Copyright is owned by the Author of the thesis. Permission is given for a copy to be downloaded by an individual for the purpose of research and private study only. The thesis may not be reproduced elsewhere without the permission of the Author.

Avian Ecological Functions in New Zealand Apple Orchards: Implications for Ecosystem Services and Disservices

A thesis presented in partial fulfilment of the

requirements for the degree of

PhD

in

Ecology

at Massey University, Manawatū campus, New Zealand.

Giuliana Caldeira Pires Ferrari

2026

Abstract

Agricultural landscapes must increasingly reconcile food production with biodiversity conservation. Birds are particularly relevant to this challenge because they can provide ecosystem services, such as pest control and pollination, while also causing ecosystem disservices, including crop damage. However, these roles are often considered separately, and little is known about how native birds use horticultural systems in Aotearoa New Zealand. This thesis investigated the occurrence, behaviour, and potential functional roles of birds in horticultural landscapes, using apple orchards as a model production system.

A systematic review of 251 studies published between 1912 and 2023 first examined global research on avian ecosystem services and disservices in horticultural systems. Pest control and crop damage dominated the literature, while relatively few studies considered services and disservices simultaneously or examined the conservation of native and endemic birds within production landscapes. Fieldwork was subsequently conducted across six apple orchards in four New Zealand regions from autumn 2024 through the 2025 harvest. Repeated bird surveys, behavioural and feeding observations, artificial sentinel-prey experiments, and crop-damage assessments were used to investigate how birds used orchards and their potential contributions to beneficial and detrimental ecological processes.

Forty-five bird species, comprising 20 native and 25 introduced species, were recorded in the orchards. Although introduced species dominated detections, several native species were widespread, including silvereyes (*Zosterops lateralis*), fantails (*Rhipidura fuliginosa*), pūkeko (*Porphyrio melanotus*), welcome swallows (*Hirundo neoxena*), and swamp harriers (*Circus approximans*). Orchard use was relatively consistent throughout the year, while seasonal differences in community composition largely reflected changes in abundance, flocking, and the occurrence of infrequent visitors. Native birds used orchards predominantly for foraging-related activities, with marked species-specific differences in behaviour, vertical habitat use, and food consumption. Silvereyes exemplified the complexity of these interactions, consuming arthropods, fruit, fallen fruit, and flowers at different times of year and therefore having the potential to contribute both services and disservices.

Experimental assessment of these functions provided a more cautious picture. Birds attacked artificial caterpillars, but at relatively low frequencies, preventing strong conclusions about the magnitude of avian pest-control services. Conversely, direct crop assessments showed that bird damage was uncommon, with fungal infection substantially more prevalent than damage attributed to birds or insects. Thus, bird presence alone was a poor indicator of either benefit or harm to apple production.

Together, these findings demonstrate that New Zealand apple orchards provide habitat for diverse avian communities and that the ecological roles of birds cannot be adequately characterised through simple classifications as beneficial species or agricultural pests. Productive landscapes should therefore not be overlooked as components of biodiversity conservation. As native bird populations expand through ongoing mammalian predator control, understanding their species-specific interactions with horticultural systems will become increasingly important for developing approaches that allow food production and native biodiversity to coexist.

Canção do Exílio	***The Song of Exile***
Minha terra tem palmeiras,	*My homeland has many palm-trees*
Onde canta o Sabiá;	*where the thrush-song fills its air;*
As aves, que aqui gorjeiam,	*no bird here can sing as well*
Não gorjeiam como lá.	*as the birds sing over there.*
Nosso céu tem mais estrelas,	*We have fields fuller of flowers*
Nossas várzeas têm mais flores,	*and a starrier sky above,*
Nossos bosques têm mais vida,	*Our woods have more life*
Nossa vida mais amores.	*and our life has more love.*
Em cismar - sozinho - à noite -	*Lonely nighttime meditations*
Mais prazer encontro eu lá;	*please me more when I am there;*
Minha terra tem palmeiras;	*my homeland has many palm-trees*
Onde canta o Sabiá.	*where the thrush-song fills its air.*
Minha terra tem primores,	*Such delights as my land offers*
Que tais não encontro eu cá;	*Are not found here nor elsewhere;*
Em cismar - sozinho - à noite -	*lonely nighttime meditations*
Mais prazer encontro eu lá;	*please me more when I am there;*
Minha terra tem palmeiras,	*My homeland has many palm-trees*
Onde canta o Sabiá.	*where the thrush-song fills its air.*
Não permita Deus que eu morra,	*Don't allow me, God, to die*
Sem que eu volte para lá;	*Without getting back there*
Sem que eu desfrute os primores	*Lest I don't relish*
Que não encontro por cá;	*On the delights found only there,*
Sem qu'inda aviste as palmeiras,	*without seeing all those palm-trees,*
Onde canta o Sabiá.	*where thrush-songs fill the air.*

Gonçalve Dias**,** 1843

Acknowledgements

To finish a thesis, it truly does take a village. My village spanned multiple time zones and continents and, to all the people that helped me along the way, these acknowledgements are for you.

This PhD would not have been possible without Massey's Doctoral Scholarship. It provided me with a stable and safe income while I was driving around the country, watching birds, and writing back at the office. The support from the fieldwork funding was also essential, including the J. P. Skipworth and Marion Cunningham scholarships. Special thanks to Plant and Food Research for not only trusting me to drive one of their fleet cars, but also for the fieldwork support. Their statisticians, Andrew McLachlan and Duncan Hedderley, also provided much-needed feedback and assurance that things were going on the right track. My sincere thanks also to Jacqui Todd for welcoming me to join her fieldwork so I could survey an amazing orchard in the South Island.

As someone that was supposed to come to New Zealand in 2020 under much different supervisory circumstances, I'm forever grateful that plans changed and I was under the tutelage of such amazing supervisors. Isabel Castro was truly a kiwi mom when my own family was so far away and provided an essential support to both field and computer work. Her extensive knowledge of bird behaviour provided the background I needed to understand a bit more the avian world I was experiencing at the orchards. Karen Mason provided invaluable connections to the apple growers and gave me a lot of perspective on the reality of their lives. Alastair Robertson had the eyes of an eagle for the tiniest details, which was much appreciated when I couldn't see a typo after staring at the same pages for hours on end. I'm forever thankful to my supervisors for allowing me to help them in small academic responsibilities, expanding my abilities towards lecturing and marking. To my honorary mentors, I will never cease to thank Kevin Parker and Doug Armstrong for not only pushing me into bird work, but also believing in me when that was important to keep me going. Special thanks to Elizabeth Parlato for validating my concerns and helping me deal with the so-prevalent impostor syndrome.

Other members of staff have continued to provide a fulfilling, engaging environment within the university. Thank you to Simon Hills for reigniting my love for snails, Murray Potter for dealing with bureaucracies that were bound to happen, and Phil for the bird identification skills that were so important throughout my work. As the essential backbone of this department, my forever thanks to Tracy Harris, Shaun Nielsen and Cleland Wallace for helping in virtually all

issues that arose throughout these last couple of years, and for providing support and encouragement when I wasn't too sure I was going in the right direction. I would also like to acknowledge the people who allow the university ecosystem to thrive: cleaning and security staff, bus drivers, IT personnel, the Registry and GRS staff, tradespeople making sure our facilities were up to the task. Thank you sincerely.

Thank you to all the growers, in no particular order, for their welcoming support of an early bird fussing around in their orchards. Brent Bertelsen, Remus Mihaila, Philip Wycherley, Mark Osborne, Neemia N. and many others involved: thank you for letting me walk around in your land and thank you for all the bird sightings and insights that you were so keen to share with me as the project ran along. Special thanks to Brent, for alerting me of the presence of New Zealand falcons in his orchard, and to Neemia for fulfilling my lifelong dream of driving a tractor. Thank you to my confirmation examiners, Svetla Sofkova-Bobcheva, for helping me secure the Hawke's Bay orchard as a fieldwork site, and David Pattermore for reminding me of looking into the presence of mammals in the orchards. Thank you to Gabor Lövei for personally introducing me to the artificial caterpillar studies, and to Eduardo Misnky for the contribution to the eBird dataset.

To my colleagues, Nyasha Chikwature, Xiaochuan Liu, Haley Johnston, Francisco Teixeira Batista Silva, Jaime Botet Rodriguez, Eliana Ramos Pallares, Azalea Anota, Anaïs Hendrikx, thank you for the afternoon breaks, the lunches, and the office talks. You made the often-solitary task of academic work more bearable, and I appreciate our random talks that provided a much-needed break from staring at endless screens. Thank you to Pauline Seymour for letting me make a difference to the university by helping pre-vet Māori and Pasifika students. Thank you to all the undergraduate students who made my PhD journey more fun, by reminding me that sharing knowledge is one of the greatest joys of being in academia.

To some people I will never meet but that have kept me sane through their literary works: C. Pinkola Estés, J. R. R. Tolkien, J. Steinbeck, T. Conroy, F. Herbert, K. St Clair, C. N. Adichie, S. Collins, J. Elphick, J. Busby, J. Le Carré, A. Roy, C. Liu, J. M. Laws, and so many more. I had to write a thesis in scientific language, but I was able to get lost in their words, and I'm grateful for the uncountable hours of reading.

As an international student, friends became my surrogate family. To Aylin Şen, Vitor Geniselli Da Silva, Adrian Grande, Manfred Goh, Aysenur Arslan, Juliette Vicente, Yusi Qin, Linda Nezbedová, Claire Chaussadas, thank you for the parties, celebrations, trips and adventures,

movie nights, dinners, and supporting talks. Thank you to Hannah and Jamie Love, David Soong, Chloe Phoon, and Hugo Pereira for all the boardgame nights. Thank you to Isaac Watson, Finn Davidson, Mikel O'Connel, James Bramley, Shaul and Mikayla Macarthur for the Magic nights and all the shenanigans involved. I promised Isaac I was going to include him especially for helping me with trade equipment for fieldwork, so here it is!

I would also like to acknowledge and thank the diverse avifauna that is my family and friends from back home. Gis and Bibs as my long-time school friends, and Carol and Bilba from university. Thank you for the laughs, tears, and memes throughout the most complicated moments of grief, homesickness, and anxiety that have marked the PhD process.

To my family, whom I miss dearly. My brother João, for giving me the privilege of being an aunt. My brother Leo, for encouraging my art and providing the support that I hope he never truly understands how necessary it was. My cousins and uncles and aunties, blood-related or not, for believing in my future. To my late grandparents Eugênio and Vera, I can only hope to know you would be proud of me arriving at this moment. To my adopted kiwi family, John and Wendy Biberstein, Cheri Butler, Daile and Jeremy Long, all the young kids and the lovely Christmas parties, thank you for making me feel welcomed.

To my companion animals, for all the love and life lessons you have shared with me: my feline friends Nala, Alaska, Morgana, Tarsila, and Layla. You might not understand human words, but we understood compassion together. To the humans and non-human companions that are no longer here, I hope heaven exists, and I hope you found peace there.

To all the birds that sprinkled happiness and serenity over these years. To the tauhou cuddling on branches and the korimako singing early morning, to the tūī going crazy on yellow plums and the riroriro eluding my subtle bird stalking. To the gulls that screamed in my ears and the soft chirps of finches, to the wariness of pūkeko and the everlasting companionship of the pīwakawaka following me around the orchards. To the inspiring laziness of kererū and the flash of bright blue from the kōtare. You made fieldwork a moment of peace in a chaotic world. To all the species I saw in sanctuaries and offshore islands, the endangered, precious taonga manu of Aotearoa. Your persistence is part of the dream that inspired this thesis.

To my love, Stefan, thank you for everything. In the small word of 'partner' fits the universe of support, attention, care and love you provided me for these past couple of years. I only hope to be able to believe in myself half as much you do.

Finally, I dedicate this thesis in honour of my own owl mother, Kátia Maria. From gifting me books when I was a wee biologist in the making, to watching me graduate from my undergrad and then my Masters. To this amazing woman that saw her little child crouched on the dirt looking at bugs and knew an unconventional path would follow. I couldn't be who I am today without you showing me the way, and homesickness is felt because you are not here with me. You taught me independence and to be proud of my roots. You managed to keep me afloat through financial and emotional hardship even when you could have had some help yourself, and you never ceased to be my number one supporter. For all the peptalks, the lunch calls, the postcards and letters, the missed birthdays, the sunrises and sunsets, the photos of birds and trees and waves, the good and sad news shared over the phone, for all the arguments and discussions and encouragements. Everything I do, I do to make you proud. *Passarinho aprende a voar, mas não esquece de que ninho veio*.

Note

This thesis is submitted as a thesis-by-publication. Chapter Two was published in Austral Ecology. Chapters Three, Four and Five were, at the time of submission, being prepared for submission to different journals. Chapters One (General Introduction) and Six (General Discussion) will not be submitted for peer-reviewed publication. All references are included in a single list at the end of this document to avoid repetition across multiple chapters. Although the chapters have been prepared for, submitted, or published in different journals, references and their corresponding list follow the standardised style of the journal Conservation Biology across all chapters. Some species have two common names in New Zealand, as they can be referred to by an English translation of traditional Māori names. In this thesis, all species are referred to by the nomenclature included in (Heather et al. 2015). Thus, a few Māori names are included as the correct common name.

The illustrations that mark the beginning of each chapter, and Figure 4.12, were drawn in ink by the author of this thesis. Cover illustrations depict the following species: Chapter One (kōtare, or sacred kingfisher *Todiramphus sanctus*); Chapter Two (goldfinch *Carduelis carduelis*); Chapter Three (tauhou, or silvereye *Zosterops lateralis*); Chapter Four (tūī *Prosthemadera novaeseelandiae*); Chapter Five (riroriro, or grey warbler *Gerygone igata*); and Chapter Six (pūkeko *Porphyrio melanotus melanotus*).

Table of Contents

Abstract 2
Acknowledgements 4
Note 8
Table of Contents 9
List of Figures 14
List of Tables 18
List of Supplementary Material (Figures) 23
List of Supplementary Material (Tables) 25
Glossary & Abbreviations 31
Chapter 1 General Introduction 33
1.1 Conservation in Human-Modified Landscapes 33
1.2 Ecosystem Services and Disservices in Agricultural Systems 34
1.2.1 Birds as Providers of Ecosystem Services and Disservices 34
1.3 Aotearoa New Zealand: A Unique Context for Bird Conservation 36
1.4 Feeding Guilds Hint at the Provision of Ecosystem Services and Disservices 37
1.4.1 Carnivory 39
1.4.2 Piscivory 39
1.4.3 Insectivory 40
1.4.4 Granivory 41
1.4.5 Frugivory 42
1.4.6 Nectarivory 43
1.4.7 Omnivory 43
1.5 The Selection of Apple Orchards as A Model Production System 45
1.6 Thesis Structure 45
Chapter 2 Not All Birds of the Same Feather: A Systematic Review of Horticultural Ecosystem Services and Disservices 48
2.1 Abstract 48
2.2 Introduction 49
2.2.1 Birds as Providers of Ecosystem Services and Disservices 49
2.3 Methods 50
2.4 Results & Discussion 51
2.4.1 Horticultural and Biological Focus 51
2.4.2 Investigating and Reporting on Ecosystem Services and Disservices 53

2.4.3 Methods Used to Investigate Ecosystem Services and Disservices....58
2.4.3.1 Estimation / Identification....59
2.4.3.2 Exclosures....59
2.4.3.3 Damage & Yield Surveys....59
2.4.3.4 Spatial Landscape Analysis....59
2.4.3.5 Use of Published Data....60
2.4.3.6 Experiments....60
2.4.3.7 Human Surveys....60
2.4.3.8 Laboratory Analysis....61
2.4.3.9 Estimation & Modelling....61
2.4.3.10 Miscellaneous....62
2.4.4 Combining Methods....62
2.4.5 Human-Wildlife Conflicts....66
2.5 Conclusions....66
Chapter 3 Spatio-Temporal Variation in Avian Communities Across Apple Orchards, New Zealand....69
3.1 Abstract....69
3.1 Introduction....70
3.1 Methods....71
3.1.1 Study Area....71
3.1.1.1 Apple Varieties....71
3.1.2 Bird Observations....75
3.1.3 Species Occupancy....76
3.1.4 Species Abundance....76
3.1.5 Flocking Patterns....76
3.1.6 Vertical Strata Use of Orchards....76
3.1.7 Mammalian Presence at Apple Orchards....77
3.1.8 Statistical Analyses....77
3.1.8.1 Species Richness Estimators....77
3.1.8.2 Species Occupancy....78
3.1.8.3 Species Abundance....78
3.1.8.4 Flocking Patterns....79
3.1.8.5 Vertical Strata Use....80
3.2 Results....80
3.2.1 Species Richness....80
3.2.2 Species Occupancy....82

3.2.3 Species Abundance 84
3.2.4 Flocking Patterns 86
3.2.5 Vertical Strata Use of Orchards 92
3.2.5.1 Blackbird 100
3.2.5.2 Chaffinch, New Zealand Fantail, Goldfinch, Greenfinch, Pūkeko, Tūī, Welcome Swallow 101
3.2.5.3 House Sparrow, Silvereye, Song Thrush, Swamp Harrier 104
3.2.6 Mammalian Presence in Orchards 105
3.3 Discussion 106
3.3.1 Species Richness and Community Composition 106
3.3.1.1 Habitat Use and Occupancy 107
3.3.1.2 Site and Seasonal Variations 108
3.3.2 Flocking Patterns and Use of Vertical Strata 109
3.3.2.1 Overhead Foragers 109
3.3.2.2 Canopy foragers 109
3.3.2.3 Ground foragers 110
3.3.2.4 Finch Assemblages 110
3.3.2.5 Seasonal Flocking 110
3.3.3 Presence of Exotic Mammals at Apple Orchards 111
3.3.4 Study Limitations 111
3.4 Conclusions 112
Chapter 4 Avian Behaviours in New Zealand Apple Orchards 114
4.1 Abstract 114
4.2 Introduction 114
4.3 Methods 116
4.3.1 Study Area 116
4.3.2 Categorising Behaviours 116
4.3.3 Feeding Behaviours of Selected Native Species 116
4.3.4 Statistical Analysis 117
4.3.4.1 Native Species Behaviours 117
4.3.4.2 Feeding behaviour 117
4.4 Results 118
4.4.1 Native Species Behaviours 118
4.4.1.1 Behaviour x Season Model (silvereyes) 124
4.4.1.2 Behaviour + Season Model (grey warblers, tūī) 124
4.4.1.3 Behaviour Only Model (fantails, pūkeko, welcome swallows) 124

4.4.2 Feeding Behaviours 126
4.5 Discussion 132
4.5.1 Foraging-Related Activities Dominated Behavioural Observations 132
4.5.2 Common Bird Visitors Feeding on Fruit Crops 134
Chapter 5 Assessing Pest Control and Crop Damage by Avian Species in New Zealand Apple Orchards 138
5.1 Abstract 138
5.2 Introduction 138
5.3 Methods 140
5.3.1 Study Area 140
5.3.2 Pest Control 140
5.3.2.1 Artificial Sentinel Prey Removal Experiments 140
5.3.2.2 Identification of Predation Marks 141
5.3.3 Crop Damage 141
5.3.4 Statistical Analyses 142
5.3.4.1 Pest Control 142
5.3.4.2 Crop Damage 143
5.4 Results 143
5.4.1 Artificial Sentinel Prey Removal Experiments 143
5.4.2 Crop Damage 150
5.5 Discussion 154
5.5.1 Provision of Pest Control as an Ecosystem Service 154
5.5.2 Provision of Crop Damage as a Disservice 156
5.5.3 Assessing Pest Control and Crop Damage Simultaneously 157
5.5.4 Implications for the New Zealand Apple Industry 157
Chapter 6 General Discussion 160
6.1 What Is Known for Birds as Providers of Ecosystem Services and Disservices? 160
6.2 What Bird Species are Actually in Apple Orchards, and How Are They Using These Systems? 162
6.3 What Are Some Typical Bird Behaviours in These Systems? 165
6.4 How Can Feeding Habits Translate into Ecosystem Services or Disservices? 166
6.5 Are Birds Acting as Pest Control and Crop Damage Agents at Apple Orchards? 167
6.6 Limitations and Recommendations 169
6.7 Implications for Human-Wildlife Conflicts 171
6.8 Tackling the Land-Sparing or Land-Sharing Debate 172
6.9 What does the Future Hold for New Zealand Birds? 174

References.....176
Supplementary Materials (Chapter One).....213
Supplementary Materials (Chapter Two).....219
Supplementary Materials (Chapter Three).....228
Supplementary Materials (Chapter Four).....298
Supplementary Materials (Chapter Five).....326

List of Figures

Figure 1.1. Conceptual framework of potential provision of ecosystem services (left column) and disservices (right column) by different avian feeding guilds (middle column). Arrows connect feeding guilds to the ecosystem services and disservices they can provide based on their feeding behaviours. Ecosystem services include pest control, seed dispersal, removal of food waste, soil disturbance, weed control and pollination. Ecosystem disservices include crop damage, herbivore release, pollinator predation, soil disturbance, weed dispersal and nectar robbing. Feeding guilds include carnivores, insectivores, frugivores, omnivores, granivores and nectarivores. Native New Zealand nectarivores often feed on soft-fleshed fruits, thus potentially causing crop damage. Apart from pollination, omnivores can provide all services and disservices. A seventh ecosystem service, soil fertilisation, was not accounted for in the diagram, because all feeding guilds can provide this service, depending on their diet. An additional feeding guild, piscivores, present in the observation records, is not accounted for in this diagram, given the feeding behaviour of such species is not directly related to horticultural systems. 38

Figure 2.1. Distribution of document publications from the first available document (1912) to 2023. Each decade is represented on the y-axis, with three decades (1911 - 1940) presenting empty values. 51

Figure 2.2. Global Distribution of Pest Control and Crop Damage Studies. Global distribution of pest control (143 occurrences, dark blue dots) and crop damage studies (124 occurrences, orange stars). Locations were retrieved from GIS coordinates provided or approximated by the researchers. Map constructed on ArcPro (ESRI 2023). 56

Figure 3.1. Regional location of the five orchards in the North Island and one in the South Island that were included in the fieldwork dataset. Pictures show the surroundings of each orchard up to a 1.5km buffer. Map constructed on QGIS (2024) from coordinates retrieved from each field site. Symbols overlapping with each orchard represent their unique orchard identities related to their regional locations: Manawatū 1 & 2 (MN), Kāpiti Coast 1 & 2 (KC), Hawke's Bay (HB), and Tasman Region (TR). 72

Figure 3.2. Species accumulation curve showing cumulative observed bird species richness across 82 surveys conducted in six apple orchards. The solid line represents the mean cumulative richness calculated from 100 random permutations of survey order, and the shaded area represents the 95% confidence interval..... 81

Figure 3.3. Observed species richness (black circles) and first-order Jackknife richness estimates (grey circles) with approximate 95% confidence intervals for each survey season. Richness estimates were calculated from incidence (presence / absence) data using individual surveys (n = 82) as sampling units..... 82

Figure 3.4. Non-metric multidimensional scaling (NMDS) ordination of bird community composition across four seasons, based on Bray-Curtis dissimilarities calculated from Hellinger-transformed abundance data (stress = 0.171). Each point represents a single orchard x season community sample. Colours indicate season, and ellipses represent the multivariate dispersion of samples within each season. NMDS1 and NMDS2 represent the major

dimensions of variation in community composition, with points located closer together indicating more similar bird assemblages. 85

Figure 3.5. Non-metric multidimensional scaling (NMDS) ordination of flocking type composition for native species: silvereyes (Zosterops lateralis), New Zealand fantails (Rhipidura fuliginosa), welcome swallows (Hirundo neoxena), and pūkeko (Porphyrio melanotus melanotus). Points represent individual sampling events, coloured by season (from autumn 2024 to summer 2025). Ellipses show 95% confidence regions for each season. Arrows represent fitted vectors from the envfit analysis, indicating the direction and relative contribution of flock-size categories (solitary individuals, pairs, small groups, medium groups, and large flocks) to the multivariate gradient. Ordinations are based on Bray-Curtis dissimilarities calculated from Hellinger-transformed flock-size data. Stress values indicate goodness of fit (stress < 0.15 = reliable; < 0.10 = good; < 0.05 = excellent). Flocking categories are distinguished between solitary individuals, pairs, small groups (3-5 individuals), medium groups (6-10 individuals), and large flocks (>10 individuals). 89

Figure 3.6. Non-metric multidimensional scaling (NMDS) ordination of flocking type composition for introduced species: blackbirds (Turdus merula), chaffinches (Fringilla coelebs), goldfinches (Carduelis carduelis), and greenfinches (Chloris chloris). Points represent individual sampling events, coloured by season (from autumn 2024 to summer 2025). Ellipses show 95% confidence regions for each season. Arrows represent fitted vectors from the envfit analysis, indicating the direction and relative contribution of flock-size categories (solitary individuals, pairs, small groups, medium groups, and large flocks) to the multivariate gradient. Ordinations are based on Bray-Curtis dissimilarities calculated from Hellinger-transformed flock-size data. Stress values indicate goodness of fit (stress < 0.15 = reliable; < 0.10 = good; < 0.05 = excellent). Flocking categories are distinguished between solitary individuals, pairs, small groups (3-5 individuals), medium groups (6-10 individuals), and large flocks (>10 individuals)..... 90

Figure 3.7. Use of the orchard's vertical strata by common New Zealand bird visitors. Presence of different species within distinct strata is informed by data collected on first-sight observations of native and introduced species across six sites and four seasons. Species are identified by abbreviations: SE = silvereye (Zosterops lateralis); PK = pūkeko (Porphyrio melanotus melanotus); SH = swamp harrier (Circus approximans); TU = tūī (Prosthemadera novaeseelandiae); FN = New Zealand fantail (Rhipidura fuliginosa); WS = welcome swallow (Hirundo neoxena); GF = goldfinch (Carduelis carduelis); CF = chaffinch (Fringilla coelebs); BB = blackbird (Turdus merula); ST = song thrush (Turdus philomelos); HS = house sparrow (Passer domesticus)..... 100

Figure 3.8. Vertical strata use by blackbird (Turdus merula). Fitted counts (± 95 % CI) from a generalised linear mixed model including the interactions between vertical stratum and season. Model was selected for inference from a candidate set of models compared using Akaike's Information Criterion values and diagnostic tools to assess for model validity..... 101

Figure 3.9. Vertical strata use by chaffinch (Fringilla coelebs), fantail (Rhipidura fuliginosa), goldfinch (Carduelis carduelis), greenfinch (Chloris chloris), pūkeko (Porphyrio melanotus melanotus), tūī (Prosthemadera novaeseelandiae) and welcome swallow (Hirundo neoxena). Fitted counts (± 95 % CI) from a generalised linear mixed model including the additive

effects of vertical stratum and season. Models were selected for inference from a candidate set of models compared using Akaike's Information Criterion values and diagnostic tools to assess model validity. Note that the y-axis (fitted counts) varies between species. 103

Figure 3.10. Vertical strata use by house sparrow (Passer domesticus), silvereye (Zosterops lateralis), song thrush (Turdus philomelos), and swamp harrier (Circus approximans). Fitted counts (± 95 % CI) from a generalised linear mixed model. House sparrows, silvereyes and swamp harriers are shown from models including the interaction between vertical stratum and season, whereas song thrushes are shown from the additive model. Models were selected for inference from a candidate set of models compared using Akaike's Information Criterion values and diagnostic tools to assess for model validity. Note that the y-axis (fitted counts) varies between species. 105

Figure 4.1. Estimated marginal means (EMMs) of behavioural observations for silvereyes (Zosterops lateralis) based on a generalised linear mixed model (GLMM) accounting for the interactions of behaviours and season. Orchard was kept as a random effect. EMMs represent estimated behavioural responses for each behaviour x season combination, with error bars indicating 95% confidence intervals. Behaviour categories were distinguished as flying; foraging; perching; hopping; vocalising; territorial behaviours; social behaviours; preening; and interacting with the observer. Extremely large confidence intervals indicate cases of near zero or zero observations. 125

Figure 4.2. Estimated marginal means (EMMs) of behavioural observations for grey warblers (Gerygone igata) and tūī (Prosthemadera novaeseelandiae) based on a generalised linear mixed model (GLMM) accounting for the main effects of behaviours and season. Orchard was kept as a random effect. EMMs represent estimated behavioural responses averaged across seasons, with error bars indicating 95% confidence intervals. Behaviour categories were distinguished as flying; foraging; perching; hopping; vocalising; territorial behaviours; social behaviours; preening; and interacting with the observer. Extremely large confidence intervals indicate cases of near zero or zero observations. 125

Figure 4.3. Estimated marginal means (EMMs) of behavioural observations for fantails (Rhipidura fuliginosa), pūkeko (Porphyrio melanotus melanotus) and welcome swallows (Hirundo neoxena). EMMs were calculated from a generalised linear mixed model (GLMM) accounting for only behaviour as the best model kept for inference. Orchard was kept as a random effect. EMMs represent estimated behavioural responses averaged across seasons, with error bars indicating 95% confidence intervals. Behaviour categories were distinguished as flying; foraging; perching; hopping; vocalising; territorial behaviours; social behaviours; preening; and interacting with the observer. Extremely large confidence intervals indicate cases of near zero or zero observations.....126

Figure 4.4. Seasonal variation in food use by silvereyes (Zosterops lateralis) in apple orchards. Points represent model-estimated relative frequencies of feeding observations for arthropods (blue), fruits (orange), fallen fruits (yellow), and flowers (pink) across seasons. Vertical lines indicate 95% confidence intervals. Estimates were derived from the best-supported negative binomial generalised linear mixed model, which included an interaction between food type and season, orchard as a random effect, and total feeding observations per orchard x season as an offset. 132

Figure 5.1. Examples of an artificial caterpillar deployed in the field (left) and a batch of five caterpillars stored individually (right). 141

Figure 5.2. Estimated marginal probabilities of artificial caterpillar predation according to season, orchard position, and predator group. Estimated marginal means were derived from a model including additive effects of season, orchard position, and predator group, with orchard included as a random intercept. Points represent estimated marginal means and error bars represent 95% confidence intervals. Estimates for each predictor are averaged across the levels of the other predictors included in the model. 149

Figure 5.3. Frequency distributions of branch-level crop damage across orchards in 2024 and 2025. Histograms show the number of fruits per branch exhibiting different levels of (A) bird damage, (B) fungal damage, and (C) insect damage. Panels for each year are faceted by orchard. 152

Figure 5.4. Non-metric multidimensional scaling (NMDS) ordination of fruit damage composition across apple orchards surveyed in 2024 and 2025. Damage composition was based on the proportional incidence of bird, insect, and fungal damage and Bray-Curtis dissimilarities. Points represent unique orchard x year x position x branch-height sampling units. Orchard position is indicated by grey (edge) or black (middle) shades, while shapes indicate the year (circles for 2024 and triangles for 2025). Panels represent branch-height categories (L = low, C = chest height, H = high). Vectors indicate the direction of association of bird, insect, and fungal damage with the ordination axes. The two-dimensional ordination had a stress value of 0.097. 153

List of Tables

Table 2.1. Types of systems and management are described in the studies retrieved from the search. The first two columns refer to the types of systems studied, with the last two columns referring to the management described by the researchers in each study. The total sum of systems will not reflect the number of documents (251), given that many studies assessed different systems. 53

Table 2.2. Types of community metrics used to measure diversity of bird communities were specified in 79 out of the 251 documents included in the review. Several metrics could be applied in the same study. The second section of the table describes the distinction between documents that presented or did not discuss human-wildlife conflicts. 53

Table 2.3. Compilation of ecosystem services studied in the 150 documents retrieved by the search, with different evidence (e.g. positive, negative, more data needed) as indicated by the researchers of each study. 128 documents presented a focus on only ecosystem services, while 22 had a focus on both ecosystem services and disservices. In some instances, researchers investigated more than one service per study. The difference between the reported and expected (column of evidence) refers to researchers presuming a certain ecosystem service but not specifically measuring or assessing it (expected but not assessed) and to interviewees reporting a certain service without the researchers assessing it (reported but not assessed)..... 56

Table 2.4. Compilation of ecosystem disservices studied in the 131 documents retrieved by the search, with different evidence (e.g. positive, negative, more data needed) as indicated by the researchers of each study. 109 documents presented a focus on only ecosystem disservices, while 22 had a focus on both ecosystem services and disservices. In some instances, researchers looked into more than one disservice per study. The difference between the reported and expected (column of evidence) refers to researchers presuming a certain ecosystem disservice but not specifically measuring or assessing it (expected but not assessed) and to interviewees reporting a certain disservice without the researchers assessing it (reported but not assessed)..... 58

Table 2.5. Compilation of different methods employed for the study of ecosystem services and disservices retrieved from the 251 documents assembled from the review. Methods were separated into distinct themes: estimation/identification of species involved in the systems; exclosures for different biological groups; surveys to assess crop yield and damage; spatial analysis of the landscape; use of published data; experiments of sentinel prey removal and provision of environmental enhancements; interviews and surveys; laboratory analysis involving DNA and isotope samples and microscope analysis; modelling of previous data and economic estimation; and a final category of miscellaneous methods. The second column distinguishes different methods within each theme. The third column further specifies the methods in each category, with others referring to biological groups other than birds. 63

Table 3.1. Identity, size, management practices, and structure of orchards included in the study. Sites are identified by regional locations. Each section is described in its configuration of crops and the number of rows. Section KC2-1 had a mix of apples, pears, feijoas, oranges

and other fruit trees. For each section, the height and distance between rows was measured five times to calculate the average height of the apple trees and the distance between the rows from one trunk to the other. In sections of mixed crops, tree height and distance between rows is given by measuring a random selection of crop trees. 73

Table 3.2. Estimated occupancy probability (Ψ) and conditional detection probability (p), with corresponding 95% confidence intervals. Estimated occupancy probabilities and detection probabilities are reported here for the 39 bird species whose best-supported occupancy models were intercept-only [null] models. Species whose best-supported models included temperature or survey period as detection covariates are presented separately in Figure S 5 and Figure S 6. 83

Table 3.3. Pairwise permutational multivariate analysis of variance (PERMANOVA) comparisons testing differences in species abundance composition between levels of season as a predictor. For each pairwise contrast, comparison groups, F-statistics, corresponding R^2 values, unadjusted p-values based on 999 permutations and Holm-adjusted p-values are reported. 85

Table 3.4. Summary of descriptive statistics for flocking composition across 92 combinations of orchard, season, survey period (AM/PM), and position (edge/middle). Arithmetic means, standard deviations (SD), and standard errors (SE) were calculated for observation counts in five flocking categories: large flocks (over 10 individuals), medium groups (6–10 individuals), small groups (3–5 individuals), pairs, and solitary individuals. Flocking analysis was calculated for five native species (silvereye Zosterops lateralis, New Zealand fantail Rhipidura fuliginosa, welcome swallow Hirundo neoxena, swamp harrier Circus approximans, and pūkeko Porphyrio melanotus melanotus); and nine introduced species (blackbird Turdus merula, chaffinch Fringilla coelebs, goldfinch Carduelis carduelis, greenfinch Chloris chloris, house sparrow Passer domesticus, song thrush Turdus philomelos, rock pigeon Columba livia, starling Sturnus vulgaris, and myna Acridotheres tristis). 87

Table 3.5. Summary of descriptive statistics for vertical strata use by native (A) and introduced (B) bird species across 23 orchard–season combinations (n = 23). Arithmetic means, standard deviations (SD), and standard errors (SE) were calculated for observation counts across six vertical strata: ground, low, medium and top tree branches, overhead, and human structures (e.g. poles, sheds and power lines).Species included in this analysis were represented by ten native species: silvereye (Zosterops lateralis), tūī (Prosthemadera novaeseelandiae), New Zealand fantail (Rhipidura fuliginosa), pūkeko (Porphyrio melanotus melanotus), welcome swallow (Hirundo neoxena), sacred kingfisher (Todiramphus sanctus), black-backed gull (Larus dominicanus), spur-winged plover (Vanellus miles), paradise shelduck (Tadorna variegata) and swamp harrier (Circus approximans); and 14 introduced species: blackbird (Turdus merula), chaffinch (Fringilla coelebs), goldfinch (Carduelis carduelis), greenfinch (Chloris chloris), house sparrow (Passer domesticus), song thrush (Turdus philomelos), starling (Sturnus vulgaris), skylark (Alauda arvensis), dunnock (Prunella modularis), magpie (Gymnorhina tibicen), eastern rosella (Platycercus eximius), yellowhammer (Emberiza citrinella), myna (Acridotheres tristis) and ring-neck pheasant (Phasianus colchicus). 93

Table 3.6. Akaike's Information Criterion (AIC) model selection results for generalised linear models examining the variation in species occupation of the vertical strata of orchards. For each species, candidate models included combinations of fixed effects, including season and orchard. Model complexity ranged from a full interaction model to a null model containing only an intercept. Models were compared using Akaike's Information Criterion (AIC), the number of estimated parameters (k), ΔAIC values, and Akaike weights. Each species' best model, providing the most parsimonious structure with acceptable diagnostics, is highlighted in bold and was selected as the model for inference. Models were constructed for blackbird (Turdus merula), chaffinch (Fringilla coelebs), New Zealand fantail (Rhipidura fuliginosa), goldfinch (Carduelis carduelis), greenfinch (Chloris chloris), house sparrow (Passer domesticus), pūkeko (Porphyrio melanotus melanotus), silvereye (Zosterops lateralis), song thrush (Turdus philomelos), starling (Sturnus vulgaris), swamp harrier (Circus approximans), tūī (Prosthemadera novaeseelandiae), and welcome swallow (Hirundo neoxena).....96

Table 4.1. Summary statistics for behaviours recorded for 10 native bird species during behavioural surveys. Species were followed for a maximum of five minutes, when possible. Total observations represent the total number of records for each species x behaviour category across the 23 surveyed orchard x season combinations. Mean represents the mean number of observations of each behaviour per orchard x season combination, with standard deviation (SD) and standard error (SE) calculated across combinations. Behaviours were categorised as foraging (behaviours associated with different feeding habits, such as hawking and gleaning by insectivorous birds, diving by carnivorous birds, and pecking and rummaging by omnivores); flying; hopping (on the ground or between branches); interacting with the observer (following the researcher in the case of New Zealand fantails, and flying or running away for other species); perching or roosting; preening (as an individual action); social behaviours (pair preening, feeding partners or fledglings, and gathering nest material); territorial behaviours (chasing conspecifics); and vocalising. Species included: black-backed gull (Larus dominicanus), New Zealand fantail (Rhipidura fuliginosa), grey warbler (Gerygone igata), sacred kingfisher (Todiramphus sanctus), paradise shelduck (Tadorna variegata), pūkeko (Porphyrio melanotus melanotus), silvereye (Zosterops lateralis), swamp harrier (Circus approximans), tūī (Prosthemadera novaeseelandiae), welcome swallow (Hirundo neoxena). 119

Table 4.2. Akaike's Information Criterion (AIC) model selection results for generalised linear mixed models (GLMMs) examining the variation in the observation of different behaviour categories for 10 native species. Candidate models included the full interactions between behaviour and season, main effects only, behaviour only, season only, and a null model. Models were compared using the number of estimated parameters (k), AIC values, ΔAIC values, and Akaike weights. Models for black-backed gulls, paradise shelducks, swamp harriers and kingfishers did not converge properly, had unstable Hessian values, and/or were too sparse to be properly calculated. These species were thus removed from further analysis. For grey warblers, tūī, and welcome swallows, an unbalanced combination of behaviour-season observations led to ΔAIC and AIC weight values not being calculated, but the models were kept for inference as they converged and passed further diagnostic tests. Models kept for inference for each species are highlighted in bold. Species included: black-backed gull (Larus dominicanus), New Zealand fantail (Rhipidura fuliginosa), grey warbler (Gerygone igata), sacred kingfisher (Todiramphus sanctus), paradise shelduck (Tadorna variegata),

pūkeko (Porphyrio melanotus melanotus), silvereye (Zosterops lateralis), swamp harrier (Circus approximans), tūī (Prosthemadera novaeseelandiae), welcome swallow (Hirundo neoxena). 122

Table 4.3. Seasonal composition of 497 feeding observations for silvereyes (Zosterops lateralis) in apple orchards. Observations represent the number of feeding events recorded for each food type (arthropods, fruits, fallen fruits, and flowers) within each season, from autumn 2024 to summer 2025. Total season observations represent the total number of feeding events recorded across all food types within that season, and percentages represent the proportion of these observations attributed to each food type. 127

Table 4.4. Model selection and diagnostic results for generalised linear mixed models (GLMMs) examining seasonal variation in food use by silvereyes (Zosterops lateralis). Candidate models included the interaction between food type and season, additive effects of food type and season, food type only, and an intercept-only model (Null). All models used a negative binomial error distribution, included orchard as a random effect, and incorporated the logarithm of total feeding observations per orchard x season as an offset. Models were compared using Akaike's Information Criterion (AIC), ΔAIC and AIC weights. Model validity was assessed using positive-definite Hessian status (pdHess) and DHARMa tests of residual uniformity, dispersion, zero inflation and outliers; values reported for DHARMa diagnostics are p-values. The model retained for inference is shown in bold. 128

Table 4.5. Model estimates and post-hoc comparisons from the best-supported model of seasonal variation in silvereye (Zosterops lateralis) feeding observations. (A) Parameter estimates from the negative binomial generalised linear mixed model including food type, season and their interaction as fixed effects, orchard as a random effect, and the logarithm of total feeding observations per orchard x season as an offset. The intercept represents the expected log observation rate at the reference levels (arthropod and autumn for food type and season, respectively). (B) Estimated marginal means on the response scale with standard errors and 95% confidence intervals. Estimates were standardised by setting the model offset to zero. (C) Pairwise seasonal comparisons within each food type derived from estimated marginal means, with p-values adjusted for multiple comparisons using the Tukey method. Ratios greater than one indicate a higher fitted relative frequency in the first season of the contrast. Asterisks indicate $p < 0.05$. 129

Table 5.1. Seasonal deployment of caterpillars. The number of artificial caterpillars deployed is given as the sample size per orchard and season, with the corresponding recovery rates after 24h in the field. Total recovery rate per season is provided as an average for each orchard. Sentinel prey removal experiments were conducted from autumn 2024 to the harvest season of 2025. Caterpillars were not deployed at Orchard TR in the spring and harvest seasons. 145

Table 5.2. Model selection and diagnostic results for binomial generalised linear mixed models examining variation in artificial caterpillar predation probability according to season, orchard position (edge or middle), and predator group (arthropod, bird, or rodent). Orchard was included as a random intercept in all models. Models were ranked using Akaike's Information Criterion (AIC), with the best-supported model shown in bold. k represents the number of estimated model parameters, ΔAIC the difference in AIC relative to the best-

supported model, and AIC weight the relative support for each model. Diagnostic columns report model convergence, positive-definite Hessian (pdHess), and p-values from DHARMa tests of dispersion, zero inflation, residual uniformity, and outliers. a indicates that the model converged successfully or had a positive-definite Hessian, as applicable. 147

Table 5.3. Model output (A), estimated marginal means (B), and pairwise contrasts (C) from the best-supported binomial generalised linear mixed model of artificial caterpillar predation. The model included additive effects of season, orchard position, and predator group, with orchard included as a random intercept. (A) Model coefficients are presented on the logit scale, with autumn, orchard edge, and arthropods as reference levels. The intercept represents the estimated log-odds of predation at these reference levels; (B) Estimated marginal means are presented as predicted probabilities of predation with standard errors (SE) and 95% confidence intervals (asymp.LCL-asymp.UCL); (C) Pairwise contrasts are presented as odds ratios with standard errors, z-statistics, and Tukey-adjusted p-values. Ratios greater than 1 indicate higher odds of predation for the first level relative to the second. Asterisks indicate statistically significant effects or contrasts ($p < 0.05$). 148

Table 5.4. Summary statistics for crop damage surveys across the six orchards surveyed. Sample size refers to the number of independent replicates (trees surveyed). Arithmetic mean, standard deviation (SD) and standard error (SE) are calculated per orchard (A), position (B), and year (C). Means, SDs and SEs are given for total fruits surveyed, yield (as a percentage), height of branches in centimetres, and bird, arthropod, and fungal damage marks. Yield was calculated as a proportion of fruits in each branch that did not contain damage marks. 151

Table 5.5. Results of (A) permutational multivariate analysis of variance (PERMANOVA) testing variation in the composition of bird, insect, and fungal fruit damage in relation to orchard position, year, and branch height, and (B) tests for homogeneity of multivariate dispersion for each factor. Damage composition was expressed as the proportion of sampled fruit exhibiting each damage type, and analyses were based on Bray-Curtis dissimilarities. PERMANOVA permutations were restricted within orchard to account for repeated sampling. R^2 represents the proportion of multivariate variation explained by each term. ... 153

List of Supplementary Material (Figures)

Figure S 1. Stacked columns of 56 native (green) and 36 introduced (orange) species in the eBird dataset grouped according to their feeding guilds. Number of observation records was log-transformed using the natural logarithm (ln) to address large disparities between the minimum and maximum values spanning several orders of magnitude. Feeding guilds are as follows: carnivores (CAR), frugivores (FRU), granivores (GRA), herbivores (HER), insectivores (INS), nectarivores (NEC), omnivores (OMN), piscivores (PSC), and piscivores-invertivores (PSC-INV). 218

Figure S 2. Flow diagram summarizing the review strategy of studies inclusion and exclusion based on PRISMA guidelines. Adapted from (Page et al. 2021).....219

Figure S 3. Global map indicating the occurrences of studies focusing on the horticultural systems with more than 10 occurrences each: fruits (71 occurrences), grains (58 occurrences), seeds & beans (35 occurrences), and greens (22). Locations were retrieved from GIS coordinates provided or approximated from studies. Map constructed on ArcPro (ESRI 2023). 227

Figure S 4. Global map indicating the location for the studies focusing on services and disservices other than pest control and crop damage. Ecosystem disservices include herbivore release (seven occurrences), disease spread (five occurrences), pollinator predation (two occurrences), seed predation (two occurrences) and killing of livestock (one occurrence). An additional disservice, repellent action, was only studied in a document that did not specify the location, therefore it is not included in this map. Ecosystem services include fertilising (five occurrences), disease control (four occurrences), pollination (four occurrences), weed control (three occurrences) and aesthetics (one occurrence). Locations were retrieved from GIS coordinates provided or approximated by the researchers. Map constructed on ArcPro (ESRI 2023). 227

Figure S 5. Estimated detection probability of dunnock (Prunella modularis) across temperature categories from the single-season occupancy model. Points represent model-estimated detection probabilities, and error bars indicate 95% confidence intervals 239

Figure S 6. Estimated detection probabilities for bird species showing a significant effect of survey period (morning AM versus afternoon PM) from single-season occupancy models. Points represent model-estimated detection probabilities, and error bars indicate 95% confidence intervals. 239

Figure S 7. Examples of rodent predation marks on chew cards (A = orchard MN2, autumn; B = orchard MN1, spring; C = orchard MN1, winter, also with possum predation marks) ..295

Figure S 8. Examples of brushtail possum (Trichosurus vulpecula) predation marks on chew cards (A = orchard TR, autumn; B = orchard MN1, winter; C = orchard MN1, summer) ...295

Figure S 9. Examples of hedgehog (Erinaceus europaeus) predation marks on chew cards (A = orchard TR, autumn; B = orchard MN2, spring; C = orchard KC1, summer) 296

Figure S 10. Examples of bird predation marks on caterpillars. Light and dark green plasticine was mixed together and rolled into 2mm wide caterpillars, cut into lengths varying between 25- and 30-mm. Caterpillars were glued to the branches or leaves of apple trees and left in the field for 24 hours. A = orchard KC1, autumn; B = orchard MN2, winter; C = orchard KC1, summer. 326

Figure S 11. Examples of rodent predation marks on caterpillars. Light and dark green plasticine was mixed together and rolled into 2mm wide caterpillars, cut into lengths varying between 25- and 30-mm. Caterpillars were glued to the branches or leaves of apple trees and left in the field for 24 hours. A = orchard HB, autumn; B = orchard MN2, summer; C = orchard KC1, harvest season 327

Figure S 12. Examples of arthropod predation marks on caterpillars. Light and dark green plasticine was mixed together and rolled into 2mm wide caterpillars, cut into lengths varying between 25- and 30-mm. Caterpillars were glued to the branches or leaves of apple trees and left in the field for 24 hours. A = orchard TR, autumn; B = orchard KC2, autumn; C = orchard MN2, winter. 327

Figure S 14. Examples of bird damage on apples. A = Orchard KC1, summer 2024; B = Orchard MN1, winter 2024; C = Orchard TR, autumn 2024 328

Figure S 15. Examples of fungal damage on apples. A = Orchard MN2, summer 2024; B = Orchard MN2, winter 2024; C = Orchard KC1, autumn 2024 329

List of Supplementary Material (Tables)

Table S 1. Compilation of 93 species included in the eBird dataset, including 56 native (A) and 36 introduced (B) species. Species are listed by their family and scientific names as retrieved from (OSNZ 2022). Common names are provided in English or in te reo Māori when appropriate. Total number of observations for each species is provided in the N column. Feeding guilds were retrieved from New Zealand Birds Online (Te Papa 2023) and were grouped into carnivores (CAR), frugivores (FRU), granivores (GRA), herbivores (HER), insectivores (INS), nectarivores (NEC), omnivores (OMN), piscivores (PSC), and piscivores-invertivores (PSC-INV). Extinction risk was retrieved from IUCN (2024) and refer to its red list categories: Least Concern (LC), Near Threatened (NT), Vulnerable (VU), Endangered (EN), and Critically Endangered (CR).....214

Table S 2. Complete description of the 251 documents included in the systematic review. Include the title, year and publication type of each document, with further information on specific details analysed by the review: filiation of the first authors, countries and regions of the case studies, types of horticultural systems, main research questions, methods of data collection, ecosystem services and disservices studied, bird species and community metrics measured, factors affecting bird communities positively and negatively, discussions on human-wildlife conflicts, and further notes if necessary. 219

Table S 3. Compilation of 99 documents out of 251 that indicated abiotic and biotic factors affecting positively and negatively bird communities in the systems surveyed. 220

Table S 4. Compilation of 77 studies that focused on particular species and / or species of special concern (native, endemic, or threatened). 224

Table S 5. Description of weather conditions of the 82 surveys conducted in the six sites surveyed from autumn 2024 to summer 2025. Data collection on fieldwork traits followed the protocol from five minute bird counts (DoC 2023). Each survey across orchards and seasons is identified by their date and survey period (AM = morning; PM = afternoon). Temperature was given as an estimated average for the duration of the survey, with the range: 1 = freezing (<0°C); 2 = cold (0 - 5°C); 3 = cool (6 - 11°C); 4 = mild (12 - 16°C); 5 = warm (17-23°C); and 6 = hot (>23°C). Wind categories were defined as 1 = leaves rustle; 2 = leaves and branchlets in constant motion; and 3 = branches or trees sway. Sun exposure was defined as 0 = cloud or grey; 1 = sun with clouds, or 2 = blue sky, with no clouds. Noise values refer to levels of human-produced noise during the surveys: 0 = not important; 1= moderate; and 2 = loud, which would include heavy machinery and construction nearby. Precipitation was defined as n = none; m = mist, and r = rain, which were subsequently identified as (1) = dripping foliage, (2) = drizzle, and (3) = light. No fieldwork was undertaken under heavy rain conditions. Asterisks marked three surveys at orchard KC2 where the grower left sprinklers to cover the entire orchard. 228

Table S 6. Distribution of apple varieties in the orchards surveyed. Orchard names represent their unique orchard identities related to their regional locations: Manawatū 1 & 2 (MN), Kāpiti Coast 1 & 2 (KC), Hawke's Bay (HB), and Tasman Region (TR). Asterisks indicate varieties present in each site. 232

Table S 7. Bird species detected during 82 surveys conducted across six apple orchards in New Zealand, between autumn 2024 and summer 2025. Seasonal columns indicate the number of surveys in which each species was detected, either natives (A) or introduced (B) species. Total detections and the frequency (%) of detections is then given for each species. 233

Table S 8. Model selection results for single-season occupancy models used to estimate species habitat use while accounting for imperfect detection. For each of the 45 bird species recorded in apple orchards, the best-supported model is presented based on Akaike's Information Criterion corrected for small sample size (AICc). The table includes the selected detection covariate (where applicable), the number of estimated parameters (K), AICc, the difference in AICc from the best-supported model (ΔAICc), model likelihood, AICc weight, log-likelihood, and cumulative AICc weight. Temperature models refer to the categories of temperature retrieved from DoC protocols (DoC 2023), while Period refers to the survey periods (morning AM or afternoon PM).....236

Table S 9. Results of tests for homogeneity of multivariate dispersion for season groups from the abundance dataset, calculated using the betadisper function in the vegan package in RStudio (Oksanen et al. 2008). PERMDISP assesses whether groups differ in their within-group dispersion (variance) in multivariate space. Non-significant p-values for orchards ($F_{5,17}$ = 0.172, p = 0.969) and seasons ($F_{3,19}$ = 0.593, p = 0.626) indicate that dispersion was homogeneous among groups, satisfying the assumption required for PERMANOVA. Df refers to the degrees of freedom for the group and residual components. SumSq refer to the total sum of squared distances from each sample to its group centroid in multivariate space. Mean Sq refer to the average squared distance, calculated as SumSq / Df. F-values were provided by the analysis of variance (ANOVA) run for the non-metric multidimensional scaling (NMDS) ordination of abundance data. P values (Pr (>F)) were provided from the permutation test and indicate whether group dispersions differ significantly ($p < 0.05$) or are homogeneous. 240

Table S 10. Results of tests for homogeneity of multivariate dispersion for the flocking composition dataset for the twelve species included in the analysis. Homogeneity was calculated using the betadisper function in the vegan package in RStudio (Oksanen et al. 2008). PERMDISP assesses whether groups differ in their within-group dispersion (variance) in multivariate space. Df refers to the degrees of freedom for the group and residual components. SumSq refer to the total sum of squared distances from each sample to its group centroid in multivariate space. F-values were provided by the analysis of variance (ANOVA) run for the non-metric multidimensional scaling (NMDS) ordination of abundance data. P values (Pr (>F)) were provided from the permutation test and indicate whether group dispersions differ significantly ($p < 0.05$) or are homogeneous. Species included: blackbird (Turdus merula), chaffinch (Fringilla coelebs), goldfinch (Carduelis carduelis), greenfinch (Chloris chloris), house sparrow (Passer domesticus), New Zealand fantail (Rhipidura fuliginosa), pūkeko (Porphyrio melanotus melanotus), rock pigeon (Columba livia), silvereye (Zosterops lateralis), song thrush (Turdus philomelos), starling (Sturnus vulgaris), swamp harrier (Circus approximans), and welcome swallow (Hirundo neoxena). 241

Table S 11. Pairwise permutational multivariate analysis of variance (PERMANOVA) comparisons testing differences in flocking composition between levels of each predictor

(season, orchard, period, and position) for the thirteen species included in the analysis. For each pairwise contrast, the table reports on the levels being compared; the number of non-zero flocking-type observations in each group after filtering rows with zero total flock counts (n1 and n2, respectively); F-statistics from PERMANOVA calculations; corresponding R^2 values; unadjusted p-values based on 999 permutations; and Holm-adjusted p-values. Significant pairwise contrasts (p.adj <0.05) are marked by asterisks. Species included: blackbird (Turdus merula), chaffinch (Fringilla coelebs), goldfinch (Carduelis carduelis), greenfinch (Chloris chloris), house sparrow (Passer domesticus), New Zealand fantail (Rhipidura fuliginosa), pūkeko (Porphyrio melanotus melanotus), rock pigeon (Columba livia), silvereye (Zosterops lateralis), song thrush (Turdus philomelos), starling (Sturnus vulgaris), swamp harrier (Circus approximans), and welcome swallow (Hirundo neoxena). 243

Table S 12. Formulas of the generalised linear mixed models (GLMMs) fitted for the vertical strata use data. Models were fitted in the 'glmmTMB' package using RStudio, using a negative binomial error distribution to account for overdispersion and an abundance of zeros in the count data. 264

Table S 13. Model diagnostics for generalised linear mixed models (GLMMs) produced to examine variation in the dataset of vertical strata use of different species across seasons and orchards surveyed. Candidate models included combinations of relevant fixed and random effects. Columns report convergence, positive-definite Hessian (pdHess), over-dispersion, zero-inflation, uniformity of residuals, and outlier influence. ✓ indicates model assumption criteria met; X indicates violations. Bold values highlight models retained for inference based on model diagnostics and Akaike's Information Criteria (AIC) selection. Species included: blackbird (Turdus merula), chaffinch (Fringilla coelebs), New Zealand fantail (Rhipidura fuliginosa), goldfinch (Carduelis carduelis), greenfinch (Chloris chloris), house sparrow (Passer domesticus), pūkeko (Porphyrio melanotus melanotus), silvereye (Zosterops lateralis), song thrush (Turdus philomelos), starling (Sturnus vulgaris), swamp harrier (Circus approximans), tūī (Prosthemadera novaeseelandiae), and welcome swallow (Hirundo neoxena). 265

Table S 14. Generalised linear mixed model (GLMM) outputs for vertical strata count across multiple species: blackbird (Turdus merula), chaffinch (Fringilla coelebs), goldfinch (Carduelis carduelis), greenfinch (Chloris chloris), house sparrow (Passer domesticus), pūkeko (Porphyrio melanotus melanotus), silvereye (Zosterops lateralis), song thrush (Turdus philomelos), swamp harrier (Circus approximans), tūī (Prosthemadera novaeseelandiae), and welcome swallow (Hirundo neoxena). Fixed-effect coefficient estimates (log scale), standard errors (SE), Wald z-statistics and associated p-values are reported. Ground and autumn were the reference levels for vertical stratum and season, respectively. The intercept represents the expected log observation count at these reference levels, with orchard effects evaluated at the reference orchard (fixed-effect models) or zero (random-effect models). Orchard was included as either a fixed effect or a random intercept, depending on the species-specific model. Significant estimates ($p < 0.05$) are marked with an asterisk. 269

Table S 15. Estimated marginal mean (EMM) pairwise contrasts from a generalised linear mixed model (GLMM) for vertical strata count across multiple species: blackbird (Turdus merula), chaffinch (Fringilla coelebs), goldfinch (Carduelis carduelis), greenfinch (Chloris

chloris), house sparrow (Passer domesticus), pūkeko (Porphyrio melanotus melanotus), silvereye (Zosterops lateralis), song thrush (Turdus philomelos), swamp harrier (Circus approximans), tūī (Prosthemadera novaeseelandiae), and welcome swallow (Hirundo neoxena). Pairwise contrasts, ratios, standard errors, Wald z-statistics and associated p-values are reported. Models that did not retain season for inference are signalled by NAs in the season column. Orchard was included as a random intercept. Significant pairwise contrasts ($p < 0.05$) are marked with an asterisk. 278

Table S 16. Seasonal variation on predation marks in chew cards deployed in six different orchards from autumn 2024 to summer 2025. Predation intensity was scored in four categories: no predation marks (0); less than 25% of chew cards marked (1), or most chew cards marked but with very few predation marks; up to 50% of chew cards marked (2); and more than 50% of chew cards marked with at least one having parts of the chew cards removed due to predation (3). Predation marks were identified to the level of brushtail possums (Trichosurus vulpecula), rodents (including rats and mice) and hedgehogs (Erinaceus europaeus) with the help of a chew card guide (Sweetapple and Nugent 2024). The presence of cats (Felis catus domesticus) and rabbits (Oryctolagus cuniculus) was detected through camera traps and observations during the surveys conducted in the orchards. The absence of observations of either species in a particular orchard and season is marked as not detected (ND).....297

Table S 18. Model diagnostics for generalised linear mixed models (GLMMs) used to examine variation in the dataset of different behaviours observed across seasons and orchards surveyed. Candidate models included combinations of relevant fixed and random effects. Columns report convergence, positive-definite Hessian (pdHess), over-dispersion, zero-inflation, uniformity of residuals, and outlier influence. ✓ indicates model assumption criteria met; X indicates violations. Bold values highlight models retained for inference based on model diagnostics and Akaike's Information Criteria (AIC) selection. Models were constructed for the following species: black-backed gull (Larus dominicanus), New Zealand fantail (Rhipidura fuliginosa), grey warbler (Gerygone igata), New Zealand sacred kingfisher (Todiramphus sanctus), paradise shelduck (Tadorna variegata), pūkeko (Porphyrio melanotus melanotus), silvereye (Zosterops lateralis), swamp harrier (Circus approximans), tūī (Prosthemadera novaeseelandiae), and welcome swallow (Hirundo neoxena). 298

Table S 19. Generalised linear mixed model (GLMM) results for silvereye (Zosterops lateralis) behavioural counts across orchards and seasons. Fixed-effect coefficient estimates (log scale), standard errors (SE), Wald z-statistics and associated p-values are reported. Foraging and autumn were the reference levels for behaviour and season, respectively. The intercept represents the expected log observation count for foraging behaviour in autumn, with the orchard random effect set to zero. Behaviour and season interaction terms indicate how seasonal effects modified the relative frequency of each behaviour. Orchard was included as a random intercept. Significant estimates ($p < 0.05$) are marked with an asterisk. 301

Table S 20. Pairwise contrasts calculated from estimated marginal means (EMMs) for silvereyes (Zosterops lateralis). EMMs were retrieved from a generalised linear mixed model (GLMM) accounting for the full interactions of behaviour and season, with orchard as a random effect. Behaviour categories were described as flying; foraging = behaviours

prominent to different feeding habits, such as hawking and gleaning for insectivorous birds, diving for carnivorous birds, and pecking and rummaging for omnivores; perching or roosting, hopping = on the ground or between branches); vocalising; territorial behaviours = chasing away conspecifics; social behaviours = couple preening, feeding mates or fledglings, gathering nest materials; preening = as an individual action; and interacting with the observer. Pairwise contrasts were calculated for all pairings of behaviours and for all seasons, from autumn 2024 to summer 2025. Significant contrasts ($p < 0.05$) are marked with an asterisk. 303

Table S 21. Generalised linear mixed model (GLMM) results for grey warbler (Gerygone igata), tūī (Prosthemadera novaeseelandiae), New Zealand fantail (Rhipidura fuliginosa), pūkeko (Porphyrio melanotus melanotus), and welcome swallow (Hirundo neoxena). Fixed-effect coefficient estimates (log scale), standard errors, Fixed-effect coefficient estimates (log scale), standard errors (SE), Wald z-statistics and associated p-values are reported. Foraging was the reference level for behaviour, while autumn was the reference level for season in models including seasonal effects. The intercept represents the expected log observation count for foraging behaviour in autumn for models including season, or for foraging behaviour irrespective of season in models without seasonal effects, with orchard random effects set to zero. Orchard was included as a random intercept. Significant estimates ($p < 0.05$) are marked with an asterisk. 309

Table S 22. Pairwise contrasts calculated from estimated marginal means (EMMs) for grey warbler (Gerygone igata), tūī (Prosthemadera novaeseelandiae), New Zealand fantail (Rhipidura fuliginosa), pūkeko (Porphyrio melanotus melanotus), and welcome swallow (Hirundo neoxena). EMMs were retrieved from a generalised linear mixed model (GLMM) accounting for the additive effects (main effects) of behaviour and season (grey warblers and tūī), and only behaviour (New Zealand fantails, pūkeko, and welcome swallows), with orchard as a random effect. Behaviour categories were described as flying; foraging = behaviours prominent to different feeding habits, such as hawking and gleaning for insectivorous birds, diving for carnivorous birds, and pecking and rummaging for omnivores; perching or roosting, hopping = on the ground or between branches); vocalising; territorial behaviours = chasing away conspecifics; social behaviours = couple preening, feeding mates or fledglings, gathering nest materials; preening = as an individual action; and interacting with the observer. Pairwise contrasts were calculated for all pairings of behaviours and for all seasons, from autumn 2024 to summer 2025. Significant contrasts ($p < 0.05$) are marked with an asterisk.....312

Table S 23. Direct observations of crop fruit consumption in the orchards surveyed, from autumn 2024 to summer 2025. Fruit crops were identified as apples and other fruits still on trees (A & C) and fruits left on the ground (B & D). 11 species were recorded consuming fruits: silvereyes (Zosterops lateralis), blackbirds (Turdus merula), tūī (Prosthemadera novaeseelandiae), pūkeko (Porphyrio melanotus melanotus), chaffinches (Fringilla coelebs), greenfinches (Chloris chloris), goldfinches (Carduelis carduelis), starlings (Sturnus vulgaris), house sparrows (Passer domesticus), eastern rosellas (Platycercus eximius), and song thrushes (Turdus philomelos). Orchard TR was not surveyed in spring. 322

Table S 24. Dates of crop-damage surveys conducted during the 2024 and 2025 apple harvest seasons at six orchards in New Zealand, following the calendar of harvest set by the growers

of each orchard. N/A indicates that an orchard was not surveyed for crop damage in that year. 326

Glossary & Abbreviations

DOC. Department of Conservation

ES. Ecosystem Services

ED. Ecosystem Disservices

IN. Introduced species

IUCN Red List Categories

LC. Least Concern

NT. Near Threatened

VU. Vulnerable

EN. Endangered

CR. Critically Endangered

GLM. Generalised linear model

GLMM. Generalised linear mixed model

NA. Native species

PFNZ 2050. Predator Free New Zealand 2050

SPR. Sentinel prey removal [experiment]

(Orchards Included in the Study)

MN1. Research apple and kiwi orchard in the Manawatū region, North Island

MN2. Conventional mix crop orchard in the Manawatū region North Island

KC1. Organic orchard in the Kāpiti Coast, North Island

KC2. Conventional mix crop orchard in the Kāpiti Coast, North Island

HB. Intensive monoculture apple orchard in Hawke's Bay, North Island

TR. Conventional monoculture apple orchard in the Tasman district, South Island



Chapter 1 General Introduction

1.1 Conservation in Human-Modified Landscapes

Agriculture has shaped ecosystems for millennia, creating diverse landscapes that reflect interactions between human societies and the natural environment (Bocquet-Appel 2011). Agricultural landscapes now represent one of the dominant forms of human land use globally, but vary widely in their structure, management intensity, and ecological outcomes. In some circumstances, production systems can provide resources and habitat that support biodiversity (Gordon et al. 2026). Although agriculture has supported the expansion of human populations and improved their quality of life, the effects of agricultural intensification rival climate change as a global driver of environmental change and biodiversity loss (Tilman et al. 2001; Maxwell et al. 2016).

The relationship between agriculture and environmental protection is often characterised by discord. There is a global need for increased food production for the foreseeable future, while also ensuring the sustainability of the surrounding environment and the biodiversity occupying this matrix (Tilman et al. 2001, 2017). Agriculture is essential for food provisioning, but its impacts on biodiversity conservation have led many researchers to believe that these targets are mutually exclusive (Balmford et al. 2012; Brambilla et al. 2017). The rise of agricultural intensification, with whole ecosystems turned into monocultures, has become the norm since the twentieth century (Lowder et al. 2021). With these rapid and drastic changes, it is now impossible to deny the scale of the biodiversity crisis associated with the Anthropocene (Quammen 1997; Gibson et al. 2015; Ceballos et al. 2020; Bradshaw et al. 2021). More recently, there has been a growing effort to acknowledge the impact these practices have on other species occupying the same environments. Rising from the conservation efforts of the mid-20th century (Gallagher 1997), these environmentalist principles have led to the establishment of conservation biology as a field to tackle biodiversity loss (Soulé 1985).

Agricultural intensification is a major issue globally, but especially pervasive in tropical regions (Green et al. 2005). The spatial variation in agriculture can be observed across regions, with cropland area increasing in developing countries and decreasing in developed countries over the past decades (Green et al. 2005). It is no coincidence that developing countries bear the burden of the biodiversity crisis. These complex social and historical drivers of the division between developed and developing countries help explain the different ways countries will deal with conservation issues (Duffy 2014, 2016; Nuwer 2018; Sollund & Runhovde 2020; Hutchinson et al. 2021). Overall, there is a clear imbalance in power dynamics between the countries in the Global North and those in the Global South (Wright 2011; Massé et al. 2020). This directly affects the ways and possibilities of conservation actions. While current and future trends point to advances in sustainable agriculture in Global North countries, conversion of agricultural land to urban areas and agricultural intensification is still expected to increase in Global South countries, which already suffer the burden of high demand for intensive production given their larger human populations (Power 2010). Social and political factors can act as barriers to adopting conservation-forward practices in human-managed lands (Johnson et al. 2011). Although issues surrounding agriculture are global, solutions need to address local and regional circumstances and their different social perspectives (Johnson et al. 2011).

1.2 Ecosystem Services and Disservices in Agricultural Systems

The need to understand the impacts of agricultural expansion and intensification has led to a discourse on the importance of environmental components that are not directly provisioned by agriculture. These other services relate to natural ecosystem functions that are - or can be - useful to humans and have been dubbed ecosystem services (MEA 2003).

Ecosystem services are primarily defined as the benefits people obtain from ecosystems (MEA 2003; Kremen 2005). They can be distinguished into four classes: provisioning, cultural, regulating and supporting services (MEA 2003). Supporting services are those that allow the production of all other services, such as soil formation and nutrient cycling. They enable provisioning services related to products obtained from ecosystems, such as food, water, and fibre. Regulating services, as the name implies, are the benefits that occur from regulation within ecosystem processes, such as disease regulation. Finally, cultural services are non-material benefits that can be obtained from ecosystems, ranging from aesthetic pleasure, spiritual inspiration, recreation, and ecotourism.

Since the Millennium Ecosystem Assessment report, it has been widely accepted that conserving natural ecosystem functions is important to maintain the basic components of human quality of life. Examples abound for biotic and abiotic components of the environment, from carbon sequestration and climate regulation to the use of nature motifs in art and ecotourism (MEA 2003; Daniel et al. 2012). More recently, the economic evaluation of such services has grown its own academic literature (Raudsepp-Hearne et al. 2010; Ojea et al. 2012).

Given that other species have ecological functions and interactions that may conflict with human interests, it is inevitable that some ecosystem functions will result in costs rather than benefits to humans (Zhang et al. 2007). This other side of the coin has been aptly named ‘ecosystem disservices’, but the extent of these disservices and their true costs are still poorly understood (Shackleton et al. 2016; Wu et al. 2021). Perhaps in the urgency of conserving nature’s last strongholds, the discourse has been skewed towards the benefits of nature to humans as a motivation for conservation (Daily 1997; Costanza et al. 1997). However, it is essential to consider the occurrence of ecosystem services and disservices as part of a continuum, lest risking a misguided understanding of their relationship with biodiversity (Shackleton et al. 2016; Gutierrez-Arellano & Mulligan 2018).

1.2.1 Birds as Providers of Ecosystem Services and Disservices

Although any species could provide ecosystem services, birds have been of special interest. Humans evolved to respond to and be influenced by colour (Prokop & Fančovičová 2013) and, with their often-colourful appearances and singing abilities, birds have always particularly fascinated humans (Frynta et al. 2010; Alves et al. 2013; Lišková & Frynta 2013).

Birds have been recognised as providers of all four classes of ecosystem services (Whelan et al. 2015; Şekercioğlu et al. 2016). As providers of services, birds are used for food, clothing and medicine (Alves et al. 2007). As regulators of services, birds can act as pollinators (Anderson et al. 2016), pest control agents (Martínez-Salinas et al. 2022; Mayne et al. 2023), and seed dispersers (Tomback 2016; Wenny et al. 2016). As supporters of services, birds can recycle nutrients (Fujita & Kameda 2016), remove potentially infectious waste and prevent the spread of diseases through scavenging (Gangoso et al. 2013), and act as ecosystem engineers (Floyd & Martin 2016). And as providers of cultural services, birds can motivate tourism

through the widely popular activity of birdwatching (Michel et al. 2020; Gorosábel et al. 2020), be used in religious ceremonies (Alves & Rosa 2010; Gosler 2012) and inspire artists throughout a vast range of disciplines (Lederer 2019).

Pest control is perhaps one of the most important ecosystem services birds can provide to humans in agricultural settings. Arthropod pests cause billions of dollars in damage to agriculture annually (Oliveira et al. 2014; Ferguson et al. 2019), especially invasive ones (Bradshaw et al. 2016). Insectivorous birds can thus act as biological pest control agents and reduce damage to crops (Chaplin-Kramer et al. 2011; Whelan et al. 2015; Díaz-Siefer et al. 2022). Even species that are not included in the insectivorous guild can still seasonally feed on insects and other arthropods (Şekercioğlu 2006). Conversely, birds of prey can act as pest control for frugivorous birds (Kross et al. 2012). Installing nest boxes for birds of prey - a relatively cheap practice - can lead to an increase in perceived predation risk, reducing fruit-eating bird abundances in orchards (Shave et al. 2018) and thus increasing yield.

Traditionally, however, birds were categorised based on costs (pests), benefits (food and other uses) or classed as irrelevant. In fact, the field of economic ornithology can be considered a predecessor to the discussions of ecosystem services, emerging in the 19th century as a response to the killing of birds considered harmful to agriculture (Kronenberg 2014). Arguments that birds can be beneficial for humans have evolved significantly, moving from the idea of birds as hunting targets to the establishment of the first modern laws of bird protection (Bonhomme 2021). The discourse was also raised in a period of rapid population growth and agricultural modernisation, leading to significant concerns regarding food supply and economic advancement (Bonhomme 2021). Nonetheless, from the onset of this subject, researchers were acutely aware of the complexity in trying to set a fixed value to birds' consumption of 'pest' species (Bonhomme 2021).

Incorporating economic considerations into conservation remains a controversial topic for many (Hughey et al. 2003; Bulte & Damania 2005; Sandbrook et al. 2013). The main criticism of both fields of economic ornithology and ecosystem services is that a utilitarian approach to deciding the usefulness of a species heavily favours human interests, establishing an excessive anthropocentric focus that hinders a holistic understanding of the environment (Kronenberg 2014). However, it would be naïve to deny the importance of the subject considering the economic and political system most of the world is currently under. If birds are to be included in political agendas and treated seriously by stakeholders other than conservationists, it seems inevitable to include their economic value (Johnson & Hackett 2016).

A majority of studies on wildlife's roles in food production systems has focused on their benefits to humans, often ignoring their disservices (Whelan et al. 2015). Nonetheless, birds cause damage to agriculture and incur other costs to humans. They can feed on and damage crops, kill livestock, disperse exotic plant species, and spread diseases (Whelan et al. 2015; Peisley et al. 2015; O'Bryan et al. 2018). Bird damage to human-managed systems, perceived or actual, can lead to human-wildlife conflicts (Lute et al. 2016; Huang et al. 2023). Additionally, because disservices are less understood and measured, landowners can have a biased negative perception of birds occupying agricultural systems (Kross et al. 2018).

Misconceptions and fearmongering can also sensationalise the perceived risks from predators and scavengers, hindering their conservation and leading to significant repercussions on human health (O'Bryan et al. 2018; Michel et al. 2020). Scavengers can save billions of dollars in

health costs by avoiding the spread of transmissible diseases (Michel et al. 2020). However, they are among the most persecuted groups of birds due to human misconceptions, resulting in them becoming a threatened bird functional guild worldwide (Şekercioğlu et al 2014; Şekercioğlu 2006; O'Bryan et al. 2018).

Growers' perceptions of the roles of birds on their lands will directly influence the adoption of practices that help or hinder wildlife permanence in human-managed systems (Kross et al. 2018), demonstrating the importance of properly investigating the extent of benefits and damages and efficiently communicating them to stakeholders. Calls for a better understanding of how agricultural changes might affect native species have been made in the past decades (Green et al. 2005), and the impact of intensification is acknowledged as a growing threat to bird species, especially in developing countries (Green et al. 2005). Current conservation cannot rely solely on protected areas with minimal human presence. While some species have shown population declines due to agricultural land use, others have adapted or become tolerant to crops (Goijman et al. 2015). Bird presence in agricultural landscapes is also linked to the availability of food resources in different systems (Goijman et al. 2015). Notwithstanding this, while much has been discussed on how birds can benefit agriculture, the role of agricultural systems in providing food for threatened species is a more recent and essential topic of research for modern conservation (Luck et al. 2015). Therefore, birds in agriculture should be viewed from both standpoints: how agricultural systems can support the survival of native bird populations, and which services and disservices those species can provide.

1.3 Aotearoa New Zealand: A Unique Context for Bird Conservation

There have been studies on the role of birds as providers of ecosystem services and disservices in agricultural systems for all main regions of the globe, with some important geographical gaps already recognised. One particularly important country where the subject has been surprisingly neglected is Aotearoa / New Zealand. This field of knowledge is extremely relevant to the country not only in terms of its historical tradition of agriculture (Moller et al. 2008), but also its unique position as a "country of birds", with many species threatened by exotic predators (Miskelly et al. 2009).

Around the world, the impact of introduced mammalian predators has been catastrophic for many island-endemic species (Blackburn et al. 2004), including the New Zealand avifauna (Craig et al. 2000). Bird species that evolved on islands without the presence of mammalian predators have been particularly affected by the introduction of such predators (Holdaway 1989; Blackburn et al. 2004; Miskelly & Powlesland 2013). Eradicating predators from islands has become a common strategy adopted for species conservation. However, climate change predictions indicate that many small island sanctuaries can lose their effectiveness (Courchamp et al. 2014). New Zealand is thus taking it one step further through Predator Free New Zealand 2050, or PFNZ 2050 (PFNZ 2022). This ambitious project, already in progress, aims to promote island sanctuary status to the whole country (Russell et al. 2015).

Before PFNZ 2050, many local and regional practices for controlling introduced predators were established across the country (PFNZ 2022). Nonetheless, PFNZ 2050 has adopted new tools and strategies required to reach such a large goal (Russell et al. 2015; Ross et al. 2020). Management ranges from intensive upkeep of predator-proofed fences to bait stations and traps (Russell et al. 2015). The goal is to eradicate the rodent, mustelid and possum species that act

as major threats to the conservation of many native and endemic birds (Russell et al. 2015). More recently, feral cats (*Felis catus domesticus*) were also included as targets of mammalian control (Morgan 2025). The main challenges include phasing out older technologies in favour of more effective control tactics at reduced cost that can garner sufficient public acceptance (Russell et al. 2015; Ross et al. 2020). However, it is also clear that there is already wide community support for PFNZ 2050, motivated by the recognition of the severe financial costs that introduced mammals cause to New Zealand's agricultural industry (Russell et al. 2015). Additionally, locals and international tourists alike seem to prefer spending time and money in predator-free reserves and parks, indicating a further economic motivation to eradicate exotic predators (Russell et al. 2015).

New Zealand also has a rather unique position, with its citizens demonstrating overwhelming support for the killing of exotic mammals (Murphy et al. 2019). The 'social license' afforded by the country the project to be undertaken on such a large scale (Murphy et al. 2019).

1.4 Feeding Guilds Hint at the Provision of Ecosystem Services and Disservices

Groups of bird species that share common foraging habitats and food types, and to some extent foraging techniques, are conceptually grouped in foraging or trophic guilds. A birds' capacity to provide ecosystem services and/or disservices in crop systems is directly related to their feeding guilds. The same bird species can often provide ecosystem services in one crop (e.g. pest control by feeding on arthropods that damage the crop) and disservices in another (e.g. crop damage by feeding on the crop), or even a combination of both, depending on the intensity of feeding on a particular diet.

It is important to note that many species can undergo seasonal diet shifts, such as omnivores becoming predominantly insectivorous during the breeding season, or nectarivores opportunistically feeding on fruits. Nonetheless, feeding guilds help guide expectations of species behaviours and their potential provision of services and disservices regarding their diet composition. A schematic diagram of these potential relationships is shown in Figure 1.1, and a discussion of each guild is presented in the next sections. The information is based on work I conducted before the fieldwork for this thesis, using observation records of birds spotted in horticultural systems across New Zealand by citizen scientists from the database eBird (Supplementary Material).

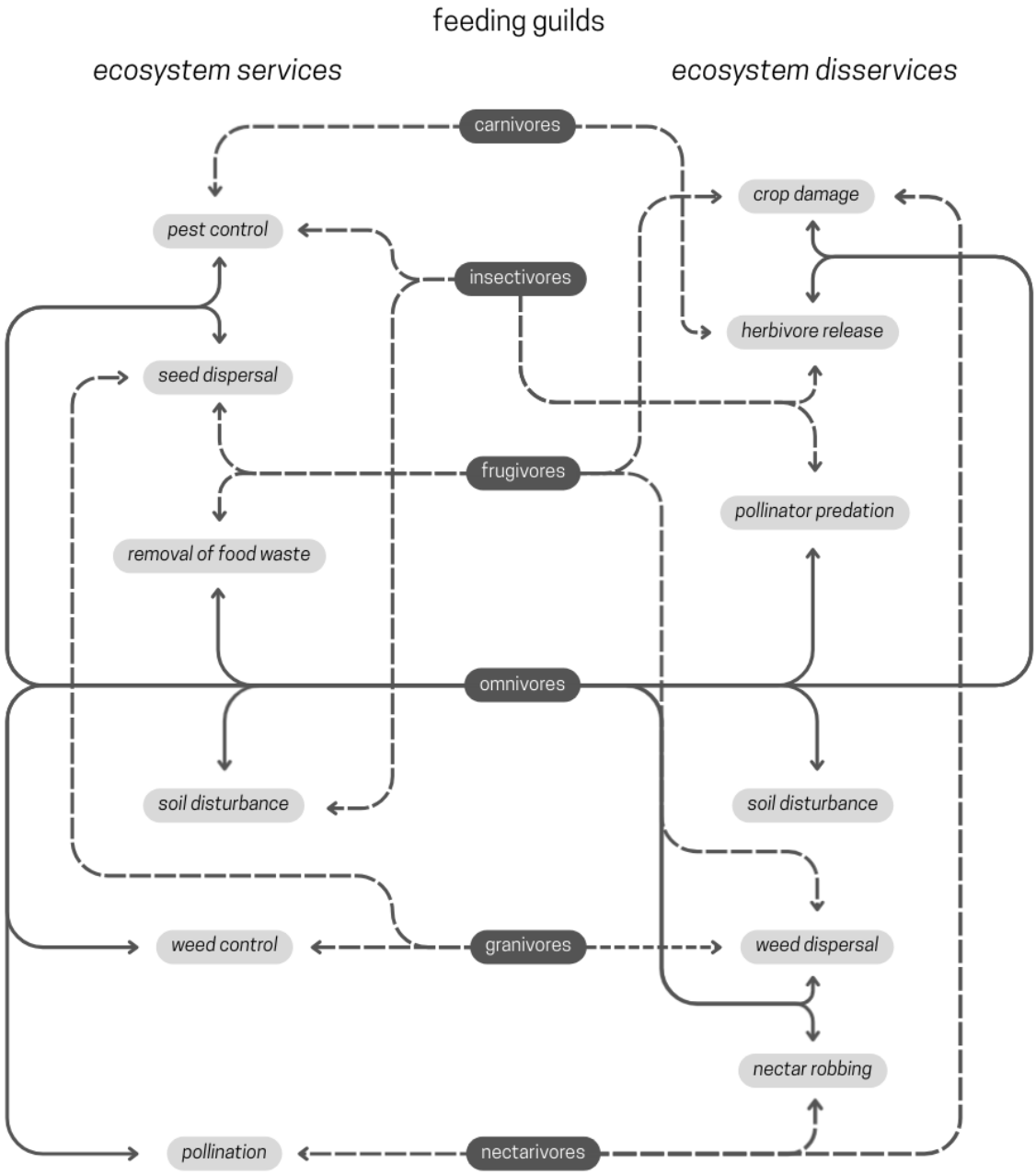


Figure 1.1. Conceptual framework of potential provision of ecosystem services (left column) and disservices (right column) by different avian feeding guilds (middle column). Arrows connect feeding guilds to the ecosystem services and disservices they can provide based on their feeding behaviours. Ecosystem services include pest control, seed dispersal, removal of food waste, soil disturbance, weed control and pollination. Ecosystem disservices include crop damage, herbivore release, pollinator predation, soil disturbance, weed dispersal and nectar robbing. Feeding guilds include carnivores, insectivores, frugivores, omnivores, granivores and nectarivores. Native New Zealand nectarivores often feed on soft-fleshed fruits, thus potentially causing crop damage. Apart from pollination, omnivores can provide all services and disservices. A seventh ecosystem service, soil fertilisation, was not accounted for in the diagram, because all feeding guilds can provide this service, depending on their diet. An additional feeding guild, piscivores, present in the observation records, is not accounted for in this diagram, given the feeding behaviour of such species is not directly related to horticultural systems.

1.4.1 Carnivory

Swamp harriers were the most abundant native species in horticultural areas in the eBird dataset and one of two native carnivores within agricultural landscapes (Table S 1). Swamp harriers have been noted as one of the few New Zealand species to be favoured by European colonisation, as they prefer to hunt in open areas (Gurr 1967). They have been observed roosting and feeding in agricultural systems, building nests close or in pasture areas (Gurr 1967), and are also commonly observed scavenging on the roads. These habits help explain their large number of observations in croplands.

Carnivorous birds can provide the ecosystem service of pest control, by reducing the number of bird pests in the crop system through predation and by inducing fear in the prey species, potentially reducing the rates of bird-induced crop damage (Luck et al. 2015). In a study conducted in New Zealand vineyards, the introduction of nest boxes for the establishment of New Zealand falcons in the systems led to a reduction of up to 95% of predation rates on grapes (Kross et al. 2012). Installing nest boxes for birds of prey can not only lead to an increase in perceived predation risk for birds damaging the crops but also enhance native populations of birds of prey (Shave et al. 2018).

However, depending on the species the carnivores are feeding on, they can also cause herbivore release. This ecosystem disservice can be caused by a cascading effect arising from consuming smaller herbivore predators (acting as mesopredators in the food chain) (Schmidt-Entling & Siegenthaler 2009; Taylor et al. 2016), leading to an increase in herbivore numbers and hence an increase in crop damage.

The dynamics of carnivore bird species in food production systems are still understudied, especially when compared to mammalian carnivory (McWherter et al. 2025). In New Zealand, evidence for ecosystem services and disservices of birds of prey in orchards, apart from the New Zealand falcon example, is lacking. Although swamp harriers are clearly seen often in croplands, no studies were found on their behaviour in these systems, and only a couple of studies reported on the birds feeding on other native species (Stephenson & Minot 2006; Stanes 2011). Further research should explore the dynamics between birds of prey and other bird species in food production systems.

1.4.2 Piscivory

Piscivory can be understood as a subset of carnivory, as piscivores feed on fish. However, they need to be treated as a distinct feeding guild because their foraging strategies and ecological impacts differ from those of terrestrial carnivory. In the eBird dataset, all piscivorous birds were native species except for the great egret (*Ardea alba*). Most piscivores belong to the Phalacrocoracidae (shags) and Laridae (gulls) taxonomic families (Table S 1). This carnivore subset also includes piscivore-invertivores, whose diets can include significant proportions of molluscs, crustaceans, and other marine or freshwater invertebrates.

Perhaps not surprisingly, none of the piscivorous species was recorded in great numbers in the croplands, with the black-billed gull (*Chroicocephalus bulleri*) having the highest number of observations at 224 (Table S 1). The black-backed gull (*Larus dominicanus*) was much more common with over 1,300 observations, but this species was not included in the piscivorous guild because of their generalist omnivorous diet.

I was unable to find any papers or theses on the potential roles of piscivorous birds in agriculture, indicating a gap in research and/or reporting. One could argue that this is to be expected, as piscivores would be quite literally out of their element in orchards. However, it is possible that these species are using horticultural systems as roosting or nesting grounds, which can differ from foraging habitats. Nonetheless, finding these species in horticultural systems indicates that they may be affecting them in ways that have not been measured or even considered previously. Therefore, I used insights from piscivorous birds in other habitats to provide background on their potential roles in horticultural systems.

By feeding primarily on fish, piscivorous birds may contribute to ecosystem services by controlling fish populations that might impact water quality in irrigation systems. Perhaps more importantly, they can serve as bioindicators of aquatic ecosystem health at a landscape scale, as horticultural systems often intersect with waterways (Luck et al. 2003).

Moreover, piscivorous birds can act as vectors of pollutants, especially in human-modified landscapes. Piscivorous birds can bioaccumulate heavy metals and other contaminants from fish or from opportunistic feeding on human waste (Kim & Koo 2007). They could also act as pathogen carriers if consuming contaminated fish, although similar scenarios have only been reported for vultures (Plaza et al. 2018). Seabirds that gather in massive colonies have also been shown to significantly affect plant and soil composition at their colonies (Ellis 2005) through their faeces and nesting activities. It is not known whether seabirds can introduce pathogens and heavy pollutants into orchards when defecating, although they do in other environments.

Therefore, while piscivorous birds might not engage directly with crops, they may influence ecosystem functions within the horticultural landscape through nutrient cycling (a service) or the spread of disease and pollutants (disservices). These roles could be even higher in horticultural systems adjacent to wetlands or waste dump areas. These considerations warrant further research into the broader landscape-level assessments of ecosystem services and disservices provided by piscivorous birds, even if they are excluded from direct metrics in horticulture.

1.4.3 Insectivory

Most of the species included in this guild were native, accounting for the second largest number of species and observations (Table S 1). A likely explanation for the relative absence of introduced species in this group is that, compared to the other feeding guilds included in this dataset, insectivorous birds tend to be highly specialised in their diets (Şekercioğlu et al. 2004). As their presence in an area is heavily dependent on the availability and abundance of their insect prey (Orłowski et al. 2014), insectivores are particularly sensitive to agricultural intensification (Şekercioğlu et al. 2004).

Furthermore, New Zealand differs from other world regions as it lacks farmland specialist native birds (e.g. (Reif et al. 2008; Hologšková et al. 2024)). Food production systems that allow for an abundance of insect species - e.g. organic practices, heterogeneous landscapes with shrub cover, a variety of food crops and crop structure - will tend to harbour a higher number of insectivorous birds (Genghini et al. 2006; Goijman et al. 2015).

Insectivorous bird species are at the forefront of pest control services by feeding on a myriad of insects considered pests to crop systems. Because compounding effects can occur when more than one pest insect species is present in the same system (Ferguson et al. 2019), having

a variety of insectivorous birds in the same system can increase the potential for pest control. Rummaging in the soil to catch insects also means that insectivorous bird species can provide the ecosystem service of soil disturbance. However, this feeding behaviour can lead to the provision of disservices such as herbivore release and pollinator predation. Understanding the impact of insectivorous birds in crop systems as providers of disservices depends on the insect species that they prey on, and whether the crop relies on insect pollination to thrive.

The large numbers of fantails, grey warblers, and welcome swallows in horticultural systems make these species excellent biological pest control agents at no observed cost to growers, as these species are not reported to feed on crops. Although fantails thrive in areas of mammalian pest control initiatives (DoC 2020), they can also coexist with mammalian pests, potentially providing services of pest control even in areas of high exotic predation pressure.

Although dunnocks have shown population declines in their native home range in Europe (Gillings et al. 2005), they have established well in New Zealand, with their diet consisting primarily of insects (Dawson & Bull 1970). The remaining insectivorous species found in agricultural areas had significantly fewer observation records, indicating an overall poor composition of introduced insectivorous species in croplands.

Thus, managing food production systems to increase the abundance of insectivorous birds could help reduce crop damage at low cost to the growers. As was the case with carnivorous birds, there was a lack of published information on the provision of ecosystem services and disservices by insectivorous birds in New Zealand, with assumptions being drawn from tropical and Northern temperate regions (Genghini et al. 2006; Garcia et al. 2023).

1.4.4 Granivory

Introduced granivores have shown important population declines in their native ranges due to agricultural intensification (Siriwardena et al. 2000; Gillings et al. 2005), but in New Zealand, they are often some of the most abundant species in bird surveys (Lemmers et al. 2014). The same agricultural intensification that can lead to a decline in granivores in their native ranges has been shown to benefit seedeaters in other regions (Angkaew et al. 2023), potentially explaining the successful establishment of these species in New Zealand.

Outside their native range, these species have been long recognised as pests in croplands, as they can opportunistically feed on small fruits and destroy grain crops (Dawson & Bull 1970; Baker 1980). Worldwide, finches are problematic species due to their consumption of grain crops (Huang et al. 2023), often involving ‘the three finches’ (goldfinches, chaffinches, greenfinches) as main culprits.

In New Zealand, introduced granivorous species are positively associated with seed densities within agricultural systems, and also feed on animal feed used for livestock (Macleod & Till 2007). Their preference for uniform, short vegetation over winter makes them highly adaptable to the New Zealand agricultural landscape.

Although these granivorous species affect New Zealand crops, their presence in horticultural systems can become beneficial during the birds’ breeding season, as they will often switch to an insect-rich diet to feed their young (Triplett et al. 2012). And in grain crops, granivorous birds can both affect the harvest yield (crop damage) and provide a sanitation service by consuming seeds that remain in orchards after harvest (Schäckermann et al. 2015). However,

there is no evidence of those services in New Zealand systems, as they have not yet been measured.

Outside New Zealand, the potential for weed control by granivorous birds has been recognised in agricultural settings, with impacts varying for perennial or annual crops (Şekercioğlu et al. 2016). However, New Zealand is at great risk of introduced weed dispersal, which has been recognised as a 'silent killer' of its ecosystems (Hooper et al. 2021). The great number of introduced granivore species is of particular concern due to the risk of weed dispersal. Although calls have been made for better control of weeds in New Zealand (Hooper et al. 2021), it remains unclear how much damage introduced granivorous birds cause by feeding on introduced weeds and potentially dispersing them across agricultural systems and forested areas.

1.4.5 Frugivory

This feeding guild was represented solely by the New Zealand pigeon, the only primarily frugivorous species (Table S 1). Although the species is considered Not Threatened, predation from introduced mammals causes a significant risk of extinction in pigeons and doves (Bennet & Owens 2002; Şekercioğlu et al. 2004; Walker 2007).

Although bird size is correlated to the size of the fruits they will feed on, and the frequency of fruit encounters (Case & Tarwater 2020), frugivores are often observed pecking at larger fruits, which could be an adaptive response for opportunistic feeding (Rey 2011). Frugivorous birds can thus be responsible for a great deal of crop damage to a variety of fruit orchards, either by directly consuming whole fruits (e.g. berries or grapes) or by inducing infections and spoilage when pecking at larger fruits (Triplett et al. 2012). Compounded crop damage can also be caused by flocking behaviour, as large groups of frugivorous birds descend into orchards to feed on the fruits (Tracey et al. 2007).

By typically swallowing seeds from fleshy fruits intact, frugivorous birds are excellent seed dispersers (Whelan et al. 2015). Although seed dispersal can be an ecosystem service, the variety of introduced fruit crops in New Zealand can make frugivores provide an ecosystem disservice through the dispersal of unwanted seeds. Flighted frugivores like the New Zealand pigeon can disperse introduced plant species across great distances. The tendency of New Zealand frugivores to be generalist feeders, coupled with introduced bird species that also feed on fruits, further promotes the risk and spread of invasive fleshy-fruited plants in the country (MacFarlane et al. 2025). This can be the case for the New Zealand pigeon, but also for other native frugivore species, such as silvereyes (*Zosterops lateralis*), tūī (*Prosthemadera novaeseelandiae*) and bellbirds (*Anthornis melanura*).

Finally, fruit-eating birds can also provide removal of food waste as an ecosystem service. Removal of food waste has been recognised as an important ecosystem service in urban areas for other taxa (Penick et al. 2015; Perfecto & Philpott 2023), but it has not been discussed adequately in the agricultural sphere or for birds. More studies need to be conducted in crop systems to quantify the impacts of birds providing a sanitation service by cleaning rotten fruits, especially in the months after the harvesting season, and in orchards with lower levels of machinery use.

1.4.6 Nectarivory

Worldwide, pollination services can increase production in approximately 75% of all food crops (Klein et al. 2007). Nectivorous birds provide pollination as an ecosystem service (Requier et al. 2023), even when bees are the top pollinators of zoogamic (animal-pollinated) crops (Giannini et al. 2015). Researchers have called for integrating agroforest ecosystems with open agricultural areas to allow for the spillover of nectarivores, thus partially making up for the decline in avian pollinators (Şekercioğlu et al. 2004).

The only nectarivores in the eBird dataset were the native tūī and bellbirds (Table S 1). They have been recognised as important pollinators and seed dispersers of several native plant species (Kelly et al. 2010). In winter, tūī will often visit urban and rural areas to feed on the nectar of introduced species (Innes et al. 2005). While they are not currently threatened with extinction, tūī tend to be sparse in deforested areas, and have become relatively common in urban areas (Robertson et al. 2017; Fitzgerald et al. 2021). These species have thrived with the removal of invasive predation pressure, with population increases markedly associated with pest control (DoC 2020).

Even as primary nectarivores, tūī and bellbirds have been shown to include fruits and insects in their diets (Craig et al. 1981; Chapter Five). Thus, New Zealand nectarivores can also provide the ecosystem disservice of crop damage. Furthermore, nectarivorous birds can also provide ecosystem disservices through nectar robbing when their feeding behaviour or morphology does not result in contact with a flower's reproductive structures (Kelly et al. 2006). Rather than pollinating the plant while feeding, birds may access nectar without contacting the anthers or stigma, sometimes by damaging the flower. Nectar robbing can occur in both native and introduced plants and depends on the interaction between the bird's feeding behaviour and floral morphology.

Nonetheless, one should have caution in assuming a disservice of nectar robbing, unless evidence demonstrates a negative effect on plant reproduction, such as damaged flowers, lower seed sets, and reduced legitimate flower visitations. Thus, while tūī and bellbirds have been recorded feeding on the nectar of introduced plant species (Innes et al. 2005; MacLeod et al. 2008), there's no confirmation of nectar robbing as a disservice. Alternatively, for example, silvereyes, native generalist omnivores, have been found to provide nectar robbing as a disservice in endemic New Zealand plants (Robertson et al. 2008). Nonetheless, information on nectar robbing of exotic horticultural plants is lacking. Further research is needed to identify the contexts in which these species can be more damaging to horticulture, as the literature on the species has focused on their role as native pollinators to native and introduced plant species.

1.4.7 Omnivory

Omnivores account for the most dominant feeding guild across avian observations within croplands in New Zealand (Figure S 1). This was to be expected, as generalist species tend to more easily adapt to fragmented habitats and high levels of human disturbance that characterise agricultural systems (Garfinkel et al. 2020; Zhang et al. 2021). Omnivores are overall less prone to extinction than more specialised functional guilds, such as scavengers, frugivores, and insectivores (Şekercioğlu et al. 2004).

Because of their generalist feeding habits, omnivores could provide all ecosystem services and disservices accounted for in horticultural systems. These include pest control when feeding on invertebrate pests, seed dispersal, weed control and dispersal, removal of food waste, pollination and pollinator predation, nectar robbing, crop damage, soil disturbance (which can be either a service or a disservice), and herbivore release.

When feeding on invertebrates, omnivore species tend to be generalist arthropod predators. Thus, omnivores may provide both services and disservices to the crop system for the same feeding behaviour (Garfinkel et al. 2020; Goijman et al. 2020). This is linked to the fact that pests of field crops can vary between years or even seasons (Kross et al. 2020; Garfinkel et al. 2020). Diet shifts will also follow ontogenetic or environmental changes (Cassano et al. 2016), and many omnivorous species will feed primarily on insects during the breeding season (Triplett et al. 2012). A complete understanding of the ecosystem services and disservices provided by omnivores will thus require behavioural and feeding studies of focal species across different crops within a temporal gradient to account for seasonal diet shifts.

Several omnivorous birds featured in the eBird dataset have also been reported in the literature within horticultural systems. Silvereyes have thrived with invasive predator control (DoC 2020) and are some of the most abundant omnivorous native species in horticultural systems. Old ornithological records already discuss the role of the species as providing damage to the crops and benefits in the form of pest control of woolly aphids (Higgins et al. 2006). A careful look at this particular species is explored in Chapters Three and Four.

Kingfishers are often seen in orchards using vertical structures as their perching grounds from where they hunt for prey (Horgan et al. 2017), and similar behaviour has been observed for the New Zealand kingfisher (*Todiramphus sanctus*). Pūkeko (*Porphyrio porphyrio*) are anecdotally considered great pests of crops, although studies on the subject have focused on their close relative, the western purple swamphen, in Europe and Asia.

Older ornithological notes provided some information on the feeding habits of paradise shelducks (*Tadorna variegata*), with a diet consisting of primarily plant material from grazing and a preference for pastures (Williams 1971; Bisset 1976). Their preference for pastoral habitats indicates their potential to act as a carrier of *Mycobacterium avium paratuberculosis*, that leads to Johne's disease in livestock (Nugent et al. 2011).

Finally, introduced omnivorous birds reported previously in the literature have been recognised as horticultural pests both in New Zealand and in other countries, such as eastern rosellas (*Platycercus eximius*), Indian mynas (*Acridotheres tristis*), and starlings (*Sturnus vulgaris*) (Galbraith 2010; Grarock et al. 2012; Prasad & Christi 2014). Starlings have adapted well to New Zealand pastures and croplands, often sustaining themselves on livestock feed and grain crops (Macleod & Till 2007). Starlings tend to flock in large numbers, which can be damaging to fruit crops (Dawson & Bull 1970; Baker 1980; Bozzo et al. 2021). Together with mynas (*Acridotheres tristes*), they are among the worst invasive species worldwide for being aggressive towards native species, displacing them and even feeding on their eggs (Lowe et al. 2000; Linz et al. 2007; Grarock et al. 2012; Rabou 2022).

House sparrows prefer grassland habitat (Macleod & Till 2007), but they will often be seen in croplands. They are extremely adaptable to urban and rural areas, and while they have suffered population declines in their home range, they are established in great numbers worldwide (Gillings et al. 2005). In New Zealand, they are often some of the most abundant species in bird surveys in agricultural land (Lemmers et al. 2014).

Belonging to the same genus (*Sturnus*) within the Turdidae family, blackbirds and song thrushes are very common introduced species across New Zealand. Blackbirds are at the forefront of many agricultural conflicts, with a long history of management towards controlling them as crop pests (Shwiff et al. 2017; Duttenhefner et al. 2024). Song thrushes face similar scrutiny, with researchers also pointing out their risk as pathogen spreaders for their behaviour

of foraging and nesting close to the ground and becoming infected with ticks (Gryczyńska et al. 2024). Both have been repeatedly pointed out by New Zealand growers as harmful to their crops (Dawson & Bull 1970; Baker 1980).

Nonetheless, there is also the potential for these introduced omnivorous birds to provide ecosystem services. In Canterbury pastures, large flocks of starlings have been reported feeding on grass grubs (*Costelytra zealandica*), indicating the potential for pest control (East & Pottinger 1975). As with other species-specific cases, further research into diets and foraging activities within horticultural systems would be required to determine their functional roles.

1.5 The Selection of Apple Orchards as A Model Production System

Agriculture can be understood as an umbrella term for the primary production of food, whether of animal protein or vegetal crops (FAO 2007). Horticulture can thus be considered a subset within agricultural techniques, referring to components pertaining to plant production, including perennial trees, fruits, vegetables, and flowers, typically on a smaller, intensive scale (Sakiyama 1991; Tigchelaar & Foley 1991). This thesis focuses on horticultural systems as they are a diverse and economically important component of New Zealand's primary industries, encompassing a range of production systems including annual vegetable crops, vineyards, and perennial fruit orchards (United Fresh 2025). Furthermore, the mechanisms and behaviours expected of birds in orchards and farmland can be very different, as farmland often consists of large expanses of grassy areas with a few rows of larger trees along the edges.

The New Zealand horticultural industry is estimated at a total export value of $6.85 billion, across 74,286 hectares of land of which approximately 8% is owned by indigenous Māori people (United Fresh 2025). In addition to their economic value, orchards can be linked to the broader indigenous concepts of *kaitiakitanga* (responsibility and stewardship of land and ecosystems) and *mahinga kai* (relationships between people, landscapes, and food resources). Among these systems, apple orchards represent one of New Zealand's major fruit industries, both in terms of production area and economic value. It is an industry marked by technological innovation, with over 80 varieties produced across the country (Dobbs & Rowling 2006; NZAP 2025). The apple industry comprises approximately 11,000 hectares across the country, behind only kiwifruit and grapes for wine (United Fresh 2025). Beyond their economic importance, apple orchards represent perennial woody production systems that maintain part of their vegetation structure throughout the year, potentially providing greater habitat complexity and resource availability for wildlife. These factors led to the selection of apple orchards as the site focus of this thesis.

1.6 Thesis Structure

This thesis is structured in five further chapters. Chapter Two includes a published systematic literature review on the ecosystem services and disservices provided by avian species worldwide, with special emphasis on methods employed in the studies and gaps in reporting data. Chapters Three to Five present the results of fieldwork conducted in six apple orchards in four regions across New Zealand (Manawatū-Whanganui, Kāpiti Coast, and Hawke's Bay in the North Island, and the Tasman region in the South Island). Fieldwork was conducted from the autumn 2024 to the harvest season of 2025. Chapter Three draws on bird surveys in the same orchards to assess seasonal variations in bird abundance and several aspects of

community composition. Chapter Four analyses the behaviours and feeding observations of some of the most abundant species seen throughout the fieldwork period, with discussions on their potential to provide pest control, crop damage, and other ecosystem services and disservices. Chapter Five investigates the provision of an ecosystem service (pest control) and a disservice (crop damage) by bird species in the orchards surveyed. Finally, Chapter Six comprises an amalgamation of the general discussions of the various chapters and posits possibilities for future research.



MASSEY UNIVERSITY
TE KUNENGA KI PŪREHUROA
UNIVERSITY OF NEW ZEALAND

GRADUATE RESEARCH SCHOOL

STATEMENT OF CONTRIBUTION
DOCTORATE WITH PUBLICATIONS/MANUSCRIPTS

We, the student and the student's main supervisor, certify that all co-authors have consented to their work being included in the thesis and they have accepted the student's contribution as indicated below in the Statement of Originality.

Student name:	Giuliana Caldeira Pires Ferrari
Name and title of main supervisor:	Professor Isabel Castro
In which chapter is the manuscript/published work?	Chapter Two

Describe the contribution that the student and members of the supervisory team have made to the manuscript/published work:[1]

GCPF (student): conceptualization / data curation / formal analysis / investigation / visualization / writing (original draft) / writing (review & editing)
KM (supervisor): investigation / writing (review & editing)
AWR (supervisor): writing (review & editing)
IC (main supervisor): investigation / writing (review & editing)

Please select one of the following three options:

(●) **The manuscript/published work is published or in press**

Please provide the full reference of the research output:

Austral Ecology. 50(9):e70110

( ) **The manuscript is currently under review for publication**

Please provide the name of the journal:

( ) **It is intended that the manuscript will be published, but it has not yet been submitted to a journal**

Student's signature:	Giuliana C. P. Ferrari 2026.01.26 10:39:34 +13'00'	Main supervisor's signature:	Isabel Castro Digitally signed by Isabel Castro Date: 2026.01.28 11:35:40 +13'00'

This form should be placed at the beginning of each relevant thesis chapter.

[1] Refer to the Massey University Publishing and Authorship guidelines (OneMassey for staff, Stream for students) and/ or Contributor Roles Taxonomy (CRediT) guidelines for guidance.

Chapter 2 Not All Birds of the Same Feather: A Systematic Review of Horticultural Ecosystem Services and Disservices

Austral Ecology. 50(**9**):e70110

Giuliana Caldeira Pires Ferrari *[1]

Karen Mason[2]

Alastair Robertson[1]

Isabel Castro[1]

1. School of Food Technology and Natural Sciences, Massey University, New Zealand

2. Plant and Food Research Palmerston North, New Zealand

* corresponding author: g.ferrari@massey.ac.nz

2.1 Abstract

Wild birds can provide essential benefits and cause significant harm in food production systems, commonly framed as ecosystem services and disservices, respectively. We conducted a systematic review of the literature on avian ecosystem services and disservices in horticultural systems, analysing 251 studies published between 1912 and 2023. Species richness and abundance were the most commonly used metrics. A total of 128 studies investigated ecosystem services, 109 addressed disservices, and only 22 considered both. Pest control (137 occurrences) and crop damage (120) were the dominant subjects within ecosystem services and disservices, respectively. However, crop damage was frequently reported without assessment, suggesting a confirmation bias toward birds as pests. The methods used to assess services and disservices were diverse, including species identification, damage and yield surveys, landscape analysis, experiments, published data, social surveys, laboratory techniques, and economic or ecological modelling. Despite this methodological diversity, most studies used only one or two approaches. Studies incorporating human-wildlife conflict were rare, despite their relevance for both conservation and horticultural management. This review reveals a bias toward studying avian contributions that are more easily measurable, such as pest control and crop damage, while more complex or less visible effects, such as pollination, disease control, or herbivore release, remain underexplored. As a result, birds' roles in horticultural systems are often understood in fragmented terms, potentially leading to ineffective or unjustified management decisions. A more holistic, species-focused, and integrative approach is needed to fully understand the trade-offs between ecosystem services and disservices. Such understanding is critical not only for enhancing the sustainability and productivity of food systems, but also for conserving wild birds in increasingly intensified agricultural landscapes.

Keywords: ecosystem services, ecosystem disservices, food production systems, avian ecology, human-wildlife dynamics, methodological shifts

2.2 Introduction

Agriculture dominates the Earth's landscape, with more than one-third of the world's terrestrial surface dedicated to agricultural production. There is a global need for increased food production while simultaneously ensuring the sustainability of the surrounding environment and the biodiversity it supports (Tilman et al. 2001). Nonetheless, although food production allowed the expansion of human populations and an increase in quality of life, the effects of agricultural intensification rival climate change as global drivers of environmental change and biodiversity loss (Tilman et al. 2001; Maxwell et al. 2016).

Agriculture is essential to human life, relying heavily on ecosystem services provided by natural ecosystems even if those are often underappreciated (Matson et al. 1997; Power 2010). With the well-documented impact of agricultural intensification on biodiversity, scientific discourse has focused on components of the natural environment that can provide indirect benefits to food production systems. Termed 'ecosystem services' (Daily 1997), these services relate to natural ecosystem functions that are, or can be, useful to humans.

Ecosystem services can be divided into four classes: provisioning, cultural, regulating and supporting services (Daily 1997). Supporting services are the ones that allow the production of all other services. They make possible provisioning services, which relate to products that can be obtained from ecosystems. Regulating services are the benefits that are obtained from regulation within ecosystem processes. Cultural services are non-material benefits that can be obtained from ecosystems.

Nature's significant benefits to humans through ecosystem services have been recognised for more than forty years (Ehrlich & Ehrlick 1981; Costanza et al. 1998, 2014; MEA 2003). Biodiversity contributes a variety of supporting services to agricultural systems, such as pest control and pollination (Daily 1997; Matson et al. 1997; Power 2010). Food production systems can thus be managed to provide natural supporting ecosystem services to the advantage of these systems (Swinton et al. 2007). However, the loss of biodiversity triggered by agricultural intensification leads researchers to believe that trade-offs between food production and ecosystem services may be unavoidable (Power 2010). Consequently, effective management, allied with the practice of maintaining biodiversity within food systems, is paramount to preserving these natural ecosystem services (Lyver et al. 2010; Power 2010).

Although it is now widely accepted that conserving natural ecosystem functions is essential for the maintenance of basic components of human quality of life, non-human species interact with human systems in ways that may result in negative outcomes for humans (Zhang et al. 2007). These costs have been aptly named 'ecosystem disservices' (Lyytimäki & Sipilä 2009). The discourse on ecosystem disservices is gaining traction (Kronenberg 2014), but their true costs are still poorly understood (Shackleton et al. 2016; Wu et al. 2021).

2.2.1 Birds as Providers of Ecosystem Services and Disservices

Biodiversity can influence food production both positively and negatively, but birds have attracted particular interest due to their behavioural diversity and broad range of feeding guilds.

These traits allow them to provide multiple ecosystem services - and at times, disservices (Triplett et al. 2012; Whelan et al. 2015; Şekercioğlu et al. 2016).

In recent decades, researchers have called for a better understanding of how agricultural practices affect native species (Green et al. 2005). Agricultural intensification is now widely recognised as a major threat to bird species, particularly in developing regions (Green et al. 2005). Current conservation cannot rely solely on protected areas with minimal human presence. While some species have shown population declines due to land use, others have adapted to or become tolerant of crops (Goijman et al. 2015). Bird occupancy in these landscapes is closely linked to the availability of food resources, highlighting the importance of agricultural systems in supporting at-risk species (Goijman et al. 2015). The role of agricultural systems in providing food for threatened species is a more recent and essential topic of research for modern conservation (Luck et al. 2015). Therefore, birds in agriculture should be viewed from both standpoints: how agricultural systems can support the permanence of native bird populations, and in turn which services and disservices those species can provide and how they can be encouraged (services) and mitigated (disservices).

To date, the literature on the costs and benefits of wild animals to agriculture has evolved independently, with few authors attempting to bridge the gaps between those subjects (Triplett et al. 2012). These gaps hinder the understanding of costs and benefits within a spectrum and their potential trade-offs (Triplett et al. 2012). In this review, we synthesise the current literature on the ecosystem services and disservices provided by birds in horticultural systems, with a focus on the biological groups studied, knowledge gaps, and methodological trends.

2.3 Methods

We conducted a systematic review following the guidelines proposed by Pullin and Stewart (2006). The search was conducted in the Dimensions CMTM platform (Hook et al. 2018). The keywords reflected the possible interactions between the three foci of the search: birds' services, birds' disservices, and the type of horticultural system (e.g, vineyard, orchard, crop, plantation). Those interactions were examined in a round of preliminary searches, then adjusted to avoid undesirable results or maximise the scope of the search. Ultimately, the review was conducted using the following keywords from the first available publication until April 2023: *(bird* OR avia* OR avifauna* or ornithol*) AND (service* OR disservice* OR pest* OR control* or pollinat* OR engineer* OR damage* or scaveng* OR release*) AND (agr* OR hort* OR orchard* OR vineyard* OR crop* OR plantation* OR coffee OR finca*),*

The search produced an initial result of 2,223 documents. We included similar keywords to services, disservices and horticultural systems to allow for a more comprehensive search, especially of older documents that would not necessarily refer to now widely used terms. For example, nuts and fruit crops studies usually include 'orchard' in the title or abstract, while 'coffee' needed to be included as a keyword to avoid missing relevant papers. In a similar logic, the keyword for agriculture was inserted in the review to avoid losing information on plant crops. However, this review focuses exclusively on plant food production systems for direct human consumption, therefore excluding pastoral studies.

Documents were screened using the Preferred Reporting Items for Systematic Reviews and Meta-Analysis (PRISMA) diagram (Page et al. 2021) (Supplementary Material, Figure S 2), The process resulted in 251 documents. Data were extracted into the following categories:

publication date, geographic location, crop systems, data collection methods, bird taxa, and community diversity metrics.

2.4 Results & Discussion

Of the 251 publications, 243 were journal articles, four were book chapters, three were pre-prints, and one was a university report (Table S 2). The earliest study dates to 1912, but the majority were published in the last 15 years (Figure 2.1).

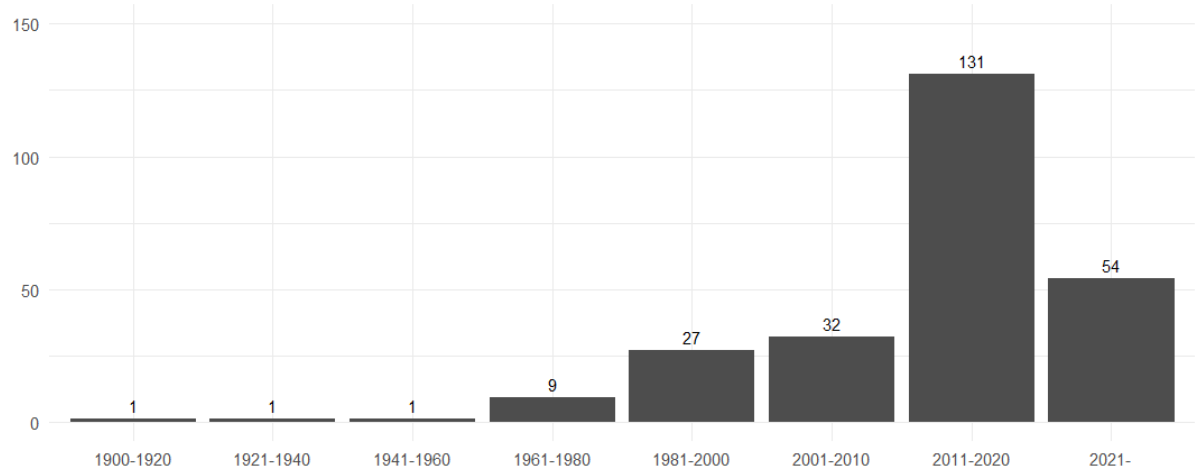


Figure 2.1. Distribution of document publications from the first available document (1912) to 2023. Each decade is represented on the y-axis, with three decades (1911 - 1940) presenting empty values.

2.4.1 Horticultural and Biological Focus

Fruits and grains were the most studied horticultural crops found in the review (Table 2.1). These are essential staples of all human societies and are recognised for their importance to human health (Awika 2011; Yahia et al. 2017). Vineyards and cacao plantations were particularly well represented - likely due to the economic relevance of wine and chocolate (Yahia et al. 2017). Greens, seeds, and beans were moderately represented (45 and 44 studies), with coffee (24) being the most represented crop in the seeds and beans category (Figure S 3). Nuts, oils, and root crops were less common (13, 9, and 3 studies, respectively). Apples (18 studies) and vineyard grapes (17) were the most cited fruit crops. Roughly one-third of publications (69) did not specify crop types, either covering multiple crops or focusing solely on bird species and their ecosystem roles. Case studies focusing on fruit orchards were concentrated in North America and Europe, with fewer case studies on the coastal regions of Africa, South America, Oceania, and Southeast Asia (Figure S 3). Publications focusing on grains were mostly distributed across Africa and Europe, with a few on North America, South America, and Southern Asia. Case studies on seed crops were mainly distributed across the tropical and subtropical regions, including the Caribbean, Central America, and Sub-Saharan Africa. Leafy crop studies were clustered in North America and Southeast Asia.

Approximately 39% of the publications (99) identified factors influencing bird communities (Table S 3). Of these, 74 focused exclusively on positive factors, 17 discussed both positive

and negative influences, and eight focused solely on negative factors. The most cited positive factors were landscape heterogeneity and proximity to natural habitats. The most common negative influences were pesticides, bird deterrents, and habitat loss. These findings echo previous literature emphasising the importance of natural habitat, shade and tree covers for the persistence of bird communities in human-managed lands (Loreau et al. 2003; Winqvist et al. 2012; Maas et al. 2015; Barbaro et al. 2021). However, there were considerably fewer documents investigating the negative factors affecting bird communities, although pesticides and other human-managed activities can be highly damaging to birds (Geiger et al. 2010; Power 2010). This indicates a research bias towards studying factors that promote or maintain bird populations, rather than those that hinder birds' survival in horticultural systems.

Most publications (133) surveyed the horticultural systems without focusing on species or taxonomic groups, but rather having a look at the general community of birds present on the system. An additional 53 publications did not include any taxonomic data, assessing services and disservices without species identification. The remaining 65 publications focus on bird species, taxonomic groups, or feeding guilds. A comprehensive list of all species and guilds studied is available in the Supplementary Material (Table S 4). While 22 publications within the review looked at species of conservation concern, only six publications expressed the importance of investigating the permanence of native or endemic species in horticultural systems (Jones et al. 2005b; Gámez-Virués et al. 2007; Kross et al. 2012; Brambilla et al. 2017; Maas et al. 2018; da Silva et al. 2022). Studies looking into the integration of conservation of endemic species, such as the Moltoni's warbler *Sylvia subalpine* (Brambilla et al. 2017) and the Azores woodpigeon *Columba palumbus azorica* (Lamelas-López & Marco 2021), into food production systems, remain rare. Most documents, in fact, failed to discern between introduced or exotic and species native to the regions of study. With the projected advance of agriculture into natural habitats (Power 2010), this represents a missed opportunity to explore how horticultural systems might support the conservation of native avifauna. Community diversity metrics were reported in 79 publications, most commonly species richness (60 studies) and abundance (48), with many studies including both (Table 2.2). Functional diversity and feeding guilds were rarely reported (9 and 4 studies, respectively). Only one study employed a weighted measure of avian abundance (Martínez-Núñez et al. 2020b). Despite frequent discussions of human-wildlife conflict, fewer than 20% of studies (45) explicitly addressed these issues.

Furthermore, many studies failed to report management practices in detail (Table 2.1). This hinders understanding how different practices can affect the provision of ecosystem services and disservices by birds. Managing horticultural systems to maintain high levels of biodiversity, while avoiding reducing crop yield, is one of the greatest conservation challenges of current times (Yahia et al. 2017). And because high levels of biodiversity can translate into ecosystem services that contribute to crop productivity, it would be desirable to pay better attention to the effects of management practices on birds and their services and disservices.

Table 2.1. Types of systems and management are described in the studies retrieved from the search. The first two columns refer to the types of systems studied, with the last two columns referring to the management described by the researchers in each study. The total sum of systems will not reflect the number of documents (251), given that many studies assessed different systems.

System	**T**	***Management***	***T***
fruits	81	not specified	122
multiple/not specified	69	conventional	51
grains/cereals	60	agroforestry	20
greens	45	organic	15
seeds/beans	44	conventional vs organic	12
nuts	13	traditional	11
other	13	small	7
oils	9	experimental	5
roots	3	sun vs shade	5
		low-intensity	3
		cooperatives	2
		indigenous practice	2
		large vs small	1
		mixed management	1

Table 2.2. Types of community metrics used to measure diversity of bird communities were specified in 79 out of the 251 documents included in the review. Several metrics could be applied in the same study. The second section of the table describes the distinction between documents that presented or did not discuss human-wildlife conflicts.

community metrics	***T***
species richness	60
abundance	48
weighed bird abundance	1
feeding guilds	9
functional diversity	4
discussion on human-wildlife conflicts	**T**
N	206
Y	45

2.4.2 Investigating and Reporting on Ecosystem Services and Disservices

Out of 251 publications, 128 investigated ecosystem services, 109 investigated ecosystem disservices, and 22 delved into both services and disservices. Six ecosystem services and seven disservices were featured, with pest control (service) and crop damage (disservice) being the focus of most publications (Table 2.3; Table 2.4). Fertilising, disease control, pollination, and weed control were the other ecosystem services studied (Table 2.3; Figure S 4), while herbivore release, disease spread, pollinator predation, seed predation, repellent action and killing of livestock are included in the list of disservices (Table 2.4; Figure S 4).

Pest control was the most frequently studied service (137 instances; Table 2.4), likely reflecting the substantial economic impacts of invertebrate pests (Ferguson et al. 2019). But the provision of pest control is often dependent on particular species and their feeding habits; insectivorous birds, for example, will be better agents of biological control of arthropod pests than granivorous species (Şekercioğlu 2006), while birds of prey can act as efficient agents of control of other birds in horticultural settings (Kross et al. 2012). Given the context-specificity between different agrosystems and geographical regions, there are still knowledge gaps on the overall effects of birds as biological pest control agents (Díaz-Siefer et al. 2022).

Other ecosystem services are likewise valuable; a third of food crops are estimated to rely on faunal pollinators, a service also valued at billions of dollars annually (Klein et al. 2007). However, pollination was only evidenced in two documents (Ndang'Ang'A et al. 2013; Requier et al. 2023). This might be explained by the higher importance of insects, which were not the focus of this review, as pollinators to crops. Nonetheless, pest control and pollination have been indicated as easier services to quantify, given the direct costs of replacing such natural agents (Power 2010). Evidence for the provision of fertilising services was confirmed in four documents (Navedo et al. 2015; Baling et al. 2016; Gorosábel et al. 2019; Plotnikov & Sinyavskiy 2020). Disease control was another ecosystem service included in the review, with three documents presenting evidence for the provision of this service (O'Bryan et al. 2018; Gorosábel et al. 2020, 2022). Weed control also had a minor representation, with a single study in the review, although the spread of weeds and their damage to crops is already a recognised issue (Peters et al. 2014). Finally, the ecosystem service of aesthetics was studied in one document (Geladi et al. 2022). This unique occurrence might be explained by the difficulty of translating a subjective notion into economic values.

Crop damage was the most reported ecosystem disservice, with 120 occurrences (Table 2.4). The main issue in this area of research is that birds are often assumed to cause damage to crops, even though the perceived losses can be significantly higher than the actual damage (Şekercioğlu et al. 2016). This became evident when comparing the assumptions of researchers for crop damage with pest control. Crop damage was seven times more likely to be reported but not assessed (Tables 3 & 4). Expectations of damage - both by researchers and growers - frequently outpaced assessments. This discrepancy suggests a bias toward negative assumptions about birds perceived as pests. The provision of crop damage is also highly dependent on the context-specifics of birds involved and the systems in question. Some bird species such as the red-billed quelea (*Quelea quelea*) and village weaver (*Ploceus cucullatus*) are consistently reported as troublesome pests, especially due to their natural history trait of feeding within big groups (Ward 1965; Adegoke 1983). However, even in those cases, damage might be overestimated, with documents reporting damage but not actually assessing it (Manyama et al. 2014; Musiwa & Mhlanga 2020). Worthy of note was the change in the methods employed to study crop damage. Until the 1980s, data was gathered by studying birds shot within the horticultural systems, then moving to the collection of faeces from live animals to study their diet content. This switch was probably inspired by the increasing importance of animal welfare in society and academic circles (Singer 2009).

Although six other disservices are accounted for in the review, only herbivore release (i.e. predation of mesopredators leading to the growth of herbivore populations and thus potential crop damage), and seed and pollinator predation featured documents presenting evidence for the provision of such disservices, with disease spread, repellent action and killing of livestock

being disproven or needing more data (Table 2.4). Birds of prey and scavengers were often assumed to be pathogenic spreaders, although this concept has been disputed (O'Bryan et al. 2018). Foodborne pathogens were also studied in other wild birds, although the researchers indicated the need for more data before conclusive evidence can be drawn (Smith et al. 2022a). Herbivore release is an example of the evidence of complex food webs within agricultural and horticultural systems, with birds indirectly affecting crops by feeding on the predators of herbivores and thus increasing the population of potential pests (Denmead et al. 2017; Garfinkel et al. 2020). Repellent action and killing of livestock were considered for specific groups, with waterfowl assumed to repel cattle from agricultural lands due to their faeces (Fox et al. 2017), and birds of prey assumed to cause mortality to livestock (O'Bryan et al. 2018). The repellent effect of waterfowl was inconclusive, while researchers on the second case study disproved the disservice to birds of prey. However, the low number of studies on these subjects hinders a definitive conclusion on whether such disservices are being provided.

There was a marked discrepancy in how services and disservices were studied. While two-thirds of pest control studies found positive evidence, only half of crop damage studies confirmed actual harm. Moreover, studies often cited growers' concerns about crop damage without measuring it. This pattern inflates the literature on disservices without robust data and may distort policy or management responses. Fundamentally, more studies on the other services and disservices included in the list would be needed to warrant conclusions on birds being de facto provisioners of such benefits and damages. There was also a low number of studies investigating services and disservices in the same system. By not approaching ecosystem services and disservices as a continuum, researchers might underestimate or ignore holistic dynamics, such as pest control being neutralised by crop damage (Gonthier et al. 2019), or vice versa (Weyell et al. 2015). A dual approach could reveal complex dynamics - where positive and negative outcomes interact in unexpected ways - which are currently underexplored.

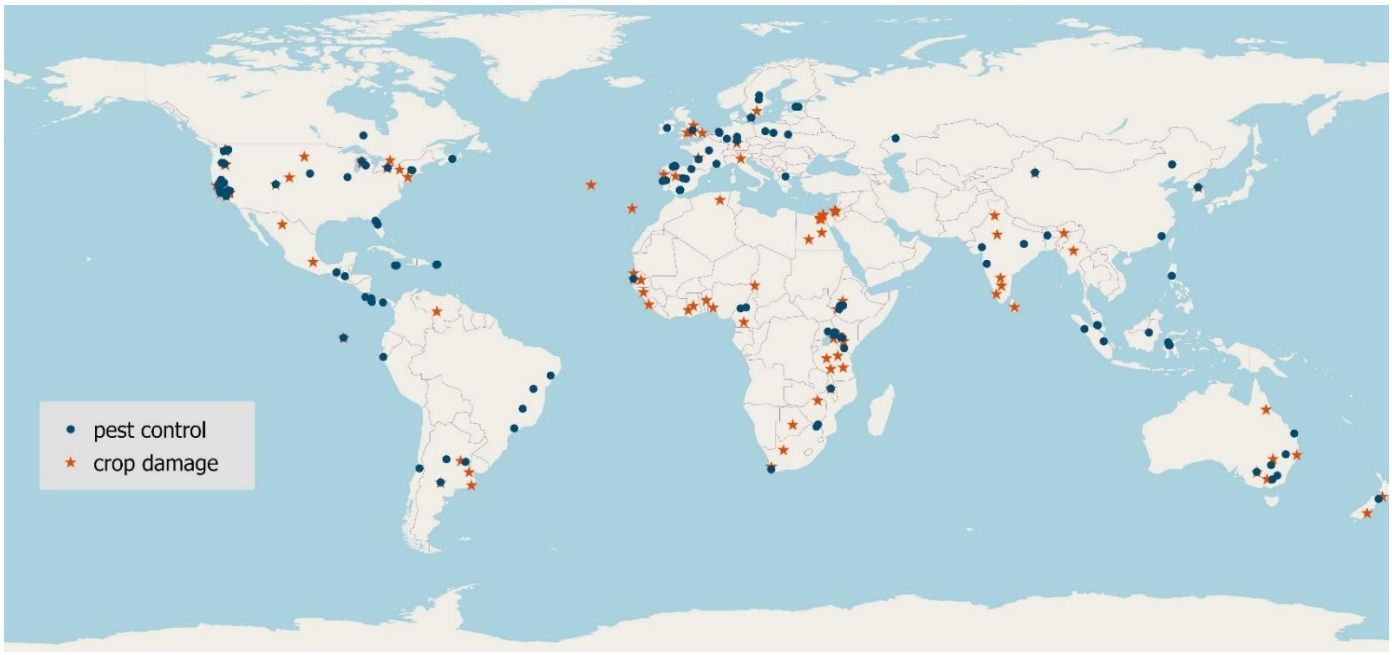


Figure 2.2. Global Distribution of Pest Control and Crop Damage Studies. Global distribution of pest control (143 occurrences, dark blue dots) and crop damage studies (124 occurrences, orange stars). Locations were retrieved from GIS coordinates provided or approximated by the researchers. Map constructed on ArcPro (ESRI 2023).

Table 2.3. Compilation of ecosystem services studied in the 150 documents retrieved by the search, with different evidence (e.g. positive, negative, more data needed) as indicated by the researchers of each study. 128 documents presented a focus on only ecosystem services, while 22 had a focus on both ecosystem services and disservices. In some instances, researchers investigated more than one service per study. The difference between the reported and expected (column of evidence) refers to researchers presuming a certain ecosystem service but not specifically measuring or assessing it (expected but not assessed) and to interviewees reporting a certain service without the researchers assessing it (reported but not assessed).

ecosystem services	***evidence***	***N***	***total***
pest control	Y	100	137
	more data needed	15	
	N	7	
	weak	6	
	reported but not assessed	4	
	expected but not assessed	2	
	neutralised by crop damage	1	
	outweighs crop damage	1	
	variable	1	
fertilising	Y	4	5
	reported but not studied	1	
disease control	Y	3	4
	N	1	
pollination	Y	2	4
	more data needed	1	
	expected but not assessed	1	
weed control	Y	1	3
	more data needed	1	

	expected but not assessed	1	
aesthetics	Y	1	1

Table 2.4. Compilation of ecosystem disservices studied in the 131 documents retrieved by the search, with different evidence (e.g. positive, negative, more data needed) as indicated by the researchers of each study. 109 documents presented a focus on only ecosystem disservices, while 22 had a focus on both ecosystem services and disservices. In some instances, researchers looked into more than one disservice per study. The difference between the reported and expected (column of evidence) refers to researchers presuming a certain ecosystem disservice but not specifically measuring or assessing it (expected but not assessed) and to interviewees reporting a certain disservice without the researchers assessing it (reported but not assessed).

ecosystem disservices	***evidence***	***N***	***total***
crop damage	Y	58	120
	reported but not assessed	24	
	N	12	
	more data needed	10	
	weak / not significant	7	
	expected but not assessed	4	
	variable	3	
	neutralised by pest control	2	
herbivore release	Y	4	7
	N	2	
	more data needed	1	
disease spread	more data needed	3	5
	N	2	
pollinator predation	N	1	2
	Y	1	
seed predation	Y	1	2
	more data needed	1	
repellent action	more data needed	1	1
killing of livestock	N	1	1

2.4.3 Methods Used to Investigate Ecosystem Services and Disservices

A key aim of this review was to examine how methodological approaches to studying ecosystem services and disservices provided by birds in food production systems have evolved over time. From the earliest records in the 1900s to contemporary studies, the development of new technologies - such as GIS in the 1960s (Maguire 1991) - has shaped how researchers approach this field.

From the 251 publications, we identified 77 methods spread over 615 occurrences. These methods could be classified into 9 groups, with an additional miscellaneous category accounting for 16 occurrences (Table 2.5). The categories are as follows:

1. Estimation of species richness and/or abundance, via bird and arthropod counts, trapping, or observations (159 occurrences)

2. Exclosures, for birds, mammals, arthropods and others (90 occurrences)

3. Damage and yield surveys (86 occurrences)

4. Spatial landscape analysis, through GIS data or digital photography (61 occurrences)

5. Use of published data, in the form of literature reviews, meta-analyses, databases and agricultural reports (61 occurrences)

6. Experimental studies, including sentinel prey experiments and habitat manipulations (52 occurrences)

7. Human surveys, such as interviews and ethnographic observations (46 occurrences)

8. Laboratory analysis, including microscopy, DNA and isotope techniques (33 occurrences)

9. Estimation and modelling of crop growth, crop losses, food consumption and pollination rates (11 occurrences).

2.4.3.1 Estimation / Identification

The most common approach involved species identification and estimation of community metrics via bird counts, mist-netting, or direct observations. Point and transect counts were the most widely used, due to their low cost, accessibility, and support from citizen science (e.g., birdwatching networks). Arthropod counts were similarly conducted on leaves and branches. Mist-netting, while effective, is resource-intensive and requires trained personnel, likely explaining its relatively limited use. Direct observations allow researchers to identify potential beneficial or damaging species in situ, but this method was only used in only a fifth of the studies in this group.

2.4.3.2 Exclosures

Exclosures represent an efficient way of investigating the effects of the absence of a certain taxonomic group in a particular system, and they were the second most common group of methods in the review (Table 2.5). Methods focused on birds and bats, indicating the importance of non-avian flying animals to agroforestry systems (Maas et al. 2013, 2019; Gras et al. 2016; Ferreira et al. 2023). Arthropods were less studied, with bees and ants being the most common groups, although this might simply reflect the inherent bias of the review by focusing on avian species. Exclosures were often combined with estimation and identification methods.

2.4.3.3 Damage & Yield Surveys

Surveys of the plants themselves configured the third most common group of the review (Table 2.5). Yield estimation, where the final yield of the crops was estimated to account for potential loss (Horgan et al. 2017; Garfinkel et al. 2020), were employed less frequently than direct damage surveys. This group was often connected to exclosures and estimation & identification. Damage made to crops often is undistinguishable at the level of family or genus, thus methods that can combine these surveys with identification of the causes of crop damage would increase the robustness of the studies.

2.4.3.4 Spatial Landscape Analysis

Spatial analyses, almost always GIS-based, were used to assess biotic and abiotic landscape features. Analysing photographs of the landscape through digital software (Filloy et al. 2023) will probably become more common in future years with the advance of GIS technologies. The use of geographical data allowed researchers to investigate factors affecting bird communities,

reaching results that promote landscape heterogeneity as an important consideration for the permanence of birds in the systems (Martínez-Núñez et al. 2020a, 2020b). This type of analysis was more strongly connected to estimation & identification, exclosures, and damage & yield surveys.

2.4.3.5 Use of Published Data

By the mid-1940s, researchers were already making use of published data to conduct reviews on the subject (Southern 1945). Most reviews had a specific focus on a species or biological group (Owen 1990; Allan et al. 1995; Mols & Visser 2002) , a service (Kirk et al. 1996; García et al. 2021; Requier et al. 2023) or disservice (Gebhardt et al. 2011; Sausse et al. 2021; Hermira & Michalski 2022), a horticultural system (Catling & Islam 1999; Chain-Guadarrama et al. 2019; Sausse & Lévy 2021), or a region (Schroth et al. 2000; Bomford & Sinclair 2002; De Mey et al. 2012). In fact, the occurrence of a wide range of perspectives was limited to three documents (Johnson et al. 2011; Triplett et al. 2012; Peisley et al. 2015), indicating the importance of this current review in systematising the available knowledge. Several reviews need to be systematically undertaken and published before the full benefits of the reviews to global knowledge can be realised (Pullin & Stewart 2006). Meta-analysis, a more robust form of review, was applied in only five publications, all within the past 15 years (Van Bael et al. 2008; Philpott et al. 2009; Weyell et al. 2015; Díaz-Siefer et al. 2022; Monteagudo et al. 2023). The global scope of the research leads to a wide range of results and how they are reported, which is a common issue in the proper development of meta-analysis (Gurevitch et al. 2018). This group of methods also included the use of available databases, reports from governmental agencies and previous data from the same or related authors (Table 2.5). This category also encompassed governmental reports and previously collected data, but was rarely combined with other methods, as many of these documents were standalone reviews (Manikowski 1984; Elliott 1988; Dhindsa & Saini 1994; Allan et al. 1995; Kirk et al. 1996; Catling & Islam 1999).

2.4.3.6 Experiments

This category included field experiments beyond exclosures, including sentinel prey removal experiments, provision and monitoring of nest boxes, perches and shelters, and the reintroduction and monitoring of species (Table 2.5).Natural prey experiments often involved the use of mealworms or common pests to the agricultural or horticultural system (Jordani et al. 2015; Garfinkel & Johnson 2015), while artificial experiments were made using plasticine models of caterpillars (Howe et al. 2015; Barbaro et al. 2017). A couple of documents reported using both types of sentinel prey, potentially increasing the accuracy of the investigation of pest control (Peisley et al. 2016; Denmead et al. 2017). This group was more strongly connected to estimation & identification, indicating the attempts of researchers to not only assess if arthropod pests are being consumed in the systems (provision of pest control), but also identify the potential agents of this biological control.

2.4.3.7 Human Surveys

Given that horticulture is directly related to human health and wellbeing, it was not surprising to find studies assessing the human component of ecosystem services and disservices through interviews - i.e. investigating the opinions and assumptions of the people who manage the lands

the birds occupy and feed in. However, social and conservation sciences traditionally are treated separately (Sandbrook et al. 2019). Some researchers utilised both qualitative and quantitative methods in their research (Schäckermann et al. 2014; Smith et al. 2021; Alemayehu & Tekalign 2022), an approach called 'triangulation'. This approach has been suggested as a way to reduce bias from a single method in the social sciences (Jupp 2001), and this rationale works here to create a more robust investigation of the provision of ecosystem services and disservices. In general, however, human surveys did not hold strong connections to other groups of methods.

2.4.3.8 Laboratory Analysis

Microscopic and other laboratory analyses compose the first group of methods in temporal order, with the analysis of the stomach content of birds killed by farmers (Hammond 1912). Examination of faeces was the most common laboratory method used, being more acceptable than killing wild birds in current times. Although microscope analysis of samples is still more common, DNA analysis has expanded in the past decade (Karp et al. 2013; Garfinkel et al. 2020) and are bound to increase in occurrence with the advancements of genetic technologies. Techniques such as barcoding (Sow et al. 2020) and next-generation sequencing (Crisol-Martínez et al. 2016) allow for better accuracy than microscope identification, and it will likely uncover discoveries in the near future. These methods were strongly connected with estimation & identification, since trapping and surveying the communities gave researchers access to faeces, and occasionally linked to damage and yield surveys.

2.4.3.9 Estimation & Modelling

This small but growing category uses economic or computational models to estimate crop losses, consumption, or pollination rates (Table 2.5). The first document within this group dates from the late 1990s (Basili & Temple 1999), but few researchers have adopted this approach. This might be due to ecologists still straying away from economics, be it for philosophical reasons (the inherent value of nature that cannot, or should not, be valued in human terms) or for what is seen as two insurmountably different theoretical fields (Hughey et al. 2003; Kaval & Baskaran 2013; Johnson & Hackett 2016). Nonetheless, incorporating economic models in food production systems has become increasingly necessary (Ferguson et al. 2019). Economic incentives are believed to be one of the most feasible methods for wildlife conservation in human-managed lands within a capitalist culture (Kareiva et al. 2012; Kross et al. 2018). Given the inclusion of only 11 documents in this group of methods, it's not surprising that it did not hold strong connections with any other group. Understanding the net return of benefits and damages to horticulture is paramount to establishing efficient management practices. Quantifying damages will include not only the direct losses of production, but also the costs of controlling techniques and potential increased processing of crops (Triplett et al. 2012). Benefits will also not be completely straightforward, since ecosystem services might fluctuate in their net return due to market prices (Luck 2013). However, although economic considerations are important in our current economic system, few documents in this review attempted to bridge this gap.

2.4.3.10 Miscellaneous

This catch-all group included less common or emergent methods. Bird-scaring trials (Murton & Jones 1973; Lindell et al. 2018), fertilisation experiments (Plotnikov & Sinyavskiy 2020), and prey recognition trials (Jones et al. 2005a) exemplify underused but potentially valuable tools. Seed removal experiments (Tschumi et al. 2018a, 2018b) also hold promise, given their similarity to established prey-removal protocols.

2.4.4 Combining Methods

The methods featured in the review have been thus far discussed separately, but in the studies, authors would often combine multiple groups. Most publications featured the use of only one or two groups (102 and 74, respectively), with 53 publications featuring three groups, 16 featuring four groups and only four publications having a combination of five different groups. We decided to examine the relationships between each group to inspect the most common pairing of methods. The most common pairings were between methods of estimation and identification with spatial landscape analysis (47 occurrences), exclosures (46), and damage and yield surveys (45); exclosures with damage and yield surveys (32) and spatial landscape analysis (29); estimation and identification with experiments (28) and damage and yield surveys with spatial landscape analysis (27). Less common pairings included laboratory analysis with estimation and identification (18 occurrences), and experiments with spatial landscape analysis (14) and exclosures (10).

The least occurring pairings were of human surveys with estimation and modelling, and laboratory analysis with experiments and estimation and modelling, with one occurrence each. Use of published data did not have any strong connections to the other groups, being featured in uncommon pairings with laboratory analysis, experiments and exclosures. Human surveys also did not feature strong connections, being the group of methods that was most featured by itself.

Only four documents presented a variety of five groups of methods in their research (Peisley et al. 2016; Kross et al. 2020; Martínez-Sastre et al. 2020; Taylor et al. 2022), all from the past decade. This indicates a potential current change towards integrating several different methods for the same study, allowing for better understanding of the complexities of birds as providers of services and disservices in horticultural systems.

Table 2.5. Compilation of different methods employed for the study of ecosystem services and disservices retrieved from the 251 documents assembled from the review. Methods were separated into distinct themes: estimation/identification of species involved in the systems; exclosures for different biological groups; surveys to assess crop yield and damage; spatial analysis of the landscape; use of published data; experiments of sentinel prey removal and provision of environmental enhancements; interviews and surveys; laboratory analysis involving DNA and isotope samples and microscope analysis; modelling of previous data and economic estimation; and a final category of miscellaneous methods. The second column distinguishes different methods within each theme. The third column further specifies the methods in each category, with others referring to biological groups other than birds.

group	***category***	***specifics***	***N***	***T***
estimation / identification	counts	point counts	31	159
		transect counts	19	
		not specified	10	
	counts (others)	arthropods	38	
		lizards	1	
		mammals	1	
	trapping	mist-nets surveys	6	
	trapping (others)	arthropods	8	
		rodents	3	
		other mammals	1	
	direct observations	general	13	
		foraging	23	
		with cameras	3	
	misc.	call recordings	1	
		faecal dropping counts	1	
exclosures	birds	birds	62	90
	mammals	bats	14	
		others	2	
	arthropods	ants	4	
		bees	2	
	others	others	4	
		lizards	1	
		weed	1	
damage	damage surveys	crops	66	86

group	*category*	*specifics*	*N*	*T*
& yield surveys		leaves	13	
	yield surveys	yield	7	
spatial landscape analysis	GIS	GIS	60	61
	digital photography	digital photography	1	
use of published data	reviews	literature reviews	37	61
		metanalysis	5	
	available data	from previous studies	9	
		databases	6	
		agricultural reports	4	
experiments	sentinel prey removal	artificial prey	21	52
		natural prey	16	
	provision and monitoring of	nest boxes	8	
		perches	5	
		shelters	1	
	species reintroduction	raptors	1	
human surveys	interviews	not specified	26	46
		semi-structured	11	
		structured	3	
		group discussions	4	
	observations	ethnographic observations	2	
laboratory analysis	microscope analysis	stomach content from regurgitation	3	33
		stomach content from culled birds	2	
		faeces collected from mistnets	4	
		faeces collected from nests	3	
		faeces collected from nest boxes	2	
		faeces collected from droppings	2	
		faeces collected from roosting sites	1	
	DNA analysis	faeces collected from mistnets	2	

group	*category*	*specifics*	*N*	*T*
		faeces and stomach content collected from mistnets	9	
		faeces collected from nest boxes	1	
		faeces from droppings	1	
		arthropods collected from pit falls	1	
	isotope analysis	blood samples	1	
		faeces collected from droppings	1	
estimation & modelling	economic estimations	crops	7	11
	estimation (others)	food consumption	1	
		pollination rates	1	
	modelling	crop losses	1	
		from previous data	1	
miscellaneous	misc.	tree traits measuring	2	16
		bird scarring	2	
		seed removal experiment	2	
		breeding and nesting monitoring	1	
		feeding trials in captivity	1	
		fertilizing experimentations	1	
		fruit measurements	1	
		leaf chemistry characterization	1	
		nest searches	1	
		pollination visitation rates	1	
		prey recognition trials	1	
		presence/absence surveys	1	
		faecal contact rates	1	

2.4.5 Human-Wildlife Conflicts

Given the importance of horticulture to human societies, it is perhaps surprising that less than a fifth of the documents (45 out of 251; Table 2.3) discussed potential or acknowledged human-wildlife conflicts arising from the interactions of wild animals in these human-managed lands. In the broader context of such conflicts, attention typically centres on mammals, particularly large species such as elephants, rhinoceros and tigers, whose impacts can be severe, especially in developing nations (Linkie et al. 2007). When avian species are considered, it's often birds of prey for their perceived threat to livestock and wildlife game, and the negative connotations associated with scavengers (Şekercioğlu 2006, Pohja-Mykrä et al. 2012; O'Bryan et al. 2018). Birds of prey represent some of the most threatened bird groups, with species suffering from lead poisoning and hunting pressure (Hallmann 1985; Heggøy & Øien 2014).

However, other bird groups are also frequently targeted. Historical and contemporary accounts reveal that farmers and growers have shot wild birds perceived as pests, regardless of the actual extent of their impact (Hammond 1912; Murton & Jones 1973). As stated previously, farmers and growers often overestimate the negative effects of native avifauna in their lands, which can lead to an increase in human-wildlife conflicts (Dickman 2010; Gorosábel et al. 2019). Population declines of scavengers can also feed into the loss of potential ecosystem services, leading to the spread of diseases and higher costs in human healthcare (Michel et al. 2020). Managing cost-benefit trade-offs of bird activity in agricultural systems can involve promoting desirable functional traits, targeted control of pest species, manage community composition, increase ecosystem diversity, and reduce agricultural intensification (Triplett et al. 2012). These practices need to be further studied and compared, so that informed recommendations can be suggested.

While it is true some bird species worldwide can cause significant damage to food production systems, the long history of confirmation bias towards ecosystem disservices by birds (Bonhomme 2021) needs to be discussed and those beliefs need to be challenged. While the scientific community has largely moved away from endorsing the killing of wild birds, this practice remains common in many regions. A comprehensive and evidence-based understanding of birds' ecological roles in horticultural systems is critical to dismantle harmful narratives and support conservation-informed management. Without this shift, unsustainable and indiscriminate practices will persist, threatening both biodiversity and the ecological stability of food production systems.

2.5 Conclusions

1. There seems to be a bias towards studying services and disservices that are arguably easier to measure (i.e. pest control, crop damage) than other harder to detect (i.e. disease spread, pollination, ecological releases of predators or herbivores). This hinders a holistic view of birds' roles in these systems, in turn deterring potential opportunities to change growers' assumptions and attitudes towards wild birds.

2. Crop damage was found to be up to seven times more likely to be reported than pest control, yet in many cases, damage was not empirically assessed. Birds' long-standing reputation as pests often leads to the unjustified targeting of species. Greater effort is needed to distinguish between harmful and beneficial species through empirical, species-specific evaluations.

3. The lack of focus on specific species or taxonomic groups hinders understanding the presence of native and/or endangered species in food production systems. A species-focused approach could thus allow the design of strategies to aid the permanence of such species in those systems.

4. Ecosystem services and disservices tend to be studied separately, hindering their comprehension in a biological continuum. Integrating these dimensions would support a more ecologically realistic understanding of avian roles and reveal unexpected synergies or trade-offs.

5. The study of ecosystem services and disservices has employed a myriad of methods throughout time, with most researchers opting for identifying and estimating bird species in the food systems. Other methods include exclosures, damage and yield surveys, spatial landscape analysis, literature reviews, sentinel prey removal experiments, human surveys, laboratory analysis and estimation and modelling of crop growth and losses. Most studies used only one or two groups of methods, but recent papers indicate a potential shifting trend towards multi-methodological approaches.

6. Effective management of bird activity in food production systems may involve promoting desirable functional traits, implementing species-specific control measures, enhancing community diversity, and reducing agricultural intensification. However, these practices require further empirical comparison to determine their efficacy and broader impacts.

7. Less than a fifth of the documents discussed potential or acknowledged human-wildlife conflicts. Because of the inherent bias of farmers and growers to assume birds as pests, the diminished number of studies focusing on this aspect of the discourse presents a clear issue for the conservation of native birds in food production systems. Without this approach, several bird groups are kept unjustifiably targeted, or not properly managed to reduce or control their impact in horticultural systems. Changing this current scenario will not only assist promoting better conservation practices for the permanence of wild birds in an ever-changing world of agricultural intensification and expansion of human-managed lands but also provide opportunities for the betterment of human societies through the reduction of the damages and the increase of potential benefits.



MASSEY UNIVERSITY
TE KUNENGA KI PŪREHUROA
UNIVERSITY OF NEW ZEALAND

GRADUATE RESEARCH SCHOOL

STATEMENT OF CONTRIBUTION
DOCTORATE WITH PUBLICATIONS/MANUSCRIPTS

We, the student and the student's main supervisor, certify that all co-authors have consented to their work being included in the thesis and they have accepted the student's contribution as indicated below in the Statement of Originality.			
Student name:	Giuliana Caldeira Pires Ferrari		
Name and title of main supervisor:	Professor Isabel Castro		
In which chapter is the manuscript/published work?	Chapter Three		
Describe the contribution that the student and members of the supervisory team have made to the manuscript/published work:[1] GCPF (student): conceptualization / data curation / formal analysis / investigation / visualization / writing (original draft) / writing (review & editing) EM (collaborator): data curation / methodology KM (supervisor): investigation / writing (review & editing) AWR (supervisor): writing (review & editing) IC (main supervisor): conceptualization / writing (review & editing)			
Please select one of the following three options:			
○	**The manuscript/published work is published or in press** Please provide the full reference of the research output:		
○	**The manuscript is currently under review for publication** Please provide the name of the journal:		
◉	**It is intended that the manuscript will be published, but it has not yet been submitted to a journal**		
Student's signature:	Giuliana C. P. Ferrari 2026.01.26 10:14:01 +13'00'	Main supervisor's signature:	Isabel Castro Digitally signed by Isabel Castro Date: 2026.01.28 11:36:11 +13'00'
This form should be placed at the beginning of each relevant thesis chapter.			

[1] Refer to the Massey University Publishing and Authorship guidelines (OneMassey for staff, Stream for students) and/ or Contributor Roles Taxonomy (CRediT) guidelines for guidance.

Chapter 3 Spatio-Temporal Variation in Avian Communities Across Apple Orchards, New Zealand

3.1 Abstract

Agricultural landscapes are increasingly recognised as potential habitats for biodiversity, yet little is known about how native and introduced birds use horticultural systems in New Zealand. This chapter assessed the occurrence, community composition and habitat use of birds across six apple orchards in four New Zealand regions over four seasons. Bird communities were surveyed using repeated transects, with 82 surveys conducted from autumn 2024 to summer 2025. Occupancy models were used to estimate habitat use while accounting for imperfect detection, and species richness estimators and multivariate analyses were used to assess sampling effort and seasonal variation in community composition. For commonly detected species, flocking patterns and use of vertical orchard strata were also examined. Introduced mammalian predators were monitored using chew cards to provide additional ecological context. A total of 45 bird species were recorded, comprising 20 native and 25 introduced species. Species richness estimators and accumulation curves indicated that sampling captured most species using the orchards, with richness being highest in summer and lowest in autumn. Introduced species dominated detections, although several native species were widespread, particularly silvereyes, fantails, pūkeko, welcome swallows and swamp harriers. Occupancy models provided little evidence that season influenced orchard use, suggesting that most commonly occurring species used orchards throughout the year. Nevertheless, community composition differed among seasons overall, although individual seasonal contrasts were not significant after correction for multiple comparisons. Seasonal patterns therefore appeared to reflect changes in the abundance of widespread species and the occurrence of infrequent visitors rather than substantial turnover in the orchard bird community. Flocking behaviour was generally consistent across seasons and orchards, with silvereyes showing the clearest seasonal shift through the formation of large winter groups. Vertical habitat use differed markedly among species and broadly reflected their foraging ecology, separating species into ground-, canopy- and aerial-associated patterns. Introduced mammals, including brushtail possums, rodents and hedgehogs, were also detected across orchards. These findings demonstrate that New Zealand apple orchards are used by diverse bird communities comprising widespread introduced species and native species, including species of conservation concern. The study provides baseline information on bird occurrence and habitat use within New Zealand apple orchards and highlights the value of considering horticultural landscapes when investigating biodiversity in modified environments. Longer-term studies across a broader range of orchards are needed to determine how management and surrounding landscape characteristics influence these communities.

3.1 Introduction

Increases in human populations and resource demands have led to an increase in the conversion of natural ecosystems into agricultural land and the intensification of food production within existing agricultural systems (MEA 2003). Agricultural intensification is a major driver of current biodiversity loss (Tilman et al. 2001; Wilson et al. 2005; Tscharntke et al. 2012; Wright et al. 2012; Angkaew et al. 2023), although the complexity of processes and potential interactions can prohibit a holistic understanding of how exactly it affects biodiversity (Firbank et al. 2008). Biodiversity within agricultural landscapes can contribute substantially to the resilience of food production systems. However, this resilience is often compromised by the very intensification practices that erode biodiversity (Moller et al. 2008).

The impacts of agricultural intensification and the creation of isolated natural habitat 'islands' has led to parallels with the Island Biogeography Theory (MacArthur & Wilson 1967). Species' traits including larger body sizes, higher trophic levels and low dispersion capabilities are deemed especially sensitive to habitat disturbance (Newbold et al. 2013). Across biological groups, birds are a valuable group to understand patterns of species persistence in human-managed systems and are often used as indicators of habitat quality (Şekercioğlu 2006; Morante-Filho et al. 2021). Native island species, due to their innate sensitivity to land changes, can be used as key indicators of the impacts of land-use change (MacLeod et al. 2012).

Overall, bird community composition is shaped by the availability of suitable resources and habitats. Species that use these agricultural systems must adapt to high levels of anthropogenic disturbance (Tscharntke et al. 2012; Zielonka et al. 2024). In fruit orchards, with irrigation patterns and straight row designs, areas of high spatial contrast are created, filtering out species unable to adapt to these environments (Zielonka et al. 2024). However, for the species that can persist in such environments, orchards can provide a variety of resources (Mangan et al. 2017). By being perennial and structurally complex, orchards are likely to provide food, cover and nesting resources for birds relative to other crops.

New Zealand has a long history of landscape transformation for agricultural use, from early indigenous Māori colonisation over 700 years ago, to the European land-changes from the 1800s onwards (Hooper et al. 2021). The country is also recognised for a unique biota of flora and fauna that had been isolated for 80 million years (Cooper & Millener 1993). Currently, New Zealand native species are suffering from global issues, such as being threatened by predation pressures from introduced species (i.e. rodents, mustelids and feral cats (*Catus domesticus)*), competition from introduced species (i.e. rodents and possums (*Trichosurus vulpecula*)), and habitat loss and degradation (Miskelly et al. 2009). This has led to a massive programme to rid New Zealand of introduced predators by 2050 (Russell et al. 2015; PFNZ 2022).

Although land-use change effects have been well documented in Europe and North America, these impacts on New Zealand's native avifauna remain relatively poorly understood (Blackwell et al. 2008; MacLeod et al. 2008; Moller et al. 2008). While some New Zealand native biodiversity can persist within agricultural systems, it has become clear that land conversion to agriculture is responsible for severe losses of natural habitat and a decline of native species (Lee et al. 2008). However, research on birds in New Zealand agricultural

landscapes, native and introduced, has focused only on species considered agricultural 'pests' (Macleod & Till 2007; MacLeod et al. 2008).

Historically, conservation initiatives in New Zealand have focused on protected areas, including fenced mainland sanctuaries and offshore islands where mammals are excluded (Holdaway 1989; Joseph et al. 2008; Galbraith & Cooper 2013). Food production systems have been historically considered devoid of native species, and therefore, of any conservation value (MacLeod et al. 2008). However, this view is being challenged with the increased recognition that native species can persist, and sometimes thrive, in human-managed ecosystems (Coleman 2010). Understanding how native species, such as birds, use these systems may provide opportunities for conserving both threatened species and maintaining common species (Frimpong 2018) in the context of ongoing agricultural intensification and land-use change.

In this chapter, I assessed the spatio-temporal occurrence and habitat use of native and introduced bird species in six apple orchards across four New Zealand regions. Species occurrence was estimated using occupancy models to account for imperfect detection, with a particular focus on seasonal patterns of orchard use. Seasonal variation in the bird community was further examined through analysis of community composition. For several common species, I also investigated their use of the orchard vertical strata and their group size tendencies, defined here as flocking (Beauchamp 2002). These later analyses were based on observations of detected individuals. Finally, I described the occurrence of introduced mammalian predators within the surveyed orchards to provide ecological context for the bird communities observed.

3.1 Methods

3.1.1 Study Area

The study was conducted across six apple orchards in four New Zealand regions (Table S 5). It included two orchards in the Manawatū region (MN), Lower North Island; two orchards on the Kāpiti Coast (KC), Lower North Island; one orchard in Hawke's Bay (HB), Eastern North Island; and one orchard in the Tasman district (TR), Northwest South Island (Figure 3.1). Orchards varied in size (2 to 44.5ha) and management practices, including a small research orchard, an organic orchard, two large monocultures, and two conventional mixed crop orchards (Table 3.1).

3.1.1.1 Apple Varieties

Across the six orchards, 20 different apple varieties were represented: Braeburn, Cherish, Crab, Dazzle, Envy, Fuji, Galaxy, Granny Smith, Golden Delicious, Jazz, King, Lady in Red, Pacific Beauty, Pacific Rose, Pacific Queen, Pink Lady, Red Delicious, Royal Gala, Sassy, and Splendour (Table S 6). The Manawatū orchards had the highest number of apple varieties, with seven and eight at MN1 and MN2, respectively. Orchard HB had the highest number of unique varieties among the sites, with four apple varieties. The most popular varieties were Royal Gala, featured in four orchards, and Braeburn, Granny Smith and Pacific Rose, featured in three out of the six orchards.

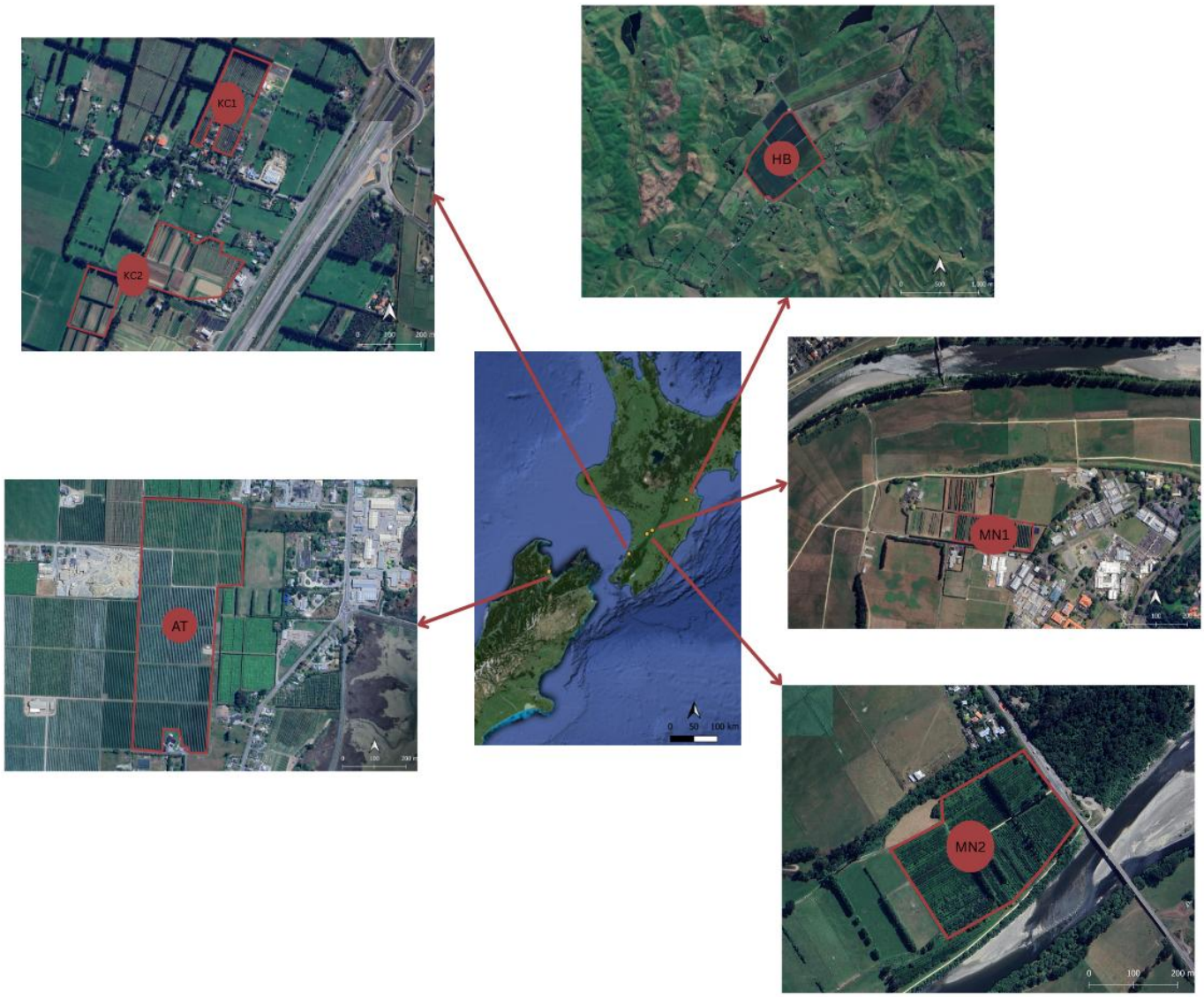


Figure 3.1. Regional location of the five orchards in the North Island and one in the South Island that were included in the fieldwork dataset. Pictures show the surroundings of each orchard up to a 1.5km buffer. Map constructed on QGIS (2024) from coordinates retrieved from each field site. Symbols overlapping with each orchard represent their unique orchard identities related to their regional locations: Manawatū 1 & 2 (MN), Kāpiti Coast 1 & 2 (KC), Hawke's Bay (HB), and Tasman Region (TR).

Table 3.1. Identity, size, management practices, and structure of orchards included in the study. Sites are identified by regional locations. Each section is described in its configuration of crops and the number of rows. Section KC2-1 had a mix of apples, pears, feijoas, oranges and other fruit trees. For each section, the height and distance between rows was measured five times to calculate the average height of the apple trees and the distance between the rows from one trunk to the other. In sections of mixed crops, tree height and distance between rows is given by measuring a random selection of crop trees.

Orchard ID	Practices	Size (ha)	Sections	Crops	Rows	Tree Height (cm)	Distance Between Rows (cm)	Management Details
Manawatū 1	research	2	MN1-1	Apples	12	317	353	regular pruning, grass mown year-round, harvest through manual labour, regular insecticide and fungicide spraying
			MN1-2	Kiwifruit	11	299	387	
			MN1-3	Kiwifruit	11	264	400	
			MN1-4	Apples	12	357	440	
Manawatū 2	conventional	9.1	MN2-1	Apples & Plums	19	494	481	irregular pruning, grass mown over spring, harvest through manual labour, regular insecticide and fungicide spraying
			MN2-2	Apples	20	420	456	
			MN2-3	Apples & Plums	42	381	437	
			MN2-4	Apples & Plums	19	396	488	
Kāpiti Coast 1	organic	3.5	KC1-1	Pears	11	362	466	regular pruning, grass mown over spring, harvest through manual labour
			KC1-2	Apples	24	380	487	
			KC1-3	Apples	25	257	466	
Kāpiti Coast 2	conventional	6.2	KC2-1	Fruit Crops (Varied)	11	396	701	regular pruning, grass mown year-round, self-picking orchard, regular insecticide and fungicide spraying
			KC2-2	Apples & Pears	25	328	577	

Orchard ID	Practices	Size (ha)	Sections	Crops	Rows	Tree Height (cm)	Distance Between Rows (cm)	Management Details
Hawke's Bay	industrial	44.5	HB-1	Apples	54	97	278	regular pruning, grass mown year-round, heavy use of machinery for spraying, pruning, and harvesting, regular insecticide and fungicide spraying
			HB-2	Apples	45	308	247	
			HB-3	Apples	56	290	283	
			HB-4	Apples	145	312	285	
Tasman Region	conventional	21	TR-1	Apples	93	310	329	regular pruning, grass mown year-round, harvest through manual and machine labour, regular insecticide and fungicide spraying
			TR-2	Apples	70	323	338	

3.1.2 Bird Observations

Bird observations were designed to capture seasonal variation in bird assemblages at each orchard. Direct observations were conducted using binoculars (Nikon Monarch M511, 10 x 42 magnification) along traversable transects that followed the orchards' tree rows and rectangular layouts. Transects were spaced approximately 15 metres apart between adjacent rows, allowing systematic coverage while minimising overlap between transects. At four of the six orchards, the entire orchard was surveyed during each survey. The two larger orchards (HB and TR) were divided into predefined sections of approximately equal size, with one section surveyed per survey to limit survey duration to approximately two hours. Each section was surveyed at least once before repeat surveys were conducted, allowing complete spatial coverage and temporal replication within each season. Smaller orchards averaged three surveys per season, alternating between morning and afternoon, while the larger orchards received additional surveys across their sections over approximately five days.

Surveys were conducted during periods of greater bird activity in the early morning and late afternoon (Bednekoff & Houston 1994), with timing defined relative to sunrise and sunset to avoid potential effects of daylight-saving changes. Morning surveys began 15-30 minutes after sunrise, while afternoon surveys concluded at least one hour before sunset to minimise observations associated with pre-roosting activity. Survey duration varied according to orchard size and bird activity, ranging from approximately one to two hours. For each survey, date, time period, mean temperature, wind and sun conditions, noise level, and precipitation were recorded (Table S 5), following standard practice for five-minute bird counts (DoC 2023). Surveys encompassed variation in sun exposure, wind, and light precipitation, but were not conducted during heavy rain because such conditions reduce bird activity and hinder visual and acoustic detection.

Transects started at a corner edge of each section, beginning from the same designated access point to maintain consistency among visits. The observer walked each transect slowly, recording the presence and behaviour of native and introduced species. Two experienced bird researchers accompanied the observer during a subset of initial surveys to assist with verification of bird identification and standardisation of data collection. When necessary, acoustic identification was supported by the eBird Merlin™ application.

Native species were followed and their behaviours recorded for up to five minutes where possible, whereas introduced species were recorded only as a first-sighting observation. As no birds were individually marked, steps were taken to minimise the risk of double-counting individuals. Identification relied primarily on visual detections, except where a species was detected only audibly. Bird movement relative to the transect and the location of each observation were considered when recording a new encounter, and birds clearly identified as the same individuals moving within the survey area or ahead of the observer were not recorded as additional detections. If an observation could not be confidently assigned to a unique individual, it was excluded. The number of individuals associated with each species encounter, including individuals, pairs, and groups, was also recorded.

Accounting for imperfect detectability is essential for more reliable estimates of species occupancy in an area (Morante-Filho et al. 2021). The repeated survey design enabled imperfect detection to be accounted for subsequently through occupancy modelling. The same surveys also provided the behavioural observations analysed in Chapter Four.

Surveys were conducted from autumn 2024 (April/May) to summer 2025 (January/February). Because orchard TR was not surveyed during spring, analyses incorporating season were based on an unbalanced design. The study included 82 surveys totalling 111.8 hours of observation and 5,024 bird encounters across six orchards. These surveys represented 23 orchard x season combinations.

3.1.3 Species Occupancy

Occupancy models were constructed to account for imperfect detection of bird occurrence within orchards. Bird home ranges extended beyond the boundaries of the survey within the orchards. Therefore, the estimates of occupancy are here considered as the species' probability of habitat use rather than true occupancy (Bailey & Adams 2005; Mangan et al. 2017).

3.1.4 Species Abundance

Species abundance was calculated for each species in each combination of orchard and season included in the surveys. Abundance was given as $Abundance = \frac{I}{A} \div n.s.$, where I = total number of individuals seen across surveys in a season; A = area of orchard in hectares; and n.s. = number of surveys conducted for that orchard per season. Relative abundance values were then given as individuals/ha per census, where census refers to the sampling unit encompassing all surveys conducted in a season.

3.1.5 Flocking Patterns

To investigate the potential of seasonal variation on birds' grouping behaviour, this analysis focused on the most frequently observed species in the orchards (Table S 7). Species were included if recorded in at least 15 out of 23 censuses. These included five native species (silvereyes *Zosterops lateralis*, New Zealand fantails *Rhipidura fuliginosa*, welcome swallows *Hirundo neoxena*, pūkeko *Porphyrio melanotus melanotus* and swamp harriers *Circus approximans*), alongside eight introduced species (blackbirds *Turdus merula*, chaffinches *Fringilla coelebs*, goldfinches *Carduelis carduelis*, greenfinches *Chloris chloris*, house sparrows *Passer domesticus*, song thrushes *Turdus philomelos*, starlings *Sturnus vulgaris* and rock pigeons *Columba livia*).

To account for the unbalanced sampling of native and introduced species (observations for up to five minutes vs snapshot observations, respectively), only the initial sighting of each native species observation was included in the analysis. The number of individuals observed in each detection was recorded in the field. Grouping categories (individual, pair, small group [three to five birds], medium-sized groups [six to ten] and large flocks [> 10 birds] were assigned during data processing based on the recorded group size.

3.1.6 Vertical Strata Use of Orchards

Here I use Pearson's definition of vertical stratification as the vertical distribution of foliage (Pearson 1971) to assess the vertical use of levels within the orchards by different bird species.

Crop trees and hedges were categorised visually into low, medium, and top branches. The initial vertical stratum of each sighting was recorded as ground, human structures (irrigation lines, fences, wooden poles, shed roofs and power lines), low, medium or top branches, and flying overhead. Birds detected exclusively through vocalisations were excluded from this analysis. Most orchard edges were composed of hedge trees with no meaningful height difference compared to the crop trees.

3.1.7 Mammalian Presence at Apple Orchards

The presence of possums, rodents, and hedgehogs was assessed through chew cards. Chew cards are a cost-effective monitoring tool that detects multiple species of small mammalian pests, including possums (common brushtail possum, *Trichosurus vulpecula*), as well as rodents and other pest animals (Sweetapple & Nugent 2024). It is specifically designed to help map the distribution of these species in low-density populations. Chew cards were deployed in transects following New Zealand's Department of Conservation guidelines (DOC 2024). Cardboard chew cards filled with peanut-based lure were folded to 45° and placed 20-30 cm above ground. Cards were spaced 20m apart, with 10 cards per transect. Chew card surveys are typically recommended for ≥ 500ha areas, as they are commonly used in large-scale pest monitoring (DoC 2024). However, deployment in smaller areas remains valid provided the minimum card spacing (20m apart) is respected, ensuring independent detection events. Accordingly, orchards MN1 and KC2 accommodated one line each, with the remaining orchards receiving two lines. In total, 380 chew cards were deployed across the six orchards, in two subsets: 10 cards/season for orchards MN1 and KC2, and 20 cards/season for orchards MN2, KC1, TR and HB.

Chew cards were left in the field for three nights. Camera traps monitored half of the cards to assist with predator identification. Cards were inspected for tooth marks, compared with diagnostic guides (Sweetapple & Nugent 2024) and identified to the level of rats and mice, possums, and hedgehogs (European hedgehog, *Erinaceus europaeus*). The intensity of damage (low, medium, and high) was recorded as a proxy for mammal activity.

3.1.8 Statistical Analyses

Given the small number of orchards and variation in management practices among sites, orchard-level effects could not be evaluated with adequate replication. Orchard-specific characteristics were therefore summarised descriptively, while inferential analyses focused on broader ecological patterns, with orchard included as a factor where appropriate to account for site-level variation rather than as a primary variable of interest. Statistical analyses were conducted in RStudio (RStudio 2016).

3.1.8.1 Species Richness Estimators

To assess whether survey effort adequately characterised bird assemblages associated with apple orchards, incidence-based species richness estimators were calculated using the 'vegan' package (Oksanen et al. 2008). Bird detections were converted into a species-by-survey incidence matrix, where each survey represented a sampling unit and each species was recorded

as detected (1) or not detected (0). Overall species richness was estimated using all surveys combined, while seasonal richness estimates were obtained by grouping surveys according to season.

Observed species richness was compared with first-order Jackknife estimates, an incidence-based estimator that accounts for undetected species by using the frequency of species detected in only a single sampling unit (Heltshe & Forrester 1983). Approximate 95% confidence intervals were calculated from the standard errors returned by the estimator. Species accumulation curves were generated using random permutations of survey order to evaluate sampling completeness and determine whether observed richness approached an asymptote (Colwell et al. 2004).

3.1.8.2 Species Occupancy

Occupancy models were fitted separately for each species using the 'unmarked' package (Fiske & Chandler 2011). Each orchard-season combination was treated as an independent sampling site, with repeated surveys conducted within that orchard during a given season serving as replicate detection occasions. This approach assumed that occupancy status remained constant throughout the repeat surveys within each orchard-season combination (MacKenzie et al. 2002).

Detection / non-detection histories were constructed for each species, with rows representing orchard-season sampling sites and columns representing repeated survey occasions. Site-level covariates included orchard and season, while observation-level covariates included the area surveyed (in hectares), the survey period (morning AM / afternoon PM), temperature, wind, sunshine, ambient noise, and precipitation. Weather conditions were categorised according to protocols from the New Zealand's Department of Conservation (DoC 2023). Weather data were matched to each survey using orchard, survey date and survey period identities.

A candidate set of occupancy models was developed for each species. A null model was first fitted, followed by models in which occupancy (ψ) was modelled as a function of season and detection probability (p) was modelled using surveyed area alone or in combination with survey period, wind, precipitation, ambient noise, sunshine or temperature. Surveyed area was retained in all non-null detection models to account for variation in sampling effort among survey occasions.

Candidate models were ranked using Akaike's Information Criterion corrected for small sample size (AICc). The model with the lowest AICc (ΔAICc = 0) was considered the best-supported model for inference. From the selected model, occupancy (ψ) and detection probability (p) estimates, together with their 95% confidence intervals, were extracted for each species. Where detection covariates were retained in the best-supported model, predicted detection probabilities were generated to illustrate the influence of survey conditions on species detectability.

3.1.8.3 Species Abundance

Bird abundance data were aggregated into a site x species matrix, with each site representing a unique orchard-season combination (n = 23). Species occurring in fewer than three samples or

with a total abundance < 2 across the dataset were excluded to reduce the influence of very rare taxa. For this multivariate ordination analysis, 16 species were included, including seven native species - silvereyes, New Zealand fantails, welcome swallows, pūkeko, paradise shelducks, tūī (*Prosthemadera novaeseelandiae*) and swamp harriers - and nine introduced - blackbirds, chaffinches, goldfinches, greenfinches, house sparrows, song thrushes, starlings, mynas (*Acridotheres tristis*) and rock pigeons.

Species abundances were Hellinger-transformed using the 'vegan' package (Oksanen et al. 2008) to reduce the influence of highly abundant species while preserving compositional differences among communities. Bird community composition was then visualised using two-dimensional non-metric multidimensional scaling (NMDS) based on Bray-Curtis dissimilarities.

Seasonal differences in community composition were tested using permutational multivariate analysis of variance (PERMANOVA) with 999 permutations. Analyses focused on seasonal variation rather than comparisons among individual orchards, as differences in orchard size, geographical location and environmental characteristics would complicate the interpretation of orchard-level differences. Homogeneity of multivariate dispersion was assessed using the *betadisper* function in the 'vegan' package (Oksanen et al. 2008). Pairwise seasonal comparisons were conducted with Holm-Bonferroni-adjusted p-values.

3.1.8.4 Flocking Patterns

To visualise patterns in flocking composition (group sizes) for each species included in the analysis, I performed non-metric multidimensional scaling ordination (NMDS) using the 'vegan' package in RStudio (Oksanen et al. 2008). Assumptions of PERMANOVA were evaluated using the 'betadisper' function within the *vegan* package for each species (Table S 10). Before ordination, I applied a Hellinger transformation to the flocking-count matrix to downweigh highly abundant categories and reduce the influence of double zeros. Community dissimilarity was then calculated using Bray-Curtis distances, which are recommended for quantitative ecological data with uninformative shared absences (Legendre & Legendre 2012). Species with insufficient variation (e.g., only one non-zero sample or no variation in flock composition across samples) were excluded from formal multivariate interpretation. For each of the retained species, site scores and species-level environmental vectors were extracted to visualise clustering across season, survey period (AM / PM), position (edge / middle) orchard, and orchard position. Ellipses representing multivariate dispersion (68% confidence) were drawn for seasons. Using the *envfit* function, arrows were drawn on the ordination space to indicate the direction and relative contribution of flock sizes to the multivariate gradient.

Because flocking observations were recorded only after a species had been detected, these analyses describe the relative composition of observed flocking events rather than the population-level probability of individuals occurring in particular group sizes. The analysis therefore does not account for potential differences in detectability among species, seasons, flock sizes, or orchard conditions, and these limitations should be considered when interpreting patterns in flock composition.

To statistically test whether flock composition differed across factors, I performed a permutational multivariate analysis of variance (PERMANOVA) fitting the following model:

Bray-Curtis distance ~ Season + Period + Orchard + Position, with 999 permutations. Pairwise tests were performed to identify differing levels. Pairwise tests were not performed for factors with fewer than two replicates or insufficient non-zero samples.

3.1.8.5 Vertical Strata Use

Analyses of the vertical strata use within orchards were performed separately for each species using generalised linear mixed models (GLMMs) fitted in the 'glmmTMB' package (Brooks et al. 2017). The response variable was the number of observations recorded within each vertical stratum. Vertical stratum (ground, human structures, low, medium and top branches, and overhead) and season (autumn, winter, spring and summer) were included as categorical fixed effects, while orchard was generally included as a random effect to account for repeated observations within orchards. A series of candidate models was fitted using a negative binomial error distribution to accommodate overdispersion in the count data. The candidate model set included models with an interaction between vertical stratum and season, additive effects of vertical stratum and season, orchard as a random effect only, an interaction between vertical stratum and season with orchard fitted as a fixed effect, and a null model (Table S 12). Orchard was specified as a random effect to account for repeated (non-independent) measures from the same orchard.

For each species, models were ranked by Akaike's Information Criterion (AIC). Diagnostics were summarised for each species to assess residual uniformity, dispersion and excessive zero inflation (Table S 13). For each species, the model with the lowest AIC ($\Delta AIC = 0$) and that passed the diagnostics was considered the best-supported model and retained for inference.

For models containing orchard as a random effect, orchard-level variability was assessed using the standard deviation (SD) of the random intercept. The negative binomial dispersion parameter (θ) was also examined, with smaller values indicating greater overdispersion. As the focus of this analysis was on vertical strata use rather than species occurrence, orchard-level predicted counts are not presented.

3.2 Results

3.2.1 Species Richness

A total of 45 bird species were recorded across the 82 surveys conducted in six apple orchards. Species richness estimators indicated that survey effort was sufficient to capture most of the bird community, with the cumulative species curve approaching an asymptote (Figure 3.2). The first-order Jackknife estimator estimated a total richness of 48.0 ± 1.7 species, while the Chao estimator estimated 45.7 ± 1.3 species, suggesting that few additional species were likely present but undetected during the study. Seasonal richness varied throughout the year (Figure 3.3). Summer supported the highest observed richness, with 40 species and the highest estimated richness (46.5 ± 3.6 species), followed by winter (35 observed; 38.7 ± 2.3 estimated) and spring (33 observed; 35.9 ± 1.7 estimated). Finally, autumn had the lowest richness (30 observed; 31.9 ± 1.3 estimated).

Bird detections were dominated by introduced species (Table S 7). Blackbirds were detected during every survey (100%), followed by song thrushes (96.5%), house sparrows (88.4%) and silvereyes (87.2%). Across the 23 orchard-season censuses, blackbirds, greenfinches and chaffinches were recorded in all censuses, while silvereyes were the most widespread native species, occurring in every orchard-season combination. House sparrows, starlings, goldfinches, song thrushes, pūkeko, fantails, welcome swallows, swamp harriers and paradise shelducks were also widespread across orchards (Table S 7). In contrast, several species were rarely detected, including black swans (*Cygnus atratus*), greylag geese (*Anser anser*), pied shags (*Phalacrocorax varius*), brown quails (*Synoicus ypsilophorus*), moreporks (*Ninox novaeseelandiae*), New Zealand falcons (*Falco novaeseelandiae*), peacocks (*Pavo cristatus*), rooks (*Corvus frugilegus*) and shining cuckoos (*Chrysococcyx lucidus*), each detected only once or twice during the study. Of these, the New Zealand falcon is classified as Vulnerable.

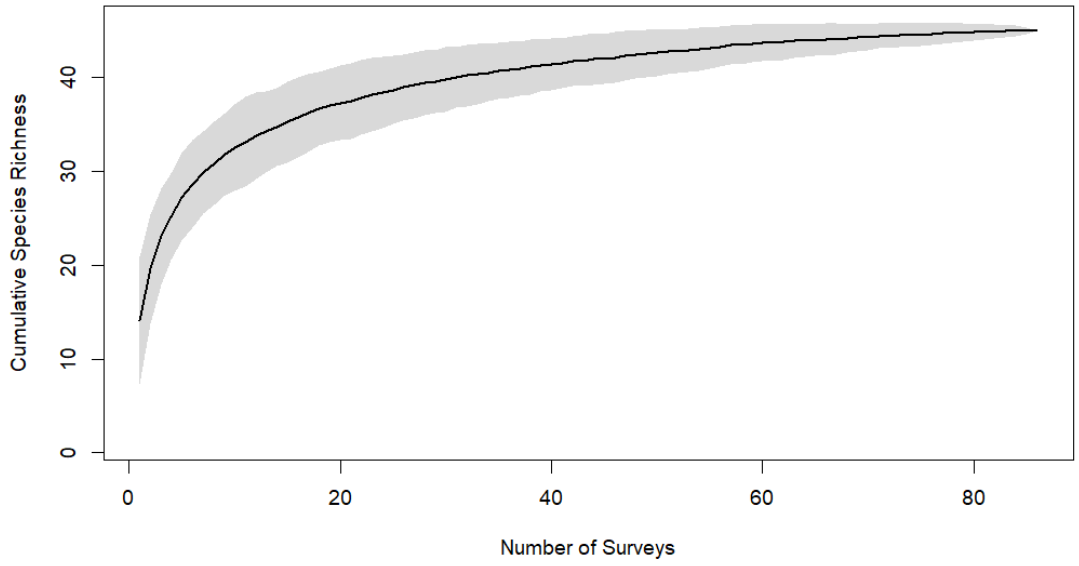


Figure 3.2. Species accumulation curve showing cumulative observed bird species richness across 82 surveys conducted in six apple orchards. The solid line represents the mean cumulative richness calculated from 100 random permutations of survey order, and the shaded area represents the 95% confidence interval.

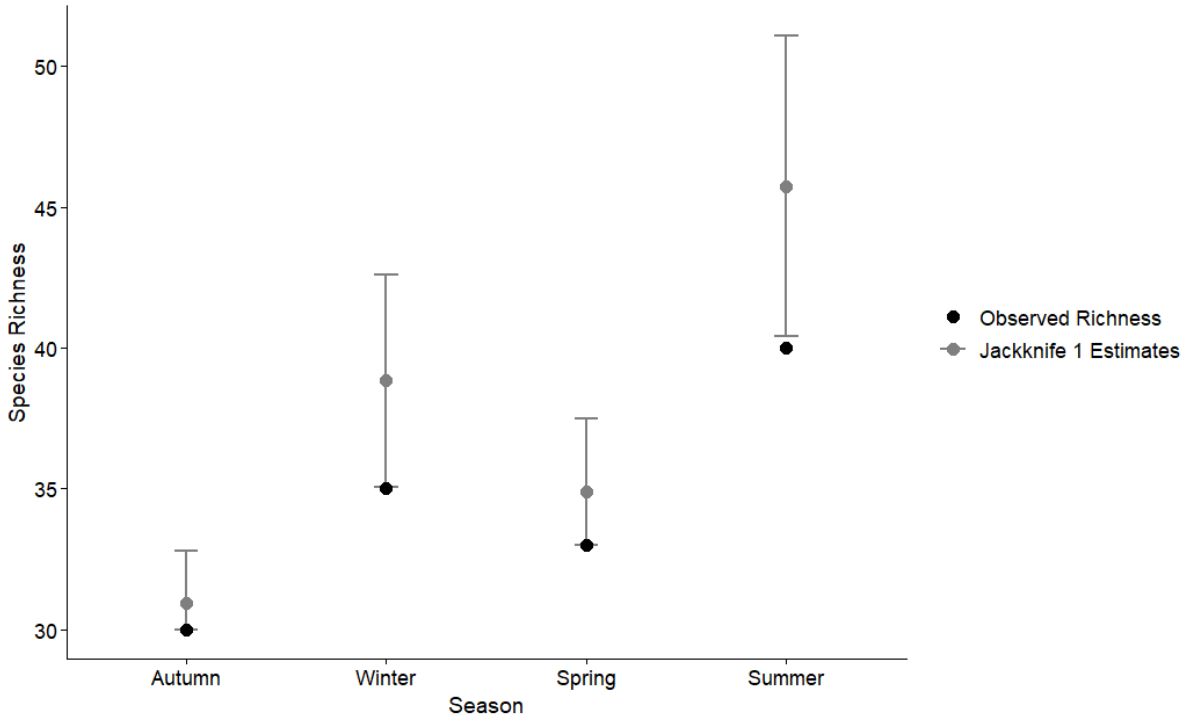


Figure 3.3. Observed species richness (black circles) and first-order Jackknife richness estimates (grey circles) with approximate 95% confidence intervals for each survey season. Richness estimates were calculated from incidence (presence / absence) data using individual surveys (n = 82) as sampling units.

3.2.2 Species Occupancy

Occupancy models were fitted for all 45 bird species recorded during the surveys to account for imperfect detection. Intercept-only models provided the best fit for 39 species, indicating that the evaluated occupancy and detection covariates (season for occupancy; surveyed area, survey period, temperature, wind, sunshine, ambient noise and precipitation for detection) did not substantially improve model performance (Table S 8). No species retained season as an occupancy predictor in the best-supported model. Detection covariates were retained in the best-supported models for six species, including temperature for dunnocks and survey period for eastern rosellas (*Platycercus eximius*), magpies (*Gymnorhina tibicen*), mallard ducks (*Anas platyrhynchos*), spur-winged plovers (*Vanellus miles*) and paradise shelducks.

After accounting for imperfect detection, blackbirds were estimated to use virtually every orchard-season combination ($\psi = 1.00$). Silvereyes, song thrushes, greenfinches, chaffinches and starlings were similarly widespread, with estimated probabilities of habitat use of at least 0.96 (Table 3.2). Welcome swallows, swamp harriers, pūkeko and rock pigeons were predicted to use approximately three-quarters to four-fifths of orchard-season combinations. In contrast, bellbirds, Canada geese, New Zealand pigeons and peacocks were predicted to use only a small proportion of orchard-season combinations. Occupancy estimates for several species were associated with wide confidence intervals, indicating substantial uncertainty in the model-derived estimates. This was particularly evident for species detected infrequently and for species recorded across all orchard-season combinations, for which occupancy estimates approached the upper boundary of the parameter space.

Detection probabilities (p) also varied among species (Table 3.2). Among species fitted with intercept-only models, detection probabilities ranged from 0.01 for black-backed gulls (*Larus dominicanus*) to 1.00 for blackbirds and mynas. Dunnock detection probability declined progressively with increasing temperature (Figure S 5). For eastern rosellas, magpies, mallard ducks, spur-winged plovers and paradise shelducks, detection probabilities were consistently higher during morning surveys than during afternoon surveys, although there was considerable overlap between periods for all five species (Figure S 6).

Table 3.2. Estimated occupancy probability (Ψ) and conditional detection probability (p), with corresponding 95% confidence intervals. Estimated occupancy probabilities and detection probabilities are reported here for the 39 bird species whose best-supported occupancy models were intercept-only [null] models. Species whose best-supported models included temperature or survey period as detection covariates are presented separately in Figure S 5 and Figure S 6.

Species	Ψ	Ψ lower	Ψ upper	p	p lower	p upper	AICc Weight
bellbird	0.154	0.047	0.402	0.430	0.144	0.772	0.918
black backed gull	0.931	0.000	1.000	0.013	0.000	0.996	0.837
black billed gull	0.270	0.126	0.488	0.676	0.478	0.826	0.950
black swan	0.284	0.130	0.513	0.532	0.302	0.749	0.758
blackbird	1.000	NA	NA	1.000	NA	NA	0.986
brown quail	0.997	0.000	1.000	0.023	0.006	0.092	0.688
California quail	0.425	0.144	0.764	0.251	0.106	0.489	0.979
Canada goose	0.141	0.045	0.364	0.550	0.258	0.811	0.804
chaffinch	1.000	0.000	1.000	0.849	0.757	0.910	0.922
fantail	0.957	0.748	0.994	0.772	0.667	0.851	0.893
goldfinch	0.961	0.721	0.996	0.828	0.728	0.896	0.938
greenfinch	1.000	0.000	1.000	0.849	0.757	0.910	0.847
grey warbler	0.459	0.203	0.739	0.320	0.140	0.576	0.978
greylag goose	0.994	0.000	1.000	0.012	0.001	0.089	0.853
house sparrow	0.966	0.678	0.997	0.900	0.810	0.950	0.848
kereru	0.103	0.023	0.357	0.419	0.088	0.844	0.774
kingfisher	1.000	0.000	1.000	0.407	0.308	0.514	0.942
morepork	0.998	0.000	1.000	0.023	0.006	0.089	0.678
myna	0.174	0.067	0.382	1.000	0.000	1.000	0.986
NZ falcon	0.293	0.000	1.000	0.088	0.000	1.000	0.852
peacock	0.045	0.006	0.263	0.642	0.119	0.960	0.905
pied cormorant	0.994	0.000	1.000	0.012	0.001	0.089	0.940
pūkeko	0.796	0.575	0.918	0.783	0.668	0.867	0.959
rainbow lorikeet	0.155	0.045	0.417	0.407	0.099	0.811	0.493

Species	Ψ	Ψ lower	Ψ upper	p	p lower	p upper	AICc Weight
red billed gull	0.268	0.076	0.620	0.261	0.078	0.595	0.916
redpoll	0.268	0.076	0.620	0.261	0.078	0.595	0.746
ring neck pheasant	0.614	0.303	0.853	0.319	0.160	0.536	0.959
rock pigeon	0.764	0.506	0.911	0.477	0.338	0.620	0.875
rook	0.997	0.000	1.000	0.023	0.006	0.092	0.642
shining cuckoo	0.981	0.000	1.000	0.024	0.002	0.239	0.727
silvereye	1.000	0.000	1.000	0.872	0.784	0.928	0.978
skylark	0.497	0.296	0.699	0.690	0.542	0.808	0.945
song thrush	1.000	0.000	1.000	0.965	0.897	0.989	0.969
starling	1.000	0.000	1.000	0.698	0.593	0.785	0.930
swamp harrier	0.798	0.576	0.920	0.768	0.650	0.855	0.977
tūī	0.438	0.254	0.641	0.795	0.609	0.906	0.899
welcome swallow	0.838	0.512	0.962	0.554	0.422	0.679	0.886
white faced heron	0.420	0.115	0.800	0.208	0.083	0.433	0.962
yellowhammer	0.321	0.159	0.542	0.627	0.444	0.780	0.613

3.2.3 Species Abundance

The two-dimensional NMDS captured the broad differences among bird communities, although some distortion remained (stress = 0.171), so small differences in the positions of samples should be interpreted cautiously. The NMDS ordination showed overlap among seasonal communities, with spring and summer samples located in broadly similar regions of ordination space, while winter samples were generally separated from these samples. Autumn samples overlapped with both winter and the spring-summer samples (Figure 3.4).

Bird assemblages showed seasonal variation in species composition, with season accounting for 27.5% of the differences among samples (PERMANOVA, pseudo-$F_{3,19} = 2.40$, $R^2 = 0.275$, $p = 0.004$). Pairwise comparisons yielded the lowest p-values for autumn versus spring, autumn versus summer, winter versus spring, and winter versus summer. However, none of the pairwise comparisons remained statistically significant after Holm correction for multiple testing (Table 3.3).

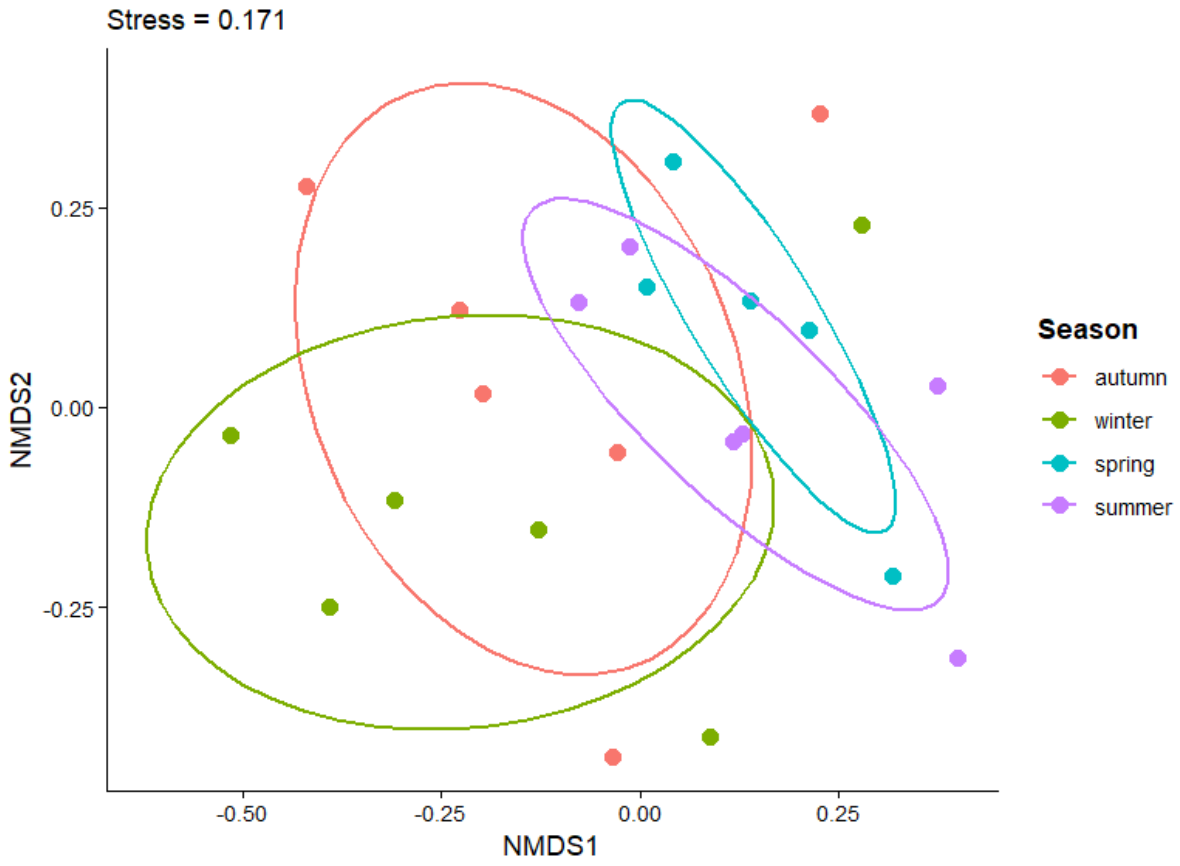


Figure 3.4. Non-metric multidimensional scaling (NMDS) ordination of bird community composition across four seasons, based on Bray-Curtis dissimilarities calculated from Hellinger-transformed abundance data (stress = 0.171). Each point represents a single orchard x season community sample. Colours indicate season, and ellipses represent the multivariate dispersion of samples within each season. NMDS1 and NMDS2 represent the major dimensions of variation in community composition, with points located closer together indicating more similar bird assemblages.

Table 3.3. Pairwise permutational multivariate analysis of variance (PERMANOVA) comparisons testing differences in species abundance composition between levels of season as a predictor. For each pairwise contrast, comparison groups, F-statistics, corresponding R^2 values, unadjusted p-values based on 999 permutations and Holm-adjusted p-values are reported.

Group 1	Group 2	F	R^2	p	Holm-adjusted p
autumn	winter	1.215	0.108	0.343	0.686
autumn	spring	2.273	0.202	0.009	0.054
autumn	summer	2.469	0.198	0.023	0.08
winter	spring	3.867	0.301	0.02	0.08
winter	summer	3.505	0.260	0.012	0.06
spring	summer	1.125	0.111	0.352	0.686

3.2.4 Flocking Patterns

Silvereyes, blackbirds and mynas had overall higher averages for all flocking types, while greenfinches and pūkeko had high averages for solitary observations (Table 3.4). Mynas were kept for descriptive purposes and were excluded from the ordination analysis as they were only recorded at one site. NMDS ordination for welcome swallows was excluded from the results because the species exhibited extremely low variation in flocking structure across sampling events, resulting in a collapsed ordination with near-zero stress. This indicates that flocking composition was virtually identical across seasons and orchards, preventing meaningful visualisation. Similarly, swamp harriers were observed almost exclusively as solitary individuals, so no figure was produced for this species.

The species composition of flocks was broadly similar across seasons, orchards, sampling periods and positions, with substantial overlap and little separation among groups in ordination space (Figure 3.5; Figure 3.6). The NMDS solutions represented the broad rank order of compositional dissimilarities with low to moderate distortion (stress < 0.001-0.15).

Within native species, only silvereyes had an identifiable seasonal shift, with large groups composing most winter observations (Figure 3.5), a result that corroborates the high number of individuals of this species observed for that season across orchards. New Zealand fantails and pūkeko had an almost complete overlap for all seasons, and were predominantly observed as solitary individuals, pairs, and small groups (Figure 3.5).

Blackbirds showed an overall overlap in their season ellipses, indicating that flocking composition was similar across seasons (Figure 3.6). The stronger likelihood was from solitary individuals and pairs, while big groups were rarer. Chaffinches had a stronger likelihood of pairs and small groups in autumn, while goldfinches had a higher likelihood of solitary individuals and small groups in autumn and large groups in summer. Likelihood of different group sizes and overlap across seasons was shown for greenfinches, house sparrows, and rock pigeons. Song thrushes had their flocking composition marked by predominantly solitary individuals, pairs, and small groups. Starlings had a seasonal shift with higher likelihood of larger groups in summer.

PERMANOVA detected no significant differences in flocking composition across the environmental and spatial factors examined, except for seasonal differences in flocks containing silvereyes (Table S 11).

Table 3.4. Summary of descriptive statistics for flocking composition across 92 combinations of orchard, season, survey period (AM/PM), and position (edge/middle). Arithmetic means, standard deviations (SD), and standard errors (SE) were calculated for observation counts in five flocking categories: large flocks (over 10 individuals), medium groups (6–10 individuals), small groups (3–5 individuals), pairs, and solitary individuals. Flocking analysis was calculated for five native species (silvereye Zosterops lateralis, New Zealand fantail Rhipidura fuliginosa, welcome swallow Hirundo neoxena, swamp harrier Circus approximans, and pūkeko Porphyrio melanotus melanotus); and nine introduced species (blackbird Turdus merula, chaffinch Fringilla coelebs, goldfinch Carduelis carduelis, greenfinch Chloris chloris, house sparrow Passer domesticus, song thrush Turdus philomelos, rock pigeon Columba livia, starling Sturnus vulgaris, and myna Acridotheres tristis).

Native Species	**silvereye**			**New Zealand fantail**			**welcome swallow**			**swamp harrier**			**pūkeko**		
	Mean	**SD**	**SE**	**Mean**	**SD**	**SE**	**Mean**	**SD**	**SE**	**Mean**	**SD**	**SE**	**Mean**	**SD**	**SE**
large flock	0.696	1.420	0.148	0	0	0	0	0	0	0	0	0	0	0	0
medium group	0.902	1.527	0.159	0	0	0	0.011	0.104	0.011	0	0	0	0.033	0.179	0.019
small group	1.750	2.375	0.248	0.098	0.299	0.031	0.141	0.459	0.048	0	0	0	0.413	0.744	0.078
pairs	1.337	2.303	0.240	0.348	0.601	0.063	0.207	0.525	0.055	0.087	0.32	0.033	0.641	1.289	0.134
solitary	1.228	1.671	0.174	0.826	1.075	0.112	0.413	0.8	0.083	1.12	1.596	0.166	1.859	3.019	0.315

Introduced Species	**blackbird**			**chaffinch**			**goldfinch**			**greenfinch**			**house sparrow**		
	Mean	**SD**	**SE**	**Mean**	**SD**	**SE**	**Mean**	**SD**	**SE**	**Mean**	**SD**	**SE**	**Mean**	**SD**	**SE**
large flock	0.033	0.179	0.019	0.011	0.104	0.011	0.359	0.921	0.096	0.022	0.147	0.015	0.565	1.44	0.15
medium group	0.174	0.381	0.040	0.043	0.253	0.026	0.348	0.791	0.082	0.12	0.626	0.065	0.663	1.092	0.114
small group	1.804	1.900	0.198	0.174	0.409	0.043	0.848	1.526	0.159	0.402	1.149	0.12	0.88	1.503	0.157
pairs	3.011	2.666	0.278	0.554	0.918	0.096	0.446	0.918	0.096	0.696	1.193	0.124	0.522	0.943	0.098
solitary	5.674	5.395	0.562	1.685	1.95	0.203	1.033	1.537	0.16	1.533	2.251	0.235	0.772	1.498	0.156

	song thrush			rock pigeon			starling			myna		
	Mean	**SD**	**SE**	**Mean**	**SD**	**SE**	**Mean**	**SD**	**SE**	**Mean**	**SD**	**SE**
large flock	0	0	0	0.272	0.853	0.089	0.185	0.838	0.087	2.083	2.151	0.621
medium group	0	0	0	0.109	0.313	0.033	0.076	0.399	0.042	1.833	1.337	0.386
small group	0.065	0.25	0.03	0.196	0.497	0.052	0.217	0.531	0.055	4.75	2.379	0.687
pairs	0.88	1.2	0.13	0.098	0.333	0.035	0.304	0.642	0.067	3.083	2.109	0.609
solitary	3.163	3.57	0.37	0.054	0.228	0.024	0.717	1.225	0.128	2.083	1.24	0.358

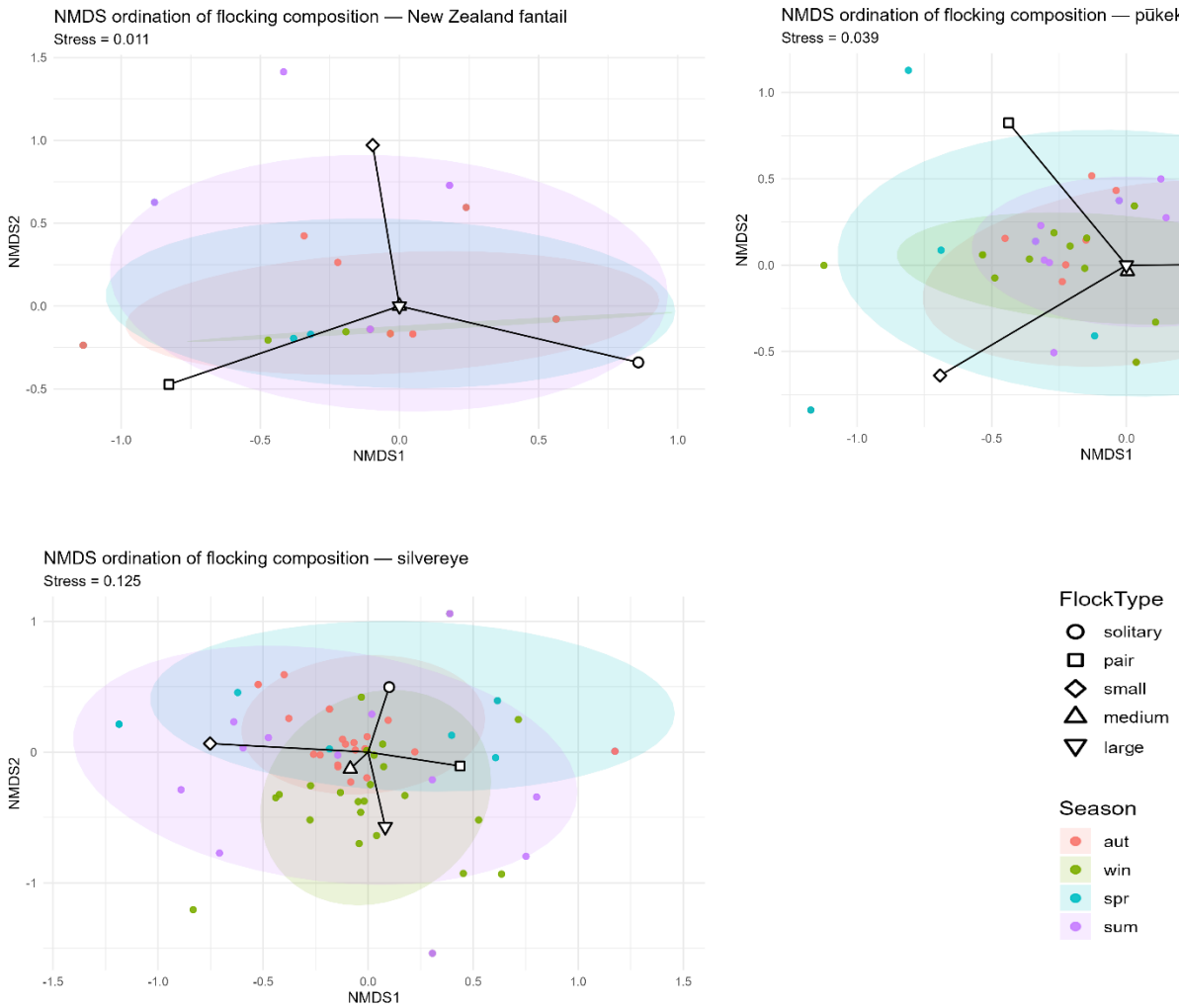


Figure 3.5. Non-metric multidimensional scaling (NMDS) ordination of flocking type composition for native species: silvereyes (Zosterops lateralis), New Zealand fantails (Rhipidura fuliginosa), welcome swallows (Hirundo neoxena), and pūkeko (Porphyrio melanotus melanotus). Points represent individual sampling events, coloured by season (from autumn 2024 to summer 2025). Ellipses show 95% confidence regions for each season. Arrows represent fitted vectors from the envfit analysis, indicating the direction and relative contribution of flock-size categories (solitary individuals, pairs, small groups, medium groups, and large flocks) to the multivariate gradient. Ordinations are based on Bray-Curtis dissimilarities calculated from Hellinger-transformed flock-size data. Stress values indicate goodness of fit (stress < 0.15 = reliable; < 0.10 = good; < 0.05 = excellent). Flocking categories are distinguished between solitary individuals, pairs, small groups (3-5 individuals), medium groups (6-10 individuals), and large flocks (>10 individuals).

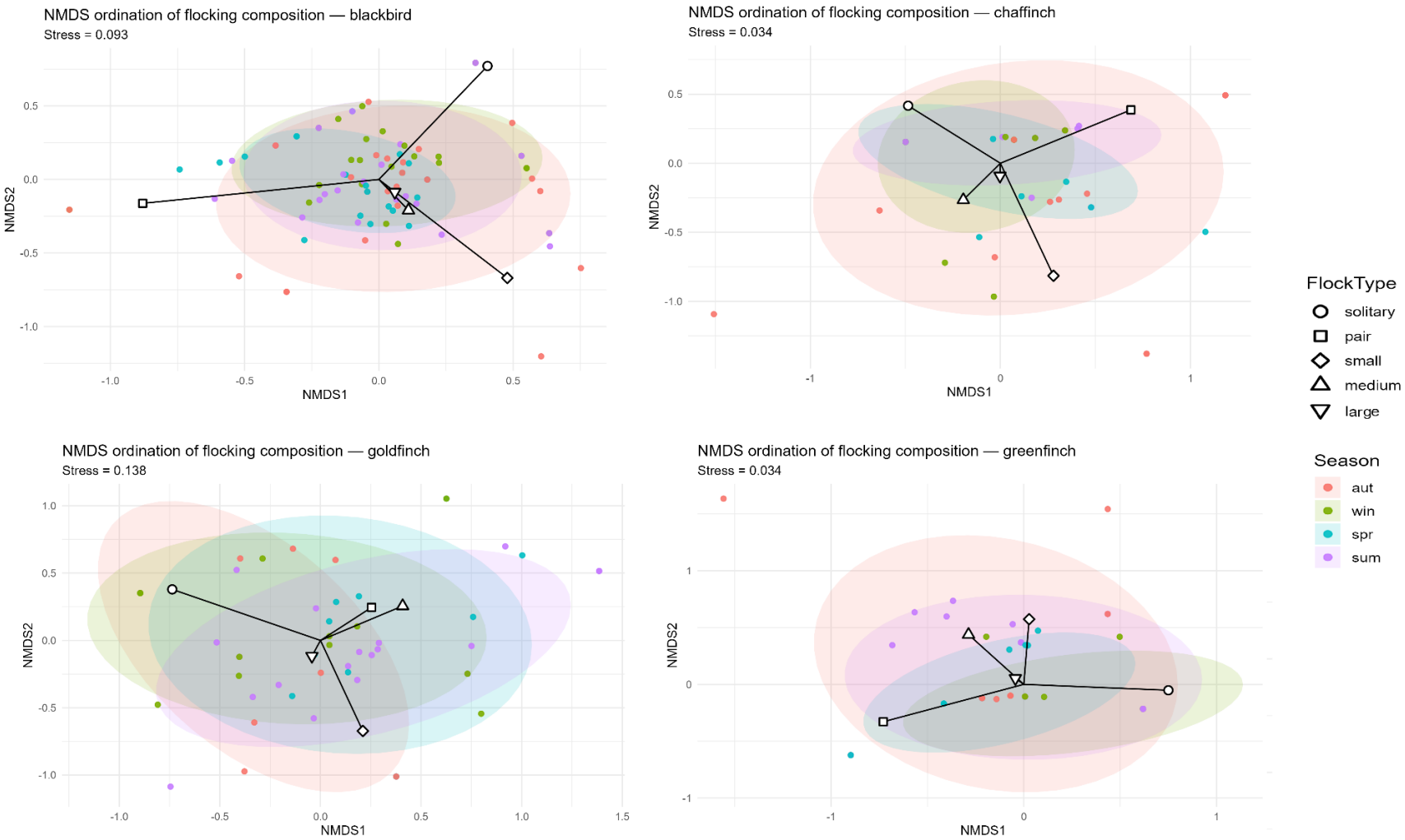


Figure 3.6. Non-metric multidimensional scaling (NMDS) ordination of flocking type composition for introduced species: blackbirds (Turdus merula), chaffinches (Fringilla coelebs), goldfinches (Carduelis carduelis), and greenfinches (Chloris chloris). Points represent individual sampling events, coloured by season (from autumn 2024 to summer 2025). Ellipses show 95% confidence regions for each season. Arrows represent fitted vectors from the envfit analysis, indicating the direction and relative contribution of flock-size categories (solitary individuals, pairs, small groups, medium groups, and large flocks) to the multivariate gradient. Ordinations are based on Bray-Curtis dissimilarities calculated from Hellinger-transformed flock-size data. Stress values indicate goodness of fit (stress < 0.15 = reliable; < 0.10 = good; < 0.05 = excellent). Flocking categories are distinguished between solitary individuals, pairs, small groups (3-5 individuals), medium groups (6-10 individuals), and large flocks (>10 individuals).

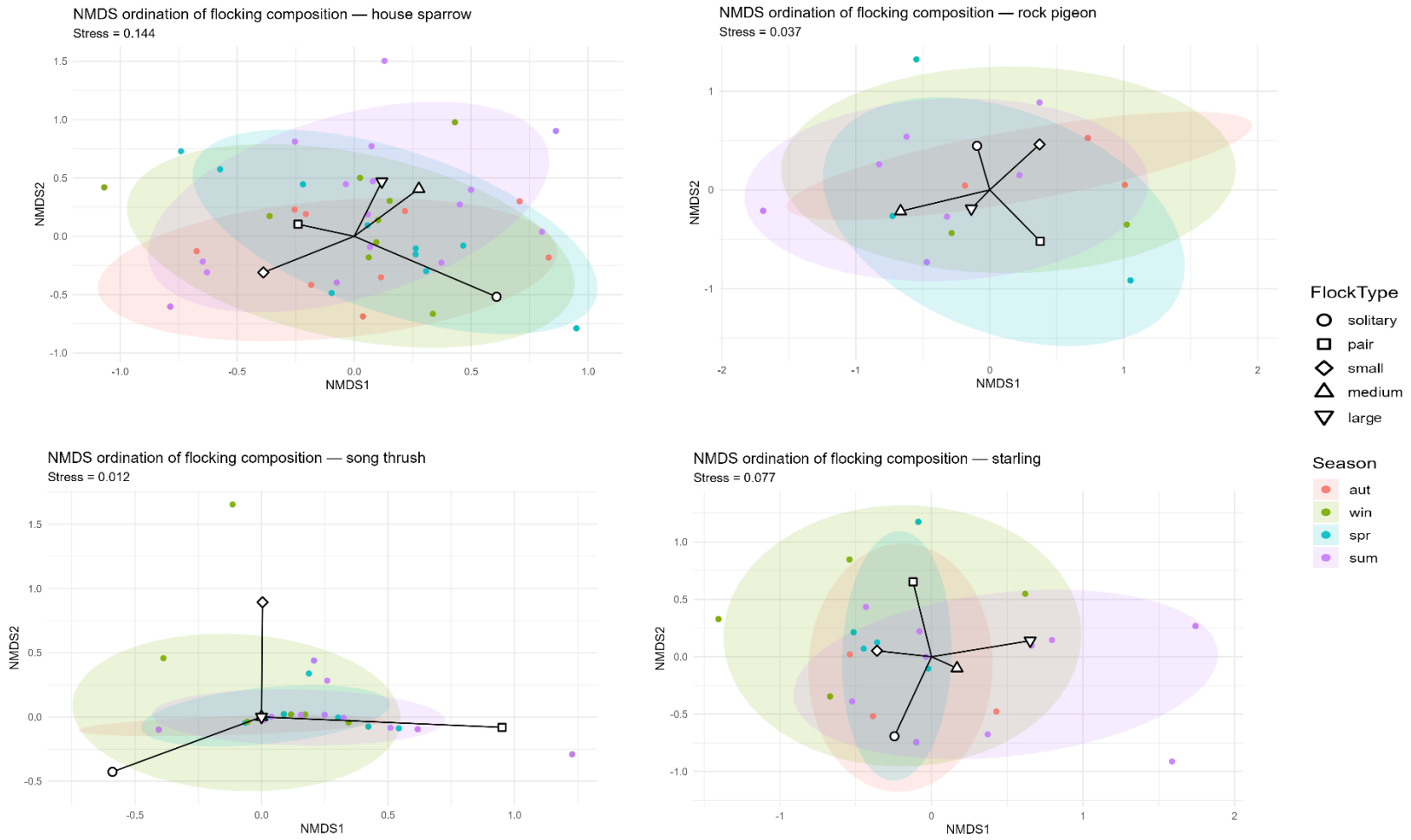


Figure 3.5 (cont.). Non-metric multidimensional scaling (NMDS) ordination of flocking type composition for introduced species: song thrushes (Turdus philomelos), starlings (Sturnus vulgaris), and rock pigeons (Columba livia). Points represent individual sampling events, coloured by season (from autumn 2024 to summer 2025). Ellipses show 95% confidence regions for each season. Arrows represent fitted vectors from the envfit analysis, indicating the direction and relative contribution of flock-size categories (solitary individuals, pairs, small groups, medium groups, and large flocks) to the multivariate gradient. Ordinations are based on Bray-Curtis dissimilarities calculated from Hellinger-transformed flock-size data. Stress values indicate goodness of fit (stress < 0.15 = reliable; < 0.10 = good; < 0.05 = excellent). Flocking categories are distinguished between solitary individuals, pairs, small groups (3-5 individuals), medium groups (6-10 individuals), and large flocks (>10 individuals).

3.2.5 Vertical Strata Use of Orchards

Use of the vertical strata within orchards was assessed for 13 bird species, comprising six native (New Zealand fantails, pūkeko, tūī, welcome swallows, silvereyes and swamp harriers) and seven introduced species (blackbirds, chaffinches, goldfinches, greenfinches, house sparrows, song thrushes and starlings). Overall, the ground and overhead strata accounted for most bird observations, whereas human structures and low branches were used least frequently (Table 3.5).

I identified three groups of best-fitting models following the use of model diagnostics and AIC values (Table 3.6). Blackbirds were best explained by an interaction between vertical stratum and season with orchard included as a random effect. Chaffinches, New Zealand fantails, goldfinches, greenfinches, pūkeko, tūī and welcome swallows were best described by additive effects of vertical stratum and season with orchard included as a random effect. House sparrows, silvereyes, song thrushes and swamp harriers were best explained by an interaction between vertical stratum and season with orchard fitted as a fixed effect.

Although the selected model for starlings converged successfully (Table S 13), standard errors could not be estimated because observations were sparse in several vertical strata. Further model simplification did not resolve this issue, as some factor levels contained very few or no observations. Consequently, starlings were excluded from subsequent analyses of vertical strata use. Overall, species could be separated into ground, canopy, and aerial foraging guilds (Figure 3.7).

Table 3.5. Summary of descriptive statistics for vertical strata use by native (A) and introduced (B) bird species across 23 orchard–season combinations (n = 23). Arithmetic means, standard deviations (SD), and standard errors (SE) were calculated for observation counts across six vertical strata: ground, low, medium and top tree branches, overhead, and human structures (e.g. poles, sheds and power lines).Species included in this analysis were represented by ten native species: silvereye (Zosterops lateralis), tūī (Prosthemadera novaeseelandiae), New Zealand fantail (Rhipidura fuliginosa), pūkeko (Porphyrio melanotus melanotus), welcome swallow (Hirundo neoxena), sacred kingfisher (Todiramphus sanctus), black-backed gull (Larus dominicanus), spur-winged plover (Vanellus miles), paradise shelduck (Tadorna variegata) and swamp harrier (Circus approximans); and 14 introduced species: blackbird (Turdus merula), chaffinch (Fringilla coelebs), goldfinch (Carduelis carduelis), greenfinch (Chloris chloris), house sparrow (Passer domesticus), song thrush (Turdus philomelos), starling (Sturnus vulgaris), skylark (Alauda arvensis), dunnock (Prunella modularis), magpie (Gymnorhina tibicen), eastern rosella (Platycercus eximius), yellowhammer (Emberiza citrinella), myna (Acridotheres tristis) and ring-neck pheasant (Phasianus colchicus).

	Vertical Stratum	Mean	SD	SE	Mean	SD	SE	Mean	SD	SE	Mean	SD	SE
A. natives		**silvereye**			**tūī**			**New Zealand fantail**			**pūkeko**		
	ground	3.330	7.590	1.550	0.080	0.280	0.060	0.62	0.88	0.18	9.88	13.78	2.81
	low branch	0.790	1.960	0.400	0.040	0.200	0.040	0.79	0.88	0.18	0.08	0.28	0.06
	medium branch	3.460	3.820	0.780	0.620	1.880	0.380	0.92	1.1	0.22	0.08	0.28	0.06
	top branch	5.710	5.190	1.060	1.120	2.400	0.490	0.88	1.3	0.26	0.75	1.59	0.33
	overhead	7.920	9.120	1.860	0.710	1.520	0.310	1.42	1.53	0.31	0.21	0.51	0.1
	human structure	1.330	2.080	0.420	0.000	0.000	0.000	0.33	0.64	0.13	0.29	0.55	0.11
		welcome swallow			**sacred kingfisher**			**black-backed gull**			**spur-winged plover**		
	ground	0.08	0.28	0.06	0	0	0	0.080	0.280	0.060	0.460	0.980	0.200
	low branch	0	0	0	0	0	0	0.000	0.000	0.000	0.000	0.000	0.000
	medium branch	0	0	0	0.12	0.45	0.09	0.000	0.000	0.000	0.000	0.000	0.000
	top branch	0.12	0.45	0.09	0.08	0.28	0.06	0.000	0.000	0.000	0.000	0.000	0.000
	overhead	3.08	3.54	0.72	0.29	0.62	0.13	1.920	5.120	1.050	0.710	1.920	0.390
	human structure	0.17	0.38	0.08	0.33	0.64	0.13	0.250	0.850	0.170	0.000	0.000	0.000

	Vertical Stratum	Mean	SD	SE	Mean	SD	SE	Mean	SD	SE	Mean	SD	SE
		paradise shelduck			swamp harrier								
	ground	0.46	1.06	0.22	0.04	0.2	0.04						
	low branch	0	0	0	0	0	0						
	medium branch	0	0	0	0.04	0.2	0.04						
	top branch	0	0	0	0.04	0.2	0.04						
	overhead	0.71	1.08	0.22	4.38	4.15	0.85						
	human structure	0	0	0	0.17	0.38	0.08						
B. introduced		blackbird			chaffinch			goldfinch			greenfinch		
	ground	17.960	13.580	2.770	17.960	13.580	2.770	2.88	4.85	0.99	1.21	2.19	0.45
	low branch	0.790	1.100	0.230	0.790	1.100	0.230	0.38	0.88	0.18	0.17	0.38	0.08
	medium branch	3.250	3.170	0.650	3.250	3.170	0.650	0.62	0.92	0.19	0.67	0.76	0.16
	top branch	1.960	1.570	0.320	1.960	1.570	0.320	1.54	1.96	0.4	2.12	3.17	0.65
	overhead	14.790	8.990	1.840	14.790	8.990	1.840	4.88	5.88	1.2	5	7.76	1.58
	human structure	2.040	1.990	0.410	2.040	1.990	0.410	1.12	2.36	0.48	0.92	1.72	0.35
		house sparrow			song thrush			starling			skylark		
	ground	3.79	5.56	1.14	5.67	5.94	1.21	0.500	0.720	0.150	1.080	2.100	0.430
	low branch	0.17	0.38	0.08	0.46	0.83	0.17	0.040	0.200	0.040	0.040	0.200	0.040
	medium branch	1.21	1.28	0.26	0.88	1.08	0.22	0.750	1.870	0.380	0.000	0.000	0.000
	top branch	2.21	2.48	0.51	2.33	2.32	0.47	1.960	2.010	0.410	0.120	0.610	0.120
	overhead	3.71	3.58	0.73	4.33	3.37	0.69	2.380	2.160	0.440	0.710	1.990	0.410
	human structure	1.58	2.87	0.59	1.83	2.2	0.45	0.750	1.390	0.280	0.500	1.350	0.280

Vertical Stratum	Mean	SD	SE	Mean	SD	SE	Mean	SD	SE	Mean	SD	SE
	dunnock			magpie			eastern rosella			yellowhammer		
ground	0.46	0.98	0.2	0.5	1.14	0.23	0	0	0	0.62	1.56	0.32
low branch	0.04	0.2	0.04	0	0	0	0	0	0	0	0	0
medium branch	0.17	0.64	0.13	0	0	0	0.04	0.2	0.04	0.04	0.2	0.04
top branch	0.5	0.72	0.15	0.12	0.34	0.07	0.25	0.61	0.12	0.12	0.61	0.12
overhead	0.38	1.06	0.22	0.71	1.08	0.22	0.46	0.78	0.16	0.96	2.61	0.53
human structure	0.25	0.61	0.12	0.08	0.41	0.08	0.04	0.2	0.04	0.25	0.68	0.14

	myna			ring-neck pheasant		
ground	1.750	4.300	0.880	0.710	0.910	0.190
low branch	0.040	0.200	0.040	0.000	0.000	0.000
medium branch	0.290	0.810	0.160	0.000	0.000	0.000
top branch	0.750	1.780	0.360	0.040	0.200	0.040
overhead	5.330	13.350	2.730	0.120	0.340	0.070
human structure	0.830	2.300	0.470	0.000	0.000	0.000

Table 3.6. Akaike's Information Criterion (AIC) model selection results for generalised linear models examining the variation in species occupation of the vertical strata of orchards. For each species, candidate models included combinations of fixed effects, including season and orchard. Model complexity ranged from a full interaction model to a null model containing only an intercept. Models were compared using Akaike's Information Criterion (AIC), the number of estimated parameters (k), ΔAIC values, and Akaike weights. Each species' best model, providing the most parsimonious structure with acceptable diagnostics, is highlighted in bold and was selected as the model for inference. Models were constructed for blackbird (Turdus merula), chaffinch (Fringilla coelebs), New Zealand fantail (Rhipidura fuliginosa), goldfinch (Carduelis carduelis), greenfinch (Chloris chloris), house sparrow (Passer domesticus), pūkeko (Porphyrio melanotus melanotus), silvereye (Zosterops lateralis), song thrush (Turdus philomelos), starling (Sturnus vulgaris), swamp harrier (Circus approximans), tūī (Prosthemadera novaeseelandiae), and welcome swallow (Hirundo neoxena).

Species	Model	k	AIC	ΔAIC	Weight
blackbird					
	Strata x Season Interaction	**26**	**647.354**	**11.118**	**0.004**
	Strata + Season Main Effects	11	659.986	23.750	6.9E-06
	Orchard Random Only	3	827.050	190.814	3.7E-42
	Strata x Season + Orchard as Fixed Effect	30	636.236	0.000	1.0E+00
	Null Model	2	825.050	188.814	1.0E-41
chaffinch					
	Strata x Season Interaction	26	459.299	6.365	0.028
	Strata + Season Main Effects	**11**	**452.934**	**0.000**	**0.678**
	Orchard Random Only	3	484.806	31.872	8.14E-08
	Strata x Season + Orchard as Fixed Effect	30	454.610	1.677	0.293
	Null Model	2	484.009	31.075	1.21E-07
New Zealand fantail					
	Strata x Season Interaction	26	357.348	NA	NA
	Strata + Season Main Effects	**11**	**352.899**	**NA**	**NA**
	Orchard Random Only	3	356.553	NA	NA
	Strata x Season + Orchard as Fixed Effect	30	NA	NA	NA
	Null Model	2	356.001	NA	NA

Species	Model	k	AIC	ΔAIC	Weight
goldfinch					
	Strata x Season Interaction	26	424.580	14.903	0.001
	Strata + Season Main Effects	**11**	**422.487**	**12.809**	**0.002**
	Orchard Random Only	3	487.172	77.494	1.48E-17
	Strata x Season + Orchard as Fixed Effect	30	409.678	0.000	0.998
	Null Model	2	507.859	98.181	4.8E-22
greenfinch					
	Strata x Season Interaction	26	418.997	15.708	0.0003
	Strata + Season Main Effects	**11**	**403.290**	**0.000**	**0.784**
	Orchard Random Only	3	453.636	50.346	9.16E-12
	Strata x Season + Orchard as Fixed Effect	30	405.872	2.582	0.216
	Null Model	2	472.560	69.271	7.12E-16
house sparrow					
	Strata x Season Interaction	26	489.521	14.093	0.001
	Strata + Season Main Effects	11	478.805	3.377	0.156
	Orchard Random Only	3	520.894	45.466	1.1E-10
	Strata x Season + Orchard as Fixed Effect	**30**	**475.428**	**0.000**	**0.843**
	Null Model	2	539.956	64.528	8.2E-15

Species	Model	k	AIC	ΔAIC	Weight
pūkeko					
	Strata x Season Interaction	26	275.108	21.403	2.2E-05
	Strata + Season Main Effects	**11**	**267.476**	**13.771**	**0.001**
	Orchard Random Only	3	359.108	105.403	1.3E-23
	Strata x Season + Orchard as Fixed Effect	30	253.705	0.000	0.999
	Null Model	2	369.455	115.749	7.3E-26
silvereye					
	Strata x Season Interaction	26	565.394	8.972	0.011
	Strata + Season Main Effects	11	575.223	18.801	8.2E-05
	Orchard Random Only	3	670.204	113.782	1.9E-25
	Strata x Season + Orchard as Fixed Effect	**30**	**556.422**	**0.000**	**0.989**
	Null Model	2	668.833	112.411	3.85E-25
song thrush					
	Strata x Season Interaction	26	534.407	17.060	0.0002
	Strata + Season Main Effects	11	517.347	0.000	0.988
	Orchard Random Only	3	599.434	82.087	1.5E-18
	Strata x Season + Orchard as Fixed Effect	**30**	**526.209**	**8.862**	**0.012**
	Null Model	2	598.195	80.848	2.7E-18
starling					
	Strata x Season Interaction	26	365.209	9.480	0.007
	Strata + Season Main Effects	11	359.305	3.576	0.142
	Orchard Random Only	3	399.264	43.535	3.0E-10
	Strata x Season + Orchard as Fixed Effect	**30**	**355.729**	**0.000**	**0.850**

Species	Model	k	AIC	ΔAIC	Weight
	Null Model	2	401.676	45.947	9.0E-11
swamp harrier					
	Strata x Season Interaction	26	187.451	13.581	0.001
	Strata + Season Main Effects	11	173.870	0.000	0.547
	Orchard Random Only	3	261.451	87.581	5.3E-20
	Strata x Season + Orchard as Fixed Effect	**30**	**174.252**	**0.382**	**0.452**
	Null Model	2	259.451	85.581	1.4E-19
tūī					
	Strata x Season Interaction	26	NA	NA	NA
	Strata + Season Main Effects	**11**	**141.425**	**NA**	**NA**
	Orchard Random Only	3	179.792	NA	NA
	Strata x Season + Orchard as Fixed Effect	30	NA	NA	NA
	Null Model	2	203.480	NA	NA
welcome swallow					
	Strata x Season Interaction	26	190.587	18.562	9.3E-05
	Strata + Season Main Effects	**11**	**172.025**	**0.000**	**0.995**
	Orchard Random Only	3	231.134	59.109	1.5E-13
	Strata x Season + Orchard as Fixed Effect	30	182.509	10.483	0.005
	Null Model	2	229.134	57.109	4.0E-13



Figure 3.7. Use of the orchard's vertical strata by common New Zealand bird visitors. Presence of different species within distinct strata is informed by data collected on first-sight observations of native and introduced species across six sites and four seasons. Species are identified by abbreviations: SE = silvereye (Zosterops lateralis); PK = pūkeko (Porphyrio melanotus melanotus); SH = swamp harrier (Circus approximans); TU = tūī (Prosthemadera novaeseelandiae); FN = New Zealand fantail (Rhipidura fuliginosa); WS = welcome swallow (Hirundo neoxena); GF = goldfinch (Carduelis carduelis); CF = chaffinch (Fringilla coelebs); BB = blackbird (Turdus merula); ST = song thrush (Turdus philomelos); HS = house sparrow (Passer domesticus).

3.2.5.1 Blackbird

Blackbirds were the only species for which the best-fitting model included the interaction between vertical stratum and season (Table 3.6). Orchard-level variation was low (SD = 0.31), indicating limited differences among orchards in vertical strata use. The ground was the most used stratum for blackbirds (Figure 3.8; Table S 14). Medium and top branches, and human structures were used significantly less (Table S 15). Season had a marginal effect on vertical strata use, with the use of overhead stratum lower for spring and summer. No other seasonal effects were detected, with estimated marginal means (EMMs) confirming a clear preference for ground and overhead strata (Figure 3.8).

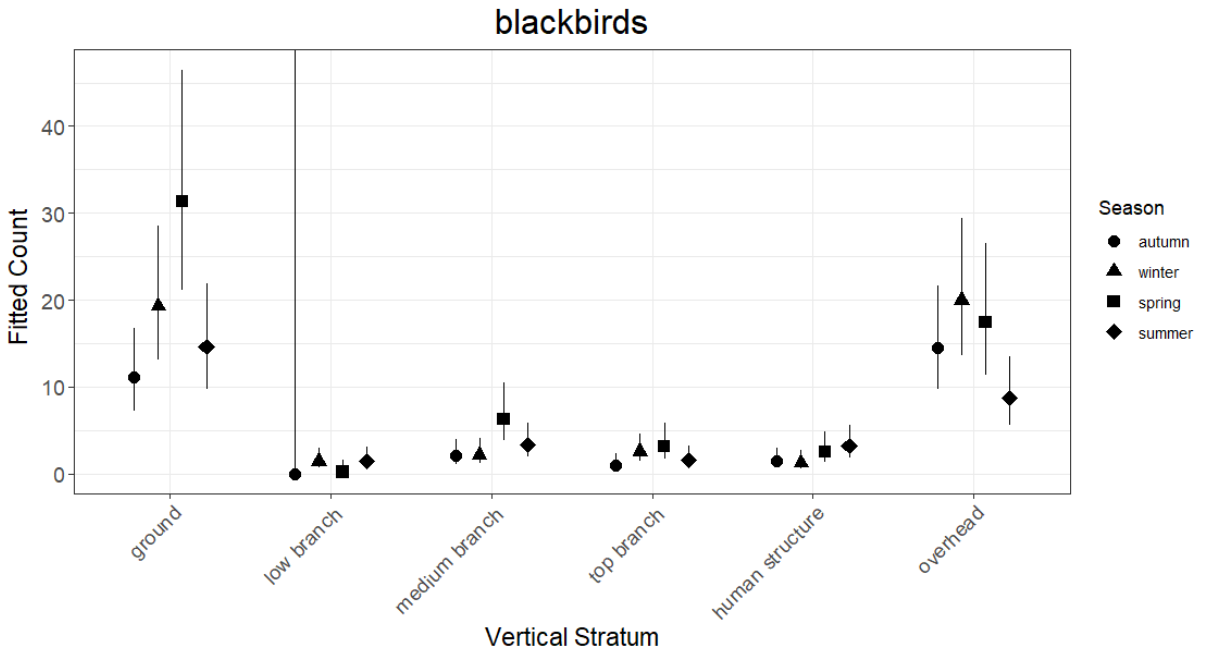


Figure 3.8. Vertical strata use by blackbird (Turdus merula). Fitted counts (± 95 % CI) from a generalised linear mixed model including the interactions between vertical stratum and season. Model was selected for inference from a candidate set of models compared using Akaike's Information Criterion values and diagnostic tools to assess for model validity.

3.2.5.2 Chaffinch, New Zealand Fantail, Goldfinch, Greenfinch, Pūkeko, Tūī, Welcome Swallow

For chaffinches, New Zealand fantails, goldfinches, greenfinches, pūkeko, tūī and welcome swallows, the best-fitting models included only the additive effects of vertical stratum and season (Table 3.6). Low orchard-level variability was detected for chaffinches and fantails (SD = 0.24 and 0.25, respectively), while moderate variability was detected for goldfinches, greenfinches and welcome swallows (SD = 0.81, 0.74 and 0.75). Pūkeko and tūī presented high orchard-level variability (SD = 1.8 and 2.1, respectively). This variability likely reflects differences in the occurrence and abundance of these species among sites, as pūkeko and tūī were not observed in all orchards.

Modelling of chaffinches' vertical use of the orchard revealed a marked use of the overhead stratum (Table S 14). Low branches and human structures were significantly less used (Table S 14; Table S 15). Overall, chaffinches used the ground and overhead strata the most, with reduced use of medium branches (Figure 3.9).

Fantails used the overhead stratum far more frequently than all other strata, although most comparisons between strata revealed non-significant results (Table S 14; Table S 15). Top branches were also used frequently, while ground and human structures had less frequent visits (Figure 3.9).

Nearly all vertical strata significantly influenced the fitted counts of goldfinches (Table S 14). The use of low, medium and top branches, as well as human structures were much lower compared to the ground level. In contrast, the overhead stratum was utilised the most by the species (Table S 15). EMMs indicated that the greatest use occurred in the overhead and ground strata, while the lower branches of trees and human structures were used infrequently (Figure

3.9). Modelling of vertical use for greenfinches revealed a similar pattern of high overhead stratum use, but the species differed in using top branches more compared to the ground and other strata (Table S 14; Table S 15). EMMs indicated that greenfinches used predominantly the upper layers of the orchard, including top branches and overhead, while infrequently seen in lower and medium branches and human structures (Figure 3.9).

Pūkeko were mainly observed using the ground stratum, with a low frequency of observations on top branches and virtually no observations on low and medium branches, human structures, and overhead. Therefore, contrasts between the ground and other strata were highly significant, but pairwise contrasts for all other strata were uninformative (Table S 14; Table S 15). Estimated marginal means substantiated these comparisons, with fitted counts of ground use estimated at 4.05 birds, compared with all other vertical layer estimations of < 0.3 birds (Figure 3.9).

Tūī were observed far more frequently within the tree and overhead strata, with rare but non-zero observations of the species on the ground (Figure 3.9; Table S 14). Use of human structures was negligible, and top branches were preferred over low branches (Table S 15). Although most pairwise contrasts were not significant, estimated marginal means indicated the primary use of the overhead stratum, with low fitted counts for all other layers (Figure 3.9).

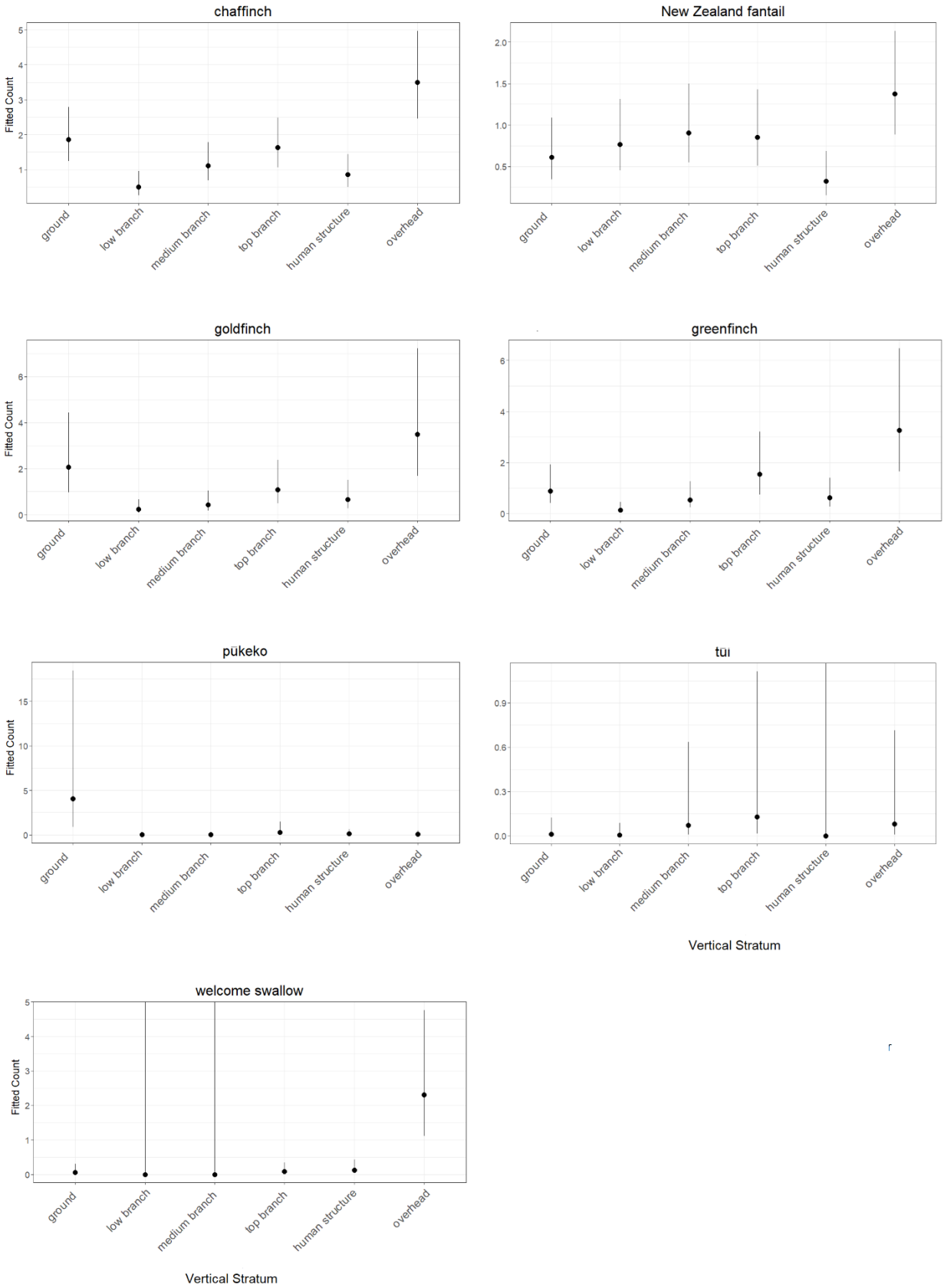


Figure 3.9. Vertical strata use by chaffinch (Fringilla coelebs), fantail (Rhipidura fuliginosa), goldfinch (Carduelis carduelis), greenfinch (Chloris chloris), pūkeko (Porphyrio melanotus melanotus), tūī (Prosthemadera novaeseelandiae) and welcome swallow (Hirundo neoxena). Fitted counts (± 95 % CI) from a generalised linear mixed model including the additive effects of vertical stratum and season. Models were selected for inference from a candidate set of models compared using Akaike's Information Criterion values and diagnostic tools to assess model validity. Note that the y-axis (fitted counts) varies between species.

3.2.5.3 House Sparrow, Silvereye, Song Thrush, Swamp Harrier

For these species, the best-fitting models included the interaction between vertical stratum and season, with orchard fitted as a fixed effect (Table 3.6).

House sparrows showed a marked preference for the ground stratum, with significantly less use of low and medium branches (Table S 14). Seasonal interactions revealed an increase in use of human structures in winter and summer, with the latter also showing an increase in top branches (Table S 14; Table S 15). Overall, house sparrows were more frequently observed using the ground and overhead strata (Figure 3.10).

Season had a strong effect on stratum use for silvereyes, related to the species' seasonal variation in abundance. Additionally, spring coefficients were unreliable due to zero or near-zero detections, increasing the predictive power of season in this analysis (Table S 14; Table S 15). Overall, silvereyes showed primary use of the medium and top branches of trees (Figure 3.10). The reduced use of medium and top branches in winter for the overhead stratum indicated that most birds in this season were observed in flight.

Song thrushes showed a marked preference for the ground compared to all other strata (Table S 15). The overhead stratum was moderately used, with low use of top branches and human structures (Figure 3.10). Model coefficients for swamp harriers were numerically unstable due to complete separation among strata (e.g., overhead Wald test, estimate = 18.45 ± 1763.3 SE, $z = 0.01$, $p = 0.99$; all other strata $< -6 \pm > 4000$ SE, $p > 0.99$), confirming that the species was virtually absent from vegetative strata, the ground, and human structures (Figure 3.10).

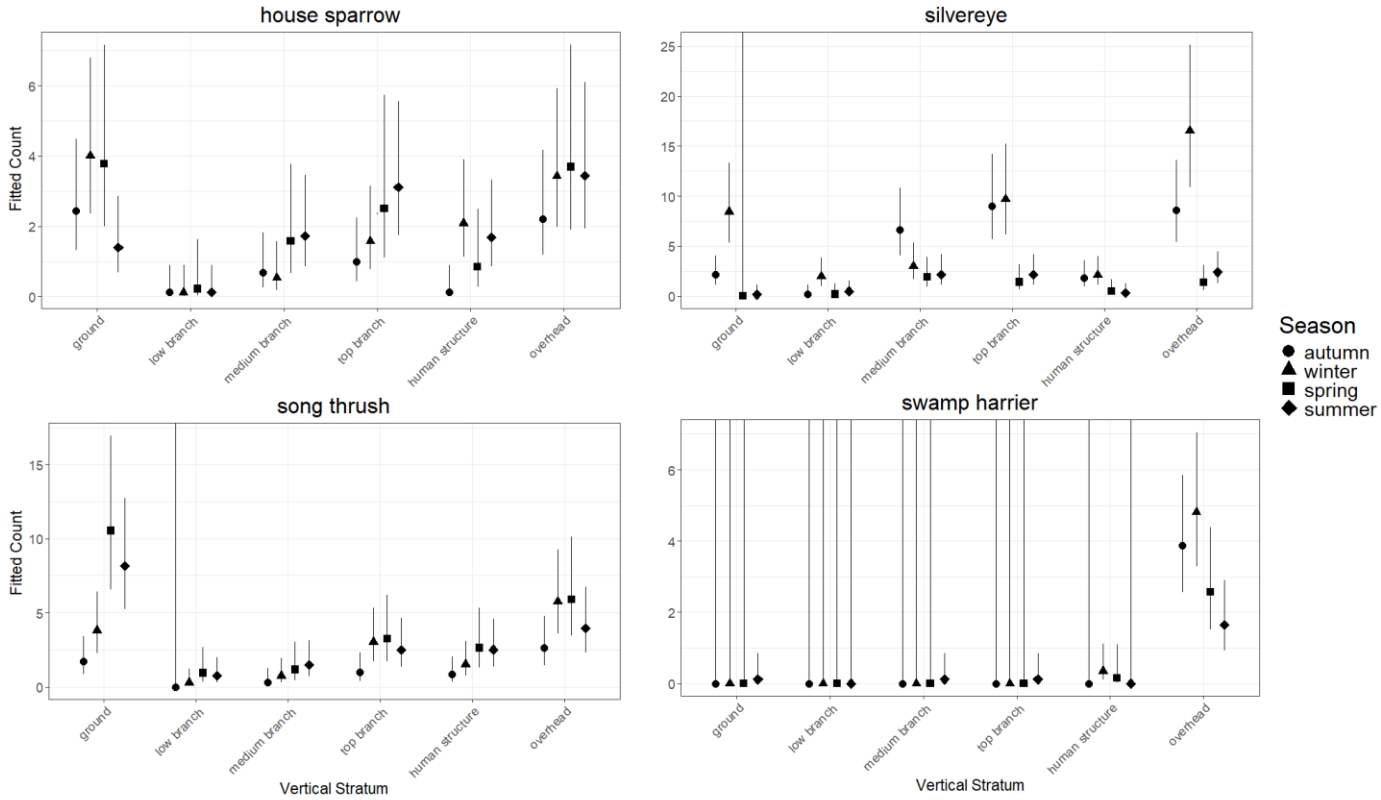


Figure 3.10. Vertical strata use by house sparrow (Passer domesticus), silvereye (Zosterops lateralis), song thrush (Turdus philomelos), and swamp harrier (Circus approximans). Fitted counts (± 95 % CI) from a generalised linear mixed model. House sparrows, silvereyes and swamp harriers are shown from models including the interaction between vertical stratum and season, whereas song thrushes are shown from the additive model. Models were selected for inference from a candidate set of models compared using Akaike's Information Criterion values and diagnostic tools to assess for model validity. Note that the y-axis (fitted counts) varies between species.

3.2.6 Mammalian Presence in Orchards

Predation marks were identified as rodents (Figure S 7), brushtail possums (Figure S 8), and hedgehogs (Figure S 9). Although proxies for densities of cats and rabbits could not be estimated, as these species did not leave marks on the chew cards, camera trap detections helped identify cat and rabbit presence at all orchards except MN1 (Table S 16). In spring, orchard MN1 also showed predation marks by cows, but their presence on the orchard was accidental due to a broken gate, and thus these marks were excluded from further interpretations. Brushtail possums were detected at orchards MN1, MN2 and TR, with most detections and higher levels of card damage at orchard MN1 (Table S 16). Rodents were detected at orchards MN1, MN2, KC1 and KC2, ranging from low to medium levels of chew card damage. Hedgehogs were detected at all orchards and featured only low levels of damage. Out of 23 orchard x season combinations, five had no mammal detections (Table S 16).

3.3 Discussion

New Zealand is an excellent country to examine primary production systems, with a culture that incentivises innovation, networking, and integration (Campbell et al. 2012). This chapter demonstrated that apple orchards support a variety of bird species. This included common introduced species, native species that are increasingly widespread across New Zealand, and threatened endemic species. Emerging patterns of flocking composition and vertical strata use across species suggest different ecological niches, foraging strategies, and seasonal resource availability.

3.3.1 Species Richness and Community Composition

Across six apple orchards, 20 native and 25 introduced bird species were recorded. The prevalence of introduced species reflects the dominance of generalist, open-habitat birds in New Zealand's modified landscapes. New Zealand has an estimated 206 terrestrial avian breeding species (Miskelly 2025), so the species list recorded for this study corresponds to approximately 22% of New Zealand's terrestrial breeding bird species despite being recorded from only six orchards.

Across all seasons, first-order Jackknife estimates exceeded observed species richness, as expected for non-parametric richness estimators that account for undetected species (Colwell & Coddington 1994; Smith & Pontius 2006). However, the relatively small differences between observed and estimated richness, together with the species accumulation curve approaching an asymptote, suggest the sampling effort was sufficient to capture most species present within the bird community.

There was a larger difference between observed and estimated richness during summer. This reflects the greater number of infrequently detected species during this season, including shining cuckoos, black swans, New Zealand pigeons (*Hemiphaga novaeseelandiae*), and pied shags.

Few studies have reported native bird abundances in New Zealand horticultural systems (Coleman 2010), as research has largely focused on crop-damaging species such as silvereyes (Baker 1980; Davies et al. 2000). In particular, studies that looked at the presence and abundance of bird species in horticultural systems have focused on the kiwifruit industry (Blackwell et al. 2005; Coleman 2010; Shaw et al. 2022). Therefore, the present data contribute new baseline information on avian community composition at apple orchards.

In contrast, introduced species have long been recognised as abundant visitors of rural New Zealand, often at much higher densities than in their native ranges (MacLeod et al. 2009). Their success has been linked to extensive forest loss, the creation of pasture-dominated landscapes and reduced climate extremes, which together provide favourable conditions for grassland and farmland species (Ewers et al. 2006; MacLeod et al. 2009). Several introduced species recorded in this study have experienced population declines in their native ranges (Gillings et al. 2005; Katuwal et al. 2021; Angkaew et al. 2023), but continue to thrive in New Zealand, highlighting the role of land-use change in shaping bird communities.

Most of the species recorded are considered of Least Concern in the categories of extinction risk, including all introduced species. This was expected, as highly disturbed habitats will filter

out more sensitive species (Zielonka et al. 2024). Additionally, many of the endangered bird species in New Zealand can only persist in predator-free and/or heavily predator-controlled areas (Miskelly et al. 2009). Nonetheless, several species of conservation concern were also detected. Black-billed (*Chroicocephalus bulleri*) and red-billed gulls (*Chroicocephalus novaehollandiae scopulinus*), both classified as Near Threatened, were observed at multiple orchards, mostly in flight, with black-billed gulls occasionally roosting and foraging at orchard TR. Gulls are highly opportunistic and often respond to human-altered environments (Schwemmer et al. 2008), but their role in New Zealand horticultural systems remains poorly understood and warrants further study.

A Vulnerable species, the New Zealand falcon, was detected in the Kāpiti region. The presence of falcons is noteworthy given their declines under agricultural intensification (Horikoshi et al. 2017) and their potential use in vineyards as biological control agents (Kross et al. 2012). During the study, Kāpiti Coast growers reported interest in attracting birds of prey into their orchards to control the population of rabbits and birds perceived as 'pests'. This highlights the potential for predator species to influence orchard communities and the importance of incorporating landowners' perspectives into ecological research (Jacobson et al. 2002, 2003; Lazaridou & Michailidis 2023).

Overall, the bird assemblages observed reflected a mixture of widespread introduced generalists and native species capable of persisting in modified landscapes. The presence of both abundant introduced species and native birds of conservation concern demonstrates that apple orchards form part of the habitats used by both widespread and conservation-relevant bird species.

3.3.1.1 Habitat Use and Occupancy

Occupancy models provided little evidence that season influenced the probability of orchard use for any of the 45 species modelled. Most species were best described by intercept-only models, indicating that the tested covariates did not substantially improve model support. Seasonal differences in observed and estimated species richness therefore appear to reflect the detection of a small number of infrequently recorded seasonal visitors rather than widespread seasonal changes in habitat use across the bird community.

Dunnock detection probability declined progressively with increasing temperature. This indicates that dunnock detection was associated with colder temperatures. In winter, dunnocks have been recorded feeding in larger groups and in more open habitats (Birkhead 1981). These factors can lead to the species becoming more conspicuous during this season and thus, easier to detect. However, because the occupancy model identified an effect of temperature rather than season, the mechanisms underlying this relationship remain uncertain.

eastern rosellas, magpies, mallard ducks, paradise shelducks and spur-winged plovers exhibited higher detection probabilities during morning than afternoon surveys. This pattern may reflect diurnal changes in activity or detectability. Explanations for these might reside outside of each species' ecology. Spur-winged plovers, eastern rosellas and magpies can be perceived as crop pests (Baker 1980; Coleman & Spurr 2001). Mallards and paradise shelducks are waterfowl and can be hunted during game bird season (Fish & Game NZ 2025). These factors may make these species more wary of human presence and more likely to avoid

orchards when worker activity is greatest. As the morning surveys were often conducted before workers entered the orchards, these species may have been easier to detect or may have remained in the orchards for longer before disturbance occurred. However, these mechanisms were not tested and are presented only as potential explanations for the observed patterns.

3.3.1.2 Site and Seasonal Variations

Due to the small number of sites and the variety of management practices, there was limited opportunity to detect site-level drivers of variation. Site-level differences were thus kept for descriptive purposes.

The expectation of organic orchard management leading to a higher species richness or abundance was not realised, contrary to previous studies (Blackburn & Arthur 2001; Genghini et al. 2006; MacLeod et al. 2008; Coleman 2010; Winqvist et al. 2012). The Kāpiti Coast orchards were very similar in their community compositions regarding the number of species detected in each, suggesting that their shared surrounding landscape overshadowed potential management drivers. In contrast, orchards TR and HB - large, intensive monocultures - were characterised by high dominance of introduced species. Monocultures reduce habitat heterogeneity (Schlötelburg et al. 2020; Martínez-Núñez et al. 2020b), and such simplified landscapes often support generalist and disturbance-tolerant birds while excluding more sensitive taxa (Kross et al. 2020; Smith et al. 2022b).

Seasonal variation in bird assemblages was modest. Although species richness was highest during summer and lowest during autumn, pairwise comparisons of community composition were not statistically significant after correcting for multiple comparisons. Nonetheless, I found moderate seasonal overlap, indicating that orchard bird communities remained broadly similar throughout the year despite changes in the occurrence and abundance of some species.

Several mechanisms may have contributed to these seasonal patterns. First, seasonal visitors such as shining cuckoos, black swans, kererū and pied shags were recorded only during spring or summer. However, these species were detected infrequently, suggesting that they were occasional rather than consistent components of orchard bird communities. Their seasonal occurrence contributed to higher estimated species richness during spring and summer without substantially altering the composition of the dominant bird assemblage.

Second, seasonal fluctuations in the abundance of common species likely contributed more to temporal variation than turnover in species identity. Silvereyes, for example, were detected throughout the year but exhibited a pronounced increase in abundance during winter, followed by a decline in spring. Winter movements of silvereyes into agricultural landscapes have been reported previously, with large migratory movements documented in parts of the South Island (Grant 1970; Dennison et al. 1981; Wearing & McCarthy 1992). Their subsequent decline in orchards during spring may reflect seasonal shifts in habitat use associated with breeding, as omnivorous birds increase their reliance on invertebrates and may move to habitats offering greater foraging opportunities. Chaffinches, similarly, have also been reported to flock in larger numbers over winter (Sibson 1983).

A similar pattern has been suggested for New Zealand fantails, which use orchards more extensively during winter but rely more heavily on adjacent semi-natural habitats during the breeding season (Steer & Burns 2008; Coleman 2010). Future research incorporating

surrounding forest remnants and other semi-natural habitats would help clarify these seasonal movements.

Overall, the results suggest that seasonal changes in orchard bird communities were driven primarily by fluctuations in the abundance of widespread species and the seasonal occurrence of a small number of infrequent visitors, rather than by major turnover in community composition. This interpretation is consistent with the occupancy analyses, which found no evidence that season influenced habitat use for any of the recorded species.

3.3.2 Flocking Patterns and Use of Vertical Strata

Flocking in birds is maintained by a balance between the benefits, such as predator avoidance and improved foraging, and costs, mainly competition and disease spreading (Thompson et al. 1974; Beauchamp 2021). The relative importance of each factor will depend on a species' ecology and environmental conditions, meaning that there's no universally optimal flocking size (Beauchamp 2002, 2022).

Birds are particularly sensitive to vertical stratification due to their high mobility (Pearson 1971). Although some studies have been conducted on vertical stratification in agricultural systems, they focused on shelterbelts and not crop trees (Yahner 1982). Although crop trees in the current study were relatively short, vertical stratification was still meaningful, with species separating into ground, canopy and aerial foraging guilds.

3.3.2.1 Overhead Foragers

Fantails, tūī, welcome swallows, swamp harriers and rock pigeons were predominantly observed in the overhead layer. Fantails and swallows, both hawking insectivores, were expectedly recorded in flight more often than perched (Heather et al. 2015). Fantails showed diverse use of canopy strata but avoided human structures, while tūī were most frequently observed in middle and upper branches, with occasional medium-sized groups limited to MN2. Swamp harriers, as wide-ranging raptors, were observed almost exclusively in solitary flight, and rock pigeons were recorded only overhead, likely reflecting both their mobility and ongoing shooting pressure within orchards (Coleman & Spurr 2001).

3.3.2.2 Canopy foragers

Silvereyes and house sparrows exemplified small-bodied, disturbance-tolerant species that exploit upper strata within orchards. Silvereyes used all strata but showed a consistent preference for top branches and overhead space, particularly during autumn and winter when flock sizes increased sharply. Their diverse strata use, and large winter aggregations align with previous work suggesting high adaptability to novel vegetation and disturbed environments (Catterall et al. 1989; Waite et al. 2013).

House sparrows have successfully colonised human-modified environments worldwide, even if experiencing population declines on their native range (Peach et al. 2008; Liebl et al. 2015). House sparrows' adaptability to human-managed systems has been linked to their generalist feeding habits, being able to consume a variety of food resources (Sætre et al. 2012). In the

orchards surveyed, house sparrows also formed predominantly small- to medium-sized flocks and used upper strata more frequently in summer and winter, but their primary association with the ground layer reflects their granivorous diet (Southern 1945). Both species demonstrate behavioural flexibility that likely contributes to their ubiquity in horticultural systems.

3.3.2.3 Ground foragers

Blackbirds, pūkeko and song thrushes were strongly associated with the ground layer, consistent with their foraging ecology (Macleod & Till 2007). Blackbirds rarely formed large flocks and occurred mostly as solitary individuals or pairs but were detected in all sites in overall large numbers. Pūkeko, although capable of forming larger groups (Moreno-Opo & Piqué 2018), were observed only in small groups or pairs in orchards. Flock size in pūkeko has been shown to vary according to habitat context, with larger flocks recorded in pastures and swamp habitats (Razalee & Norazlimi 2023). The relatively small groups observed in this study may therefore reflect the particular characteristics of orchard habitats, although human disturbance may also contribute to their flocking behaviour.

Song thrushes, likewise, used the ground most frequently, with limited use of higher strata or human structures. This pattern was consistent with their predominantly ground-based foraging behaviour (Gryczyńska et al. 2024).

3.3.2.4 Finch Assemblages

Chaffinches, goldfinches and greenfinches demonstrated broadly similar flocking patterns, dominated by solitary birds, pairs and small groups, with rare formation of large flocks. All three species used the ground and overhead layers frequently, with limited use of intermediate strata. Goldfinches were the most likely of the finches to use top branches, whereas greenfinches made comparatively greater use of the canopy but avoided human structures, consistent with similar patterns observed in vineyards (Cabodevilla et al. 2021). These patterns highlight the role of orchard ground cover and open canopy structure in supporting widespread granivorous species.

3.3.2.5 Seasonal Flocking

Starlings were the only species to form consistently large flocks over summer, with aggregations of several hundred individuals observed in summer at the Kāpiti orchards. Despite these pronounced seasonal peaks, overall flocking composition showed strong overlap across seasons, with solitary birds, pairs and small groups contributing substantially to ordination structure. The formation of large flocks in summer aligns with international patterns of post-breeding aggregation, where starlings exploit high-energy food resources before dispersing more broadly (Fischl & Caccamise 1985; Whitehead 1995). In New Zealand, older studies had already pointed out that starling's flocking composition is heavily influenced by season. Starlings will gather in larger flocks after breeding, with foraging behaviour being tied to the local availability of seasonal food resources (Coleman 1972).

Importantly, large aggregations of starlings can have functional consequences in agricultural systems. In Canterbury pastures, starlings concentrated their foraging in areas of high grass-grub (*Costelytra zealandica*) density, with predation substantially reducing grass-grub populations under conditions of high starling abundance (East & Pottinger 1975). However, these effects were strongly context-dependent and were not detected at sites supporting fewer starlings. Although the ecological effects of the large flocks observed in the present study were not assessed, their occurrence highlights the potential for starlings to contribute to pest consumption in horticultural systems as well as to recognised crop-related disservices. Further research into their diet and foraging activity within orchards would be required to determine their functional role.

3.3.3 Presence of Exotic Mammals at Apple Orchards

Chew cards provided a descriptive assessment of introduced mammal presence across the surveyed orchards. Interpretation is conservative because the limited replication precluded formal statistical analyses of mammal detections. Nevertheless, brushtail possums, rodents and hedgehogs were recorded across the surveyed orchards, indicating that these introduced mammals were widespread within the surveyed apple production systems. Their occurrence highlights that birds using orchards share these habitats with a range of introduced mammalian species, several of which are recognised predators of native wildlife or competitors for resources (Russell et al. 2015; Murphy et al. 2019).

Cats and rabbits were not detected by chew cards but were recorded opportunistically during bird surveys and by camera traps. Chew cards were designed to detect primarily possum presence (Sweetapple & Nugent 2024), meaning they might not be adequate to assess the occurrence of cats. Their presence in the orchards is still worthy of note, as cats have been recognised as main culprits of bird population declines, especially on islands (Miskelly & Powlesland 2013; Short 2016; Brain & Anderson 2019). Cats would rarely interact with the chew cards; therefore, a species-targeted study of this species would be needed to assess their presence at the orchards and potential interactions with the bird species visiting the systems.

Overall, although mammalian abundance was not quantified, the widespread occurrence of introduced mammals alongside a diverse bird community illustrates that orchard ecosystems support multiple interacting vertebrate taxa. Future studies should investigate how mammalian predators within the orchards are influencing bird habitat use and the potential provision of avian ecosystem services and disservices.

3.3.4 Study Limitations

In this study, human structures were rarely used by the avian species, contrasting with studies from colder climates (Johnson & Glahn 1994; Elser et al. 2019). Edge habitats appeared to support additional species, but observations were insufficient to quantify their contribution. Some bias is possible from first-sighting observations, as birds may have been recorded in flight after disturbance; however, consistent patterns across species suggest that recorded strata use reflects genuine behavioural patterns.

In forested systems, birds often move into denser vegetation during the warmest part of the day to reduce heat stress (Walther 2002). Orchards lack such structural refuges, which may explain why shelterbelts function as microhabitat "coolers" and why diversity tended to be higher at orchard edges than in interior rows (Walther 2002). Previous research from the ARGOS programme in New Zealand kiwifruit orchards identified shelterbelts, neighbouring bush patches and other non-crop habitats as potentially important influences on bird distribution within orchards (Coleman 2010). Although diversity tended to be higher at orchard edges than in interior rows in the present study, these differences were not statistically significant and should therefore be interpreted cautiously. Nevertheless, the observed pattern is consistent with the recognised importance of local habitat and landscape composition in shaping bird communities within New Zealand agricultural landscapes (MacLeod et al. 2008). These findings warrant further investigation across a larger number of apple orchards.

Finally, an important limitation of this study is that the data analysed represent a single year of seasonal variation. As interannual variation in bird abundance and community composition can be expected, particularly in response to variation in climatic conditions and resource availability, it is not possible to determine whether the seasonal patterns observed here would remain consistent across years.

3.4 Conclusions

New Zealand apple orchards supported diverse bird communities, including widespread native species and species of conservation concern, despite the overall dominance of introduced birds. Rather than undergoing major seasonal turnover, orchard bird communities remained relatively consistent throughout the year, with seasonal variation largely reflecting changes in the abundance, flocking behaviour and occurrence of particular species. Species also differed markedly in their use of orchard vertical strata, demonstrating that even the relatively simple structure of apple orchards provides distinct opportunities for ground-, canopy- and aerial-associated birds. These findings show that apple orchards form part of the habitat used by New Zealand birds and provide new baseline information on how native and introduced species use horticultural environments. Their value for biodiversity, however, is likely to depend on interactions among orchard management, surrounding landscape features and the wider ecological community. Broader, multi-year studies are needed to determine how these factors influence bird communities and whether horticultural systems can be managed to better support native biodiversity alongside food production.



MASSEY UNIVERSITY
TE KUNENGA KI PŪREHUROA
UNIVERSITY OF NEW ZEALAND

GRADUATE RESEARCH SCHOOL

STATEMENT OF CONTRIBUTION
DOCTORATE WITH PUBLICATIONS/MANUSCRIPTS

We, the student and the student's main supervisor, certify that all co-authors have consented to their work being included in the thesis and they have accepted the student's contribution as indicated below in the Statement of Originality.			
Student name:	Giuliana Caldeira Pires Ferrari		
Name and title of main supervisor:	Professor Isabel Castro		
In which chapter is the manuscript/published work?	Chapter Four		
Describe the contribution that the student and members of the supervisory team have made to the manuscript/published work:[1] GCPF (student): conceptualization / data curation / formal analysis / funding acquisition / investigation / methodology / visualization / writing (original draft) / writing (review & editing) KM (supervisor): conceptualization / funding acquisition / methodology / investigation / writing (review & editing) AWR (supervisor): conceptualization / formal analysis / methodology / writing (review & editing) IC (main supervisor): conceptualization / formal analysis / investigation / methodology/ writing (review & editing)			
Please select one of the following three options:			
○	**The manuscript/published work is published or in press** Please provide the full reference of the research output:		
○	**The manuscript is currently under review for publication** Please provide the name of the journal:		
◉	**It is intended that the manuscript will be published, but it has not yet been submitted to a journal**		
Student's signature:	Giuliana C. P. Ferrari 2026.01.26 10:17:11 +13'00'	Main supervisor's signature:	Isabel Castro Digitally signed by Isabel Castro Date: 2026.01.28 11:36:57 +13'00'
This form should be placed at the beginning of each relevant thesis chapter.			

[1] Refer to the Massey University Publishing and Authorship guidelines (OneMassey for staff, Stream for students) and/ or Contributor Roles Taxonomy (CRediT) guidelines for guidance.

Chapter 4 Avian Behaviours in New Zealand Apple Orchards

4.1 Abstract

Birds can contribute to both beneficial and detrimental ecological processes in horticultural systems, but functional traits alone provide limited information about how species impact crops. Direct behavioural observations can therefore provide important insights into how birds use agricultural habitats and how their potential roles vary through time. This chapter investigated the behaviour and feeding ecology of native birds across six apple orchards in New Zealand, with particular emphasis on seasonal variation. Native birds were followed for up to five minutes, with behaviours recorded at 10-second intervals and classified into nine behavioural categories. Behavioural patterns were analysed for ten sufficiently widespread native species using generalised linear mixed models, although sparse data restricted statistical inference to six species. Direct feeding observations were used to characterise food use, with seasonal changes in silvereye (*Zosterops lateralis*) feeding analysed separately. Foraging and flying were the most frequently recorded behaviours across the native species examined, although behavioural patterns differed among species. Silvereyes were the only species for which the best-supported model included an interaction between behaviour and season, indicating seasonal variation in behavioural composition, whereas simpler behavioural models were supported for the remaining species. Species-specific observations also revealed distinctive patterns including aerial foraging by New Zealand fantails (*Rhipidura fuliginosa*) and welcome swallows (*Hirundo neoxena*), ground foraging by pūkeko (*Porphyrio melanotus*), and territorial behaviour by tūī (*Prosthemadera novaeseelandiae*). Direct feeding observations revealed seasonal variation in resource use by silvereyes. Silvereyes accounted for most recorded fruit consumption and also consumed arthropods, fallen fruit and flowers, with the relative use of these resources changing among seasons. Overall, native birds used apple orchards predominantly for foraging-related activities, while species-specific and seasonal patterns demonstrated that broad functional classifications alone do not fully describe bird-crop interactions. In particular, the diverse feeding behaviour of silvereyes illustrates how a single species may have the potential to contribute to both beneficial and detrimental processes within orchards. These findings provide a behavioural basis for identifying bird-crop interactions that warrant direct experimental assessment before their net effects on orchard production can be determined.

4.2 Introduction

Increasing attention is being paid to the conservation of native species in agro-ecosystems, as balancing agricultural productivity with the protection of threatened biodiversity remains an urgent global challenge. Birds are an excellent model group for targeting conservation in human-managed lands. They are easy to identify and generally well-known in terms of their ecology and behaviour (Genghini et al. 2006; Mirski et al. 2024), making them reliable bioindicators of ecosystem health in agricultural systems (Whelan et al. 2015).

Furthermore, the interactions between birds and humans, including their benefits and damages, have been studied and recognised for over a century (Whelan et al. 2008; Kronenberg 2014; Bonhomme 2021). Much has been discussed regarding the potential provision of ecosystem services and disservices by avian species in horticulture (Ferrari et al. 2025; Chapter 2).

Although ecosystem services and disservices provided by birds are closely linked to the foraging behaviours, detailed behavioural studies in horticultural systems remain relatively uncommon, particularly at the species level (Whelan et al. 2008).

Studies in perennial crops have demonstrated that bird communities and their functional composition vary among crop types, with apple orchards and vineyards supporting distinct assemblages of birds with different potential ecological roles (Luck et al. 2015; Katayama et al. 2022). However, functional classifications alone do not establish how birds interact with crops. Direct behavioural observations in vineyards have demonstrated that foraging activity can determine the spatial distribution of crop damage, with starling movements and feeding behaviour influencing patterns of grape consumption (Somers & Morris 2002).

Functional traits such as diet, body size and foraging strategy can provide useful proxies for the potential ecological functions performed by birds. However, the ecological function inferred from traits does not necessarily correspond to the realised effect of a species within a particular crop, and conclusions may depend on the traits selected (Philpott et al. 2009; Hordley et al. 2021).

Birds' foraging behaviour reflects a trade-off between foraging efficiency and the risks of starvation and predation (Bednekoff & Krebs 1995; Macleod et al. 2005; Quinn et al. 2012). Fruit orchards can therefore serve as valuable refuges for food resources within an agricultural matrix, providing a multi-strata habitat with vertical tree structures and a grassy ground cover (Simon et al. 2010). Nonetheless, birds that are present in these systems must adapt to high levels of anthropogenic disturbance, including irrigation methods, use of heavy machinery and pesticides, and artificial rows (Tscharntke et al. 2012; Zielonka et al. 2024; Peria & Francis 2025).

The impermanent nature of horticultural habitats, including crop rotations and regular tree pruning, and the overall impermanence of horticultural habitats can lead to changes in the foraging habits of wild birds (Wilson et al. 2005). These can reduce nesting success, which can disrupt site fidelity behaviours (Best et al. 1995). Furthermore, the openness of orchard environments can lead to high nest mortality (Mitchell et al. 2015). Behavioural changes are often the first response of wild animals to environmental change, but most studies on land use change focus only on changes in species occurrence and abundance (Ke et al. 2024). Variation in bird behaviour and community composition across landscapes (Mihai et al. 2017; Ke et al. 2024) highlights the importance of studying how bird visitors use horticultural systems to assess their ecosystem services and disservices.

Finally, bird behaviour and their potential consequences for crops are also expected to vary seasonally following the intrinsic seasonality of the crop system. Additionally, changes in breeding activity, energy requirements and resource availability can alter both bird activity and their diet. This means that a species' functional role within the system may change throughout the year (Smith et al. 2022b).

In this chapter, I investigated the typical behaviours of native avian visitors to New Zealand apple orchards. I predicted that behavioural composition would vary among seasons, reflecting seasonal changes in resource availability and bird energetic and reproductive requirements. Furthermore, I expected that native birds would use orchards predominantly for foraging-related activities. Finally, I also examined the feeding behaviours of native species, trying to assess how the consumption of different food resources varied across seasons.

4.3 Methods

4.3.1 Study Area

The study was conducted across six apple orchards in four New Zealand regions: Manawatū, Lower North Island (two orchards), Kāpiti Coast, Lower North Island (two orchards), Hawke's Bay, Eastern North Island (one orchard), and Tasman District, Northwest South Island (one orchard). Orchard size varied significantly, and management practices included research purposes, organic practices, and conventional or industrial practices as shown in the previous chapter (Table 3.1).

4.3.2 Categorising Behaviours

Behaviours were recorded by direct observation using binoculars (Nikon Monarch M511, 10x42 magnification) during each visit to an orchard as part of the abundance surveys (Chapter Four). Native birds were followed for up to five minutes to obtain more detailed behavioural observations. Behaviours of native species were recorded every 10 seconds, dictated on a Sony Digital Voice Recorder, to allow quick recording of data for later transcription into an Excel sheet.

Behaviours were distinguished into nine categories: foraging (hawking and gleaning by insectivorous birds, diving by carnivorous birds, and pecking and rummaging by omnivores); flying, hopping (on the ground or between branches); interacting with observer (following the researcher in the case of the New Zealand fantail (*Rhipidura fuliginosa*), and flying or running away for other species); perching or roosting, preening (as an individual action); social behaviours (pair preening, feeding mates or fledglings, gathering nest material); territorial behaviours (chasing away conspecifics); and vocalising.

Behavioural data were compiled for all native bird species recorded across surveys; however, only 10 of the 22 species had sufficient observations (in at least three of the six sites surveyed) for inclusion in behavioural analyses: silvereye (*Zosterops lateralis*), fantail, pūkeko (*Porphyrio melanotus melanotus*), tūī (*Prosthemadera novaeseelandiae*), welcome swallow (*Hirundo neoxena*), swamp harrier (*Circus approximans*), New Zealand sacred kingfisher (*Todiramphus sanctus*), black-backed gull (*Larus dominicanus*), grey warbler (*Gerygone igata*), and paradise shelduck (*Tadorna variegata*).

4.3.3 Feeding Behaviours of Selected Native Species

During the behavioural observations of native birds, I recorded plant or animal items being consumed where visible. Visits to the crops were noted if feeding was done on fruits still on the trees, fruits left on the ground, or on flowers. Prey capture manoeuvres helped identify events of invertebrate predation, and were categorised as gleaning (a standing or moving bird picks a stationary prey item from a substrate); probing (the bird manipulates the substrate by pecking or rummaging); hovering (a bird captures prey from substrate while in stationary flight); chasing or diving (a bird pursues prey, often in a downward flight); and hawking (the bird attacks flying insects around the foliage) (Thiollay 1988; Castro 1996). Silvereyes had 497 feeding observations, allowing testing for seasonal changes and the types of food consumed. Fruit consumption by other species, including introduced species, was kept for descriptive purposes only.

4.3.4 Statistical Analysis

4.3.4.1 Native Species Behaviours

To evaluate variation in the behavioural activity within native species across a potential seasonal and spatial gradient, I fitted a series of candidate generalised linear mixed models (GLMMs) with a negative binomial error structure to accommodate overdispersion in the count data. GLMMs were constructed using the *glmmTMB* package on RStudio (Brooks et al. 2017).

For each of the ten species included in this analysis, an information-theoretic approach included five models in decreasing order of complexity, starting with a model testing all behaviour and season interactions, a model with only the main effects of behaviour and season, a model accounting only for behaviour, a model accounting only for season, and a null model with an intercept only. Due to the relatively low number of observations within each category, orchard was fitted as a random effect for all models. Behaviour and season were treated as fixed effects. An offset term (log(total observations per orchard x season)) was incorporated to standardise behavioural counts by sampling effort.

For each species, model selection followed a two-step approach. Firstly, models were ranked using Akaike's Information Criterion (AIC) values. Secondly, all competing models were tested on model diagnostics using the *DHARMa* package (Hartig 2025). Model convergence was assessed using both the optimiser convergence code and the positive-definite Hessian test (pdHess). Models were also tested for overdispersion and zero-inflation, residual uniformity, and outliers (Table S 17).

Only models that converged, had positive-definite Hessians, and passed all DHARMa diagnostic tests were considered valid candidates for inference. Models showing severe overdispersion, unstable positive-definite Hessians, or failed convergence were discarded even if ranked highly by AIC values. Therefore, species included in the dataset were retained for behavioural modelling only when 1. there was a clear AIC-supported model with a valid structure; and 2. diagnostic tests indicated acceptable convergence, residual uniformity, and an absence of overdispersion, lack of uniformity, and Hessian instability.

For the GLMMs of native species behaviour, pairwise comparisons were conducted using estimated marginal means (EMMs) derived from the fitted models. For silvereye feeding behaviour, EMMs were calculated on the response scale for each food type within each season using the *emmeans* package in R (Lenth et al. 2018), with Tukey's adjustment applied to control for multiple comparisons. Predictions were standardised by setting the model offset to zero, corresponding to one total feeding observation. To evaluate seasonal variation in food use, pairwise comparisons among seasons were conducted separately within each food type, with Tukey's adjustment applied to account for multiple comparisons. Model-estimated relative feeding frequencies and associated 95% confidence intervals were used to visualise seasonal patterns in food use.

4.3.4.2 Feeding behaviour

Analysis of the feeding behaviour of silvereyes considered all food consumption recorded during observations: fruits, fallen fruits, flowers, and arthropods. Feeding observations were analysed using generalised linear mixed models (GLMMs) with a negative binomial error distribution using the *glmmTMB* package on RStudio (Brooks et al. 2017). The response variable was the number of observations recorded for each food type (arthropod, fruit, fallen

fruit and flower) within each orchard x season combination. Food type and season (autumn, winter, spring and summer) were treated as categorical fixed effects, while orchard was included as a random effect to account for repeated observations within orchards.

To account for differences in the total number of feeding observations among orchard x season combinations, an offset was included in all models, defined as the natural logarithm of the total number of feeding observations recorded within each orchard x season combination. This allowed models to assess variation in the relative frequency of different food types rather than differences arising from variation in the overall number of feeding observations. Orchard x season combinations with no feeding observations were excluded because relative food use could not be estimated, whereas zero observations for individual food types within otherwise sampled orchard x season combinations were retained.

Four candidate models were fitted for silvereyes: an interaction between food type and season; additive effects of food type and season; food type only; and an intercept-only null model. Orchard was retained as a random effect and the offset was included in all candidate models. Models were ranked using Akaike's Information Criterion (AIC), ΔAIC and AIC weights. Model convergence and identifiability were assessed using optimiser convergence codes and positive-definite Hessian diagnostics (pdHess). Residual diagnostics were evaluated using the *DHARMa* package (Hartig 2025), including tests for dispersion, zero inflation, residual uniformity and outliers. The diagnostically acceptable model with the greatest AIC support was retained for inference.

4.4 Results

4.4.1 Native Species Behaviours

From the 22 native species observed across the study, ten species were assessed for patterns in their behaviours, as they were observed in at least three of the six sites surveyed, and in at least one season. However, GLMMs could not be generated for black-backed gulls, paradise shelducks, swamp harriers and kingfishers due to a lack of observations across multiple categories of behaviours.

Species assessed included two omnivores (silvereyes and pūkeko), three insectivores (New Zealand fantails, grey warblers, and welcome swallows), and a nectarivore, the tūī. Most observations recorded were of birds foraging and flying (Table 4.1). The least recorded behaviours were territorial behaviours and preening. Interacting with the observer was recorded almost exclusively for fantails and pūkeko.

Using an information-theoretic approach to construct the GLMMs, the best models for each species were categorised into three types: (1) full interactions of behaviour and season, (2) additive (main) effects of behaviour and season, and (3) behaviour only (Table 4.2). The GLMM outputs revealed species-specific behavioural patterns across seasons, which are presented in detail in the following sections. Except for silvereyes, behavioural patterns were summarised across all seasons.

Table 4.1. Summary statistics for behaviours recorded for 10 native bird species during behavioural surveys. Species were followed for a maximum of five minutes, when possible. Total observations represent the total number of records for each species x behaviour category across the 23 surveyed orchard x season combinations. Mean represents the mean number of observations of each behaviour per orchard x season combination, with standard deviation (SD) and standard error (SE) calculated across combinations. Behaviours were categorised as foraging (behaviours associated with different feeding habits, such as hawking and gleaning by insectivorous birds, diving by carnivorous birds, and pecking and rummaging by omnivores); flying; hopping (on the ground or between branches); interacting with the observer (following the researcher in the case of New Zealand fantails, and flying or running away for other species); perching or roosting; preening (as an individual action); social behaviours (pair preening, feeding partners or fledglings, and gathering nest material); territorial behaviours (chasing conspecifics); and vocalising. Species included: black-backed gull (Larus dominicanus), New Zealand fantail (Rhipidura fuliginosa), grey warbler (Gerygone igata), sacred kingfisher (Todiramphus sanctus), paradise shelduck (Tadorna variegata), pūkeko (Porphyrio melanotus melanotus), silvereye (Zosterops lateralis), swamp harrier (Circus approximans), tūī (Prosthemadera novaeseelandiae), welcome swallow (Hirundo neoxena).

Species	By Behaviour	Total Observations	Mean	SD	SE
black-backed gull	flying	46	2	4.95	1.03
	foraging	4	0.17	0.58	0.12
	hopping	0	0	0	0
	interacting with observer	0	0	0	0
	perching	6	0.26	0.86	0.18
	preening	0	0	0	0
	social	0	0	0	0
	territorial	0	0	0	0
	vocalising	2	0.09	0.29	0.06
grey warbler	flying	9	0.39	1.12	0.23
	foraging	8	0.35	1.11	0.23
	hopping	6	0.26	0.86	0.18
	interacting with observer	0	0	0	0
	perching	5	0.22	0.52	0.11
	preening	0	0	0	0
	social	0	0	0	0
	territorial	0	0	0	0
	vocalising	2	0.09	0.42	0.09
New Zealand fantail	flying	159	6.91	5.68	1.18
	foraging	225	9.78	10.42	2.17
	hopping	45	1.96	2.23	0.46
	interacting with observer	11	0.48	0.95	0.2
	perching	105	4.57	4.96	1.03
	preening	10	0.43	0.95	0.2
	social	23	1	1.51	0.31
	territorial	15	0.65	1.11	0.23
	vocalising	87	3.78	2.81	0.59

Species	By Behaviour	Total Observations	Mean	SD	SE
paradise shelduck	flying	16	0.7	1.11	0.23
	foraging	11	0.48	1.08	0.23
	hopping	0	0	0	0
	interacting with observer	0	0	0	0
	perching	0	0	0	0
	preening	3	0.13	0.46	0.1
	social	1	0.04	0.21	0.04
	territorial	0	0	0	0
	vocalising	14	0.61	1.59	0.33
pūkeko	flying	37	1.61	2.25	0.47
	foraging	254	11.04	16.34	3.41
	hopping	2	0.09	0.29	0.06
	interacting with observer	70	3.04	3.14	0.65
	perching	23	1	1.88	0.39
	preening	7	0.3	0.63	0.13
	social	23	1	1.71	0.36
	territorial	3	0.13	0.46	0.1
	vocalising	15	0.65	1.03	0.21
sacred kingfisher	flying	16	0.7	0.97	0.2
	foraging	3	0.13	0.46	0.1
	hopping	0	0	0	0
	interacting with observer	0	0	0	0
	perching	13	0.57	0.9	0.19
	preening	0	0	0	0
	social	3	0.13	0.46	0.1
	territorial	0	0	0	0
	vocalising	32	1.39	1.83	0.38
silvereye	flying	602	26.17	26.53	5.53
	foraging	542	23.57	27.86	5.81
	hopping	94	4.09	4.93	1.03
	interacting with observer	2	0.09	0.29	0.06
	perching	190	8.26	8.34	1.74
	preening	37	1.61	2.35	0.49
	social	58	2.52	4.81	1
	territorial	36	1.57	2.39	0.5
	vocalising	108	4.7	4.4	0.92

Species	By Behaviour	Total Observations	Mean	SD	SE
swamp harrier	flying	63	2.74	2.14	0.45
	foraging	86	3.74	4.07	0.85
	hopping	0	0	0	0
	interacting with observer	0	0	0	0
	perching	11	0.48	0.85	0.18
	preening	0	0	0	0
	social	0	0	0	0
	territorial	0	0	0	0
	vocalising	0	0	0	0
tūī	flying	86	3.74	7.57	1.58
	foraging	100	4.35	11.27	2.35
	hopping	28	1.22	3.410	0.710
	interacting with observer	0	0	0.000	0.000
	perching	30	1.3	2.950	0.610
	preening	6	0.26	0.920	0.190
	social	14	0.61	2.500	0.520
	territorial	13	0.57	1.56	0.33
	vocalising	56	2.43	4.44	0.93
welcome swallow	flying	56	2.43	3.33	0.69
	foraging	34	1.48	1.81	0.38
	hopping	0	0	0	0
	interacting with observer	0	0	0	0
	perching	4	0.17	0.39	0.08
	preening	0	0	0	0
	social	0	0	0	0
	territorial	0	0	0	0
	vocalising	0	0	0	0

Table 4.2. Akaike's Information Criterion (AIC) model selection results for generalised linear mixed models (GLMMs) examining the variation in the observation of different behaviour categories for 10 native species. Candidate models included the full interactions between behaviour and season, main effects only, behaviour only, season only, and a null model. Models were compared using the number of estimated parameters (k), AIC values, ΔAIC values, and Akaike weights. Models for black-backed gulls, paradise shelducks, swamp harriers and kingfishers did not converge properly, had unstable Hessian values, and/or were too sparse to be properly calculated. These species were thus removed from further analysis. For grey warblers, tūī, and welcome swallows, an unbalanced combination of behaviour-season observations led to ΔAIC and AIC weight values not being calculated, but the models were kept for inference as they converged and passed further diagnostic tests. Models kept for inference for each species are highlighted in bold. Species included: black-backed gull (Larus dominicanus), New Zealand fantail (Rhipidura fuliginosa), grey warbler (Gerygone igata), sacred kingfisher (Todiramphus sanctus), paradise shelduck (Tadorna variegata), pūkeko (Porphyrio melanotus melanotus), silvereye (Zosterops lateralis), swamp harrier (Circus approximans), tūī (Prosthemadera novaeseelandiae), welcome swallow (Hirundo neoxena).

Species	Model	k	AIC	ΔAIC	Weight
black-backed gull					
	Behaviour x Season	38	NA	NA	NA
	Behaviour + Season	14	NA	NA	NA
	Behaviour Only	11	66.689	NA	NA
	Season Only	6	118.062	NA	NA
	Null Model	3	112.06	NA	NA
New Zealand fantail					
	Behaviour x Season	38	639.005	21.326	2.23E-05
	Behaviour + Season	14	623.679	6.000	0.047
	Behaviour Only	**11**	**617.679**	**0**	**0.953**
	Season Only	6	845.621	227.942	3.03E-50
	Null Model	3	839.62	221.942	6.09375E-49
grey warbler					
	Behaviour x Season	38	NA	NA	NA
	Behaviour + Season	**14**	**98.194**	**NA**	**NA**
	Behaviour Only	11	NA	NA	NA
	Season Only	6	112.948	NA	NA
	Null Model	3	106.948	NA	NA
kingfisher					
	Behaviour x Season	38	NA	NA	NA
	Behaviour + Season	14	179.232	NA	NA
	Behaviour Only	11	NA	NA	NA
	Season Only	6	254.161	NA	NA
	Null Model	3	248.161	NA	NA
paradise shelduck					
	Behaviour x Season	29	NA	NA	NA
	Behaviour + Season	13	NA	NA	NA
	Behaviour Only	11	NA	NA	NA
	Season Only	5	158.178	NA	NA
	Null Model	3	154.178	NA	NA

Species	Model	k	AIC	ΔAIC	Weight
pūkeko					
	Behaviour x Season	38	488.337	24.423	4.61E-06
	Behaviour + Season	14	469.014	5.100	0.072
	Behaviour Only	**11**	**463.914**	**0.000**	**0.928**
	Season Only	6	596.036	132.122	1.89E-29
	Null Model	3	590.036	126.122	3.80E-28
silvereye					
	Behaviour x Season	**38**	**803.285**	**0**	**0.925**
	Behaviour + Season	14	814.336	11.051	0.004
	Behaviour Only	11	808.414	5.129	0.071
	Season Only	6	1094.969	291.684	4.24E-64
	Null Model	3	1088.969	285.684	8.52E-63
swamp harrier					
	Behaviour x Season	38	220.639	NA	NA
	Behaviour + Season	14	186.877	NA	NA
	Behaviour Only	11	NA	NA	NA
	Season Only	6	380.156	NA	NA
	Null Model	3	374.156	NA	NA
tūī					
	Behaviour x Season	38	NA	NA	NA
	Behaviour + Season	**14**	**277.554**	**NA**	**NA**
	Behaviour Only	11	NA	NA	NA
	Season Only	6	338.265	NA	NA
	Null Model	3	332.265	NA	NA
welcome swallow					
	Behaviour x Season	38	203.693	NA	NA
	Behaviour + Season	14	NA	NA	NA
	Behaviour Only	**11**	**158.845**	**NA**	**NA**
	Season Only	6	273.031	NA	NA
	Null Model	3	267.031	NA	NA

4.4.1.1 Behaviour x Season Model (silvereyes)

Silvereyes were the most abundant species across orchards (Chapter Three), with hundreds of observations within different categorised behaviours. The species was the only one for which the full interaction model of behaviour-season was retained for inference.

The behavioural patterns of silvereyes were remarkably consistent across all orchards, with flying dominating their activity patterns across all seasons (Figure 4.1, Table S 18). Foraging was the second most observed behaviour, tied closely to flying except for the summer season (Wald test, estimate = 0.307 ± 0.09, z = -4, $p < 0.005$; Table S 19). These results suggest that movements within the orchard are closely tied to searching for food rather than other activities. Compared to flying and foraging, most other behaviours (such as hopping, perching, preening, vocalising, social interactions and territorial displays) were recorded far less frequently (Table S 19). Vocalising was observed more strongly in summer compared to other seasons (Table S 18). Interactions with the observer were extremely rare.

4.4.1.2 Behaviour + Season Model (grey warblers, tūī)

Behavioural patterns of grey warblers were consistent across sites, with most behaviours recorded at very low frequencies (Table 4.1). Because of these low frequencies, estimates from Wald tests and EMM contrasts were non-informative (Table S 20; Table S 21). Flying and foraging were the most observed behaviours for the species, with no significant differences among behaviours (Figure 4.2).

Tūī were observed across all behavioural categories, except interacting with the researcher (Table 4.1). Flying and foraging were the most observed behaviours, with all other categories recorded far less frequently (Figure 4.2). Vocalising behaviours were far more common than other social (Wald test, estimate = 6.199 ± 2.67, z = 4.22, $p < 0.001$) and territorial behaviours (= 6.06 ± 2.57, z = 4.25, $p < 0.001$).

4.4.1.3 Behaviour Only Model (fantails, pūkeko, welcome swallows)

Behavioural patterns of New Zealand fantails remained consistent across sites. Due to the characteristic insectivore behaviour of hawking and gleaning, it was easier for the observer to distinguish foraging activities from flying for other purposes. Foraging was significantly more frequently observed than other behaviours (Table S 20). Other commonly observed behaviours were flying and perching (Figure 4.3). The species was observed interacting with the observer, namely following them along the transects, at a low frequency (Table S 20). Nonetheless, these interactions were observed significantly more frequently than preening and perching behaviours (Table S 21).

Like fantails, pūkeko were most often observed foraging (Figure 4.3). All other behaviours were recorded less frequently (Table S 20). Interactions with the observer constituted the second most frequently recorded behavioural category (Figure 4.3). Pūkeko, together with fantails, were the only species for which interactions with the observer were recorded. Pūkeko-observer interactions primarily involved avoidance behaviours, such as moving away from the observer.

Only flying, foraging and perching were recorded for welcome swallows (Table 4.1). Flying was significantly more frequently observed than foraging and perching (Table S 20). The lack

of observations for other categories led to a majority of uninformative pairwise contrasts (Table S 21). Overall, flying was observed more frequently than foraging (Wald test, estimate = -1.014 ± 0.17, z = -5.77, $p < 0.05$), and perching was observed at a significantly lower ratio (Figure 4.3).

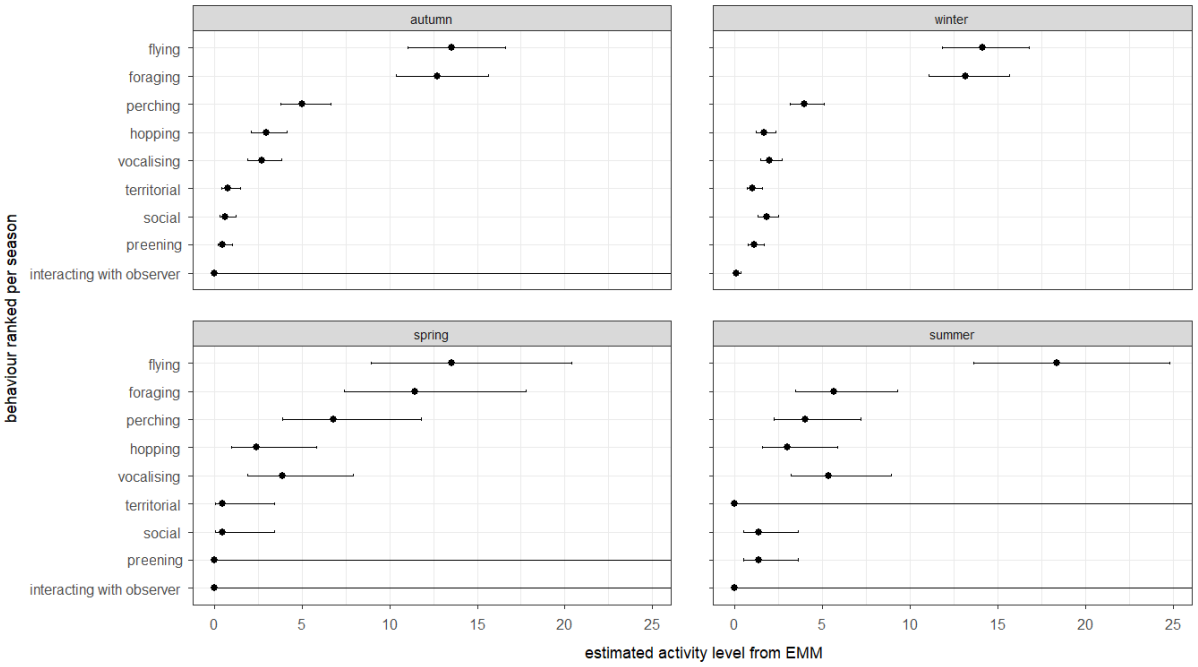


Figure 4.1. Estimated marginal means (EMMs) of behavioural observations for silvereyes (Zosterops lateralis) based on a generalised linear mixed model (GLMM) accounting for the interactions of behaviours and season. Orchard was kept as a random effect. EMMs represent estimated behavioural responses for each behaviour x season combination, with error bars indicating 95% confidence intervals. Behaviour categories were distinguished as flying; foraging; perching; hopping; vocalising; territorial behaviours; social behaviours; preening; and interacting with the observer. Extremely large confidence intervals indicate cases of near zero or zero observations.

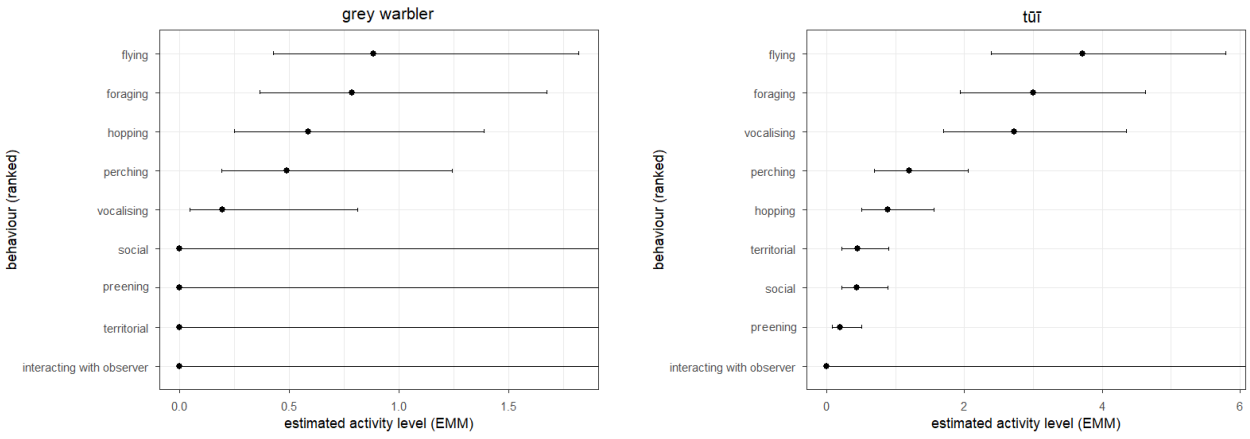


Figure 4.2. Estimated marginal means (EMMs) of behavioural observations for grey warblers (Gerygone igata) and tūī (Prosthemadera novaeseelandiae) based on a generalised linear mixed model (GLMM) accounting for the main effects of behaviours and season. Orchard was kept as a random effect. EMMs represent estimated behavioural responses averaged across seasons, with error bars indicating 95% confidence intervals. Behaviour categories were distinguished as flying; foraging; perching; hopping; vocalising; territorial behaviours; social behaviours; preening; and interacting with the observer. Extremely large confidence intervals indicate cases of near zero or zero observations.

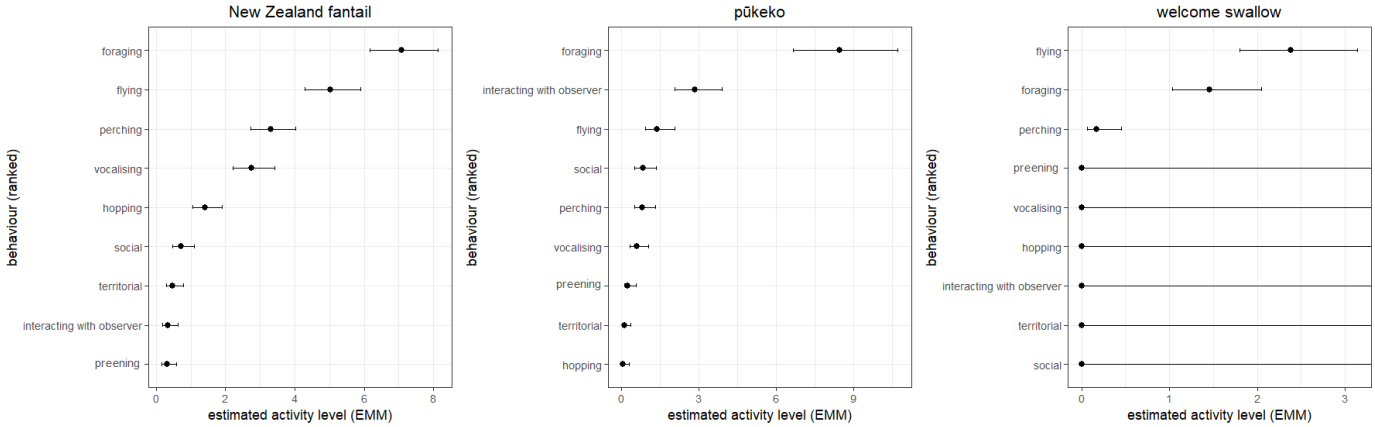


Figure 4.3. Estimated marginal means (EMMs) of behavioural observations for fantails (Rhipidura fuliginosa), pūkeko (Porphyrio melanotus melanotus) and welcome swallows (Hirundo neoxena). EMMs were calculated from a generalised linear mixed model (GLMM) accounting for only behaviour as the best model kept for inference. Orchard was kept as a random effect. EMMs represent estimated behavioural responses averaged across seasons, with error bars indicating 95% confidence intervals. Behaviour categories were distinguished as flying; foraging; perching; hopping; vocalising; territorial behaviours; social behaviours; preening; and interacting with the observer. Extremely large confidence intervals indicate cases of near zero or zero observations.

4.4.2 Feeding Behaviours

Foraging behaviours were observed for 10 native and 15 introduced species (from the 22 and 24 species recorded across sites, respectively). However, observations of direct food consumption (Table 4.3) were less frequent, as predation events on small invertebrates or the quick diving of carnivores into far sections of the orchard could be missed when attempting to observe all bird species within the site with a pair of binoculars. Fruit crop consumption was recorded for eleven bird species (Table S 22). These eleven species can be grouped into generalist omnivores (silvereyes, blackbirds, pūkeko, house sparrows, starlings, eastern rosellas and song thrushes), granivores (chaffinches, goldfinches and greenfinches), and a nectarivore (tūī). Most species had <5 recorded feeding events on fruits (Table S 22). Silvereyes accounted for 334 of the 385 observations of fruit consumption.

Across different fruit types, silvereyes, tūī, pūkeko, chaffinches and greenfinches were observed consuming apples still on the trees, while consumption of apples on the ground was recorded for silvereyes, blackbirds, chaffinches, greenfinches, goldfinches, starlings and house sparrows. Other fruit crops, including kiwi-fruit, pears, oranges and feijoas were consumed by silvereyes, blackbirds, eastern rosellas and song thrushes. Blackbirds and song thrushes were more often seen feeding on fallen apples. Across the orchards surveyed, tūī almost exclusively consumed fruit crops, always still on the trees. Silvereyes and blackbirds were the only species observed feeding on other fruits on the ground (Table S 22). Overall, fruit consumption observations were sporadic and did not allow discerning potential patterns of food choice.

The exception was for silvereyes. The model containing the interaction between food type and season received overwhelming AIC support, and showed no evidence of residual non-uniformity, overdispersion, excessive zero inflation or problematic outlier (Table 4.4). This analysis indicates that silvereyes shifted their feeding behaviour across seasons, with arthropod feeding significantly higher in summer than autumn, while the relative frequency of other food types also varied across seasons.

Silvereye food use varied markedly among seasons (Table 4.5A). Fruit consumption was tied to seasonal differences, with lower relative fruit feeding in winter (β = -1.41 ± 0.47 SE, z = -3.02, $p < 0.05$) and summer (β = -3.74 ± 1.14 SE, z = -3.27, $p < 0.05$) relative to autumn. Several coefficients associated with zero, or very sparse, food x season combinations that had extremely large standard errors were not interpreted.

Seasonal patterns in feeding reflected shifts in the food resources used by birds across the year (Table 4.5B; Figure 4.4). Arthropod consumption increased from autumn to summer, with fitted relative frequency rising from 0.24 ± 0.06 SE to 0.95 ± 0.34. In contrast, fruit consumption was highest in autumn (0.65 ± 0.14) and declined in winter (0.23 ± 0.05), while feeding on fallen fruit showed the opposite pattern, increasing from autumn (0.11 ± 0.03) to winter (0.42 ± 0.09). Flower feeding events were less common, and concentrated in spring, when its fitted relative frequency reached 0.58 ± 0.24.

Pairwise comparisons supported these seasonal shifts in feeding (Table 4.5C). Arthropod feeding was significantly more frequent in summer than autumn, while fruit feeding was more frequent in autumn than winter. Conversely, feeding on fallen fruit was more frequent in winter than autumn, and flower feeding was more frequent in spring than winter (all $p < 0.05$). No other reliably estimable seasonal comparisons were significant.

Table 4.3. Seasonal composition of 497 feeding observations for silvereyes (Zosterops lateralis) in apple orchards. Observations represent the number of feeding events recorded for each food type (arthropods, fruits, fallen fruits, and flowers) within each season, from autumn 2024 to summer 2025. Total season observations represent the total number of feeding events recorded across all food types within that season, and percentages represent the proportion of these observations attributed to each food type.

Season	Food Type	Observations	Total Season Observations	Percentage (%)
autumn	arthropod	39	158	24.68
	fruit	101	158	63.92
	fallen fruit	18	158	11.39
	flower	0	158	0
winter	arthropod	103	306	33.66
	fruit	73	306	23.86
	fallen fruit	129	306	42.16
	flower	1	306	0.33
spring	arthropod	6	17	35.29
	fruit	0	17	0
	fallen fruit	1	17	5.88
	flower	10	17	58.82
summer	arthropod	15	16	93.8
	fruit	1	16	6.25
	fallen fruit	0	16	0
	flower	0	16	0

Table 4.4. Model selection and diagnostic results for generalised linear mixed models (GLMMs) examining seasonal variation in food use by silvereyes (Zosterops lateralis). Candidate models included the interaction between food type and season, additive effects of food type and season, food type only, and an intercept-only model (Null). All models used a negative binomial error distribution, included orchard as a random effect, and incorporated the logarithm of total feeding observations per orchard x season as an offset. Models were compared using Akaike's Information Criterion (AIC), ΔAIC and AIC weights. Model validity was assessed using positive-definite Hessian status (pdHess) and DHARMa tests of residual uniformity, dispersion, zero inflation and outliers; values reported for DHARMa diagnostics are p-values. The model retained for inference is shown in bold.

Model	AIC	DeltaAIC	AIC Weight	pdHess	Uniformity	Dispersion	ZeroInflation	Outliers
Food Type x Season	**304.449**	**0**	**1**	**TRUE**	**0.992**	**0.69**	**0.86**	**1**
Food Type Only	367.245	62.797	2.31E-14	TRUE	0.522	0.19	0.286	0.14
Food Type + Season	369.430	64.981	7.75E-15	TRUE	0.876	0.21	0.336	1
Null	376.612	72.164	2.13E-16	TRUE	0.458	0.246	0.522	1

Table 4.5. Model estimates and post-hoc comparisons from the best-supported model of seasonal variation in silvereye (Zosterops lateralis) feeding observations. (A) Parameter estimates from the negative binomial generalised linear mixed model including food type, season and their interaction as fixed effects, orchard as a random effect, and the logarithm of total feeding observations per orchard x season as an offset. The intercept represents the expected log observation rate at the reference levels (arthropod and autumn for food type and season, respectively). (B) Estimated marginal means on the response scale with standard errors and 95% confidence intervals. Estimates were standardised by setting the model offset to zero. (C) Pairwise seasonal comparisons within each food type derived from estimated marginal means, with p-values adjusted for multiple comparisons using the Tukey method. Ratios greater than one indicate a higher fitted relative frequency in the first season of the contrast. Asterisks indicate $p < 0.05$.

A. GLMM Output	term	estimate	Std. Error	z value	p value	
	(Intercept)	-1.420	0.261	-5.432	5.59E-08	*
	feedingfruit	0.990	0.341	2.898	3.75E-03	*
	feedingfallen fruit	-0.798	0.408	-1.958	5.02E-02	
	feedingflower	-21.798	8757.860	-0.002	9.98E-01	
	seasonwinter	0.374	0.341	1.095	2.73E-01	
	seasonspring	0.387	0.553	0.699	4.85E-01	
	seasonsummer	1.369	4.40E-01	3.11E+00	1.84E-03	*
	feedingfruit:seasonwinter	-1.406	0.465	-3.021	2.52E-03	*
	feedingfallen fruit:seasonwinter	0.972	0.510	1.904	5.69E-02	
	feedingflower:seasonwinter	17.111	8757.860	0.002	9.98E-01	
	feedingfruit:seasonspring	-26.088	114633.049	0.000	1.00E+00	
	feedingfallen fruit:seasonspring	-0.992	1.21E+00	-8.17E-01	4.14E-01	
	feedingflower:seasonspring	22.289	8.76E+03	2.54E-03	9.98E-01	
	feedingfruit:seasonsummer	-3.737	1.142	-3.272	1.07E-03	*
	feedingfallen fruit:seasonsummer	-26.930	269235.663	0.000	1.00E+00	
	feedingflower:seasonsummer	-6.155	3.01E+05	-2.04E-05	1.00E+00	

B. EMMs	Season	Food Type	Response	SE	asymp.LCL	asymp.UCL
	autumn	arthropod	0.242	0.063	0.145	0.403
	winter	arthropod	0.351	0.077	0.228	0.540
	spring	arthropod	0.356	0.173	0.137	0.924
	summer	arthropod	0.951	0.336	0.475	1.900
	autumn	fruit	0.650	0.143	0.423	1.000
	winter	fruit	0.232	0.053	0.148	0.362
	spring	fruit	4.48E-12	5.13E-07	2.22E-16	Inf
	summer	fruit	0.061	0.063	0.008	0.460
	autumn	fallen fruit	0.109	0.034	0.059	0.201
	winter	fallen fruit	0.418	0.090	0.274	0.636
	spring	fallen fruit	0.059	0.061	0.008	0.451
	summer	fallen fruit	8.62E-13	2.32E-07	2.22E-16	Inf
	autumn	flower	8.25E-11	7.23E-07	2.22E-16	Inf
	winter	flower	0.003	0.003	0.0004	0.0240
	spring	flower	0.581	0.240	0.2586	1.3055
	summer	flower	6.89E-13	2.07E-07	2.22E-16	Inf

C. Pairwise Contrasts	Seasonal Contrast	Food Type	ratio	SE	z value	p value	
	autumn / winter	arthropod	0.69	0.23	-1.095	0.692	
	autumn / spring	arthropod	0.68	0.38	-0.699	0.897	
	autumn / summer	arthropod	0.25	0.11	-3.115	0.010	*
	winter / spring	arthropod	0.99	0.53	-0.023	1.000	
	winter / summer	arthropod	0.37	0.15	-2.392	0.079	
	spring / summer	arthropod	0.37	0.23	-1.633	0.360	
	autumn / winter	fruit	2.81	0.89	3.264	0.006	*
	autumn / spring	fruit	1.45E+11	1.67E+16	0.0002	1	
	autumn / summer	fruit	10.68	11.25	2.2464	0.1109	
	winter / spring	fruit	5.176E+10	5.934E+15	0.0002	1	
	winter / summer	fruit	3.81	4.017	1.2659	0.5848	
	spring / summer	fruit	7.35E-11	8.42E-06	-0.0002	1	
	autumn / winter	fallen fruit	0.260	0.099	-3.5489	0.0022	*
	autumn / spring	fallen fruit	1.832	1.981	0.5601	0.9438	
	autumn / summer	fallen fruit	1.26E+11	3.39E+16	9.49E-05	1	
	winter / spring	fallen fruit	7.037	7.438	1.8459	0.2518	
	winter / summer	fallen fruit	4.84624E+11	1.30E+17	9.99E-05	1	
	spring / summer	fallen fruit	6.89E+10	1.85E+16	9.27E-05	1	
	autumn / winter	flower	2.55E-08	0.000	-0.0020	1.0000	
	autumn / spring	flower	1.42E-10	1.24E-06	-0.0026	1.0000	
	autumn / summer	flower	119.837	3.61E+07	1.59E-05	1	
	winter / spring	flower	0.006	0.006	-4.7104	1.47E-05	*
	winter / summer	flower	4.70E+09	1.41E+15	7.39E-05	1	
	spring / summer	flower	8.43E+11	2.54E+17	9.12E-05	1	

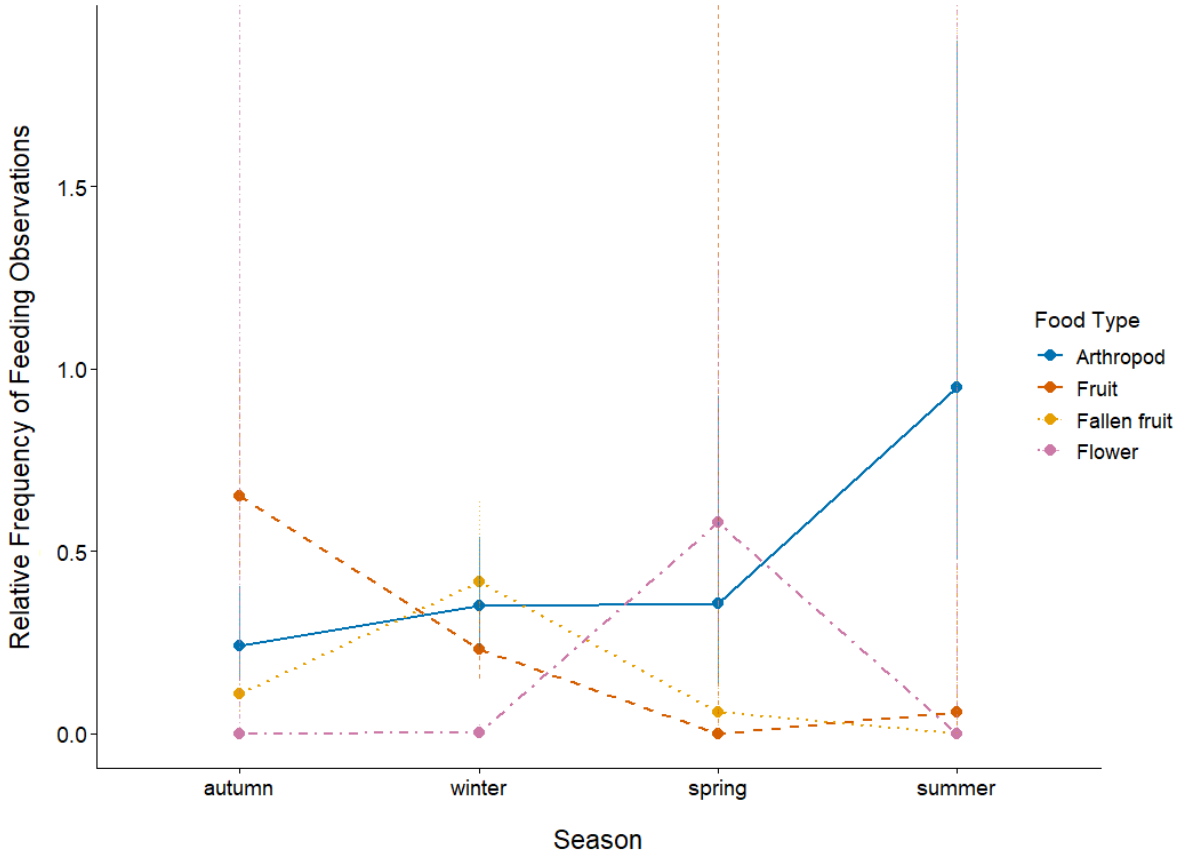


Figure 4.4. Seasonal variation in food use by silvereyes (Zosterops lateralis) in apple orchards. Points represent model-estimated relative frequencies of feeding observations for arthropods (blue), fruits (orange), fallen fruits (yellow), and flowers (pink) across seasons. Vertical lines indicate 95% confidence intervals. Estimates were derived from the best-supported negative binomial generalised linear mixed model, which included an interaction between food type and season, orchard as a random effect, and total feeding observations per orchard x season as an offset.

4.5 Discussion

4.5.1 Foraging-Related Activities Dominated Behavioural Observations

The primary motivation for the behavioural study was to understand how birds, particularly natives, interact with horticultural systems and the beneficial or detrimental activities they undertake within them. Behavioural observations indicated that most native bird species visiting New Zealand apple orchards were primarily engaged in foraging activities. Even among species for which flying was the most frequently observed behaviour (e.g., silvereye, tūī, grey warbler), the behaviour seemed to be closely associated with foraging movement rather than non-foraging purposes. This aligns with growing evidence recognising agricultural landscapes as important feeding habitats for many bird taxa (Wilson et al. 2005; Macleod & Till 2007; Htay et al. 2024), particularly where adjacent natural habitats are degraded (Zhong et al. 2025). The present findings therefore indicate that foraging is a major component of native avifaunal use of New Zealand apple orchards.

However, the predominance of foraging observations does not necessarily indicate that orchards function exclusively as feeding habitats. A small number of nests were encountered opportunistically during fieldwork, suggesting that some species may also use orchards for breeding. As nest searching and reproductive monitoring were outside the scope of this study, the importance of orchards as breeding habitat could not be assessed. Future studies combining

behavioural observations with systematic nest surveys and measures of reproductive success would help determine whether orchards provide habitat throughout multiple stages of birds' life cycle. Establishing breeding use alone would not demonstrate habitat quality, as the presence of individuals or nests does not necessarily indicate that a habitat supports successful reproduction rates (van Horne 1983; Pulliam 1988). Quantifying nest success, juvenile recruitment and survival would therefore be necessary to determine whether orchards function as productive breeding habitats or as potential sink habitats (Dias 1996).

Social, vocal and territorial behaviours were detected far less frequently than foraging or flying, although this likely reflects methodological and classification challenges rather than behavioural rarity. Subtle social interactions are difficult to identify without extensive species-specific knowledge (Morris 1956), and the treatment of vocalisations as a separate category may have artificially reduced apparent social activity. Vocalisation intensity also varies seasonally (McGovern et al. 2024), and distinguishing mate-calling from territorial signalling was not feasible. Hence, low frequencies of social or territorial behaviours should be interpreted as detection artefacts rather than evidence that such behaviours are biologically unimportant in orchard landscapes.

The low frequencies of territorial behaviours may not reflect true rarity within orchards. This nuance is particularly relevant for species known to exhibit strong territorial behaviours during the breeding season, such as fantails and tūī (Innes et al. 2022). Intermittent records of conspecific chasing do not necessarily indicate territory establishment, and confirming territorial occupation would require targeted monitoring of breeding pairs, territory boundaries, nest-building and territory defence. Although a small number of nests were encountered opportunistically, nest searching and assessment were not included formally in the study and could not be considered representative.

A notable species-specific pattern emerged for tūī at orchard MN2, where conspecific exclusion around fruiting trees was observed in late autumn, early winter and summer. These behaviours diminished in spring when fruit availability at the site was low, suggesting seasonal defence of feeding resources rather than long-term territory holding. This aligns well with previous descriptions of tūī defending exclusive feeding territories (Stewart & Craig 1985).

Interactions with field observers were likewise distinctive among the two main species in which the behaviour was recorded. Fantails regularly followed surveyors to exploit insects disturbed by human movement, consistent with known opportunistic foraging strategies (Heather et al. 2015). In contrast, pūkeko frequently fled from observers at distances greater than 15 metres, indicating a strong avoidance response. Growers anecdotally reported actively persecuting pūkeko as crop pests, including outside regulated hunting permits. Comparable persecution of closely related swamphen species occurs in cropping regions overseas (Moreno-Opo & Piqué 2018; Razalee & Norazlimi 2023). These observations offer a plausible ecological explanation for heightened wariness in pūkeko and highlight the need to investigate how human disturbance affects their foraging efficiency and habitat use in food production systems.

These behavioural interpretations should, however, be considered in the context of a few limitations. Statistical modelling was only feasible for a subset of common native species (fantail, grey warbler, pūkeko, silvereye, tūī, and welcome swallow), meaning that patterns identified here may not be transferable to other species. Furthermore, orchard was included as

a random effect to account for variation among study sites rather than explicitly testing differences among individual orchards.

Flight behaviour also warrants cautious interpretation. Flying was often one of the most recorded behaviours, potentially reflecting detectability bias, as birds in motion are easier to identify. Similar overestimation associated with disturbance responses has been documented for blackbirds (Coleman 2010). Two factors lessen this concern here. First, birds using managed landscapes often exhibit high tolerance to noise and disturbance relative to forest-dependent species (Zielonka et al. 2024; Peria & Francis 2025). Second, many flight events were recorded at substantial distances, facilitated by the high visibility of the orchard layout. Consequently, while observer effects cannot be discounted, the behavioural patterns reported likely reflect genuine tendencies rather than artefacts of disturbance avoidance.

Orchard identity alone may also provide a limited representation of the spatial factors influencing bird behaviour. Bird communities in agricultural systems are influenced not only by local habitat characteristics but also by landscape-scale factors, including the amount and configuration of surrounding vegetation, habitat connectivity, patch size and landscape heterogeneity (Johnson et al. 2011; Weller 2011; Kross et al. 2016; Innes et al. 2022; Díaz-Siefer et al. 2022). Consequently, orchard identity alone may provide a limited representation of the spatial factors influencing bird behaviour. Future studies across a wider network of orchards should explicitly quantify orchard size, connectivity to native vegetation, surrounding habitat composition and landscape heterogeneity. Such an approach would help determine whether behavioural tendencies within orchards are consistent across landscapes or depend on the availability and configuration of complementary habitats surrounding orchards.

Despite the limitations outlined above, the consistency of behavioural patterns associated with foraging across species suggests that these patterns are meaningful across the avian community using apple orchard habitats in New Zealand. Taken together, they provide a foundation for understanding how native birds use these systems and for evaluating how behavioural tendencies translate into functional roles within orchard ecosystems.

4.5.2 Common Bird Visitors Feeding on Fruit Crops

Silvereyes are generalist omnivores (Heather et al. 2015) and accounted for nearly 87% of fruit consumption observations. This indicates their potential contribution to crop damage. However, the interpretation of these results needs to consider that introduced species were not followed for up to five minutes, therefore their true feeding rates were not estimated. Nonetheless, fruit consumption for silvereyes was particularly high during winter, coinciding with the post-harvest season for apples, when uncollected fruit commonly remained on the ground. As harvest progressed, fallen fruit became readily available, and silvereyes frequently exploited this resource. The high winter abundance of silvereyes, combined with their scavenging behaviour of fallen fruits, indicates their potential to provide a sanitation service through the removal of rotting fruit. Studies on other taxonomically distinct groups have pointed out that abundant species can remove substantial volumes of food waste (Penick et al. 2015; Schäckermann et al. 2015), but further research needs to be conducted with silvereyes to test this hypothesis.

Conversely, silvereyes were also recorded feeding on flowers in spring, primarily from apples, although whether the birds were consuming nectar or the flower themselves was not recorded.

Although silvereyes do not have a nectarivorous feeding apparatus, they have been recognised as important pollinators of native New Zealand plants (Kelly et al. 2006). Nonetheless, their role as apple tree pollinators was not tested in this thesis, nor did I find definitive evidence in the literature supporting this role. Further research is needed to assess their potential as pollinators of introduced fruit crops. In the scenario of damaging the flowers when feeding on them, silvereyes would be providing an indirect form of crop damage, by preventing subsequent fruit formation.

Altogether, the number of flower-feeding events was small, and silvereye presence at the orchards was lowest in spring. These factors indicate that their impact on this form of crop damage is likely minimal. Additionally, silvereyes fed primarily on arthropods across seasons, which may reflect the more stable availability of arthropods across seasons than fruit crops. Support for this idea comes from the observation that, apart from the mixed-crop orchards (MN1 and KC2), fruit availability was largely restricted to autumn and early winter. Silvereyes, like many omnivorous species, can also shift to a highly insectivorous diet during the breeding and fledgling season due to higher protein requirements (Triplett et al. 2012; Heather et al. 2015). These contrasting feeding behaviours position silvereyes as a species capable of both ecosystem services and disservices across a seasonal gradient, warranting further focused studies to quantify their net effect across orchard functioning.

Other species could not be assessed statistically in their food use, but the data kept for descriptive purposes still allowed some worthy observations. Tūī are iconic native nectarivores with important roles in native pollination and seed dispersal and have been recognised as opportunistic frugivores (Kelly et al. 2010; Heather et al. 2015). Across the orchards surveyed, tūī almost exclusively consumed fruit crops, contrasting with their reported winter reliance on nectar (Innes et al. 2005). Their relatively low abundance among sites likely reflects their broad home range exceeding orchard sizes (Innes et al. 2022). However, where they were present, individuals appeared to exploit available fruit resources as a primary food source. As predator control initiatives increase tūī populations (DoC 2020), this may translate into higher rates of soft-fruit damage if access to mature fruit crops is not managed. However, given their aggressive territorial behaviour (Heather et al. 2015), tūī may interfere with smaller passerines such as silvereyes, potentially reducing the frequency with which silvereyes feed on fruit. Although such interactions were not identified during this study, they represent an important avenue for future research in fruit orchards where tūī are more abundant visitors.

Blackbirds were also recorded feeding regularly on fruit crops. Blackbirds have been identified as major contributors to crop damage (Dawson & Bull 1970; Coleman & Spurr 2001), however, in this study, most feeding observations were of arthropods rather than fruit. This pattern may reflect the high presence of silvereyes, which tended to use the vertical strata of the crop trees and may have limited blackbird access to fruit resources. As introduced species were not followed continuously for the behavioural study, fruit consumption for blackbirds was likely underestimated. Consequently, any conclusion drawn from the observations should be interpreted cautiously and warrants further studies.

Overall, only silvereyes could be analysed in detail for feeding behaviours. Nonetheless, this species exemplifies the divergent ways orchards visitors engage with fruit crops, illustrating the potential for simultaneously providing ecosystem services (e.g. pest control, sanitation through fallen-fruit removal) and disservices (crop damage). While fruit consumption events were documented in this chapter, quantitative estimation of crop damage was beyond its scope.

In the next chapter, I examine sentinel prey predation and crop damage to assess potential beneficial and detrimental bird-crop interactions within apple orchards.



MASSEY UNIVERSITY
TE KUNENGA KI PŪREHUROA
UNIVERSITY OF NEW ZEALAND

GRADUATE RESEARCH SCHOOL

STATEMENT OF CONTRIBUTION
DOCTORATE WITH PUBLICATIONS/MANUSCRIPTS

We, the student and the student's main supervisor, certify that all co-authors have consented to their work being included in the thesis and they have accepted the student's contribution as indicated below in the Statement of Originality.			
Student name:	Giuliana Caldeira Pires Ferrari		
Name and title of main supervisor:	Professor Isabel Castro		
In which chapter is the manuscript/published work?	Chapter Five		
Describe the contribution that the student and members of the supervisory team have made to the manuscript/published work:[1] GCPF (student): conceptualization / data curation / formal analysis / funding acquisition / investigation / methodology / visualization / writing (original draft) / writing (review & editing) KM (supervisor): conceptualization / funding acquisition / investigation / methodology / writing (review & editing) AWR (supervisor): conceptualization / formal analysis / methodology / writing (review & editing) IC (main supervisor): conceptualization / formal analysis / investigation / methodology / writing (review & editing)			
Please select one of the following three options:			
○	**The manuscript/published work is published or in press** Please provide the full reference of the research output:		
○	**The manuscript is currently under review for publication** Please provide the name of the journal:		
◉	**It is intended that the manuscript will be published, but it has not yet been submitted to a journal**		
Student's signature:	Giuliana C. P. Ferrari 2026.01.28 11:32:18 +13'00'	Main supervisor's signature:	Isabel Castro Digitally signed by Isabel Castro Date: 2026.01.28 11:37:20 +13'00'
This form should be placed at the beginning of each relevant thesis chapter.			

[1] Refer to the Massey University Publishing and Authorship guidelines (OneMassey for staff, Stream for students) and/ or Contributor Roles Taxonomy (CRediT) guidelines for guidance.

Chapter 5 Assessing Pest Control and Crop Damage by Avian Species in New Zealand Apple Orchards

5.1 Abstract

Birds can provide both ecosystem services and disservices in agricultural systems, yet these functions are rarely assessed simultaneously. This chapter evaluated the potential contributions of birds to pest control and crop damage in New Zealand apple orchards using artificial sentinel prey removal experiments and direct surveys of fruit damage. Artificial caterpillars were deployed across six orchards and multiple seasons to quantify predation by birds, arthropods, and rodents, while crop-damage surveys conducted during the 2024 and 2025 harvests quantified damage attributed to birds, insects, and fungi. Arthropods had the highest estimated probability of attacking artificial caterpillars, followed by birds and rodents. Predation probability was significantly higher at orchard edges than in orchard middles but did not differ among seasons. However, the relatively low frequency of bird attacks and limitations inherent to artificial sentinel prey constrain their interpretation as a direct measure of avian pest-control services. Crop-damage surveys showed that fungal damage was substantially more frequent than damage attributed to birds or insects. Multivariate analysis provided no evidence that the composition of bird, insect, and fungal damage differed with orchard position, year, or branch height. Bird-related damage was uncommon overall, indicating that birds were not the predominant source of recorded fruit damage within the orchards surveyed. These findings challenge perceptions of birds as major horticultural pests and highlight the importance of directly quantifying crop damage rather than inferring impacts from bird presence alone. At the same time, uncertainty surrounding the relationship between attacks on artificial prey and removal of actual crop pests prevented a conclusive assessment of the magnitude of avian pest-control services. Consequently, the net functional contribution of birds to apple production could not be resolved from the two approaches used here. Integrating direct crop-damage assessment with complementary measures of pest consumption, such as dietary analyses or exclusion experiments, would provide a stronger basis for evaluating avian ecosystem services and disservices simultaneously. Overall, birds represented a comparatively minor source of recorded crop damage in these New Zealand apple orchards, while their contribution to pest control remains promising but uncertain.

5.2 Introduction

Agriculture dominates the Earth's landscape, with more than one third of the world's terrestrial surface dedicated to agricultural production. Meeting the global demand for increased agricultural output while ensuring environmental sustainability and protecting biodiversity remains one of the defining challenges of the 21st century (Tilman et al. 2001; Hemler & Frank 2019). Modern agriculture depends heavily on natural ecological processes, even if these benefits are often underappreciated (Matson et al. 1997; Power 2010). These benefits, known as ecosystem services, arise from natural ecosystem functions that support or enhance human well-being (Daily 1997).

It is now widely accepted that conserving natural ecosystem functions is essential for the maintenance of basic components of human quality of life. Nonetheless, non-human species have their own interests which often lead to human costs, which are recognised as ecosystem

disservices (Zhang et al. 2007; Lyytimäki & Sipilä 2009). The discourse on ecosystem disservices is gaining traction (Kronenberg 2014), but their true costs are still poorly understood (Shackleton et al. 2016; Wu et al. 2021).

Biodiversity can thus contribute significantly to food production in positive and negative ways, but birds have garnered special attention in the research of ecosystem services. Avian behaviour and the expansive variety of feeding guilds lend birds the ability to provide a variety of potential ecosystem services and disservices (Triplett et al. 2012; Whelan et al. 2015; Şekercioğlu et al. 2016). In contrast, wild species that are successful in competing with humans in food production systems are deemed 'pests', and managing or excluding them has long been a fixture of agricultural practices (Marzluff et al. 1994).

For the most part, the literature on the costs and benefits of birds to agriculture has evolved independently, with few authors attempting to bridge the gaps between those subjects (Triplett et al. 2012; Peisley et al. 2016). These gaps hinder the understanding of costs and benefits within a spectrum and their potential trade-offs. This is especially important in agriculture, as farmers will often only tolerate a disservice in their systems if the wildlife involved is recognised as otherwise valuable, or also a provider of ecosystem services (Lute et al. 2016). As people tend to care about what they can directly observe, ecosystem services provided by birds, such as pest control, may be concealed by disservices such as crop damage (Huang et al. 2023). This imbalance in perception can influence management decisions by shaping grower's willingness to coexist with wildlife (Jacobson et al. 2002; Lazaridou & Michailidis 2023).

In New Zealand, it is estimated that invertebrate pests cause annual losses of up to 2.3 billion dollars in agricultural systems (Ferguson et al. 2019). In this context, the presence of biological pest control agents, such as insectivorous birds, could prove to be an immensely valuable resource for food production systems. New Zealand has a long history of agricultural expansion and intensification (MacLeod et al. 2008; Moller et al. 2008), coupled with a native fauna composed primarily of birds, many of which face varying degrees of extinction threats (Craig et al. 2000; Miskelly et al. 2009). Within the New Zealand agricultural landscape, birds are studied primarily when seen as pests (MacLeod et al. 2008). Little scientific information is yet available on the potential benefits they can bring to food production systems.

A common proxy to assess the provision of pest control is the predation of arthropods and other 'pests' within the horticultural system by the focal group of predators. However, birds move fast and through vast distances, hindering the capture of discrete events of predation. An alternative involves focusing on the outcome of these events (Valdés-Correcher et al. 2022). Real or artificial prey models are offered in bait stations, known as sentinel prey removal experiments (SPR). Sentinel prey removal studies have been historically associated with entomological research to study predation pressure, but they are increasingly used to measure vertebrate predator activity (Jedlicka et al. 2011). They can be used to measure the speed and magnitude of avian responses to ecosystem changes (Garfinkel & Johnson 2015), especially pervasive in the context of human-managed ecosystems characterised by high disturbance and rapid changes. Although artificially increasing prey availability in SPR experiments may elevate observed attack rates, this method is widely used because it allows predation rates to be quantified when direct evidence of predation is otherwise difficult to obtain (Jedlicka et al. 2011; Lövei & Ferrante 2017; Bateman et al. 2017; Martínez-Sastre et al. 2020).

Traditionally, SPR experiments involve offering live or dead prey (MacLellan 1958; Geiger et al. 2010; Winqvist et al. 2011). This can lead to maintenance issues, namely keeping the prey alive and associated costs, or potential low access to dead model prey. Live prey can be highly contentious, as growers can be wary of the risk of releasing crop pests into their orchards. An alternative consists of using artificial models, often made from soft clay. These artificial sentinel prey are increasingly favoured for the ease of replicability, cheaper costs, and the lack of need for maintaining organic prey in the field (Howe et al. 2009; Lövei & Ferrante 2017; Bateman et al. 2017).

This chapter aimed to investigate the provision of an ecosystem service (pest control) through artificial sentinel prey removal experiments and an ecosystem disservice (crop damage) through damage surveys. I aimed to assess the potential trade-offs between the benefits of avian pest control and the consumption of fruit crops by birds in New Zealand apple orchards. I expected predation rates to vary among seasons and between orchard edges and interiors, while the composition of crop damage was expected to vary between years, orchard positions, and branch heights.

5.3 Methods

5.3.1 Study Area

The study was conducted across six apple orchards in four New Zealand regions: Manawatū (orchards MN1 and MN2), Kāpiti Coast (orchards KC1 and KC2), Hawke's Bay (orchard HB), and Tasman district (orchard TR). Orchard size varied across sites, ranging from 2ha at MN1 to 44.5 ha at HB. Fieldwork coincided with the occupancy and behaviour studies (Chapters Three and Four), and additionally extended into the 2025 harvest season (early autumn). A detailed description of the orchards' structures, management practices, and apple varieties is included in Chapter Three.

5.3.2 Pest Control

5.3.2.1 Artificial Sentinel Prey Removal Experiments

Model caterpillars were constructed from green non-toxic plasticine to reduce the risk of toxicity if ingested by birds. Light and dark green plasticine were mixed and rolled into ~2mm-diameter caterpillars, each 25-30mm long (Figure 5.1). Caterpillars were deployed in batches of five, with a minimum of five batches per orchard and up to 20 batches for orchard HB. Batches were separated by at least 10m to maintain spatial independence. Caterpillars were primarily placed in apple trees; however, in mixed-crop orchards, deployment included other fruit trees where required to maintain spacing. Caterpillars were deployed in mid-afternoon to allow full exposure during peak morning foraging periods and retrieved after 24 hours. Deployments proceeded under most weather conditions except heavy rain, when glue adhesion was unreliable. During spring and summer, caterpillars were kept in cooler bags prior to deployment and placed in shaded sites to avoid melting (Muchula et al. 2019).



Figure 5.1. Examples of an artificial caterpillar deployed in the field (left) and a batch of five caterpillars stored individually (right).

5.3.2.2 Identification of Predation Marks

After retrieval, caterpillars were stored individually inside labelled plastic vials and inspected under a dissection microscope, with all potential predation marks photographed. Caterpillars exhibiting ambiguous or accidental damage marks were excluded from further analysis. Predator identity was assigned using a reference guide of predation marks from arthropods, mammals, birds, and reptiles (Low et al. 2014). Marks were classified into coarse taxonomic groups, and identifications were independently assessed by the author and three supervisors, with uncertain cases resolved by consensus. To support mark identification for New Zealand fauna, a supplementary calibration trial was conducted at a rural property, where artificial caterpillars were deployed in ground-based locations accessible only to invertebrates and in above-ground locations accessible to birds. Reference impressions from these deployments were used to refine identification of bird and arthropod predation marks commonly observed in the field samples. To ensure independence of predation events, all marks attributable to a single predator group on an individual caterpillar were treated as originating from the same predation event (Ferrante et al. 2017a). Each recovered caterpillar was therefore scored independently for the presence or absence of predation by each of three predator groups: arthropods, birds, and rodents.

5.3.3 Crop Damage

Crop damage was assessed during the 2024 and 2025 harvest seasons using a branch-level survey approach adapted from Peisley et al. (2016). Exclusion experiments are commonly used to partition crop damage among birds, insects, and other agents (Johnson et al. 2009; Classen et al. 2014; Maas et al. 2019; Bouarakia et al. 2023). However, for this study, exclosures were not feasible across all orchards due to narrow row spacing, machinery access requirements, and

logistical constraints. A non-exclosure approach was therefore adopted to allow consistent sampling across sites.

At each orchard section, ten apple trees were randomly selected, spaced at least 10 m apart to ensure independence. Trees were selected from both edge and interior positions, with four trees sampled at each of two section edges and two from the middle; where edge trees were unavailable, nearby trees were substituted to maintain sample size. On each tree, one branch was randomly selected from one of three height categories (low: <100 cm; chest height: 100-179 cm; high: ≥180 cm), with height categories assigned before the field surveys.

Prior to harvest, all apples on the selected branch were counted, and fruits showing visible signs of damage were recorded. Damage was classified as bird, insect, or fungal based on established reference guides (Beckerman 2000; Gauthier et al. 2013; Pipfruit NZ 2025). There is a possibility of other types of pathogen damage (e.g. bacterial) being mistaken for fungal infections, such as fire blight (Peil et al. 2009). However, no instances of fire blight damage were recorded during the surveys, nor was the pathogen an immediate concern raised by the growers of the included orchards.

Bird damage was characterised by distinct beak marks or gouges, insect damage by circular feeding marks, and fungal damage by superficial or internal lesions. Sick or rotten fruit remaining on branches were also recorded. Damage incidence was quantified as the number of damaged fruits per branch, while yield was expressed as the proportion of undamaged fruit per branch. This approach allowed estimation of both absolute damage rates and proportional yield loss.

5.3.4 Statistical Analyses

5.3.4.1 Pest Control

The effects of season and orchard position on artificial caterpillar predation were analysed using generalised linear mixed models (GLMMs) fitted using the glmmTMB package in R (Brooks et al. 2017). Predation was modelled using a binomial error distribution with a logit link. For each sampling unit and predator group, the response was specified as the number of caterpillars exhibiting predation marks relative to the number without marks, thereby modelling the probability that an exposed caterpillar showed evidence of predation. Predator identity was classified as arthropod, bird, or rodent. Season comprised five levels (autumn, harvest, winter, spring, and summer), and orchard position comprised two levels (edge and middle). Orchard identity was included as a random intercept to account for repeated sampling within orchards.

Model selection followed an information-theoretic approach consistent with analyses in the preceding chapters. A small candidate set was constructed to evaluate the effects of season and orchard position while accounting for differences among predator groups. Candidate models included: an interaction between season and orchard position with an additive effect of predator group (Season x Position + Predator); additive effects of season, orchard position, and predator group (Season + Position + Predator); predator group only; and a null model containing only the orchard random intercept. Models were ranked using Akaike's Information Criterion (AIC), with models within $\Delta AIC < 2$ considered to have equivalent support. The diagnostically acceptable model with the lowest AIC was retained for inference.

Model diagnostics were assessed using simulated residuals in the DHARMa package. Models were evaluated for convergence, positive-definite Hessian matrices, dispersion, excessive zero inflation, residual uniformity, and outliers. Estimated marginal means and 95% confidence intervals were subsequently calculated on the response scale using the emmeans package (Lenth et al. 2018).

5.3.4.2 Crop Damage

To assess variation in the composition of fruit damage, a multivariate ordination was conducted using non-metric multidimensional scaling (NMDS). Damage data were aggregated into sampling units representing unique orchard x year x position x branch-height combinations. For each sampling unit, bird, insect, and fungal damage counts were summed and divided by the total number of apples examined to account for variation in the number of fruits sampled. Rotten fruits were excluded because the original cause of damage could not be reliably attributed to birds, insects, fungi, or a combination of these agents. Sampling units with no bird, insect, or fungal damage were excluded from the multivariate analysis, resulting in 45 sampling units.

NMDS was performed on the proportional damage data using Bray-Curtis dissimilarities in the vegan package in RStudio. A two-dimensional solution was fitted, and ordination stress was used to assess the representation of among-sample dissimilarities. The final ordination had a stress value of 0.097. Differences in damage composition were subsequently tested using permutational multivariate analysis of variance (PERMANOVA) with the function 'adonis2' within the *vegan* package, with 999 permutations and Bray-Curtis dissimilarities (Oksanen et al. 2008). Orchard position (edge or middle), year (2024 or 2025), and branch height (low, chest height, or high) were included as predictors. An initial model also included the interaction between position and year; as this interaction was not supported, the final additive model included position, year, and branch height. Marginal effects were tested, with permutations restricted within orchard to account for repeated sampling within orchards.

Homogeneity of multivariate dispersion was assessed separately for position, year, and branch height using the 'betadisper' function, with significance evaluated using permutation tests with 999 permutations. These tests were used to assess whether differences in within-group dispersion could influence interpretation of the PERMANOVA results.

5.4 Results

5.4.1 Artificial Sentinel Prey Removal Experiments

Across six apple orchards, 1,575 caterpillars were deployed across four seasons (autumn 2024 to summer 2025) and the 2025 harvest period (Table 5.1). Sampling was conducted in all orchards in each season except orchard TR, which was not surveyed during spring and harvest. Caterpillar recovery rates ranged from 92-98%, with 85 caterpillars not retrieved. Because missing caterpillars could not be reliably attributed to predation, they were excluded from predation rate analyses (Schillé et al. 2024).

122 predation events were identified in 113 caterpillars, accounting for 7.6% of all recovered caterpillars. Although it was possible to identify a single predation mark by a non-arthropod invertebrate (a snail), predation marks were broadly classified into rodents (Figure S 10), birds

(Figure S 11), and arthropods (Figure S 12). Arthropod marks comprised 86 of the 122 predation events (70.5%), followed by birds (31 events, 25.4%), rodents (4 events, 3.3%), and one non-arthropod invertebrate event (0.8%). Out of the 113 caterpillars with predation marks, 81 were positioned in the middle of the orchard and 32 at the edges.

Most depredated caterpillars (n = 103) had marks by a single taxonomic group (arthropods, birds, or rodents). A small set of 10 caterpillars had marks by two taxonomic groups, with most (n = 8) showing both bird and arthropod marks, and two showing rodent and arthropod marks. There was no evidence of the same caterpillar being marked by birds and rodents.

The additive model containing season, orchard position, and predator group received the greatest AIC support (AIC = 308.89, AIC weight = 0.506), although the predator-only model received similar support (ΔAIC = 0.20, AIC weight = 0.458; Table 5.2). The model containing the interaction between season and position received substantially less support (ΔAIC = 5.28), providing little evidence that positional differences in predation varied among seasons. The retained additive model met all model diagnostic criteria (Table 5.2).

Estimated predation probability did not differ significantly among seasons (Table 5.3A; Figure 5.2). Predation probabilities ranged from 0.012 (95% CI: 0.007-0.021) during harvest to 0.021 (95% CI: 0.013-0.035) in spring. Tukey-adjusted pairwise comparisons of estimated marginal means, evaluated using asymptotic *z*-tests (degrees of freedom = ∞), detected no significant differences among seasons (all $p > 0.05$).

Predation probability differed between orchard positions, with caterpillars deployed at orchard edges having an estimated predation probability of 0.022 (95% CI: 0.014-0.034), compared with 0.012 (95% CI: 0.009-0.018) in orchard middles (Table 5.3B; Figure 5.2). A Tukey-adjusted pairwise comparison based on an asymptotic *z*-test indicated that predation odds at edges were 1.77 times those in orchard middles ($z = 2.70$, $p < 0.05$).

Predation also differed strongly among predator groups (Table 5.3C; Figure 5.2). Arthropods had the highest estimated predation probability (0.063, 95% CI: 0.050-0.079), followed by birds (0.023, 95% CI: 0.016-0.033) and rodents (0.003, 95% CI: 0.001-0.008). Arthropod predation was approximately 2.89 times that attributed to birds ($z = 4.98$, $p < 0.001$) and 22.80 times that attributed to rodents ($z = 6.10$, $p < 0.001$). Bird predation was approximately 7.90 times greater than rodent predation ($z = 3.88$, $p < 0.001$).

Table 5.1. Seasonal deployment of caterpillars. The number of artificial caterpillars deployed is given as the sample size per orchard and season, with the corresponding recovery rates after 24h in the field. Total recovery rate per season is provided as an average for each orchard. Sentinel prey removal experiments were conducted from autumn 2024 to the harvest season of 2025. Caterpillars were not deployed at Orchard TR in the spring and harvest seasons.

Orchard	Season	Sample Size	Recovery Rate	Caterpillars Total	Recovery Rate (Average)
Manawatū 1					
	autumn	50	88%		
	winter	50	98%		
	spring	25	100%	225	95%
	summer	50	92%		
	harvest	50	96%		
Manawatū 2					
	autumn	50	92%		
	winter	50	96%		
	spring	50	96%	250	95%
	summer	50	100%		
	harvest	50	92%		
Kāpiti Coast 1					
	autumn	50	94%		
	winter	50	100%		
	spring	50	98%	250	94%
	summer	50	86%		
	harvest	50	90%		

Orchard	Season	Sample Size	Recovery Rate	Caterpillars Total	Recovery Rate (Average)
Kāpiti Coast 2					
	autumn	25	96%		
	winter	50	92%		
	spring	50	98%	225	93%
	summer	50	84%		
	harvest	50	94%		
Hawke's Bay					
	autumn	75	82.60%		
	winter	75	100%		
	spring	75	98.60%	425	93.84%
	summer	100	92%		
	harvest	100	96%		
Tasman Region					
	autumn	50	98%		
	winter	75	98%	175	98%
	summer	75	97.30%		

Table 5.2. Model selection and diagnostic results for binomial generalised linear mixed models examining variation in artificial caterpillar predation probability according to season, orchard position (edge or middle), and predator group (arthropod, bird, or rodent). Orchard was included as a random intercept in all models. Models were ranked using Akaike's Information Criterion (AIC), with the best-supported model shown in bold. k represents the number of estimated model parameters, ΔAIC the difference in AIC relative to the best-supported model, and AIC weight the relative support for each model. Diagnostic columns report model convergence, positive-definite Hessian (pdHess), and p-values from DHARMa tests of dispersion, zero inflation, residual uniformity, and outliers. a indicates that the model converged successfully or had a positive-definite Hessian, as applicable.

Model	k	AIC	Delta_AIC	AIC_weight	convergence	pdHess	dispersion	zero-inflation	uniformity	outliers
Season + Position + Predator Group	**9**	**308.89**	**0**	**0.506**	✔	✔	**0.7**	**0.992**	**0.9745**	**1**
Predator Only	4	309.09	0.2	0.458	✔	✔	0.712	0.492	0.769	1
Season x Position + Predator	13	314.17	5.28	0.036	✔	✔	0.744	1	0.441	1
Null	2	402.8	93.91	0	✔	✔	0.024	0.068	0.122	1

Table 5.3. Model output (A), estimated marginal means (B), and pairwise contrasts (C) from the best-supported binomial generalised linear mixed model of artificial caterpillar predation. The model included additive effects of season, orchard position, and predator group, with orchard included as a random intercept. (A) Model coefficients are presented on the logit scale, with autumn, orchard edge, and arthropods as reference levels. The intercept represents the estimated log-odds of predation at these reference levels; (B) Estimated marginal means are presented as predicted probabilities of predation with standard errors (SE) and 95% confidence intervals (asymp.LCL-asymp.UCL); (C) Pairwise contrasts are presented as odds ratios with standard errors, z-statistics, and Tukey-adjusted p-values. Ratios greater than 1 indicate higher odds of predation for the first level relative to the second. Asterisks indicate statistically significant effects or contrasts ($p < 0.05$).

A. Model Output

term	estimate	SE	z	p	
(Intercept)	-2.287	0.260	-8.801	1.35E-18	*
Seasonharvest	-0.446	0.319	-1.400	0.161	
Seasonspring	0.131	0.291	0.449	0.653	
Seasonsummer	-0.189	0.282	-0.671	0.502	
Seasonwinter	-0.116	0.282	-0.411	0.681	
positionmiddle	-0.569	0.211	-2.701	0.007	*
predatorbird.marks	-1.060	0.213	-4.978	6.41E-07	*
predatorrodent.marks	-3.127	0.513	-6.096	1.09E-09	*

B. Estimate Marginal Means	probability	SE	asymp.LCL	asymp.UCL
Season				
autumn	0.019	0.005	0.011	0.030
harvest	0.012	0.003	0.007	0.021
spring	0.021	0.006	0.013	0.035
summer	0.015	0.004	0.009	0.025
winter	0.017	0.004	0.010	0.027
Position				
edge	0.022	0.005	0.014	0.034
middle	0.012	0.002	0.009	0.018
Predator Group				
arthropods	0.063	0.007	0.050	0.079
birds	0.023	0.004	0.016	0.033
rodents	0.003	0.001	0.001	0.008

C. Pairwise Contrasts	odds ratio	SE	z	p	
Season					
autumn / harvest	1.562	0.498	1.400	0.628	
autumn / spring	0.877	0.256	-0.449	0.992	
autumn / summer	1.208	0.34	0.671	0.963	
autumn / winter	1.123	0.316	0.411	0.994	
harvest / spring	0.562	0.182	-1.778	0.386	
harvest / summer	0.773	0.244	-0.815	0.926	
harvest / winter	0.719	0.227	-1.046	0.834	
spring / summer	1.377	0.397	1.110	0.801	
spring / winter	1.280	0.369	0.856	0.913	
summer / winter	0.929	0.259	-0.263	0.999	
Position					
edge / middle	1.767	0.372	2.701	0.007	*
Predator Group					
arthropods / birds	2.886	0.615	4.978	2.00E-06	*
arthropods / rodents	22.798	11.69	6.096	3.30E-09	*
birds / rodents	7.899	4.207	3.880	3.07E-04	*

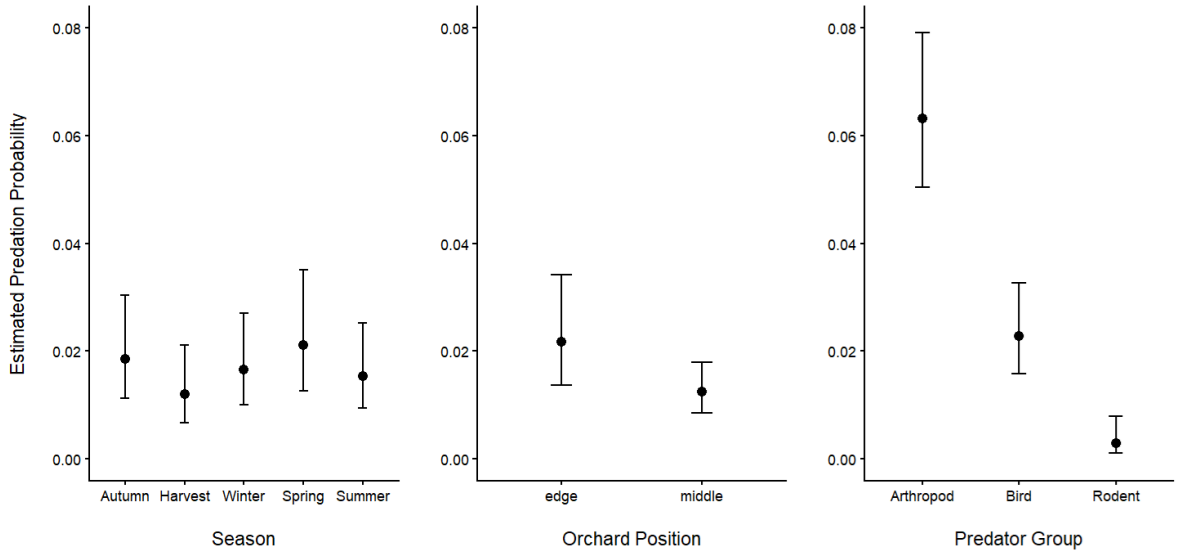


Figure 5.2. Estimated marginal probabilities of artificial caterpillar predation according to season, orchard position, and predator group. Estimated marginal means were derived from a model including additive effects of season, orchard position, and predator group, with orchard included as a random intercept. Points represent estimated marginal means and error bars represent 95% confidence intervals. Estimates for each predictor are averaged across the levels of the other predictors included in the model.

5.4.2 Crop Damage

Four orchards were surveyed in 2024 and five in 2025 (Table S 23). Orchards MN2, KC1 and KC2 were surveyed in both years, while TR was surveyed in 2024 and MN1 and HB in 2025. In 2024, 70 apple trees were surveyed, totalling 374 fruits, compared with 120 trees and 584 fruits in 2025. The mean number of fruits per sampled branch ranged from 3.65 at HB to 5.85 at MN1 (Table 5.4). The mean proportion of undamaged fruit per branch was 79% in 2024 and 72% in 2025 and ranged among orchards from 49% at KC1 to 91% at TR (Table 5.4).

Across both years, 28 fruits showed evidence of bird damage (Figure S 13), comprising 10 fruits in 2024 and 18 in 2025. Fungal damage was more frequent, occurring on 45 fruits in 2024 and 130 in 2025 (Figure S 14). Insect damage was comparatively uncommon, with 17 damaged fruits recorded across both years, comprising seven in 2024 and ten in 2025. The distribution of these damage types among orchards is shown in Figure 5.3.

The NMDS ordination provided a two-dimensional representation of variation in proportional fruit-damage composition (stress = 0.097; Figure 5.4). PERMANOVA provided no evidence that damage composition differed with orchard position ($F = 1.83$, $R^2 = 0.042$, $p > 0.05$), year ($F = 0.96$, $R^2 = 0.022$, $p > 0.05$), or branch height ($F = 0.23$, $R^2 = 0.011$, $p > 0.05$; Table 5.5A). Together, these predictors accounted for approximately 7.5% of the variation in damage composition, with most variation remaining unexplained ($R^2 = 0.924$). Tests of multivariate dispersion showed no significant differences in dispersion between orchard positions, years, or branch-height categories (all $p > 0.05$; Table 5.5B).

Table 5.4. Summary statistics for crop damage surveys across the six orchards surveyed. Sample size refers to the number of independent replicates (trees surveyed). Arithmetic mean, standard deviation (SD) and standard error (SE) are calculated per orchard (A), position (B), and year (C). Means, SDs and SEs are given for total fruits surveyed, yield (as a percentage), height of branches in centimetres, and bird, arthropod, and fungal damage marks. Yield was calculated as a proportion of fruits in each branch that did not contain damage marks.

		Total Fruits			Yield (%)			Height of Branches			Bird Damage			Arthropod Damage			Fungal Damage		
	sample size	Mean	SD	SE	Mean	SD	SE	Mean	SD	SE	Mean	SD	SE	Mean	SD	SE	Mean	SD	SE
by orchard																			
MN1	20	5.85	4.63	1.03	74.89	26.29	5.88	145.35	51.01	11.41	0.5	0.830	0.180	0.1	0.31	0.07	0.7	1.13	0.25
MN2	30	4.8	3.23	0.59	64.02	30.14	5.50	153.67	48.83	8.92	0.33	0.660	0.120	0.2	0.48	0.09	0.8	1.00	0.18
KC1	30	5.6	3.54	0.65	48.75	32.82	5.99	128.97	49.27	9	0	0.000	0.000	0.07	0.25	0.05	2.6	2.24	0.41
KC 2	30	5.63	4.05	0.74	72.00	26.96	4.92	132.57	53.12	9.7	0.07	0.250	0.050	0.1	0.4	0.07	1.27	1.62	0.30
HB	40	3.65	1.89	0.30	86.99	24.97	3.95	135.82	52.54	8.31	0	0.000	0.000	0.03	0.160	0.02	0.42	0.68	0.11
TR	40	5.35	2.40	0.38	91.16	19.63	3.10	128.02	54.75	8.66	0.15	0.360	0.060	0.070	0.270	0.040	0.100	0.30	0.05
by position																			
edge	136	4.95	3.13	0.27	78.63	28.02	2.40	138.07	51.88	4.45	0.12	0.430	0.040	0.070	0.280	0.020	0.800	1.46	0.13
middle	54	5.28	3.63	0.49	64.32	33.06	4.50	132.20	52.51	7.15	0.20	0.490	0.070	0.150	0.410	0.060	1.220	1.54	0.21
by year																			
2024	70	5.34	3.040	0.360	79.01	28.87	3.451	130.36	51.33	6.140	0.14	0.390	0.050	0.100	0.350	0.040	0.640	1.26	0.15
2025	120	4.87	3.410	0.310	71.97	30.70	2.803	139.93	52.26	4.770	0.15	0.480	0.040	0	0	0	1.080	1.60	0.15

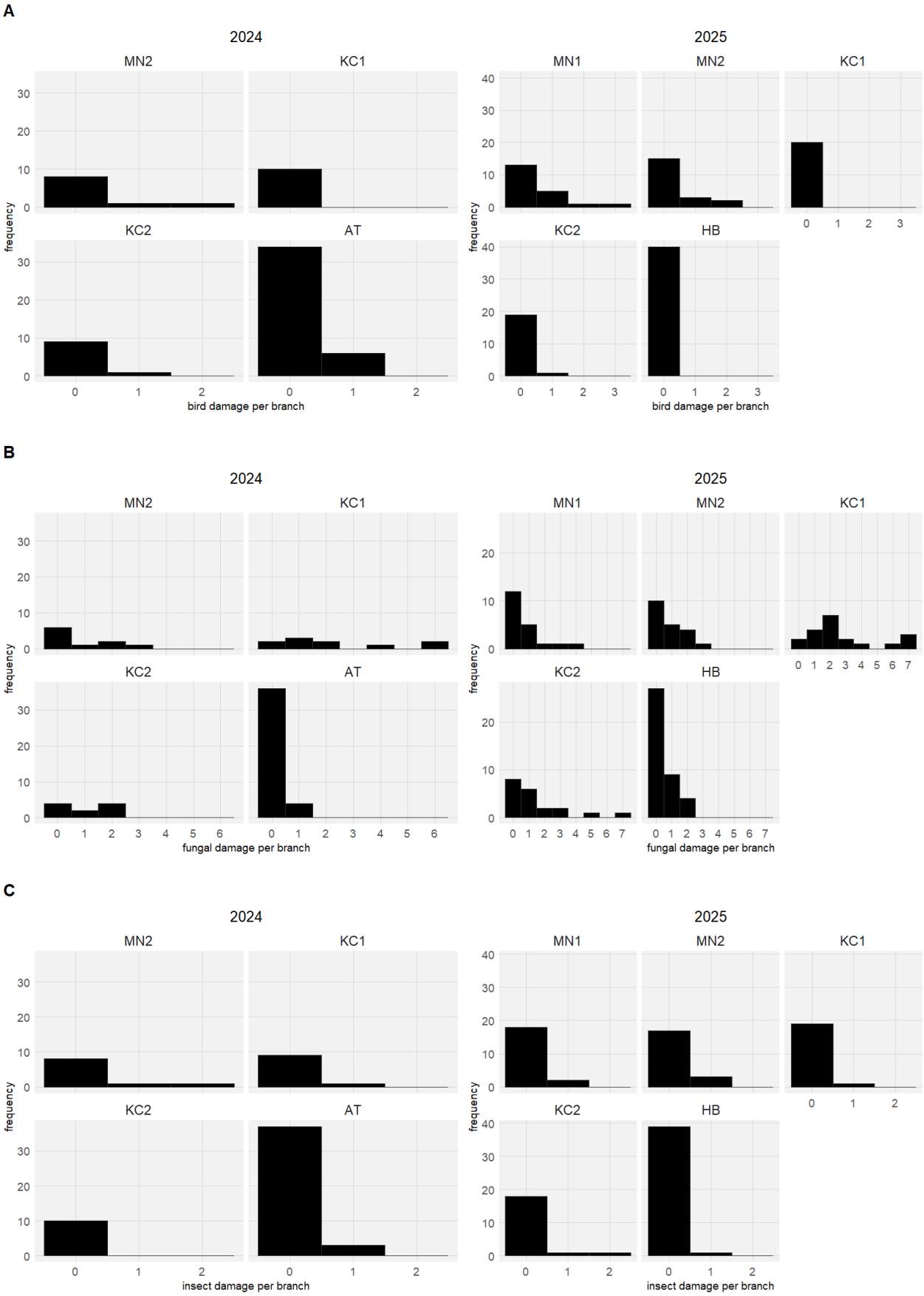


Figure 5.3. Frequency distributions of branch-level crop damage across orchards in 2024 and 2025. Histograms show the number of fruits per branch exhibiting different levels of (A) bird damage, (B) fungal damage, and (C) insect damage. Panels for each year are faceted by orchard.

Table 5.5. Results of (A) permutational multivariate analysis of variance (PERMANOVA) testing variation in the composition of bird, insect, and fungal fruit damage in relation to orchard position, year, and branch height, and (B) tests for homogeneity of multivariate dispersion for each factor. Damage composition was expressed as the proportion of sampled fruit exhibiting each damage type, and analyses were based on Bray-Curtis dissimilarities. PERMANOVA permutations were restricted within orchard to account for repeated sampling. R^2 represents the proportion of multivariate variation explained by each term.

A. PERMANOVA

term	Df	SumOfSqs	R^2	F	p
Position	1	0.400	0.042	1.832	0.053
Year	1	0.210	0.022	0.961	0.473
Height	2	0.101	0.011	0.231	0.972
Residual	40	8.734	0.924	NA	NA
Total	44	9.448	1	NA	NA

B. Homogeneity of Multivariate Dispersion	Df	F	p
Position	1	0.271	0.622
Year	1	1.965	0.171
Height	2	0.538	0.59

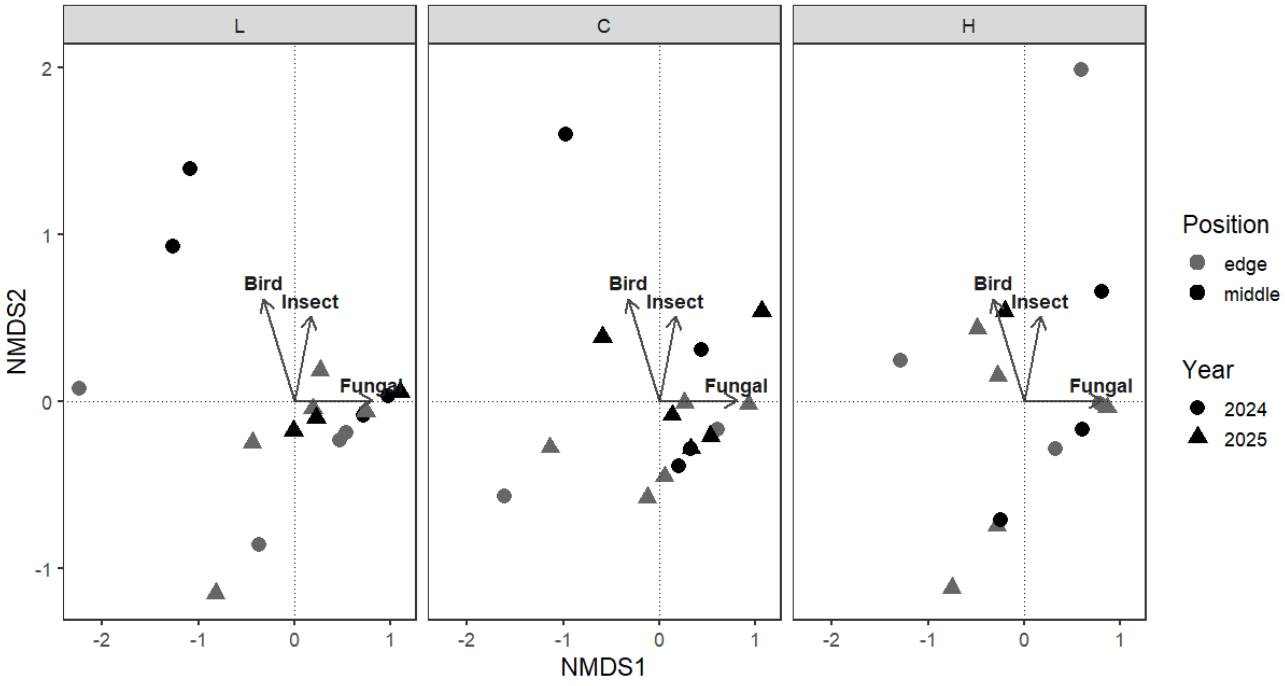


Figure 5.4. Non-metric multidimensional scaling (NMDS) ordination of fruit damage composition across apple orchards surveyed in 2024 and 2025. Damage composition was based on the proportional incidence of bird, insect, and fungal damage and Bray-Curtis dissimilarities. Points represent unique orchard x year x position x branch-height sampling units. Orchard position is indicated by grey (edge) or black (middle) shades, while shapes indicate the year (circles for 2024 and triangles for 2025). Panels represent branch-height categories (L = low, C = chest height, H = high). Vectors indicate the direction of association of bird, insect, and fungal damage with the ordination axes. The two-dimensional ordination had a stress value of 0.097.

5.5 Discussion

Results from the SPR experiments showed that the main predators of sentinel caterpillars in the apple orchards surveyed were arthropods, with birds contributing substantially lower predation rates and rodents the lowest overall rate. Predation probability was higher at orchard edges than in orchard middles but did not differ significantly among seasons. Crop-damage surveys showed that fungal damage was substantially more frequent than damage attributed to birds or insects, while multivariate damage composition did not differ significantly with orchard position, year, or branch height.

5.5.1 Provision of Pest Control as an Ecosystem Service

Previous SPR studies have indicated that edges of orchards show more predation rates than the middle (Kolkert et al. 2021), a pattern that was confirmed in this study. This was the case even with an overall higher deployment of sentinel prey in the middle of orchards, indicating the strength of this result. Artificial sentinel prey caterpillars were significantly more attacked by arthropods than birds or rodents, a pattern recognised in other studies (Ferrante et al. 2014, 2017a, 2017b). In contrast, predation marks by birds on recovered caterpillars were only recorded for 2.1% of the recovered sentinel prey, compared to 24-50% reported in other studies (Ferrante et al. 2014, 2017a, 2017b). Potentially due to these lower numbers, no significant seasonal differences in predation probability were detected. For caterpillars showing evidence of predation, a clear pattern emerged in which attacks were attributable either to a single taxonomic group (birds, rodents, or arthropods) or to combined predation by birds and arthropods or rodents and arthropods. No caterpillars showed evidence of predation by both rodents and birds, which may be explained by the strong scent left by rodents during foraging (Koivula et al. 1997).

The relatively low number of bird predation marks recorded on artificial caterpillars may have several, non-mutually exclusive explanations. First, the abundance and composition of insectivorous birds using the orchards may have limited interactions with the sentinel prey. Second, birds present in the orchards may not have recognised or selected the artificial caterpillars as prey. Third, characteristics of sentinel-prey deployment, including prey presentation and sampling effort, may have affected the probability of detecting bird attacks.

Regarding the first explanation, several native and introduced bird species recorded in the orchards are known to consume caterpillars or other arthropods, including silvereyes (*Zosterops lateralis*), fantails (*Rhipidura fuliginosa*), grey warblers (*Gerygone igata*), shining cuckoos (*Chrysococcyx lucidus*), blackbirds (*Turdus merula*), and mynas (*Acridotheres tristis*) (Heather et al. 2015). However, the presence or abundance of these species does not necessarily translate directly into predation on sentinel prey, as birds differ in diet and foraging behaviour. Fantails, for example, predominantly capture prey in flight (McLean 1989) and may therefore have been less likely to attack stationary artificial caterpillars.

The relatively small gaps between branches and foliage within apple canopies may also have restricted access to the sentinel prey for species that require greater space for aerial or manoeuvring foraging, potentially including fantails and grey warblers. Grey warblers and shining cuckoos were also recorded infrequently across the study orchards. Silvereyes, although abundant during parts of the year and known to increase their consumption of invertebrates during the breeding season, were largely absent from the orchards during spring

(as shown in Chapter Three). These patterns may have reduced opportunities for attacks on stationary artificial caterpillars. This possibility could not be directly evaluated in the present study, and the relationship between insectivorous bird abundance and pest removal may be more complex than suggested by studies reporting associations between bird communities and pest-control activity (Martínez-Sastre et al. 2020).

Orchard management may further influence interactions between birds and arthropod prey. Insecticide use can complicate evaluations of pest control by birds by altering the availability of natural arthropod prey (Garfinkel et al. 2020), and all orchards except KC1 regularly used pesticides. However, as shown in Chapter Three, the organic orchard did not support greater bird species diversity or abundance than the other study orchards. Pesticide use alone is therefore unlikely to explain the relatively low frequency of bird attacks observed here, although effects on arthropod availability and bird foraging behaviour were not directly assessed.

The second explanation concerns the extent to which artificial caterpillars represent prey that birds recognise and choose to attack. Even where insectivorous or omnivorous birds were present, individuals may have failed to detect the artificial caterpillars, recognised but rejected them, or preferentially selected naturally occurring prey. Artificial caterpillars therefore provide an index of interactions with standardised model prey rather than a direct measurement of consumption of orchard pests. This distinction is particularly important when interpreting bird-mediated pest control, because species-specific foraging strategies may influence the likelihood that a bird encounters and attacks stationary artificial prey.

A third explanation involves the deployment of the sentinel prey. Sentinel-prey experiments using artificial caterpillars have frequently attached prey to cardboard panels or placed them on sticks or other conspicuous substrates (Ferrante et al. 2014; Peisley et al. 2016). In the present study, caterpillars were instead deployed directly on tree branches and leaves to more closely represent prey encountered by birds foraging within orchard vegetation. Although this provided a more natural presentation, it may also have made the caterpillars less conspicuous and reduced their probability of detection. Differences in deployment methods may therefore contribute to the lower attack rates observed here relative to those reported in other artificial-prey studies (Ferrante et al. 2014, 2017a, 2017b). In addition, the relatively small number of bird predation events recorded limits the precision with which patterns in bird attacks can be inferred, even though the overall number of sentinel prey deployed was substantial.

The use of real sentinel prey, either dead or alive, may produce different predation rates from artificial prey, as suggested by previous studies (Peisley et al. 2016; Lövei & Ferrante 2017). However, deploying live agricultural pests in commercial orchards presents practical and biosecurity concerns. Growers may understandably be reluctant to introduce crop pests such as codling moth (*Cydia pomonella*) into orchards in which considerable resources are invested in pest suppression. Moreover, relatively few studies have compared artificial and real sentinel prey under the same field conditions (e.g., Peisley et al. 2016), limiting the extent to which differences between the two approaches can currently be generalised.

Despite these limitations, artificial prey provided a practical and standardised method for repeated monitoring across orchards and seasons, including winter conditions and periods of high UV exposure during spring and summer. The use of non-toxic plasticine also avoided the risks associated with introducing live pest organisms into commercial orchards. Nevertheless,

the observed attack rates should be interpreted as evidence of interactions between predators and artificial sentinel prey rather than as a direct estimate of the magnitude of pest-control services provided by birds in apple orchards.

5.5.2 Provision of Crop Damage as a Disservice

Approaches to quantify crop losses tend to vary considerably and are often not comparable between sites, as different units of measurement and spatial scales are used (Gutierrez-Arellano & Mulligan 2018). By applying a consistent survey method across orchards and years, this study assessed damage attributed to birds, fungi, and insects during the harvest seasons of two consecutive years across orchards with different management practices.

Most recorded crop damage was attributed to fungi, and potentially other pathogens, while comparatively few fruits showed evidence of bird or insect damage. Damage composition did not differ significantly with orchard position, year, or branch height, suggesting that these factors did not explain substantial variation in the relative occurrence of the three damage types. Fungal damage nevertheless accounted for most of the observed damage, particularly at the Kāpiti Coast orchards. At the organic orchard KC1, fungal control was limited to copper-based spraying. In 2025, growers at both Kāpiti Coast orchards also reported a dry summer followed by wet conditions before harvest, which may have favoured fungal damage. These observations provide potential explanations for the patterns recorded but were not formally tested in the present analysis.

Bird-related crop damage was low overall, although MN1 and MN2 accounted for a comparatively large proportion of the recorded bird-damaged fruit. Silvereyes were particularly abundant at MN1 during winter and are known to consume fruit, as discussed in Chapter Four, providing one possible explanation for the bird damage observed at this orchard. Fruit consumption by tūī (*Prosthemadera novaeseelandiae*) was also observed at MN2. However, because orchard identity and species abundance were not tested as predictors of crop damage in the present analysis, these observations should be regarded as possible ecological explanations rather than evidence of causal relationships.

Taken together with the high incidence of fungal damage, these results indicate that within the orchards surveyed, birds were not the predominant source of recorded crop damage. This contrasts with much of the New Zealand horticultural literature, where birds have traditionally been considered the major contributors of crop damage (Baker 1980; Davies et al. 2000; Saxton et al. 2004b). Even when measured bird-related damage is low, fruit growers frequently perceive birds as principal pests within orchards (Wright & Inglis 1979; Kronenberg 2014; Kross et al. 2018).

Birds have been regarded as agricultural pests throughout the long history of crop production, with deterrent methods documented as early as ancient civilisations (Abdelhakim 2020). Chapter Two highlighted how birds may be targeted as crop-damage culprits even when evidence attributing losses to them is limited (Chapter Two, Ferrari et al. 2025). The findings of the present study reinforce the value of directly assessing crop damage rather than relying solely on expectations of damage. Although field-based damage assessments can be more expensive and time-consuming, they can provide more direct estimates of crop damage (Elser et al. 2019).

The interpretation of crop damage as an ecosystem disservice is further complicated by evidence that individual bird species may provide benefits to some crops or during some periods while causing damage under other circumstances (Kross et al. 2020). Crop damage can vary spatially and temporally with bird behaviour, population dynamics, and crop phenology (Triplett et al. 2012). Furthermore, the presence or abundance of birds within an orchard does not necessarily correspond to their contribution to crop damage, because species differ substantially in their likelihood of consuming fruit. Consequently, perceptions of bird damage based primarily on bird presence may overestimate their contribution to crop losses (Lindell et al. 2012; Elser et al. 2019).

5.5.3 Assessing Pest Control and Crop Damage Simultaneously

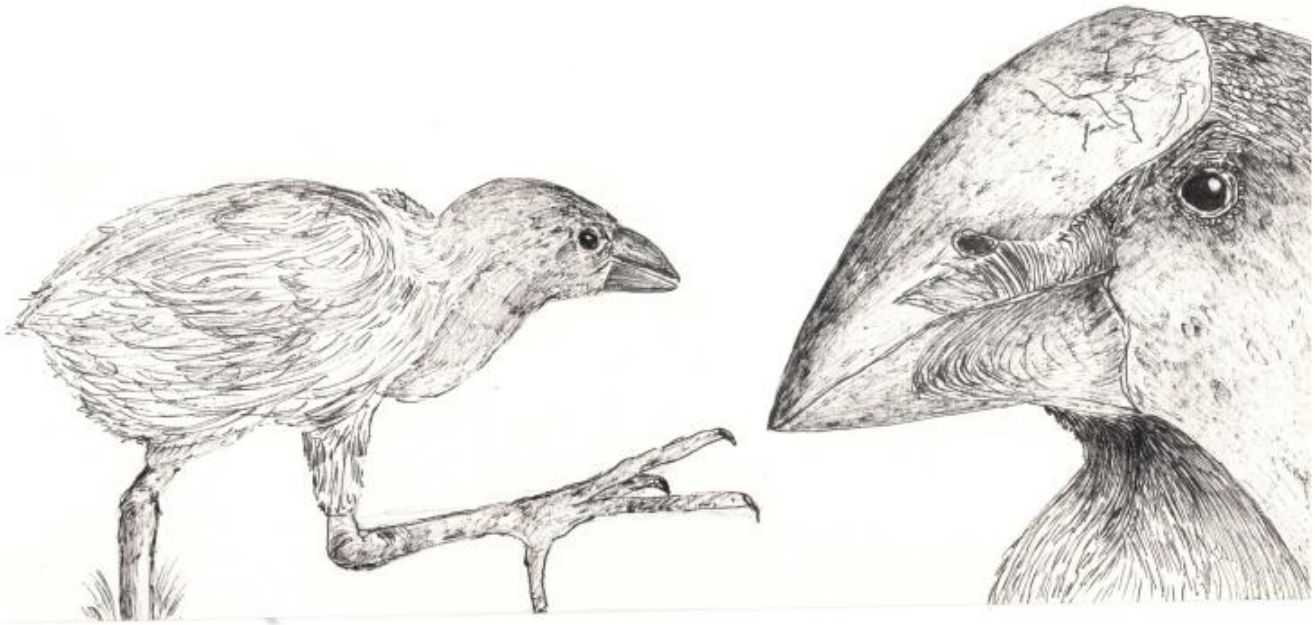
Most studies on ecosystem services or disservices tend to study them separately (Chapter Two). The objective of this study was to assess the potential for birds to provide ecosystem services and disservices simultaneously in New Zealand apple orchards. However, the limitations identified through the sentinel prey removal experiment constrain the extent to which pest control and crop damage can be evaluated concurrently. Although relatively little crop damage was attributed to birds, particularly compared with fungal damage, the extent to which birds contribute to pest control remains uncertain and warrants further investigation.

5.5.4 Implications for the New Zealand Apple Industry

New Zealand is a small export-oriented nation, yet it has maintained a leading position in the global apple market through the development of innovative production practices and cultivars (Christopher 1999). Even the smaller production systems included in this study supported at least five apple varieties, with each site containing at least one cultivar not recorded elsewhere. Such cultivar diversity may itself contribute positively to agricultural biodiversity and should therefore not be considered synonymous with agricultural intensification. Nevertheless, other developments associated with the Green Industrial Revolution have driven agricultural intensification at unprecedented scales, characterised by increased pesticide inputs and reliance on heavy machinery (Pretty & Bharucha 2014). Compounding the issue, agriculture intensification is a leading global cause of biodiversity declines, including among avian species (BirdLife International 2018).

Even with increased innovation and technological advances, many smaller New Zealand growers have been forced out of the industry due to hardships and global economic crises, which have also affected larger operations (Dobbs & Rowling 2006). Under this scenario, factors within crop systems that can reduce damage to crops and bring increased revenue to growers are of utmost importance. Reducing pesticide frequency in horticulture not only addresses consumers' concerns about adverse health effects but may also reduce impacts on biodiversity (MacLeod et al. 2012). Using birds as habitat indicators can not only guide sustainable management practices (Coleman 2010), but also enhance market access for growers by signalling sustainable orchard practices to the wider public (Blackwell et al. 2005). However, to realise these benefits, growers must balance potential damage caused by birds against their potential contribution to pest control and the increased appeal to a 'green' market associated with the presence of native species.

These benefits can only be properly assessed if ecosystem services and disservices are recognised at the species or taxonomic-group level. In the next and final chapter, I synthesise the findings on bird species presence and behaviour in orchards and consider what these patterns indicate about their potential contributions to pest control and crop damage.



Chapter 6 General Discussion

This thesis was born out of a dream and a concern, both derived from Predator Free New Zealand 2050. This incredibly ambitious project aims to rid the entire country of the main mammalian pests that restrict native species populations, to the point that very few people see some of them. The dream is one day seeing New Zealand's native species thriving everywhere. A day where tīeke (*Philesturnus carunculatus*), hihi (*Notiomystis cincta*), kākāriki (*Cyanoramphus spp*) and many other avian species can feast on insects, reptiles, and plants in our backyards. The concern is that a dream could turn into a nightmare if flocks of kākāriki, kākā (*Nestor meridionalis*) or New Zealand pigeons (*Hemiphaga novaeseelandiae*) decimate fruit trees in orchards. What if the tīeke establish themselves in orchards and not only feed on insects, but also on the crops? Realistically, we have not been concerned about these issues because the overlap of endemic and/or endangered birds in New Zealand and human-modified landscapes was tenuous, as many species are confined to offshore islands and fenced sanctuaries. But is it so rare for a native New Zealand bird to be present in horticultural systems? How much do we actually know about the use of human-modified land by these birds? How much do we know about the use of orchards, arguably a type of forest (albeit a rigid and often homogenous one), by these native species? Which of the native New Zealand birds, currently imprisoned by exotic mammalian predation pressure, could adapt to modified landscapes when freed from this pressure?

Each chapter of my thesis aimed to bring us closer to answering these questions, and as it is always the case, each answer led to many other questions. In many cases, my answers could be improved by increasing the sample size, the common burden of PhD theses. This was the result of one person's effort, which could only be at a few sites per season, only one site at a time. Nonetheless, being so close to the birds continuously, day after day and season after season, allowed me to start unravelling the holistic interactions of these precious native birds with introduced species, each other, and the system where they are present. In this discussion, I aim to remind the reader of the main findings of this thesis, presenting the next questions to be answered along with them. This discussion is organised to follow the chapter-by-chapter structure of the thesis to facilitate reading, but connections are made between them to tie the ideas together in a way that would not be possible within the thesis given its manuscript-for-publication style.

6.1 What Is Known for Birds as Providers of Ecosystem Services and Disservices?

During the initial stages of this project, I found that while there were increasing numbers of studies investigating ecosystem services and disservices provided by avian species in horticultural systems, reviews would often fall short of trying to condense a global view on the subject. My global systematic review of the provision of ecosystem services and disservices by birds in horticultural systems revealed that researchers often studied a particular system without considering avian community identity in the system (Ferrari et al. 2025). Very few studies investigated the permanence of native or endemic species in horticultural systems (Jones et al. 2005b; Gámez-Virués et al. 2007; Kross et al. 2012; Brambilla et al. 2017; Maas et al. 2018; da Silva et al. 2022). This gap clearly represents a missed opportunity to explore how food

production systems can support the conservation of native avifauna, a pressing issue in the context of rapid land use changes and widespread human-managed systems.

Additionally, many studies did not report on orchard management practices, hindering understanding of how different practices (e.g. organic and conventional management) may influence the provision of services and disservices. However, establishing the effects of management practices requires more than documenting differences among orchards, as management occurs alongside variation in factors such as orchard structure, surrounding habitat, location, and crop characteristics. This thesis was similarly unable to isolate the effects of individual management practices because the orchards represented existing production systems rather than experimentally controlled management treatments. Disentangling these effects would require a study specifically designed and sufficiently replicated to compare management systems while accounting for potentially confounding environmental and production variables.

Managing horticultural systems to maintain biodiversity while sustaining crop yield remains a significant conservation challenge (Yahia et al., 2017). Evidence from agricultural systems indicates that biodiversity can support crop production through ecosystem services such as pollination and biological pest control, with the richness of service-providing organisms contributing to these functions independently of their abundance (Dainese et al., 2019). Future research using targeted and sufficiently replicated study designs could therefore help establish which horticultural management practices support biodiversity and associated ecosystem services while maintaining crop production.

Overall, birds are strongly recognised as providers of ecosystem services (ES) in food production systems and, more recently, of ecosystem disservices (ED). Although a variety of ES and ED were reported for different horticultural systems (e.g. fertilising, disease control, disease spread, pollination, seed predation), pest control and crop damage are the most studied service and disservice across the literature (Ferrari et al. 2025). The reasons for this preference are twofold. Firstly, both pest control and crop damage are important components of the dynamics between wildlife and humans, as these can directly impact food production systems as benefits or damages. Both invertebrate and bird ‘pests’ can cause a substantial impact on crops (Collinge 1918; Ferguson et al. 2019; Montràs-Janer et al. 2019; Sausse & Lévy 2021). Secondly, pest control and crop damage are arguably easier to measure when compared to other services and disservices. Calculating the costs of replacing natural biological control agents is simple (Power 2010), and crop damage surveys, although time-consuming, can be done with a low budget. However, the more recent influx of complex techniques to study ES and ED at orchards (e.g. spatial landscape analysis, next-generation sequencing) and the integration of several different methods indicate the capability of handling larger volumes of data across wider temporal and spatial scopes (e.g. Peisley et al. 2016; Kross et al. 2020; Martínez-Sastre et al. 2020; Taylor et al. 2022).

A large issue evidenced by the review was the fact that crop damage is consistently overestimated, with studies reporting on it even without measuring the rates of damage (Ferrari et al. 2025). Some studies simply reported on the damage as assessed by growers (Dawson & Bull 1970; Manyama et al. 2014; Musiwa & Mhlanga 2020). Even in New Zealand, with a long history of avian conservation, growers will consider birds as the primary cause of crop damage even if the true extent is uncertain (Watkins et al. 2000). Although it is necessary to acknowledge the inherent connection growers have to their lands, it is also important to note

that social and economic factors all tie into the perceptions and attitudes of farmers towards wildlife in their systems (Greiner et al. 2009; Lazaridou & Michailidis 2023). Thus, ecosystem services provided by birds might be 'concealed' by crop damage, as growers will often mainly care about what can be directly observed (Huang et al. 2023). Once a species is categorised as a pest, it will be treated accordingly (Caughley & Sinclair 1994), often involving shooting at the birds even when not legally sanctioned (Coleman & Spurr 2001; Htay et al. 2024). Birds' long-standing reputation as pests often leads to the unjustified targeting of species, and a greater effort is needed to distinguish between harmful and beneficial species through empirical, species-specific evaluations.

Finally, another topic highlighted by the review was that ecosystem services and disservices tend to be studied separately, hindering their comprehension on a biological continuum (Triplett et al. 2012). By not considering their synergetic dynamics, researchers might underestimate negative outcomes when they interact in unexpected ways (Weyell et al. 2015; Gonthier et al. 2019). Effectively managing bird activity within food production systems requires potentially promoting desirable functional traits and implementing species-specific control measures. These measures may involve enhancing community diversity and reducing agricultural intensification to maintain high levels of biodiversity. However, these practices will require further empirical comparison to determine their efficacy and broader impacts.

Once global perspectives were assessed, a current background of expected species was investigated, to help identify and assess the identity of the bird communities occurring within orchard systems. Citizen data was essential for this information, as eBird records were able to provide data on almost 20 years of bird observations across the entire country. Although there's always an inherent bias to citizen science initiatives (Johnston et al. 2021), eBird has proved to be reliable and an excellent tool to account for large temporal and/or spatial datasets (Sullivan et al. 2009; Wood et al. 2011).

Across 19 years, 92 species were observed at least four times within horticultural systems, including 56 native and 36 introduced species. This background study allowed a better understanding of which species to expect in my own fieldwork and helped highlight the importance of horticultural systems by recording threatened species within these systems. These included New Zealand falcons (*Falco novaeseelandiae*, seen also during the fieldwork portion of this thesis), which are recovering from important population declines (Seaton & Hyde 2013). Additionally, North Island brown kiwi (*Apteryx mantelli*) and kākā are currently under the Vulnerable category of extinction risk, while black-fronted terns (*Chlidonias albostriatus*) are Endangered and the New Zealand dotterel (*Anarhynchus obscurus*) is currently considered Critically Endangered (IUCN 2024).

6.2 What Bird Species are Actually in Apple Orchards, and How Are They Using These Systems?

A year of bird surveys provided a reliable estimation of the abundance and species richness of the apple orchards surveyed. Considering the six sites, I found 22 native and 24 introduced bird species. These 46 species contrast with the 92 species compiled from the eBird dataset in the previous chapter. Spanning the entire country and across a variety of horticultural systems, it is not surprising that the eBird dataset had twice as many species as the dataset for the apple

orchards. Comparing them revealed 50 species unique to the eBird dataset and four unique to the apple orchard dataset. The unique species in orchards were two introduced (redpoll *Acanthis flammea* and rainbow lorikeet *Trichoglossus moluccanus*) and two native species (morepork *Ninox novaeseelandiae* and long-tailed cuckoo *Urodynamis taitensis*). All four species were seen in low numbers and in very few surveys, indicating their uncommon status in the orchards. Moreporks, for example, were only heard, not seen, and only at orchard HB during early mornings, reflecting the species' nocturnal habits and my diurnal surveys. Their presence in orchards is likely to be more common than I recorded, as the high levels of small birds and rodents in orchards may make these systems very profitable for moreporks.

Long-tailed cuckoos nest in New Zealand, migrating to Australia and the Pacific Islands outside of their breeding season (Gill 2023). Their low presence among the orchards was not surprising, as long-tailed cuckoos will mainly parasitise nests of whiteheads (*Mohoua albicilla*) and yellowheads (*Mohoua ochrocephala*), two native species that are threatened by exotic mammalian predation and are considered forest-dependent (Elliott 1996; Leuschner 2013). Where farmland edges protected areas, whiteheads and long-tailed cuckoos can be seen in the agricultural landscape (I. Castro, pers. comm.). These species may therefore be better represented in the future after PFNZ 2050.

The rainbow lorikeet is an unwanted species in New Zealand, after an illegal release of dozens of individuals in the Auckland area in the 1990s (Miskelly 2015). A few individuals were recorded in the current fieldwork over 500km away from the Auckland area, in the Kāpiti Coast. Although these individuals could be descendants of the Auckland population, the most likely scenario is that they were lost pets from owners in the region, as parrots feature as the main group of lost bird pets in the country (Stanley et al. 2023).

Overall, I found that species richness and abundance reflected a composition of generalised introduced and native species that can tolerate highly disturbed landscapes. Few studies have focused on bird communities across New Zealand horticultural systems, as the main goal of such studies is often to investigate crop-damaging species. By focusing on a few 'main culprits', such as silvereyes (*Zosterops lateralis*), blackbirds (*Turdus merula*), and house sparrows (*Passer domesticus*), research has largely ignored the presence and dynamics of the wider avian composition and underestimated the potential conservation value of these systems. New Zealand falcons, especially, were notable due to their recognised decline due to agricultural intensification, but also because of their potential as biological control agents of bird species considered 'pests' (Kross et al. 2012; Horikoshi et al. 2017).

Another example was the presence of threatened species in the dataset, such as black-billed and red-billed gulls (*Chroicocephalus bulleri* and *C. novaehollandiae scopulinus*, respectively) and the long-tailed cuckoo. However, the use of eBird records limits the extent to which these observations can be interpreted as evidence of habitat use. Although records were spatially associated with areas classified as cropland, the observational data do not provide sufficient context to determine whether individuals were actively using horticultural habitats, using adjacent habitats, or were recorded incidentally, for example while passing over these areas. Consequently, the occurrence of threatened species in the dataset should be interpreted as evidence of their presence within or in close association with horticultural landscapes rather than evidence that these systems provide suitable habitat or conservation value for those species.

Seasonal shifts were evident in avian community composition. Spring and summer had broadly similar communities, and winter was the most distinct season. I proposed three likely mechanisms to explain those results: 1. a winter decline in introduced species' abundance in winter; 2. the presence of seasonal visitors; and 3. the seasonal shifts in the abundance of silvereyes. Although some authors have reported declines in some of the introduced species' abundance in winter in their native ranges (Chamberlain & Crick 1999; Bradbury et al. 2000; Gillings et al. 2005; Schwemmer et al. 2008), I did not detect any declines in this study. Seasonal spring and summer visitors were rare across all surveys, and therefore, their abundance would influence species richness across seasons, but their presence or absence could not be the primary explanation for seasonal variation in community composition. The most likely mechanism to explain the differences between the seasons was therefore the changes in silvereyes' abundance. As the most abundant species in most orchards, their sharp dominance over winter communities across the orchards surveyed helps explain the distinctiveness of that season's composition.

The way the species used the spatial components of the orchards also varied, reflecting ecological niches and foraging strategies of the species present. Foraging communities were separated into overhead, upper strata, and ground foragers, with no species showing preference for the lower strata within the crop trees, and all species avoided human structures. Although behavioural explanations for this result could not be confidently stated, it seems that even for species adapted to highly disturbed environments, such as the introduced species, their persistence is still tied to more natural components of the human-managed systems. Further research should include a behavioural focus on potential reasons for an apparent avoidance of human structures.

I also investigated the presence of exotic mammals within apple orchards. With the recognised impact of exotic mammalian predators on New Zealand avifauna (Blackburn et al. 2004; Russell et al. 2015; Murphy et al. 2019), it was perhaps tempting to expect higher mammalian densities to negatively impact the abundance and community composition of bird species across the sites. However, I concluded that the avian community within orchards is already filtered by species that must adapt to high levels of human disturbance - heavy machinery, regular tree pruning, pesticide and fungicide spraying - and, additionally, mammalian predators. I was unable to compare the effects of mammalian predators on bird species' abundance directly, and no significant seasonal or orchard differences in predator presence could be detected. This could be linked to the low number of sites, prompting future studies to compare avian communities within horticultural systems in areas of varying degrees of management control of exotic mammalian predators.

This chapter demonstrated that New Zealand orchards can and are functioning as relevant habitats for a broad range of bird species, including natives. Although orchard-level effects were generally weak, large monocultures had the lowest native species richness, evidencing the importance of heterogeneous systems to the persistence of a diverse bird community. A few gaps in knowledge remain after this chapter, including whether birds provide the removal of food waste in orchards as an ecosystem service, and whether there is a trade-off between this service and crop damage when feeding on fruits before the harvest. Silvereyes would be an excellent target for such future studies, where their potential for these roles remains to be identified.

6.3 What Are Some Typical Bird Behaviours in These Systems?

Typical behaviours of different native species highlighted the variable ways they interacted with the orchards. Especially noteworthy was the human avoidance expressed by pūkeko (*Porphyrio melanotus*), which spend a considerable amount of time running or flying away from human observers. As observed elsewhere, pūkeko and their close relatives are often persecuted in agricultural systems due to their behaviour of ripping stems off the ground to feed (Moreno-Opo & Piqué 2018; Razalee & Norazlimi 2023). Although this can mean substantial damage to establishing orchards, in older orchards with mature trees, the pūkeko may be unjustifiably targeted. In fact, in the orchards included in this study, most crop fruit consumption involving native species was due to silvereyes and tūī (*Prosthemadera novaeseelandiae*), which tend to be well-liked species and thus, less vilified.

However, there are also a few caveats to these conclusions. First, given the human wariness of pūkeko, it is likely that fruit predation events were recorded in low numbers as the birds were focused on escaping the prying eyes of the observer. Second, although tūī have sufficiently strong bills to damage fruit, their bill morphology is specialised for nectar feeding and may make them less likely to initiate feeding on intact, firm fruit. Tūī had low observation numbers for apple consumption, and although not tested, there is a possibility that they were feeding on apples that had already been opened by other birds. Additionally, in a pilot study conducted in summer 2024, tūī were observed feeding primarily on yellow plums that were not harvested that year, indicating that they would likely prefer softer fruits to feed on. Nonetheless, I am not advocating for the persecution of tūī or silvereye instead of pūkeko, but growers should challenge their preconceptions and measure the damage caused by birds they consider pests.

Very few dead birds were observed across over 80 surveys. This could suggest that mortality rates could be low due to an abundance of resources, or that any dead birds may be readily eaten or carried away (Shaw et al. 2022). However, it was not possible to assess which of these possibilities, or alternative ones, were at play. Could the swamp harrier (*Circus approximans*), a hunter and carrion eater, and an abundant species across croplands, perform this role? It is still not clear what swamp harriers are doing in the orchards, although hunting behaviours lead to the hypothesis of them using orchards as foraging grounds. Nonetheless, following them around was particularly difficult, given their ability to traverse great distances (Innes et al. 2022). The species is recognised to roost communally (Gurr 1967), but was mainly observed as individuals or pairs at the orchards, once again reinforcing the plausibility of orchards as mainly foraging grounds. Future research should be carried out on the feeding behaviours of swamp harriers within these systems and especially which species they are feeding on. This could help clarify if swamp harriers could disrupt conservation attempts of integrating threatened bird species into human-managed food production systems.

The prevalence of foraging behaviours among several native species within horticultural systems is consistent with findings from other studies (Ke et al. 2024; Zamora-Marín et al. 2025). They highlight the impact of land-use changes in agricultural systems on avian behaviours, which is still relatively underexplored (Ke et al. 2024). Future work should assess the feeding diets of native species that were deemed common in orchards from both the eBird and apple orchards datasets. The diets should be compared for the same species in orchards, their natural habitats (e.g. forests), and urban areas.

6.4 How Can Feeding Habits Translate into Ecosystem Services or Disservices?

Birds' food choices are directly related to which ecosystem services and disservices they can provide within horticultural systems. Therefore, preliminary work was conducted to try to distinguish the species in different feeding guilds, such as carnivores, insectivores, nectarivores, and omnivores. However, it becomes clear that this attempt placed species in boxes that would often limit their overall feeding behaviours. Tūī and bellbirds (*Anthornis melanura*), for example, are classified as nectarivores, but they are closely associated with frugivory and tūī can also often be seen feeding on invertebrates (Craig et al. 1981; Kelly et al. 2006). Therefore, here I used species' feeding guilds as a baseline to understand their primary food sources, and how these behaviours can be translated into potential services or disservices.

The presence of native fruit- and nectar-feeders in orchards might lead to a higher provision of ecosystem disservices than services. The high mobility of New Zealand pigeons and tūī and their flocking behaviours can promote higher levels of crop damage and the spread of invasive fleshy-fruited plants across New Zealand (Innes et al. 2022; MacFarlane et al. 2025). And although these native nectarivores are important pollinators and seed dispersers of native plants (Kelly et al. 2010), these roles might not be as important for fruit crops, which are often self-pollinating, artificially pollinated, or bee-pollinated. Therefore, developing strategies to mitigate their potential damage within orchards becomes increasingly important as mammalian control initiatives release these species from protected forested habitats into food production matrices. Nonetheless, New Zealand pigeons, tūī and bellbirds are well-liked in New Zealand, eliciting positive attitudes from the public. Additionally, as observed personally and through anecdotal reporting, tūī are territorial around their feeding trees and can potentially act as deterrents for other species that feed more heavily on fruit. However, this mechanism has yet to be assessed empirically.

Another curious finding within the orchards was the presence of primarily marine habitat birds, including red-billed gulls and black-backed gulls (*Larus dominicanus*). Although clearly these species wouldn't be engaging directly with the crops, they can still influence ecosystem functions through nutrient recycling and the potential spread of pollutants. These species are also not exclusively marine feeders, and pasture invertebrates can form a significant portion of their diets (Mills 2022; Miskelly 2022). How do these birds relate to the provision of landscape-level ecosystem services and disservices, considering their high mobility and their primary use of habitat outside of horticultural systems? Are they bypassing the orchards as foraging habitats and using them as nesting and roosting grounds? Are they feeding on resources within the food production systems that have yet to be identified? Their roles could be even more significant in horticultural systems close to wetlands and waste dump areas, but this is a topic that requires further research.

The dynamics of carnivorous birds in food production systems are still understudied (McWherter et al. 2025). Although swamp harriers were present in all orchards surveyed and the most commonly observed native bird in the citizen science data, only a few studies were found on swamp harriers feeding on other native species (Stephenson & Minot 2006; Stanes 2011). I could not find studies on their behaviours in horticultural systems. Therefore, their potential for the control of crop damage by preying on other birds has not been tested, as it has been for the New Zealand falcon (Kross et al. 2012). New Zealand falcons, however, are still

uncommon throughout New Zealand, recovering from population declines associated with habitat loss and exotic mammalian predation (Seaton & Hyde 2013). Nonetheless, the potential for native birds of prey to negatively impact the conservation of threatened species in these systems is not yet understood.

Native birds that feed primarily or exclusively on insects are a positive indicator of their potential beneficial role within horticultural systems. Fantails (*Rhipidura fuliginosa*) and welcome swallows (*Hirundo neoxena*) were recorded in most of the orchards surveyed, while grey warblers (*Gerygone igata*) were less common but still present in some of the sites. . Insectivores are particularly sensitive to agricultural intensification (Şekercioğlu et al. 2004; Orłowski et al. 2014). Because these species also thrive with mammalian pest control initiatives (DoC 2020), managing orchards to increase the abundance of insectivores at a low cost for growers can be directly tied to the efforts of PFNZ 2050.

Perhaps not surprisingly, most species recorded during the survey, in number of species and individuals, can be loosely categorised as omnivores. This could be expected, as horticultural birds need to survive in fragmented habitats and tolerate high levels of human disturbance (Garfinkel et al. 2020; Zhang et al. 2021). Due to their generalist behaviours, omnivores could be responsible for providing all ecosystem services accounted for in horticultural systems (pest and weed control, seed dispersal, removal of food waste, soil disturbance, and pollination). Similarly, they could also be providing a variety of ecosystem disservices, including crop damage, predation of pollinators, nectar robbing, weed dispersal, and soil disturbance. Their potential for these services and disservices, however, can only be recognised with species-focused studies.

6.5 Are Birds Acting as Pest Control and Crop Damage Agents at Apple Orchards?

The final data component of this thesis planned to assess the provision of pest control and crop damage simultaneously at the orchards surveyed. However, the unexpectedly low rates of predation marks on the sentinel prey caterpillars raised some concerns about the interpretability of the results, with further research required in these systems to assess whether the findings were influenced by behavioural or deployment constraints. The presentation of the caterpillars in the field followed a more naturalistic design, with caterpillars placed directly on leaves or branches, compared with studies in which artificial prey was made more conspicuous to predators. This may have reduced their detectability and consequently the number of recorded predation events. However, making artificial prey more conspicuous could also artificially increase encounter rates, meaning that the low attack rates observed here may partly reflect predator-prey encounters under a more naturalistic presentation. It remains unclear whether the low number of bird attacks resulted primarily from the presentation of the artificial prey, avoidance or non-recognition of artificial prey by New Zealand birds, or genuinely low rates of interaction with caterpillar-like prey within the orchards.

For crop damage, it became clear that the main culprit of crop loss at the orchards surveyed was fungal infections, not bird damage. Fungal damage was especially prevalent in the Kāpiti Coast region, whereas the larger monoculture orchards in Hawke's Bay and Tasman Region showed lower levels of fungal infection. Fungal damage is a major issue in the apple industry,

affecting the pre-harvest, harvest, and post-harvest stages (Patriarca 2019). Orchard KC1, with its organic certification, was only allowed to control fungal damage with copper spraying. Combined with unfavourable weather conditions for both harvest seasons of 2024 and 2025, according to the grower, the orchard suffered the highest rates of crop damage by fungal infections across sites.

The low incidence of direct bird damage to the crops leads to the conclusion that, for the apple orchards surveyed, birds are not the main drivers of crop damage. However, indirect effects may still occur; birds can increase the risk of fungal infections by damaging the fruits or dispersing fungal propagules (Watkins et al. 2000; Xu et al. 2001; Johansson et al. 2025). At the same time, birds can also help control fungal infections by reducing populations of arthropods that can provide a similar pathway of risk facilitation by damaging the fruits and spreading fungi across the orchard. Evidence for the potential of fungal control by bird species, however, is remarkably lacking in the literature. Therefore, I believe the apple industry would greatly benefit from a deeper understanding of the trade-offs of having birds in these systems regarding the potential to increase or mitigate the risks of fungal infections.

Combining the findings from the previous chapters, it was possible to point out native species likely to have the largest impacts on apple orchards currently. Notably, silvereyes were the dominant species across most sites. Even at Orchard HB, where they were occasionally supplanted by mynas (*Acridotheres tristis*) as the most dominant species, silvereyes were still present in high numbers. As mentioned previously in this chapter, there is a high possibility of their provision of a sanitation service, by feeding on fruits left on trees after harvest and on the ground, and arthropod pest control. However, for winter fruit crops, silvereyes could be potentially very damaging, as this season has a markedly increased abundance. Additionally, for smaller fruit crops, silvereyes can provide compounding damage by pecking on fruits instead of swallowing them whole (Porter et al. 1994; Saxton et al. 2004a), and thus increasing risks of fungal infections. This could be a similar problem for other small birds, such as finches, although observations of fruit consumption for these species were very low. Blackbirds, which are often considered bird pests in New Zealand and elsewhere (Dawson & Bull 1970; Davies et al. 2000; Shwiff et al. 2017), were also surprisingly infrequent in observations of crop damage, indicating that either the perceived consumption of apples by this species has been vastly exaggerated, or the birds in these orchards preferred to consume a mainly arthropod diet year-round. However, as mentioned previously, any inference on the introduced species needs to be considered carefully, as these species were not subjected to follow-up behavioural surveys.

Tūī were also shown to be damaging to crops in areas where their abundance is high. In orchard MN2, for example, they were recorded feeding on yellow plums and apples, taking advantage of the ample seasonal resources. Their potential for provisioning of crop damage, however, will likely be linked to their access to soft-fleshed fruit or mature fruits that are already opened by other birds. Therefore, as PFNZ 2050 advances, we may see higher rates of soft-fruit damage in areas of higher tūī abundance if access to mature fruit crops is not managed, but these mechanisms need to be assessed before control measures are put in place.

Following on the data collected in the data chapters and the advances on mammalian control across the country, inferences can be drawn for additional species, even if they were absent in the current study or recorded in low numbers. New Zealand pigeons are potential trouble for fruit orchards. The species' main threat has been identified as exotic mammalian predation

(Clout et al. 1995), which could explain their low number of observations among croplands across the country (171 observations, Chapter Three) and in the orchards surveyed (summer visitors to Orchard MN2, Chapter Four). With increased mammalian control, the species will likely increase in numbers and form larger flocks. Flocking behaviour has been recognised as a compounded factor of crop damage in other countries, such as Australia, with large groups of frugivorous birds descending into orchards to feed (Tracey et al. 2007). Finally, their generalist feeding habits (Heather et al. 2015) could also lead to increased risk of dispersal of invasive fleshy-fruited plants across New Zealand, an important issue that has not received enough attention (MacFarlane et al. 2025). However, their role in orchards has not been confirmed by empirical evidence. Additionally, New Zealand pigeons have a slow reproductive rate, with a single egg laid for each nesting event (Powlesland 2013), meaning they could take a long time to reach high population numbers. Therefore, their potential as providers of crop damage to orchards is currently speculative, warranting future research on the subject to confirm or disprove these conclusions.

Not only are fruit-damaging species thriving under mammalian control measures. The removal of invasive predation pressure has led to an increase in fantail numbers (DoC 2020). Their behaviour of catching most of their prey on the wing (Moeed & Fitzgerald 1982) makes fantails effective aerial insectivores of moths, flies and wasps, all potential causes of crop damage. However, their movement, range sizes, and overall behaviour have seldom been assessed (Innes et al. 2022). Therefore, further studies are needed on the fantail consumption of insect pests inside the orchards to assess the realised or potential role of a biological control agent.

Introduced species also warrant consideration in these systems, even if they were not the focus of this thesis. Starlings (*Sturnus vulgaris*) and blackbirds, for example, have been recognised as both abundant visitors to New Zealand orchards (Davies et al. 2000; Shaw et al. 2022) and as providers of crop damage (Dawson & Bull 1970; Watkins 1999; Saxton et al. 2004a). However, starlings have also been shown to feed extensively on grass grubs, an agricultural pest, with up to 90% of their diets being composed of arthropods (Coleman 1977). In that regard, starlings could also be providers of pest control. At the same time, starlings are also recognised as aggressive competitors of native cavity-nesting birds (Linz et al. 2007), although similar information is lacking for New Zealand. PFNZ 2050 could lead to disadvantageous situations, where some native species are threatened by competition from introduced birds released from predation pressure (Fea et al. 2020). These questions remain unanswered but raise important concerns that need to be addressed for the overall success of the eradication program.

6.6 Limitations and Recommendations

This project had limitations that influenced the data collected during the fieldwork. Categorisations of avian behaviours, for example, were mainly guided by pilot studies conducted at orchards MN2, KC1 and KC2 during spring 2023 and summer 2024. These preliminary surveys helped identify the most common behaviours recorded, leading to the nine categories analysed in Chapter Four. However, other studies have simplified categories into smaller, discrete groups, such as only reproductive, foraging, and passive behaviours (e.g. Ke et al. 2024). I chose not to simplify the categories in order to capture subtle differences in bird

behaviours; however, having too many categories may have inflated the models and reduced the ability to detect predictive effects.

In retrospect, I should have paid closer attention to the regularity and intensity of pesticide spraying within the orchards, because these can be highly toxic and directly affect bird presence (MacLeod et al. 2012). However, restrictions prohibiting visitors inside the orchards for 24 hours after spraying made it challenging to compare bird activity before and after pesticide applications. Future studies should record detailed information on pesticide types at each site and assess immediate bird responses to their application.

I did not track individual species continuously throughout a survey period, as the goal was to sample entire bird communities. Thus, I could not determine whether species were more active at specific times of the day, as has been done in other studies (Watkins 1999), where video camera footage was used to record the species causing crop damage. This was a methodology I explored in the pilot studies, but it was time-consuming and many species were wary of the equipment. Collecting faecal samples could have provided information on the diets of native species; however, I was unable to acquire the necessary permits in time. Quantifying arthropods could also have helped explain site-level variation in abundance and diversity of insectivorous birds. Although these considerations arose retrospectively during data analysis, they are retained here as recommendations for future studies.

Another suggestion that I consider of utmost importance is understanding the perceptions and attitudes of growers towards wildlife in their systems, a topic that for logistical reasons could not be fully explored in this thesis. Drivers of growers' tolerance of wildlife will directly affect the persistence of species deemed as 'pests' in those systems, and literature on this subject has grown in the past decades (Coleman & Spurr 2001; Greiner et al. 2009; Kross et al. 2018; Huang et al. 2023; McWherter et al. 2025). However, extensive studies of this nature are still lacking in New Zealand, warranting future research on the subject.

Finally, in a study conducted only with blackbirds and silvereyes in New Zealand vineyards, researchers pointed out that blackbirds preferred grapes with higher sugar content (approximately 40%), while silvereyes preferred the 10-20% range (Saxton et al. 2004b). Other studies have also pointed out that birds can choose between different crop varieties using biochemical signals (Nereu et al. 2018). With 20 apple varieties represented across the sites, there was a missed opportunity to identify the varieties prior to the fieldwork. This would allow noting which ones were being consumed by the birds to identify if sugar content, or even variation in the colour hues of fruits, would lead to different predation rates. This could be done by mapping the distribution of apple varieties on different sites and quantifying predation rates on these varieties.

I would have liked to include more sites, as this would have improved the statistical analyses. In most of the statistical analyses, it was not possible to detect predictive effects of orchard identity, hindering assessment of how different management practices influenced bird diversity and abundance. The lack of a strong predictive effect of organic practices on species diversity contrasted with other studies (Chamberlain et al. 2010; Coleman 2010; Winqvist et al. 2011). However, it needs to be considered with the caveat of only one organic site among the orchards. The decision to include only a few sites was not taken lightly, and factors outside of my control also determined the spatial possibilities for the studies. In early 2023, at the beginning of this thesis, Cyclone Gabrielle devastated a significant portion of major horticultural regions in the

country. Additionally, not all growers, understandably, were enthusiastic about researchers inconveniently poking around their systems, arriving early morning and leaving after work hours, and deploying foreign objects in their orchards. Some growers would also prefer to cover their crop trees year-round, not allowing for birds to perform their typical roles within the system. Growers who were curious about which bird species were present in their orchards, and how birds used these systems, were more willing to participate in the study.

This study can be seen as a complement to past studies in food production systems, especially the ARGOS project. The Agriculture Research Group on Sustainability scheme was explicitly designed to evaluate social, economic and ecological aspects of sustainable food production, focusing on kiwi orchards and pastures (Campbell et al. 2012; Merfield et al. 2015). Insights from the project indicated that monitoring programmes can gain from a higher number of visits to each sampled site each year (Weller 2012). This strengthens the importance of the frequent visits to the few apple orchards selected for the current study.

Overall, the project revealed important insights into the roles of birds in the New Zealand apple industry, while also raising further questions discussed here. Drawing on the inferences collated from this thesis, the following recommendations are intended to inform orchard management practices. Rather than prescribing uniform management actions, the recommendations emphasise the importance of recognising context-dependent factors within the orchards.

There is a persistent prejudice towards pūkeko as a major bird pest. There is validity to those claims, as the birds can cause significant crop damage in early-establishment orchards, delicate ground crops, or orchards with a large population of this species. However, this study highlighted the importance of measuring crop damage instead of relying on perceptions that are often skewed by individual and communal biases. Overall, the damaging potential of pūkeko at New Zealand orchards is still mainly anecdotal evidence, and further studies focusing on this species are needed to understand their roles in these systems.

Bird use of orchards changed markedly across seasons, meaning that potential bird-deterring practices need to be strategised to account for these variations. Such practices could include increased effort in attracting birds of prey in the pre-harvest period and bird nets that are deployed only during the critical stages of flower and fruit development. Growers often prefer to perform a broad-scale exclusion of birds by covering the crop trees with nets for long periods of time, including year-round. For smaller fruits (e.g. berries), this practice is often necessary to avoid high rates of crop damage. However, for other crops, trade-offs can be lost by hindering the provision of pest control services, thus keeping the orchard reliant on chemical control practices. By focusing on seasonal effects and not year-round measures, these approaches could reduce costs and be more effective in finding measures to reduce crop damage.

6.7 Implications for Human-Wildlife Conflicts

The expected increase in populations for both common and threatened species from invasive predation pressure does not mean solely positive aspects. Wildlife can cause many damages to humans, including in food production systems, by providing ecosystem disservices that affect peoples' health, livelihood, and perceived wellbeing. These struggles, emerging from actual or

perceived, direct or indirect threats to human interests and needs, are described as human-wildlife conflicts (IUCN 2023).

Human-wildlife conflicts (HWC) can be exacerbated by the socioeconomic impacts of crop losses (Sausse et al. 2021), as damages ultimately cost money to growers. Additionally, one's cultural and social beliefs will directly influence one's perception of wildlife-related risks (McWherter et al. 2025). How to adequately mediate those conflicts is an integral part of modern conservation, especially in human-managed systems. Negative impacts need to minimised while ensuring the protection of biological diversity (Moreno-Opo & Piqué 2018).

New evidence and perceptions can also shift the narrative on HWC. Silvereyes, for example, have long been considered agricultural pests in New Zealand (Higgins et al. 2006). In fact, multiple sources indicate that the birds would be shot at and driven away from orchards already in the early 20th century (Chisholm 1908a, 1908b). A couple of decades later, however, research showed that the birds were capable of decimating populations of important crop pests, such as woolly aphids (Drummond 1909). This is an important contrast to other countries, such as in Germany, where aphid control is not directly linked to birds (Martin et al. 2015). From despised agricultural 'villain' to some of the most common native birds in croplands, silvereyes have held a contentious role, alternating between a crop damage or pest control provider depending on who's evaluating them.

A peaceful coexistence depends on humans and wildlife sharing the same landscape and adapting jointly to their environment (Rey 2011; Carter & Linnell 2016). And as pointed out in the previous chapter, impacts of perceived bird 'pests' need to be carefully analysed, so species are not unjustifiably targeted. Recognising these complex and often synergetic roles can help integrate biodiversity conservation with agricultural productivity in a world of increasingly pressing demands for food production. This need to reconcile biodiversity conservation with food production also places the findings of this thesis within the broader land-sharing and land-sparing debate.

6.8 Tackling the Land-Sparing or Land-Sharing Debate

For several decades now, conservationists have discussed whether food production systems and conservation land management should be split or integrated, dubbed the 'land-sparing' and 'land-sharing' debate (Green et al. 2005; Brussaard et al. 2010; Phalan et al. 2011; Grass et al. 2019). This debate has arisen from the competing demands of food production and biodiversity conservation (Phalan et al. 2011). However, the question of how to harmonise food production with conservation is not new (Waggoner 1996). Essentially, the debate concerns the allocation of the finite resource of available land (Tscharntke et al. 2012; Fischer et al. 2014). Land sparing proposes setting aside areas for biodiversity while allowing agricultural systems to be intensively farmed for higher food production outputs, whereas land sharing includes approaches that facilitate the persistence of wildlife within food-production systems (Green et al. 2005).

Evidence has been produced in favour of land sparing for increasing wildlife populations and mitigating greenhouse gas emissions (Phalan et al. 2011). However, the feasibility and effectiveness of land-sparing strategies depend on specific environmental, economic and social contexts. Increasing the volume of food production does not necessarily result in land being spared or meet all human needs, while the conservation benefits of agricultural intensification

also depend on the relationship between crop yield and biodiversity (Matson & Vitousek 2006; Tscharntke et al. 2012; Wright et al. 2012; Garfinkel & Johnson 2015). Consequently, approaches to the debate increasingly recognise a mixture of alternatives, including wildlife-friendly farming practices that can reduce the impacts of agriculture on biodiversity (Green et al. 2005; Fischer et al. 2008, 2014; Johnson et al. 2011; Maas et al. 2013).

New Zealand provides a particularly relevant context for this debate. Conservation has historically focused strongly on protected areas, including reserves, fenced sanctuaries and offshore islands, with intensive management of exotic mammalian predators (Norton & Miller 2000). At the same time, the country has undergone extensive transformation from its pre-human forested state into a landscape dominated by agricultural land uses, including pastures, woodlots and shelterbelts (MacLeod et al. 2008; Moller et al. 2008). This strong emphasis on separating areas managed primarily for biodiversity conservation from productive landscapes broadly reflects a land-sparing approach.

However, the findings of this thesis demonstrate that productive landscapes should not be overlooked as potential components of biodiversity conservation. Native bird species were consistently recorded within working apple orchards, where they used the available habitat for foraging and other behaviours while potentially contributing both ecosystem services and disservices. In this sense, these findings provide support for a land-sharing perspective in which horticultural systems are not considered exclusively as areas of food production, but also as habitats in which agricultural production and native biodiversity can coexist.

This consideration may become increasingly important with the advancement of Predator Free 2050 and other mammalian predator-control initiatives. If predator suppression allows threatened or uncommon native species to increase in abundance and expand beyond reserves, sanctuaries and offshore islands, productive landscapes may increasingly form part of the environments encountered by recovering bird populations. Understanding how birds already use horticultural systems, and the services and disservices associated with their presence, can therefore provide a basis for anticipating how native species might interact with these systems as their populations recover.

Grower responses will also be important in determining whether such coexistence is feasible. If birds are not perceived to cause crop damage, growers can be willing to maintain or increase bird abundance on their land (Jacobson et al. 2002). Different species may therefore elicit different responses according to perceptions of the benefits or damage associated with them. Understanding the functional roles of birds within productive landscapes could help land managers foster beneficial interactions while mitigating potential disservices, allowing native avifauna to be incorporated into horticultural management without compromising economic viability.

The land-sparing and land-sharing approaches therefore need not represent mutually exclusive alternatives in the New Zealand context. Protected areas will remain essential for species requiring intensive conservation management, but the recovery of native biodiversity may increasingly require consideration of the landscapes surrounding those areas. Horticultural systems that accommodate native birds while maintaining agricultural production could complement protected areas, extending conservation opportunities into human-managed landscapes while potentially providing benefits to both biodiversity and agriculture.

6.9 What does the Future Hold for New Zealand Birds?

Mammalian predator control across New Zealand has led to increases in native bird species and a spillover of individuals into urban and rural areas (McArthur et al. 2021). Bird species, common and endangered, are thriving under mammalian predator control measures, expanding in population and distribution (DoC 2020). Similar predator-release dynamics have been observed in other countries, indicating the potential for these control measures to allow birds to expand or persist in human-managed landscapes (Ratcliffe et al. 2010; Niemczynowicz et al. 2017). Overall, measuring the role of birds in New Zealand horticulture proved challenging, as most crops and many bird species present in these systems are introduced (Whyte 2023). Nonetheless, both citizen science data and field-based evidence from this thesis demonstrated that native, endemic, and/or endangered species persist in these intensively managed horticultural environments. This is an excellent outcome for New Zealand and elsewhere. High rates of natural habitat loss and degradation (i.e. conversion to highly intensified agricultural systems) have led to global declines in bird populations (Foley et al. 2005). With pressing food production needs for an ever-growing human population, it becomes clear that recreating natural habitats cannot be the main response; rather, wild species are bound to coexist in agroecosystems as surrounding forests and wetlands are lost. By focusing on raising ecosystem services across orchards, be they organic, intensively managed, or conventional, will enable growers to efficiently use their land while guaranteeing the system's persistence for future generations (Merfield et al. 2015).

At the core of many human-wildlife conflicts lies the realisation that human perceived values for wildlife will greatly differ on whether they hold in higher regard nature protection or economic development (McMahon et al. 2024). This helps explain why crop damage caused by birds tends to be perceived as higher for farmers than what is quantified in scientific studies. What does that mean for the species persisting in horticultural systems? For some, 'bad behaviour' might be excusable to a greater degree due to the species' popularity (Cote et al. 2013). For others, like the pūkeko, perceived damage might be the trigger for growers to be their own jury and executioners. Conflict can be further exacerbated by the behavioural flexibility and cognitive abilities of birds, which often make them difficult to exclude from crops, as they learn to circumvent preventative measures (Duttenhefner et al. 2024). As a result, bird deterrence can be costly, labour-intensive, and highly dependent on species-specific behaviour.

This thesis also highlighted that much has yet to be learned from the growers themselves. One of the Kāpiti Coast orchard growers, who held views on both the beneficial and damaging roles of birds in the orchard, was able to identify a wide range of species visiting the site, including less common species such as the New Zealand falcon. The owner of one of the Manawatū orchards stated that, once logistical issues delayed their plans of harvesting the yellow plums, they decided to leave them on the trees as a food resource for the tūī. Meaning that the answer lies somewhere in the middle. Instead of admonishing any animal behaviour that turns out to be inconvenient for humans, we need to reframe human-wildlife conflicts as coexistence issues (Peterson et al. 2013; Whyte 2023). Ensuring the continued presence of birds in horticultural systems requires approaches that are ecologically effective while remaining economically viable. Although addressing this challenge lies beyond the scope of a single thesis, the present work highlights that bird visitors to apple orchards encompass a broader range of interactions than it was previously assumed. The findings presented here underscore that bird presence in

orchards involves complex and multifaceted interactions that extend beyond simplistic classifications of benefit or damage.

References

Abdelhakim WM. 2020. Scaring Birds: The concept of the Scarecrow in Ancient Egypt. International Journal of Heritage, Tourism and Hospitality 14:42-51.

Adegoke AS. 1983. The pattern of migration of village weaverbirds (*Ploceus cucullatus*) in Southwestern Nigeria. The Auk 100:863-870.

Alemayehu N, Tekalign W. 2022. Prevalence of crop damage and crop-raiding animals in southern Ethiopia: the resolution of the conflict with the farmers. GeoJournal 87:845-859.

Allan JR, Kirby JS, Feare CJ. 1995. The biology of Canada geese *Branta canadensis* in relation to the management of feral populations. Wildlife Biology 1:129-143.

Alves RRN, Lima JRF, Araujo HFP. 2013. The live bird trade in Brazil and its conservation implications: An overview. Bird Conservation International 23:53-65.

Alves RRN, Rosa IL. 2010. Trade of Animals Used in Brazilian Traditional Medicine: Trends and Implications for Conservation. Human Ecology 38:691-704.

Alves RRN, Rosa IL, Santana GG. 2007. The role of animal-derived remedies as complementary medicine in Brazil. BioScience 57:949-955.

Anderson SH, Kelly D, Robertson AW, Ladley JJ. 2016. Pollination by Birds: A Functional Evaluation. Pages 73-106 in Şekercioğlu ÇH, Wenny DG, Whelan CJ, editors. Why Birds Matter: Avian Ecological Function and Ecosystem Services. University of Chicago Press, Chicago.

Angkaew R, Ngoprasert D, Powell LA, Limparungpatthanakij W, Round PD, Gale GA. 2023. Variation in avian responses to rice intensification in the central plains of Thailand guides conservation opportunities. Biological Conservation 286:110307.

Awika JM. 2011. Major Cereal Grains Production and Use around the World. Pages 1-13 in Awika JM, Piironen V, Bean S, editors. Advances in Cereal Science: Implications to Food Processing and Health Promotion. American Chemical Society, Washington, DC.

Bailey L, Adams M. 2005. Occupancy Models to Study Wildlife. US Geological Survey, Reston, USA. Available from https://pubs.usgs.gov/fs/2005/3096/fs20053096.pdf.

Baker RT. 1980. Birds in an apple orchard. Notornis 27:331-334.

Baling M, Stuart-Fox D, Brunton DH, Dale J. 2016. Habitat suitability for conservation translocation: The importance of considering camouflage in cryptic species. Biological Conservation 203:298-305.

Balmford A, Green R, Phalan B. 2012. What conservationists need to know about farming. Proceedings of the Royal Society B: Biological Sciences 279:2714-2724.

Barbaro L, Assandri G, Brambilla M, Castagneyrol B, Froidevaux J, Giffard B, Pithon J, Puig-Montserrat X, Torre I, Calatayud F, Gaüzère P, Guenser J, Macià-Valverde FX, Mary

S, Raison L, Sirami C, Rusch A. 2021. Organic management and landscape heterogeneity combine to sustain multifunctional bird communities in European vineyards. Journal of Applied Ecology 58:1261-1271.

Barbaro L, Rusch A, Muiruri EW, Gravellier B, Thiery D, Castagneyrol B. 2017. Avian pest control in vineyards is driven by interactions between bird functional diversity and landscape heterogeneity. Journal of Applied Ecology 54:500-508.

Barceló I, Guzmán-Aranda JC, Cháves-Ramírez F, Powell LA. 2012. Rural inhabitant perceptions of sandhill cranes in wintering areas of Northern Mexico. Human Dimensions of Wildlife, 17:4.

Basili GD, Temple SA. 1999. Dickcissels and crop damage in Venezuela: defining the problem with ecological models. Ecological Applications 9:732-739.

Bateman PW, Fleming PA, Wolfe AK. 2017. A different kind of ecological modelling: the use of clay model organisms to explore predator-prey interactions in vertebrates. Journal of Zoology 301:251-262.

Beauchamp G. 2002. Higher-level evolution of intraspecific flock-feeding in birds. Behavioral Ecology and Sociobiology 51:480-487.

Beauchamp G. 2021. Flocking in birds increases annual adult survival in a global analysis. Oecologia 197:387-394.

Beauchamp G. 2022. Flocking in birds is associated with diet, foraging substrate, timing of activity, and life history. Behavioral Ecology and Sociobiology 76:e74.

Beckerman J. 2000. Apple Scab on Tree Fruit in the Home Orchard. Purdue University, West Lafayette, USA.

Bednekoff PA, Houston AI. 1994. Avian daily foraging patterns: effects constraints and variability of digestive. Evolutionary Ecology 8:36-52.

Bednekoff PA, Krebs JR. 1995. Great tit fat reserves: effects of changing and unpredictable feeding day length. Functional Ecology 9:457-462.

Benjamini L. 1980. Feeding behaviour of the chukar (*Alectoris chukar*) in sugar beet plantations. Phytoparasitica 8:3-18.

Benras H, Guezoul O, Neffar S, Chenchouni H. 2023. Disclosing the determinants, drivers and predictors of bird depredation on date palm (*Phoenix dactylifera* L.) production. Journal of the Saudi Society of Agricultural Sciences 22:231-244.

Bennett PM, Owens IPF. 2002. Evolutionary Ecology of Birds: Life Histories, Mating Systems, and Extinction. Oxford University Press, Oxford, UK.

Best LB, Freemark KE, Dinsmore JJ, Camp M. 1995. A review and synthesis of habitat use by breeding birds in agricultural landscapes of Iowa. The American Midland Naturalist 134:1-29.

BirdLife International. 2018. State of the world's birds: Taking the pulse of the planet. Cambridge, UK.

Birkhead ME. 1981. The social behaviour of the dunnock (*Prunella modularis*). Ibis 123:75-84.

Bisset SA. 1976. Foods of the paradise shelduck *Tadorna variegata* in the high country of North Canterbury, New Zealand. Notornis 23:106-119.

Blackburn J, Arthur W. 2001. Comparative abundance of centipedes on organic and conventional farms, and its possible relation to declines in farmland bird populations. Basic and Applied Ecology 2:373-381.

Blackburn TM, Cassey P, Duncan RP, Evans KL, Gaston KJ. 2004. Avian extinction and mammalian introductions on oceanic islands. Science 305:1955-1958.

Blackwell G, Fukuda Y, Maegli T, MacLeod CJ. 2008. Room for everyone? Refugia and native biodiversity in New Zealand's agricultural landscapes. New Zealand Journal of Agricultural Research 51:473-476.

Blackwell G, O'Neill E, Buzzi F, Clarke D, Dearlove T, Green M, Moller H, Rate S, Wright J. 2005. Bird community composition and relative abundance in production and natural habitats of New Zealand. Dunedin.

Bocquet-Appel J. 2011. When the world's population took off: the springboard of the Neolithic demographic transition. Science 333:560-561.

Boesing AL, Nichols E, Metzger JP. 2017. Effects of landscape structure on avian-mediated insect pest control services: a review. Landscape Ecology 32:931-944.

Bomford M, Sinclair R. 2002. Australian research on bird pests: Impact, management and future directions. Emu 102:29-45.

Bonhomme B. 2021. Indispensable allies or overly-sentimentalized critters?: Debating the merits of insectivorous birds as defenders of crop, 1850-1914. The Historian 83:44-69.

Borkhataria RR, Colazzo JA, Groom MJ. 2012. Species abundance and potential biological control services in shade vs. sun coffee in Puerto Rico. Agriculture, Ecosystems and Environment 151:1-5.

Bouarakia O, Linden VMG, Joubert E, Weier SM, Grass I, Tscharntke T, Foord SH, Taylor PJ. 2023. Bats and birds control tortricid pest moths in South African macadamia orchards. Agriculture, Ecosystems and Environment 352:108527.

Bozzo F, Tarricone S, Petrontino A, Cagnetta P, Maringelli G, La Gioia G, Fucilli V, Ragni M. 2021. Quantification of the starling population, estimation and mapping of the damage to olive crops in the apulia region. Animals 11:1-12.

Bradbury RB, Kyrkos A, Morris AJ, Clark SC, Perkins AJ, Wilson JD. 2000. Habitat associations and breeding success of yellowhammers on lowland farmland. Journal of Applied Ecology 37:789-805.

Bradshaw CJA, Ehrlich PR, Beattie A, Ceballos G, Crist E, Diamond J, Dirzo R, Ehrlich AH, Harte J, Harte ME, Pyke G, Raven PH, Ripple WJ, Saltré F, Turnbull C, Wackernagel M, Blumstein DT. 2021. Underestimating the challenges of avoiding a ghastly future. Frontiers in Conservation Science 1:615419.

Bradshaw CJA, Leroy B, Bellard C, Roiz D, Albert C, Fournier A, Barbet-Massin M, Salles JM, Simard F, Courchamp F. 2016. Massive yet grossly underestimated global costs of invasive insects. Nature Communications 7:1-8.

Brain RA, Anderson JC. 2019. The agro-enabled urban revolution, pesticides, politics, and popular culture: a case study of land use, birds, and insecticides in the USA. Environmental Science and Pollution Research 26:21717-21735.

Brambilla M, Ilahiane L, Assandri G, Ronchi S, Bogliani G. 2017. Combining habitat requirements of endemic bird species and other ecosystem services may synergistically enhance conservation efforts. Science of the Total Environment 586:206-214.

Brennan EB. 2020. Sparrow preferences for winter cover crops in California's Central Coast. Frontiers in Sustainable Food Systems 4:567579.

Brooks ME, Kristensen K, Van Benthem KJ, Magnusson A, Berg CW. 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. The R Journal 9:378-400.

Brussaard L, Caron P, Campbell B, Lipper L, Mainka S, Rabbinge R, Babin D, Pulleman M. 2010. Reconciling biodiversity conservation and food security: Scientific challenges for a new agriculture. Current Opinion in Environmental Sustainability 2:34-42.

Bulte EH, Damania R. 2005. An economic assessment of wildlife farming and conservation. Conservation Biology 19:1222-1233.

Burger HF, Hylander K, Ayalew B, van Dam NM, Mendesil E, Schedl A, Shimales T, Zewdie B, Tack AJM. 2022. Bottom-up and top-down drivers of herbivory on Arabica coffee along an environmental and management gradient. Basic and Applied Ecology 59:21-32.

Cabodevilla X, Arroyo B, Wright AD, Salguero AJ, Mougeot F. 2021. Vineyard modernization drives changes in bird and mammal occurrence in vineyard plots in dry farmland. Agriculture, Ecosystems and Environment 315:e107448.

Campbell H, Rosin C, Hunt L, Fairweather J. 2012. The social practice of sustainable agriculture under audit discipline: Initial insights from the ARGOS project in New Zealand. Journal of Rural Studies 28:129-141.

Canavelli SB, Swisher ME, Branch LC. 2014. Factors related to farmers' preferences to decrease monk parakeet damage to crops. Human Dimensions of Wildlife 18:124-137.

Canavelli SB, Branch LC, Cavallero P, González C, Zaccagnini ME. 2014b. Multi-level analysis of bird abundance and damage to crop fields. Agriculture, Ecosystems and Environment 197:128-136.

Carter NH, Linnell JDC. 2016. Co-adaptation is key to coexisting with large carnivores. Trends in Ecology and Evolution 31:575-578.

Case SB, Tarwater CE. 2020. Functional traits of avian frugivores have shifted following species extinction and introduction in the Hawaiian Islands. Functional Ecology 34:2467-2476.

Cassano CR, Silva RM, Mariano-Neto E, Schroth G, Faria D. 2016. Bat and bird exclusion but not shade cover influence arthropod abundance and cocoa leaf consumption in agroforestry landscape in northeast Brazil. Agriculture, Ecosystems and Environment 232:247-253.

Castro I. 1996. Behavioural ecology and management of hihi (*Notiomystis cincta*), an endemic New Zealand honeyeater. PhD thesis. Massey University, Palmerston North.

Catling HD, Islam Z. 1999. Pests of deepwater rice and their management. Integrated Pest Management Reviews 4:193-229.

Catterall CP, Green RJ, Jones DN. 1989. Occurrence of birds in relation to plants in a sub-tropical city. Wildlife Research 16:289-305.

Caughley G, Sinclair J. 1994. Wildlife Ecology and Management. Blackwell Publishing Inc., Cambridge, UK.

Ceballos G, Ehrlich PR, Raven PH. 2020. Vertebrates on the brink as indicators of biological annihilation and the sixth mass extinction. Proceedings of the National Academy of Sciences 117:13596-13602.

Chain-Guadarrama A, Martínez-Salinas A, Aristizábal N, Ricketts TH. 2019. Ecosystem services by birds and bees to coffee in a changing climate: a review of coffee berry borer control and pollination. Agriculture, Ecosystems and Environment 280:53-67.

Chamberlain DE, Crick HQP. 1999. Population declines and reproductive performance of Skylarks *Alauda arvensis* in different regions and habitats of the United Kingdom. Ibis 141:38-51.

Chamberlain DE, Joys A, Johnson PJ, Norton L, Feber RE, Fuller RJ. 2010. Does organic farming benefit farmland birds in winter? Biology Letters 6:82-84.

Chaplin-Kramer R, O'Rourke ME, Blitzer EJ, Kremen C. 2011. A meta-analysis of crop pest and natural enemy response to landscape complexity. Ecology Letters 14:922-932.

Chisholm AH. 1908a. The white-eye (*Zosterops coerulescens*): Its relation to the orchardist. Emu - Austral Ornithology 8:35-36.

Chisholm AH. 1908b. *Zosterops coerulescens* nesting. Emu - Austral Ornithology 8:38.

Christopher AJ. 1999. Core issues in New Zealand's apple industry: global-local challenges. Geography 84:275-280.

Classen A, Peters MK, Ferger SW, Helbig-Bonitz M, Schmack JM, Maassen G, Schleuning M, Kalko EKV, Böhning-Gaese K, Steffan-Dewenter I. 2014. Complementary ecosystem services provided by pest predators and pollinators increase quantity and quality of coffee yields. Proceedings of the Royal Society B: Biological Sciences 281:e20133148.

Clout MN, Karl BJ, Pierce RJ, Robertson HA. 1995. Breeding and survival of New Zealand Pigeons *Hemiphaga novaeseelandiae*. Ibis 137:264-271.

Coleman GJ. 2010. Birds as indicators of sustainable management practices on New Zealand kiwifruit orchards. MSc dissertation. University of Otago, Dunedin.

Coleman JD. 1972. The feeding ecology, productivity and management of Starlings in Canterbury, New Zealand. PhD thesis. University of Canterbury, Christchurch, New Zealand.

Coleman JD. 1977. The foods and feeding of starlings in Canterbury. Proceedings (New Zealand Ecological Society) 24:94-109.

Coleman JD, Spurr EB. 2001. Farmer perceptions of bird damage and control in arable crops. New Zealand Plant Protection 54:184-187.

Collinge WE. 1918. The damage to agriculture by vermin and birds. Nature 101:48.

Colwell RK, Chang XM, Chang J. 2004. Interpolating, extrapolating, and comparing incidence-based species accumulation curves. Ecology 85:2717-2727.

Colwell RK, Coddington JA. 1994. Estimating terrestrial biodiversity through extrapolation. Philosophical Transactions of the Royal Society of London B Biological Sciences 345:101-118.

Cooper RA, Millener PR. 1993. The New Zealand biota: historical background and new research. Trends in Ecology & Evolution 8:429-433.

Costanza R, d'Arge R, de Groot R, Farber S, Grasso M, Hannon B, Limburg K, Naeem S, O'Neill RV, Paruelo J, Raskin RG, Sutton P, van den Belt M. 1997. The value of the world's ecosystem services and natural capital. Nature 387:253-260.

Costanza R, de Groot R, Sutton P, van der Ploeg S, Anderson SJ, Kubiszewski I, Farber S, Turner RK. 2014. Changes in the global value of ecosystem services. Global Environmental Change 26:152-158.

Cote S, Durand O, Laroche E, Warden R. 2013. Evaluating the Interactions between Wellington Residents and the Threatened Kaka Parrot. BSc report. Worcester Polytechnic Institute, Worcester, USA.

Courchamp F, Hoffmann BD, Russell JC, Leclerc C, Bellard C. 2014. Climate change, sea-level rise, and conservation: Keeping island biodiversity afloat. Trends in Ecology and Evolution 29:127-130.

Craig J, Anderson S, Clout M, Creese B, Mitchell N, Ogden J, Roberts M, Ussher G. 2000. Conservation issues in New Zealand. Annual Review of Ecology and Systematics 31:61-78.

Craig JL, Stewart AM, Douglas ME. 1981. The foraging of New Zealand honeyeaters. New Zealand Journal of Zoology 8:87-91.

Crisol-Martínez E, Moreno-Moyano LT, Wormington KR, Brown PH, Stanley D. 2016. Using next-generation sequencing to contrast the diet and explore pest-reduction services of sympatric bird species in macadamia orchards in Australia. PLoS ONE 11:1-19.

da Silva LP, Oliveira D, Ferreira S, Gonçalves CI, Valente C, Mata VA. 2022. Birds as potential suppressing agents of eucalypt plantations' insect pests. BioControl 67:571-582.

Daily GC. 1997. Nature's Services: Societal Dependence on Natural Ecosystems. 1st ed. Island Press, Washington, DC.

Dainese M, Martin EA, Aizen MA, Albrecht M, Bartomeus I, Bommarco R, Carvalheiro LG, Chaplin-Kramer R, Gagic V, Garibaldi LA, Ghazoul J, Grab H, Jonsson M, Karp DS, Kennedy CM, Kleijn D, Kremen C, Landis DA, Letourneau DK, Marini L, Poveda K, Rader R, Smith HG, Tscharntke T, Andersson GKS, Badenhausser I, Baensch S, Bezerra ADM, Bianchi FJJA, Boreux V, Bretagnolle V, Caballero-Lopez B, Cavigliasso P, Ćetković A, Chacoff NP, Classen A, Cusser S, da Silva e Silva FD, de Groot GA, Dudenhöffer JH, Ekroos J, Fijen T, Franck P, Freitas BM, Garratt MPD, Gratton C, Hipólito J, Holzschuh A, Hunt L, Iverson AL, Jha S, Keasar T, Kim TN, Kishinevsky M, Klatt BK, Klein AM, Krewenka KM, Krishnan S, Larsen AE, Lavigne C, Liere H, Maas B, Mallinger RE, Martinez Pachon E, Martínez-Salinas A, Meehan TD, Mitchell MGE, Molina GAR, Nesper M, Nilsson L, O'Rourke ME, Peters MK, Plećaš M, Potts SG, Ramos DL, Rosenheim JA, Rundlöf M, Rusch A, Sáez A, Scheper J, Schleuning M, Schmack JM, Sciligo AR, Seymour C, Stanley DA, Stewart R, Stout JC, Sutter L, Takada MB, Taki H, Tamburini G, Tschumi M, Viana BF, Westphal C, Willcox BK, Wratten SD, Yoshioka A, Zaragoza-Trello C, Zhang W, Zou Y, Steffan-Dewenter I. 2019. A global synthesis reveals biodiversity-mediated benefits for crop production. Science Advances 5:eaax0121.

Daniel TC, Muhar A, Arnberger A, Aznar O, Boyd JW, Chan KMA, Costanza R, Elmqvist T, Flint CG, Gobster PH, Grêt-Regamey A, Lave R, Muhar S, Penker M, Ribe RG, Schauppenlehner T, Sikor T, Soloviy I, Spierenburg M, Taczanowska K, Tam J, von der Dunk A. 2012. Contributions of cultural services to the ecosystem services agenda. Proceedings of the National Academy of Sciences 109:8812-8819.

Davies V, Trought MCT, Hickling G. 2000. Bird Behaviour in Marlborough Vineyards. Lincoln University, Marlborough District, New Zealand.

Dawson DG, Bull PC. 1970. A questionnaire survey of bird damage to fruit. New Zealand Journal of Agricultural Research 13:362-371.

De Mey Y, Demont M, Diagne M. 2012. Estimating bird damage to rice in Africa: evidence from the Senegal River Valley. Journal of Agricultural Economics 63:175-200.

Denmead LH, Darras K, Clough Y, Diaz P, Grass I, Hoffmann MP, Nurdiansyah F, Fardiansah R, Tscharntke T. 2017. The role of ants, birds and bats for ecosystem functions and yield in oil palm plantations. Ecology 98:1945-1956.

Dennison MD, Heather BD, Robertson HA. 1981. Migratory movement of silvereyes at Farewell Spit. Notornis 28:119-120.

Dhindsa MS, Saini HK. 1994. Agricultural ornithology: an Indian perspective. Journal of Biosciences 19:391-402.

Dias PC. 1996. Sources and sinks in population biology. Trends in Ecology & Evolution 11:326-330.

Díaz-Siefer P, Olmos-Moya N, Fontúrbel FE, Lavandero B, Pozo RA, Celis-Diez JL. 2022. Bird-mediated effects of pest control services on crop productivity: a global synthesis. Journal of Pest Science 95:567-576.

Dickman AJ. 2010. Complexities of conflict: the importance of considering social factors for effectively resolving human-wildlife conflict. Animal Conservation 13:458-466.

Dix ME, Johnson RJ, Harrell MO, Case RM, Wright RJ, Hodges L, Brandle JR, Schoeneberger MM, Sunderman NJ, Fitzmaurice RL, Young LJ, Hubbard KG. 1995. Influences of trees on abundance of natural enemies of insect pests: a review. Agroforestry Systems 29:303-311.

Dobbs M, Rowling D. 2006. Revisiting the New Zealand apple industry: the impacts of change. British Food Journal 108:574-585.

DoC. 2020. Heaphy Management Area Bird Survey - September 2019. Department of Conservation, Wellington, New Zealand. 16p.

DoC. 2023. Five Minute Bird Count Standard Data Field Form. Department of Conservation, Wellington, New Zealand. Available from https://www.doc.govt.nz/our-work/five-minute-bird-counts/.

DoC. 2024. Predator Free 2050: A Practical Guide to Trapping. Department of Conservation, Wellington, New Zealand.

Drummond J. 1909. Reviews. Austral Ornithology 8:226-228.

Duffy R. 2014. Waging a war to save biodiversity: the rise of militarized conservation. International Affairs 90:819-834.

Duffy R. 2016. War, by Conservation. Geoforum 69:238-248.

Duttenhefner JL, Greives TJ, Klug PE. 2024. Spraying drones: efficacy of integrating an avian repellent with drone hazing to elicit blackbird flock dispersal and abandonment of sunflower fields. Wildlife Biology:e01333.

East R, Pottinger RP. 1975. Starling (*Sturnus vulgaris* L.) predation on grass grub (*Costelytra zealandica* (White), Melolonthinae) populations in Canterbury. New Zealand Journal of Agricultural Research 18:417-452.

Ehrlich PR, Ehrlich AH. 1981. Extinction: the causes and consequences of the disappearance of species. 1st edition. Random House, New York. 305p.

Eilers EJ, Klein AM. 2009. Landscape context and management effects on an important insect pest and its natural enemies in almond. Biological Control 51:388-394.

Elliott CCH. 1988. The assessment of on-farm losses due to birds and rodents in Eastern Africa. International Journal of Tropical Insect Science 9:717-720.

Elliott GE. 1996. Productivity and mortality of mohua (*Mohoua ochrocephala*). New Zealand Journal of Zoology 23:229-237.

Ellis JC. 2005. Marine birds on land: a review of plant biomass, species richness, and community composition in seabird colonies. Plant Ecology 181:227-241.

Elser JL, Lindell CA, Steensma KMM, Curtis PD, Leigh DK, Siemer WF, Boulanger JR, Shwiff SA. 2019. Measuring bird damage to three fruit crops: a comparison of grower and field estimates. Crop Protection 123:1-4.

Ewers RM, Kliskey AD, Walker S, Rutledge D, Harding JS, Didham RK. 2006. Past and future trajectories of forest loss in New Zealand. Biological Conservation 133:312-325.

FAO. 2007. The State of Food and Agriculture. Food and Agriculture Organization of the United Nations, Rome, Italy. 222p.

Fea N, Linklater W, Hartley S. 2020. Responses of New Zealand forest birds to management of introduced mammals. Conservation Biology 35:35-49.

Ferguson CM, Barratt BIP, Bell N, Goldson SL, Hardwick S, Jackson M, Jackson TA, Phillips CB, Popay AJ, Rennie G, Sinclair S, Townsend R, Wilson M. 2019. Quantifying the economic cost of invertebrate pests to New Zealand's pastoral industry. New Zealand Journal of Agricultural Research 62:255-315.

Ferrante M, Barone G, Kiss M, Bozóné-Borbáth E, Lövei GL. 2017a. Ground-level predation on artificial caterpillars indicates no enemy-free time for lepidopteran larvae. Community Ecology 18:280-286.

Ferrante M, González E, Lövei GL. 2017b. Predators do not spill over from forest fragments to maize fields in a landscape mosaic in central Argentina. Ecology and Evolution 7:7699-7707.

Ferrante M, Lo Cacciato A, Lövei GL. 2014. Quantifying predation pressure along an urbanisation gradient in Denmark using artificial caterpillars. European Journal of Entomology 111:649-654.

Ferrari GCP, Mason K, Robertson A, Castro I. 2025. Not All Birds of the Same Feather: A Systematic Review of Ecosystem Services and Disservices in Horticulture. Austral Ecology 50:e070110.

Ferreira DF, Jarrett C, Wandji AC, Atagana PJ, Rebelo H, Maas B, Powell LL. 2023. Birds and bats enhance yields in Afrotropical cacao agroforests only under high tree-level shade cover. Agriculture, Ecosystems and Environment 345:e108325.

Filloy J, Oxbrough A, Oddi JA, Ramos CS, Ribero MN, Santoandré S, Vaccaro AS. 2023. Understorey structural complexity mediated by plantation management as a driver of predation events on potential eucalypt pests. Forest Ecology and Management 531:e120799.

Firbank LG, Petit S, Smart S, Blain A, Fuller RJ. 2008. Assessing the impacts of agricultural intensification on biodiversity: a British perspective. Philosophical Transactions of the Royal Society B: Biological Sciences 363:777-787.

Fischer J, Brosi B, Daily GC, Ehrlich PR, Goldman R, Goldstein J, Lindenmayer DB, Manning AD, Mooney HA, Pejchar L, Ranganathan J, Tallis H. 2008. Should agricultural

policies encourage land sparing or wildlife-friendly farming? Frontiers in Ecology and the Environment 6:380-385.

Fischer J, Abson DJ, Butsic V, Chappell MJ, Ekroos J, Hanspach J, Kuemmerle T, Smith HG, von Wehrden H. 2014. Land sparing versus land sharing: Moving forward. Conservation Letters 7:149-157.

Fischl J, Caccamise DF. 1985. Influence of habitat and season on foraging flock composition in the European Starling (*Sturnus vulgaris*). Oecologia 67:532-539.

Fish & Game NZ. 2025. Hunting in Action. Available from https://www.fishandgame.org.nz/game-bird-hunting-in-new-zealand/ (accessed November 28, 2025).

Fiske I, Chandler R. 2011. Unmarked: an R package for fitting hierarchical models of wildlife occurrence and abundance. Journal of Statistical Software 43:1-23.

Fitzgerald N, Innes J, Watts C, Thornburrow D, Bartlam S, Collins K, Byers D, Burns B. 2021. Increasing urban abundance of tūī (Prosthemadera novaeseelandiae) by pest mammal control in surrounding forests. Notornis 68:93-107.

Fleming PJS, Gilmour A, Thompson JA. 2002. Chronology and spatial distribution of cockatoo damage to two sunflower hybrids in south-eastern Australia, and the influence of plant morphology on damage. Agriculture, Ecosystems and Environment 91:127–137.

Floyd C, Martin K. 2016. Bird Ecosystem Engineers: Birds That Excavate Cavities. Pages 298-320 in Şekercioğlu ÇH, Wenny DG, Whelan CJ, editors. Why Birds Matter: Avian Ecological Function and Ecosystem Services. University of Chicago Press, Chicago, USA.

Foley JA, Defries RS, Asner GP, Barford CC. 2005. Global consequences of land use. Science 309:570-574.

Fox AD, Elmberg J, Tombre IM, Hessel R. 2017. Agriculture and herbivorous waterfowl: A review of the scientific basis for improved management. Biological Reviews 92:854-877.

Frimpong EA. 2018. A case for conserving common species. PLoS Biology 16:1-6.

Frynta D, Lišková S, Bültmann S, Burda H. 2010. Being attractive brings advantages: The case of parrot species in captivity. PLoS ONE 5:1-9.

Fujita M, Kameda KO. 2016. Nutrient Dynamics and Nutrient Cycling by Birds. Pages 271-297 in Şekercioğlu ÇH, Wenny DG, Whelan CJ, editors. Why Birds Matter: Avian Ecological Function and Ecosystem Services. University of Chicago Press, Chicago.

Galbraith JA. 2010. The ecology and impact of the introduced eastern rosella (*Platycercus eximius*) in New Zealand. MSc dissertation. University of Auckland, Auckland, New Zealand.

Galbraith M, Cooper H. 2013. Tiritiri Matangi - an overview of 25 years of ecological restoration. New Zealand Journal of Ecology 37:258-260.

Gallagher CL. 1997. The movement to create an environmental bill of rights: from Earth Day, 1970 to the present. Fordham Environmental Law Journal 9:107-154.

Gámez-Virués S, Bonifacio RS, Gurr GM, Kinross C, Raman A, Nicol HI. 2007. Arthropod prey of shelterbelt-associated birds: linking faecal samples with biological control of agricultural pests. Australian Journal of Entomology 46:325-331.

Gangoso L, Agudo R, Anadón JD, De la Riva M, Suleyman AS, Porter R, Donázar JA. 2013. Reinventing mutualism between humans and wild fauna: Insights from vultures as ecosystem services providers. Conservation Letters 6:172-179.

García D, Miñarro M, Martínez-Sastre R. 2018. Birds as suppliers of pest control in cider apple orchards: Avian biodiversity drivers and insectivory effect. Agriculture, Ecosystems and Environment 254:233-243.

García D, Miñarro M, Martínez-Sastre R. 2020. Enhancing ecosystem services in apple orchards: nest boxes increase pest control by insectivorous birds. Journal of Applied Ecology 58:465-475.

Garcia K, Olimpi EM, Karp DS, Gonthier DJ. 2020. The Good, the Bad, and the Risky: Can birds be incorporated as biological control agents into integrated pest management programs? Journal of Integrated Pest Management 11:1-11.

Garcia K, Olimpi EM, M'Gonigle L, Karp DS, Wilson-Rankin EE, Kremen C, Gonthier DJ. 2023. Semi-natural habitats on organic strawberry farms and in surrounding landscapes promote bird biodiversity and pest control potential. Agriculture, Ecosystems and Environment 347: 108353.

Garfinkel M, Johnson M. 2015. Pest-removal services provided by birds on small organic farms in northern California. Agriculture, Ecosystems and Environment 211:24-31.

Garfinkel MB, Minor ES, Whelan CJ. 2020. Birds suppress pests in corn but release them in soybean crops within a mixed prairie/agriculture system. Condor 122(2): duaa009.

Gauthier NW, Bessin R, Strang J, Wright S, Kaiser C. 2013. An IPM Scouting Guide for Common Problems of Apple in Kentucky. Lexington. Available from http://www.ca.uky.edu/.

Gebhardt H. 1996. Ecological and economic consequences of introductions of exotic wildlife (birds and mammals) in Germany. Wildlife Biology 2:205-211.

Gebhardt K, Anderson AM, Kirkpatrick KN, Shwiff SA. 2011. A review and synthesis of bird and rodent damage estimates to select California crops. Crop Protection 30:1109-1116.

Geiger F, Bengtsson J, Berendse F, Weisser WW, Emmerson M, Morales MB, Ceryngier P, Liira J, Tscharntke T, Winqvist C, Eggers S, Bommarco R, Pärt T, Bretagnolle V, Plantegenest M, Clement LW, Dennis C, Palmer C, Oñate JJ, Guerrero I, Hawro V, Aavik T, Thies C, Flohre A, Hänke S, Fischer C, Goedhart PW, Inchausti P. 2010. Persistent negative effects of pesticides on biodiversity and biological control potential on European farmland. Basic and Applied Ecology 11:97-105.

Geladi I, Henry P-Y, Couenberg P, Welsh R, Fessl B. 2022. What are farmers' perceptions about farmland landbirds? A Galapagos Islands perspective. Renewable Agriculture and Food Systems 37:504-515.

Genghini M, Gellini S, Gustin M. 2006. Organic and integrated agriculture: The effects on bird communities in orchard farms in northern Italy. Biodiversity and Conservation 15:3077-3094.

Giannini TC, Boff S, Cordeiro GD, Cartolano EA, Veiga AK, Imperatriz-Fonseca VL, Saraiva AM. 2015. Crop pollinators in Brazil: a review of reported interactions. Apidologie 46:209-223.

Gibson K, Rose D, Fincher R. 2015. Manifesto for living in the Anthropocene. Punctum Books, New York.

Gill BJ. 2023. Long-tailed cuckoo | Koekoeā. Available from www.nzbirdsonline.org.nz (accessed November 18, 2025).

Gillespie GD. 1982. Greenfinch feeding behaviour and impact on a rapeseed crop in Oamaru, New Zealand, New Zealand Journal of Zoology, 9:481-486.

Gillings S, Newson SE, Noble DG, Vickery JA. 2005. Winter availability of cereal stubbles attracts declining farmland birds and positively influences breeding population trends. Proceedings of the Royal Society B: Biological Sciences 272:733-739.

Goijman AP, Conroy MJ, Bernardos JN, Zaccagnini ME. 2015. Multi-season regional analysis of multi-species occupancy: Implications for bird conservation in agricultural lands in east-central Argentina. PLoS ONE 10.

Goijman AP, Conroy MJ, Varni VD, Thompson JJ, Zaccagnini ME. 2020. Occupancy of avian foraging guilds in soybean fields and borders in Entre Ríos, Argentina: responses to vegetation structure and prey resources. Avian Research 11:1-14.

Golawski A, Golawska S. 2013. Are the birds dangerous for insect pollinators? The relationship between hymenopterans and the red-backed shrike. Journal of Insect Conservation 17:1155-1160.

Gonthier DJ, Sciligo AR, Karp DS, Lu A, Garcia K, Juarez G, Chiba T, Gennet S, Kremen C. 2019. Bird services and disservices to strawberry farming in Californian agricultural landscapes. Journal of Applied Ecology 56:1948-1959.

Gordon JD, Fagan B, Finch J, Gillson L, Milner N, Thomas CD. 2026. Black Death Land Abandonment Drove European Diversity Losses. Ecology Letters 29:1-12.

Gorosábel A, Bernad L, Muñoz SD, Pedrana J. 2022. Using the ecosystem services approach to link raptors with human well-being in the Southeast Pampas of Argentina. Biodiversity and Conservation 31:949-970.

Gorosábel A, Bernad L, Pedrana J. 2020. Ecosystem services provided by wildlife in the Pampas region, Argentina. Ecological Indicators 117.

Gorosábel A, Pedrana J, Bernad L, Caballero VJ, Muñoz SD, Maceira NO. 2019. Evaluating the impacts and benefits of sheldgeese on crop yields in the Pampas region of

Argentina: A contribution for mitigating the conflicts with agriculture. Agriculture, Ecosystems and Environment 279:33-42.

Gosler A. 2012. Ethno-ornithology: Birds, Indigenous Peoples, Culture and Society. (Gosler A, Tidemann SC, editors). 2nd edition. Earthscan, Oxford, UK. 368p.

Govind SK, Jayson EA. 2018. Crop damage by wild animals in Thrissur District, Kerala, India. Pages 309-323 in Sivaperuman C, Venkataraman K, editors. Indian Hotspots: Vertebrate Faunal Diversity, Conservation and Management. Springer, Singapore.

Grant P. 1970. Northern movement of silvereyes in winter on the West Coast, South Island. Notornis 17:322-323.

Grarock K, Tidemann CR, Wood J, Lindenmayer DB. 2012. Is it benign or is it a pariah? Empirical evidence for the impact of the common myna (*Acridotheres tristis*) on Australian birds. PLoS ONE 7:e40622.

Gras P, Tscharntke T, Maas B, Tjoa A, Hafsah A, Clough Y. 2016. How ants, birds and bats affect crop yield along shade gradients in tropical cacao agroforestry. Journal of Applied Ecology 53:953-963.

Grass I, Loos J, Baensch S, Batáry P, Librán-Embid F, Ficiciyan A, Klaus F, Riechers M, Rosa J, Tiede J, Udy K, Westphal C, Wurz A, Tscharntke T. 2019. Land-sharing/-sparing connectivity landscapes for ecosystem services and biodiversity conservation. People and Nature 1:262-272.

Green RE, Cornell SJ, Scharlemann JPW, Balmford A. 2005. Farming and the fate of wild nature. Science 307:550-555.

Greiner R, Patterson L, Miller O. 2009. Motivations, risk perceptions and adoption of conservation practices by farmers. Agricultural Systems 99:86-104.

Gryczyńska A, Polaczyk J, Welc-Falęciak R. 2024. *Toxoplasma gondii* infection in ticks infesting migratory birds: the blackbird (*Turdus merula*) and the song thrush (*Turdus philomelos*). Experimental and Applied Acarology 92:233-240.

Guenat S, Kaartinen R, Jonsson M. 2019. Shade trees decrease pest abundances on brassica crops in Kenya. Agroforest Systems 93:641-652.

Gurevitch J, Koricheva J, Nakagawa S, Stewart G. 2018. Meta-analysis and the science of research synthesis. Nature 555:175-182.

Gurr L. 1967. Communal roosting behaviour of the Australasian harrier *Circus approximans* in New Zealand. Ibis 110:332-337.

Gutierrez-Arellano C, Mulligan M. 2018. A review of regulation ecosystem services and disservices from faunal populations and potential impacts of agriculturalisation on their provision, globally. Nature Conservation 30:1-39.

Hallmann B. 1985. Status and conservation problems of birds of prey in Greece. ICBP Technical Publication 5:55-59.

Hammond JB. 1912. An investigation concerning the food of certain birds. The Journal of Agricultural Science 4:380-409.

Hartig F. 2025. DHARMa: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models. Available from https://CRAN.R-project.org/package=DHARMa (accessed November 24, 2025).

Hassan AAE, Abd El-Halem MA, Omar MMA, Elhanbaly Ruwaida AA. 2022. Assessement of damage caused by house sparrow, *Passer domesticus niloticus* on wheat and sorghum crops at Sohag governorate, Egypt. Archives of Agriculture Sciences Journal 5:127-133.

Heath SK, Long RE. 2019. Multiscale habitat mediates pest reduction by birds in an intensive agricultural region. Ecosphere 10:e02884.

Heather B, Robertson H, Onley D. 2015. The Field Guide to the Birds of New Zealand. Penguin Random House New Zealand, Auckland.

Heggøy O, Øien IJ. 2014. Conservation status of birds of prey and owls in Norway. BirdLife Norway, Trondheim, Norway. 129p.

Heltshe JF, Forrester NE. 1983. Estimating Species Richness Using the Jackknife Procedure. Biometrics 39:1-11.

Hemler EC, Frank BH. 2019. Plant-based diets for personal, population, and planetary health. Advances in Nutrition 10:S275-S283.

Herrera JM, Silva B, Jiménez-Navarro G, Barreiro S, Melguizo-Ruiz N, Moreira F, Vasconcelos S, Morgado R, Rodriguez-Pérez J. 2021. A food web approach reveals the vulnerability of biocontrol services by birds and bats to landscape modification at regional scale. Scientific Reports 11:23662.

Hermira AAC, Michalski F. 2022. Crop damage by vertebrates in Latin America: current knowledge and potential future management directions. PeerJ 10:e13185.

Higgins PJ, Peter JM, Cowling SJ. 2006. Family Zosteropidae. Pages 1728-1792 in Higgins PJ, Peter JM, Cowling SJ, editors. Handbook of Australian, New Zealand and Antarctic Birds. Volume 7, Part B: Boatbill to Starlings. Oxford University Press, Melbourne, Australia.

Hiron M, Rubene D, Mweresa CK, Ajamma YUO, Owino EA, Low M. 2014. Crop damage by granivorous birds despite protection efforts by human bird scarers in a sorghum field in western Kenya. Ostrich, 85:153-159.

Holdaway RN. 1989. New Zealand's pre-human avifauna and its vulnerability. New Zealand Journal of Ecology 12:11-25.

Hološková A, Cíbik J, Reif J. 2024. Why do open-farmland specialist birds prefer small fields? The evaluation of mechanisms using a cross-border study. Global Ecology and Conservation 56:e03327.

Hook DW, Porter SJ, Herzog C. 2018. Dimensions: building context for search and evaluation. Frontiers in Research Metrics and Analytics 3:23.

Hooper A, Brandt A, Newman J. 2021. Space Invaders: A Review of How New Zealand Manages Weeds That Threaten Native Ecosystems. Parliamentary Commissioner for the Environment - Te Kaitiaki Taiao a Te Whare Paremata, Wellington, New Zealand. 239p.

Hordley LA, Gillings S, Petchey OL, Tobias JA, Oliver TH. 2021. Diversity of response and effect traits provides complementary information about avian community dynamics linked to ecological function. Functional Ecology 35:1938-1950.

Horgan FG, Ramal AF, Villegas JM, Almazan MLP, Bernal CC, Jamoralin A, Pasang JM, Orboc G, Agreda V, Arroyo C. 2017. Ecological engineering with high diversity vegetation patches enhances bird activity and ecosystem services in Philippine rice fields. Regional Environmental Change 17:1355-1367.

Horgan FG, Kudavidanage EP. 2020. Farming on the edge: farmer training to mitigate human-wildlife conflict at an agricultural frontier in south Sri Lanka. Crop protection 127:e104981.

Horikoshi C, Battley PF, Seaton R, Minot EO. 2017. Winter habitat use of New Zealand falcons (*Falco novaeseelandiae ferox*) in an intensively managed pine plantation. New Zealand Journal of Ecology 41:193-206.

Howe A, Lövei GL, Nachman G. 2009. Dummy caterpillars as a simple method to assess predation rates on invertebrates in a tropical agroecosystem. Entomologia Experimentalis et Applicata 131:325-329.

Howe AG, Nachman G, Lövei GL. 2015. Predation pressure in Ugandan cotton fields measured by a sentinel prey method. Entomologia Experimentalis et Applicata 154:161-170.

Htay T, Htoo KK, Røskaft E, Ringsby TH, Ranke PS. 2024. Environmental factors affecting spatio-temporal distribution of crop-exploiting species: implications for coexistence between agricultural production and avifauna conservation in wetlands. Environmental Management 74:664-683.

Huang C, Zhou K, Huang Y, Fan P, Liu Y, Lee TM. 2023. Insights into the coexistence of birds and humans in cropland through meta-analyses of bird exclosure studies, crop loss mitigation experiments, and social surveys. PLoS Biology 21.

Hughey KFD, Cullen R, Moran E. 2003. Integrating economics into priority setting and evaluation in conservation management. Conservation Biology 17:93-103.

Hutchinson A, Stephens-Griffin N, Wyatt T. 2021. Speciesism and the wildlife trade: Who gets listed, downlisted and uplisted in CITES? International Journal for Crime, Justice and Social Democracy 11:191-209.

Innes J, Fitzgerald N, Watts C, Thornburrow D, Blackwell H, Lancaster E, Burns B. 2005. Distribution, movements and nesting success of Waikato tui. Notornis 52:173.

Innes J, Miskelly CM, Armstrong DP, Fitzgerald N, Parker KA, Stone ZL. 2022. Movements and habitat connectivity of New Zealand forest birds. New Zealand Journal of Ecology 46:1-21.

Issa MA, El-Bakhshawngi MIA. 2018. An estimation of bird damages on some field, vegetable and fruit crops at Sharkia Governorate, Egypt. Zagazig Journal of Agricultural Research 45:1273-1281.

IUCN. 2023. IUCN SSC Guidelines on Human-Wildlife Conflict and Coexistence. International Union for Conservation of Nature, Gland, Switzerland.

IUCN. 2024. The IUCN Red List of Threatened Species. Available from https://www.iucnredlist.org/ (accessed December 10, 2024).

Jacobson SK, Sieving KE, Jones G, Mcelroy J, Chen B, Hostetler ME, Miller SW. 2002. Farmers' opinions about bird conservation and pest management on organic and conventional North Florida farms. University of Florida, Gainesville, USA.

Jacobson SK, Sieving KE, Jones GA, Van Doorn A. 2003. Assessment of farmer attitudes and behavioral intentions toward bird conservation on organic and conventional Florida farms. Conservation Biology 17:595-606.

Jasinski M, Hughes M, Fraser HW, Fitzgerald S, Willwerth JJ. 2021. Kestrel nest box occupancy and fledging rates and the effect of kestrel presence and absence on bird abundance and activity in fruiting crops in the Niagara Region and Norfolk County. Crop Protection 139:e105377.

Jedlicka JA, Greenberg R, Letourneau DK. 2011. Avian conservation practices strengthen ecosystem services in California vineyards. PLoS ONE 6(11):e27347.

Jedlicka JA, Vo ATE, Almeida RPP. 2016. Molecular scatology and high-throughput sequencing reveal predominately herbivorous insects in the diets of adult and nestling Western Bluebirds (*Sialia mexicana*) in California vineyards. The Auk 134:116-127.

Johansson NR, Kaasalainen U, Rikkinen J. 2025. Diversity of fungi attached to birds corresponds to the habitat ecologies of their avian dispersal vectors. Annals of Botany 136:721-732.

Johnson MD, Hackett SC. 2016. Why Birds Matter Economically: Values, Markets, and Policies. Pages 27-48 in Şekercioğlu ÇH, Wenny DG, Whelan CJ, editors. Why Birds Matter: Avian Ecological Function and Ecosystem Services. University of Chicago Press, Chicago.

Johnson MD, Levy NJ, Kellermann JL, Robinson DE. 2009. Effects of shade and bird exclusion on arthropods and leaf damage on coffee farms in Jamaica's Blue Mountains. Agroforestry Systems 76:139-148.

Johnson RJ, Glahn JF. 1994. European Starlings. The Handbook: Prevention and Control of Wildlife Damage. USDA Animal & Plant Health Inspection Service, Riverdale Park, USA.

Johnson RJ, Jedlicka JA, Quinn JE, Brandle JR. 2011. Global Perspectives on Birds in Agricultural Landscapes. Pages 55-140 in Campbell WB, Ortíz SL, editors. Integrating Agriculture, Conservation and Ecotourism: Examples from the Field. Springer, New York, USA.

Johnston A, Hochachka WM, Strimas-Mackey ME, Gutierrez VR, Robinson OJ, Miller ET, Auer T, Kelling ST, Fink D. 2021. Analytical guidelines to increase the value of community science data: an example using eBird data to estimate species distributions. Diversity and Distributions 27:1265-1277.

Jones GA, Sieving KE, Avery ML, Meagher RL. 2005a. Parasitized and non-parasitized prey selectivity by an insectivorous bird. Crop Protection 24:185-189.

Jones GA, Sieving KE, Jacobson SK. 2005b. Avian diversity and functional insectivory on North-Central Florida farmlands. Conservation Biology 19:1234-1245.

Jones GA, Sieving KE. 2006. Intercropping sunflower in organic vegetables to augment bird predators of arthropods. Agriculture, Ecosystems and Enviroment 117:171-177.

Jordani MX, Hasui É, da Silva VX. 2015. Natural enemies depend on remnant habitat size in agricultural landscapes. Journal of Forestry Research 26:469-477.

Joseph LN, Maloney RF, O'Connor SM, Cromarty P, Jansen P, Stephens T, Possingham HP. 2008. Improving methods for allocating resources among threatened species: the case for a new national approach in New Zealand. Pacific Conservation Biology 14:154-158.

Jupp V. 2001. Triangulation. In McLaughlin E, Muncie J, editors. The SAGE Dictionary of Criminology. SAGE Publications, London, UK.

Kareiva P, Lalasz R, Marvier M. 2012. Conservation in the Anthropocene: beyond solitude and fragility. Breakthrough Journal 2:29-37.

Karp DS, Mendenhall CD, Sandí RF, Chaumont N, Ehrlich PR, Hadly EA, Daily GC. 2013. Forest bolsters bird abundance, pest control and coffee yield. Ecology Letters 16:1339-1347.

Katayama N, Uchida H, Kusumoto Y, Iida T. 2022. Bird use of fruit orchards and vineyards in Japan: Mitigating a knowledge gap with a systematic review of published and grey literature. Ornithol Sci 21:93-114.

Katuwal HB, Zhang M, Baral HS, Sharma HP, Quan RC. 2021. Assessment of farmers' knowledge and perceptions towards farmland birds show the need of conservation interventions. Global Ecology and Conservation 27:e01563.

Kaval P, Baskaran R. 2013. Key Ideas and Concepts from Economics for Understanding the Roles and Value of Ecosystem Services. Pages 28-42 in Wratten S, Sandhu H, Cullen R, Costanza R, editors. Ecosystem Services in Agricultural and Urban Landscapes. Wiley-Blackwell, Oxford, UK.

Kay BJ, Twigg LE, Korn TJ, Nicol HI. 1994. The use of artificial perches to increase predation on house mice (*Mus domesticus*) by raptors. Wildlife Research 21:95-106.

Ke A, Sollmann R, Frishkoff L, Echeverri A, Zook J, Karp DS. 2024. Effects of agriculture and nature reserves on avian behavior in northwestern Costa Rica. Conservation Biology 38:e14241.

Kellerman JL, Johnson MD, Stercho AM, Hackett SC. 2008. Ecological and economic services provided by birds on Jamaican Blue Mountains coffee farms. Conservation Biology 22:1177-1185.

Kelly D, Ladley JJ, Robertson AW, Anderson SH, Wotton DM, Wiser SK. 2010. Mutualisms with the wreckage of an avifauna: the status of bird pollination and fruit-dispersal in New Zealand. New Zealand Journal of Ecology 34:66-85.

Kelly D, Robertson AW, Ladley JJ, Anderson SH, McKenzie RJ. 2006. The relative (un)importance of introduced animals as pollinators and dispersers of native plants. Pages 227-245 in Allen RB, Lee WG, editors. Biological Invasions in New Zealand. 1st edition. Springer, Berlin, Germany.

Kim J, Koo TH. 2007. The use of feathers to monitor heavy metal contamination in herons, Korea. Arch Environ Contam Toxicol 53:435-441.

Kirk DA, Evenden MD, Mineau P. 1996. Past and Current Attempts to Evaluate the Role of Birds as Predators of Insect Pests in Temperate Agriculture. Pages 175-262 in Nolan V, Ketterson ED, editors. Current Ornithology. Plenum Press, New York.

Klein AM, Vaissière BE, Cane JH, Stefaan-Dewenter I, Cunningham SA, Kremen C, Tscharntke T. 2007. Importance of pollinators in changing landscapes for world crops. Proceedings of the Royal Society B 274:303-313.

Klosterman ME, Linz GM, Slowik AA, Homan HJ. 2013. Comparisons between blackbird damage to corn and sunflower in North Dakota. Crop Protection 53:1-5.

Koivula M, Korpimäki E, Viitala J. 1997. Do Tengmalm's owls see vole scent marks visible in ultraviolet light? Animal Behaviour 54:873-877.

Kolkert HL, Smith R, Rader R, Reid N. 2021. Prey removal in cotton crops next to woodland reveals periodic diurnal and nocturnal invertebrate predation gradients from the crop edge by birds and bats. Scientific Reports 11:e5256.

Kremen C. 2005. Managing ecosystem services: What do we need to know about their ecology? Ecology Letters 8:468-479.

Kronenberg J. 2014. What can the current debate on ecosystem services learn from the past? Lessons from economic ornithology. Geoforum 55:164-177.

Kross SM, Ingram KP, Long RF, Niles MT. 2018. Farmer perceptions and behaviors related to wildlife and on-farm conservation actions. Conservation Letters 11:1-9.

Kross SM. 2016. Insect pest control and bird damage as a function of distance from riparian habitat in a California vineyard. Proceedings of the Vertebrate Pest Conference, 27:204-208.

Kross SM, Kelsey TR, McColl CJ, Townsend JM. 2016. Field-scale habitat complexity enhances avian conservation and avian-mediated pest-control services in an intensive agricultural crop. Agriculture, Ecosystems and Environment 225:140-149.

Kross SM, Martinico BL, Bourbour RP, Townsend JM, McColl C, Kelsey RT. 2020. Effects of field and landscape scale habitat on insect and bird damage to sunflowers. Frontiers in Sustainable Food Systems 4:e40.

Kross SM, Tylianakis JM, Nelson XJ. 2012. Effects of introducing threatened falcons into vineyards on abundance of passeriformes and bird damage to grapes. Conservation Biology 26:142-149.

Lamelas-López L, Marco F. 2021. Using camera-trapping to assess grape consumption by vertebrate pests in a World Heritage vineyard region. Journal of Pest Science 94:585-590.

Langowska A, Yosef R, Skórka P, Tryjanowski P. 2018. Mist-netting of migrating bee-eaters positively influences honey bee colony performance. Journal of Apicultural Science 62:67-78.

Lazaridou D, Michailidis A. 2023. Assessment of farmers' attitudes toward pest control services provided by birds. KnE Social Sciences:138-147.

Lederer RJ. 2019. The Art of the Bird: The History of Ornithological Art through Forty Artists. 1st edition. University of Chicago Press, Chicago.

Lee WG, Meurk CD, Clarkson BD. 2008. Agricultural intensification: Whither indigenous biodiversity? New Zealand Journal of Agricultural Research 51:457-460.

Legendre P, Legendre L. 2012. Ordination in Reduced Space. Numerical Ecology (3rd edition). Elsevier, Amsterdam.

Lemessa D, Samnegård U, Hambäck PA, Hylander K. 2015. Tree cover mediates the effect on rapeseed leaf damage of excluding predatory arthropods, but in an unexpected way. Agriculture, Ecosystems and Environment 211:57-64.

Lemmers P, Davidson MM, Butler RC. 2014. Relative abundance of introduced European birds varies with field margin type on arable farms in Canterbury, New Zealand. New Zealand Journal of Zoology 41:203-209.

Lenth R, Singmann H, Love J, Buerkner P, Herve M. 2018. Package "emmeans." Available from http://cran.r-project.org/package=emmeans (accessed May 2, 2025).

Leuschner N. 2013. Whitehead / Pōpokotea. Available from https://www.nzbirdsonline.org.nz/species/whitehead (accessed January 19, 2026).

Librán-Embid F, de Coster G, Metzer JP. 2017. Effects of bird and bat exclusion on coffee pest control at multiple spatial scales. Landscape Ecology 32:1907-1920.

Liebl AL, Schrey AW, Andrew SC, Sheldon EL, Griffith SC. 2015. Invasion genetics: Lessons from a ubiquitous bird, the house sparrow *Passer domesticus*. Current Zoology 61:465-476.

Lindell CA, Eaton RA, Lizotte EM, Rothwell NL. 2012. Bird consumption of sweet and tart cherries. Human-Wildlife Interactions 6:283-290.

Lindell CA, Steensma KMM, Curtis PD, Boulanger JR, Carroll JE, Burrows C, Lusch DP, Rothwell NL, Wieferich SL, Henrichs HM, Leight DK, Eaton RA, Linz GM. 2016. Proportion of bird damage in tree fruits are higher in low-fruit-abundance contexts. Crop Protection 90:40-48.

Lindell CA, Hannay MB, Hawes BC. 2018. Bird management in blueberries and grapes. Agronomy 8:1-16.

Lindell CA, Eaton RA, Howard PH, Roels SM, Shave ME. 2018b. Enhancing agricultural landscapes to increase crop pest reduction by vertebrates. Agriculture, Ecosystems and Environment 257:1-11.

Linden VMG, Grass I, Joubert E, Tscharntke T, Weier SM, Taylor PJ. 2019. Ecosystem services and disservices by birds, bats and monkeys change with macadamia landscape heterogeneity. Journal of Applied Ecology 56:2069-2078.

Linkie M, Dinata Y, Nofrianto A, Leader-Williams N. 2007. Patterns and perceptions of wildlife crop raiding in and around Kerinci Seblat National Park, Sumatra. Animal Conservation 10:127-135.

Linz GM, Homan HJ, Gaulker SM, Penry LB, Bleier WJ. 2007. European starlings: a review of an invasive species with far-reaching impacts. Fort Collins, USA.

Lišková S, Frynta D. 2013. What determines bird beauty in human eyes? Anthrozoos 26:27-41.

Loreau M, Mouquet N, Gonzalez A, Mooney HA. 2003. Biodiversity as spatial insurance in heterogeneous landscapes. Proceedings of the National Academy of Sciences 100:12765-12770.

Lövei GL, Ferrante M. 2017. A review of the sentinel prey method as a way of quantifying invertebrate predation under field conditions. Insect Science 24:528-542.

Low PA, Sam K, McArthur C, Posa MRC, Hochuli DF. 2014. Determining predator identity from attack marks left in model caterpillars: Guidelines for best practice. Entomologia Experimentalis et Applicata 152:120-126.

Lowder SK, Sánchez MV, Bertini R. 2021. Which farms feed the world and has farmland become more concentrated? World Development 142:105455.

Lowe S, Browne M, Boudkelas S, de Poorter M. 2000. 100 of the World's Worst Invasive Alien Species: A Selection from the Global Invasive Species Database. Invasive Species Specialist Group, Auckland, New Zealand. 11p.

Luck GW. 2013. The net return from animal activity in agro-ecosystems: trading off benefits from ecosystem services against costs from crop damage. F1000Research 2:239.

Luck GW, Daily GC, Ehrlich PR. 2003. Population diversity and ecosystem services. Trends in Ecology & Evolution 18:331-336.

Luck GW, Hunt K, Carter A. 2015. The species and functional diversity of birds in almond orchards, apple orchards, vineyards and eucalypt woodlots. Emu 115:99-109.

Luna AP, Bintanel H, Viñuela J, Villanúa D. 2020. Nest-boxes for raptors as biological control system of vole pests: high local success with moderate negative consequences for non-target species. Biological Control 146:e104267.

Lute ML, Navarrete CD, Nelson MP, Gore ML. 2016. Moral dimensions of human-wildlife conflict. Conservation Biology 30:1200-1211.

Lyver PO, Moller H, Thomas WH, Muiruri MN, Maundu P, Sault N, Barua M, Jepson P. 2010. Birds and Conservation. Pages 241-330 Ethno-ornithology: Birds, Indigenous Peoples, Culture and Society, 1ed edition. Earthscan, London, UK.

Lyytimäki J, Sipilä M. 2009. Hopping on one leg - The challenge of ecosystem disservices for urban green management. Urban Forestry and Urban Greening 8:309-315.

Maas B, Clough Y, Tscharntke T. 2013. Bats and birds increase crop yield in tropical agroforestry landscapes. Ecology Letters 16:1480-1487.

Maas B, Tscharntke T, Saleh S, Dwi Putra D, Clough Y. 2015. Avian species identity drives predation success in tropical cacao agroforestry. Journal of Applied Ecology 52:735-743.

Maas B, Tscharntke T, Tjoa A, Saleh S, Edy N, Anshary A, Basir M. 2018. Effects of Ecosystem Services Provided by Birds and Bats in Smallholder Cacao Plantations of Central Sulawesi. University of Göttingen, Germany.

Maas B, Heath S, Grass I, Cassano C, Classen A, Faria D, Gras P, Williams-Guillén K, Johnson M, Karp DS, Linden V, Martínez-Salinas A, Schmack JM, Kross S. 2019. Experimental field exclosure of birds and bats in agricultural systems — Methodological insights, potential improvements, and cost-benefit trade-offs. Basic and Applied Ecology 35:1-12.

MacArthur RH, Wilson EO. 1967. The Theory of Island Biogeography. Princeton University Press, Princeton.

MacFarlane AET, Briskie JV, Kelly D. 2025. Dispersal of invasive Berberis glaucocarpa in secondary forest occurs mainly by exotic frugivores. Notornis 72:91.

MacKenzie DI, Nichols JD, Lachman GB, Droege S, Royle AA, Langtimm CA. 2002. Estimating site occupancy rates when detection probabilities are less than one. Ecology 83:2248-2255.

MacLellan CR. 1958. Role of woodpeckers in control of the codling moth in Nova Scotia. The Canadian Entomologist 90:18-22.

MacLeod CJ, Blackwell G, Benge J. 2012. Reduced pesticide toxicity and increased woody vegetation cover account for enhanced native bird densities in organic orchards. Journal of Applied Ecology 49:652-660.

MacLeod CJ, Blackwell G, Moller H, Innes J, Powlesland R. 2008. The forgotten 60%: bird ecology and management in New Zealand's agricultural landscape. New Zealand Journal of Ecology 32:240-255.

MacLeod CJ, Newson SE, Blackwell G, Duncan RP. 2009. Enhanced niche opportunities: Can they explain the success of New Zealand's introduced bird species? Diversity and Distributions 15:41-49.

Macleod CJ, Till A. 2007. Crop use by introduced bird species in winter in relation to crop structure and seed resources. Bird Study 54:80-86.

Macleod R, Gosler AG, Cresswell W. 2005. Diurnal mass gain strategies and perceived predation risk in the great tit Parus major. Journal of Animal Ecology 74:956-964.

Maguire DJ. 1991. An overview and definition of GIS. Geographical Information Systems: Principles and Applications 1:9-20.

Mangan AM, Pejchar L, Werner SJ. 2017. Bird use of organic apple orchards: frugivory, pest control and implications for production. PLoS ONE 12:1-15.

Manikowski S. 1984. Birds injurious to crops in west Africa. Tropical Pest Management 30:379-387.

Manyama F, Nyahongo JW, Roskaft E. 2014. Factors affecting attitudes of local people toward the red-billed quelea (*Quelea quelea*) in Kondoa District, Tanzania. International Journal of Biodiversity and Conservation 6:138-147.

Marrero P, Oliveira P, Nogales M. 2004. Diet of the endemic Madeira laurel pigeon *Columba trocaz* in agricultural and forest areas: implications for conservation. Bird Conservation International 14:165-172.

Martin EA, Reineking B, Seo B, Steffan-Dewenter I. 2013. Natural enemy interactions constrain pest control in complex agricultural landscapes. Proceedings of the Natural Academy of Sciences 110:5534-5539.

Martin EA, Reineking B, Seo B, Steffan-Dewenter I. 2015. Pest control of aphids depends on landscape complexity and natural enemy interactions. PeerJ 3:e1095.

Martin EA, Seo B, Park CR, Reineking B, Steffan-Dewenter I. 2016. Scale-dependent effects of landscape composition and configuration on natural enemy diversity, crop herbivory, and yields. Ecological Applications 26:448-462.

Martínez-Núñez C, Rey PJ, Manzaneda AJ, Tarifa R, Molina JL, Salido T. 2020a. Landscape drivers and effectiveness of pest control by insectivorous birds in a landscape-dominant woody crop. BioRxiv.

Martínez-Núñez C, Rey PJ, Manzaneda AJ, Tarifa R, Salido T, Isla J, Pérez AJ, Camacho FM, Molina JL. 2020b. Direct and indirect effects of agricultural practices, landscape complexity and climate on insectivorous birds, pest abundance and damage in olive groves. Agriculture, Ecosystems and Environment 304:107145.

Martínez-Salinas A, Chain-Guadarrama A, Aristizábal N, Vilchez-Mendoza S, Cerda R, Ricketts TH. 2022. Interacting pest control and pollination services in coffee systems. Proceedings of the National Academy of Sciences 119:e2119959119.

Martínez-Sastre R, Miñarro M, García D. 2020. Animal biodiversity in cider apple orchards: simultaneous environmental drivers and effects on insectivory and pollination. Agriculture, Ecosystems and Environment 295:106918.

Marzluff JM, Boone RB, Cox GW. 1994. Historical changes in populations and perceptions of native pest bird species in the West. Studies in Avian Biology 15:202-220.

Massé F, Dickinson H, Margulies J, Joanny L, Lappe-Osthege T, Duffy R. 2020. Conservation and crime convergence? Situating the 2018 London Illegal Wildlife Trade Conference. Journal of Political Ecology 27:23-42. University of Arizona Libraries.

Matson PA, Parton WJ, Power AG, Swift MJ. 1997. Agricultural intensification and ecosystem properties. Science 277:504-509.

Matson PA, Vitousek PM. 2006. Agricultural intensification: Will land spared from farming be land spared for nature? Conservation Biology 20:709-710.

Maxwell SL, Fuller RA, Brooks TM, Watson JEM. 2016. Biodiversity: The ravages of guns, nets and bulldozers. Nature 536:143-145.

Mayne SJ, King DI, Andersen JC, Elkinton JS. 2023. Crop-specific effectiveness of birds as agents of pest control. Agriculture, Ecosystems and Environment 348:e108395.

McArthur N, Flux I, Harvey A. 2021. State and trends in the diversity, abundance and distribution of birds in Wellington City. Greater Wellington Regional Council, Wellington, New Zealand. 80p.

McGovern J, Giese J, Schulte L. 2024. Springtime bird use of agricultural landscapes examined by using autonomous recording units. Journal of Field Ornithology 95:1-17.

McInnes RS, Carne PB. 1978. Predation of cossid moth larvae by yellow-tailed black cockatoos causing losses in plantations of Eucalyptus grandis in north coastal New South Wales. Australian Wildlife Research 5:101-121.

McKay H, Watola GV, Langton SD, Langton SA. 2006. The use of agricultural fields by re-established greylag geese (Anser anser) in England: A risk assessment. Crop Protection 25:996-1003.

McLean IG. 1989. Feeding behaviour of the fantail (Rhipidura fuliginosa). Notornis 36:99-106.

McMahon BJ, Arroyo B, Bunnefeld N, Carrete M, Daunt F, Young JC. 2024. Birds and people: from conflict to coexistence. Ibis 166:23-37.

McWherter B, Ma Z, Wahl M, Zollner P, Humberg LA, Kluever BM, Burcham GN. 2025. Drivers of agricultural producers' tolerance towards less-charismatic avian species. Biological Conservation 301:110884.

MEA. 2003. Millennium Ecosystem Assessment: Ecosystems and Human Well-being - A Framework for Assessment. Island Press, Washington, DC.

Merfield C, Moller H, Manhire J, Rosin C, Norton S, Carey P, Hunt L, Reid J, Fairweather J, Benge J, Le Quellec I, Campbell H, Lucock D, Saunders C, MacLeod C, Barber A,

McCarthy A. 2015. Are organic standards sufficient to ensure sustainable agriculture? Lessons from New Zealand's ARGOS and Sustainability Dashboard projects. Sustainable Agriculture Research 4:158-172.

Metwally AM, Ahmed MA, Mahmoud NA, Abdel-Aal MM. 2009. Field trials to evaluate damage caused by wild birds to certain field crops under different habitats at Assiut Governorate. Journal of Agricultural Sciences 34:1291-1300.

Michel N. L, Whelan CJ, Verutes GM. 2020. Ecosystem services provided by Neotropical birds. The Condor 122:1-21.

Mihai CA, Stănică F, Stănică MRI. 2017. Monitoring of artificial nests in horticultural ecosystems - observation of woodpeckers ethology. Pages 631-638 2nd International Conference on Sustainable Agriculture and Food Security: A Comprehensive Approach. KnE Life Sciences, Dubai, UAE.

Milligan MC, Johnson MD, Garfinkel M, Smith CJ, Njoroge P. 2016. Quantifying pest control services by birds and ants in Kenyan coffee farms. Biological Conservation 194:58-65.

Mills JA. 2022. Red-billed gull | tarāpunga. Available from www.nzbirdsonline.org.nz (accessed November 18, 2025).

Mirski P, Grosberg J, Kull T, Mellov P, Tõnisalu G, Väli V, Väli Ü. 2024. Movement of avian predators points to biodiversity hotspots in agricultural landscape. Royal Society Open Science 11:231543.

Miskelly C. 2025, December. Bird Taxa. Available from https://collections.tepapa.govt.nz/topic/2872 (accessed January 17, 2026).

Miskelly CM. 2015. Rainbow lorikeet. Available from www.nzbirdsonline.org.nz (accessed August 9, 2025).

Miskelly CM. 2022. Southern black-backed gull | karoro. Available from www.nzbirdsonline.org.nz (accessed November 18, 2025).

Miskelly CM, Dowding JE, Elliott GP, Hitchmough RA, Powlesland RG, Robertson HA, Sagar PM, Scofield RP, Taylor GA. 2009. Conservation status of New Zealand birds, 2008: Science or assertion? Notornis 55:117-135.

Miskelly CM, Powlesland RG. 2013. Conservation translocations of New Zealand birds, 1863-2012. Notornis 60:3-28.

Mitchell MC, Best LB, Gionfriddo JP. 2015. Avian nest-site selection and nesting. The Wilson Bulletin 108:573-583.

Moeed A, Fitzgerald BM. 1982. Foods of insectivorous birds in forest of the Orongorongo Valley, Wellington, New Zealand. New Zealand Journal of Zoology 9:391-403.

Moller H, MacLeod CJ, Haggerty J, Rosin C, Blackwell G, Perley C, Meadows S, Weller F, Gradwohl M. 2008. Intensification of New Zealand agriculture: Implications for biodiversity. New Zealand Journal of Agricultural Research 51:253-263.

Mols CMM, Visser ME. 2002. Great tits can reduce caterpillar damage in apple orchards. Journal of Applied Ecology 39:888-899.

Monteagudo N, Benayas JMR, Andivia E, Rebollo S. 2023. Avian regulation of crop and forest pests, a meta-analysis. Pest Management Science 79:2380-2389.

Montoya A, Cabodevilla X, Fargallo JA, Biescas E, Mentaberre G, Villanúa D. 2021. Vertebrate diet of the common kestrel (Falco tinnunculus) and barn owl (*Tyto alba*) in rain-fed crops: implications to the pest control programs. European Journal of Wildlife Research 67:79.

Montràs-Janer T, Knape J, Nilsson L, Tombre I, Pärt T, Månsson J. 2019. Relating national levels of crop damage to the abundance of large grazing birds: Implications for management. Journal of Applied Ecology 56:2286-2297.

Morante-Filho JC, Benchimol M, Faria D. 2021. Landscape composition is the strongest determinant of bird occupancy patterns in tropical forest patches. Landscape Ecology 36:105-117.

Moreno-Opo R, Piqué J. 2018. Reconciling the conservation of the purple swamphen (*Porphyrio porphyrio*) and its damage in Mediterranean rice fields through sustainable non-lethal techniques. PeerJ 6:e4518.

Morgan J. 2025. The tide turns: feral cats join the predator free mission. Available from https://predatorfreenz.org/research/predators/feral-cats-join-the-predator-free-mission/ (accessed January 28, 2026).

Morris D. 1956. The feather postures of birds and the problem of the origin of social signals. Behaviour 9:75-113.

Muchula K, Xie G, Gurr GM. 2019. Ambient temperature affects the utility of plasticine caterpillar models as a tool to measure activity of predators across latitudinal and elevational gradients. Biological Control 129:12-17.

Murphy EC, Russell JC, Broome KG, Ryan GJ, Dowding JE. 2019. Conserving New Zealand's native fauna: a review of tools being developed for the Predator Free 2050 programme. Journal of Ornithology 160:883-892.

Murton RK, Jones BE. 1973. The ecology and economics of damage to Brassicae by wood-pigeons *Columba palumbus*. Annals of Applied Biology 75:107-122.

Musiwa AR, Mhlanga W. 2020. Human-wildlife conflict in Mhokwe Ward, Mbire District, North-East Zimbabwe. African Journal of Ecology 58:786-795.

Navedo JG, Hahn S, Parejo M, Abad-Gómez JM, Gutiérrez JS, Villegas A, Sánchez-Guzmán JM, Masero JA. 2015. Unravelling trophic subsidies of agroecosystems for biodiversity conservation: Food consumption and nutrient recycling by waterbirds in Mediterranean rice fields. Science of the Total Environment 511:288-297.

Ndang'Ang'A PK, Njoroge JBM, Ngamau K, Kariuki W, Atkinson PW, Vickery J. 2013. Avian foraging behaviour in relation to provision of ecosystem services in a highland East African agroecosystem. Bird Study 60:156-168.

Nereu M, Heleno RH, Lopez-Núñez F, Agostinho M, Ramos JA. 2018. Effects of native biodiversity on grape loss of four castes: Testing the biotic resistance hypothesis. Web Ecology 18:15-27.

Nevard TD, Leiper I, Archibald G, Garnett ST. 2019. Farming and cranes on the Atherton Tablelands, Australia. Pacific Conservation Biology 25:184-192.

Newbold T, Scharlemann JPW, Butchart SHM, Şekercioğlu ÇH, Alkemade R, Booth H, Purves DW. 2013. Ecological traits affect the response of tropical forest bird species to land-use intensity. Proceedings of the Royal Society B: Biological Sciences 280:20122131.

Niemczynowicz A, Świętochowski P, Brzeziński M, Zalewski A. 2017. Non-native predator control increases the nesting success of birds: American mink preying on wader nests. Biological Conservation 212:86-95.

Norton DA, Miller CJ. 2000. Some issues and options for the conservation of native biodiversity in rural New Zealand. Ecological Management and Restoration 1:26-34.

Nugent G, Whitford EJ, Hunnam JC, Wilson PR, Cross ML, de Lisle GW. 2011. *Mycobacterium avium* subsp. paratuberculosis infection in wildlife on three deer farms with a history of Johne's disease. New Zealand Veterinary Journal 59:293-298.

Nurdiansyah F, Denmead LH, Clough Y, Wiegand K, Tscharntke T. 2016. Biological control in Indonesian oil palm potentially enhanced by landscape context. Agriculture, Ecosystems and Environment 232:141-149.

Nuwer RL. 2018. Poached: Inside the Dark World of Wildlife Trafficking. Da Capo Press, Boston, USA.

NZAP. 2025. Our Apples. Available from https://www.applesandpears.nz/our-apples-pears/our-apples/ (accessed July 14, 2025).

O'Bryan CJ, Braczkowski AR, Beyer HL, Carter NH, Watson JEM, McDonald-Madden E. 2018. The contribution of predators and scavengers to human well-being. Nature Ecology and Evolution 2:229-236.

O'Connor T, García GÓ, Isacch JP. 2022. Avian biodiversity and frugivory in an agroecological cherry orchard in the Pampas region of Argentina. Ardeola 69:249-262.

Ojea E, Martin-Ortega J, Chiabai A. 2012. Defining and classifying ecosystem services for economic valuation: the case of forest water services. Environmental Science and Policy 19-20:1-15.

Oksanen J, Kindt R, Legendre P, O'Hara B, Simpson GL, Solymos P, Stevens MHH, Wagner H. 2008. vegan: Community Ecology Package. https://vegandevs.github.io/vegan/, R package version 2.7.2.

Oliveira CM, Auad AM, Mendes SM, Frizzas MR. 2014. Crop losses and the economic impact of insect pests on Brazilian agriculture. Crop Protection 56:50-54.

Olimpi EM, Garcia K, Gonthier DJ, de Master KT, Echeverri A, Kremen C, Sciligo AR, Snyder WE, Wilson-Rankin EE, Karp DS. 2020. Shifts in species interactions and farming

contexts mediate net effects of birds in agroecosystems. Ecological Applications 30:e02115.

Olimpi EM, Garcia K, Gonthier DJ, Kremen C, Snyder WE, Wilson-Rankin EE, Karp DS. 2021. Semi-natural habitat surrounding farms promotes multifunctionality in avian ecosystem services. Journal of Applied Ecology 59:898-908.

Olmos-Moya N, Díaz-Siefer P, Pozo RA, Fontúrbel FE, Lavandero B, Abades S, Celis-Diez JL. 2022. The use of cavity-nesting wild birds as agents of biological control in vineyards of Central Chile. Agriculture, Ecosystems and Environment 334:e107975.

Orłowski G, Karg J, Karg G. 2014. Functional invertebrate prey groups reflect dietary responses to phenology and farming activity and pest control services in three sympatric species of aerially foraging insectivorous birds. PLoS ONE 9:1-18.

Osie M, Shibru S, Nemomissa S. 2023. Birds and arthropods predation in mosaic agricultural landscapes: implication of habitat heterogeneity for ecosystem services. Research Square:e 2787812.

Otieno NE, Jacobs SM, Pryke JS. 2019. Maize-field complexity and farming system influence insectivorous birds' contribution to arthropod herbivore regulation. Biotropica 51:851-861.

Owen M. 1990. The damage-conservation interface illustrated by geese. Ibis 132:238-252.

Page MJ, McKenzie JE, Bossuyt PM, Boutron I, Hoffmann TC, Mulrow CD, Shamseer L, Tetzlaff JM, Akl EA, Brennan SE, Chou R, Glanville J, Grimshaw JM, Hróbjartsson A, Lalu MM, Li T, Loder EW, Mayo-Wilson E, McDonald S, McGuinness LA, Stewart LA, Thomas J, Tricco AC, Welch VA, Whiting P, Moher D. 2021. The PRISMA 2020 statement: an updated guideline for reporting systematic reviews. British Journal of Management 372:n71.

Pande S, Dahanukar N. 2011. The diet of Indian eagle owl *Bubo bengalensis* and its agronomic significance. JoTT Communication 3:2011-2017.

Paranjpe DA, Dange P. 2020. A tale of two species: human and peafowl interactions in human-dominated landscapes influence each other's behaviour. Current Science 119:670-679.

Patriarca A. 2019. Fungi and mycotoxin problems in the apple industry. Current Opinion in Food Science 29:42-47.

Peach WJ, Vincent KE, Fowler JA, Grice PV. 2008. Reproductive success of house sparrows along an urban gradient. Animal Conservation 11:493-503.

Pearson DL. 1971. Vertical stratification of birds in a tropical dry forest. The Condor 73:46-55.

Peer BD, Homan HJ, Linz GM, Bleier WJ. 2003. Impact of blackbird damage to sunflower: bioenergetic and economic models. Ecological Applications 13:248-256.

Peil A, Bus VGM, Geider K, Richter K, Flachowsky H, Hanke MV. 2009. Improvement of fire blight resistance in apple and pear. International Journal of Plant Breeding 3:1-27.

Peisley RK, Saunders ME, Luck GW. 2015. A systematic review of the benefits and costs of birds and insect activity in agroecosystems. Springer Science Reviews 3:113-125.

Peisley RK, Saunders ME, Luck GW. 2016. Cost-benefit trade-offs of bird activity in apple orchards. PeerJ 2016:1-20.

Penick CA, Savage AM, Dunn RR. 2015. Stable isotopes reveal links between human food inputs and urban ant diets. Proceedings of the Royal Society B - Biological Sciences 282:2014608.

Perfecto I, Vandermeer JH, Bautista GL, Nuñez GI, Greenberg R, Bichier P, Langridge S. 2004. Greater predation in shaded coffee farms: the role of resident neotropical birds. Ecology 85:2677-2681.

Perfecto I, Philpott SM. 2023. Ants (Hymenoptera: Formicidae) and ecosystem functions and services in urban areas: a reflection on a diverse literature. Myrmecological News 33:103-122.

Peria L, Francis CD. 2025. Avian biodiversity in central California vineyards. PeerJ 13:e19904.

Pescador M, Peris SJ. 1998. Effects of great bustards (*Otis tarda*) on cultivated areas in west-central Spain. Journal of Agricultural Science 130:9-15.

Peters VE, Greenberg R. 2013. Fruit supplementation affects birds but not arthropod predation by birds in Costa Rican agroforestry systems. Biotropica 45:102-110.

Peters K, Breitsameter L, Gerowitt B. 2014. Impact of climate change on weeds in agriculture: a review. Agronomy for Sustainable Development 34:707-721.

Peterson MN, Peterson MJ, Peterson TR, Leong K. 2013. Why transforming biodiversity conservation conflict is essential and how to begin. Pacific Conservation Biology 19:94-103.

PFNZ. 2022. Predator Free New Zealand. Available from https://predatorfreenz.org/ (accessed January 26, 2026).

Phalan B, Onial M, Balmford A, Green RE. 2011. Reconciling food production and biodiversity conservation: Land sharing and land sparing compared. Science 333:1289-1291.

Philpott SM, Soong O, Lowenstein JH, Pulido AL, Lopez DT, Flynn DFB, Declerck F. 2009. Functional richness and ecosystem services: bird predation on arthropods in tropical agroecosystems. Ecological Applications 19:1858-1867.

Pipfruit NZ. 2025. Integrated Fruit Production (IFP) Manual. Available from https://ifp.pipfruitnz.co.nz/manual (accessed January 26, 2026).

Plaza PI, Blanco G, Madariaga MJ, Boeri E, Teijeiro ML, Bianco G, Lambertucci SA. 2018. Scavenger birds exploiting rubbish dumps: pathogens at the gates. Transboundary and Emerging Diseases 66:873-881.

Plotnikov A, Sinyavskiy I. 2020. The use of bird droppings, mineral and organomineral fertilizers in solving the issue of increasing productivity of agricultural lands of the Trans-Urals. BIO Web of Conferences 27:00111.

Pohja-Mykrä M, Vuorisalo T, Mykrä S. 2012. Organised persecution of birds of prey in Finland: historical and population biological perspectives. Ornis Fennica 89:1-19.

Porter RER, Rudge MR, McLennan J. 1994. Birds and small mammals: a pest control manual. Manaaki Whenua Press, Lincoln.

Power AG. 2010. Ecosystem services and agriculture: Tradeoffs and synergies. Philosophical Transactions of the Royal Society B: Biological Sciences 365:2959-2971.

Powlesland RG. 2013. Kererū | New Zealand pigeon. Available from https://www.nzbirdsonline.org.nz/species/new-zealand-pigeon (accessed January 25, 2026).

Prasad RR, Christi K. 2014. Physical method of control on common myna (*Acridotheres tristis*) in Sigatoka-Fiji Islands. The International Journal of Engineering and Science 3:26-31.

Pretty J, Bharucha ZP. 2014. Sustainable intensification in agricultural systems. Annals of Botany 114:1571-1596.

Prokop P, Fančovičová J. 2013. Does colour matter? The influence of animal warning coloration on human emotions and willingness to protect them. Animal Conservation 16:458-466.

Puan CL, Goldizen AW, Zakaria MH, Mohd N, Baxter GS. 2011. Absence of differential predation on rats by Malaysian barn owls in oil palm plantations. Journal of Raptor Research 45:71-78.

Pucket HL, Brandle JR, Johnson RJ, Blankenship EE. 2009. Avian foraging patterns in crop field edges adjacent to woody habitat. Agriculture, Ecosystems and Environment 131:9-15.

Pulliam HR. 1988. Sources, sinks, and population regulation. The American Naturalist 132:652-661.

Pullin AS, Stewart GB. 2006. Guidelines for systematic review in conservation and environmental management. Conservation Biology 20:1647-1656.

Quammen D. 1997. The Song of the Dodo: Island Biogeography in an Age of Extinction. Scribner, New York City.

Quinn JL, Cole EF, Bates J, Payne RW, Cresswell W. 2012. Personality predicts individual responsiveness to the risks of starvation and predation. Proceedings of the Royal Society B: Biological Sciences 279:1919-1926.

Rabou AFNA. 2022. On the occurrence, trapping and potential risks of the invasive Indian Myna (*Acridotheres tristis* Linnaeus, 1766) in the Gaza Strip: Palestine. International Journal of Fauna and Biological Studies 9:45-55.

Ratcliffe N, Bell M, Pelembe T, Boyle D, Benjamin R, White R, Godley B, Stevenson J, Sanders S. 2010. The eradication of feral cats from Ascension Island and its subsequent recolonization by seabirds. Oryx 44:20-29.

Raudsepp-Hearne C, Peterson GD, Teng M, Bennett EM, Holland T, Benessaiah K, MacDonald GK, Pfeifer L. 2010. Untangling the environmentalist's paradox: Why is human well-being increasing as ecosystem services degrade? BioScience 60:576-589.

Razalee ML, Norazlimi NA. 2023. Investigating pest birds problems and potential solutions in Sawah Ring, Tangkak. Journal of Sustainable Natural Resources 4:38-46.

Redlich S, Martin EA, Steffan-Dewenter I. 2017. Landscape-level crop diversity benefits biological pest control. Journal of Applied Ecology 55:2419-2428.

Reif J, Voříšek P, Šťastný K, Bejček V, Petr J. 2008. Agricultural intensification and farmland birds: New insights from a central European country. Ibis 150:596-605.

Requier F, Pérez-Méndez N, Andersson GKS, Blareau E, Merle I, Garibaldi LA. 2023. Bee and non-bee pollinator importance for local food security. Trends in Ecology and Evolution 38:196-205.

Rey PJ. 2011. Preserving frugivorous birds in agro-ecosystems: Lessons from Spanish olive orchards. Journal of Applied Ecology 48:228-237.

Rey Benayas JM, Meltzer J, de las Heras-Bravo D, Cayuela L. 2017. Potential of pest regulation by insectivorous birds in Mediterranean woody crops. PLoS ONE 12:e0180702.

Robertson AW, Ladley JJ, Kelly D, McNutt KL, Peterson PG, Merrett MF, Karl BJ. 2008. Assessing pollination and fruit dispersal in *Fuchsia excorticata* (Onagraceae). New Zealand Journal of Botany 46:299-314.

Robertson HA, Baird K, Dowding JE, Elliott GP, Hitchmough RA, Miskelly CM, McArthur N, O'Donnell CJ, Sagar PM, Scofield RP, Taylor GA. 2017. Conservation status of New Zealand birds, 2016. Wellington. Available from www.doc.govt.nz.

Ross J, Ryan G, Jansen M, Sjoberg T. 2020. Predator-free New Zealand 2050: fantasy or reality? Pages 1-6 in Woods DM, editor. Proceedings of the 29th Vertebrate Pest Conference. University of California Agriculture and Natural Resources, Santa Barbara, USA.

RStudio. 2016. RStudio: Integrated Development for R. RStudio, Inc., Boston. Available from http://www.rstudio.com/.

Russell JC, Innes JG, Brown PH, Byrom AE. 2015. Predator-Free New Zealand: Conservation country. BioScience 65:520-525.

Sætre GP, Riyahi S, Aliabadian M, Hermansen JS, Hogner S, Olsson U, Gonzalez Rojas MF, Sæther SA, Trier CN, Elgvin TO. 2012. Single origin of human commensalism in the house sparrow. Journal of Evolutionary Biology 25:788-796.

Sakiyama R. 1991. What Is Horticulture? Chronica Horticulturae:17.

Sandbrook C, Fisher JA, Holmes G, Luque-Lora R, Keane A. 2019. The global conservation movement is diverse but not divided. Nature Sustainability 2:316-323.

Sandbrook CG, Fisher JA, Vira B. 2013. What do conservationists think about markets? Geoforum 50:232-240.

Sandhu PS, Sandhu JS. 1994. Parakeet damage to marigold. Japanese Journal of Ornithology 43:73-78.

Sausse C, Chevalot A, Lévy M. 2021. Hungry birds are a major threat for sunflower seedlings in France. Crop Protection 148:105712.

Sausse C, Lévy M. 2021. Bird damage to sunflower: International situation and prospects. Oilseeds and Fats, Crops and Lipids 28:1-18.

Saxton VP, Creasy GL, Paterson AM, Trought MCT. 2004a. Experimental method to investigate and monitor bird behavior and damage in vineyards. American Journal of Enology and Viticulture 55:288-291.

Saxton VP, Hickling GJ, Trought MCT, Creasy GL. 2004b. Comparative behavior of free-ranging blackbirds (*Turdus merula*) and silvereyes (*Zosterops lateralis*) with hexose sugars in artificial grapes. Applied Animal Behaviour Science 85:157-166.

Schäckermann J, Weiss N, von Wehrden H, Klein A-M. 2014. High trees increase sunflower seed predation by birds in an agricultural landscape of Israel. Frontiers in Ecology and Evolution 2:1-9.

Schäckermann J, Pufal G, Mandelik Y, Klein AM. 2015. Agro-ecosystem services and dis-services in almond orchards are differentially influenced by the surrounding landscape. Ecological Entomology 40:12-21.

Schillé L, Valdés-Correcher E, Archaux F, Bălăcenoiu F, Bjørn MC, Bogdziewicz M, Boivin T, Branco M, Damestoy T, de Groot M, Dobrosavljević J, Duduman ML, Dulaurent AM, Green S, Grünwald J, Eötvös CB, Faticov M, Fernandez-Conradi P, Flury E, Funosas D, Galmán A, Gossner MM, Gripenberg S, Grosu L, Hagge J, Hampe A, Harvey D, Houston R, Isenmann R, Kavčič A, Kozlov MV, Lanta V, Le Tilly B, Lopez-Vaamonde C, Mallick S, Mäntylä E, Mårell A, Milanović S, Molnár M, Moreira X, Moser V, Mrazova A, Musolin DL, Perot T, Piotti A, Popova AV, Prinzing A, Pukinskaya L, Sallé A, Sam K, Sedikhin NV, Shabarova T, Tack AJM, Thomas R, Thrikkadeeri K, Toma D, Vaicaityte G, van Halder I, Varela Z, Barbaro L, Castagneyrol B. 2024. Decomposing drivers in avian insectivory: large-scale effects of climate, habitat and bird diversity. Journal of Biogeography 51:1079-1094.

Schlötelburg A, Plekat A, Bellingrath-Kimura S, Jacob J. 2020. Self-service traps inspected by avian and terrestrial predators as a management option for rodents. Pest Management Science 76:103-110.

Schmidt-Entling MH, Siegenthaler E. 2009. Herbivore release through cascading risk effects. Biology Letters 5:773-776.

Schroth G, Krauss U, Gasparotto L, Aguilar JAD, Vohland K. 2000. Pests and diseases in agroforestry systems of the humid tropics. Agroforestry Systems 50:199-241.

Schwemmer P, Garthe S, Mundry R. 2008. Area utilization of gulls in a coastal farmland landscape: Habitat mosaic supports niche segregation of opportunistic species. Landscape Ecology 23:355-367.

Seaton R, Hyde N. 2013. New Zealand falcon / Kārearea. Available from https://www.nzbirdsonline.org.nz/species/new-zealand-falcon (accessed January 28, 2026).

Şekercioğlu ÇH. 2006. Increasing awareness of avian ecological function. Trends in Ecology and Evolution 21:464-471.

Şekercioğlu ÇH, Daily GC, Ehrlich PR. 2004. Ecosystem consequences of bird declines. Proceedings of the National Academy of Sciences 101:18042-18047.

Şekercioğlu ÇH, Wenny DG, Whelan CJ. 2016. Why Birds Matter: Avian Ecological Function and Ecosystem Service. University of Chicago Press, Chicago.

Shackleton CM, Ruwanza S, Sinasson Sanni GK, Bennett S, De Lacy P, Modipa R, Mtati N, Sachikonye M, Thondhlana G. 2016. Unpacking Pandora's Box: understanding and categorising ecosystem disservices for environmental management and human wellbeing. Ecosystems 19:587-600.

Shave ME, Shwiff SA, Elser JL, Lindell CA. 2018. Falcons using orchard nest boxes reduce fruit-eating bird abundances and provide economic benefits for a fruit-growing region. Journal of Applied Ecology 55:2451-2460.

Shaw W, Bycroft C, Gurney F, Giejsztowt J, Deacon L. 2022. Bird Use of Kiwifruit Orchards Around the Time of Application of Hydrogen Cyanamide. Wildlands, Mt Maunganui, New Zealand. 53p.

Short J. 2016. Predation by feral cats key to the failure of a long-term reintroduction of the western barred bandicoot (*Perameles bougainville*). Wildlife Research 43:38-50.

Shwiff SA, Ernest KL, DeGroot SL, Anderson AM, Shwiff SS. 2017. The Economic Impact of Blackbird Damage to Crops. Pages 207-216 in Linz GM, Avery ML, Dolbeer RA, editors. Ecology and Management of Blackbirds (Icteridae) in North America. CRC Press, Boca Raton, USA.

Sibson RB. 1983. Winter flocking of chaffinches in northern New Zealand. Notornis 30:70-72.

Simon S, Bouvier JC, Debras JF, Sauphanor B. 2010. Biodiversity and pest management in orchard systems. A review. Agronomy for Sustainable Development 30:139-152.

Singer P. 2009. Animal Liberation: The Definitive Classic of the Animal Movement. Harper Perennial Modern Classics, New York, USA.

Siriwardena GM, Baillie SR, Crick HQP, Wilson JD. 2000. The importance of variation in the breeding performance of seed-eating birds in determining their population trends on farmland. Journal of Applied Ecology 37:128-148.

Smith CD, Pontius JS. 2006. Jackknife Estimator of Species Richness with S-PLUS. Journal of Statistical Software 15:1-12.

Smith OM, Taylor JM, Echeverri A, Northfield T, Cornell KA, Jones MS, Latimer CE, Owen JP, Snyder WE, Kennedy CM. 2021. Big wheel keep on turnin': linking grower attitudes, farm management, and delivery of avian ecosystem services. Biological Conservation 254:108970.

Smith OM, Olimpi EM, Navarro-Gonzalez N, Cornell KA, Frishkoff LO, Northfield TD, Bowles TM, Edworthy M, Eilers J, Fu Z, Garcia K, Gonthier DJ, Jones MS, Kennedy CM, Latimer CE, Owen JP, Sato C, Taylor JM, Wilson-Rankin EE, Snyder WE, Karp DS. 2022a. A trait-based framework for predicting foodborne pathogen risk from wild birds. Ecological Applications 32:e2523.

Smith OM, Kennedy CM, Echeverri A, Karp DS, Latimer CE, Taylor JM, Wilson-Rankin EE, Owen JP, Snyder WE. 2022b. Complex landscapes stabilize farm bird communities and their expected ecosystem services. Journal of Applied Ecology 59:927-941.

Sollund R, Runhovde SR. 2020. Responses to wildlife crime in post-colonial times: Who fares best? British Journal of Criminology 60:1014-1033.

Somers CM, Morris RD. 2002. Birds and wine grapes: Foraging activity causes small-scale damage patterns in single vineyards. Journal of Applied Ecology 39:511-523.

Soulé ME. 1985. What is Conservation Biology? BioScience 35:727-734.

Southern HN. 1945. The economic importance of the house sparrow, *Passer domesticus* L.: a review. Annals of Applied Biology 32:57-67.

Sow A, Haran J, Benoit L, Galan M, Brévault T. 2020. DNA metabarcoding as a tool for disentangling food webs in agroecosystems. Insects 11:1-19.

Stanes A. 2011. Predation of a small pied stilt (*Himantopus himantopus*) colony by a swamp harrier (*Circus approximans*). Notornis 58:51-52.

Stanley M, McNaughton E, Fewster R, Galbraith J. 2023. Invasion risks of exotic parrots via the pet trade. Page 21, 2023 Birds New Zealand Conference Programme and Abstracts. Birds New Zealand, New Plymouth, New Zealand.

Steer J, Burns KC. 2008. Seasonal variation in male-female competition, cooperation and selfish hoarding in a monogamous songbird. Behavioural Ecology and Sociobiology 62:1175-1183.

Stephenson BM, Minot EO. 2006. Breeding biology of morepork (*Ninox novaeseelandiae*) on Mokoia Island, Lake Rotorua, New Zealand. Notornis 53:308-315.

Stewart AM, Craig JL. 1985. Movements, status, access to nectar, and spatial organisation of the tui. New Zealand Journal of Zoology 12:649-666.

Subramanya S. 1994. Non-random foraging in certain bird species of field crops. Journal of Bioscience 19:369-380.

Sullivan BL, Wood CL, Iliff MJ, Bonney RE, Fink D, Kelling S. 2009. eBird: A citizen-based bird observation network in the biological sciences. Biological Conservation 142:2282-2292.

Sweetapple P, Nugent G. 2024. Chewcards: A guide to the Interpretation of Animal Tooth Impressions. Manaaki Whenua Landcare Research, New Zealand.

Swinton SM, Lupi F, Robertson GP, Hamilton SK. 2007. Ecosystem services and agriculture: Cultivating agricultural ecosystems for diverse benefits. Ecological Economics 64:245-252.

Taylor JM, Smith OM, Edworthy M, Kennedy CM, Latimer CE, Owen JP, Wilson-Rankin EE, Snyder WE. 2022. Bird predation and landscape context shape arthropod communities on broccoli. Ornithological Applications 124:1-16.

Taylor RA, Ryan SJ, Brashares JS, Johnson LR. 2016. Hunting, food subsidies, and mesopredator release: The dynamics of crop-raiding baboons in a managed landscape. Ecology 97:951-960.

Tela M, Cresswell W, Chapman H. 2021. Pest-removal services provided by birds on subsistence farms in south-eastern Nigeria. PLoS ONE 16:e0255638.

Thiollay JM. 1988. Comparative foraging success of insectivorous birds in tropical and temperate forests: ecological implications. Oikos 53:17-30.

Thompson WA, Vertinsky I, Krebs JR. 1974. The Survival Value of Flocking in Birds: A Simulation Model. Journal of Animal Ecology 43:785-820.

Tigchelaar EC, Foley VL. 1991. Horticultural technology. HortTechnology 1:7-16.

Tilman D, Clark M, Williams DR, Kimmel K, Polasky S, Packer C. 2017. Future threats to biodiversity and pathways to their prevention. Nature 546:73-81.

Tilman D, Fargione J, Wolff B, D'Antonio C, Dobson A, Howarth R, Schindler D, Schlensinger WH, Simberloff D, Swackhamer D. 2001. Forecasting agricultural driven global environmental change. Science 292:281-284.

Tomback DF. 2016. Seed Dispersal by Corvids: Birds That Build Forests. Pages 196-234 in Şekercioğlu ÇH, Wenny DG, Whelan CJ, editors. Why Birds Matter: Avian Ecological Function and Ecosystem Services. University of Chicago Press, Chicago.

Tracey JP, Bomford M, Hart Q, Saunders G, Sinclair R. 2007. Managing Bird Damage to Fruit and Other Horticultural Crops. Canberra. Available from https://www.researchgate.net/publication/265663349.

Triplett S, Luck GW, Spooner P. 2012. The importance of managing the costs and benefits of bird activity for agricultural sustainability. International Journal of Agricultural Sustainability 10:268-288.

Tscharntke T, Clough Y, Wanger TC, Jackson L, Motzke I, Perfecto I, Vandermeer J, Whitbread A. 2012. Global food security, biodiversity conservation and the future of agricultural intensification. Biological Conservation 151:53-59.

Tschumi M, Ekroos J, Hjort C, Smith HG, Birkhofer K. 2018a. Rodents, not birds, dominate predation-related ecosystem services and disservices in vertebrate communities of agricultural landscapes. Oecologia 188:863-873.

Tschumi M, Ekroos J, Hjort C, Smith HG, Birkhofer K. 2018b. Predation-mediated ecosystem services and disservices in agricultural landscapes. Ecological Applications 28:2109-2118.

United Fresh. 2025. Fresh Facts 2025: New Zealand's Fresh Fruit & Vegetable Industry. Beach Haven, Auckland. Available from www.unitedfresh.co.nz.

Valdés-Correcher E, Mäntylä E, Barbaro L, Damestoy T, Sam K, Castagneyrol B. 2022. Following the track: accuracy and reproducibility of predation assessment on artificial caterpillars. Entomologia Experimentalis et Applicata 170:914-921.

Van Bael SA, Philpott SM, Greenberg R, Bichier P, Barber NA, Mooney KA, Gruner DS. 2008. Birds as predators in tropical agroforestry systems. Ecology 89:928-934.

van Horne B. 1983. Density as a misleading indicator of habitat quality. The Journal of Wildlife Management:893-901.

Vansynghel J, Ocampo-Ariza C, Maas B, Martin EA, Thomas E, Hanf-Dressler T, Schumacher NC, Ulloque-Samatelo C, Yovera FF, Tscharntke T, Steffan-Dewenter I. 2022. Quantifying services and disservices provided by insects and vertebrates in cacao agroforestry landscapes. Proceedings of the Royal Society B 289:e20221309.

van Velden JL, Smith T, Ryan PG. 2016. Cranes and crops: Investigating farmer tolerances toward crop damage by threatened blue cranes (*Anthropoides paradiseus*) in the Western Cape, South Africa. Environmental Management 58:972-983.

Waggoner PE. 1996. How much land can ten billion people spare for nature? Daedalus 125:73-93.

Waite E, Closs GP, Van Heezik Y, Dickinson KJM. 2013. Resource availability and foraging of Silvereyes (*Zosterops lateralis*) in urban trees. Emu 113:26-32.

Walker JS. 2007. Geographical patterns of threat among pigeons and doves (Columbidae). Oryx 41:289-299.

Walther BA. 2002. Vertical stratification and use of vegetation and light habitats by Neotropical forest birds. Journal of Ornithology 143:64-81.

Ward P. 1965. Feeding ecology of the black-faced dioch *Quelea quelea* in Nigeria. Ibis 107:173-214.

Watkins N, Davies V, Hickling G, Trought M. 2000. Bird Behaviour in Vineyards: A Review. Marlborough District.

Watkins NG. 1999. Ecological Correlates of Bird Damage in a Canterbury Vineyard. PhD thesis. Lincoln University, Lincoln, New Zealand.

Wearing CH, McCarthy K. 1992. Predation of Codling Moth *Cydia pomonella* L. by the Silvereye *Zosterops lateralis* (Latham). Biocontrol Science and Technology 2:285-295.

Weller F. 2011. Testing the power of an experiment to measure predator control and habitat complexity impacts on farmland bird abundance. New Zealand Journal of Ecology 35:44-51.

Weller F. 2012. A comparison of different approaches to monitoring bird density on New Zealand sheep and beef farms. New Zealand Journal of Ecology 36(3):1-9.

Wenny DG, Şekercioğlu ÇH, Cordeiro NJ, Rogers HS, Kelly D. 2016. Seed Dispersal by Fruit-Eating Birds. Pages 107-147 in Şekercioğlu ÇH, Wenny DG, Whelan CJ, editors. Why Birds Matter: Avian Ecological Function and Ecosystem Services. University of Chicago Press, Chicago.

Weyell J, Eigenbrod F, Hudson M, Kafumbata D, Tsirizeni M, Chiotha S, Poppy G, Willcock S. 2015. The impact of animals on crop yields in Malawian rural villages. African Journal of Agricultural Research 10:3016-3028.

Whelan CJ, Şekercioğlu ÇH, Wenny DG. 2015. Why birds matter: from economic ornithology to ecosystem services. Journal of Ornithology 156:227-238.

Whelan CJ, Wenny DG, Marquis RJ. 2008. Ecosystem services provided by birds. Annals of the New York Academy of Sciences 1134:25-60.

Whitehead SC. 1995, June. Foraging behaviour and habitat use in the European starling, *Sturnus vulgaris*, in an agricultural environment. PhD thesis. University of Oxford, Oxford, UK.

Whyte D. 2023. Birds in the orchard, friend or foe? Nelson. Available from www.treecrops.org.nz.

Williams M. 1971. The distribution and abundance of the paradise shelduck (*Tadorna variegata*, Gmelin) in New Zealand from pre-European times to the present day. Notornis 18:71-86.

Wilson JD, Whittingham MJ, Bradbury RB. 2005. The management of crop structure: A general approach to reversing the impacts of agricultural intensification on birds? Ibis 147:453-463.

Winqvist C, Bengtsson J, Aavik T, Berendse F, Clement LW, Eggers S, Fischer C, Flohre A, Geiger F, Liira J, Pärt T, Thies C, Tscharntke T, Weisser WW, Bommarco R. 2011. Mixed effects of organic farming and landscape complexity on farmland biodiversity and biological control potential across Europe. Journal of Applied Ecology 48:570-579.

Winqvist C, Ahnström J, Bengtsson J. 2012. Effects of organic farming on biodiversity and ecosystem services: taking landscape complexity into account. Annals of the New York Academy of Sciences 1249:191-203.

Witt ABR, Little RM, Crowe TM. 1995. The effectiveness of helmeted guineafowl *Numida meleagris* (Linnaeus 1766) in controlling the banded fruit weevil *Phlyctinus callosus* (Schönherr 1826), and their impact on other invertebrates in apple orchards in the Western Cape Province, South Africa. Agriculture, Ecosystems & Environment 55:169-179.

Wood C, Sullivan B, Iliff M, Fink D, Kelling S. 2011. eBird: Engaging Birders in Science and Conservation. PLoS Biology 9:1-6.

Wright EN, Inglis IR. 1979. Bird Problems in Agriculture. Pages 1-110 Understanding Agricultural Bird Problems. BCPC Publications, London.

Wright G. 2011. Conceptualising and combating transnational environmental crime. Trends in Organized Crime 14:332-346. Springer Science and Business Media, LLC.

Wright HL, Lake IR, Dolman PM. 2012. Agriculture-a key element for conservation in the developing world. Conservation Letters 5:11-19.

Wu S, Li BV, Li S. 2021. Classifying ecosystem disservices and valuating their effects - a case study of Beijing, China. Ecological Indicators 129:107977.

Xu XM, Robinson JD, Berrie AM, Harris DC. 2001. Spatio-temporal dynamics of brown rot (*Monilinia fructigena*) on apple and pear. Plant Pathology 50:569-578.

Yahia EM, Maldonado MEC, Svendsen M. 2017. The Contribution of Fruit and Vegetable Consumption to Human Health. Pages 1-52 in Yahia EM, editor. Fruit and Vegetable Phytochemicals: Chemistry and Human Health. Wiley-Blackwell, Hoboken.

Yahner RH. 1982. Avian use of vertical strata and plantings in farmstead shelterbelts. The Journal of Wildlife Management 46:50-60.

Zamora-Marín JM, Zamora-López A, León-Ortega M, Sáez-Gómez P, García-Castellanos FA, Sánchez-Zapata JA, Camacho C. 2025. Breeding performance of an aerial insectivorous bird under contrasting farming systems. Ecological Applications 35:e70059.

Zhang J, Pannell JL, Case BS, Hinchliffe G, Stanley MC, Buckley HL. 2021. Interactions between landscape structure and bird mobility traits affect the connectivity of agroecosystem networks. Ecological Indicators 129:107962.

Zhang W, Ricketts TH, Kremen C, Carney K, Swinton SM. 2007. Ecosystem services and dis-services to agriculture. Ecological Economics 64:253-260.

Zhong L, Li Y, Li Y, Dai C. 2025. Hungry wintering birds and angry farmers: crop damage and management implications in a protected wetland in China. Global Ecology and Conservation 57:e03402.

Zielonka NB, Arellano E, Crowther LP, Ferreira V, Muñoz-Sáez A, Oliveira-Rebouças P, da Silva FO, Butler SJ, Dicks LV. 2024. Distinct bird communities in forests and fruit farms of Caatinga landscapes. Ibis 166(3):1081-1091.

Supplementary Materials (Chapter One)

This Supplementary Material refers to a preliminary data collection that was conducted previous to the fieldwork data presented in Chapters Three-Five. The purpose of this work was to conduct a search on observation records from citizen science data to understand which species of native and introduced birds were already spotted within horticultural systems. The analysis was retained as supplementary material as it primarily provided descriptive national context rather than addressing the central research questions of the thesis. The appendix is included to document these findings and complement the field-based analyses presented in the main chapters.

Observation records were obtained from the platform eBird (Sullivan et al. 2009) through the collaboration of Birds New Zealand, which validates submissions using a national network of ornithological reviewers. The dataset comprised 5,172,814 observations of 451 bird species recorded between January 2003 and March 2023. Records were spatially intersected with Land Use and Carbon Analysis System (LUCAS) maps (MfE 2023) to identify observations within cropland habitats (LUCAS classes 77 and 78, including orchards and vineyards). Observation dates were matched to the corresponding LUCAS land-use period to account for changes in land use over time.

Scientific nomenclature was standardised following the Ornithological Society of New Zealand checklist (OSNZ 2022). Duplicate taxonomic entries were merged, and species represented by fewer than four records were excluded, resulting in a final dataset of 92 species. Information on conservation status, origin (native or introduced) and main habitat (terrestrial, aquatic or marine) was compiled from ornithological sources (Te Papa et al. 2023; IUCN 2024).

Table S 1. Compilation of 93 species recorded within croplands according to eBird sightings, including 56 native (A) and 36 introduced (B) species. Species are listed by their family and scientific names as retrieved from (OSNZ 2022). Common names are provided in English or in te reo Māori when appropriate. Total number of observations for each species is provided in the N column. Feeding guilds were retrieved from New Zealand Birds Online (Te Papa 2023) and were grouped into carnivores (CAR), frugivores (FRU), granivores (GRA), herbivores (HER), insectivores (INS), nectarivores (NEC), omnivores (OMN), piscivores (PSC), and piscivores-invertivores (PSC-INV). Extinction risk was retrieved from IUCN (2024) and refer to its red list categories: Least Concern (LC), Near Threatened (NT), Vulnerable (VU), Endangered (EN), and Critically Endangered (CR).

	Family	Species	Common Name	N	Guild	Habitat	IUCN
A. native							
	Acanthizidae	*Gerygone igata*	grey warbler	893	INS	T	LC
	Accipitridae	*Circus approximans*	swamp harrier	2419	CAR	T	LC
	Alcedinidae	*Todiramphus sanctus*	kingfisher	1104	OMN	T	LC
	Anatidae	*Anas gracilis*	grey teal	413	OMN	A	LC
	Anatidae	*Anas superciliosa*	Pacific black duck	72	OMN	A	LC
	Anatidae	*Aythya novaeselandiae*	NZ scaup	603	OMN	A	LC
	Anatidae	*Spatula rhynchotis*	Australasian shoveler	503	OMN	A	LC
	Anatidae	*Tadorna variegata*	paradise shelduck	1338	OMN	A	LC
	Apterygidae	*Apteryx mantelli*	brown kiwi	10	OMN	T	VU
	Ardeidae	*Ardea alba*	great egret	26	PSC	A	LC
	Ardeidae	*Botaurus poiciloptilus*	Australasian bittern	16	OMN	A	VU
	Ardeidae	*Egretta novaehollandiae*	white-faced heron	618	OMN	A	LC
	Charadriidae	*Charadrius bicinctus*	double-banded plover	50	OMN	A	LC
	Charadriidae	*Charadrius obscurus*	NZ dotterel	22	OMN	M	VU
	Charadriidae	*Vanellus miles*	spur-winged plover	1947	OMN	T	LC
	Charadriidae	*Anarhynchus frontalis*	wrybill	6	INS	A	VU
	Charadriidae	*Elseyornis melanops*	black-fronted dotterel	61	OMN	A	LC
	Columbidae	*Hemiphaga novaeselandiae*	New Zealand pigeon	171	FRU	T	LC
	Cuculidae	*Chrysococcyx lucidus*	shining bronze cuckoo	74	INS	T	LC
	Falconidae	*Falco novaeselandiae*	New Zealand falcon	185	CAR	T	VU
	Haematopodidae	*Haematopus finschi*	South Island pied oystercatcher	342	OMN	M	LC
	Haematopodidae	*Haematopus unicolor*	variable oystercatcher	53	OMN	M	LC
	Hirundinidae	*Hirundo neoxena*	welcome swallow	2368	INS	T	LC
	Laridae	*Chlidonias albostriatus*	black-fronted tern	244	OMN	M	EN
	Laridae	*Chroicocephalus bulleri*	black-billed gull	224	OMN	M	NT
	Laridae	*C. novaehollandiae scopulinus*	red-billed gull	201	OMN	M	NT
	Laridae	*Hydroprogne caspia*	Caspian tern	74	PSC	M	VU

Family	Species	Common Name	N	Guild	Habitat	IUCN
Laridae	*Larus dominicanus*	black-backed gull	1373	OMN	M	LC
Laridae	*Sterna striata*	white-fronted tern	58	PSC	M	NT
Locustellidae	*Poodytes punctatus*	NZ fernbird	5	OMN	T	LC
Meliphagidae	*Anthornis melanura*	bellbird	254	NEC	T	LC
Meliphagidae	*Prothesmadera novaeselandiae*	tūī	709	NEC	T	LC
Mohouidae	*Mohoua novaeseelandiae*	pīpipi	7	INS	T	LC
Motacillidae	*Anthus novaeselandiae*	Australian pipit	55	OMN	T	LC
Petroicidae	*Petroica macrocephala*	tomtit	15	INS	T	LC
Phalacrocoracidae	*Phalacrocorax carbo*	great cormorant	295	PSC	A	LC
Phalacrocoracidae	*Phalacrocorax punctatus*	spotted shag	35	OMN	A	LC
Phalacrocoracidae	*Phalacrocorax sulcirostris*	little black cormorant	81	PSC	A	LC
Phalacrocoracidae	*Phalacrocorax varius*	Australian pied cormorant	110	PSC	A	LC
Phalacrocoracidae	*Microcarbo melanoleucos brevirostris*	little shag	586	OMN	A	LC
Podicipedidae	*Podiceps cristatus*	great crested grebe	41	OMN	A	VU
Podicipedidae	*Poliocephalus rufopectus*	NZ grebe	54	INS	A	VU
Procellariidae	*Pachyptila turtur*	fairy prion	65	OMN	T	LC
Rallidae	*Fulica atra*	Eurasian coot	177	OMN	A	LC
Rallidae	*Gallirallus australis*	weka	15	OMN	T	VU
Rallidae	*Porphyrio melanotus melanotus*	pūkeko	1729	OMN	T	LC
Rallidae	*Zapornia tabuensis*	spotless crake	5	OMN	T / A	LC
Recurvirostridae	*Himantopus himantopus*	pied stilt	318	INS	M	LC
Recurvirostridae	*Himantopus novaezelandiae*	black stilt	12	OMN	A	CR
Rhipiduridae	*Rhipidura fuliginosa*	NZ fantail	1874	INS	T	LC
Scolopacidae	*Limosa tapponica*	bar-tailed godwit	27	CAR	M	NT
Stercorariidae	*Stercorarius pomarinus*	pomarine jaeger	6	OMN	M	LC
Strigopidae	*Nestor meridionalis*	kākā	25	OMN	T	VU
Sulidae	*Morus serrator*	Australasian gannet	8	PSC	A	LC
Threskiornithidae	*Platalea regia*	royal spoonbill	89	OMN	A	LC
Zosteropidae	*Zosterops lateralis*	silvereye	2003	OMN	T	LC

	Family	Species	Common Name	N	Guild	Habitat	IUCN
B. introduced							
	Accipitridae	*Milvus migrans*	black kite	33	OMN	T	LC
	Alaudidae	*Alauda arvensis*	skylark	1535	GRA	T	LC
	Alcedinidae	*Dacelo novaeguineae*	laughing kookaburra	15	OMN	T	LC
	Anatidae	*Anas platyrhynchos*	mallard	1327	OMN	A	LC
	Anatidae	*Anser anser*	feral goose	99	OMN	A	LC
	Anatidae	*Branta canadensis*	Canada goose	262	OMN	A	LC
	Anatidae	*Cairina moschata*	Muscovy duck	27	OMN	A	LC
	Anatidae	*Cygnus atratus*	black swan	703	HER	A	LC
	Anatidae	*Cygnus olor*	mute swan	149	OMN	A	LC
	Ardeidae	*Bubulcus ibis*	cattle egret	27	INS	A	LC
	Artamidae	*Gymnorhina tibicen*	Australian magpie	1717	OMN	T	LC
	Cacatuidae	*Cacatua galerita*	sulphur-crested cockatoo	8	OMN	T	LC
	Columbidae	*Columba livia*	rock pigeon	730	OMN	T	LC
	Columbidae	*Streptopelia chinensis*	spotted dove	187	GRA	T	LC
	Columbidae	*Streptopelia risoria*	African collared dove	92	OMN	T	LC
	Corvidae	*Corvus frugilegus*	rook	11	OMN	T	LC
	Emberizidae	*Emberiza cirlus*	cirl bunting	37	OMN	T	LC
	Emberizidae	*Emberiza citrinella*	yellowhammer	1185	GRA	T	LC
	Fringillidae	*Carduelis carduelis*	goldfinch	2774	GRA	T	LC
	Fringillidae	*Chloris chloris*	European greenfinch	1788	GRA	T	LC
	Fringillidae	*Fringilla coelebs*	chaffinch	2279	GRA	T	LC
	Numididae	*Numida meleagris*	helmeted guineafowl	10	OMN	T	LC
	Odontophoridae	*Callipepla californica*	California quail	443	OMN	T	LC
	Passeridae	*Passer domesticus*	house sparrow	3781	OMN	T	LC
	Phasianidae	*Meleagris gallopavo*	wild turkey	46	OMN	T	LC
	Phasianidae	*Pavo cristatus*	peafowl	67	OMN	T	LC
	Phasianidae	*Phasianus colchicus*	ring-neck pheasant	312	OMN	T	LC
	Prunellidae	*Prunella modularis*	dunnock	1152	INS	T	LC
	Phasianidae	*Synoicus ypsilophorus*	brown quail	5	OMN	T	LC
	Psittaculidae	*Platycercus eximius*	eastern rosella	182	OMN	T	LC
	Strigidae	*Athena noctua*	little owl	253	OMN	T	LC
	Sturnidae	*Acridotheres tristis*	common myna	675	OMN	T	LC

Family	Species	Common Name	N	Guild	Habitat	IUCN
Sturnidae	*Sturnus vulgaris*	common starling	3436	OMN	T	LC
Threskiornithidae	*Plegadis falcinellus*	glossy ibis	6	CAR	A	LC
Turdidae	*Turdus merula*	blackbird	3287	OMN	T	LC
Turdidae	*Turdus philomelos*	song thrush	2637	OMN	T	LC

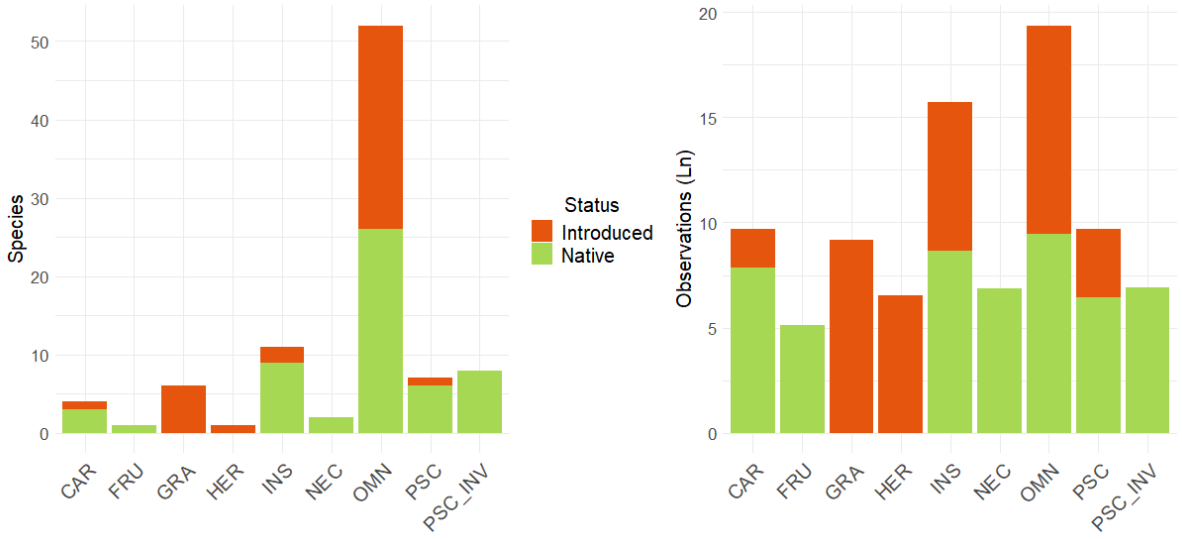


Figure S 1. Stacked columns of 56 native (green) and 36 introduced (orange) species in the eBird dataset grouped according to their feeding guilds. Number of observation records was log-transformed using the natural logarithm (ln) to address large disparities between the minimum and maximum values spanning several orders of magnitude. Feeding guilds are as follows: carnivores (CAR), frugivores (FRU), granivores (GRA), herbivores (HER), insectivores (INS), nectarivores (NEC), omnivores (OMN), piscivores (PSC), and piscivores-invertivores (PSC-INV).

Supplementary Materials (Chapter Two)

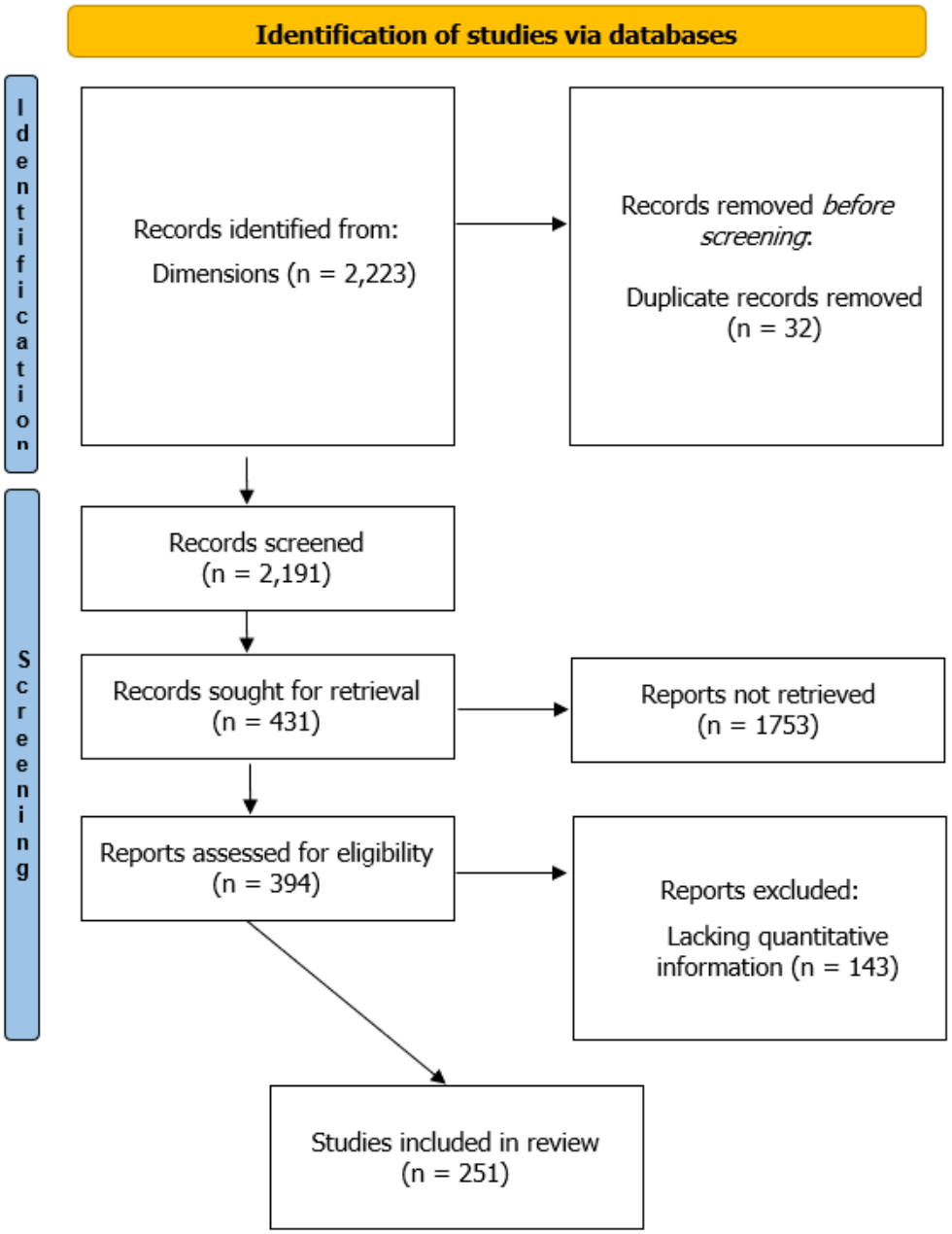


Figure S 2. Flow diagram summarizing the review strategy of studies inclusion and exclusion based on PRISMA guidelines. Adapted from (Page et al. 2021).

Table S 2. Complete description of the 251 documents included in the systematic review. Include the title, year and publication type of each document, with further information on specific details analysed by the review: filiation of the first authors, countries and regions of the case studies, types of horticultural systems, main research questions, methods of data collection, ecosystem services and disservices studied, bird species and community metrics measured, factors affecting bird communities positively and negatively, discussions on human-wildlife conflicts, and further notes if necessary.

(Table SM.2.1 is included as an excel table due to its larger size; it can be accessed here: https://onlinelibrary.wiley.com/action/downloadSupplement?doi=10.1111%2Faec.70110&file=aec70110-sup-0002-TableS1.xlsx)

Table S 3. Compilation of 99 documents out of 251 that indicated abiotic and biotic factors affecting positively and negatively bird communities in the systems surveyed.

Reference	***factors affecting bird communities (+)***	***factors affecting bird communities (-)***
Barbaro et al. 2017	landscape and local heterogeneity	N/A
Benjamini 1980	soil humidity	N/A
Boesing et al. 2017	proximity to habitat patches, forest cover, crop diversity, landscape complexity	forest cover, edge density
Borkhataria et al. 2012	presence of shade trees	N/A
Bouarakia et al. 2023	availability of prey	N/A
Brambilla et al. 2017	N/A	soil loss
Brennan 2020	N/A	canopy cover
Burger et al. 2022	canopy cover	N/A
Canavelli et al. 2014b	proximity to mand-made structures and adjacent trees, tree cover	N/A
Chain-Guadarrama et al. 2019	N/A	climate change
Classen et al. 2014	not established	not established
Díaz-Siefer et al. 2021	proximity to natural areas	N/A
Dix et al. 1995	forest edges, tree	pesticide
Eilers & Klein 2009	proximity to natural habitat, surrounding natural habitat	N/A
Escobar-Ramírez et al. 2019	forest patches	N/A
Ferrante et al. 2017b	landscape complexity	N/A
Ferreira et al. 2023	shade cover	N/A
Filloy et al. 2023	structural complexity of vegetation (understorey)	N/A
Fox et al. 2016	field size, presence of standing water, snow cover	disturbance
Gámez-Virués et al. 2007	shelterbelts (tree edges)	N/A
García et al. 2018	woody vegetation cover	N/A
García et al. 2020	nest boxes	N/A
Garcia et al. 2023	seminatural habitats	availability of nests
Garfinkel & Johnson 2015	proximity to natural areas, landscape heterogeneity	N/A
Gonthier et al. 2019	semi-natural habitat	N/A
Gras et al. 2016	canopy cover	N/A
Guenat et al. 2019	shade trees	N/A
Heath & Long 2019	woody vegetation cover, woody edges, seminatural cover	N/A

Reference	*factors affecting bird communities (+)*	*factors affecting bird communities (-)*
Herrera et al. 2021	natural vegetation cover, landscape complexity	N/A
Hiron et al. 2014	N/A	scaring devices
Horgan et al. 2017	presence of vegetable supports for perching	N/A
Howe et al. 2015	N/A	pesticide
Htay et al. 2022	proximity to body of water	N/A
Jedlicka 2011	nest boxes	N/A
Johnson et al. 2009	shade	N/A
Johnson et al. 2011	multiple	multiple
Jones & Sieving 2006	presence of intercrops	N/A
Jones et al. 2005b	field border vegetation, connectivity within matrix	N/A
Jordani et al. 2015	adjacent forest fragment size	N/A
Karp et al. 2013	forest cover	N/A
Kay et al. 1994	perches	N/A
Kellerman et al. 2008	landscape heterogeneity	N/A
Kolkert 2021	forest cover, crop edge proximity	N/A
Kross 2016	complexity of field edge habitat	N/A
Kross et al. 2016	local habitat complexity	N/A
Kross et al. 2020	proximity to natural areas	N/A
Lemessa et al. 2015	forest cover	N/A
Librán-Embid et al. 2017	forest cover	N/A
Lindell et al. 2016	forest cover	N/A
Lindell et al. 2018b	landscape enhancements	N/A
Linden et al. 2019	natural vegetation	N/A
Luck et al. 2013	resource availability, proximity to natural areas	proximity to human settlements
Luna et al. 2020	nest boxes	nest boxes
Maas et al. 2015	forest cover, forest proximity	connectivity
Maas et al. 2018	shade trees	N/A
Mangan et al. 2017	natural habitat	grass habitat
Martin et al. 2013	landscape complexity	N/A
Martin et al. 2015	landscape complexity	N/A

Reference	*factors affecting bird communities (+)*	*factors affecting bird communities (-)*
Martin et al. 2016	organic practices, landscape complexity	N/A
Martínez-Núñez et al. 2020a	landscape heterogeneity	N/A
Martínez-Núñez et al. 2020b	edge density, high patch diversity	landscape homogeneity
Martínez-Salinas et al. 2016	canopy cover	N/A
Martínez-Sastre et al. 2020	apple canopy cover (wider and more continuous)	N/A
Milligan et al. 2016	shade tree canopy	distance to an adjacent forest fragment0
Navedo et al. 2015	proximity to natural areas	N/A
Ndang'ang'a et al. 2013	natural vegetation cover	N/A
Nurdiansyah et al. 2016	vegetation surrounding plantation, distance from the border	N/A
O'Bryan et al. 2018	N/A	poisoning
O'Connor et al. 2022	proximity to adjacent forest	N/A
Olimpi et al. 2020	seminatural habitats	habitat loss
Olimpi et al. 2021	semi-natural habitat surrounding farms	N/A
Olmos-Moya et al. 2022	nest boxes	habitat loss
Orłowski et al. 2014	natural variation in food abundance; woody borders	N/A
Osie et al. 2023	landscape heterogeneity	N/A
Otieno et al. 2019	organic practices, landscape heterogeneity, trees	N/A
Peisley et al. 2016	lower orchard management	N/A
Perfecto et al. 2004	diverse shade	N/A
Peters & Greenberg 2013	food provisioning	N/A
Philpott et al. 2009	not established	not established
Puckett et al. 2009	proximity to woody edges	N/A
Redlich et al. 2018	crop diversification, landscape heterogeneity, semi-natural habitat	N/A
Rey Benayas et al. 2017	presence of nesting resources	N/A
Sausse & Lévy 2021	landscape complexity	bird scaring devices
Schackerman et al. 2014	N/A	proximity to semi-natural habitats
Schäckermann et al. 2015	proximity to semi-natural habitats	N/A
Schroth et al. 2000	proximity to forest edge	N/A
Shave et al. 2018	nest boxes	N/A
Simon et al. 2010	provision and monitoring of nest boxes, landscape complexity	pesticide

Reference	*factors affecting bird communities (+)*	*factors affecting bird communities (-)*
Smith et al. 2021	crop-livestock interactions, farm size	N/A
Smith et al. 2022b	seminatural habitats, landscape complexity	N/A
Somers & Morris 2002	tree abundance, proximity to edges	N/A
Sow et al. 2020	tree abundance and diversity	N/A
Subramanya 1994	vegetation complexity	N/A
Taylor et al. 2022	proximity to natural areas	N/A
Tela et al. 2021	proximity to trees	N/A
van Bael et al. 2008b	canopy cover	N/A
Vansynghel et al. 2022	forest shade, connectivity to forest patches	N/A
Winqvist et al. 2011	landscape complexity, organic farming	proportion of arable land

Table S 4. Compilation of 77 studies that focused on particular species and / or species of special concern (native, endemic, or threatened).

Reference	***Birds Studied***	***Species of Special Concern***
Adegoke 1983	village weaverbirds	N
Allan et al. 1995	Canada goose	N
Barceló et al. 2012	sandhill crane	N
Benjamini 1980	chukar	N
Benras et al. 2023	Hybrid sparrow	N
Brambilla et al. 2017	Moltoni's warbler	Y (endemic)
Brennan 2020	sparrows	N
Canavelli et al. 2014	monk parakeet	N
Canavelli et al. 2014b	monk parakeet	N
da Silva et al. 2022	birds present in the system	Y (native species)
Fleming et al. 2002	sulphur-crested cockatoo	N
Fox et al. 2016	waterfowl	N
Gámez-Virués et al. 2007	birds present in the system	Y (all but one natives)
Garfinkel & Johnson 2015	birds present in the system	Y (7/105)
Gebhardt 1996	introduced birds	N
Gebhardt 2011	birds present in the system, corvids	N
Basili & Temple 1999	dickcissel	Y (declining)
Gillespie 1982	greenfinch	N
Golawski & Golawska 2013	red-backed shrike	N
Gorosábel et al. 2019	waterfowl	Y
Gorosábel et al. 2022	raptors	N/A
Govind & Jayson 2018	Indian peafowl	N
Hammond 1912	starlings	N
Hassan et al. 2022	birds present in the system, house sparrow	N
Hiron et al. 2014	birds present in the system, weavers, doves	N
Horgan & Kudavidanage 2020	birds present in the system, peafowl	N
Horgan et al. 2017	passerine birds present in the system	N
Issa & El-Bakhshawngi 2018	house sparrow, hooded crow	N

Reference	*Birds Studied*	*Species of Special Concern*
Jasinski et al. 2021	American kestrel, birds present in the system	Y
Jedlicka 2011	passerine birds present in the system; western blue jay	N
Jedlicka et al. 2016	Western bluebird	N
Jones et al. 2005a	red-winged blackbirds	N
Jones et al. 2005b	birds present in the system	Y (native species)
Kay et al. 1994	raptors	N
Klosterman et al. 2013	blackbirds	N
Kross et al. 2012	NZ falcon	Y (endemic)
Kross et al. 2018	perching birds, raptors	N
Lamelas-López & Marco 2021	birds present in the system	Y (Azorean blackbird EN)
Langowska et al. 2018	bee-eaters	N
Luck et al. 2013	birds present in the system	Y (regent parrot)
Luna et al. 2020	birds present in the system	Y (rare species)
Maas et al. 2018	birds present in the system	Y (a third endemic)
MacLellan 1958	eastern hairy and northern downy woodpecker	N
Manyama et al. 2014	red-billed Quelea	N
Marrero et al. 2004	Madeira Laurel pigeon	Y (EN)
McInnes & Carne 1978	yellow-tailed black cockatoo	Y (VU)
McKay et al. 2006	Greylag geese	Y (reintroduced)
Metwally et al. 2009	birds present in the system, house sparrow	N
Mols & Visser 2002	great tits	N
Montoya et al. 2021	common kestrel / barn owl	N
Montràs-Janer et al. 2019	geese, swans and cranes	N
Murton & Jones 1973	wood-pigeon	N
Musiwa & Mhlanga 2020	quelea	N
Navedo et al. 2015	waterbirds	N
Nevard et al. 2019	brolga and Australian sarus crane	Y
O'Bryan et al. 2018	falcons & vultures	Y
Orłowski et al. 2014	insectivorous birds (common swifts, house martins and barn swallows)	N

Reference	*Birds Studied*	*Species of Special Concern*
Otieno et al. 2019	insectivorous	N
Owen 1990	geese	N
Pande & Dahanukar 2011	Indian Eagle Owl	N
Paranjpe & Dange 2018	Indian peafowl	N
Peer et al. 2003	red winged blackbirds, common grackles, yellow headed blackbirds	N
Peisley et al. 2015	birds studied by each research	N
Peisley et al. 2017	raptors	N
Pescador & Peris 1998	great bustards	Y (VU)
Puan et al. 2011	barn owl	N
Rey Benayas et al. 2017	insectivorous birds	N
Sandhu & Sandhu 1994	blossom-headed and roseringed parakeet	N
Shave et al. 2018	American kestrel, fruit-eating brids	Y
Smith et al. 2021	raptors	Y
Southern 1945	house sparrow	N
Sow et al. 2020b	village weaverbirds	N
Subramanya 1994	roseringed parakeet, munia and weaverbird	N
Taylor et al. 2022	American goldfinch, robin, savannah, song, and white-crowned sparrow	N
van Velden et al. 2016	blue Crane	Y
Ward 1965	quelea	N
Witt et al. 1995	helmeted guineafowl	N



Figure S 3. Global map indicating the occurrences of studies focusing on the horticultural systems with more than 10 occurrences each: fruits (71 occurrences), grains (58 occurrences), seeds & beans (35 occurrences), and greens (22). Locations were retrieved from GIS coordinates provided or approximated from studies. Map constructed on ArcPro (ESRI 2023).



Figure S 4. Global map indicating the location for the studies focusing on services and disservices other than pest control and crop damage. Ecosystem disservices include herbivore release (seven occurrences), disease spread (five occurrences), pollinator predation (two occurrences), seed predation (two occurrences) and killing of livestock (one occurrence). An additional disservice, repellent action, was only studied in a document that did not specify the location, therefore it is not included in this map. Ecosystem services include fertilising (five occurrences), disease control (four occurrences), pollination (four occurrences), weed control (three occurrences) and aesthetics (one occurrence). Locations were retrieved from GIS coordinates provided or approximated by the researchers. Map constructed on ArcPro (ESRI 2023).

Supplementary Materials (Chapter Three)

Table S 5. Description of weather conditions of the 82 surveys conducted in the six sites surveyed from autumn 2024 to summer 2025. Data collection on fieldwork traits followed the protocol from five minute bird counts (DoC 2023). Each survey across orchards and seasons is identified by their date and survey period (AM = morning; PM = afternoon). Temperature was given as an estimated average for the duration of the survey, with the range: 1 = freezing (<0°C); 2 = cold (0 - 5°C); 3 = cool (6 - 11°C); 4 = mild (12 - 16°C); 5 = warm (17-23°C); and 6 = hot (>23°C). Wind categories were defined as 1 = leaves rustle; 2 = leaves and branchlets in constant motion; and 3 = branches or trees sway. Sun exposure was defined as 0 = cloud or grey; 1 = sun with clouds, or 2 = blue sky, with no clouds. Noise values refer to levels of human-produced noise during the surveys: 0 = not important; 1= moderate; and 2 = loud, which would include heavy machinery and construction nearby. Precipitation was defined as n = none; m = mist, and r = rain, which were subsequently identified as (1) = dripping foliage, (2) = drizzle, and (3) = light. No fieldwork was undertaken under heavy rain conditions. Asterisks marked three surveys at orchard KC2 where the grower left sprinklers to cover the entire orchard.

orchard	date	period	temperature	wind	sun	noise	precipitation
autumn							
Tasman Region	07_05_24	AM	3	0	2	2	n
Tasman Region	07_05_24	PM	4	0	2	1	n
Tasman Region	08_05_24	AM	3	0	2	2	n
Tasman Region	09_05_24	PM	4	0	2	1	n
Manawatū 2	11_05_24	AM	3	0	1	1	n
Manawatū 2	12_05_24	AM	3	0	0	0	n
Manawatū 2	12_05_24	PM	4	1	0	0	r (2)
Kāpiti Coast 1	16_05_24	PM	4	0	1	0	n
Kāpiti Coast 2	17_05_24	AM	3	0	0	0	n
Kāpiti Coast 1	17_05_24	AM	3	1	1	0	n
Kāpiti Coast 2	18_05_24	AM	3	0	0	1	r (1)
Kāpiti Coast 1	18_05_24	AM	4	1	0	1	r (2)
Kāpiti Coast 2	18_05_24	PM	4	0	0	0	r (2)
Hawke's Bay	24_05_24	AM	3	0	2	1	n
Hawke's Bay	24_05_24	PM	3	1	0	0	n
Hawke's Bay	25_05_24	AM	3	0	2	0	n
Hawke's Bay	25_05_24	PM	4	1	1	0	n
Manawatū 1	27_05_24	PM	4	2	0	0	r (1)
Manawatū 1	30_05_24	AM	1	0	2	0	n

	orchard	date	period	temperature	wind	sun	noise	precipitation
winter								
	Manawatū 1	22_07_24	AM	3	0	0	0	n
	Manawatū 1	22_07_24	PM	3	0	0	0	r (1)
	Manawatū 1	23_07_24	AM	2	0	1	0	r (1)
	Manawatū 2	24_07_24	AM	2	0	1	1	n
	Manawatū 2	24_07_24	PM	3	1	1	1	n
	Manawatū 2	26_07_24	AM	2	0	2	0	n
	Manawatū 2	26_07_24	PM	4	1	0	1	n
	Kāpiti Coast 2	29_07_24	PM	4	1	0	1	n
	Kāpiti Coast 2	30_07_24	AM	3	0	0	0	n
	Kāpiti Coast 2	30_07_24	PM	3	0	0	1	n
	Kāpiti Coast 1	30_07_24	PM	3	0	0	0	n
	Kāpiti Coast 1	31_07_24	AM	3	0	0	0	n
	Kāpiti Coast 1	31_07_24	PM	3	1	1	0	n
	Hawke's Bay	05_08_24	PM	3	0	1	2	n
	Hawke's Bay	06_08_24	AM	2	0	2	0	n
	Hawke's Bay	06_08_24	PM	3	1	2	1	n
	Hawke's Bay	07_08_24	AM	2	0	2	0	n
	Hawke's Bay	07_08_24	PM	4	1	2	1	n
	Hawke's Bay	08_08_24	AM	3	0	1	1	n
	Tasman Region	06_09_24	AM	2	0	2	2	n
	Tasman Region	06_09_24	PM	4	0	1	2	n
	Tasman Region	07_09_24	AM	4	0	0	0	n
	Tasman Region	07_09_24	PM	4	0	1	0	n
	Tasman Region	08_09_24	AM	3	0	1	0	n
	Tasman Region	08_09_24	PM	3	1	2	0	n
	Tasman Region	09_09_24	AM	3	0	1	1	r (2)

	orchard	date	period	temperature	wind	sun	noise	precipitation
spring								
	Manawatū 1	07_10_24	AM	3	1	0	0	r (1)
	Manawatū 1	07_10_24	PM	3	1	0	0	r (3)
	Manawatū 1	08_10_24	AM	3	2	0	0	r (2)
	Manawatū 1	08_10_24	PM	4	3	1	0	n
	Manawatū 2	09_10_24	AM	3	1	0	0	r (1)
	Manawatū 2	10_10_24	AM	3	0	0	0	r (1)
	Manawatū 2	10_10_24	PM	4	2	1	0	r (2)
	Kāpiti Coast 2	14_10_24	PM	3	0	0	1	n
	Kāpiti Coast 1	15_10_24	AM	3	0	1	0	n
	Kāpiti Coast 2	15_10_24	PM	4	2	2	1	n
	Kāpiti Coast 2	16_10_24	AM	3	0	1	0	n
	Kāpiti Coast 1	16_10_24	PM	4	0	2	1	n
	Kāpiti Coast 1	17_10_24	AM	2	1	2	0	n
	Hawke's Bay	18_11_24	PM	4	2	2	0	n
	Hawke's Bay	19_11_24	AM	3	0	2	0	n
	Hawke's Bay	19_11_24	PM	4	2	2	0	n
	Hawke's Bay	20_11_24	AM	3	0	1	0	n
	Hawke's Bay	20_11_24	PM	6	3	1	0	n
	Hawke's Bay	21_11_24	AM	4	0	1	1	n

	orchard	date	period	temperature	wind	sun	noise	precipitation
summer								
	Manawatū 1	06_01_25	AM	4	0	0	0	n
	Manawatū 1	07_01_25	AM	4	0	1	0	n
	Manawatū 1	08_01_25	PM	4	1	0	0	r (1)
	Manawatū 2	07_01_25	PM	5	1	1	0	n
	Manawatū 2	08_01_25	AM	4	0	0	0	r (1)
	Manawatū 2	09_01_25	AM	3	0	2	0	n
	Kāpiti Coast 1	13_01_25	PM	6	2	2	0	n
	Kāpiti Coast 1	14_01_25	AM	4	0	2	0	n
	Kāpiti Coast 2	14_01_25	PM	5	2	1	1	*
	Kāpiti Coast 1	15_01_25	AM	4	0	0	0	n
	Kāpiti Coast 2	15_01_25	PM	6	0	2	1	*
	Kāpiti Coast 2	16_01_25	AM	5	0	2	1	*
	Hawke's Bay	20_01_25	PM	6	1	0	0	n
	Hawke's Bay	21_01_25	AM	5	0	1	1	n
	Hawke's Bay	21_01_25	PM	6	1	0	0	n
	Hawke's Bay	22_01_25	AM	4	0	0	0	r (1)
	Hawke's Bay	22_01_25	PM	5	0	0	0	n
	Hawke's Bay	23_01_25	AM	4	0	2	1	m (1)

Table S 6. Distribution of apple varieties in the orchards surveyed. Orchard names represent their unique orchard identities related to their regional locations: Manawatū 1 & 2 (MN), Kāpiti Coast 1 & 2 (KC), Hawke's Bay (HB), and Tasman Region (TR). Asterisks indicate varieties present in each site.

Apple Variety	MN1	MN2	KC1	KC2	HB	TR
Braeburn	*	*		*		
Cherish						*
Crab			*			
Dazzle	*				*	
Envy	*					*
Fuji					*	
Galaxy					*	
Granny Smith		*	*	*		
Golden Delicious	*					
Jazz	*					
King					*	
Lady in Red				*		
Pacific Beauty		*	*			
Pacific Rose	*	*	*			
Pacific Queen		*		*		
Pink Lady	*					
Red Delicious		*				
Royal Gala		*	*	*		*
Sassy					*	
Splendour		*				
Total Varieties	7	8	5	5	5	3

Table S 7. Bird species detected during 82 surveys conducted across six apple orchards in New Zealand, between autumn 2024 and summer 2025. Seasonal columns indicate the number of surveys in which each species was detected, either natives (A) or introduced (B) species. Total detections and the frequency (%) of detections is then given for each species.

	Scientific Name	Species	Autumn	Winter	Spring	Summer	Total Detections	Detection %
A. natives								
	Zosterops lateralis	silvereye	19	24	13	19	75	87.2
	Rhipidura fuliginosa	New Zealand fantail	17	15	13	16	61	70.9
	Porphyrio melanotus melanotus	pūkeko	14	18	11	14	57	66.3
	Circus approximans	swamp harrier	14	17	11	14	56	65.1
	Hirundo neoxena	welcome swallow	8	4	10	20	42	48.8
	Todiramphus sanctus	sacred kingfisher	6	8	10	11	35	40.7
	Prosthemadera novaeseelandiae	tūī	8	7	4	5	24	27.9
	Vanellus miles	spur-winged plover	0	7	8	6	21	24.4
	Tadorna variegata	paradise shelduck	7	12	2	0	21	24.4
	Larus dominicanus	black-backed gull	4	6	3	7	20	23.3
	Chroicocephalus bulleri	black-billed gull	3	8	0	1	12	14
	Gerygone igata	grey warbler	3	2	2	4	11	12.8
	Egretta novaehollandiae	white-faced heron	2	2	4	1	9	10.5
	Chroicocephalus novaehollandiae	red-billed gull	4	1	0	1	6	7
	Anthornis melanura	bellbird	1	2	0	2	5	5.8
	Hemiphaga novaeseelandiae	New Zealand pigeon	0	0	0	3	3	3.5
	Ninox novaeseelandiae	morepork	0	0	1	1	2	2.3

	Scientific Name	Species	Autumn	Winter	Spring	Summer	Total Detections	Detection %
	Falco novaeseelandiae	NZ falcon	0	1	1	0	2	2.3
	Chrysococcyx lucidus	shining cuckoo	0	0	0	2	2	2.3
	Phalacrocorax varius	pied shag	0	0	0	1	1	1.2
B. introduced								
	Turdus merula	blackbird	19	25	18	24	86	100
	Turdus philomelos	song thrush	17	24	18	24	83	96.5
	Passer domesticus	house sparrow	16	18	18	24	76	88.4
	Fringilla coelebs	chaffinch	15	23	16	19	73	84.9
	Chloris chloris	greenfinch	14	18	18	23	73	84.9
	Carduelis carduelis	goldfinch	13	16	16	24	69	80.2
	Sturnus vulgaris	starling	14	16	13	17	60	69.8
	Alauda arvensis	skylark	3	11	11	11	36	41.9
	Gymnorhina tibicen	magpie	6	6	8	9	29	33.7
	Columba livia	rock pigeon	6	6	7	10	29	33.7
	Prunella modularis	dunnock	8	10	5	2	25	29.1
	Acridotheres tristis	myna	4	6	6	6	22	25.6
	Emberiza citrinella	yellowhammer	0	11	7	4	22	25.6
	Platycercus eximius	eastern rosella	7	4	0	5	16	18.6

Scientific Name	Species	Autumn	Winter	Spring	Summer	Total Detections	Detection %
Phasianus colchicus	ring-neck pheasant	4	4	4	3	15	17.4
Callipepla californica	California quail	3	1	3	3	10	11.6
Anas platyrhynchos	mallard duck	0	3	3	3	9	10.5
Branta canadensis	Canada goose	0	0	3	4	7	8.1
Acanthis flammea	redpoll	2	0	0	4	6	7
Trichoglossus moluccanus	rainbow lorikeet	0	2	2	0	4	4.7
Synoicus ypsilophorus	brown quail	0	0	0	2	2	2.3
Pavo cristatus	peacock	0	0	0	2	2	2.3
Corvus frugilegus	rook	0	0	2	0	2	2.3
Cygnus atratus	black swan	0	0	0	1	1	1.2
Anser anser	greylag goose	0	1	0	0	1	1.2

Table S 8. Model selection results for single-season occupancy models used to estimate species habitat use while accounting for imperfect detection. For each of the 45 bird species recorded in apple orchards, the best-supported model is presented based on Akaike's Information Criterion corrected for small sample size (AICc). The table includes the selected detection covariate (where applicable), the number of estimated parameters (K), AICc, the difference in AICc from the best-supported model (ΔAICc), model likelihood, AICc weight, log-likelihood, and cumulative AICc weight. Temperature models refer to the categories of temperature retrieved from DoC protocols (DoC 2023), while Period refers to the survey periods (morning AM or afternoon PM).

Species	Best Model	K	AICc	Delta AICc	ModelLik	AICc Weight	Log-Likelihood	Cumulative Weight
bellbird	Null	2	35.483	0	1	0.918	-15.441	0.918
black backed gull	Null	2	66.515	0	1	0.950	-30.958	0.950
black billed gull	Null	2	58.810	0	1	0.758	-27.105	0.758
black swan	Null	2	15.498	0	1	0.837	-5.449	0.837
blackbird	Null	2	4.600	0	1	0.986	0.000	0.986
brown quail	Null	2	23.598	0	1	0.688	-9.499	0.688
California quail	Null	2	63.128	0	1	0.979	-29.264	0.979
Canada goose	Null	2	38.281	0	1	0.804	-16.841	0.804
chaffinch	Null	2	77.653	0	1	0.922	-36.527	0.922
dunnock	Temperature	7	103.992	0	1	0.326	-41.263	0.326
eastern rosella	Period	7	71.019	0	1	0.464	-24.776	0.464
fantail	Null	2	97.618	0	1	0.893	-46.509	0.893
goldfinch	Null	2	87.936	0	1	0.938	-41.668	0.938
greenfinch	Null	2	77.653	0	1	0.847	-36.527	0.847
grey warbler	Null	2	66.404	0	1	0.978	-30.902	0.978
greylag goose	Null	2	15.498	0	1	0.853	-5.449	0.853
house sparrow	Null	2	65.241	0	1	0.848	-30.320	0.848
kereru	Null	2	25.974	0	1	0.774	-10.687	0.774

Species	Best Model	K	AICc	Delta AICc	ModelLik	AICc Weight	Log-Likelihood	Cumulative Weight
kingfisher	Null	2	120.829	0	1	0.942	-58.114	0.942
magpie	Period	7	95.032	0	1	0.640	-36.783	0.640
mallard duck	Period	7	61.122	0	1	0.523	-19.828	0.523
masked lapwing	Period	7	82.572	0	1	0.603	-30.553	0.603
morepork	Null	2	23.599	0	1	0.678	-9.499	0.678
myna	Null	2	25.855	0	1	0.986	-10.627	0.986
NZ falcon	Null	2	23.577	0	1	0.852	-9.489	0.852
paradise shellduck	Period	7	89.930	0	1	0.277	-34.232	0.277
peacock	Null	2	16.574	0	1	0.905	-5.987	0.905
pied cormorant	Null	2	15.498	0	1	0.940	-5.449	0.940
pūkeko	Null	2	101.783	0	1	0.959	-48.591	0.959
rainbow lorikeet	Null	2	32.736	0	1	0.493	-14.068	0.493
red billed gull	Null	2	44.548	0	1	0.916	-19.974	0.916
redpoll	Null	2	44.548	0	1	0.746	-19.974	0.746
ring neck pheasant	Null	2	81.148	0	1	0.959	-38.274	0.959
rock pigeon	Null	2	107.488	0	1	0.875	-51.444	0.875
rook	Null	2	23.598	0	1	0.642	-9.499	0.642
shining cuckoo	Null	2	23.599	0	1	0.727	-9.499	0.727
silvereye	Null	2	70.372	0	1	0.978	-32.886	0.978
skylark	Null	2	97.422	0	1	0.945	-46.411	0.945
song thrush	Null	2	30.629	0	1	0.969	-13.015	0.969

Species	Best Model	K	AICc	Delta AICc	ModelLik	AICc Weight	Log-Likelihood	Cumulative Weight
starling	Null	2	110.007	0	1	0.930	-52.703	0.930
swamp harrier	Null	2	104.264	0	1	0.977	-49.832	0.977
tūī	Null	2	65.985	0	1	0.899	-30.692	0.899
welcome swallow	Null	2	121.425	0	1	0.886	-58.413	0.886
white faced heron	Null	2	59.658	0	1	0.962	-27.529	0.962
yellowhammer	Null	2	76.308	0	1	0.613	-35.854	0.613

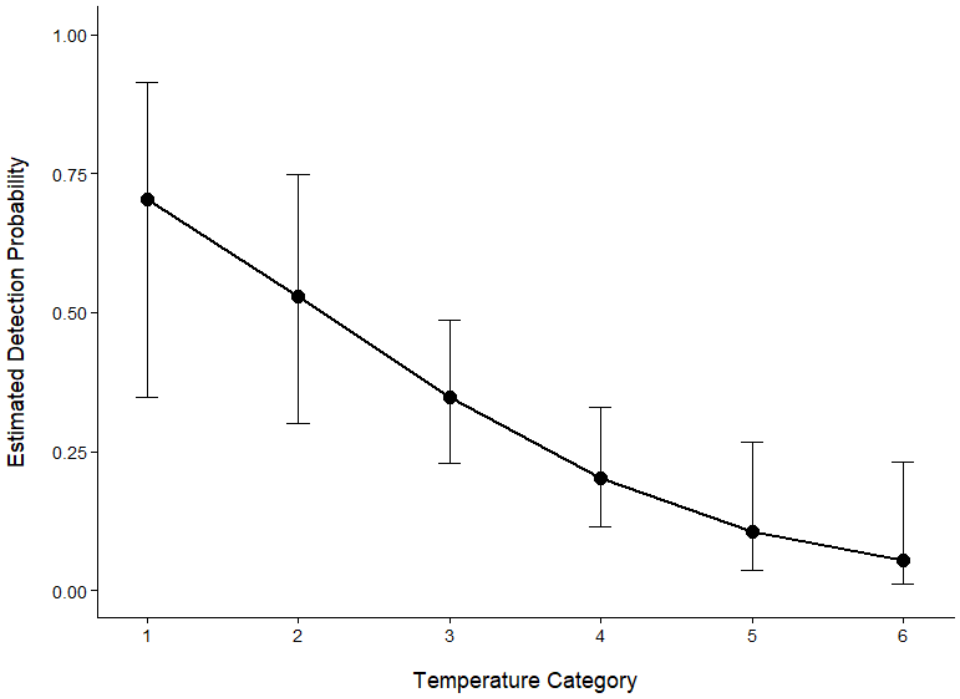


Figure S 5. Estimated detection probability of dunnock (Prunella modularis) across temperature categories from the single-season occupancy model. Points represent model-estimated detection probabilities, and error bars indicate 95% confidence intervals

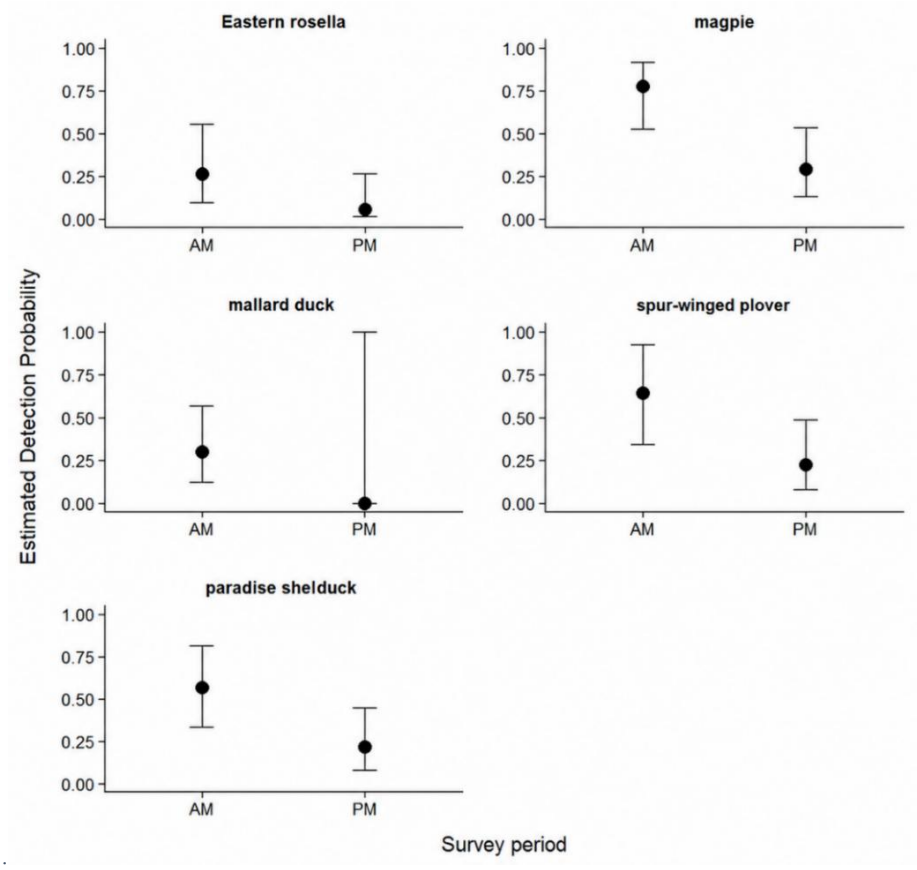


Figure S 6. Estimated detection probabilities for bird species showing a significant effect of survey period (morning AM versus afternoon PM) from single-season occupancy models. Points represent model-estimated detection probabilities, and error bars indicate 95% confidence intervals.

Table S 9. Results of tests for homogeneity of multivariate dispersion for season groups from the abundance dataset, calculated using the betadisper function in the vegan package in RStudio (Oksanen et al. 2008). PERMDISP assesses whether groups differ in their within-group dispersion (variance) in multivariate space. Non-significant p-values for orchards ($F_{5,17} = 0.172$, $p = 0.969$) and seasons ($F_{3,19} = 0.593$, $p = 0.626$) indicate that dispersion was homogeneous among groups, satisfying the assumption required for PERMANOVA. Df refers to the degrees of freedom for the group and residual components. SumSq refer to the total sum of squared distances from each sample to its group centroid in multivariate space. Mean Sq refer to the average squared distance, calculated as SumSq / Df. F-values were provided by the analysis of variance (ANOVA) run for the non-metric multidimensional scaling (NMDS) ordination of abundance data. P values (Pr (>F)) were provided from the permutation test and indicate whether group dispersions differ significantly ($p < 0.05$) or are homogeneous.

Orchard	**Df**	**Sum Sq**	**Mean Sq**	**F value**	**PR(>f)**
Groups	5.000	0.004	0.001	0.172	0.969
Residuals	17.000	0.009	0.005		
Season	**Df**	**Sum Sq**	**Mean Sq**	**F value**	**PR(>f)**
Groups	3.000	0.011	0.004	0.593	0.626
Residuals	19.000	0.124	0.007		

Table S 10. Results of tests for homogeneity of multivariate dispersion for the flocking composition dataset for the twelve species included in the analysis. Homogeneity was calculated using the betadisper function in the vegan package in RStudio (Oksanen et al. 2008). PERMDISP assesses whether groups differ in their within-group dispersion (variance) in multivariate space. Df refers to the degrees of freedom for the group and residual components. SumSq refer to the total sum of squared distances from each sample to its group centroid in multivariate space. F-values were provided by the analysis of variance (ANOVA) run for the non-metric multidimensional scaling (NMDS) ordination of abundance data. P values (Pr (>F)) were provided from the permutation test and indicate whether group dispersions differ significantly ($p < 0.05$) or are homogeneous. Species included: blackbird (Turdus merula), chaffinch (Fringilla coelebs), goldfinch (Carduelis carduelis), greenfinch (Chloris chloris), house sparrow (Passer domesticus), New Zealand fantail (Rhipidura fuliginosa), pūkeko (Porphyrio melanotus melanotus), rock pigeon (Columba livia), silvereye (Zosterops lateralis), song thrush (Turdus philomelos), starling (Sturnus vulgaris), swamp harrier (Circus approximans), and welcome swallow (Hirundo neoxena).

Species	NDMS stress	Term	Df	SumofSq	R^2	F	Pr(>F)
blackbird	0.093	Model	10	0.939	0.170	1.655	0.060
		Residual	81	4.596	0.830	NA	NA
		Total	91	5.535	1.000	NA	NA
chaffinch	0.034	Model	10	1.134	0.152	0.966	0.510
		Residual	54	6.334	0.848	NA	NA
		Total	64	7.468	1.000	NA	NA
goldfinch	0.138	Model	10	3.482	0.258	1.774	0.019
		Residual	51	10.011	0.742	NA	NA
		Total	61	13.493	1.000	NA	NA
greenfinch	0.034	Model	10	1.838	0.218	1.339	0.198
		Residual	48	6.588	0.782	NA	NA
		Total	58	8.426	1.000	NA	NA
house sparrow	0.144	Model	10	2.629	0.199	1.242	0.225
		Residual	50	10.579	0.801	NA	NA
		Total	60	13.207	1	NA	NA
New Zealand fantail	0.011	Model	10	0.916	0.121	0.594	0.846
		Residual	43	6.635	0.879	NA	NA
		Total	53	7.551	1	NA	NA
pūkeko	0.039	Model	9	1.437	0.295	1.956	0.053
		Residual	42	3.428	0.705	NA	NA
		Total	51	4.864	1	NA	NA

Species	NDMS stress	Term	Df	SumofSq	R^2	F	Pr(>F)
rock pigeon	0.037	Model	9	4.292	0.414	1.724	0.034
		Residual	22	6.087	0.586	NA	NA
		Total	31	10.379	1	NA	NA
silvereye	0.125	Model	10	4.381	0.313	3.059	0.001
		Residual	67	9.597	0.687	NA	NA
		Total	77	13.978	1	NA	NA
song thrush	0.012	Model	10	0.616	0.155	1.120	0.366
		Residual	61	3.355	0.845	NA	NA
		Total	71	3.970	1	NA	NA
starling	0.077	Model	10	1.886	0.167	0.722	0.828
		Residual	36	9.401	0.833	NA	NA
		Total	46	11.286	1	NA	NA
swamp harrier	0	Model	9	0.133	0.200	0.969	0.481
		Residual	35	0.533	0.800	NA	NA
		Total	44	0.666	1	NA	NA
welcome swallow	0	Model	10	3.406	0.453	1.989	0.048
		Residual	24	4.109	0.547	NA	NA
		Total	34	7.515	1	NA	NA

Table S 11. Pairwise permutational multivariate analysis of variance (PERMANOVA) comparisons testing differences in flocking composition between levels of each predictor (season, orchard, period, and position) for the thirteen species included in the analysis. For each pairwise contrast, the table reports on the levels being compared; the number of non-zero flocking-type observations in each group after filtering rows with zero total flock counts (n1 and n2, respectively); F-statistics from PERMANOVA calculations; corresponding R^2 values; unadjusted p-values based on 999 permutations; and Holm-adjusted p-values. Significant pairwise contrasts (p.adj <0.05) are marked by asterisks. Species included: blackbird (Turdus merula), chaffinch (Fringilla coelebs), goldfinch (Carduelis carduelis), greenfinch (Chloris chloris), house sparrow (Passer domesticus), New Zealand fantail (Rhipidura fuliginosa), pūkeko (Porphyrio melanotus melanotus), rock pigeon (Columba livia), silvereye (Zosterops lateralis), song thrush (Turdus philomelos), starling (Sturnus vulgaris), swamp harrier (Circus approximans), and welcome swallow (Hirundo neoxena).

	Group 1	Group 2	n1	n2	F	R^2	p	p.adj
blackbird	By Season							
	autumn	winter	24	24	3.333	0.068	0.047	0.282
	autumn	spring	24	20	2.467	0.055	0.102	0.51
	autumn	summer	24	24	2.331	0.048	0.119	0.51
	winter	spring	24	20	2.120	0.048	0.164	0.51
	winter	summer	24	24	0.519	0.011	0.605	0.605
	spring	summer	20	24	1.624	0.037	0.219	0.51
	By Orchard							
	Tasman Region	Hawke's Bay	14	14	1.752	0.063	0.244	1.000
	Tasman Region	Kāpiti Coast 1	14	16	0.136	0.005	0.819	1
	Tasman Region	Kāpiti Coast 2	14	16	4.887	0.149	0.012	0.180
	Tasman Region	Manawatū 1	14	16	1.440	0.049	0.280	1.000
	Tasman Region	Manawatū 2	14	16	0.632	0.022	0.535	1.000
	Hawke's Bay	Kāpiti Coast 1	14	16	1.013	0.035	0.385	1.000
	Hawke's Bay	Kāpiti Coast 2	14	16	1.042	0.036	0.387	1
	Hawke's Bay	Manawatū 1	14	16	0.820	0.028	0.463	1

	Group 1	Group 2	n1	n2	F	R^2	p	p.adj
	Hawke's Bay	Manawatū 2	14	16	0.773	0.027	0.450	1.000
	Kāpiti Coast 1	Kāpiti Coast 2	16	16	4.680	0.135	0.014	0.196
	Kāpiti Coast 1	Manawatū 1	16	16	2.035	0.064	0.168	1.000
	Kāpiti Coast 1	Manawatū 2	16	16	0.209	0.007	0.726	1.000
	Kāpiti Coast 2	Manawatū 1	16	16	0.066	0.002	0.848	1.000
	Kāpiti Coast 2	Manawatū 2	16	16	3.194	0.096	0.084	1.000
	Manawatū 1	Manawatū 2	16	16	0.585	0.019	0.614	1.000
	By Period							
	AM	PM	46	46	2.200	0.024	0.130	0.130
	By Position							
	edge	middle	46	46	0.433	0.005	0.640	0.640
chaffinch	By Season							
	autumn	winter	18	16	2.704	0.078	0.068	0.408
	autumn	spring	18	16	1.502	0.045	0.244	0.976
	autumn	summer	18	15	1.898	0.058	0.157	0.785
	winter	spring	16	16	0.273	0.009	0.667	1
	winter	summer	16	15	0.592	0.020	0.528	1
	spring	summer	16	15	0.621	0.021	0.489	1

Group 1	Group 2	n1	n2	F	R^2	p	p.adj
By Orchard							
Tasman Region	Hawke's Bay	11	12	1.429	0.064	0.287	1.000
Tasman Region	Kāpiti Coast 1	11	9	0.683	0.037	0.613	1
Tasman Region	Kāpiti Coast 2	11	10	0.026	0.001	0.858	1.000
Tasman Region	Manawatū 1	11	11	1.497	0.070	0.246	1.000
Tasman Region	Manawatū 2	11	12	0.228	0.011	0.707	1.000
Hawke's Bay	Kāpiti Coast 1	12	9	0.750	0.038	0.578	1.000
Hawke's Bay	Kāpiti Coast 2	12	10	-0.670	-0.035	0.991	1
Hawke's Bay	Manawatū 1	12	11	1.670	0.074	0.217	1
Hawke's Bay	Manawatū 2	12	12	1.307	0.056	0.319	1.000
Kāpiti Coast 1	Kāpiti Coast 2	9	10	0.406	0.023	0.726	1.000
Kāpiti Coast 1	Manawatū 1	9	11	2.589	0.126	0.068	1.000
Kāpiti Coast 1	Manawatū 2	9	12	1.161	0.058	0.299	1.000
Kāpiti Coast 2	Manawatū 1	10	11	0.956	0.048	0.435	1.000
Kāpiti Coast 2	Manawatū 2	10	12	0.610	0.030	0.501	1.000
Manawatū 1	Manawatū 2	11	12	1.786	0.078	0.175	1.000
By Period							
AM	PM	42	23	0.335	0.005	0.701	0.701

	Group 1	Group 2	n1	n2	F	R^2	p	p.adj
	By Position							
	edge	middle	38	27	0.315	0.005	0.737	0.737
goldfinch	By Season							
	autumn	winter	12	13	0.227	0.010	0.827	1
	autumn	spring	12	15	2.057	0.076	0.119	0.714
	autumn	summer	12	22	1.305	0.039	0.273	1
	winter	spring	13	15	1.020	0.038	0.381	1
	winter	summer	13	22	1.042	0.031	0.375	1
	spring	summer	15	22	1.141	0.032	0.330	1
	By Orchard							
	Tasman Region	Hawke's Bay	12	13	3.332	0.127	0.029	0.324
	Tasman Region	Kāpiti Coast 1	12	7	4.623	0.214	0.014	0.196
	Tasman Region	Kāpiti Coast 2	12	12	3.906	0.151	0.011	0.165
	Tasman Region	Manawatū 1	12	8	0.155	0.009	0.852	1.000
	Tasman Region	Manawatū 2	12	10	-0.006	0.000	0.923	1.000
	Hawke's Bay	Kāpiti Coast 1	13	7	1.825	0.092	0.167	1.000
	Hawke's Bay	Kāpiti Coast 2	13	12	0.450	0.019	0.716	1

	Group 1	Group 2	n1	n2	F	R^2	p	p.adj
	Hawke's Bay	Manawatū 1	13	8	3.300	0.148	0.027	0.324
	Hawke's Bay	Manawatū 2	13	10	1.836	0.080	0.168	1.000
	Kāpiti Coast 1	Kāpiti Coast 2	7	12	0.845	0.047	0.473	1.000
	Kāpiti Coast 1	Manawatū 1	7	8	2.998	0.187	0.080	0.720
	Kāpiti Coast 1	Manawatū 2	7	10	3.888	0.206	0.024	0.312
	Kāpiti Coast 2	Manawatū 1	12	8	3.004	0.143	0.043	0.430
	Kāpiti Coast 2	Manawatū 2	12	10	2.390	0.107	0.091	0.728
	Manawatū 1	Manawatū 2	8	10	0.604	0.036	0.598	1.000
	By Period							
	AM	PM	36	26	0.930	0.015	0.444	0.444
	By Position							
	edge	middle	36	26	0.864	0.014	0.453	0.453
greenfinch	By Season							
	autumn	winter	12	14	0.634	0.026	0.598	1
	autumn	spring	12	14	0.340	0.014	0.766	1
	autumn	summer	12	19	-1.077	-0.039	1.000	1
	winter	spring	14	14	2.609	0.091	0.113	0.678

Group 1	Group 2	n1	n2	F	R^2	p	p.adj
winter	summer	14	19	1.594	0.049	0.210	1
spring	summer	14	19	0.422	0.013	0.578	1
By Orchard							
Tasman Region	Hawke's Bay	13	14	5.079	0.169	0.016	0.240
Tasman Region	Kāpiti Coast 1	13	9	0.477	0.023	0.573	1
Tasman Region	Kāpiti Coast 2	13	5	1.107	0.065	0.327	1.000
Tasman Region	Manawatū 1	13	10	3.029	0.126	0.076	1.000
Tasman Region	Manawatū 2	13	8	1.626	0.079	0.206	1.000
Hawke's Bay	Kāpiti Coast 1	14	9	1.791	0.079	0.189	1.000
Hawke's Bay	Kāpiti Coast 2	14	5	1.147	0.063	0.373	1
Hawke's Bay	Manawatū 1	14	10	1.931	0.081	0.177	1
Hawke's Bay	Manawatū 2	14	8	2.016	0.092	0.165	1.000
Kāpiti Coast 1	Kāpiti Coast 2	9	5	0.087	0.007	0.927	1.000
Kāpiti Coast 1	Manawatū 1	9	10	0.552	0.031	0.484	1.000
Kāpiti Coast 1	Manawatū 2	9	8	0.139	0.009	0.732	1.000
Kāpiti Coast 2	Manawatū 1	5	10	0.336	0.025	0.712	1.000
Kāpiti Coast 2	Manawatū 2	5	8	0.255	0.023	0.834	1.000
Manawatū 1	Manawatū 2	10	8	0.132	0.008	0.697	1.000
By Period							

	Group 1	Group 2	n1	n2	F	R^2	p	p.adj	
	AM	PM	32	27	-0.061	-0.001	0.945	0.945	
	By Position								
	edge	middle	33	26	3.706	0.061	0.046	0.046	*
house sparrow	By Season								
	autumn	winter	14	15	1.669	0.058	0.223	0.669	
	autumn	spring	14	13	2.601	0.094	0.069	0.345	
	autumn	summer	14	19	2.994	0.088	0.047	0.282	
	winter	spring	15	13	0.803	0.030	0.459	0.68	
	winter	summer	15	19	1.238	0.037	0.340	0.68	
	spring	summer	13	19	1.892	0.059	0.142	0.568	
	By Orchard								
	Tasman Region	Hawke's Bay	14	12	0.761	0.031	0.544	1.000	
	Tasman Region	Kāpiti Coast 1	14	12	0.970	0.039	0.390	1	
	Tasman Region	Kāpiti Coast 2	14	9	0.891	0.041	0.505	1.000	
	Tasman Region	Manawatū 1	14	6	2.386	0.117	0.083	1.000	
	Tasman Region	Manawatū 2	14	8	1.075	0.051	0.363	1.000	
	Hawke's Bay	Kāpiti Coast 1	12	12	0.600	0.027	0.602	1.000	

	Group 1	Group 2	n1	n2	F	R^2	p	p.adj
	Hawke's Bay	Kāpiti Coast 2	12	9	0.805	0.041	0.468	1
	Hawke's Bay	Manawatū 1	12	6	0.696	0.042	0.572	1
	Hawke's Bay	Manawatū 2	12	8	0.830	0.044	0.478	1.000
	Kāpiti Coast 1	Kāpiti Coast 2	12	9	0.658	0.033	0.584	1.000
	Kāpiti Coast 1	Manawatū 1	12	6	0.617	0.037	0.590	1.000
	Kāpiti Coast 1	Manawatū 2	12	8	0.588	0.032	0.648	1.000
	Kāpiti Coast 2	Manawatū 1	9	6	0.463	0.034	0.677	1.000
	Kāpiti Coast 2	Manawatū 2	9	8	-0.061	-0.004	0.939	1.000
	Manawatū 1	Manawatū 2	6	8	0.160	0.013	0.890	1.000
	By Period							
	AM	PM	31	30	0.697	0.012	0.584	0.584
	By Position							
	edge	middle	41	20	2.428	0.040	0.075	0.075
New Zealand fantail	By Season							
	autumn	winter	17	12	0.466	0.017	0.492	1
	autumn	spring	17	10	0.043	0.002	0.785	1
	autumn	summer	17	15	0.680	0.022	0.479	1

Group 1	Group 2	n1	n2	F	R^2	p	p.adj
winter	spring	12	10	0.665	0.032	0.431	1
winter	summer	12	15	1.473	0.056	0.262	1
spring	summer	10	15	0.164	0.007	0.780	1
By Orchard							
Tasman Region	Hawke's Bay	5	9	1.000	0.077	0.460	1.000
Tasman Region	Kāpiti Coast 1	5	11	1.502	0.097	0.272	1
Tasman Region	Kāpiti Coast 2	5	8	0.104	0.009	0.860	1.000
Tasman Region	Manawatū 1	5	8	0.487	0.042	0.515	1.000
Tasman Region	Manawatū 2	5	13	1.995	0.111	0.185	1.000
Hawke's Bay	Kāpiti Coast 1	9	11	-0.598	-0.034	0.989	1.000
Hawke's Bay	Kāpiti Coast 2	9	8	1.267	0.078	0.295	1
Hawke's Bay	Manawatū 1	9	8	-0.213	-0.014	0.970	1
Hawke's Bay	Manawatū 2	9	13	0.685	0.033	0.522	1.000
Kāpiti Coast 1	Kāpiti Coast 2	11	8	2.083	0.109	0.150	1.000
Kāpiti Coast 1	Manawatū 1	11	8	0.378	0.022	0.624	1.000
Kāpiti Coast 1	Manawatū 2	11	13	-0.100	-0.005	0.855	1.000
Kāpiti Coast 2	Manawatū 1	8	8	0.553	0.038	0.591	1.000

	Group 1	Group 2	n1	n2	F	R^2	p	p.adj
	Kāpiti Coast 2	Manawatū 2	8	13	1.347	0.066	0.277	1.000
	Manawatū 1	Manawatū 2	8	13	-0.619	-0.034	0.981	1.000
	By Period							
	AM	PM	28	26	0.330	0.006	0.632	0.632
	By Position							
	edge	middle	40	14	1.594	0.030	0.206	0.206
pūkeko	By Season							
	autumn	winter	14	16	0.685	0.024	0.494	1
	autumn	spring	14	11	0.128	0.006	0.849	1
	autumn	summer	14	11	0.179	0.008	0.800	1
	winter	spring	16	11	0.162	0.006	0.777	1
	winter	summer	16	11	0.434	0.017	0.565	1
	spring	summer	11	11	0.169	0.008	0.807	1
	By Orchard							
	Tasman Region	Hawke's Bay	12	10	2.074	0.094	0.124	0.868
	Tasman Region	Kāpiti Coast 1	12	15	-0.277	-0.011	0.979	1
	Tasman Region	Kāpiti Coast 2	12	10	0.413	0.020	0.617	1.000

	Group 1	Group 2	n1	n2	F	R^2	p	p.adj	
	Tasman Region	Manawatū 1	12	0	NA	NA	NA	NA	
	Tasman Region	Manawatū 2	12	5	3.208	0.176	0.075	0.600	
	Hawke's Bay	Kāpiti Coast 1	10	15	2.458	0.097	0.125	0.868	
	Hawke's Bay	Kāpiti Coast 2	10	10	1.410	0.073	0.240	0.96	
	Hawke's Bay	Manawatū 1	10	0	NA	NA	NA	NA	
	Hawke's Bay	Manawatū 2	10	5	4.662	0.264	0.027	0.270	
	Kāpiti Coast 1	Kāpiti Coast 2	15	10	0.921	0.039	0.396	1.000	
	Kāpiti Coast 1	Manawatū 1	15	0	NA	NA	NA	NA	
	Kāpiti Coast 1	Manawatū 2	15	5	4.441	0.198	0.034	0.306	
	Kāpiti Coast 2	Manawatū 1	10	0	NA	NA	NA	NA	
	Kāpiti Coast 2	Manawatū 2	10	5	2.290	0.150	0.162	0.868	
	Manawatū 1	Manawatū 2	0	5	NA	NA	NA	NA	
	By Period								
	AM	PM	28	24	4.898	0.089	0.022	0.022	*
	By Position								
	edge	middle	32	20	1.588	0.031	0.225	0.225	
rock pigeon	By Season								
	autumn	winter	6	7	0.553	0.048	0.702	1	

Group 1	Group 2	n1	n2	F	R^2	p	p.adj	
autumn	spring	6	9	3.135	0.194	0.041	0.246	
autumn	summer	6	10	2.030	0.127	0.124	0.62	
winter	spring	7	9	1.150	0.076	0.359	1	
winter	summer	7	10	0.797	0.050	0.521	1	
spring	summer	9	10	0.776	0.044	0.544	1	
By Orchard								
Tasman Region	Hawke's Bay	1	4	0.337	0.101	1.000	1.000	
Tasman Region	Kāpiti Coast 1	1	6	0.623	0.111	0.873	1	
Tasman Region	Kāpiti Coast 2	1	11	0.186	0.018	1.000	1.000	
Tasman Region	Manawatū 1	1	0	NA	NA	NA	NA	
Tasman Region	Manawatū 2	1	10	3.687	0.291	0.177	1.000	
Hawke's Bay	Kāpiti Coast 1	4	6	0.818	0.093	0.630	1.000	
Hawke's Bay	Kāpiti Coast 2	4	11	0.394	0.029	0.810	1	
Hawke's Bay	Manawatū 1	4	0	NA	NA	NA	NA	
Hawke's Bay	Manawatū 2	4	10	1.568	0.116	0.230	1.000	
Kāpiti Coast 1	Kāpiti Coast 2	6	11	1.128	0.070	0.332	1.000	
Kāpiti Coast 1	Manawatū 1	6	0	NA	NA	NA	NA	
Kāpiti Coast 1	Manawatū 2	6	10	5.909	0.297	0.001	0.010	*
Kāpiti Coast 2	Manawatū 1	11	0	NA	NA	NA	NA	

	Group 1	Group 2	n1	n2	F	R^2	p	p.adj	
	Kāpiti Coast 2	Manawatū 2	11	10	5.870	0.236	0.003	0.027	*
	Manawatū 1	Manawatū 2	0	10	NA	NA	NA	NA	
	By Period								
	AM	PM	20	12	1.434	0.046	0.244	0.244	
	By Position								
	edge	middle	14	18	0.590	0.019	0.649	0.649	
silvereye	By Season								
	autumn	winter	24	24	8.477	0.156	0.001	0.006	*
	autumn	spring	24	14	1.483	0.040	0.243	0.243	
	autumn	summer	24	16	4.170	0.099	0.009	0.036	*
	winter	spring	24	14	5.401	0.130	0.001	0.006	*
	winter	summer	24	16	3.606	0.087	0.017	0.051	
	spring	summer	14	16	2.780	0.090	0.057	0.114	
	By Orchard								
	Tasman Region	Hawke's Bay	10	14	4.499	0.170	0.005	0.075	
	Tasman Region	Kāpiti Coast 1	10	13	2.495	0.106	0.081	0.88	
	Tasman Region	Kāpiti Coast 2	10	11	3.107	0.141	0.058	0.696	
	Tasman Region	Manawatū 1	10	15	3.873	0.144	0.013	0.169	

	Group 1	Group 2	n1	n2	F	R^2	p	p.adj
	Tasman Region	Manawatū 2	10	15	2.170	0.086	0.095	0.880
	Hawke's Bay	Kāpiti Coast 1	14	13	1.756	0.066	0.201	1.000
	Hawke's Bay	Kāpiti Coast 2	14	11	0.034	0.001	0.898	1
	Hawke's Bay	Manawatū 1	14	15	0.614	0.022	0.612	1
	Hawke's Bay	Manawatū 2	14	15	0.768	0.028	0.511	1.000
	Kāpiti Coast 1	Kāpiti Coast 2	13	11	1.072	0.046	0.369	1.000
	Kāpiti Coast 1	Manawatū 1	13	15	4.190	0.139	0.008	0.112
	Kāpiti Coast 1	Manawatū 2	13	15	0.117	0.004	0.868	1.000
	Kāpiti Coast 2	Manawatū 1	11	15	1.291	0.051	0.295	1.000
	Kāpiti Coast 2	Manawatū 2	11	15	0.587	0.024	0.624	1.000
	Manawatū 1	Manawatū 2	15	15	2.488	0.082	0.080	0.880
	By Period							
	AM	PM	40	38	1.054	0.014	0.389	0.389
	By Position							
	edge	middle	43	35	1.985	0.025	0.119	0.119
song thrush	By Season							
	autumn	winter	12	21	0.509	0.016	0.596	1
	autumn	spring	12	17	1.278	0.045	0.274	0.976

Group 1	Group 2	n1	n2	F	R^2	p	p.adj
autumn	summer	12	22	4.492	0.123	0.060	0.36
winter	spring	21	17	0.393	0.011	0.717	1
winter	summer	21	22	2.550	0.059	0.102	0.51
spring	summer	17	22	1.586	0.041	0.244	0.976
By Orchard							
Tasman Region	Hawke's Bay	14	13	-0.118	-0.005	0.993	1.000
Tasman Region	Kāpiti Coast 1	14	11	0.188	0.008	0.644	1
Tasman Region	Kāpiti Coast 2	14	14	1.566	0.057	0.218	1.000
Tasman Region	Manawatū 1	14	10	-0.058	-0.003	0.975	1.000
Tasman Region	Manawatū 2	14	10	0.273	0.012	0.579	1.000
Hawke's Bay	Kāpiti Coast 1	13	11	0.327	0.015	0.574	1.000
Hawke's Bay	Kāpiti Coast 2	13	14	0.742	0.029	0.494	1
Hawke's Bay	Manawatū 1	13	10	-0.032	-0.002	0.986	1
Hawke's Bay	Manawatū 2	13	10	-0.152	-0.007	0.998	1.000
Kāpiti Coast 1	Kāpiti Coast 2	11	14	0.557	0.024	0.609	1.000
Kāpiti Coast 1	Manawatū 1	11	10	0.175	0.009	0.626	1.000

	Group 1	Group 2	n1	n2	F	R^2	p	p.adj
	Kāpiti Coast 1	Manawatū 2	11	10	-0.100	-0.005	0.710	1.000
	Kāpiti Coast 2	Manawatū 1	14	10	0.818	0.036	0.478	1.000
	Kāpiti Coast 2	Manawatū 2	14	10	0.666	0.029	0.574	1.000
	Manawatū 1	Manawatū 2	10	10	-0.009	-0.001	0.949	1.000
	By Period							
	AM	PM	41	31	2.665	0.037	0.088	0.088
	By Position							
	edge	middle	40	32	1.097	0.015	0.343	0.343
starling	By Season							
	autumn	winter	7	15	0.657	0.032	0.551	1
	autumn	spring	7	11	0.269	0.017	0.700	1
	autumn	summer	7	14	1.330	0.065	0.289	1
	winter	spring	15	11	1.304	0.052	0.301	1
	winter	summer	15	14	1.644	0.057	0.188	0.94
	spring	summer	11	14	3.065	0.118	0.037	0.222
	By Orchard							
	Tasman Region	Hawke's Bay	5	8	0.358	0.032	0.659	1.000

Group 1	Group 2	n1	n2	F	R²	p	p.adj
Tasman Region	Kāpiti Coast 1	5	10	0.959	0.069	0.456	1
Tasman Region	Kāpiti Coast 2	5	10	0.495	0.037	0.702	1.000
Tasman Region	Manawatū 1	5	6	1.972	0.180	0.085	1.000
Tasman Region	Manawatū 2	5	8	0.341	0.030	0.759	1.000
Hawke's Bay	Kāpiti Coast 1	8	10	0.080	0.005	0.916	1.000
Hawke's Bay	Kāpiti Coast 2	8	10	-0.248	-0.016	0.996	1
Hawke's Bay	Manawatū 1	8	6	0.766	0.060	0.554	1
Hawke's Bay	Manawatū 2	8	8	0.241	0.017	0.812	1.000
Kāpiti Coast 1	Kāpiti Coast 2	10	10	0.079	0.004	0.927	1.000
Kāpiti Coast 1	Manawatū 1	10	6	1.203	0.079	0.348	1.000
Kāpiti Coast 1	Manawatū 2	10	8	0.047	0.003	0.922	1.000
Kāpiti Coast 2	Manawatū 1	10	6	0.678	0.046	0.561	1.000
Kāpiti Coast 2	Manawatū 2	10	8	-0.166	-0.010	0.994	1.000
Manawatū 1	Manawatū 2	6	8	1.285	0.097	0.301	1.000
By Period							
AM	PM	26	21	0.066	0.001	0.933	0.933
By Position							
edge	middle	37	10	0.703	0.015	0.558	0.558

	Group 1	Group 2	n1	n2	F	R^2	p	p.adj
swamp harrier	By Season							
	autumn	winter	12	11	0.002	0.000	1.000	1
	autumn	spring	12	12	0.171	0.008	0.709	1
	autumn	summer	12	10	-0.025	-0.001	1.000	1
	winter	spring	11	12	0.122	0.006	0.744	1
	winter	summer	11	10	-0.025	-0.001	1.000	1
	spring	summer	12	10	0.189	0.009	1.000	1
	By Orchard							
	Tasman Region	Hawke's Bay	9	12	0.228	0.012	0.753	1.000
	Tasman Region	Kāpiti Coast 1	9	10	0.033	0.002	1.000	1
	Tasman Region	Kāpiti Coast 2	9	11	0.949	0.050	0.377	1.000
	Tasman Region	Manawatū 1	9	0	NA	NA	NA	NA
	Tasman Region	Manawatū 2	9	3	0.313	0.030	1.000	1.000
	Hawke's Bay	Kāpiti Coast 1	12	10	0.049	0.002	1.000	1.000
	Hawke's Bay	Kāpiti Coast 2	12	11	0.280	0.013	0.645	1
	Hawke's Bay	Manawatū 1	12	0	NA	NA	NA	NA
	Hawke's Bay	Manawatū 2	12	3	0.484	0.036	0.821	1.000

	Group 1	Group 2	n1	n2	F	R^2	p	p.adj
	Kāpiti Coast 1	Kāpiti Coast 2	10	11	0.501	0.026	0.600	1.000
	Kāpiti Coast 1	Manawatū 1	10	0	NA	NA	NA	NA
	Kāpiti Coast 1	Manawatū 2	10	3	0.282	0.025	1.000	1.000
	Kāpiti Coast 2	Manawatū 1	11	0	NA	NA	NA	NA
	Kāpiti Coast 2	Manawatū 2	11	3	0.907	0.070	0.701	1.000
	Manawatū 1	Manawatū 2	0	3	NA	NA	NA	NA
	By Period							
	AM	PM	20	25	2.314	0.051	0.144	0.144
	By Position							
	edge	middle	28	17	5.084	0.106	0.053	0.053
welcome swallow	By Season							
	autumn	winter	5	5	0.556	0.065	0.505	1
	autumn	spring	5	9	1.108	0.085	0.332	1
	autumn	summer	5	16	1.003	0.050	0.366	1
	winter	spring	5	9	-0.223	-0.019	0.990	1
	winter	summer	5	16	-0.021	-0.001	0.949	1

Group 1	Group 2	n1	n2	F	R^2	p	p.adj
spring	summer	9	16	-0.090	-0.004	0.949	1
By Orchard							
Tasman Region	Hawke's Bay	8	9	-0.034	-0.002	0.928	1.000
Tasman Region	Kāpiti Coast 1	8	3	1.876	0.173	0.305	1
Tasman Region	Kāpiti Coast 2	8	3	1.437	0.138	0.290	1.000
Tasman Region	Manawatū 1	8	5	0.014	0.001	0.936	1.000
Tasman Region	Manawatū 2	8	7	2.310	0.151	0.124	1.000
Hawke's Bay	Kāpiti Coast 1	9	3	1.706	0.146	0.365	1.000
Hawke's Bay	Kāpiti Coast 2	9	3	1.172	0.105	0.408	1
Hawke's Bay	Manawatū 1	9	5	-0.107	-0.009	0.962	1
Hawke's Bay	Manawatū 2	9	7	2.012	0.126	0.152	1.000
Kāpiti Coast 1	Kāpiti Coast 2	3	3	1.000	0.200	1.000	1.000
Kāpiti Coast 1	Manawatū 1	3	5	4.654	0.437	0.128	1.000
Kāpiti Coast 1	Manawatū 2	3	7	4.008	0.334	0.055	0.825
Kāpiti Coast 2	Manawatū 1	3	5	3.332	0.357	0.121	1.000
Kāpiti Coast 2	Manawatū 2	3	7	2.563	0.243	0.143	1.000
Manawatū 1	Manawatū 2	5	7	1.830	0.155	0.188	1.000

Group 1	Group 2	n1	n2	F	R^2	p	p.adj	
By Period								
AM	PM	18	17	3.917	0.106	0.047	0.047	*
By Position								
edge	middle	22	13	6.189	0.158	0.008	0.008	*

Table S 12. Formulas of the generalised linear mixed models (GLMMs) fitted for the vertical strata use data. Models were fitted in the 'glmmTMB' package using RStudio, using a negative binomial error distribution to account for overdispersion and an abundance of zeros in the count data.

Model	Model Formula
Strata x Season Interaction	observations ~ vertical stratum * season + (1 | orchard)
Main Effects Only	observations ~ vertical stratum + season + (1 | orchard)
Orchard Random Only	observations ~ 1 + (1 | orchard)
Strata x Season + Orchard as Fixed Effect	observations ~ vertical stratum * season + orchard
Null Model	observations ~ 1

Table S 13. Model diagnostics for generalised linear mixed models (GLMMs) produced to examine variation in the dataset of vertical strata use of different species across seasons and orchards surveyed. Candidate models included combinations of relevant fixed and random effects. Columns report convergence, positive-definite Hessian (pdHess), over-dispersion, zero-inflation, uniformity of residuals, and outlier influence. ✓indicates model assumption criteria met; X indicates violations. Bold values highlight models retained for inference based on model diagnostics and Akaike's Information Criteria (AIC) selection. Species included: blackbird (Turdus merula), chaffinch (Fringilla coelebs), New Zealand fantail (Rhipidura fuliginosa), goldfinch (Carduelis carduelis), greenfinch (Chloris chloris), house sparrow (Passer domesticus), pūkeko (Porphyrio melanotus melanotus), silvereye (Zosterops lateralis), song thrush (Turdus philomelos), starling (Sturnus vulgaris), swamp harrier (Circus approximans), tūī (Prosthemadera novaeseelandiae), and welcome swallow (Hirundo neoxena).

Species	Model	convergence	pdHess	dispersion	zero-inflation	uniformity	outliers
blackbird							
	Strata x Season Interaction	**a**	**a**	**0.652**	**0.378**	**0.960**	**1**
	Main Effects Only	a	a	0.79	0.17	0.684	1
	Orchard Random Only	a	a	0.724	1	0.608	1
	Strata x Season + Orchard as Fixed Effect	a	a	0.29	0.264	0.914	0.38
	Null Model	a	a	0.744	1	0.657	1
chaffinch							
	Strata x Season Interaction	a	a	0.728	0.846	0.558	1
	Main Effects Only	**a**	**a**	**0.824**	**1**	**0.906**	**1**
	Orchard Random Only	a	a	0.818	0.8	0.989	1
	Strata x Season + Orchard as Fixed Effect	a	a	0.96	0.758	0.868	1
	Null Model	a	a	0.744	0.744	0.974	1
New Zealand fantail							
	Strata x Season Interaction	a	a	0.744	0.93	0.228	1
	Main Effects Only	**a**	**a**	**0.808**	**0.97**	**0.946**	**1**
	Orchard Random Only	a	a	0.798	1	0.821	1
	Strata x Season + Orchard as Fixed Effect	a	X	0.618	0.79	0.718	1
	Null Model	a	a	0.774	0.966	0.774	1

Species	Model	convergence	pdHess	dispersion	zero-inflation	uniformity	outliers
goldfinch							
	Strata x Season Interaction	a	a	0.694	0.962	0.868	1
	Main Effects Only	**a**	**a**	**0.766**	**1**	**0.587**	**1**
	Orchard Random Only	a	a	0.664	1	0.788	1
	Orchard as Fixed Effect	a	a	0.868	1	0.681	1
	Null Model	a	a	0.368	0.676	0.810	1
greenfinch							
	Strata x Season Interaction	a	a	0.328	0.974	0.430	1
	Main Effects Only	**a**	**a**	**0.378**	**0.998**	**0.355**	**1**
	Orchard Random Only	a	a	0.424	0.866	0.618	1
	Strata x Season + Orchard as Fixed Effect	a	a	0.608	0.782	0.998	1
	Null Model	a	a	0.102	0.536	0.255	0.42
house sparrow							
	Strata x Season Interaction	a	a	0.696	0.58	0.239	1
	Main Effects Only	a	a	0.938	0.704	0.740	1
	Orchard Random Only	a	a	0.994	0.71	0.760	1
	Strata x Season + Orchard as Fixed Effect	**a**	**a**	**0.684**	**0.446**	**0.207**	**0.24**
	Null Model	a	a	0.814	1	0.959	1
pūkeko							
	Strata x Season Interaction	a	a	0.868	0.944	0.464	1
	Main Effects Only	**a**	**a**	**0.926**	**0.996**	**0.579**	**1**
	Orchard Random Only	a	a	0.922	0.954	0.875	1
	Strata x Season + Orchard as Fixed Effect	X	a	0.63	0.834	0.982	1
	Null Model	a	a	0.508	0.928	0.577	1

Species	Model	convergence	pdHess	dispersion	zero-inflation	uniformity	outliers
silvereye							
	Strata x Season Interaction	a	a	0.91	0.882	0.921	1.000
	Main Effects Only	a	a	0.94	0.716	0.987	1
	Orchard Random Only	a	a	0.646	0.886	0.904	1
	Strata x Season + Orchard as Fixed Effect	**a**	**a**	**0.834**	**0.786**	**0.853**	**1**
	Null Model	a	a	0.628	0.89	0.261	1
song thrush							
	Strata x Season Interaction	a	a	0.828	0.982	0.287	0.3
	Main Effects Only	a	a	0.818	0.938	0.329	1
	Orchard Random Only	a	a	0.65	1	0.977	0.26
	Strata x Season + Orchard as Fixed Effect	**a**	**a**	**0.526**	**1**	**0.959**	**1**
	Null Model	a	a	0.534	0.928	0.301	0.36
starling							
	Strata x Season Interaction	a	a	0.806	0.982	0.598	1
	Main Effects Only	a	a	0.918	1	0.347	0.1
	Orchard Random Only	a	a	0.99	1	0.711	1
	Strata x Season + Orchard as Fixed Effect	**a**	**a**	**0.836**	**0.866**	**0.925**	**1**
	Null Model	a	a	0.998	1	0.993	1

Species	Model	convergence	pdHess	dispersion	zero-inflation	uniformity	outliers
swamp harrier							
	Strata x Season Interaction	a	a	0.896	1	0.356	1
	Main Effects Only	a	a	0.982	0.95	0.489	1
	Orchard Random Only	a	a	0.792	1	0.112	1
	Strata x Season + Orchard as Fixed Effect	**a**	**a**	**0.502**	**0.802**	**0.386**	**1**
	Null Model	a	a	0.798	1	0.187	1
tūī							
	Strata x Season Interaction	a	X	0.726	0.77	0.562	1
	Main Effects Only	**a**	**a**	**0.722**	**0.832**	**0.669**	**1**
	Orchard Random Only	a	a	0.738	0.83	0.973	1
	Strata x Season + Orchard as Fixed Effect	a	X	0.042	0.648	0.361	1
	Null Model	a	a	0.93	1	0.998	1
welcome swallow							
	Strata x Season Interaction	X	a	0.82	1	0.957	1
	Main Effects Only	**a**	**a**	**0.87**	**0.854**	**0.946**	**1**
	Orchard Random Only	a	a	0.974	1	0.588	1
	Strata x Season + Orchard as Fixed Effect	a	a	0.88	1	0.200	1
	Null Model	a	a	0.928	1	0.836	1

Table S 14. Generalised linear mixed model (GLMM) outputs for vertical strata count across multiple species: blackbird (Turdus merula), chaffinch (Fringilla coelebs), goldfinch (Carduelis carduelis), greenfinch (Chloris chloris), house sparrow (Passer domesticus), pūkeko (Porphyrio melanotus melanotus), silvereye (Zosterops lateralis), song thrush (Turdus philomelos), swamp harrier (Circus approximans), tūī (Prosthemadera novaeseelandiae), and welcome swallow (Hirundo neoxena). Fixed-effect coefficient estimates (log scale), standard errors (SE), Wald z-statistics and associated p-values are reported. Ground and autumn were the reference levels for vertical stratum and season, respectively. The intercept represents the expected log observation count at these reference levels, with orchard effects evaluated at the reference orchard (fixed-effect models) or zero (random-effect models). Orchard was included as either a fixed effect or a random intercept, depending on the species-specific model. Significant estimates ($p < 0.05$) are marked with an asterisk.

species	term	estimate	SE	z	p	
blackbird						
	(Intercept)	2.4016	0.2136	11.2443	2.5E-29	*
	locationlow branch	-21.251	4940.730	-0.004	1.0E+00	
	locationmedium branch	-1.670	0.348	-4.797	0.000002	*
	locationtop branch	-2.453	0.459	-5.340	0.0000001	*
	locationhuman structure	-2.047	0.394	-5.190	0.0000002	*
	locationoverhead	0.270	0.234	1.158	0.247	
	seasonwinter	0.559	0.228	2.450	0.014	*
	seasonspring	1.042	0.232	4.491	0.000	*
	seasonsummer	0.279	0.235	1.189	0.234	
	locationlow branch:seasonwinter	18.645	4940.730	0.004	0.997	
	locationmedium branch:seasonwinter	-0.508	0.479	-1.060	0.289	
	locationtop branch:seasonwinter	0.424	0.558	0.760	0.447	
	locationhuman structure:seasonwinter	-0.673	0.564	-1.193	0.233	
	locationoverhead:seasonwinter	-0.237	0.315	-0.753	0.451	
	locationlow branch:seasonspring	16.238	4940.730	0.003	0.997	
	locationmedium branch:seasonspring	0.066	0.442	0.150	0.881	
	locationtop branch:seasonspring	0.157	0.565	0.278	0.781	
	locationhuman structure:seasonspring	-0.486	0.530	-0.918	0.358	
	locationoverhead:seasonspring	-0.857	0.329	-2.603	0.009	*
	locationlow branch:seasonsummer	18.940	4940.730	0.004	0.997	
	locationmedium branch:seasonsummer	0.201	0.458	0.439	0.660	
	locationtop branch:seasonsummer	0.228	0.593	0.385	0.700	

species	term	estimate	SE	z	p	
	locationhuman structure:seasonsummer	0.525	0.496	1.058	0.290	
	locationoverhead:seasonsummer	-0.789	0.337	-2.343	0.019	*
chaffinch						
	(Intercept)	0.368	0.259	1.422	0.155	
	locationlow branch	-1.295	0.355	-3.643	0.0003	*
	locationmedium branch	-0.514	0.286	-1.799	0.072	
	locationtop branch	-0.131	0.263	-0.497	0.619	
	locationhuman structure	-0.769	0.305	-2.521	0.012	*
	locationoverhead	0.634	0.234	2.707	0.007	*
	seasonwinter	0.304	0.231	1.317	0.188	
	seasonspring	0.512	0.240	2.129	0.033	*
	seasonsummer	0.184	0.241	0.762	0.446	
New Zealand fantail						
	(Intercept)	-0.126	0.325	-0.387	0.699	
	locationlow branch	0.232	0.372	0.625	0.532	
	locationmedium branch	0.396	0.362	1.094	0.274	
	locationtop branch	0.337	0.366	0.922	0.357	
	locationhuman structure	-0.634	0.459	-1.381	0.167	
	locationoverhead	0.815	0.339	2.401	0.016	*
	seasonwinter	-0.429	0.269	-1.594	0.111	
	seasonspring	-0.560	0.295	-1.897	0.058	
	seasonsummer	-0.497	0.272	-1.823	0.068	
goldfinch						
	(Intercept)	0.026	0.439	0.059	0.953	

species	term	estimate	SE	z	p	
	locationlow branch	-2.128	0.424	-5.024	5.06E-07	*
	locationmedium branch	-1.572	0.363	-4.331	1.48E-05	*
	locationtop branch	-0.653	0.300	-2.180	0.029	*
	locationhuman structure	-1.156	0.323	-3.576	0.000	*
	locationoverhead	0.519	0.260	1.992	0.046	*
	seasonwinter	0.653	0.293	2.230	0.026	*
	seasonspring	0.877	0.303	2.897	0.004	*
	seasonsummer	1.288	0.279	4.619	3.9E-06	*
greenfinch						
	(Intercept)	-0.821	0.456	-1.800	0.072	
	locationlow branch	-1.905	0.585	-3.257	0.001	*
	locationmedium branch	-0.492	0.390	-1.263	0.207	
	locationtop branch	0.555	0.324	1.710	0.087	
	locationhuman structure	-0.346	0.365	-0.947	0.344	
	locationoverhead	1.297	0.299	4.338	0.00001	*
	seasonwinter	0.444	0.320	1.386	0.166	
	seasonspring	1.277	0.321	3.981	0.0001	*
	seasonsummer	1.099	0.298	3.690	0.0002	*
house sparrow						
	(Intercept)	2.12	0.34	6.31	2.86E-10	*
	locationlow branch	-3.01	1.07	-2.81	0.005	*
	locationmedium branch	-1.28	0.59	-2.17	0.030	*
	locationtop branch	-0.91	0.52	-1.75	0.080	
	locationhuman structure	-3.01	1.07	-2.81	0.005	*
	locationoverhead	-0.09	0.44	-0.21	0.831	

species	term	estimate	SE	z	p	
	seasonwinter	0.5	0.4	1.23	0.219	
	seasonspring	0.44	0.45	0.98	0.328	
	seasonsummer	-0.56	0.47	-1.17	0.241	
	orchardHB	-0.45	0.22	-2.01	0.045	*
	orchardKC1	-1.52	0.27	-5.58	2.36E-08	*
	orchardKC2	-1.45	0.27	-5.48	4.29E-08	*
	orchardMN1	-2.27	0.34	-6.78	1.19E-11	*
	orchardMN2	-1.68	0.28	-5.95	2.62E-09	*
	locationlow branch:seasonwinter	-0.5	1.51	-0.33	0.742	
	locationmedium branch:seasonwinter	-0.74	0.85	-0.87	0.384	
	locationtop branch:seasonwinter	-0.03	0.68	-0.04	0.968	
	locationhuman structure:seasonwinter	2.36	1.14	2.06	0.039	*
	locationoverhead:seasonwinter	-0.06	0.58	-0.1	0.919	
	locationlow branch:seasonspring	0.16	1.52	0.1	0.918	
	locationmedium branch:seasonspring	0.4	0.8	0.5	0.617	
	locationtop branch:seasonspring	0.5	0.74	0.67	0.503	
	locationhuman structure:seasonspring	1.51	1.25	1.21	0.225	
	locationoverhead:seasonspring	0.07	0.64	0.11	0.912	
	locationlow branch:seasonsummer	0.56	1.53	0.36	0.716	
	locationmedium branch:seasonsummer	1.49	0.77	1.93	0.054	
	locationtop branch:seasonsummer	1.71	0.7	2.44	0.015	*
	locationhuman structure:seasonsummer	3.2	1.18	2.71	0.007	*
	locationoverhead:seasonsummer	1	0.64	1.55	0.121	
pūkeko						
	(Intercept)	1.677	0.798	2.102	0.036	*
	locationlow branch	-4.789	0.734	-6.527	6.7E-11	*

species	term	estimate	SE	z	p	
	locationmedium branch	-4.767	0.734	-6.497	8.2E-11	*
	locationtop branch	-2.604	0.303	-8.599	8.0E-18	*
	locationhuman structure	-3.530	0.424	-8.316	9.1E-17	*
	locationoverhead	-3.856	0.488	-7.909	2.6E-15	*
	seasonwinter	0.020	0.295	0.068	0.946	
	seasonspring	-0.504	0.351	-1.434	0.151	
	seasonsummer	-0.629	0.320	-1.965	0.049	*
silvereye						
	(Intercept)	0.029	0.386	0.076	0.940	
	locationlow branch	-2.672	1.069	-2.499	0.012	*
	locationmedium branch	1.124	0.410	2.742	0.006	*
	locationtop branch	1.431	0.400	3.579	0.0003	*
	locationhuman structure	-0.187	0.475	-0.393	0.694	
	locationoverhead	1.385	0.398	3.483	0.000	*
	seasonwinter	1.365	0.394	3.465	0.001	*
	seasonspring	-19.817	5549.282	-0.004	0.997	
	seasonsummer	-2.672	1.069	-2.499	0.012	*
	orchardHB	1.467	0.262	5.592	2.24E-08	*
	orchardKC1	0.696	0.276	2.520	0.012	*
	orchardKC2	0.644	0.274	2.354	0.019	*
	orchardMN1	0.703	0.282	2.492	0.013	*
	orchardMN2	0.906	0.271	3.342	0.001	*
	locationlow branch:seasonwinter	1.220	1.144	1.066	0.286	
	locationmedium branch:seasonwinter	-2.171	0.556	-3.903	9.51E-05	*
	locationtop branch:seasonwinter	-1.290	0.513	-2.515	0.012	*
	locationhuman structure:seasonwinter	-1.206	0.621	-1.942	0.052	

species	term	estimate	SE	z	p	
	locationoverhead:seasonwinter	-0.709	0.506	-1.402	0.161	
	locationlow branch:seasonspring	19.929	5549.282	0.004	0.997	
	locationmedium branch:seasonspring	18.562	5549.282	0.003	0.997	
	locationtop branch:seasonspring	17.952	5549.282	0.003	0.997	
	locationhuman structure:seasonspring	18.525	5549.282	0.003	0.997	
	locationoverhead:seasonspring	17.979	5549.282	0.003	0.997	
	locationlow branch:seasonsummer	3.822	1.599	2.390	0.017	*
	locationmedium branch:seasonsummer	1.552	1.150	1.350	0.177	
	locationtop branch:seasonsummer	1.242	1.146	1.084	0.278	
	locationhuman structure:seasonsummer	0.891	1.345	0.662	0.508	
	locationoverhead:seasonsummer	1.391	1.140	1.220	0.223	
song thrush						
	(Intercept)	1.380	0.380	3.631	0.0003	*
	locationlow branch	-20.223	7337.719	-0.003	0.998	
	locationmedium branch	-1.740	0.813	-2.139	0.032	*
	locationtop branch	-0.571	0.571	-1.000	0.317	
	locationhuman structure	-0.711	0.574	-1.239	0.215	
	locationoverhead	0.425	0.469	0.906	0.365	
	seasonwinter	0.801	0.440	1.819	0.069	
	seasonspring	1.819	0.431	4.222	2.42E-05	*
	seasonsummer	1.563	0.421	3.716	0.000	*
	orchardHB	-1.158	0.250	-4.633	3.60E-06	*
	orchardKC1	-0.880	0.241	-3.647	0.000	*
	orchardKC2	-0.885	0.240	-3.696	0.000	*
	orchardMN1	-1.224	0.254	-4.820	1.44E-06	*
	orchardMN2	-0.924	0.240	-3.847	0.000	*

species	term	estimate	SE	z	p
	locationlow branch:seasonwinter	17.649	7337.719	0.002	0.998
	locationmedium branch:seasonwinter	0.119	0.983	0.121	0.903
	locationtop branch:seasonwinter	0.342	0.688	0.498	0.619
	locationhuman structure:seasonwinter	-0.205	0.723	-0.283	0.777
	locationoverhead:seasonwinter	-0.010	0.587	-0.016	0.987
	locationlow branch:seasonspring	17.799	7337.719	0.002	0.998
	locationmedium branch:seasonspring	-0.452	0.977	-0.463	0.644
	locationtop branch:seasonspring	-0.604	0.701	-0.861	0.389
	locationhuman structure:seasonspring	-0.673	0.717	-0.938	0.348
	locationoverhead:seasonspring	-1.004	0.595	-1.687	0.092
	locationlow branch:seasonsummer	17.865	7337.719	0.002	0.998
	locationmedium branch:seasonsummer	0.045	0.926	0.048	0.962
	locationtop branch:seasonsummer	-0.611	0.690	-0.886	0.376
	locationhuman structure:seasonsummer	-0.467	0.689	-0.678	0.498
	locationoverhead:seasonsummer	-1.148	0.587	-1.954	0.051
swamp harrier					
	(Intercept)	-16.448	1763.016	-0.009	0.993
	locationlow branch	-7.512	75430.736	0.000	1.000
	locationmedium branch	-6.260	40363.538	0.000	1.000
	locationtop branch	-6.269	40548.005	0.000	1.000
	locationhuman structure	-3.637	11005.187	0.000	1.000
	locationoverhead	18.446	1763.016	0.010	0.992
	seasonwinter	0.005	2490.316	0.000	1.000
	seasonspring	1.444	2013.234	0.001	0.999
	seasonsummer	14.950	1763.016	0.008	0.993
	orchardHB	0.201	0.286	0.703	0.482

species	term	estimate	SE	z	p	
	orchardKC1	-0.375	0.325	-1.151	0.250	
	orchardKC2	0.201	0.286	0.703	0.482	
	orchardMN1	-2.572	0.742	-3.467	0.001	*
	orchardMN2	-1.319	0.440	-3.001	0.003	*
	locationlow branch:seasonwinter	-0.358	117416.419	0.000	1.000	
	locationmedium branch:seasonwinter	-2.347	136197.417	0.000	1.000	
	locationtop branch:seasonwinter	-2.356	137397.232	0.000	1.000	
	locationhuman structure:seasonwinter	19.680	11144.846	0.002	0.999	
	locationoverhead:seasonwinter	0.212	2490.316	0.000	1.000	
	locationlow branch:seasonspring	-0.383	90695.811	0.000	1.000	
	locationmedium branch:seasonspring	-1.917	70647.613	0.000	1.000	
	locationtop branch:seasonspring	-1.923	71127.842	0.000	1.000	
	locationhuman structure:seasonspring	17.396	11048.033	0.002	0.999	
	locationoverhead:seasonspring	-1.854	2013.234	-0.001	0.999	
	locationlow branch:seasonsummer	-4.591	75431.932	0.000	1.000	
	locationmedium branch:seasonsummer	6.260	40363.538	0.000	1.000	
	locationtop branch:seasonsummer	6.269	40548.005	0.000	1.000	
	locationhuman structure:seasonsummer	-13.939	12809.203	-0.001	0.999	
	locationoverhead:seasonsummer	-15.807	1763.016	-0.009	0.993	
tūī						
	(Intercept)	-3.718	1.293	-2.875	0.004	*
	locationlow branch	-0.693	1.225	-0.566	0.571	
	locationmedium branch	2.015	0.753	2.677	0.007	*
	locationtop branch	2.603	0.733	3.552	0.000	*
	locationhuman structure	-14.216	864.020	-0.016	0.987	
	locationoverhead	2.140	0.748	2.863	0.004	*

species	term	estimate	SE	z	p	
	seasonwinter	-1.504	0.451	-3.333	0.001	*
	seasonspring	-2.190	0.609	-3.597	0.0003	*
	seasonsummer	-0.038	0.275	-0.137	0.891	
welcome swallow						
	(Intercept)	-2.788	0.855	-3.260	0.001	*
	locationlow branch	-20.352	18439.806	-0.001	0.999	
	locationmedium branch	-20.352	18439.806	-0.001	0.999	
	locationtop branch	0.344	0.943	0.365	0.715	
	locationhuman structure	0.717	0.896	0.800	0.424	
	locationoverhead	3.623	0.752	4.820	1.44E-06	*
	seasonwinter	-0.959	0.535	-1.791	0.073	
	seasonspring	0.335	0.488	0.687	0.492	
	seasonsummer	0.625	0.425	1.472	0.141	

Table S 15. Estimated marginal mean (EMM) pairwise contrasts from a generalised linear mixed model (GLMM) for vertical strata count across multiple species: blackbird (Turdus merula), chaffinch (Fringilla coelebs), goldfinch (Carduelis carduelis), greenfinch (Chloris chloris), house sparrow (Passer domesticus), pūkeko (Porphyrio melanotus melanotus), silvereye (Zosterops lateralis), song thrush (Turdus philomelos), swamp harrier (Circus approximans), tūī (Prosthemadera novaeseelandiae), and welcome swallow (Hirundo neoxena). Pairwise contrasts, ratios, standard errors, Wald z-statistics and associated p-values are reported. Models that did not retain season for inference are signalled by NAs in the season column. Orchard was included as a random intercept. Significant pairwise contrasts ($p < 0.05$) are marked with an asterisk.

species	contrast	season	ratio	SE	z	p.value	
blackbird							
	ground / low branch	autumn	1.695E+09	8.376E+12	0.004	1.0E+00	
	ground / medium branch	autumn	5.310	1.848	4.797	2.38E-05	*
	ground / top branch	autumn	11.628	5.342	5.340	1.4E-06	*
	ground / human structure	autumn	7.747	3.056	5.190	3.1E-06	*
	ground / overhead	autumn	0.763	0.178	-1.158	8.6E-01	
	low branch / medium branch	autumn	0.000	0.000	-0.004	1	
	low branch / top branch	autumn	0.000	0.000	-0.004	1	
	low branch / human structure	autumn	0.000	0.000	-0.004	1	
	low branch / overhead	autumn	0.000	0.000	-0.004	1	
	medium branch / top branch	autumn	2.190	1.145	1.499	0.665	
	medium branch / human structure	autumn	1.459	0.681	0.809	0.966	
	medium branch / overhead	autumn	0.144	0.049	-5.671	2.13E-07	*
	top branch / human structure	autumn	0.666	0.370	-0.732	0.978	
	top branch / overhead	autumn	0.066	0.030	-5.988	3.18E-08	*
	human structure / overhead	autumn	0.098	0.038	-5.956	3.87E-08	*
	ground / low branch	winter	13.547	5.223	6.759	2.08E-10	*
	ground / medium branch	winter	8.825	2.913	6.596	6.32E-10	*
	ground / top branch	winter	7.609	2.406	6.418	2.08E-09	*
	ground / human structure	winter	15.188	6.126	6.745	2.30E-10	*
	ground / overhead	winter	0.968	0.205	-0.156	1.000	
	low branch / medium branch	winter	0.651	0.300	-0.930	0.939	
	low branch / top branch	winter	0.562	0.253	-1.278	0.797	

species	contrast	season	ratio	SE	z	p.value	
	low branch / human structure	winter	1.121	0.578	0.222	1.000	
	low branch / overhead	winter	0.071	0.028	-6.852	1.09E-10	*
	medium branch / top branch	winter	0.862	0.349	-0.366	0.999	
	medium branch / human structure	winter	1.721	0.819	1.141	0.864	
	medium branch / overhead	winter	0.110	0.036	-6.706	3.00E-10	*
	top branch / human structure	winter	1.996	0.931	1.482	0.676	
	top branch / overhead	winter	0.127	0.040	-6.532	9.76E-10	*
	human structure / overhead	winter	0.064	0.026	-6.834	1.24E-10	*
	ground / low branch	spring	150.433	153.553	4.912	1.34E-05	*
	ground / medium branch	spring	4.969	1.358	5.865	6.72E-08	*
	ground / top branch	spring	9.940	3.270	6.980	4.42E-11	*
	ground / human structure	spring	12.600	4.457	7.162	1.20E-11	*
	ground / overhead	spring	1.798	0.416	2.533	0.115	
	low branch / medium branch	spring	0.033	0.034	-3.299	0.012	*
	low branch / top branch	spring	0.066	0.069	-2.588	0.100	
	low branch / human structure	spring	0.084	0.089	-2.344	0.176	
	low branch / overhead	spring	0.012	0.012	-4.325	0.000	*
	medium branch / top branch	spring	2.000	0.735	1.887	0.410	
	medium branch / human structure	spring	2.536	0.988	2.387	0.161	
	medium branch / overhead	spring	0.362	0.103	-3.583	0.005	*
	top branch / human structure	spring	1.268	0.546	0.551	0.994	
	top branch / overhead	spring	0.181	0.061	-5.062	6.16E-06	*
	human structure / overhead	spring	0.143	0.052	-5.377	1.13E-06	*
	ground / low branch	summer	10.084	3.932	5.926	4.64E-08	*
	ground / medium branch	summer	4.343	1.291	4.939	1.16E-05	*
	ground / top branch	summer	9.254	3.476	5.924	4.70E-08	*
	ground / human structure	summer	4.584	1.381	5.052	6.48E-06	*

species	contrast	season	ratio	SE	z	p.value	
	ground / overhead	summer	1.680	0.408	2.136	0.269	
	low branch / medium branch	summer	0.431	0.187	-1.940	0.378	
	low branch / top branch	summer	0.918	0.451	-0.175	1.000	
	low branch / human structure	summer	0.455	0.199	-1.804	0.463	
	low branch / overhead	summer	0.167	0.066	-4.491	0.000	*
	medium branch / top branch	summer	2.131	0.898	1.796	0.468	
	medium branch / human structure	summer	1.055	0.377	0.151	1.000	
	medium branch / overhead	summer	0.387	0.120	-3.072	0.026	*
	top branch / human structure	summer	0.495	0.210	-1.657	0.561	
	top branch / overhead	summer	0.182	0.070	-4.432	0.000	*
	human structure / overhead	summer	0.367	0.115	-3.205	0.017	*
chaffinch							
	ground / low branch	NA	3.650	1.297	3.643	0.004	*
	ground / medium branch	NA	1.672	0.478	1.799	0.466	
	ground / top branch	NA	1.140	0.300	0.497	0.996	
	ground / human structure	NA	2.158	0.658	2.521	0.118	
	ground / overhead	NA	0.531	0.124	-2.707	0.074	
	low branch / medium branch	NA	0.458	0.173	-2.068	0.304	
	low branch / top branch	NA	0.312	0.113	-3.224	0.016	*
	low branch / human structure	NA	0.591	0.232	-1.339	0.763	
	low branch / overhead	NA	0.145	0.050	-5.663	2.22E-07	*
	medium branch / top branch	NA	0.682	0.199	-1.312	0.778	
	medium branch / human structure	NA	1.291	0.426	0.772	0.972	
	medium branch / overhead	NA	0.317	0.085	-4.309	0.0002	*
	top branch / human structure	NA	1.893	0.589	2.050	0.314	
	top branch / overhead	NA	0.466	0.113	-3.157	0.020	*

species	contrast	season	ratio	SE	z	p.value	
	human structure / overhead	NA	0.246	0.071	-4.880	1.57E-05	*
New Zealand fantail							
	ground / low branch	NA	0.793	0.295	-0.625	0.989	
	ground / medium branch	NA	0.673	0.244	-1.094	0.884	
	ground / top branch	NA	0.714	0.261	-0.922	0.941	
	ground / human structure	NA	1.886	0.866	1.381	0.738	
	ground / overhead	NA	0.443	0.150	-2.401	0.156	
	low branch / medium branch	NA	0.849	0.291	-0.479	0.997	
	low branch / top branch	NA	0.901	0.312	-0.302	1.000	
	low branch / human structure	NA	2.379	1.055	1.954	0.369	
	low branch / overhead	NA	0.559	0.178	-1.831	0.446	
	medium branch / top branch	NA	1.061	0.356	0.178	1.000	
	medium branch / human structure	NA	2.803	1.222	2.365	0.169	
	medium branch / overhead	NA	0.658	0.202	-1.365	0.748	
	top branch / human structure	NA	2.641	1.158	2.216	0.230	
	top branch / overhead	NA	0.620	0.192	-1.540	0.638	
	human structure / overhead	NA	0.235	0.098	-3.478	0.007	*
goldfinch							
	ground / low branch	NA	8.401	3.559	5.024	7.5E-06	*
	ground / medium branch	NA	4.816	1.748	4.331	0.0002	*
	ground / top branch	NA	1.922	0.576	2.180	0.247	
	ground / human structure	NA	3.178	1.028	3.576	0.005	*
	ground / overhead	NA	0.595	0.155	-1.992	0.347	
	low branch / medium branch	NA	0.573	0.277	-1.153	0.859	
	low branch / top branch	NA	0.229	0.100	-3.366	0.010	*

species	contrast	season	ratio	SE	z	p.value	
	low branch / human structure	NA	0.378	0.170	-2.158	0.258	
	low branch / overhead	NA	0.071	0.029	-6.387	2.5E-09	*
	medium branch / top branch	NA	0.399	0.151	-2.427	0.147	
	medium branch / human structure	NA	0.660	0.261	-1.051	0.901	
	medium branch / overhead	NA	0.124	0.043	-5.979	3.4E-08	*
	top branch / human structure	NA	1.654	0.563	1.479	0.678	
	top branch / overhead	NA	0.310	0.087	-4.166	0.000	*
	human structure / overhead	NA	0.187	0.058	-5.422	0.000	*
greenfinch							
	ground / low branch	NA	6.723	3.933	3.257	0.014	*
	ground / medium branch	NA	1.636	0.638	1.263	0.805	
	ground / top branch	NA	0.574	0.186	-1.710	0.525	
	ground / human structure	NA	1.413	0.516	0.947	0.934	
	ground / overhead	NA	0.273	0.082	-4.338	0.0002	*
	low branch / medium branch	NA	0.243	0.148	-2.318	0.187	
	low branch / top branch	NA	0.085	0.049	-4.303	0.0002	*
	low branch / human structure	NA	0.210	0.125	-2.614	0.094	
	low branch / overhead	NA	0.041	0.023	-5.720	2E-07	*
	medium branch / top branch	NA	0.351	0.129	-2.844	0.051	
	medium branch / human structure	NA	0.864	0.351	-0.361	0.999	
	medium branch / overhead	NA	0.167	0.058	-5.116	5E-06	*
	top branch / human structure	NA	2.460	0.845	2.621	0.092	
	top branch / overhead	NA	0.476	0.130	-2.715	0.072	
	human structure / overhead	NA	0.193	0.062	-5.125	4E-06	*

species	contrast	season	ratio	SE	z	p.value	
house sparrow							
	ground / low branch	autumn	20.337	21.793	2.811	0.056	
	ground / medium branch	autumn	3.588	2.117	2.165	0.254	
	ground / top branch	autumn	2.477	1.285	1.748	0.500	
	ground / human structure	autumn	20.337	21.793	2.811	0.056	
	ground / overhead	autumn	1.100	0.488	0.214	1.000	
	low branch / medium branch	autumn	0.176	0.202	-1.517	0.654	
	low branch / top branch	autumn	0.122	0.135	-1.900	0.402	
	low branch / human structure	autumn	1.000	1.451	0.000	1	
	low branch / overhead	autumn	0.054	0.058	-2.714	0.073	
	medium branch / top branch	autumn	0.690	0.451	-0.567	0.993	
	medium branch / human structure	autumn	5.667	6.482	1.517	0.654	
	medium branch / overhead	autumn	0.306	0.183	-1.985	0.351	
	top branch / human structure	autumn	8.211	9.097	1.900	0.402	
	top branch / overhead	autumn	0.444	0.233	-1.545	0.635	
	human structure / overhead	autumn	0.054	0.058	-2.714	0.073	
	ground / low branch	winter	33.416	35.370	3.315	0.012	*
	ground / medium branch	winter	7.495	4.610	3.274	0.014	*
	ground / top branch	winter	2.545	1.111	2.140	0.267	
	ground / human structure	winter	1.916	0.770	1.619	0.586	
	ground / overhead	winter	1.167	0.439	0.410	0.999	
	low branch / medium branch	winter	0.224	0.261	-1.282	0.795	
	low branch / top branch	winter	0.076	0.083	-2.374	0.165	
	low branch / human structure	winter	0.057	0.062	-2.665	0.082	
	low branch / overhead	winter	0.035	0.037	-3.157	0.020	*
	medium branch / top branch	winter	0.340	0.222	-1.651	0.564	
	medium branch / human structure	winter	0.256	0.163	-2.140	0.267	

species	contrast	season	ratio	SE	z	p.value	
	medium branch / overhead	winter	0.156	0.096	-3.007	0.032	*
	top branch / human structure	winter	0.753	0.353	-0.605	0.991	
	top branch / overhead	winter	0.458	0.204	-1.752	0.497	
	human structure / overhead	winter	0.609	0.252	-1.197	0.839	
	ground / low branch	spring	17.402	18.750	2.651	0.085	
	ground / medium branch	spring	2.400	1.314	1.599	0.599	
	ground / top branch	spring	1.506	0.800	0.771	0.972	
	ground / human structure	spring	4.478	2.862	2.346	0.176	
	ground / overhead	spring	1.024	0.478	0.051	1.000	
	low branch / medium branch	spring	0.138	0.154	-1.772	0.484	
	low branch / top branch	spring	0.087	0.096	-2.205	0.235	
	low branch / human structure	spring	0.257	0.300	-1.164	0.854	
	low branch / overhead	spring	0.059	0.064	-2.620	0.092	
	medium branch / top branch	spring	0.628	0.380	-0.769	0.973	
	medium branch / human structure	spring	1.866	1.318	0.883	0.951	
	medium branch / overhead	spring	0.427	0.236	-1.537	0.640	
	top branch / human structure	spring	2.973	2.066	1.568	0.620	
	top branch / overhead	spring	0.680	0.361	-0.727	0.979	
	human structure / overhead	spring	0.229	0.148	-2.282	0.201	
	ground / low branch	summer	11.659	12.681	2.258	0.211	
	ground / medium branch	summer	0.808	0.410	-0.420	0.998	
	ground / top branch	summer	0.449	0.211	-1.708	0.527	
	ground / human structure	summer	0.830	0.413	-0.374	0.999	
	ground / overhead	summer	0.406	0.189	-1.936	0.380	
	low branch / medium branch	summer	0.069	0.075	-2.457	0.137	
	low branch / top branch	summer	0.039	0.041	-3.045	0.028	*
	low branch / human structure	summer	0.071	0.077	-2.441	0.142	

species	contrast	season	ratio	SE	z	p.value	
	low branch / overhead	summer	0.035	0.037	-3.144	0.021	*
	medium branch / top branch	summer	0.556	0.255	-1.278	0.797	
	medium branch / human structure	summer	1.028	0.507	0.055	1.000	
	medium branch / overhead	summer	0.502	0.229	-1.512	0.657	
	top branch / human structure	summer	1.849	0.840	1.352	0.756	
	top branch / overhead	summer	0.903	0.373	-0.247	1.000	
	human structure / overhead	summer	0.488	0.220	-1.588	0.607	
pūkeko							
	ground / low branch	NA	120.177	88.182	6.527	1.01E-09	*
	ground / medium branch	NA	117.564	86.256	6.497	1.23E-09	*
	ground / top branch	NA	13.511	4.091	8.599	5.35E-14	*
	ground / human structure	NA	34.115	14.480	8.316	6.64E-14	*
	ground / overhead	NA	47.260	23.040	7.909	1.24E-13	*
	low branch / medium branch	NA	0.978	0.996	-0.022	1.000	
	low branch / top branch	NA	0.112	0.086	-2.845	0.051	
	low branch / human structure	NA	0.284	0.234	-1.529	0.645	
	low branch / overhead	NA	0.393	0.337	-1.088	0.886	
	medium branch / top branch	NA	0.115	0.088	-2.815	0.055	
	medium branch / human structure	NA	0.290	0.239	-1.502	0.663	
	medium branch / overhead	NA	0.402	0.345	-1.062	0.896	
	top branch / human structure	NA	2.525	1.217	1.921	0.389	
	top branch / overhead	NA	3.498	1.884	2.325	0.184	
	human structure / overhead	NA	1.385	0.852	0.530	0.995	

species	contrast	season	ratio	SE	z	p.value	
silvereye							
	ground / low branch	autumn	14.474	15.478	2.499	0.124	
	ground / medium branch	autumn	0.325	0.133	-2.742	0.067	
	ground / top branch	autumn	0.239	0.096	-3.579	0.005	*
	ground / human structure	autumn	1.206	0.573	0.393	0.999	
	ground / overhead	autumn	0.250	0.100	-3.483	0.007	*
	low branch / medium branch	autumn	0.022	0.024	-3.610	0.004	*
	low branch / top branch	autumn	0.017	0.017	-3.916	0.001	*
	low branch / human structure	autumn	0.083	0.090	-2.303	0.193	
	low branch / overhead	autumn	0.017	0.018	-3.874	0.001	*
	medium branch / top branch	autumn	0.736	0.251	-0.899	0.947	
	medium branch / human structure	autumn	3.708	1.607	3.024	0.030	*
	medium branch / overhead	autumn	0.770	0.266	-0.758	0.974	
	top branch / human structure	autumn	5.040	2.137	3.815	0.002	*
	top branch / overhead	autumn	1.046	0.348	0.137	1.000	
	human structure / overhead	autumn	0.208	0.088	-3.718	0.003	*
	ground / low branch	winter	4.275	1.733	3.583	0.005	*
	ground / medium branch	winter	2.851	1.086	2.749	0.066	
	ground / top branch	winter	0.869	0.285	-0.428	0.998	
	ground / human structure	winter	4.026	1.607	3.489	0.006	*
	ground / overhead	winter	0.509	0.160	-2.143	0.265	
	low branch / medium branch	winter	0.667	0.301	-0.898	0.947	
	low branch / top branch	winter	0.203	0.083	-3.906	0.001	*
	low branch / human structure	winter	0.942	0.439	-0.129	1.000	
	low branch / overhead	winter	0.119	0.047	-5.357	1.3E-06	*
	medium branch / top branch	winter	0.305	0.116	-3.128	0.022	*
	medium branch / human structure	winter	1.412	0.628	0.776	0.972	

species	contrast	season	ratio	SE	z	p.value	
	medium branch / overhead	winter	0.178	0.066	-4.658	4.7E-05	*
	top branch / human structure	winter	4.634	1.856	3.828	0.002	*
	top branch / overhead	winter	0.586	0.184	-1.702	0.531	
	human structure / overhead	winter	0.126	0.049	-5.292	1.8E-06	*
	ground / low branch	spring	0.000	0.000	-0.003	1	
	ground / medium branch	spring	0.000	0.000	-0.004	1	
	ground / top branch	spring	0.000	0.000	-0.003	1	
	ground / human structure	spring	0.000	0.000	-0.003	1	
	ground / overhead	spring	0.000	0.000	-0.003	1	
	low branch / medium branch	spring	0.088	0.096	-2.234	0.222	
	low branch / top branch	spring	0.119	0.132	-1.928	0.385	
	low branch / human structure	spring	0.339	0.405	-0.906	0.945	
	low branch / overhead	spring	0.122	0.134	-1.911	0.395	
	medium branch / top branch	spring	1.354	0.748	0.548	0.994	
	medium branch / human structure	spring	3.847	2.762	1.877	0.417	
	medium branch / overhead	spring	1.379	0.762	0.582	0.992	
	top branch / human structure	spring	2.842	2.107	1.409	0.722	
	top branch / overhead	spring	1.019	0.594	0.032	0.999999995	
	human structure / overhead	spring	0.359	0.266	-1.384	0.737	
	ground / low branch	summer	0.317	0.377	-0.967	0.928	
	ground / medium branch	summer	0.069	0.074	-2.486	0.128	
	ground / top branch	summer	0.069	0.074	-2.483	0.129	
	ground / human structure	summer	0.495	0.622	-0.560	0.994	
	ground / overhead	summer	0.062	0.067	-2.597	0.098	
	low branch / medium branch	summer	0.217	0.152	-2.180	0.247	
	low branch / top branch	summer	0.218	0.153	-2.176	0.249	
	low branch / human structure	summer	1.562	1.495	0.466	0.997	

species	contrast	season	ratio	SE	z	p.value	
	low branch / overhead	summer	0.197	0.136	-2.359	0.171	
	medium branch / top branch	summer	1.003	0.482	0.006	1	
	medium branch / human structure	summer	7.184	5.828	2.431	0.146	
	medium branch / overhead	summer	0.904	0.422	-0.215	1.000	
	top branch / human structure	summer	7.162	5.809	2.428	0.147	
	top branch / overhead	summer	0.902	0.420	-0.222	1.000	
	human structure / overhead	summer	0.126	0.101	-2.586	0.101	
song thrush							
	ground / low branch	autumn	6.063E+08	4.449E+12	0.003	1	
	ground / medium branch	autumn	5.697	4.633	2.139	0.267	
	ground / top branch	autumn	1.770	1.011	1.000	0.918	
	ground / human structure	autumn	2.035	1.167	1.239	0.818	
	ground / overhead	autumn	0.654	0.307	-0.906	0.945	
	low branch / medium branch	autumn	0.000	0.000	-0.003	1	
	low branch / top branch	autumn	0.000	0.000	-0.003	1	
	low branch / human structure	autumn	0.000	0.000	-0.003	1	
	low branch / overhead	autumn	0.000	0.000	-0.003	1	
	medium branch / top branch	autumn	0.311	0.267	-1.361	0.751	
	medium branch / human structure	autumn	0.357	0.307	-1.197	0.838	
	medium branch / overhead	autumn	0.115	0.091	-2.722	0.071	
	top branch / human structure	autumn	1.150	0.733	0.219	1.000	
	top branch / overhead	autumn	0.369	0.201	-1.831	0.446	
	human structure / overhead	autumn	0.321	0.176	-2.069	0.304	
	ground / low branch	winter	13.118	10.182	3.316	0.012	*
	ground / medium branch	winter	5.055	2.782	2.945	0.038	*
	ground / top branch	winter	1.257	0.484	0.595	0.991	

species	contrast	season	ratio	SE	z	p.value	
	ground / human structure	winter	2.498	1.094	2.090	0.292	
	ground / overhead	winter	0.660	0.235	-1.169	0.852	
	low branch / medium branch	winter	0.385	0.339	-1.085	0.887	
	low branch / top branch	winter	0.096	0.075	-2.984	0.034	*
	low branch / human structure	winter	0.190	0.155	-2.038	0.321	
	low branch / overhead	winter	0.050	0.039	-3.875	0.001	*
	medium branch / top branch	winter	0.249	0.140	-2.474	0.132	
	medium branch / human structure	winter	0.494	0.297	-1.172	0.850	
	medium branch / overhead	winter	0.131	0.071	-3.758	0.002	*
	top branch / human structure	winter	1.987	0.905	1.507	0.660	
	top branch / overhead	winter	0.525	0.196	-1.727	0.514	
	human structure / overhead	winter	0.264	0.114	-3.093	0.024	*
	ground / low branch	spring	11.289	6.623	4.132	0.001	*
	ground / medium branch	spring	8.954	4.853	4.045	0.001	*
	ground / top branch	spring	3.237	1.315	2.892	0.044	*
	ground / human structure	spring	3.989	1.715	3.218	0.016	*
	ground / overhead	spring	1.785	0.653	1.584	0.609	
	low branch / medium branch	spring	0.793	0.573	-0.321	1.000	
	low branch / top branch	spring	0.287	0.180	-1.994	0.346	
	low branch / human structure	spring	0.353	0.227	-1.621	0.585	
	low branch / overhead	spring	0.158	0.095	-3.069	0.026	*
	medium branch / top branch	spring	0.362	0.212	-1.739	0.506	
	medium branch / human structure	spring	0.445	0.268	-1.344	0.760	
	medium branch / overhead	spring	0.199	0.111	-2.892	0.044	*
	top branch / human structure	spring	1.232	0.596	0.432	0.998	
	top branch / overhead	spring	0.551	0.235	-1.396	0.730	
	human structure / overhead	spring	0.447	0.201	-1.790	0.472	

species	contrast	season	ratio	SE	z	p.value	
	ground / low branch	summer	10.573	5.665	4.401	0.0002	*
	ground / medium branch	summer	5.448	2.412	3.829	0.002	*
	ground / top branch	summer	3.261	1.265	3.046	0.028	*
	ground / human structure	summer	3.247	1.247	3.066	0.026	*
	ground / overhead	summer	2.060	0.728	2.046	0.316	
	low branch / medium branch	summer	0.515	0.318	-1.075	0.891	
	low branch / top branch	summer	0.308	0.178	-2.033	0.323	
	low branch / human structure	summer	0.307	0.177	-2.054	0.312	
	low branch / overhead	summer	0.195	0.108	-2.944	0.038	*
	medium branch / top branch	summer	0.599	0.296	-1.039	0.905	
	medium branch / human structure	summer	0.596	0.292	-1.055	0.899	
	medium branch / overhead	summer	0.378	0.177	-2.083	0.296	
	top branch / human structure	summer	0.996	0.440	-0.010	1	
	top branch / overhead	summer	0.632	0.262	-1.106	0.879	
	human structure / overhead	summer	0.634	0.261	-1.106	0.879	
swamp harrier							
	ground / low branch	autumn	1829.561	1.380E+08	0.000	1	
	ground / medium branch	autumn	523.162	2.112E+07	0.000	1	
	ground / top branch	autumn	527.964	2.141E+07	0.000	1	
	ground / human structure	autumn	37.966	4.178E+05	0.000	1	
	ground / overhead	autumn	0.000	0.000	-0.010	1	
	low branch / medium branch	autumn	0.286	24452.953	0.000	1	
	low branch / top branch	autumn	0.289	24702.569	0.000	1	
	low branch / human structure	autumn	0.021	1581.008	0.000	1	
	low branch / overhead	autumn	0.000	0.000	0.000	1	
	medium branch / top branch	autumn	1.009	57683.538	0.000	1	

species	contrast	season	ratio	SE	z	p.value	
	medium branch / human structure	autumn	0.073	3030.694	0.000	1	
	medium branch / overhead	autumn	0.000	0.000	-0.001	1	
	top branch / human structure	autumn	0.072	3015.952	0.000	1	
	top branch / overhead	autumn	0.000	0.000	-0.001	1	
	human structure / overhead	autumn	0.000	0.000	-0.002	1	
	ground / low branch	winter	2616.408	2.354E+08	0.000	1	
	ground / medium branch	winter	5468.790	7.114E+08	0.000	1	
	ground / top branch	winter	5570.081	7.312E+08	0.000	1	
	ground / human structure	winter	0.000	0.000	-0.009	1	
	ground / overhead	winter	0.000	0.000	-0.011	1	
	low branch / medium branch	winter	2.090	330561.827	0.000	1	
	low branch / top branch	winter	2.129	338786.759	0.000	1	
	low branch / human structure	winter	0.000	0.000	0.000	1	
	low branch / overhead	winter	0.000	0.000	0.000	1	
	medium branch / top branch	winter	1.019	188214.939	0.000	1	
	medium branch / human structure	winter	0.000	0.000	0.000	1	
	medium branch / overhead	winter	0.000	0.000	0.000	1	
	top branch / human structure	winter	0.000	0.000	0.000	1	
	top branch / overhead	winter	0.000	0.000	0.000	1	
	human structure / overhead	winter	0.073	0.044	-4.372	0.000	*
	ground / low branch	spring	2682.850	1.351E+08	0.000	1	
	ground / medium branch	spring	3556.961	2.062E+08	0.000	1	
	ground / top branch	spring	3613.221	2.112E+08	0.000	1	
	ground / human structure	spring	0.000	0.001	-0.014	1	
	ground / overhead	spring	0.000	0.000	-0.017	1	
	low branch / medium branch	spring	1.326	1.018E+05	0.000	1	
	low branch / top branch	spring	1.347	1.039E+05	0.000	1	

species	contrast	season	ratio	SE	z	p.value
	low branch / human structure	spring	0.000	0.000	0.000	1
	low branch / overhead	spring	0.000	0.000	0.000	1
	medium branch / top branch	spring	1.016	8.361E+04	0.000	1
	medium branch / human structure	spring	0.000	0.000	0.000	1
	medium branch / overhead	spring	0.000	0.000	0.000	1
	top branch / human structure	spring	0.000	0.000	0.000	1
	top branch / overhead	spring	0.000	0.000	0.000	1
	human structure / overhead	spring	0.059	0.061	-2.753	0.065
	ground / low branch	summer	1.804E+05	7.662E+07	0.028	0.999999997
	ground / medium branch	summer	1.000	1.414	0.000	1
	ground / top branch	summer	1.000	1.414	0.000	1
	ground / human structure	summer	4.296E+07	2.816E+11	0.003	1
	ground / overhead	summer	0.071	0.074	-2.550	0.110
	low branch / medium branch	summer	0.000	0.002	-0.028	0.999999997
	low branch / top branch	summer	0.000	0.002	-0.028	0.999999997
	low branch / human structure	summer	238.159	1.564E+06	0.001	1
	low branch / overhead	summer	0.000	0.000	-0.035	1.000
	medium branch / top branch	summer	1.000	1.414	0.000	1
	medium branch / human structure	summer	4.296E+07	2.816E+11	0.003	1
	medium branch / overhead	summer	0.071	0.074	-2.550	0.110
	top branch / human structure	summer	4.296E+07	2.816E+11	0.003	1
	top branch / overhead	summer	0.071	0.074	-2.550	0.110
	human structure / overhead	summer	0.000	0.000	-0.003	1

species	contrast	season	ratio	SE	z	p.value	
tūī							
	ground / low branch	NA	2.000	2.449	0.566	0.993	
	ground / medium branch	NA	0.133	0.100	-2.677	0.080	
	ground / top branch	NA	0.074	0.054	-3.552	0.005	*
	ground / human structure	NA	1.493E+06	1.290E+09	0.016	1	
	ground / overhead	NA	0.118	0.088	-2.863	0.048	*
	low branch / medium branch	NA	0.067	0.069	-2.622	0.092	
	low branch / top branch	NA	0.037	0.038	-3.236	0.015	*
	low branch / human structure	NA	7.465E+05	6.450E+08	0.016	1	
	low branch / overhead	NA	0.059	0.061	-2.753	0.065	
	medium branch / top branch	NA	0.556	0.179	-1.825	0.449	
	medium branch / human structure	NA	1.120E+07	9.675E+09	0.019	1	
	medium branch / overhead	NA	0.882	0.313	-0.353	0.999	
	top branch / human structure	NA	2.016E+07	1.742E+10	0.019	1	
	top branch / overhead	NA	1.588	0.492	1.494	0.668	
	human structure / overhead	NA	0.000	0.000	-0.019	1	
welcome swallow							
	ground / low branch	NA	6.900E+08	1.3E+13	1.1E-03	1	
	ground / medium branch	NA	6.900E+08	1.3E+13	1.1E-03	1	
	ground / top branch	NA	0.708	6.7E-01	-3.7E-01	0.999	
	ground / human structure	NA	0.488	4.4E-01	-8.0E-01	0.968	
	ground / overhead	NA	0.027	2.0E-02	-4.8E+00	2.1E-05	*
	low branch / medium branch	NA	1	2.6E+04	-1.4E-19	1	
	low branch / top branch	NA	1.0E-09	1.9E-05	-1.1E-03	1	
	low branch / human structure	NA	7.1E-10	1.3E-05	-1.1E-03	1	
	low branch / overhead	NA	3.9E-11	7.1E-07	-1.3E-03	1	

species	contrast	season	ratio	SE	z	p.value	
	medium branch / top branch	NA	1.0E-09	1.9E-05	-1.1E-03	1	
	medium branch / human structure	NA	7.1E-10	1.3E-05	-1.1E-03	1	
	medium branch / overhead	NA	3.9E-11	7.1E-07	-1.3E-03	1	
	top branch / human structure	NA	0.689	5.5E-01	-4.7E-01	0.997	
	top branch / overhead	NA	0.038	2.4E-02	-5.2E+00	3.5E-06	*
	human structure / overhead	NA	0.055	3.1E-02	-5.2E+00	3.1E-06	*

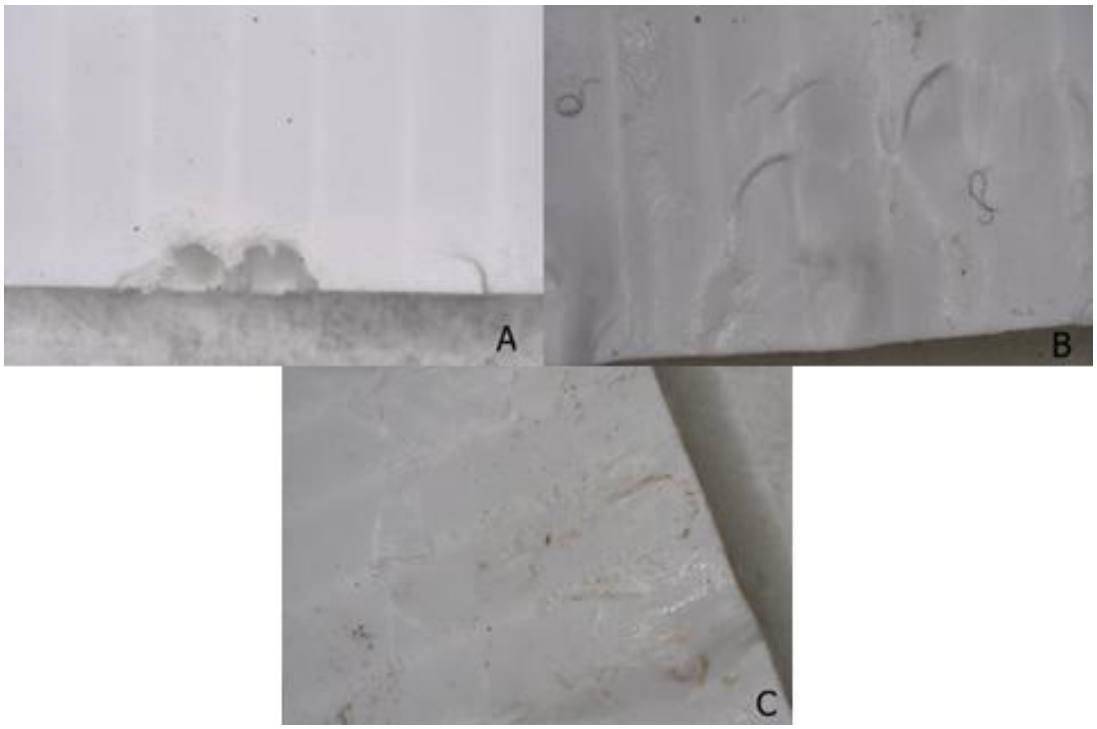


Figure S 7. Examples of rodent predation marks on chew cards (A = orchard MN2, autumn; B = orchard MN1, spring; C = orchard MN1, winter, also with possum predation marks)



Figure S 8. Examples of brushtail possum (Trichosurus vulpecula) predation marks on chew cards (A = orchard TR, autumn; B = orchard MN1, winter; C = orchard MN1, summer)

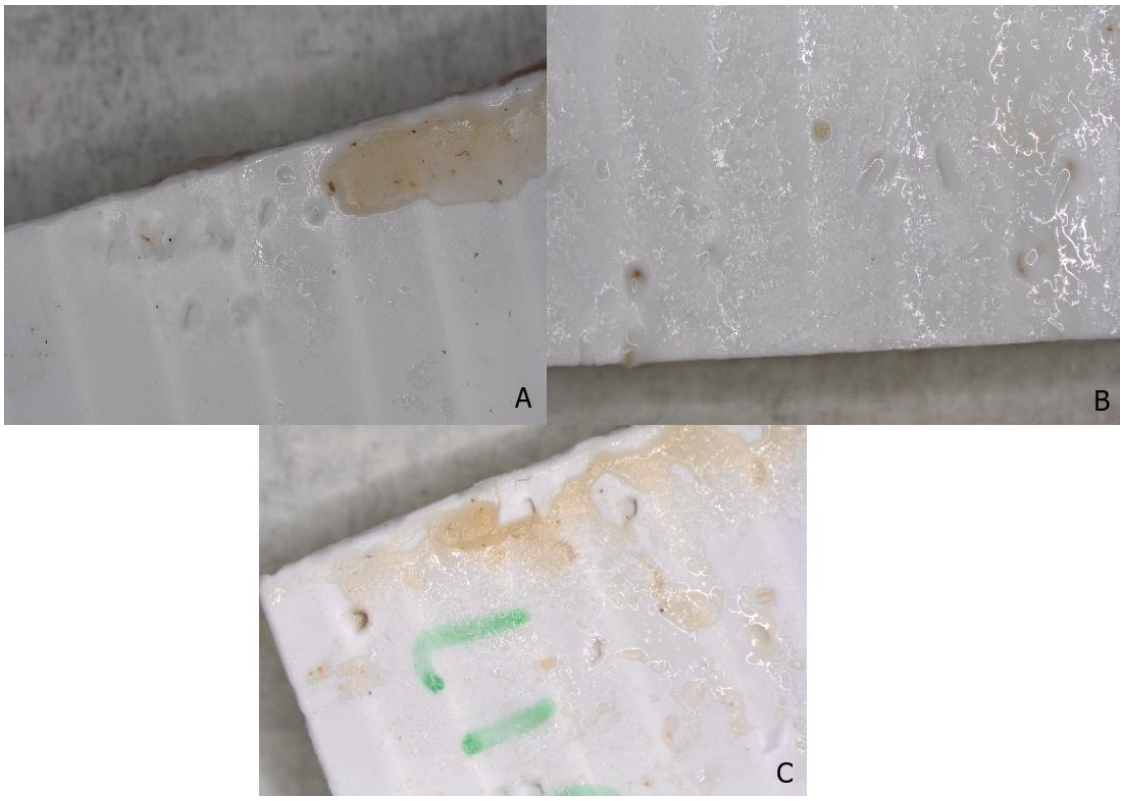


Figure S 9. Examples of hedgehog (Erinaceus europaeus) predation marks on chew cards (A = orchard TR, autumn; B = orchard MN2, spring; C = orchard KC1, summer)

Table S 16. Seasonal variation on predation marks in chew cards deployed in six different orchards from autumn 2024 to summer 2025. Predation intensity was scored in four categories: no predation marks (0); less than 25% of chew cards marked (1), or most chew cards marked but with very few predation marks; up to 50% of chew cards marked (2); and more than 50% of chew cards marked with at least one having parts of the chew cards removed due to predation (3). Predation marks were identified to the level of brushtail possums (Trichosurus vulpecula), rodents (including rats and mice) and hedgehogs (Erinaceus europaeus) with the help of a chew card guide (Sweetapple and Nugent 2024). The presence of cats (Felis catus domesticus) and rabbits (Oryctolagus cuniculus) was detected through camera traps and observations during the surveys conducted in the orchards. The absence of observations of either species in a particular orchard and season is marked as not detected (ND).

		predation marks			**presence detected**	
orchard	**season**	**possum**	**rodent**	**hedgehog**	**cat**	**rabbit**
Manawatū 1						
	autumn	low	-	-	ND	ND
	winter	low	low	-	ND	ND
	spring	medium	medium	-	ND	ND
	summer	medium	-	low	ND	ND
Manawatū 2						
	autumn	-	medium	-	Y	Y
	winter	low	-	-	Y	Y
	spring	-	-	low	ND	Y
	summer	low	-	-	ND	Y
Kāpiti Coast 1						
	autumn	-	medium	-	Y	ND
	winter	-	-	-	Y	ND
	spring	-	-	low	Y	Y
	summer	-	-	low	Y	Y
Kāpiti Coast 2						
	autumn	-	low	-	ND	ND
	winter	-	-	low	ND	ND
	spring	-	-	-	ND	ND
	summer	-	-	-	Y	Y
Hawke's Bay						
	autumn	low	-	low	ND	Y
	winter	-	-	low	Y	Y
	spring	N/A	N/A	N/A	ND	ND
	summer	-	-	low	Y	Y
Tasman Region						
	autumn	-	-	-	ND	Y
	winter	-	-	-	Y	Y
	summer	-	-	low	Y	Y

Supplementary Materials (Chapter Four)

Table S 17. Model diagnostics for generalised linear mixed models (GLMMs) used to examine variation in the dataset of different behaviours observed across seasons and orchards surveyed. Candidate models included combinations of relevant fixed and random effects. Columns report convergence, positive-definite Hessian (pdHess), over-dispersion, zero-inflation, uniformity of residuals, and outlier influence. ✓indicates model assumption criteria met; X indicates violations. Bold values highlight models retained for inference based on model diagnostics and Akaike's Information Criteria (AIC) selection. Models were constructed for the following species: black-backed gull (Larus dominicanus), New Zealand fantail (Rhipidura fuliginosa), grey warbler (Gerygone igata), New Zealand sacred kingfisher (Todiramphus sanctus), paradise shelduck (Tadorna variegata), pūkeko (Porphyrio melanotus melanotus), silvereye (Zosterops lateralis), swamp harrier (Circus approximans), tūī (Prosthemadera novaeseelandiae), and welcome swallow (Hirundo neoxena).

Species	Model	Convergence	pdHess	dispersion	zero-inflation	uniformity	outliers
black-backed gull							
1	Behaviour x Season	X	X	0	0.238	0.921	1
2	Behaviour + Season	X	X	0.004	1	0.577	1
3	**Behaviour Only**	✔	✔	**0.01**	**1**	**0.710**	**1**
4	Season Only	✔	✔	0.858	1	0.992	1
5	Null Model	✔	✔	0.86	1.000	0.992	1
New Zealand fantail							
1	Behaviour x Season	✔	✔	0.126	0.948	0.516	1.00E+00
2	Behaviour + Season	✔	✔	0.902	0.4	0.992	0.240
3	**Behaviour Only**	✔	✔	**0.878**	**0.394**	**0.888**	**0.260**
4	Season Only	✔	✔	0.782	0.608	0.559	1.00E+00
5	Null Model	✔	✔	0.78	0.608	0.559	1

Species	Model	Convergence	pdHess	dispersion	zero-inflation	uniformity	outliers
grey warbler							
1	Behaviour x Season	✔	X	0.00	0.118	0.220	1
2	**Behaviour + Season**	✔	✔	**0.392**	**1**	**0.282**	**1**
3	Behaviour Only	✔	X	0.394	1	0.282	1
4	Season Only	✔	✔	0.954	1	0.432	1
5	Null Model	✔	✔	0.954	1	0.432	1
kingfisher							
1	Behaviour x Season	✔	X	0	0.378	0.425	1
2	**Behaviour + Season**	✔	✔	**0.708**	**1**	**0.991**	**1**
3	Behaviour Only	✔	X	0.708	1	0.991	1
4	Season Only	✔	✔	0.774	0.93	0.909	1
5	Null Model	✔	✔	0.774	0.93	0.909	1
paradise shelduck							
1	Behaviour x Season	✔	X	0.15	0.636	0.994	1
2	Behaviour + Season	✔	X	0.81	0.798	0.778	1
3	Behaviour Only	X	X	0.788	0.778	0.836	1
4	Season Only	✔	✔	0.95	1	0.751	1
5	**Null Model**	✔	✔	**0.95**	**1**	**0.751**	**1**
pūkeko							
1	Behaviour x Season	X	✔	0.97	0.954	0.278	1.00E+00
2	Behaviour + Season	✔	✔	0.674	0.980	0.546	1.000
3	**Behaviour Only**	✔	✔	**0.97**	**0.912**	**0.800**	**1.000**
4	Season Only	✔	✔	0.314	0.746	0.766	1.00E+00
5	Null Model	✔	✔	0.314	0.746	0.766	1.00E+00

Species	Model	Convergence	pdHess	dispersion	zero-inflation	uniformity	outliers
silvereye							
1	**Behaviour x Season**	✔	✔	**0.744**	**0.45**	**0.907**	**1.000**
2	Behaviour + Season	✔	✔	0.246	0.156	0.923	0.420
3	Behaviour Only	✔	✔	0.238	0.154	0.858	0.460
4	Season Only	✔	✔	0.852	0.684	0.738	1.00E+00
5	Null Model	✔	✔	0.852	0.684	0.738	1.00E+00
swamp harrier							
1	**Behaviour x Season**	✔	✔	**0**	**0.396**	**0.126**	**1.000**
2	Behaviour + Season	X	✔	0	0.814	0.776	1.000
3	Behaviour Only	✔	X	0.004	0.772	0.732	1.000
4	Season Only	✔	✔	0.572	0.834	0.346	1.00E+00
5	Null Model	✔	✔	0.572	0.834	0.346	1.00E+00
tūī							
1	Behaviour x Season	✔	X	0.004	0.482	0.194	1
2	**Behaviour + Season**	✔	✔	**0.878**	**0.072**	**0.780**	**1**
3	Behaviour Only	✔	X	0.86	0.058	0.774	1
4	Season Only	✔	✔	0.596	0.368	0.167	1
5	Null Model	✔	✔	0.596	0.368	0.167	1
welcome swallow							
1	Behaviour x Season	✔	✔	0.662	0.56	0.983	1
2	Behaviour + Season	✔	X	0.828	0.698	0.718	1
3	**Behaviour Only**	✔	✔	**0.92**	**0.752**	**0.885**	**1**
4	Season Only	✔	✔	0.822	1	0.846	1
5	Null Model	✔	✔	0.822	1	0.846	1

Table S 18. Generalised linear mixed model (GLMM) results for silvereye (Zosterops lateralis) behavioural counts across orchards and seasons. Fixed-effect coefficient estimates (log scale), standard errors (SE), Wald z-statistics and associated p-values are reported. Foraging and autumn were the reference levels for behaviour and season, respectively. The intercept represents the expected log observation count for foraging behaviour in autumn, with the orchard random effect set to zero. Behaviour and season interaction terms indicate how seasonal effects modified the relative frequency of each behaviour. Orchard was included as a random intercept. Significant estimates ($p < 0.05$) are marked with an asterisk.

term	estimate	SE	z	p	
(Intercept)	-1.115	0.105	-10.66	1.57E-26	*
behaviourflying	0.06	0.147	0.411	0.681	
behaviourhopping	-1.465	0.205	-7.15	8.7E-13	*
behaviourperching	-0.935	0.178	-5.239	0.0000002	*
behaviourpreening	-3.343	0.428	-7.813	5.57E-15	*
behaviourvocalising	-1.557	0.21	-7.414	1.23E-13	*
behavioursocial	-3.04	0.376	-8.08	6.46E-16	*
behaviourterritorial	-2.809	0.342	-8.224	1.97E-16	*
behaviourinteracting with observer	-28.19	101887.929	0	1.000	
seasonwinter	0.033	0.137	0.238	0.812	
seasonspring	-0.106	0.247	-0.431	0.666	
seasonsummer	-0.814	0.273	-2.981	0.003	*
behaviourflying:seasonwinter	0.009	0.193	0.046	0.964	
behaviourhopping:seasonwinter	-0.611	0.282	-2.167	0.030	*
behaviourperching:seasonwinter	-0.262	0.234	-1.119	0.263	
behaviourpreening:seasonwinter	0.858	0.483	1.777	0.076	
behaviourvocalising:seasonwinter	-0.342	0.28	-1.223	0.221	
behavioursocial:seasonwinter	1.054	0.421	2.507	0.012	*
behaviourterritorial:seasonwinter	0.252	0.412	0.612	0.541	
behaviourinteracting with observer:seasonwinter	23.101	101887.929	0.0002	1.000	
behaviourflying:seasonspring	0.105	0.34	0.308	0.758	
behaviourhopping:seasonspring	-0.108	0.548	-0.197	0.844	
behaviourperching:seasonspring	0.411	0.402	1.021	0.307	

term	estimate	SE	z	p	
behaviourpreening:seasonspring	-18.07	9139.033	-0.002	0.998	
behaviourvocalising:seasonspring	0.47	0.477	0.984	0.325	
behavioursocial:seasonspring	-0.137	1.096	-0.125	0.901	
behaviourterritorial:seasonspring	-0.368	1.084	-0.34	0.734	
behaviourinteracting with observer:seasonspring	0.142	271958.94	0.000001	1.000	
behaviourflying:seasonsummer	1.121	0.33	3.400	0.001	*
behaviourhopping:seasonsummer	0.836	0.471	1.777	0.076	
behaviourperching:seasonsummer	0.591	0.429	1.379	0.168	
behaviourpreening:seasonsummer	1.905	0.708	2.689	0.007	*
behaviourvocalising:seasonsummer	1.504	0.418	3.595	0.000	*
behavioursocial:seasonsummer	1.6	0.678	2.359	0.018	*
behaviourterritorial:seasonsummer	-17.554	6431.248	-0.003	0.998	
behaviourinteracting with observer:seasonsummer	4.03	110575.735	0.00004	1.000	

Table S 19. Pairwise contrasts calculated from estimated marginal means (EMMs) for silvereyes (Zosterops lateralis). EMMs were retrieved from a generalised linear mixed model (GLMM) accounting for the full interactions of behaviour and season, with orchard as a random effect. Behaviour categories were described as flying; foraging = behaviours prominent to different feeding habits, such as hawking and gleaning for insectivorous birds, diving for carnivorous birds, and pecking and rummaging for omnivores; perching or roosting, hopping = on the ground or between branches); vocalising; territorial behaviours = chasing away conspecifics; social behaviours = couple preening, feeding mates or fledglings, gathering nest materials; preening = as an individual action; and interacting with the observer. Pairwise contrasts were calculated for all pairings of behaviours and for all seasons, from autumn 2024 to summer 2025. Significant contrasts (p < 0.05) are marked with an asterisk.

contrast	season	ratio	SE	df	z.ratio	p value	p < 0.05
foraging / flying	autumn	0.941	0.14	1	-0.411	1.000	
foraging / hopping	autumn	4.327	0.89	1	7.150	3.138E-11	*
foraging / perching	autumn	2.547	0.45	1	5.239	5.751E-06	*
foraging / pruning	autumn	28.316	12.12	1	7.813	2.519E-13	*
foraging / vocalising	autumn	4.744	1.00	1	7.414	4.479E-12	*
foraging / social	autumn	20.909	7.87	1	8.080	1.370E-13	*
foraging / territorial	autumn	16.588	5.67	1	8.224	1.102E-13	*
foraging / interacting with observer	autumn	1.750E+12	1.783E+17	1	0.000	1	
flying / hopping	autumn	4.597	0.94	1	7.465	3.050E-12	*
flying / perching	autumn	2.705	0.48	1	5.611	7.189E-07	*
flying / pruning	autumn	30.082	12.87	1	7.958	1.863E-13	*
flying / vocalising	autumn	5.040	1.06	1	7.714	4.931E-13	*
flying / social	autumn	22.213	8.35	1	8.250	1.076E-13	*
flying / territorial	autumn	17.622	6.01	1	8.415	9.137E-14	*
flying / interacting with observer	autumn	1.859E+12	1.894E+17	1	0.000	1	
hopping / perching	autumn	0.589	0.13	1	-2.328	0.325	
hopping / pruning	autumn	6.544	2.95	1	4.167	0.001	*
hopping / vocalising	autumn	1.096	0.28	1	0.363	1.000	
hopping / social	autumn	4.832	1.94	1	3.918	0.003	*
hopping / territorial	autumn	3.833	1.42	1	3.635	0.008	*
hopping / interacting with observer	autumn	4.043E+11	4.119E+16	1	0.000	1	
perching / pruning	autumn	11.119	4.89	1	5.482	1.506E-06	*

contrast	season	ratio	SE	df	z.ratio	p value	p < 0.05
perching / vocalising	autumn	1.863	0.43	1	2.674	0.157	
perching / social	autumn	8.210	3.19	1	5.413	2.210E-06	*
perching / territorial	autumn	6.514	2.31	1	5.274	4.739E-06	*
perching / interacting with observer	autumn	6.870E+11	7.000E+16	1	0.000	1	
pruning / vocalising	autumn	0.168	0.08	1	-3.942	0.003	*
pruning / social	autumn	0.738	0.41	1	-0.551	1.000	
pruning / territorial	autumn	0.586	0.31	1	-1.014	0.985	
pruning / interacting with observer	autumn	6.179E+10	6.295E+15	1	0.000	1	
vocalising / social	autumn	4.407	1.78	1	3.664	0.008	*
vocalising / territorial	autumn	3.497	1.30	1	3.359	0.022	*
vocalising / interacting with observer	autumn	3.688E+11	3.758E+16	1	0.000	1	
social / territorial	autumn	0.793	0.39	1	-0.476	1.000	
social / interacting with observer	autumn	8.367E+10	8.525E+15	1	0.000	1	
territorial / interacting with observer	autumn	1.055E+11	1.075E+16	1	0.000	1	
foraging / flying	winter	0.933	0.12	1	-0.549	1.000	
foraging / hopping	winter	7.971	1.54	1	10.709	8.160E-14	*
foraging / perching	winter	3.310	0.50	1	7.861	2.697E-13	*
foraging / pruning	winter	12.004	2.69	1	11.085	4.197E-14	*
foraging / vocalising	winter	6.680	1.24	1	10.271	9.903E-14	*
foraging / social	winter	7.286	1.37	1	10.565	8.893E-14	*
foraging / territorial	winter	12.893	2.98	1	11.075	4.396E-14	*
foraging / interacting with observer	winter	162.265	116.26	1	7.103	4.388E-11	*
flying / hopping	winter	8.543	1.66	1	11.060	4.796E-14	*
flying / perching	winter	3.547	0.54	1	8.309	1.009E-13	*
flying / pruning	winter	12.865	2.88	1	11.399	0	*
flying / vocalising	winter	7.159	1.32	1	10.677	8.971E-14	*
flying / social	winter	7.809	1.47	1	10.917	8.915E-14	*

contrast	season	ratio	SE	df	z.ratio	p value	p < 0.05
flying / territorial	winter	13.819	3.19	1	11.388	0	*
flying / interacting with observer	winter	173.908	124.59	1	7.200	2.168E-11	*
hopping / perching	winter	0.415	0.09	1	-4.146	0.001	*
hopping / pruning	winter	1.506	0.40	1	1.526	0.844	
hopping / vocalising	winter	0.838	0.20	1	-0.748	0.998	
hopping / social	winter	0.914	0.22	1	-0.376	1.000	
hopping / territorial	winter	1.618	0.44	1	1.756	0.711	
hopping / interacting with observer	winter	20.358	14.89	1	4.120	0.001	*
perching / pruning	winter	3.627	0.87	1	5.368	2.837E-06	*
perching / vocalising	winter	2.018	0.41	1	3.448	0.016	*
perching / social	winter	2.201	0.45	1	3.818	0.004	*
perching / territorial	winter	3.895	0.96	1	5.524	1.187E-06	*
perching / interacting with observer	winter	49.024	35.37	1	5.394	2.453E-06	*
pruning / vocalising	winter	0.556	0.15	1	-2.240	0.379	
pruning / social	winter	0.607	0.16	1	-1.890	0.621	
pruning / territorial	winter	1.074	0.32	1	0.242	1.000	
pruning / interacting with observer	winter	13.518	10.00	1	3.519	0.013	*
vocalising / social	winter	1.091	0.25	1	0.375	1.000	
vocalising / territorial	winter	1.930	0.52	1	2.461	0.251	
vocalising / interacting with observer	winter	24.292	17.71	1	4.376	4.126E-04	*
social / territorial	winter	1.770	0.48	1	2.115	0.463	
social / interacting with observer	winter	22.271	16.26	1	4.251	7.158E-04	*
territorial / interacting with observer	winter	12.585	9.34	1	3.413	0.019	*
foraging / flying	spring	0.848	0.26	1	-0.539	1.000	
foraging / hopping	spring	4.820	2.45	1	3.092	0.051	
foraging / perching	spring	1.689	0.61	1	1.454	0.876	
foraging / pruning	spring	1.994E+09	1.822E+13	1	0.002	1	

contrast	season	ratio	SE	df	z.ratio	p value	p < 0.05
foraging / vocalising	spring	2.966	1.27	1	2.537	0.214	
foraging / social	spring	23.972	24.67	1	3.088	0.052	
foraging / territorial	spring	23.972	24.67	1	3.088	0.052	
foraging / interacting with observer	spring	1.518E+12	3.828E+17	1	0.000	1	
flying / hopping	spring	5.687	2.86	1	3.456	0.016	*
flying / perching	spring	1.993	0.70	1	1.958	0.573	
flying / pruning	spring	2.353E+09	2.150E+13	1	0.002	1	
flying / vocalising	spring	3.499	1.48	1	2.971	0.073	
flying / social	spring	28.281	29.02	1	3.257	0.031	*
flying / territorial	spring	28.281	29.02	1	3.257	0.031	*
flying / interacting with observer	spring	1.791E+12	4.516E+17	1	0.000	1	
hopping / perching	spring	0.350	0.19	1	-1.951	0.578	
hopping / pruning	spring	4.137E+08	3.781E+12	1	0.002	1	
hopping / vocalising	spring	0.615	0.36	1	-0.830	0.996	
hopping / social	spring	4.973	5.49	1	1.454	0.877	
hopping / territorial	spring	4.973	5.49	1	1.454	0.877	
hopping / interacting with observer	spring	3.149E+11	7.941E+16	1	0.000	1	
perching / pruning	spring	1.180E+09	1.079E+13	1	0.002	1	
perching / vocalising	spring	1.756	0.81	1	1.218	0.953	
perching / social	spring	14.191	14.81	1	2.542	0.212	
perching / territorial	spring	14.191	14.81	1	2.542	0.212	
perching / interacting with observer	spring	8.986E+11	2.266E+17	1	0.000	1	
pruning / vocalising	spring	0.000	0.00	1	-0.002	1	
pruning / social	spring	0.000	0.00	1	-0.002	1	
pruning / territorial	spring	0.000	0.00	1	-0.002	1	
pruning / interacting with observer	spring	761.243	1.921E+08	1	0.000	1	
vocalising / social	spring	8.083	8.64	1	1.955	0.575	

contrast	season	ratio	SE	df	z.ratio	p value	p < 0.05
vocalising / territorial	spring	8.083	8.64	1	1.955	0.575	
vocalising / interacting with observer	spring	5.118E+11	1.291E+17	1	0.000	1	
social / territorial	spring	1.000	1.42	1	0.000	1	
social / interacting with observer	spring	6.332E+10	1.597E+16	1	0.000	1	
territorial / interacting with observer	spring	6.332E+10	1.597E+16	1	0.000	1	
foraging / flying	summer	0.307	0.09	1	-4.000	0.002	*
foraging / hopping	summer	1.875	0.79	1	1.483	0.864	
foraging / perching	summer	1.410	0.55	1	0.882	0.994	
foraging / pruning	summer	4.216	2.38	1	2.549	0.209	
foraging / vocalising	summer	1.054	0.38	1	0.145	1.000	
foraging / social	summer	4.221	2.38	1	2.551	0.208	
foraging / territorial	summer	6.970E+08	4.482E+12	1	0.003	1	
foraging / interacting with observer	summer	3.110E+10	1.336E+15	1	0.001	1	
flying / hopping	summer	6.108	2.28	1	4.847	4.411E-05	*
flying / perching	summer	4.595	1.54	1	4.563	1.740E-04	*
flying / pruning	summer	13.735	7.25	1	4.966	2.409E-05	*
flying / vocalising	summer	3.434	1.03	1	4.094	0.001	*
flying / social	summer	13.750	7.25	1	4.968	2.384E-05	*
flying / territorial	summer	2.271E+09	1.460E+13	1	0.003	1	
flying / interacting with observer	summer	1.013E+11	4.354E+15	1	0.001	1	
hopping / perching	summer	0.752	0.34	1	-0.630	0.999	
hopping / pruning	summer	2.249	1.37	1	1.331	0.922	
hopping / vocalising	summer	0.562	0.24	1	-1.345	0.918	
hopping / social	summer	2.251	1.37	1	1.332	0.922	
hopping / territorial	summer	3.717E+08	2.391E+12	1	0.003	1	
hopping / interacting with observer	summer	1.659E+10	7.127E+14	1	0.001	1	
perching / pruning	summer	2.989	1.75	1	1.870	0.635	

contrast	season	ratio	SE	df	z.ratio	p value	p < 0.05
perching / vocalising	summer	0.747	0.29	1	-0.739	0.998	
perching / social	summer	2.993	1.75	1	1.871	0.634	
perching / territorial	summer	4.942E+08	3.178E+12	1	0.003	1	
perching / interacting with observer	summer	2.205E+10	9.475E+14	1	0.001	1	
pruning / vocalising	summer	0.250	0.14	1	-2.442	0.261	
pruning / social	summer	1.001	0.71	1	0.002	1	
pruning / territorial	summer	1.653E+08	1.063E+12	1	0.003	1	
pruning / interacting with observer	summer	7.378E+09	3.170E+14	1	0.001	1	
vocalising / social	summer	4.004	2.27	1	2.444	0.260	
vocalising / territorial	summer	6.613E+08	4.253E+12	1	0.003	1	
vocalising / interacting with observer	summer	2.951E+10	1.268E+15	1	0.001	1	
social / territorial	summer	1.651E+08	1.062E+12	1	0.003	1	
social / interacting with observer	summer	7.370E+09	3.166E+14	1	0.001	1	
territorial / interacting with observer	summer	44.628	1.939E+06	1	0.000	1	

Table S 20. Generalised linear mixed model (GLMM) results for grey warbler (Gerygone igata), tūī (Prosthemadera novaeseelandiae), New Zealand fantail (Rhipidura fuliginosa), pūkeko (Porphyrio melanotus melanotus), and welcome swallow (Hirundo neoxena). Fixed-effect coefficient estimates (log scale), standard errors, Fixed-effect coefficient estimates (log scale), standard errors (SE), Wald z-statistics and associated p-values are reported. Foraging was the reference level for behaviour, while autumn was the reference level for season in models including seasonal effects. The intercept represents the expected log observation count for foraging behaviour in autumn for models including season, or for foraging behaviour irrespective of season in models without seasonal effects, with orchard random effects set to zero. Orchard was included as a random intercept. Significant estimates (p < 0.05) are marked with an asterisk.

term	estimate	SE	z	p	
		grey warbler			
(Intercept)	-1.322	0.508	-2.601	0.009	*
behaviourflying	0.118	0.486	0.242	0.808	
behaviourhopping	-0.288	0.540	-0.533	0.594	
behaviourperching	-0.470	0.570	-0.824	0.410	
behaviourpreening	-22.384	25645.288	-0.001	0.999	
behaviourvocalising	-1.386	0.791	-1.754	0.080	
behavioursocial	-22.384	25645.288	-0.001	0.999	
behaviourterritorial	-22.384	25645.288	-0.001	0.999	
behaviourinteracting with observer	-22.384	25645.288	-0.001	0.999	
seasonwinter	2.82875E-07	0.475	5.95704E-07	1.000	
seasonspring	6.8612E-07	0.816	8.40322E-07	1.000	
seasonsummer	4.32154E-07	0.606	7.13679E-07	1.000	
		tūī			
(Intercept)	-1.434	0.255	-5.621	1.90E-08	*
behaviourflying	0.216	0.315	0.686	0.493	
behaviourhopping	-1.219	0.344	-3.538	0.000	*
behaviourperching	-0.917	0.346	-2.650	0.008	*
behaviourpreening	-2.704	0.507	-5.335	9.57E-08	*
behaviourvocalising	-0.096	0.327	-0.294	0.769	
behavioursocial	-1.920	0.403	-4.765	1.89E-06	*

term	estimate	SE	z	p	
behaviourterritorial	-1.899	0.403	-4.716	2.41E-06	*
behaviourinteracting with observer	-22.441	8198.629	-0.003	0.998	
seasonwinter	0.123	0.240	0.511	0.609	
seasonspring	-0.036	0.352	-0.101	0.919	
seasonsummer	-0.034	0.256	-0.135	0.893	
New Zealand fantail					
(Intercept)	-1.109	0.070	-15.756	6.23E-56	*
behaviourflying	-0.342	0.110	-3.100	0.002	*
behaviourhopping	-1.607	0.166	-9.707	2.82E-22	*
behaviourperching	-0.761	0.120	-6.331	2.43E-10	*
behaviourpreening	-3.112	0.324	-9.603	7.75E-22	*
behaviourvocalising	-0.944	0.135	-6.986	2.83E-12	*
behavioursocial	-2.279	0.220	-10.343	4.49E-25	*
behaviourterritorial	-2.706	0.268	-10.101	5.47E-24	*
behaviourinteracting with observer	-3.016	0.310	-9.736	2.13E-22	*
pūkeko					
(Intercept)	-0.627	0.121	-5.199	2.00E-07	*
behaviourflying	-1.802	0.233	-7.716	1.20E-14	*
behaviourhopping	-4.740	0.727	-6.516	7.23E-11	*
behaviourperching	-2.322	0.266	-8.727	2.62E-18	*
behaviourpreening	-3.485	0.414	-8.410	4.10E-17	*
behaviourvocalising	-2.652	0.311	-8.518	1.63E-17	*
behavioursocial	-2.303	0.268	-8.587	8.96E-18	*
behaviourterritorial	-4.341	0.602	-7.212	5.49E-13	*
behaviourinteracting with observer	-1.087	0.202	-5.371	7.84E-08	*

term	estimate	SE	z	p	
welcome swallow					
(Intercept)	-1.014	0.176	-5.771	7.86E-09	*
behaviourflying	0.492	0.230	2.137	0.033	*
behaviourhopping	-19.409	2806.505	-0.007	0.994	
behaviourperching	-2.141	0.530	-4.039	5.37E-05	*
behaviourpreening	-19.409	2806.505	-0.007	0.994	
behaviourvocalising	-19.409	2806.505	-0.007	0.994	
behavioursocial	-19.409	2806.505	-0.007	0.994	
behaviourterritorial	-19.409	2806.505	-0.007	0.994	
behaviourinteracting with observer	-19.409	2806.505	-0.007	0.994	

Table S 21. Pairwise contrasts calculated from estimated marginal means (EMMs) for grey warbler (Gerygone igata), tūī (Prosthemadera novaeseelandiae), New Zealand fantail (Rhipidura fuliginosa), pūkeko (Porphyrio melanotus melanotus), and welcome swallow (Hirundo neoxena). EMMs were retrieved from a generalised linear mixed model (GLMM) accounting for the additive effects (main effects) of behaviour and season (grey warblers and tūī), and only behaviour (New Zealand fantails, pūkeko, and welcome swallows), with orchard as a random effect. Behaviour categories were described as flying; foraging = behaviours prominent to different feeding habits, such as hawking and gleaning for insectivorous birds, diving for carnivorous birds, and pecking and rummaging for omnivores; perching or roosting, hopping = on the ground or between branches); vocalising; territorial behaviours = chasing away conspecifics; social behaviours = couple preening, feeding mates or fledglings, gathering nest materials; preening = as an individual action; and interacting with the observer. Pairwise contrasts were calculated for all pairings of behaviours and for all seasons, from autumn 2024 to summer 2025. Significant contrasts ($p < 0.05$) are marked with an asterisk.

contrast	ratio	SE	df	z.ratio	p value	p < 0.05
grey warbler						
foraging / flying	0.889	0.432	1	-0.242	1.000	
foraging / hopping	1.333	0.720	1	0.533	1.000	
foraging / perching	1.600	0.912	1	0.824	0.996	
foraging / preening	5.261E+09	1.349E+14	1	0.001	1.000	
foraging / vocalising	4.000	3.162	1	1.754	0.713	
foraging / social	5.261E+09	1.349E+14	1	0.001	1.000	
foraging / territorial	5.261E+09	1.349E+14	1	0.001	1.000	
foraging / interacting with observer	5.261E+09	1.349E+14	1	0.001	1.000	
flying / hopping	1.500	0.791	1	0.769	0.998	
flying / perching	1.800	1.004	1	1.054	0.980	
flying / preening	5.919E+09	1.518E+14	1	0.001	1.000	
flying / vocalising	4.500	3.518	1	1.924	0.597	
flying / social	5.919E+09	1.518E+14	1	0.001	1.000	
flying / territorial	5.919E+09	1.518E+14	1	0.001	1.000	
flying / interacting with observer	5.919E+09	1.518E+14	1	0.001	1.000	
hopping / perching	1.200	0.727	1	0.301	1.000	
hopping / preening	3.946E+09	1.012E+14	1	0.001	1.000	
hopping / vocalising	3.000	2.449	1	1.346	0.918	
hopping / social	3.946E+09	1.012E+14	1	0.001	1.000	

contrast	ratio	SE	df	z.ratio	p value	p < 0.05
hopping / territorial	3.946E+09	1.012E+14	1	0.001	1.000	
hopping / interacting with observer	3.946E+09	1.012E+14	1	0.001	1.000	
perching / preening	3.288E+09	8.433E+13	1	0.001	1.000	
perching / vocalising	2.500	2.092	1	1.095	0.975	
perching / social	3.288E+09	8.433E+13	1	0.001	1.000	
perching / territorial	3.288E+09	8.433E+13	1	0.001	1.000	
perching / interacting with observer	3.288E+09	8.433E+13	1	0.001	1.000	
preening / vocalising	7.602E-10	1.950E-05	1	-0.001	1.000	
preening / social	1.000	36267.915	1	0.000	1.000	
preening / territorial	1.000	36267.915	1	0.000	1.000	
preening / interacting with observer	1.000	36267.915	1	0.000	1.000	
vocalising / social	1.315E+09	3.373E+13	1	0.001	1.000	
vocalising / territorial	1.315E+09	3.373E+13	1	0.001	1.000	
vocalising / interacting with observer	1.315E+09	3.373E+13	1	0.001	1.000	
social / territorial	1.000	36267.915	1	0.000	1.000	
social / interacting with observer	1.000	36267.915	1	0.000	1.000	
territorial / interacting with observer	1.000	36267.915	1	0.000	1.000	

contrast	ratio	SE	df	z.ratio	p value	p < 0.05
tūī						
foraging / flying	0.806	0.254	1	-0.686	0.999	
foraging / hopping	3.383	1.165	1	3.538	0.012	*
foraging / perching	2.502	0.866	1	2.650	0.166	
foraging / preening	14.937	7.571	1	5.335	0.000	*
foraging / vocalising	1.101	0.360	1	0.294	1.000	
foraging / social	6.824	2.750	1	4.765	0.000	*
foraging / territorial	6.681	2.691	1	4.716	0.000	*
foraging / interacting with observer	5.574E+09	4.570E+13	1	0.003	1.000	
flying / hopping	4.199	1.533	1	3.930	0.003	*
flying / perching	3.106	1.078	1	3.264	0.030	*
flying / preening	18.540	9.653	1	5.608	0.000	*
flying / vocalising	1.366	0.434	1	0.984	0.987	
flying / social	8.470	3.584	1	5.050	0.000	*
flying / territorial	8.293	3.445	1	5.093	0.000	*
flying / interacting with observer	6.919E+09	5.673E+13	1	0.003	1.000	
hopping / perching	0.740	0.290	1	-0.769	0.998	
hopping / preening	4.416	2.376	1	2.760	0.127	
hopping / vocalising	0.325	0.122	1	-2.994	0.068	
hopping / social	2.017	0.889	1	1.593	0.809	
hopping / territorial	1.975	0.873	1	1.539	0.837	
hopping / interacting with observer	1.648E+09	1.351E+13	1	0.003	1.000	
perching / preening	5.970	3.226	1	3.306	0.026	*
perching / vocalising	0.440	0.157	1	-2.304	0.340	
perching / social	2.727	1.218	1	2.247	0.375	
perching / territorial	2.670	1.175	1	2.232	0.385	

contrast	ratio	SE	df	z.ratio	p value	p < 0.05
perching / interacting with observer	2.228E+09	1.827E+13	1	0.003	1.000	
preening / vocalising	0.074	0.039	1	-4.937	0.000	*
preening / social	0.457	0.263	1	-1.360	0.913	
preening / territorial	0.447	0.258	1	-1.392	0.901	
preening / interacting with observer	3.732E+08	3.060E+12	1	0.002	1.000	
vocalising / social	6.199	2.674	1	4.229	0.001	*
vocalising / territorial	6.069	2.572	1	4.255	0.001	*
vocalising / interacting with observer	5.064E+09	4.152E+13	1	0.003	1.000	
social / territorial	0.979	0.479	1	-0.043	1.000	
social / interacting with observer	8.169E+08	6.697E+12	1	0.003	1.000	
territorial / interacting with observer	8.343E+08	6.840E+12	1	0.003	1.000	

contrast	ratio	SE	df	z.ratio	p value	p < 0.05
New Zealand fantail						
foraging / flying	1.408	0.156	1	3.100	0.0502	
foraging / hopping	4.987	0.825	1	9.707	0.0000	*
foraging / perching	2.140	0.257	1	6.331	0.0000	*
foraging / preening	22.460	7.278	1	9.603	0.0000	*
foraging / vocalising	2.569	0.347	1	6.986	0.0000	*
foraging / social	9.762	2.151	1	10.343	0.0000	*
foraging / territorial	14.966	4.009	1	10.101	0.0000	*
foraging / interacting with observer	20.410	6.323	1	9.736	0.0000	*
flying / hopping	3.541	0.605	1	7.407	0.0000	*
flying / perching	1.520	0.197	1	3.226	0.0342	*
flying / preening	15.949	5.220	1	8.461	0.0000	*
flying / vocalising	1.825	0.247	1	4.442	0.0003	*
flying / social	6.932	1.558	1	8.613	0.0000	*
flying / territorial	10.627	2.885	1	8.707	0.0000	*
flying / interacting with observer	14.493	4.536	1	8.543	0.0000	*
hopping / perching	0.429	0.077	1	-4.709	0.0001	*
hopping / preening	4.504	1.578	1	4.297	0.0006	*
hopping / vocalising	0.515	0.096	1	-3.554	0.0114	*
hopping / social	1.958	0.503	1	2.612	0.1813	
hopping / territorial	3.001	0.897	1	3.677	0.0073	*
hopping / interacting with observer	4.093	1.379	1	4.182	0.0010	*
perching / preening	10.494	3.480	1	7.089	0.0000	*
perching / vocalising	1.201	0.181	1	1.213	0.9540	
perching / social	4.561	1.055	1	6.564	0.0000	*
perching / territorial	6.992	1.936	1	7.024	0.0000	*

contrast	ratio	SE	df	z.ratio	p value	p < 0.05
perching / interacting with observer	9.536	3.029	1	7.100	0.0000	*
preening / vocalising	0.114	0.038	1	-6.451	0.0000	*
preening / social	0.435	0.165	1	-2.196	0.4079	
preening / territorial	0.666	0.272	1	-0.993	0.9866	
preening / interacting with observer	0.909	0.398	1	-0.219	1.0000	
vocalising / social	3.799	0.901	1	5.626	0.0000	*
vocalising / territorial	5.824	1.641	1	6.254	0.0000	*
vocalising / interacting with observer	7.943	2.558	1	6.436	0.0000	*
social / territorial	1.533	0.510	1	1.285	0.9360	
social / interacting with observer	2.091	0.768	1	2.009	0.5372	
territorial / interacting with observer	1.364	0.542	1	0.781	0.9974	

contrast	ratio	SE	df	z.ratio	p value	p < 0.05
pūkeko						
foraging / flying	6.060	1.415	1	7.716	4.85E-13	*
foraging / hopping	114.413	83.228	1	6.516	2.60E-09	*
foraging / perching	10.201	2.715	1	8.727	7.19E-14	*
foraging / preening	32.613	13.513	1	8.410	9.19E-14	*
foraging / vocalising	14.178	4.414	1	8.518	8.39E-14	*
foraging / social	10.008	2.685	1	8.587	7.95E-14	*
foraging / territorial	76.772	46.205	1	7.212	1.98E-11	*
foraging / interacting with observer	2.967	0.601	1	5.371	2.80E-06	*
flying / hopping	18.881	14.054	1	3.947	2.56E-03	*
flying / perching	1.683	0.522	1	1.678	7.60E-01	
flying / preening	5.382	2.386	1	3.797	4.63E-03	*
flying / vocalising	2.340	0.812	1	2.450	2.57E-01	
flying / social	1.652	0.514	1	1.613	7.98E-01	
flying / territorial	12.670	7.884	1	4.080	1.48E-03	*
flying / interacting with observer	0.490	0.125	1	-2.797	1.16E-01	
hopping / perching	0.089	0.067	1	-3.199	3.72E-02	*
hopping / preening	0.285	0.234	1	-1.532	8.41E-01	
hopping / vocalising	0.124	0.096	1	-2.706	1.45E-01	
hopping / social	0.087	0.066	1	-3.223	3.46E-02	*
hopping / territorial	0.671	0.623	1	-0.430	1.00E+00	
hopping / interacting with observer	0.026	0.019	1	-4.970	2.37E-05	*
perching / preening	3.197	1.477	1	2.515	2.24E-01	
perching / vocalising	1.390	0.517	1	0.885	9.94E-01	
perching / social	0.981	0.331	1	-0.057	1.00E+00	
perching / territorial	7.526	4.784	1	3.175	4.01E-02	*

contrast	ratio	SE	df	z.ratio	p value	p < 0.05
perching / interacting with observer	0.291	0.084	1	-4.294	5.93E-04	*
preening / vocalising	0.435	0.212	1	-1.708	7.42E-01	
preening / social	0.307	0.142	1	-2.553	2.07E-01	
preening / territorial	2.354	1.672	1	1.205	9.56E-01	
preening / interacting with observer	0.091	0.039	1	-5.610	7.24E-07	*
vocalising / social	0.706	0.262	1	-0.937	9.91E-01	
vocalising / territorial	5.415	3.546	1	2.580	1.95E-01	
vocalising / interacting with observer	0.209	0.068	1	-4.808	5.34E-05	*
social / territorial	7.671	4.881	1	3.202	3.68E-02	*
social / interacting with observer	0.296	0.085	1	-4.224	8.07E-04	*
territorial / interacting with observer	0.039	0.024	1	-5.324	3.62E-06	*

contrast	ratio	SE	df	z.ratio	p value	p < 0.05
welcome swallow						
foraging / flying	0.611	0.141	1	-2.137	0.447	
foraging / hopping	2.685E+08	7.537E+11	1	0.007	1.000	
foraging / perching	8.512	4.513	1	4.039	0.002	*
foraging / preening	2.685E+08	7.537E+11	1	0.007	1.000	
foraging / vocalising	2.685E+08	7.537E+11	1	0.007	1.000	
foraging / social	2.685E+08	7.537E+11	1	0.007	1.000	
foraging / territorial	2.685E+08	7.537E+11	1	0.007	1.000	
foraging / interacting with observer	2.685E+08	7.537E+11	1	0.007	1.000	
flying / hopping	4.393E+08	1.233E+12	1	0.007	1.000	
flying / perching	13.923	7.262	1	5.049	0.000	*
flying / preening	4.393E+08	1.233E+12	1	0.007	1.000	
flying / vocalising	4.393E+08	1.233E+12	1	0.007	1.000	
flying / social	4.393E+08	1.233E+12	1	0.007	1.000	
flying / territorial	4.393E+08	1.233E+12	1	0.007	1.000	
flying / interacting with observer	4.393E+08	1.233E+12	1	0.007	1.000	
hopping / perching	3.170E-08	8.895E-05	1	-0.006	1.000	
hopping / preening	1.000	3968.998	1	0.000	1.000	
hopping / vocalising	1.000	3968.998	1	0.000	1.000	
hopping / social	1.000	3968.998	1	0.000	1.000	
hopping / territorial	1.000	3968.998	1	0.000	1.000	
hopping / interacting with observer	1.000	3968.998	1	0.000	1.000	
perching / preening	3.155E+07	8.854E+10	1	0.006	1.000	
perching / vocalising	3.155E+07	8.854E+10	1	0.006	1.000	
perching / social	3.155E+07	8.854E+10	1	0.006	1.000	
perching / territorial	3.155E+07	8.854E+10	1	0.006	1.000	

contrast	ratio	SE	df	z.ratio	p value	p < 0.05
perching / interacting with observer	3.155E+07	8.854E+10	1	0.006	1.000	
preening / vocalising	1.000	3968.998	1	0.000	1.000	
preening / social	1.000	3968.998	1	0.000	1.000	
preening / territorial	1.000	3968.998	1	0.000	1.000	
preening / interacting with observer	1.000	3968.998	1	0.000	1.000	
vocalising / social	1.000	3968.998	1	0.000	1.000	
vocalising / territorial	1.000	3968.998	1	0.000	1.000	
vocalising / interacting with observer	1.000	3968.998	1	0.000	1.000	
social / territorial	1.000	3968.998	1	0.000	1.000	
social / interacting with observer	1.000	3968.998	1	0.000	1.000	
territorial / interacting with observer	1.000	3968.998	1	0.000	1.000	

Table S 22. Direct observations of crop fruit consumption in the orchards surveyed, from autumn 2024 to summer 2025. Fruit crops were identified as apples and other fruits still on trees (A & C) and fruits left on the ground (B & D). 11 species were recorded consuming fruits: silvereyes (Zosterops lateralis), blackbirds (Turdus merula), tūī (Prosthemadera novaeseelandiae), pūkeko (Porphyrio melanotus melanotus), chaffinches (Fringilla coelebs), greenfinches (Chloris chloris), goldfinches (Carduelis carduelis), starlings (Sturnus vulgaris), house sparrows (Passer domesticus), eastern rosellas (Platycercus eximius), and song thrushes (Turdus philomelos). Orchard TR was not surveyed in spring.

crop	orchard	season	silvereye	blackbird	tūī	pūkeko	chaffinch	greenfinch	goldfinch	starling	house sparrow	eastern rosella	song thrush
A. apple													
	MN1	autumn	12	0	0	0	0	0	0	0	0	0	0
	MN1	winter	33	0	0	0	0	0	0	0	0	0	0
	MN1	spring	0	0	0	0	0	0	0	0	0	0	0
	MN1	summer	0	0	0	0	0	0	0	0	0	0	0
	MN2	autumn	42	0	7	0	0	0	0	0	0	0	0
	MN2	winter	16	0	2	0	3	0	0	0	0	0	0
	MN2	spring	2	0	0	0	0	0	0	0	0	0	0
	MN2	summer	0	0	0	0	0	0	0	0	0	0	0
	KC1	autumn	30	0	5	1	0	1	0	0	0	0	0
	KC1	winter	8	0	0	0	0	0	0	0	0	0	0
	KC1	spring	0	0	0	0	0	0	0	0	0	0	0
	KC1	summer	0	0	0	0	0	0	0	0	0	0	0
	KC2	autumn	16	0	0	0	0	0	0	0	0	0	0
	KC2	winter	10	0	0	0	0	0	0	0	0	0	0
	KC2	spring	0	0	0	0	0	0	0	0	0	0	0
	KC2	summer	0	0	0	0	0	0	0	0	0	0	0
	HB	autumn	10	0	0	0	0	0	0	0	0	0	0
	HB	winter	2	0	0	0	0	0	0	0	0	0	0
	HB	spring	0	0	0	0	0	0	0	0	0	0	0
	HB	summer	0	0	0	0	0	0	0	0	0	0	0
	TR	autumn	1	0	0	0	0	0	0	0	0	0	0
	TR	winter	0	0	0	0	0	0	0	0	0	0	0
	TR	summer	0	0	0	0	0	0	0	0	0	0	0

crop	orchard	season	silvereye	blackbird	tūī	pūkeko	chaffinch	greenfinch	goldfinch	starling	house sparrow	eastern rosella	song thrush
B. apple (ground)													
	MN1	autumn	1	1	0	0	0	0	0	0	0	0	0
	MN1	winter	19	3	0	0	0	0	0	0	0	0	0
	MN1	spring	0	0	0	0	0	0	0	0	0	0	0
	MN1	summer	0	0	0	0	0	0	0	0	0	0	0
	MN2	autumn	1	0	0	0	0	0	0	0	0	0	0
	MN2	winter	26	1	0	0	0	0	0	0	0	0	0
	MN2	spring	0	4	0	0	0	0	0	0	0	0	0
	MN2	summer	0	0	0	0	0	0	0	0	0	0	0
	KC1	autumn	0	2	0	0	0	0	0	0	2	0	0
	KC1	winter	10	0	0	0	0	0	0	0	0	0	0
	KC1	spring	0	1	0	0	1	2	0	1	0	0	0
	KC1	summer	0	0	0	0	0	0	0	0	0	0	0
	KC2	autumn	0	0	0	0	0	0	0	0	0	0	0
	KC2	winter	17	0	0	0	0	0	0	0	0	0	0
	KC2	spring	0	0	0	0	0	0	0	0	0	0	0
	KC2	summer	0	0	0	0	0	0	0	0	0	0	0
	HB	autumn	15	0	0	0	0	0	0	0	0	0	0
	HB	winter	51	0	0	0	1	1	1	0	0	0	0
	HB	spring	0	0	0	0	0	0	0	0	0	0	0
	HB	summer	0	0	0	0	0	0	0	0	0	0	0
	TR	autumn	0	0	0	0	0	0	0	0	0	0	0
	TR	winter	5	0	0	0	0	0	0	0	0	0	0
	TR	summer	0	0	0	0	0	0	0	0	0	0	0

crop	orchard	season	silvereye	blackbird	tūī	pūkeko	chaffinch	greenfinch	goldfinch	starling	house sparrow	eastern rosella	song thrush
C. other fruits													
	MN1	autumn	0	0	0	0	0	0	0	0	0	0	0
	MN1	winter	3	0	0	0	0	0	0	0	0	0	0
	MN1	spring	2	0	0	0	0	0	0	0	0	0	0
	MN1	summer	0	0	0	0	0	0	0	0	0	0	0
	MN2	autumn	0	0	0	0	0	0	0	0	0	0	0
	MN2	winter	0	0	0	0	0	0	0	0	0	0	0
	MN2	spring	0	0	0	0	0	0	0	0	0	0	0
	MN2	summer	0	0	0	0	0	0	0	0	0	0	0
	KC1	autumn	0	0	0	0	0	0	0	0	0	0	0
	KC1	winter	0	0	0	0	0	0	0	0	0	0	0
	KC1	spring	0	0	0	0	0	0	0	0	0	0	0
	KC1	summer	0	2	0	0	0	0	0	0	0	0	0
	KC2	autumn	1	1	0	0	0	0	0	0	0	1	0
	KC2	winter	0	0	0	0	0	0	0	0	0	0	0
	KC2	spring	0	1	0	0	0	0	0	0	0	0	3
	KC2	summer	0	0	0	0	0	0	0	0	0	0	0
	HB	autumn	0	0	0	0	0	0	0	0	0	0	0
	HB	winter	0	0	0	0	0	0	0	0	0	0	0
	HB	spring	0	0	0	0	0	0	0	0	0	0	0
	HB	summer	0	0	0	0	0	0	0	0	0	0	0
	TR	autumn	0	0	0	0	0	0	0	0	0	0	0
	TR	winter	0	0	0	0	0	0	0	0	0	0	0
	TR	summer	0	0	0	0	0	0	0	0	0	0	0

crop	orchard	season	silvereye	blackbird	tūī	pūkeko	chaffinch	greenfinch	goldfinch	starling	house sparrow	eastern rosella	song thrush
D. other fruits (ground)													
	MN1	autumn	0	0	0	0	0	0	0	0	0	0	0
	MN1	winter	0	0	0	0	0	0	0	0	0	0	0
	MN1	spring	0	1	0	0	0	0	0	0	0	0	0
	MN1	summer	0	0	0	0	0	0	0	0	0	0	0
	MN2	autumn	0	0	0	0	0	0	0	0	0	0	0
	MN2	winter	0	0	0	0	0	0	0	0	0	0	0
	MN2	spring	0	0	0	0	0	0	0	0	0	0	0
	MN2	summer	0	0	0	0	0	0	0	0	0	0	0
	KC1	autumn	0	0	0	0	0	0	0	0	0	0	0
	KC1	winter	0	0	0	0	0	0	0	0	0	0	0
	KC1	spring	0	0	0	0	0	0	0	0	0	0	0
	KC1	summer	0	0	0	0	0	0	0	0	0	0	0
	KC2	autumn	1	1	0	0	0	0	0	0	0	0	0
	KC2	winter	0	0	0	0	0	0	0	0	0	0	0
	KC2	spring	0	1	0	0	0	0	0	0	0	0	0
	KC2	summer	0	0	0	0	0	0	0	0	0	0	0
	HB	autumn	0	0	0	0	0	0	0	0	0	0	0
	HB	winter	0	0	0	0	0	0	0	0	0	0	0
	HB	spring	0	0	0	0	0	0	0	0	0	0	0
	HB	summer	0	0	0	0	0	0	0	0	0	0	0
	TR	autumn	0	0	0	0	0	0	0	0	0	0	0
	TR	winter	0	0	0	0	0	0	0	0	0	0	0
	TR	summer	0	0	0	0	0	0	0	0	0	0	0

Supplementary Materials (Chapter Five)

Table S 23. Dates of crop-damage surveys conducted during the 2024 and 2025 apple harvest seasons at six orchards in New Zealand, following the calendar of harvest set by the growers of each orchard. N/A indicates that an orchard was not surveyed for crop damage in that year.

Orchard	Harvest 2024	Harvest 2025
MN1	N/A	18 / 03
MN2	16 / 03	25 / 03
KC1	25 / 02	03 / 03
KC2	26 / 02	03 / 03
HB	N/A	01 / 03
TR	19 / 02	N/A



Figure S 10. Examples of bird predation marks on caterpillars. Light and dark green plasticine was mixed together and rolled into 2mm wide caterpillars, cut into lengths varying between 25- and 30-mm. Caterpillars were glued to the branches or leaves of apple trees and left in the field for 24 hours. A = orchard KC1, autumn; B = orchard MN2, winter; C = orchard KC1, summer.



Figure S 11. Examples of rodent predation marks on caterpillars. Light and dark green plasticine was mixed together and rolled into 2mm wide caterpillars, cut into lengths varying between 25- and 30-mm. Caterpillars were glued to the branches or leaves of apple trees and left in the field for 24 hours. A = orchard HB, autumn; B = orchard MN2, summer; C = orchard KC1, harvest season.



Figure S 12. Examples of arthropod predation marks on caterpillars. Light and dark green plasticine was mixed together and rolled into 2mm wide caterpillars, cut into lengths varying between 25- and 30-mm. Caterpillars were glued to the branches or leaves of apple trees and left in the field for 24 hours. A = orchard TR, autumn; B = orchard KC2, autumn; C = orchard MN2, winter.

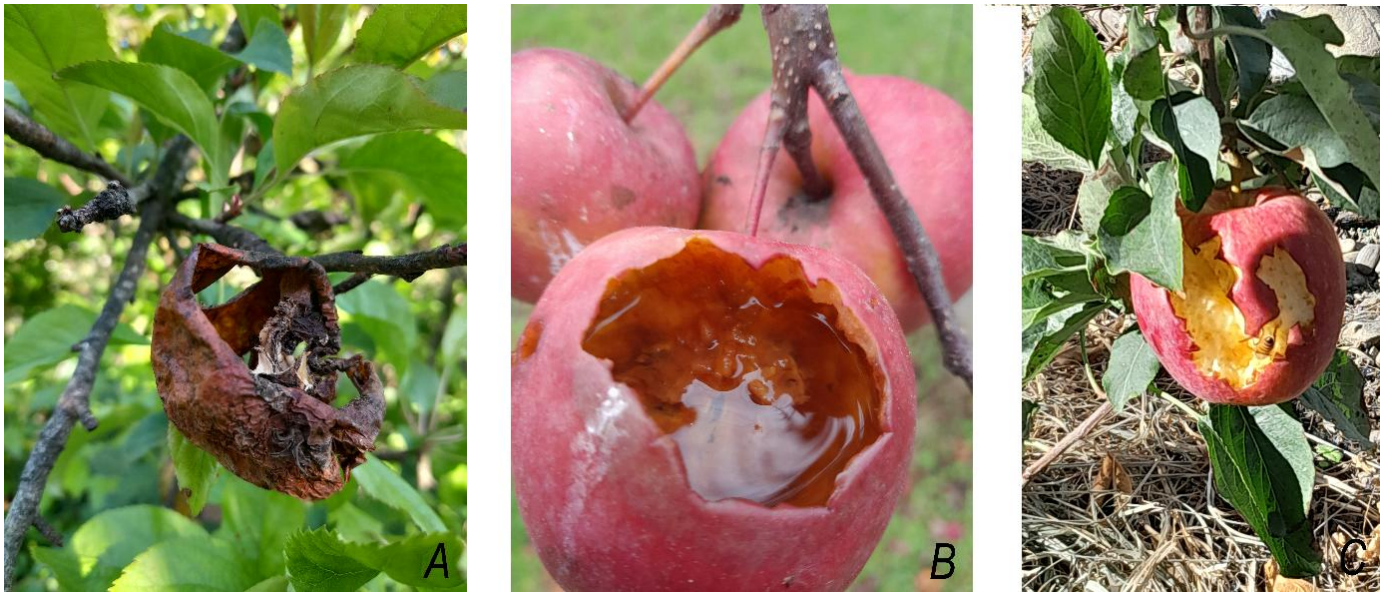


Figure S 13. Examples of bird damage on apples. A = Orchard KC1, summer 2024; B = Orchard MN1, winter 2024; C = Orchard TR, autumn 2024.



Figure S 14. Examples of fungal damage on apples. A = Orchard MN2, summer 2024; B = Orchard MN2, winter 2024; C = Orchard KC1, autumn 2024