Impact of human colonisation history on New Zealand Avian diversity

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Frontispiece

New Zealand Fantail (Photo: Amiot C.)

"It is obvious that modern civilised man upsets the 'natural' ecosystems or 'biotic communities' on a very large scale. But it would be difficult, not to say impossible, to draw a natural line between the activities of the human tribes which presumably fitted into and formed parts of 'biotic communities 'and the destructive human activities of the modern world. Is man part of 'nature ' or not ? Can his existence be harmonised with the conception of the 'complex organism' ? Regarded as an exceptionally powerful biotic factor which increasingly upsets the equilibrium of preexisting ecosystems and eventually destroys them, at the same time forming new ones of very different nature, human activity finds its proper place in ecology."

Tansley, 1935

Abstract

Human activity has transformed earth's ecology and exerts new selection forces on entire species communities. This thesis examines the influence of evolutionary and human history on the composition of local biodiversity in New Zealand terrestrial habitats. The Auckland region of New Zealand provides an excellent model system because these areas have only recently been colonised by humans, and there is a gradient of habitats ranging from urban to protected native bush. The history of humans in New Zealand is used to inform the response of naïve biodiversity to anthropogenic transformation. First, a general concept of the effect of human societies on biodiversity responses to anthropogenic impacts is explained in chapter one. I focus on three major historical phases - hunter-gather, Agrarian and Industrial- to outline the contrasting influences of each society on native species extinction and extirpation legacies. I then examine the impact of two waves of colonization by humans in New Zealand on avifauna, to establish an understanding of the influence of different human societies on species communities. My results show that New Zealand's extinction rates are the highest recorded, and are associated with the post-colonisation period by European society and a more advanced human niche construction. This caused more advanced cultural, ecological transformations at various spatial scales. In addition, for exotic bird species in New Zealand, I examined whether the extent of previous coexistence with humans was a potential determinant of establishment success. My findings suggest that previously co-existing with humans is a potential key factor driving the establishment success of exotic species, particularly in habitats transformed by humans. To verify the idea that species functional diversity responds in different ways to human civilisation, I characterise differences in species biological traits among a gradient of habitats with variable degrees of anthropogenic disturbance. I show that no clear assemblages of traits are currently found along extant New Zealand native avifauna. I argue that this can be explained by the different experiences that NZ native avifauna has had with humans in comparison

to exotic species. To investigate the possibility of a time-lag response of birds to human habitat transformations, the response of an avifauna assemblage in a remnant forest in the urban habitat is investigated over a period of 26 years of human habitat changes. My results suggest that the community assemblage changed over that time, driven by the arrival of new exotic species. This resulted in a change of community composition to one dominated by exotic species. Finally, nest-site selection of exotic and native avifauna is examined across an anthropogenic gradient to understand the role of evolutionary history in shaping their behavioural response to habitat change. I found further support for the effect of species past-experience with humans. Indeed only native species more naive to anthropogenic habitats and its disturbance tend to alter their nest site strategy in relation to the degree of terrestrial predation. By using the history of a recently colonised location like New Zealand, this research has been able to show the potential importance of human society characteristics during colonisation and how previous levels of human coexistence of biodiversity has implications for current and future ecological consequences in an Anthropogenic world. This thesis highlights the importance of considering species' past-experiences with humans to inform ecological and evolutionary research and conservation strategies

Keywords : New Zealand, anthropogenic disturbance, anthrosequence, environmental change, time-lag, past-evolutionary history

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Chapter 1

General Introduction

1.1 Emergence of human systems on Earth, a novel evolutionary trajectory

Since the appearance of tools (Harmand *et al.* 2015) made by early hominids 3.3 to 3.5 million years ago, humans have influenced and transformed earth's ecosystems, including causing changes to the atmosphere, hydrosphere, lithosphere and biosphere (Foley *et al.* 2005, Ellis and Ramankutty 2008, Ellis 2011, Steffen *et al.* 2011). Human populations have modified the Earth's environment by altering it for their own needs (Balée 1998, Smith 2007, Steffen *et al.* 2011). Humans have differed from other species in their impact on the environment and ecosystems due to a combination of different capacities such as sociality (Ellis 2011), ecosystem engineering (Smith 2007, Ellis 2011) and handling a wide array of powerful tools (Terborgh 1999, Steffen *et al.* 2011, Ellis 2011) to improve food acquisition and to sustain their populations. The development of human competencies in the 'Anthropocene period', tool construction for hunting, control of fire, agricultural or domestication systems and industrialisation, have resulted in the transformation of the terrestrial biosphere through the establishment of human-dominated ecosystems (Steffen *et al.* 2011, Ellis 2015) and have altered the evolutionary trajectory of entire ecosystems (Steffen *et al.* 2011, Ellis 2015).

Evolutionary theorists and social research have highlighted that human capacity for environmental transformation (Diamond 1984, 1992, Balée 1996) had diverged in correlation with the growth and the development of human societies (Steffen *et al.* 2009, Ellis 2011, Steffen *et al.* 2011, Ellis 2015). Hunter-gatherer societies have caused the first human-induced species extinctions around the earth with the extinction of the megafauna (Grayson 2001, Pimm *et al.* 2014) and also increased the abundance of some other animals (resulting from the appearance of a new source of food across regenerating forests and reduction of other competitors like the megafauna; Balée 1998). Such societies also caused changes of land-cover (i.e., deforestation) through the use of the hunting techniques (i.e., landscape burning; Clark and Royall 1996, McWhethy *et al.* 2009, Bird *et al.* 2013) across most of the Earth's ecosystems (see Ellis 2015) and some regional development of plant biodiversity through new growth of plants after burning of the original vegetation (e.g., in North America: Pyne 2017, Cromon 1983, Marquardt 1992; in Australia: Walsh 1990). Thus human society, with the creation of a human landscape, has driven the first unnatural

community change at the regional scale for plant and animal, with a notable increase of species biodiversity (Pyne 2017) and also the extinction of species due to overkill (Grayson 1984). Agrarian societies, whose economy is based on producing and maintaining crops and farmland, through the development of agriculture and domestication of plants and animals (via artificial selection), have caused landscape-level transformation with an increase in cultivated area. This has been helped by technological innovations, such as multiple cropping, crop rotations, and mechanisation (Ellis 2013), which have changed biogeochemical cycles and net primary production (Ellis 2011). Thus, as human populations have spread across the globe, the human colonisation and establishment of human societies at new locations will have acted differently on colonised ecosystems, displaying divergent anthropogenic complexity due to the direct interaction of human society on landscapes (Ellis and Ramankutty 2008, Ellis 2011, Ellis 2015) and their consequences on biodiversity (Balée 1998). As a result, ecosystems and biodiversity should reflect both current and past human action (Helmus *et al.* 2014). However, few studies have used an explicit temporal perspective to determine the current biodiversity structure or response to human habitat modification.

An explicit temporal perspective is crucial for comparing biodiversity across different locations (Carpenter *et al.* 2009). Indeed, to determine current biodiversity, human colonisation legacies may be one of the most important factors. Contemporary colonisation (e.g., Hawai'i, New Zealand, islands of east Polynesia) may display similar anthromes (= anthropogenic biomes) to countries with older colonised habitats (e.g., Europe, Asia). But these anthromes may have had a different rate for the human-induced landscape changes. Indeed, an older colonised habitat could have been exposed for a longer period of time to human sociocultural disturbance processes than a country with recent colonisation. Consequently, the time-lag response (= relaxation time; Kuussaari *et al.* 2009) of organisms (both in terms of population numbers and evolutionary adaptations) to the ongoing transformation will be greatly shaped by the capacity of species to cope or fail with major environmental changes (Tilman *et al.* 1994, Essl *et al.* 2015a, 2015b, Haddad *et al.* 2015). Considering this aspect is very important because it may help to understand community response trajectories under human legacies, and account for potential transient species (i.e., shorter temporal delays in time-lag response in new habitats, or relaxation time).

Furthermore, a change in human systems (a system is composed of a human population and its social

institutions, culture, and material products ; Nolan and Lenski 2010, Ellis 2015) will be reflected directly in the biosphere and its dynamics (Athens and Ward 1993, Ellis 2011, Stephen *et al.* 2011, Ellis 2015, Wood *et al.* 2017). The longer the process of gradual changes occurring under the action of human society (i.e., energy use, material consumption), the more that human impacts will be coupled with long-term transformations on natural ecosystems (Ellis 2015). Therefore, two things remain important to understand: firstly, the effect of cohabitation with human society of species (i.e., period and sociocultural regime) on the ecosystem transformation, and secondly, wether the different human systems will generate similar ecological inheritance on the local biodiversity and, if not, how they differ in their effects (Essl *et al.* 2015a).

1.2 New Zealand and its biodiversity

1.2.1 Unique biological diversity of New Zealand

The New Zealand continent was originally linked to the super-continent Gondwana (including what is now South America, Africa, Madagascar, Antarctica, Australia, New Zealand, Tasmania, India and parts of Southeast Asia). Plate tectonic movement led to Gondwana breaking up around 80 to 50 million years ago, into three major pieces of land; Australia, Antarctica and New Zealand (Department of Conservation 2006, Waters and Craw 2006). Before the separation from Gondwana, New Zealand flora shared characteristics with the flora of other parts of the super-continent, such as Southern beech (*Nothofagus sp.*) and an early primitive family of conifers.

Conversely, New Zealand's fauna was distinct from the rest of Gondwana, because it separated prior to mammals arriving, resulting in the evolution of native fauna without terrestrial mammals with the exception of few species of bats. A recent discovery of a fossil species of mammal, 'Saint Barthans mammal' (Worthy *et al.* 2006) suggests that mammals may have been present, but were not ecologically significant and are missing for much of the geological history of New Zealand. Consequently, New Zealand biodiversity has presented a unique evolution, in comparison with other locations, without the presence of terrestrial species from the mammal class and their potential influence.

1.2.2. First human arrival and its impact on biodiversity (1280-1890)

Despite major modern human movement around the earth having occurred since 2 million years ago, altering the ecological and evolutionary process on earth's ecosystems, New Zealand's biodiversity and ecosystems have only been recently affected by human populations, with the arrival of the Polynesian hunter-gatherer society settlement around AD 1280 (Whilmshurts *et al.* 2008, Whilmshurts *et al.* 2011). During this period, island biodiversity has only been affected by the direct effects of human activity. Human establishment in New Zealand has led to considerable changes in biodiversity, by putting pressure on plant and animal resources via broadening of foraging strategies (Cumberland 1941) and predation on megafauna (Grayson 2001). The Polynesian also brought in exotic terrestrial mammals: the polynesian rats (*Rattus exulans*) and polynesian domestic dog 'Kurī' (*Canis lupus familiaris*) (Grayson 2001), to the ecosystem with the terrestrial fauna dominated by large, flightless and naive birds (Duncan and Blackburn 2004, Perry *et al.* 2014). The establishment of human settlements was accompanied by use of fire leading to deforestation (Anderson 2002b, Perry *et al.* 2014) and fragmentation of habitat. During this period, New Zealand terrestrial avifauna (e.g., moa, Haast's eagle, penguins) were driven to rapid extinction through direct demographic pressure via intense hunting activity (McGlone *et al.* 1994, Holdaway *et al.* 2001, Duncan *et al.* 2002), significant loss of habitat in little more than 200 years after human arrival (Perry *et al.* 2014) and the arrival of new alien species, including predators and their associated diseases (Smith and Banks 2014). The reduction to extinction of the moa populations, a large and easily harvested prey, was led by the prehistoric Polynesian hunters across the New Zealand archipelago (Anderson 1998), due to its rich source of easily hunted animal protein and its high foraging return rate (Nagaoka 2001). Thus, during this period, a wide variety of bird became extinct along with the moa population, such as petrel, penguins, waterfowl, birds of prey, rails and several passerine species (Roff and Roff 2003, Boessenkool *et al.* 2009) due to the direct or indirect effect of the human settlement. This consequently reduced one of the major sources of available animal protein from the large easily harvested prey species (e.g., moa, penguins) that sustained human population growth, which led to the late arrival of new food sources (McGlone *et al.* 1994). At this time, Polynesian horticultural and agrarian society emerged, with the shift to cultivation of taro (*Colocasia*

antiquorum) or kūmara (*Ipomoea batatas)* using farming technologies, such as terracing or the use of fertiliser (ash produced by burning the covering vegetation; Schaniel 2001). This period also includes cultural changes (Anderson 2002a), with a transition to sedentary societies with larger population, and the development of fortified villages (McGlone 1989, Wood *et al.* 2016). This change of sociocultural system, resulting from the depletion of easily exploited stocks of protein-rich food (bird and animal resources), has been an important transition for the ecosystem with an intense increase of landscape use resulting in large-scale deforestation for crop farming and the development of starch-rich bracken and cabbage tree (*Cordyline australis*) and the over exploitation of swamp vegetation (rich in eels, and fish, and attractive to waterfowl) (McGlone 1989).

During the period of colonisation by the first human society, New Zealand's biota had undergone considerable changes with the extinction of a large range of the native avifauna (loss of 34 native birds species ; Diamond and Veitch 1981, Holdaway 1989, Holdaway *et al.* 2001, Duncan *et al.* 2002) due to human hunting, vegetation burning and predation by introduced mammalian predators (i.e., polynesian rat, polynesian dog) which had different predatory strategies compared to the native avian predators (McGlone 1989). The introduction of alien species, more specifically the pacific rat, during the Polynesian settlement has caused the extinction of smaller species (< 3.75 kg) and cavity-nesting species like petrel (Roff and Roff 2003). New Zealand's ecosystems started to undergo its first unnatural habitat transformation with notable human-induced deforestation using controlled or uncontrolled fire along coastal plains (Glade 2003), and clearing that led to open habitats (i.e., steppe, grassland, pasture). Some changes in vegetation were also observed to obtain adequate nutrition with development and pioneer vegetation (early successional system) along the new pasture (i.e., manuka, bracken, shrubby vegetation, edible fruit and berries; Oliver 1933, Cumberland 1941), disruption in plant dispersal and the introduction of exotic species (i.e., kūmara, taro) (Cumberland 1941, Yen 1961, Hargreaves 1963).

1.2.3 European society's arrival and its impact on biodiversity (1890 to present)

There were two stages of colonisation by European society: discovery and the settlement itself (Cumberland 1941), both having a major impact on NZ's biodiversity:

First, under an exploration expedition into the Pacific Ocean, Abel Tasman was the first European explorer to discover New Zealand in AD 1642. Many European expeditions took place after that, notably by explorers such as sealers, whalers, and timber groups as well as missionaries (e.g., Vancouver in 1791, Malaspina in 1793). Those different expeditions, through their trade and their settlers, represented the first contact with a European society by New Zealand's native species. Those European explorers introduced exotic species such as the Norway rat (*Rattus norvegicu*s), chickens (in 1773 during the second voyage of Captain James Cook to New Zealand; Wood *et al.* 2016) and wild pigs (*Sus scrofa,* in 1773 by Captain James Cook and Captain Furneaux; Reed and Reed 1951) to their temporary coastal itinerant settlements (Brocklie 2015). The European settlers also introduced white potatoes turnips, carrots and cabbage (Schaniel 2001, Keane 2010, Wood *et al.* 2016), which led to the development of agricultural land for potato crops, resulting in further natural habitat loss. European explorers also indirectly affected biodiversity, through the trade of flax (*Phormium tenax*) with Māori tribes and contributed towards the exploitation of natural flax (Keane 2010) and therefore habitat loss for native fauna. Through this period, European society produced only a small disturbance and transformation of the natural landscape. But this period represented the first experimentation of acclimatisation of exotic plants and animals (i.e. voyage of Cook in 1773 or from Furneaux in 1777; see Thomson 1922).

The second wave of European colonisation, with the arrival of large number of migrants and their establishment across the country, was the most important in terms of the environmental impact, on some ecosystem already in a fragile state. European settlers were originally from an industrialising-agrarian society (hybrid systems between industrial and agrarian societies; Ellis 2015) with their culture (e.g., religious, justice), institutions (e.g., bank, concept of ownership) and technological innovations (e.g., weapons, mechanisation; Wakefield and Stout 2010), as well as having a subsistence regime (described in

Ellis 2015) differing greatly from that of the Polynesians. These new settlers started to establish subsistence and commercial agriculture, as well as developing commercial manufacturing using local natural resources (e.g., timber). The arrival of large numbers of migrants led to the intensification of land-use (Nightingale 2008) for food production, water management systems (e.g., Auckland domain) and the establishment of a road network, resulting in pronounced environmental impact not only on flat plains like those settled by Polynesians but also on steep slopes (Glade 2003). European settlers, as a premodern society, have produced technological change by trading bows and arrow for firearms (Terborgh 1999). Consequently, the European hunter with more efficient technology should have taken similar native prey to the Polynesians, but in less time (Bates and Tucker 2010). Over the expansion of European settlers across the country has conducted to the emergence two new important anthropogenic landscapes in New Zealand: agricultural and residential (Ellis 2015).

The farming of European settlers was for commercial purposes (in contrast with the subsistence farming of Māori) and was more intensive (Glade 2003). Sheep and cattle were imported in large numbers, fire was used to clear native vegetation for developing pasture and agricultural land which has led to a significant loss of forested areas. The bush clearing was intensified by the need to export produce to the British Empire and other British colonies (Glasby 1991), resulting in more significant loss of natural habitats, due to converting more natural area to pasture (Glade 2003). Based on their past experience in Europe, settlers developed two different agricultural production systems, livestock production and crop cultivation, and consequently affected the native biota in different ways. Indeed, the major driver of biodiversity transformation, caused by livestock production systems with free-range feeding, resulted in significant loss of biomass, trampling and destruction of root systems of native plants, and replacement of wild grazers by livestock (Alkemade *et al.* 2013). The major transformation by crop cultivation systems include land deterioration or erosion due to deforestation and overexploitation of the soil (land deterioration via deforestation or erosion), increased competition with exotic flora, changes in community structure and dominance.

Another major impact of European settlers on natural ecosystems were through the introduction of a significant numbers of exotic species (Thomson 1922, Esler 1987, 1991). The European farmers introduced

European vegetable and exotic plants (Williams and Cameron 2001 in Allen and Lee 2001). The acclimatisation societies intentionally released exotic animal species including birds and mammals. These species have had major impact on the indigenous flora and fauna through competition, the introduction of novel diseases, and predation (Thomson 1922).

The improvement in agricultural productivity due to technological innovation in agriculture (e.g., mechanisation, fertilisation) led to the growth and concentration of settlements and the fast emergence of residential areas and cities (Gibson 1973). Urban areas and their growing populations resulted in a change of land-cover to infrastructure built in response to human needs (Lambin *et al.* 2001, Croci *et al.* 2008). Such landscape modifications are irreversible and permanent to the detriment of the local landscapes and its biodiversity (Blair 1996). Such changes are characterised by a landscape with more exposed ground, excavation and disturbance by anthropogenic movement (Goudie and Viles 2016).

Although many studies have demonstrated the impact of human colonisation on natural ecosystems and biodiversity (Athens and Ward 1993, Ellis 2011, Ellis 2015), few have investigated how the degrees of socioeconomic and technological development of human coloniser differ in their impact. New Zealand, with its Polynesian and European colonisations provide a good system for such a study. In less than two centuries, the degree of changes to the natural ecosystems in New Zealand are equivalent to that in Europe and North America over more than twenty centuries and four centuries respectively (Lambin *et al.* 2001). With such a short human colonisation history, the evolutionary changes in native biodiversity and changes of traits of organisms in response to human impact are more recent and may still be in the early stages of response to the human disturbances (Hughes *et al.* 2013). Furthermore, with the presence of introduced species with a longer history of coexisting with humans, New Zealand provides a good model for investigating the influence of society on the impact of natural ecosystems.

1.3 The effect of island history on New Zealand avifauna

During their colonisation, humans have influenced the New Zealand fauna through a non-random species

loss as previously described, through deforestation, hunting (e.g., of megafauna such as moa), the introduction of mammal predators, and a large number of attempts to introduce avifauna (Diamond and Veitch 1981, Duncan and Blackburn 2004). New Zealand presents the only place in the world where the pre-human community was thoroughly reshaped (Duncan and Blackburn 2004). Thus, following the first human arrival and the first introduction of mammal predators (e.g., kiore, and polynesian dog), the novel hunting strategy of both predators on the native avifauna presented the first unnatural filtering selection, on specific life history traits, by targeting large-body and ground- or burrow-nesting birds (Newton 1998, Duncan *et al.* 2002, Duncan and Balckburn 2004). The species characterised by such features were more likely to suffer from extirpation and extinction during this period. European colonisation (c. 168 years ago) was accompanied by an extensive introduction of mammal predators, which imposed the second unnatural filtering selection on native with a predation pressure on species with a broad range of body-size, driving a second wave of extirpation and extinction of the New Zealand native species.

Evolved in isolation, New Zealand avian species has evolved several traits under reduced ground-predation, such as reduction or loss of flight ability, ground- or burrow-nesting behaviour with extended incubation and fledging times (Dowding and Murphy 2001). Such traits are not adaptive in the presence of novel predator species like humans and mammals (predator naivety, explained by Milberg and Tyrberg 1993, Duncan and Blackburn 2004). Predator naivety has been widely reported and acknowledged as a cause of population decline and extinction of native species (Diamond and Veitch 1981, Atkinson 1989, Holdaway 1989, Vitousek *et al.* 1997, Holdaway 1999, Dowding and Murphy 2001, Steadman 2006, Innes *et al.* 2009, O'Donnell *et al.* 2015). Animal predation events occur at different stages of birds' life cycle, especially during the egg and chick stages (Brown *et al.* 2008). Endemic birds have evolved in the presence of a range of diurnal avian predators that probably hunted by sight. However, the traits evolved with such predators are less effective against mammal predators that hunt using visual and olfactory cues (Sanders and Maloney 2002). Our knowledge on the evolution of traits in response to such novel predation strategies by island avifauna is not well established. In New Zealand, few studies have investigated such aspect. However, a recent study on bellbirds observed that birds in the presence of predators are more prone to

reduce activities, such as nest visitation, around the nest (Massaro *et al.* 2011). Previous studies have considered predation pressure as a significant limiting factor for a bird population and an important parameter that influences the evolution of bird life-history traits and community assemblages, and a major cause of mortality in most birds (Lack 1968, Newton 1998, Martin 1988, 1992, 1995). Consequently, understanding of the New Zealand avifauna response to the new predation pressure is important for understanding predator-prey coevolution and for conservation of native species.

The island ecosystem of New Zealand, where humans have only present for 720 years, the humans can be perceived as a novel predator for the native avifauna, which could predispose them to an inappropriate response to human presence, anthropogenic habitat change. For Example, the presence inadequate responses of the giant birds (e.g., moa) could explain the fast decline of their population after the Polynesian arrival (Gemmell *et al.* 2004). Indeed, overhunting could have been facilitated by the naivety of the species to human and not due to the human density at that time (Holdaway *et al.* 2014). That moa extinction over a short period after human arrival suggested the absence of any anti-predation strategies of the species to humans (Wroe *et al.* 2004, Holdaway *et al.* 2014) and the presence of inappropriate responses such as the no-fear response, as observed in the Galapagos Islands by Darwin (1839) or by Stetson when visiting Howland Island in 1854 (Howland 1955), that predisposed them to overhunting, as easy sizeable meals. This, rather than the evolution of weapon technology by Europeans and the appearance of the shotgun in New Zealand, may better explain the increase in population depletion of some native species, as a contrast to observations in Manu National Park in Peru, where the gun offered a halving of hunting effort compared with the bow and arrow (Levi *et al.* 2009).

Native avifauna have also suffered from humans through large-scale habitat modification (e.g., deforestation and pasturalisation), which have driven a decline and extinction of forest species (e.g., huia *Heteralocha acutirostris* , New Zealand quail *Coturnix novaezelandiae*, laughing owl *Sceloglaux albifacies*, New Zealand little bittern *Ixobrychus novaezelandiae,* bush wren *Xenicus longipes*), with a combination of other factors (e.g., mammal and human predations). Habitat specialisation of some New Zealand species

(i.e., forest and swamp specialists) may have predisposed them to succeed despite the fragmentation of their landscapes caused by the human activity (Diamond 1984, Keinath *et al.* 2017) and in the presence of a novel, complex ecological system established by humans. The constraints developed by anthropogenic ecological systems are known as limiting factors for biodiversity and could drive a new pattern of biodiversity through the selection of life-history attributes correlating with the occupied area and the local trajectory of landscape change. New Zealand and its landscape, along with its human history, have not shown a uniform transformation of habitats across the two islands by the humans that had different effects on its avifauna. Indeed, a study on native avifauna has shown that species did not present the same degree of sensitivity to size and isolation (Diamond 1984), so the species do not share similar biological traits that could give them the same advantages when faced with anthropogenic habitats.

Thus, an approach to analyse the interaction of biological traits and habitat type including human modified habitats can offer knowledge for both fundamental ecology and conservation biology (Statzner *et al.* 2004, Croci *et al.* 2008, Croci *et al.* 2009).

Studies on the response of biodiversity to habitat modification using biological traits and discrimination between native and exotic species across the anthropogenic habitat are lacking. Van Heezick *et al.* (2008), through an urban gradient of a South Island city, have shown that nearly half of the species recorded along the gradient were exotic birds and that native species responded differently to the habitat gradient and without a potential effect from vegetation structure. Avian diversity has been well surveyed in Wellington (Duncan and Duncan 2005) and Hamilton (Fitzgerald and Innes 2013). Avian diversity and community structure in the largest city of New Zealand, Auckland are less known. In addition, only a few studies have examined temporal variations in bird assemblages over time. Nevertheless, such information may provide insight for management of native diversity in anthropogenic habitats and could be completed by a better understanding of the relationships between birds' life-history traits and specific anthropogenic landscape features.

Introduced avian fauna in New Zealand has been an important component of local human habitat change and potentially impact on a local community via food or nesting competition (Ingold 1998, Wiebe

2003), direct predation (Massaro *et al.* 2007, Hudges *et al.* 2008) or transmitting novel a diseases (van Ripper III *et al.* 1986). Invasion success of exotic species has been well studied using parameters related to the suitability of alien species to the abiotic environment and the location of introduction. Nevertheless, the influence of their past evolutionary history has not been included. Humankind, as one of the leading forces of evolution of the planet through its activities and its habitat changes, is known to play an important role in shaping the local biodiversity. The processes of human niche construction that have shaped biodiversity will tend to follow similar evolutionary trajectories and it allow introduced species with past histories of coexisting with human to succeed in the new habitat. An understanding of the influence of human experiences on invasion success of a species can could help determine the effect of past evolutionary history on the community responses (e.g., biological trait selection) to ongoing anthropogenic factors. Thus, an understanding of how evolutionary history has shaped the response of the exotic community in terms of key biological traits or behavioural trait in the anthropogenic habitat in New Zealand, can also help predict which native community will have problems coping with the new anthropogenic habitats of New Zealand. Such information could help conservation practitioners to determine the viability of species in anthropogenic habitats.

1.4 Thesis structure and objectives

This research aims to provide a better understanding of the influence of humans and their societies on native biodiversity, in a country with a recent human history and understand the role of humans and their societies in the evolutionary processes of local biodiversity in colonised ecosystems. The thesis includes three main aspects:

Firstly, to identify, in a country with recent human history, the influence of colonisation by a modern human society on biodiversity and more particularly on bird communities. This will help to establish an understanding of the impacts of human societies on intact ecosystems and their biodiversity. There is a

notable lack of research into the influence of human societies on the evolution of the community structure and the potential filtering effect of each sociocultural society on current ecosystems.

Secondly, to determine if the past evolutionary history of species with a human sociocultural society shapes the key life history traits and the species' ability to cope and persist with modified habitats. In addition, whether a species' past evolutionary experiences with humans could help to develop appropriate responses to adapt to the new environment shaped by human societies. These may provide a better understanding of the role of evolutionary history in shaping a species' response to anthropogenic effects.

Thirdly, to describe the influence of human filtering on life history traits of species in anthropogenic landscapes. So far, only a minimal amount of research has explored the impact of past human activity on life history traits. Such a study will help to understand the evolutionary drive of local species assemblages in human-dominated landscapes and predict the evolutionary trends of communities in ecosystems newly colonised by humans.

This thesis contains six research chapters (Chapters 2 to 7) with a general introduction (Chapter 1) and a general discussion (Chapter 8). Each chapters (2 to 7) has been written in publication format, and therefore they may contain some common information around the key concept of the thesis. The chapters are:

Chapter 1 gives background information relating to the topic of the study. A literature review on the emergence of the human system on earth is presented, followed by an overview of New Zealand history of human emergence and biodiversity evolution responses across their biological trait and their behaviour.

Chapter 2 highlights the importance of human society's legacies on biodiversity patterns and structures. It reviews the current knowledge of anthropogenic filtering and proposes a new key concept of an ecological framework linking human-induced changes with native species extinction and selections for adaptive traits. It highlights the importance of understanding the relationship between society type, timing of societal colonisation and the adaptive responses of native species.

Chapter 3 examines the effect of human societies on native biodiversity, across the two waves of settlers who established themselves in New Zealand, by assessing what role human societies and their sociocultural regimes, have played on the change of habitat and native avifauna during colonisation. More specifically, the chapter investigates the response of native avifauna through extinctions recorded in each colonisation by a human society and their habitat modifications.

Chapter 4 investigates the influence of the history of coexisting with humans on the potential capacity of species to establish in different habitats modified by human sociocultural societies. The relationships between the natural niche of a species and their past experience with human society were examined in order to provide another potential determinant of invasion success, co-evolutionary history with human, in addition to o other well-known determinants (i.e., propagule pressure).

Chapter 5 examines the influence of human colonial history as a filter on biological traits in New Zealand avifauna, across both a natural habitat and anthropogenic habitats. This chapter assesses the importance of species status (native/exotic), phylogeny and past experiences with human to determine species assemblages in modern-day New Zealand.

Chapter 6 investigates the change on the local community structure in a forest fragment remnant within a recently urbanised habitat. The influence of human development on avian biodiversity over time was assessed in the local and regional community, by exploring transition in bird assemblage. This chapter examines the potential effect of changes in urban surrounding and forest remnant cover over 26 years on native and exotic bird assemblages

Chapter 7 assesses the effects of past-evolutionary experience with human-induced habitat changes and its related predation on species' nest-site selection strategies. I investigate whether species with different evolutionary history with human-induced habitats changes are similar in nest-site selection strategies along an urban gradient.

Chapter 8 synthesises the findings of different chapters and discusses the contribution and limitations of the thesis and future research directions.

Chapter 2

Temporal and sociocultural effects of human colonisation on native biodiversity: filtering and rates of adaptation

Abstract

Modern human societies have impacted native species richness and their adaptive capacity on every continent, in clearly contrasting ways. I propose a general model explaining how the sequence, duration, and type of colonising society alters native species richness patterns through changes in evolutionary pressures. These changes causes different 'filtering effect' on native species, while simultaneously altering the capacity of surviving species to adapt to further societal pressures. Using this model may better explain the observed native species extinction rates and extirpation legacies following human societies colonisations, as well as predict likely future patterns.

2.1 Introduction

Human societies radically change local and regional native species richness and the ecological and evolutionary processes of colonised ecosystems (Koch and Barnosky 2006, Barnosky 2008, Ellis 2015). As a hypothesis to explain these changes, I propose that the rates and types of changes in native species richness following human colonisation are mediated by the temporal dynamics and types of the coloniser's societies. Specifically, rates of extinction and extirpation following human colonisation can be understood as analogous to habitat filtering processes (Cornwell *et al.* 2006, Kraft *et al.* 2015). In this framework, time elapsed since colonisation, the number of times colonised by a different society type and its sociocultural regime at the time of colonisation all play significant roles in shaping the ecological and evolutionary responses to sociocultural filtering processes.

Recent studies have shown a divergence in life history traits through nest predation constraints between regions colonised by humans at different times (Martin and Colbert 1996). Rates of change (e.g., alterations of reproductive strategies) may be more rapid in more recently colonised sites (Cartwright *et al.* 2014). I propose that these patterns result from anthropogenic filtering and adaptation processes and that these processes can be applied together with well-established biogeographic principles, such as latitude, altitude, habitat area and degree of isolation (Mc Arthur 1972, Helmus *et al.* 2014), to predict current and future patterns of native species richness and life-history traits, especially with regard to the capacity of species to adapt to changing environments and climate. By incorporating the temporal and sociocultural aspects of human colonisation alongside the classic dimensions of biogeography, it may be possible to develop a more comprehensive framework for understanding biodiversity patterns in an increasingly anthropogenic biosphere. Indeed, previous studies using chronometric resolution have highlighted that megafauna extinction were more related to anthropogenic causes than to a climatic role, in Australia (Rule *et al.* 2012), Patagonia (Villavicencio *et al.* 2016), and in New Zealand (Holdaway *et al.* 2001, Trewick and Gibb 2010).

2.2 Changes in human societies

In this study, I consider the differing effects of human colonisation on species richness by three major types of human societies: hunter-gatherer, agrarian and industrial, each with profoundly different levels of societal complexity, subsistence regimes, resource use, and ecosystem engineering practices (Ellis 2015, Table 2.1). Hunter-gatherer societies, while still present today, represents the earliest forms of human societies (Ellis 2015). These societies generally depend for subsistence on mobile to moderately sedentary social foraging strategies for subsistence, which maximise the use of seasonally available local or regional food resources. Typical patterns of resources of exploitations are first by hunting the most desirable megafauna, then by broadening hunting and foraging strategies across taxa (niche broadening), and later by the intentional use of fire to maintain more productive early successional ecosystems (Hamilton *et al.* 2007, Ellis 2015, Ellis *et al.* 2016; Table 2.1). Harvesting pressures by these societies filter biodiversity, causing extirpation and range shifts with ecosystem engineering using fire, both intentionally and unintentionally (Grayson 2001, Barnosky *et al.* 2004, Koch and Barnosky 2006, Boivin *et al.* 2016).

A transition from hunter-gatherer to early agrarian societies produces even greater alterations of native biodiversity (Table 2.1). Agrarian societies systematically denude vegetation from landscapes (e.g., grazing by livestock; Brigg *et al.* 2006), with practices ranging from temporary shifting cultivation, resembling burning by hunter-gatherers, to the continuous use of land by annual cultivation and the use of irrigation, causing permanent habitat loss and fragmentation (Ellis 2015, Boivin *et al.* 2016). Further impacts of agrarian societies include the introduction of domesticates, diseases, ruderals, and feral species, as well as additional pressures from larger, denser, and more rapidly growing human populations (Grayson 2001, Koch and Barnosky 2006, Ellis 2015, Boivin *et al.* 2016).

Most recently, the industrial revolution and the massive food requirements of growing human populations have led to agricultural intensification, with the use of toxic agrichemicals and excess nutrients, loss of remaining habitat fragments, increased drainage of land, intensive grassland management, and the construction of transportation networks and movement of materials and biota across the planet (Ellis 2015, Boivin *et al.* 2016; Table 2.1). Modern agricultural techniques have therefore resulted in a further increase of

land-use intensity (Benton *et al.* 2003), the development of non-agricultural land use (i.e., urbanization; Ramalho and Hobbs 2012), and therefore new forms of biodiversity decline. Furthermore, the cultural evolution that occurred during the industrial stage societies also resulted in new combinations of constraints, most notably via the appearance of new philosophical concepts, such as alterations for the sake of 'improvements' or 'aesthetics' of the landscape. These ideas that led to the creation of the acclimatisation movement (Wallace 1911, Osborne 2000) that translocated familiar biodiversity into unfamiliar environments colonised by settlers (Carruthers *et al.* 2011, Boivin *et al.* 2016). This was done to improve the productivity of the land for agriculture, hunting, or for nostalgic reasons (Osborne 2000). Thus the appearance of this concept of acclimatisation was characterised at a local scale by an increase in species richness, but was often detrimental to native ecological inheritance and its biodiversity.

Table 2.1: Human sociocultural systems classified by primary subsistence regime, in order of historical emergence (based on Nolan and Lenski 2010, and Ellis 2015) in relation to anthropogenic transformation and their impact on local ecosystems and biodiversity ([a] Kune š *et al.* 2008, [b] Grayson 2001, [c] Huston 2005, [d] Smith 2011, [e] Cartwright *et al.* 2014, [f] Croci *et al.* 2008, [g] Stockwell *et al.* 2003).т

Sociocultural system	Subsistence regime	Technological innovation	Ecological impact	Introduced species	Impact on native species				General impact native ecosystems
					Flora		Fauna		
					Observed	Potential traits selected by humans	Observed	Potential traits selected by humans	
Hunter gatherer	Hunting foraging	Land clearing using fire, social hunting, food processing and cooking, projectiles, ceramics	Extensive use of ecosystem resources, resource depression, diet breadth strategy	Dispersion of commensal species (e.g. rat, dog) and consumed species (e.g. seed), consumed species translocation (e.g. kumara).	Reduced abundance of harvested native plants for consumption in located area	Light, nitrogen, nutriment rich soil demanding taxa [a]	Population decline of prey, favoured for hunting (i.e. large vertebrates), diversification of prey resource with appearance of smaller prey	Small species, earlier sexual maturity, reduced antler size [b]	Human predation pressure at local scale, abundance of higher return prey (i.e. larger) reduced first. The abundance of lower return prey (i.e. smaller) reduced as a secondary effect. Exotic species impact native species via predation pressure on native flora and fauna, or via dispersion of novel diseases.
Agrarian	Continuous subsistence agriculture, handicrafts	Plough, animal tractions	Strong use of high net primary productivity area for food production, landscape modification to increase prey abundance(clam garden, fish-weirs, diversion dams), released of nutriment in soil.	Dispersion of annual crops, translocation of domesticated species (i.e. herbivores), transplantation of perennial fruit , nut-bearing, and root crops species.	Early successional stage plant communities increase, higher ratio of production to respiration, loss of perennial plants, slower growing species decline. Reduction of woody biomass and shift to earlier successional sequence vegetation communities.	Smaller sized, annually reproducing species and higher ratio of production to respiration favoured [c]. fallow-cycle vegetation community lost of germination dormancy, increase of seed size [d].	Native grazers favoured, reduction in population size of large vertebrates and species diversity.	Grazing herbivores [c], selection of early life reproduction [e].	Mosaic vegetation landscape, native vegetation converted to annual crops, domesticated herbivores substituted for native ones. Dispersion of rare and/or endemic species to marginal habitats (low productive area). Increased animal diversity (species richness) due to translocation.
Industrial	Commercial, agriculture, manufacturing.	Fossil energy, synthetics, rapid bulk transport, telecommunication.	Intensification in land use (reduced energy availability, high human population density in settlements), colonisation of new land near high NPP (net primary production) land (lakes , rivers, aridity, wetness area) marginal lands due to their transportation requirements, resource extraction increases, urban/industrial growth, drainage of wet area, flood control.	Introduction of exotic predators, translocation of exotic species to enrich the diversity of the region (i.e., acclimatisation society).	Decline of vegetation with slow growth, invasion by exotic species	Fast growth species, speed of germination, tolerance to metal [g].	Extinction of native vertebrates due to introduction of exotic predator species, decline of native predator and herbivore species remaining in marginal habitats.	Sedentary, omnivorous, long life expectancy, importance parental care [f], pesticide resistance [g].	Switch of biodiversity composition with appearance of introduced species replacing native species but increase of richness.

2.3 Native biodiversity response through filtering and adaptations

Throughout each of these sociocultural regimes, human-induced habitat changes, such as altered land use, introduction of exotic species and exploitation of native species (Table 2.1), have acted as a 'filter' that some native species will pass through or persist, and others do not (Kraft *et al.* 2015, Boivin *et al.* 2016), leading to associated extinctions and extirpations. The number of surviving species after these filtering periods will be the result of two factors: 1) the numbers of species initially present (biogeographic principles) and 2) the adaptive capacities of native species to cope and persist with altered environments and climate change, which will be determined by their species specific traits (Cornwell *et al.* 2006). So, following each filtering period, co-existing species sharing a trait or combination of traits that cope with anthropogenic change tend to have a higher probability of survival, a process termed 'inheritance ecology' (Kraft *et al.* 2015). Thus, as human societies and their associated habitat alterations change through time, species with suitable life history strategies will tend to be selected and survive (Figure 2.1). Consequently, the current native species richness of an ecosystem and its community structure are the product of initial regional species richness mediated by a combination of phylogenetically conserved and convergent traits that are adaptive in the face of anthropogenic pressures (Pavoine and Bonsall 2011).

The adaptive capacity of a species in responding to dynamic anthropogenic environments depends on life history and other complex genetic traits (Helm *et al.* 2009). Natural selection for life history and other traits under earlier environmental conditions (i.e., initial human arrival), therefore, shape evolutionary responses to later environmental changes (Sih *et al.* 2011). Species face three main outcomes in responding to rapid environmental change: (1) survival through adaptive traits already selected through evolutionary history without further evolutionary change, (2) survival without an evolutionary history of selection for adaptive traits or phenotypic plasticity or (3) extirpation or extinction in the absence of adaptive traits or phenotypic plasticity (Sih *et al.* 2011, Hendry *et al.* 2011).
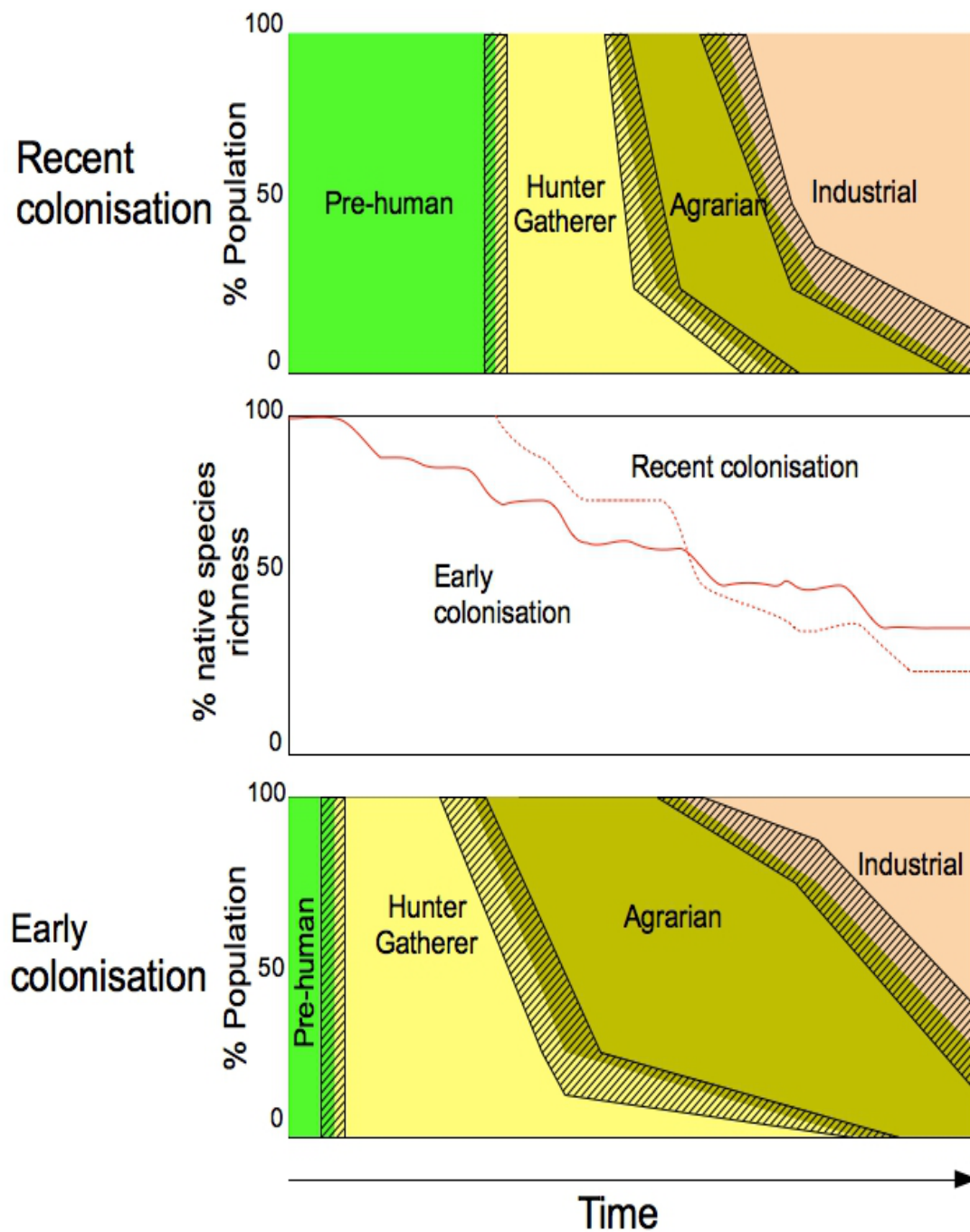
Figure 2.1: A stylised depiction illustrating differing temporal impacts of human colonisation patterns on native species richness and their evolutionary response under two colonisation patterns (early and recent) using three major colonisation periods of human sociocultural system: (1) hunter-gatherers, (2) agrarian societies and (3) industrial societies. Hatched zones represent filtering events during the transition period between sociocultural regimes. Extinction events may occur because of filtering during transition periods or failing to adapt within each sociocultural niche. Shorter transition periods and shorter duration of each cultural development stage may result in more rapid extinction or extirpation rates of native species.

Similar adaptive patterns have been observed in environments undergoing urbanization and are categorised as exploiter, adapter and avoider (Blair 1996). Thus, the evolutionary past shapes the persistence of native species in rapidly changing anthropogenic habitats (Pavoine and Bonsall 2011, Essl *et al.* 2015a).

Different types of societies act as different filters for native biodiversity and species traits, acting first to determine whether species go extinct or persist, and acting then on surviving species through extended periods of selection and adaptation within anthropogenic environments. As the scale of societies has increased, so has human capacity for ecosystem engineering, such that anthropogenic filtering of biodiversity has changed substantially over human history, creating different ecological constraints acting to filter the biological traits of persisting native species (Essl *et al.* 2015a).

Native species richness within continents like Africa, Asia and Europe received the earliest selective pressure from behaviourally modern humans (Panel 1). The earliest anthropogenic filtering processes caused the extinction of many species, in particular megafauna species that were hunted to extinction, with cascading consequences across entire ecosystems (Grayson 2001, Barnosky *et al.* 2004, Barnosky 2008, Ellis 2015, Boivin *et al.* 2016). This was followed by the first adaptive responses to anthropogenic environmental changes and pressures. For example, mollusc populations declined in size and altered age structure due to harvesting pressure from prehistoric humans (Grayson 2001, Boivin *et al.* 2016).

With agrarian and industrial societies, anthropogenic filtering pressures continue to increase and expand, driving continuing species extirpation and extinction, community shifts and increasing the rates, intensity and extent of anthropogenic ecological changes. Time elapsed between major changes in society type also moderate the severity of filtering effects, by increasing the time available for species to adapt to dynamic anthropogenic habitats. At the time of first colonisation of native habitats, different types of human societies present different degrees of filtering (Balée 1998), with larger scale societies (agrarian, industrial) tending to induce more rapid rates of environmental change and more extreme filtering than smaller scale societies (e.g., hunter-gatherer; Panel 1).

Figure 2.2: Long-term global changes based on the percentage of pre-human anthropocene megafauna (mammal and avifauna weighing > 0.7 kg, Dirzo *et al.* 2014) that went extinct as a function of estimated times of major categories of human sociocultural systems in Africa (Green), Europe (Yellow), North America (Blue) and New Zealand (Orange) (supplementary form for methodology). The x axis is a logarithmic scale (year), trend-lines shows temporal changes of extant megafauna species for each location, and the onset of human population exhibiting major categories of sociocultural systems are indicated by symbols (hunter gatherer: Δ , Agrarian: □, industrial: ◇)

Panel 1. Case study

Our planet has experienced a large mass extinction event caused by human activities over millennia through human interaction (e.g., hunting, harvesting...) or transformation (e.g., human niche constructing activities like cleared lands, biotic exchange, erosion). Thus this model has been used in three different contexts of selective pressure from behaviourally modern human, (1) Europe and Africa, which had the earliest selective pressures from humans (> 45,000 years before present [YBP]; Fu *et al.* 2014, Suppl. 1); (2) North America (~10,000 YBP; Bourgeon *et al.* 2017, Suppl. 1) and (3) New Zealand, which observed a later selective pressure from humans (~737 YBP; Wilmshurst *et al.* 2008, Suppl. 1). The ultimate goal is to identify divergence between the change of human societies and their associated habitat alterations are affiliated to reduction of native megafauna richness.

In these three contexts, similar process of sociocultural niche construction have been observed, also with similar sequences of changes sociocultural systems (i.e., hunter-gatherer, agrarian, industrial societies), but with different durations and overlaps between each type of system (Figure 2.2). Thus countries more recently colonised by humans have experienced shorter transitions times between sociocultural systems that could help explain the longer temporal delays in biodiversity responses to society change. The proportion of megafauna species that went extinct following colonisation of hunter gatherer societies (Figure 2.2) in Europe (0.8% biodiversity reduction) and Africa (8.8%) were more fewer than those in North America (30.6%) and New Zealand (55.9%). Humans in Europe and Africa became established over a much longer period and had less impact on local megafauna extinctions, a pattern that is clearly contrasted by North America and New Zealand. However, such extinction rates cannot fully be explained by human impacts alone, as other effects such as environmental impacts, either working alone or in tandem with human impacts can contribute to extinction or extirpation events. Similar results have also been observed during the later sociocultural niche construction during the onset of industrial societies (Figure 2.2), which are more characteristic of the Anthropocene period. Indeed, Europe (13.9%) and Africa (8.8%) had a lower extinction rate during the industrial period and the anthropocene period than North America (18.7%) and New Zealand (25.0%) where extinction was more pronounced. The time-lagged between the onsets of a news human sociocultural systems and the subsequent extinction events appears to vary with the duration of human association. In locations with longer periods of human association, the extinction rates of native biodiversity was lower (see Figure 2.2 for European and Africa) following transitions between sociocultural systems, likely due to longer periods for evolutionary change to occur between transitions.

However, in New Zealand, one of the last locations to be colonised by humans with particularly rapid transitions between sociocultural systems, the native community of megafauna has undertaken a faster magnitude of extinction. So, the transition period between human sociocultural systems combined with climatic change may favour an evolutionary responses of biodiversity to anthropogenic impacts (i.e., past experience with humans provides the evolutionary history that could shape how biodiversity responds to human impacts; Sih *et al.* 2011).

The importance of temporal dynamics in ecology has been well recognised. Our approach highlights the importance of temporal effect of human societies of the study of human impacts on biodiversity and landscape.

Native species in African and European regions experienced the longest and most gradual forms of filtering pressures by preindustrial societies. This enabled traits adaptive to dynamic anthropogenic environments to become established and lessened rates of extinction both during societal regime transitions and during the period between the transitions (Panel 1). In North America, hunter-gatherer societies arrived much later than in Europe and Africa, driving a rapid phase of extinction at the time of first colonisation (Martin 1973, 1984); This rapid filtering effect is even more pronounced in the very recent first arrival of hunter-gatherers to New Zealand (Barnosky *et al.* 2004, Barnosky 2008, see Figure 2.2).

Species exposed to shorter periods between anthropogenic filtering events (Figure 2.1) would be expected to experience higher risks of extinction when faced with a subsequent filtering event, owing to inadequate prior evolutionary shifts in adaptive traits (Essl *et al.* 2015a, 2015c). This may explain why North America's more recent establishment of larger scale agrarian and industrial societies is related to higher extinction rates than in Europe, as native species have had less time to adapt to anthropogenic environmental changes in the Americas (Figure 2.2 see Panel 1)

To fully understand the long-term prospects for native species' persistence and adaptation in the face of anthropogenic pressures, rigorous comparative investigations of long-term anthropogenic filtering that focus on the timing and types of societal colonisations and sociocultural regime shifts may serve as critical observational laboratories (Cartwright *et al.* 2014). While it seems fairly well established that more recent colonisations are associated with higher rates of native megafauna loss, the causes of this are not fully understood, nor are they necessarily generalisable to other species. Nevertheless, it is clear that failure to consider the effects of societal legacies and sociocultural transitions on native species loss and the presence of adaptations that might prevent future losses can have major consequences (Ramalho and Hobbs 2012). By presenting an integrated framework for investigating the processes of native species extinction and adaptation in response to anthropogenic filtering, it is hoped that ecological science and its application to biodiversity conservation can be advanced, ideally through further studies, models, and conservation strategies informed by a deeper empirical and theoretical understanding of native species' adaptations to anthropogenic environments (see potential applications and additional considerations, Table 2.2).

Acknowledgments

Table 2.2: Potential applications and additional considerations following our framework

Research fields	Suggested applications	Additional consideration (limitation, alternative hypothesis, other factors)
Evolution	- Understanding of how human society affects species adaptation rate. - Add new understanding to the evolution of genetic response and phenotype variation in biodiversity. - Understand the ability of species or individuals to cope with anthropogenic habitats. - Develop conceptual framework to explain how past human history influences the evolution cue-responses relationships between organisms and environments.	- Lack of available data on early human colonisation history - Lack of understanding of the effect of human population growth and size on biodiversity. - Lack of knowledge about interactions of multiple stressor interactions (e.g., climate change, invasive species, and habitat clearance).
Conservation	- Probability of extinction or extirpation of native species. - Aid in the understanding of the causes of species population declines. - Further understanding of the factors that lead to the establishment of invasive species.	- Current rate of habitat clearance. - Population size / propagule pressure of invasive species. - Rate of invasive species introduction. - Vulnerability of native species (e.g. island species). - Lack of inclusion of interdisciplinary approaches.
Ecology	- Add to biogeographical parameter to help to refine the process of species extinction. - Understand biodiversity dynamic and response to novel cues. - Understand behavioural response flexibility of species to anthropogenic habitats. - Understand the behavioural response to ecological change.	- Uncertainty about the effect of climate change. - Habitat loss and fragmentation. - Introduction of novel enemies (e.g. diseases, predator or parasites). - Lack of knowledge about interaction of multiple stressors. - Problem of interpretation due to complexity of biodiversity response and individual potential adaptations.
Anthroecology	- Understand human-induced ecological pattern changes and their influence on the complexities of socioecological systems. - Understand the dynamic interplay between human society and ecological systems. - Aid in understanding the evolution of the anthropogenic global-warming system and its effect on biodiversity. - Understand the relation between human sociocultural systems transitions, landscape alteration and their long-term impact.	- Required the time depth accessible on the area on human societies. - Lack of knowledge of major anthropogenic roles in shaping biodiversity in each societies. - More multidisciplinary research required with ecologists and archaeologists.

Supplementary forms

Suppl. 1: Material and Methods:

I obtained the date of non-human anthropocene megafauna (mammal and avifauna weighing > 0.7 kg; Dirzo *et al.* 2014, Pimm *et al.* 2014) considered as extinct or extirpated from four geographic regions (Africa, Europe, North America and New Zealand; see *Appendices*), from published information on IUCN (2015), New Zealand birds online [Accessed 7 July 2017], the sixth extinction [Accessed 7 July 2017] and in primary literatures (Kingdon 1997, Palumbo and Gallo-Orsi 1999, Reumer *et al.* 2003, Baillie *et al.* 2004, Fontaine *et al.* 2007, Bover and Alcover 2008, Jackson and Nowell 2011). The number of non-human anthropocene megafauna was extracted from IUCN [Accessed 7 July 2017]. The percentage of non-human anthropocene megafauna that went extinct in relation to times was established based on the total number of pre-human megafauna species present.

Suppl.1-Table 1 Estimated date of occurrences of major categories of sociocultural systems (time in YBP).

Sociocultural system	Africa	Europe	North America	New Zealand
Hunter Gatherer	~ 200,000	~ 45,000	~ 10,000	~737
Agrarian	~ 6,000	~ 3,000	~ 5,000	~ 567
Industrial	~ 127	~217	~ 207	~ 137

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Chapter 3

How human colonisation history has impacted the community structure of New Zealand birds leading to the highest known extinction rates

Abstract

Anthropogenic impacts on ecosystems and biodiversity have been widely recognised. However, the chronology of human colonisation is rarely considered as a factor in ecological studies attempting to understand anthropogenic impacts. I investigated habitat and biodiversity changes resulting from human colonisation within the Auckland Region and the North Island of New Zealand; an island nation with very recent human history. Specifically, I quantified the effects of Polynesian and European societies on landscape changes and native avian species diversity. My results demonstrate dramatic changes in landscape structure and biodiversity during the settlement of these human societies. The development of anthropogenic ecosystems and the introduction of exotic fauna by different human societies have brought fast, unprecedented changes on native biodiversity structure. The colonisation of New Zealand was correlated with an extremely high rate of extinction of native birds; the highest extinction rate recorded for any taxonomic group to date worldwide. I found a significantly higher extinction rates following European colonisation (1760 E/MSY) than following Polynesian colonisation (421 E/MSY). My results indicate that biodiversity responses to human-induced changes are the result of the interaction between past evolutionary history of the local biota and the sociocultural regime of the colonising human social groups. Thus, my results highlight the importance of incorporating a human historical dimension into ecological and conservation studies.

3.1 Introduction

Human societies have altered the ecological and evolutionary processes of natural ecosystems (Vitousek *et al.* 1997, Lambin *et al.* 2003, Barnosky *et al.* 2012), replacing natural landscapes with man-made systems such as farmland, roads, and buildings (Pauchard *et al.* 2006). Since the earliest ancestor of modern humans, an increasing range of the earth's ecosystems have been colonised by small social groups. To satisfy the needs associated with increasing population sizes, such as food sources, leading to range expansions of human populations across a wider area (Ellis 2011, Ellis 2015, Boivin *et al.* 2016). Pre-human ecosystems have thus been transformed dramatically, in terms of biodiversity composition and landscape structure. The human social and cultural transformation (Ellis 2015) has had a major effect on the degree of human impact on the native ecosystems. These changes have in turn altered the ecological and evolutionary trajectories of species within these ecosystems (Ellis 2011, Steffen *et al.* 2011, Šizling *et al.* 2016). However, the changes brought by humans have not been homogeneous across the areas colonised (Ellis 2011, Ellis 2015). There is evidence indicating that these changes are the result, at least in part, of the sociocultural system of the colonising society (e.g., hunter-gatherer, horticultural, agrarian, industrial) (Ellis 2011, Steffen *et al.* 2011, Ellis 2015). The impact of sociocultural system of a given society is characterised by a particular level of changes to local biogeographic, evolutionary, and ecosystem processes, due to its social institutions, which tend to be altered in ways that may lead to heritable benefits and lead to a 'social niche construction' (Ellis, 2011; Ellis 2015).

Ecosystems that have been colonised only recently, by more culturally advanced human social groups in term of sociocultural systems (defined in Ellis 2015), experience a different sociocultural niche construction than ecosystems colonised by prior, less culturally advanced human social groups. The ecosystem changes under a human social niche construction can be influenced across the habitat by different human cultural, material and ecological inheritance (i.e., fire regime, farming, domestication) which result in species loss, trophic displacement of megafauna, and higher species turnover causing shifts in ecosystem structure (Ellis

2015). For example, a more recent human group would have more advanced means to modify the natural system to suit its needs (i.e. agricultural tools *vs* agricultural machinery) and would cause a faster and larger impact on the native ecosystem transitions (Willis *et al.* 2004, Pimm *et al.* 2006, Ellis 2015).

So, human-induced habitat changes during the colonisation process are correlated with the degree of the sociocultural system (i.e., expressed in their use of technology and engineering) of the society (Ellis 2015), which acted as an anthropogenic filter (Dawkins 1982, Croci *et al.* 2008, Gámez-Virués *et al.* 2015) depending on its ecological inheritance (see Ellis 2015). Thus, the current community structure of colonised habitats will vary according to the colonisation history by human societies and the degree of the sociocultural system of those societies. These differences may lead to different anthropogenic filters (i.e., different heritable ecological patterns and processes), causing contrasting extirpation or extinction (Steadmand 1995) of a non-random subset of species. Indeed during the social niche construction of new human social groups, ecosystems and communities will be exposed to a new anthroecological succession (i.e., order of sequences of different societies acting on the biome, or anthrosequence) and its anthropogenic transformation of the ecological pattern and processes (Ellis 2015). The resulting ecological communities will thus retain a reduced array of species (Sih *et al.* 2011), due to the extirpation or extinction of some species.

During the filtering process, the capacity of a species to cope or adjust to a modified habitat will depend on a species' life-history and its behavioural traits (Sih *et al.* 2011, Hendry *et al.* 2011, Essl *et al.* 2015a). Species that have coexisted with humans for longer periods can be considered as pre-adapted to anthropogenic change and can be expected to possess key traits or behaviours that make them more likely to pass through, and survive further filtering events and adapt more quickly to the new environmental conditions (Martin and Clobert 1996, Sih *et al.* 2011, Hendry *et al.* 2011, Essl *et al.* 2015a, Boivin *et al.* 2016). Therefore, human-experienced avifauna and human-naïve fauna are also likely to differ in their ability to cope with anthropogenic changes 'ecological inheritance' (Olding -Smee 1988, Olding -Smee and Laland 2012).

New Zealand represents one of the last land masses colonised by humans (Anderson 1991, Craig *et al.* 2000) and the general consensus indicates two human colonisation events: Polynesian society (Māori) around AD 1280 (Wilmshurst *et al.* 2008, Wilmshurst *et al.* 2011) followed by European societies around the mid-

1800s (Duncan and Young 2000). Thus, New Zealand native biodiversity has undergone at least two anthropogenic filtering events within the last 500 years (approx. 25 human generations).

This period represents a short time-frame for species to adapt (Essl *et al.* 2015a) and reach a new evolutionary equilibrium (Heaney 2000, Rabosky and Glor 2010). The discrepancies in the subsistence regime and technological asymmetry (technology-gap) between these two sociocultural regimes may have each favoured a different subset of species within the resulting anthroecosystems (Ellis 2015, see Suppl. 2).

Thus, the colonisation history of New Zealand offers a useful model to understand: (1) the impacts of human colonisation on local ecosystems and (2) the responses of species to environmental changes caused by humans with asymmetrical sociocultural developments.

In this chapter, I investigate the effect of two anthropogenic filtering events in the native biodiversity and ecosystems of New Zealand by two human groups with asymmetrical sociocultural niches (see Ellis 2015), using two scales of analysis: (1) at an island level, using the North Island of New Zealand (the area in New Zealand with the higher rate of species extinction since human contact, Holdaway *et al.* 2001), and (2) at a regional level, using the Auckland region. I highlight the divergence in sociocultural niche and anthropogenic filtering processes, between the first and second colonisation events, by modern humans of New Zealand. Using historical records, I examine the effects of anthropogenic filtering on the structure of New Zealand ecosystems and the native avifauna composition at these two geographic scales. I chose the New Zealand avifauna as an indicator of changes in native biodiversity. Avifauna has one of the best fossil records from the late Quaternary, with a great level of details of distribution and changes in distribution. Birds are also the dominant terrestrial vertebrate group in New Zealand (Holdaway *et al.* 2001). More New Zealand avifauna extinctions have resulted from the human colonisation than from climate change (Holdaway *et al.* 2001, Trewick and Gibb 2010).

3.2 Materials and methods

3.2.1 Study area.

The North Island of New Zealand (113,729 km²) is part of the New Zealand biodiversity hotspot (Conservation International) and the 14th-largest island in the world. It is the most populated island of New Zealand, supporting around 75.5% of the country's human population. The North Island is defined by two ecoregions, temperate broadleaf and mixed forest (e.g., Northland temperate forest, Northland temperate Kauri Forest), high in native species richness for both flora and fauna.

The Auckland region (4,894 km²) is one of the nine governmental regions of the North Island. This region has attracted large populations of settlers during both the human colonisation events, due to its landscape and its milder climate. Consequently, the region is currently the most populated of New Zealand (2013 Census; 1.415 million people, ~ 33.4% of NZ population; New Zealand Government Statistic 2016). The first human contact in the region is estimated at around 1300 AD (Davidson 1978a).

3.2.2 Ecosystem structure and dynamics of change

Anthropogenic effects on natural ecosystems were estimated using the degree of forest lost following each period of colonisation. The area of pre-human forest cover was obtained from Ewer *et al.* (2006). Forest cover in 1840 was estimated for the North Island and the Auckland region based on work by McGlone (1983). Current estimates of land cover for agriculture, forest and artificial cover (e.g., road, building) were obtained from the Statistics New Zealand website (New Zealand Government Statistics 2009).

3.2.3 Bird species

To estimate the response of native terrestrial birds to human settlement, I determined the presence or absence of avian species in the North Island of New Zealand and in the Auckland region based on historical records. Terrestrial bird species that were only present on offshore islands in each area were considered as absent. I

established a list of avian species for the three main time periods (pre-human, post Polynesian settlement and post European settlement), based on unpublished reports, publications and personal observations (Hutton 1870, Buller 1870, Anonymous 1940, Anonymous 1942 – 1944, Anonymous 1946, Lovegrove 1980, Robertson *et al.* 2007) (see Suppl. 3). Native species from the Order Anseriformes were not included in the list due to their potential to migrate outside the study zone.

3.2.4 Extinction rate

Using the New Zealand avifauna records and the extinction records during each period of human colonisation (Holdaway *et al.* 2001, New Zealand online 2013), I calculated the extinction rate for each colonisation period using the number of species extinctions (E) per year per total number of species following Pimm *et al.* (2006). In order to allow comparison with other research (Pimm *et al.* 2006, Pimm *et al.* 2014), I adjusted it to per million species years (MSY), rather than using the absolute numbers.

3.2.5 Data analysis

I used the well-established mathematical model of the species-area relationship (SAR) equation ($S = cA^z$), to calculate the extinction of species after deforestation (McWethy *et al.* 2010, Hanski 1998, May and Stumpf 2000, Brook *et al.* 2003). In this equation, S is the number of species, A is the habitat size (area) and c and z are two constants (Diamond 1972, Drakare *et al.* 2006). When the size of a habitat A is reduced to A_{now}, the number of species in the reduced habitat S_{now} can be predicted using the equation:

$$\frac{S_{now}}{S} = \left(\frac{A_{now}}{A}\right)^2 \quad \textbf{(1)}$$

Previous research has established that if z = 0.1, this offers a good estimation of the number of short-term species extinctions that will occur following habitat loss (Rybicki and Hanski 2013). Conversely, long-term extinction patterns are more likely to occur when z = ~0.25 (Rybicki and Hanski 2013). To estimate the

long term extinction, I used the estimated value z = 0.27 that has been established using a meta-analysis of SAR (Diamond 1972).

To estimate the amount of time elapsed between European settlement and the new equilibrium in native terrestrial avian species richness, I calculated the 'relaxation index' (I), using the ratio of the number of extinctions after a given time period (T) (Brooks *et al.* 1999):

$$I = \frac{\left(S_{\text{now}}\right)}{\left(S_{\text{original}}\right)} \quad \textbf{(2)}$$

where S_{now} represents the number of species available at a given time, and S_{original} is the number of species present at the start of the period of change. At the start of the relaxation process (i.e., initial urbanisation development), when $S_{\text{now}} = S_{\text{original}}$, I will be equal to 1, and it will subsequently decline with time and urbanisation progress. I calculated the half-life of the declining avifauna using the equation of Books *et al.* (1999) and assumed that the species decline, represented by *I*, follows a first-approximation exponential relationship (Diamond 1972).

$$I = \exp\left(-k \times T\right) \quad \textbf{(3)}$$

where *T* is the time after the start of urbanisation and *k* is a constant. Half-life was calculated using *I* = 0.5 to represent the potential time taken for the extinction of half of the species from the community to occur.

3.3 Results

3.3.1 Changes in landscape structure since human colonisation.

The landscape-level impacts on the North Island following human colonisation (AD ~1280-present)

were considerable. Large changes in the composition of natural ecosystems occurred, with a 76.5% reduction of native forest cover (8,395,828 ha) and a concomitant increase in agricultural land (6,858,441 ha) and urban area (607,900 ha) (Table 3.1). Similar patterns were observed in the Auckland region where intense deforestation has occurred with the loss of 55.7% of the forest since human colonisation of the region around AD 1350. Since European settlement in AD 1840, the Auckland region's ecosystem has been characterised by a rapid expansion of urban areas, averaging 298.3 ha.year^{-1} (range: 16.6 to 927.9 ha.year^{-1} between 1840 and2008) and extensive conversion of forest to agricultural areas (318,311 ha between 1840 and 2008, ~1,894.7 ha.year^{-1}). During this period, intensive deforestation has occurred with the loss of 72% (117,704 ha between 1840and 2008, -700.6 ha.year^{-1}) of the forest that remained after pre-Polynesian occupation of the region (Table 3.1).

Table 3.1: Changes in land cover due to deforestation following human settlement (from 1280 to 2008) and the current land cover for the North Island of New Zealand and the Auckland region. Percentage values represent the proportion of the total area (in ha).

		North Island	Auckland Region
Area size		11,401,800	489,400
Forest Cover	Pre-human	10,969,272 (96.2%)	327,396 (66.9%)
	Pre-european	5,484,636 (48.1%)	163,698 (33.45%)
	Current	2,573,444 (22.6%)	45,994 (9.4%)
Current land cover	Urban area	607,900 (5.3%)	49,520 (10.1%)
	Agricultural area	6,858,441 (60.1%)	318,311 (65.0%)

3.3.2. Response of Native avifauna to human colonisation

Before human colonisation, 57 species of terrestrial birds were present on the North Island (only including species where breeding populations are/were known to be present or fossil evidence indicated the presence of a breeding population, see Holdaway *et al.* 2001). The extinction of 12 species occurred during colonisation by Polynesians (AD ~ 1280–1800; ~ 421.05E/MSY) and a further 14 extinctions occurred during European colonisation (AD 1800–2015; ~ 1447.03E/MSY). As such, the current North Island avifauna represents only 54.4% of the pre-human species pool. I used measures of historical changes in forest cover and the native avifauna populations, to predict the total number of species that will become extinct post-European colonisation. These estimates included 31 native species plus four species of birds self-introduced from Australia and naturalised: the welcome swallow (*Hirundo neoxana*), silvereyes (*Zosterops lateralis*), spur-winged plover (*Vanellis spinosus*) and white-faced heron (*Egretta novaehollandia*) (n = 35 species). Predictions of bird extinctions during each human society were made by calculating the slope *z* (see methods) based on deforestation trajectories during human colonisation of the North Island. The z-value was higher during European (*z* = 0.49) than during the pre-Polynesian (*z* = 0.34) period; thus the extinction rate in relation to deforestation was significantly greater during the European period in the North Island. Based on the post-colonisation extinction rates of native avifauna for the North Island (AD ~ 1280–2014), I found a relaxation rate of *k* = 0.0004 year^{-1}, which gives a half-life of 734 years (AD 2034).

Using a lower estimate for the value of the slope *z* = 0.1 and an upper estimate of *z* = 0.27, based on the remnant forest habitat in the North Island (2,573,444 ha, see Table 3.1), my estimates of the number of native avifauna species that will be likely to survive European settlement vary between 42 species in the short term to 37 species in the long term following habitat loss, excluding the 4 self-introduced species. The North Island of New Zealand has therefore exhibited higher extinction rates during the European period than predicted, with only 31 species remaining, much lower than the estimate of 37 to 42 species. Analogous trends during the pre-Polynesian period were observed, because using the same calculation methods based on the amount of forest remaining at the time of European arrival, I estimated a reduction of the avifauna species pool of 4 to 10 species (i.e., 47–53 species remaining), whereas the observed extinctions during this period were higher with

14 extinctions (43 species remaining). This suggests that the species/area relationship is insufficient for predicting extinction rates in the North Island of New Zealand, and that other factors have had a significant impact on the extinction rates of native avifauna species.

For the Auckland region, I estimated from published records that there were 33 species present in 1870 in the Auckland region, 23 species in 1939-45 and 24 species in 1980 (North Island brown kiwi recorded, missing in previous survey). In 2014, 23 species still remained, thus exhibiting a reduction of 30.3% of native avifauna during European settlement (1870–2014) in the area.

Using values of the slope $z = 0.1$ and $z = 0.27$ based on the remnant forest in the Auckland region (45,994 ha, see Table 3.1), my estimates of the number of native avifauna species that will survive following the completion of the European settlement and urban development process (in 1840; Duncan and Young 2000), vary between 23 species in the short term to 19 species in the long term, excluding the 4 self-introduced species. When the observed number of bird species found in the Auckland area is included in the equation, I found a value for the slope of SAR, $z = 0.2844$. From the avifauna history of the Auckland region between AD 1870 and AD 1945, I found a relaxation rate of $k = 0.0021$ year^{-1} using the z-value of 0.28, which gives a half-life of 143 years (AD2013).

3.4 Discussion

The global expansion of humans has transformed ecosystems, following clearly defined successional stages of sociocultural niche constructions by human societies (Ellis 2015, Šizling *et al.* 2016). In spite of relatively recent colonisation by humans, the ecosystems of New Zealand have experienced anthrosequences comparable to other regions worldwide, but over a much shorter timeframe. In this study, I have shown that the regime shift between sociocultural systems is associated with very high rates of species extinctions. European settlement, a society more complex and characterised by high sociocultural inheritance and technological capacity (see Suppl. 2), caused a more dramatic change to native ecosystems and the avifauna community.

During this transition, I have observed a change in the magnitude of anthropogenic impact on biodiversity from a small-scale society (Polynesian) to a large industrial scale society (European), with more societal complexity, specialisation, technological capacity and cultural innovation (Ellis 2015).

The colonisation of New Zealand by humans has resulted in a multitude of ecological impacts (i.e., habitat transformation, exotic species introductions and native species extinctions or extirpation). The first human group colonising New Zealand ecosystems from AD 1280 to 1800 was a simple horticultural society (see Suppl. 2) which spread along the coast of the country, and initiated the process of environmental transformation for the purpose of food. The New Zealand landscape experienced its first anthropogenic transformation and anthroecological succession (i.e., 'anthropogenic filter') via the introduction of exotic mammalian predators (see Suppl. 2), the use of fire regimes (McWethey *et al.* 2010) to facilitate an early successional stage for harvesting food (Ewers *et al.* 2006) and hunting (Stevens *et al.* 1988). Thus, archaeological records of this period in the Auckland region show exploitation of a wide range of birds and other animals (Davidson 1978a). This period was mainly characterised by over-exploitation of avifauna and other animals leading to extinction of species (Anderson 2003, King 2003). By the first fire regimes leading to forest clearance and the appearance of open shrub-land bracken taxa such as *Pteridium esculentum* and *Coriaria* along water banks (McGlone and Wilmshurst 1999). Later around the 14th century, coinciding with a global decrease in temperature (Yen 1961), the Polynesian society started to boost food returns from land by exploiting seed crops (Hargreaves 1963) and tubers such as kūmara, taro, hue (gourd) and uwhi (yam) (Yen 1961, Hargreaves 1963), and exploited the most productive part of the landscape for agriculture (Davidson, 1978b). Polynesian settlers of the Auckland region have thus changed their habits concerning animal protein resources by exploiting more fish and shellfish (Davidson 1978a). Consequently, the pre-human lowland forest landscape near water sites of the North Island and Auckland region (McGlone 1983, McWhethy *et al.* 2009) shifted into an open landscape of secondary scrubland, fern and tussock grassland during Polynesian colonisation (Anderson 2002b) and there is evidence of their gardening activities (Lowe *et al.* 2000). Thus Polynesian society (Māori) in New Zealand has caused similar landscape transformation and modification (i.e.,

forest decline) as other simple horticultural societies and observed similar ecological inheritance patterns (i.e., heritable ecological patterns or processes that confer adaptive advantage / disadvantage to a population or to sociocultural systems), via the use of fire (Anderson 2002b) and stone technologies (e.g., adzes, Davidson 1978a,b), and which favoured open spaces for agriculture. This period had a great biodiversity loss with a high extinction rate of avifauna, particularly megafauna (e.g. North Island Giant Moa, *Dinornis novaezealandiae*; Hodgen's waterhen, *Gallinula hodgenorum*), due to over-exploitation as a high-value animal protein resource in the early human diet (Hargreaves 1963, Trotter and McCulloch 1984, Holdaway 1989, Steadman 1989, Pimm *et al.* 2006) and also by an active deforestation process caused by controlled and uncontrolled fires (Anderson 1984, Steadman 1989, McGlone and Wilmshurst 1999). Furthermore, during this period, the anthrome (anthropogenic biome) formed (Ellis 2011) by this society which is characterised by a transformation of ecosystems via hunting and burning, and a change in landscape structure of habitat near water banks with low land clearing (see Table 3.1, showing 50% reduction of forest cover in the North Island [5,484,636 ha to 11,401,800 ha] and in the Auckland region [136,698 ha to 489,400 ha]), overcrowding, and alteration of productive ecosystems, like wetlands or forests, (caused by changes in vegetation composition or via habitat destruction) (McGlone 1989). Biodiversity structure was also altered via a process of selective extinction of terrestrial mega-avifauna (Duncan *et al.* 2002) and the species in trophic levels that were directly associated with mega-avifauna (i.e., mega-avifauna predatory species such as Eyle's Harrier, *Circus teauteensis* and Haast's Eagle, *Aquila moorei*). These ecosystem and species level changes led to new ecological patterns associated with more open landscapes cover by bracken with open low and scrubby vegetation (Table 3.1, McGlone and Wilmshurst 1999), leading to erosion / degradation of the soil and also to the heterogeneity of biodiversity.

The arrival of Europeans to New Zealand in the 1800s exposed the local ecosystems to advanced agrarian sociocultural systems (see Table 3.1) that transformed already modified ecosystems and also untouched native ecosystem, with a different array of tools (e.g. plough, garden tools) and technological resources (e.g., crop rotation techniques, shifting cultivation, use of fertilisers, firearms, nursery gardens). In addition to exotic species brought by Polynesians (see Suppl. 3), further exotic species beyond those required

for agricultural purposes were introduced, through the establishment of an acclimatisation society (see Suppl. 3; Steadman 1989, McGlone 1989, Glade 2003). Thus, the rate of exploitation of natural landscapes for resources was boosted, for export to Great Britain (e.g., native timber, wool, grain, kauri gum) and to provide sufficient food resources from agricultural practice for an expanding population. Consequently, from the time of their first arrival, Europeans have pursued an aggressive policy of deforestation to develop European style farming practices (Schaniel 2001) road infrastructure and the rapid creation of urban settlements (Gibson 1973) that lead to rapid change in local ecological patterns and processes. These changes produced a more intense filtering process than previously experienced by New Zealand ecosystems, during the primary anthroecological succession. Thus habitat change during this period has resulted in the appearance of new ecological constraints (secondary anthroecological succession), such as overgrazing via the introduction of herbivorous species, or further natural habitat transformation via the intentional or unintentional introduction of exotic flora (Esler 1987, Duncan and Young 2000) and fauna (Steadman 1989), habitat loss via exploitation of steep slopes unexploited by Polynesians, nutrient saturation, and high sedimentation rates (Schaniel 2001). These impacts were all resulted from a subsistence and commercial agriculture (e.g., meat and dairy products), which harness food energy through domestication, in contrast to the previous society, which collected energy via harvesting and hunting directly from native ecosystems. From AD 1860 to 1920, around 50% of the remnant forest of New Zealand was transformed to pastoral grassland and crop land (Schaniel 2001, Trustrum and Hawley 1986) to increase food productivity. This period, between 1890 and 1900, had an average forest clearance rate of 2.7% per year (Glasby 1991) and one of the greatest and most rapid habitat changes of any country (Trustrum and Hawley 1986). As a British colony specialising in the exportation of foods (Glasby 1991) via refrigerated shipping, New Zealand has been able to rapidly reach a high degree of agriculture mechanisation (Gibson 1973), leading to early industrial development when compared with other European colonies (Alvarez *et al.* 2011). The fast mechanisation and industrialisation combined with the economic growth of the country has increased the rate of land exploitation, via the expansion and intensification of agricultural land cover and the processing of raw materials (e.g., wood, aluminium, iron and gold). These factors have thus contributed to impacts on local ecological patterns and processes (e.g., pollution, extractive industrial damage, nutrient

saturation; disturbance in ecological regime; see ref. Ellis 2015). In addition, mechanisation of crop production has increased labour productivity and led to a fast and earlier migration of people to cities (Gibson 1973, Alvarez *et al.* 2011). The concentrated European settler colonisation has favoured the development of industrial land use and urban land cover (i.e., pavement, building) which impacted on the structure of biodiversity via fragmentation of remnant ecosystems, erosion, pollution, competition with non-native species that are adapted to highly disturbed environments or ornamental species introductions (Thomson 1922).

3.4.1 Rates of species extinction.

Since human colonisation, native habitats and terrestrial avifauna of the North Island have undergone significant transformation, initially due to anthropogenic filtering processes by pre-Polynesian society (Holdaway 1989, Atkinson and Cameron 1993, Holdaway and Jacomb 2000), resulting in an extinction rate of its terrestrial avifauna of 21% in about 500 years (~ 421.05 E/MSY) and a strong change in landscape cover with 50% reduction in forest cover (Table 3.1, McGlone 1983, McWethy *et al.* 2009). The extinction rates observed in New Zealand during the different phases of human colonisation are markedly higher than the estimated current global average extinction rate of 100 E/MSY and the estimated background extinction rate of about 0.1 E/MSY without human action (Pimm *et al.* 2014). This shows the severity of the impact of human colonisation processes and the associated anthropogenic filtering on biodiversity extinction rates. Thus during this period, habitats and ecosystems experienced the first direct modification and filtering from humans as well as indirect modification caused by human society activities (i.e., introduction of new predator species, subsistence regime of the society). Consequently, this period represented the first unnatural filtering effect or selection for local biodiversity (global warming excluded as a direct effect). Indeed, humans have acted as a direct selection pressure on native terrestrial mega-avifauna through hunting pressure, but also on other smaller species with the introduction of the Pacific rat (Holdaway 1999). Consequently, at the time of European arrival, native biodiversity and its avifauna had already experienced an anthropogenic filtering event and observed a change in selection pressures. Thus, the arrival of Europeans and the transformations that followed have caused a second filtering process on the remnant terrestrial avifauna, via range restriction, habitat modification and the

appearance of new predators with different predatory strategies. Since AD 1800, North Island avifauna has lost 31.1% of its species (~1447.03E/MSY). At a regional level in Auckland, the species reduction was 27.3% (~1759.53E/MSY) since AD 1870. To the best of my knowledge, these are the highest extinction rates ever recorded (see in Ceballos *et al.* 2015). My data showed a stronger effect from European colonisation on the avifauna community at both national and regional levels, in comparison to the previous colonisation by a Polynesian society.

The local rate of extinction observed in the case of the North Island of New Zealand and Auckland region avifauna after European settlement was much higher than the extinction rate recorded in other countries colonised by Europeans, such as Australia where the extinction rate was 88 E/MSY (Brooke *et al.* 2008). However, this lower extinction rate may be due to the larger land area of Australia and the longer period of coexistence (~ 40,000 years; Hiscock 2008) of the native fauna with Australia's Aboriginal peoples. By contrast, Hawaii, another island ecosystem lacking native mammalian predators, experienced a similar pattern of extinction rates to New Zealand, with lower extinction rates of 315.3 E/MSY during the Polynesian occupation compared with 1197.6 E/MSY during the European occupation (extracted from Brower 2008). The high proportion of Hawaiian native avian species that are endemic (72% of the avifauna; Brower 2008, Myers *et al.* 2000) may explain the high degree of extinction that has occurred following each of the two human colonisation phases, as has been suggested by Pimm and Askins (1995). However the level of endemicity alone, cannot explain the rapidity of the extinction process that occurred following the colonisation of New Zealand. The extinction rate of North Island avifauna was nearly four times higher during European colonisation than that during Polynesian colonisation. Therefore, the impacts from European colonisation (e.g., habitat fragmentation, exotic species invasion, nutrient saturation, pollution) affected native species indirectly as well as through biogeographical processes, rather than just via direct human behaviour, such as hunting. Additionally, the introduction of a wide range of mammalian predators with novel predatory strategies to native species (Holdaway 1999), resulted in greater impacts (i.e., a stronger filter) on native avifauna than in countries evolved with mammalian predators.

3.4.2 Human historical legacies influence the shape of biodiversity.

Settlement by both European and Polynesian societies in the North Island and the Auckland region has led to a significant transformation of natural habitat to anthropogenic habitat as previously described, with a reduction of natural ecosystems (e.g., forests; Table 3.1, Hanski 1998) and the introduction of new predators (see Suppl. 4, Holdaway 1999). The impact of human settlements led to new population equilibrium levels for native species. Thus, on the North Island, I predicted a sharper decline of species during European colonisation than during the Polynesian period, solely due to the combined effect of deforestation and an increase in exotic predator species. These factors add to the indirect extinction debt that resulted from adaptation to the new biodiversity components (Martin and Clobert 1996) during Polynesian settlement. My results suggest that the rate and magnitude of disturbance that has occurred during colonisation by each society had very different impacts on avian extinction rates. My outcome demonstrated also that the number of bird extinctions in the North Island was not only due to the result of habitat destruction and new predation but also from a wide range of factors caused by human society, such as the introduction of new avifauna. Previous studies have established the half-life of doomed species to be around 50 years (Brooks *et al.* 1999, Ferraz *et al.* 2003, Ferraz *et al.* 2007). In the case of the Auckland region, the half-life for the local bird community was estimated to be 144 years after AD 1870 (i.e., half-life reached in AD 2014). As predicted, only one native species has gone locally extinct since 1980, with the loss of the last remnant population of North Island brown kiwi during the last 24 years (ecologically extinct). This observation can also explain the requirement of a long time lag (relaxation time) for New Zealand native avifauna to respond to environmental changes and to establish a sustainable population without active management. Recent work on the time-lag response suggests that species with long historical legacies of coexisting with human-induced habitat change may have shorter time-lag delays in their response (Hendry *et al.* 2011). Indeed species with an evolutionary history of dealing with human-induced habitat change will likely have increased sensitivity to perceive a human habitat change (Cartwright *et al.* 2014) and greater ability to induce an optimal response to the novel environment (Sih 2013). Along this line, New Zealand avifauna has only co-existed for a short period with human-induced habitat change (i.e., 500 years of Polynesian habitat change) at the time of European colonisation, allowing little time for species to

exhibit an appropriate evolutionary response to cope with the multiple novel stressors caused by the first colonisation event, before a second colonisation event occurred. Consequently, the slow response of native biodiversity to human-induced habitat change may be due to this short period of association with human-induced habitat change and may not have provided enough evolutionary time for species to adapt.

3.5 Conclusion

The impact of human societies on ecosystems and biodiversity has greatly differed in New Zealand from other colonisation events. During each colonisation event, native ecosystems have suffered from a different intensity of habitat alteration and ecosystem transformation caused by the differences in sociocultural niche construction of the settler societies. Thus native avifauna, have suffered from different levels of constraints during the human societies filtering that has led to the extinction and extirpation of some native species, and adaptation by others. Throughout the sociocultural and anthroecological succession of societies established in New Zealand, the advanced agrarian system of European society has displayed a stronger anthropogenic filtering process on native avifauna, via direct (e.g., hunting) and indirect actions (e.g., introductions of exotic predators). Consequently, these two anthroecological successions (i.e., Polynesian and European societies) have created an anthropogenic filter that has resulted in changing selection pressures for native biodiversity.

Consequently, an understanding of societal legacies (e.g., technological innovations, cultural and institutional innovations) across global ecosystems and the frameworks of ecological successions are important for interpreting the current trajectory of ecosystem changes.

Acknowledgements

Supplementary forms

Suppl. 2: Societal classification of New Zealand settlers by, the chronosequence of historical colonisation. To understand the basic pattern of each societal types of New Zealand settlers, data for each sociocultural system at their arrival were extracted from Hargreaves 1963, McGlone 1983, Stevens *et al.* 1988, Mc Wethy *et al.* 2010, Anderson 1991 and summarised in a table based on Nolan and Lenski 2010 and Ellis 2015.

Settler society	Sociocultural system	Subsistence regime	Technological innovation	Cultural and institutional innovation	Introduction species
Polynesian	Simple horticultural	Forest clearance for hunting, travelling, security, dwelling	Domestication (dogs, chicken)	Land ownership at different level, tribe (iwi), clan (hapū), family group (whānau)=> communal enterprise	Fauna : Mammals: 2 species (kiore and dogs), insect (fleas, lice)
		Permanent horticulture (kūmara, taro, potatoes, maize)	Horticulture innovation : plot rotation, tillage	Trade with travel within tribal district and between districts (stones and foods)	Flora : few plants (kumara, taro, maize, tī, Karaka)
		Pastoralism	Wooden or stone tools (adzes, hoe, chisels, fishhooks, harpoon points)	Wooden dwelling, village, fortification and security	
		Hunting megafauna (moa, seals....)	Watercraft and walked track	Oral culture transmission, wood and stone carving / Basic maritime culture	
European	Advanced Agrarian	Subsistence and commercial agriculture (self-sufficient farmer)	Iron tools, animal traction, biological control	Literacy	Fauna : Mammals 48 (4) species; Marsupial 12 species; Birds 130 species , Fish 33 species, insects
		Subsistence and commercial hunting (whaler, sealer...)	Road network, waterways	Transport (horse bus, coach services, bullock carts...)	Flora : up to 26000 species
			Agriculture innovation : irrigation, fertilizer, shifting cultivation, plough	Expansion trade and empire	
			Hunting tools : traps, firearms	Strong maritime culture	
			Communication : electric telegraph		

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Suppl. 3: List of native avifauna species in New Zealand North Island for the three main time period (prehuman, Pre European and current) and in Auckland area for the two major period (Pre-European and current) and their conservation status.

Conservation status is based on the New Zealand threat classification system (Robertson *et al.* 2012) and are **D** Declining, **R** Recovering, **Re** Relict, **Nu** Naturally Uncommon, **E** Extinct, **NV** Nationally Vulnerable, **NE** Nationally Endangered, **NC** Nationally Critical, **NT** Not Threatened. * Self-introduction

Common name	Scientific name	Old scientific name	Conservation Status	date of establishment	Pre human	Pre European	Current	Pre European		During European		Current
								1870	1873	Between 1939-1945	1980	2005-14
Little bush moa	*Anomalopteryx didiformis*		E		X							
Mappin's moa	*Pachyornis mappini*		E		X							
Coastal moa	*Euryapteryx curtus*		E		X							
Large bush moa	*Dinornis novaezelandiae*		E		X							
North Island brown kiwi	*Apteryx mantelli*		NV		X	X	X	X	X		X	
Little spotted kiwi	*Apteryx owenii*		R		X	X						
Reef heron	*Egretta sacra*		NE		X	X	X					
White faced heron *	*Egretta novaehollandiae*		NT	1940			X				X	X
Great white egret	*Ardea modesta*	*Egretta alba*	NC		X	X	X					
New Zealand little bittern	*Ixobrychus novaezelandiae*		E		X	X						
Eyle's harrier	*Circus eylesi*		E		X							
Swamp harrier	*Circus approximans*	*Circus assimilis*	NT		X	X	X	X	X	X	X	X
New Zealand falcon	*Falco novaeseelandiae*	*Hieracidae novaezelandiae*	NV		X	X	X	X	X	X		
New Zealand quail	*Couturix novaezelandia*		E		X	X		X	X			
North Island adzebill	*Aptornis otidiformis*		E		X							
Banded rail	*Gallirallus philippensis*		D		X	X	X	X	X		X	X
Weka	*Gallirallus australis*	*Ocydromus Earli*	D		X	X	X	X	X	X	X	X
Snipe rail	*Capellirallus karamu*		E		X							
Spotless crake	*Porzana tabuensis*		Re		X	X	X	X	X		X	X
March crake	*Porzana pusilla*		Re		X	X	X	X	X		X	X
Hodgens' waterhen	*Gallinula hodgenorum*		E		X							
North Island takahe	*Porphyrio mantelli*		E		X	X						
Pukeko	*Porphyrio melanotus*	*Porphyrio melanonotus*	NT		X	X	X	X	X	X	X	X
New Zealand coot	*Fulica prisca*		E		X							
Variable oystercatcher *	*Haematopus unicolor*		R		X	X	X	X	X		X	X
Spur-winger plover	*Vanellus miles*		NT	1970			X					X
South island pied oystercatcher	*Haematopus finschi*		D		X	X	X	X	X		X	X
Black stilt	*Himantopus novaezelandiae*		NC		X	X	X	X	X		X	X
New Zealand pigeon	*Hemiphaga novaeseelandiae*	*Carpophaga novaezelandiae*	NT		X	X	X	X	X	X	X	X
Kakapo	*Strigops habroptilus*		NC		X	X						
Kaka	*Nestor meridionalis*		NV		X	X	X	X	X	X	X	X
Red-crowned parakeet	*Cyanoramphus novaezelandiae*	*Platycercus novaezelandia*	Re		X	X		X	X			
Yellow-crowned parakeet	*Cyanoramphus auriceps*	*Platycercus auriceps*	NT		X	X		X	X		X	X
Orange-fronted parakeet	*Cynoramphus malherbi*		NV		X	X						
Morepork	*Ninox novaeseelandiae*	*Athene novaezelandiae*	NT		X	X	X	X	X	X	X	X
Laughing owl	*Sceloglaux albifacies*		E		X	X						
Shining cuckoo	*Chrysococcys lucidus*		NE		X	X	X	X	X	X	X	X
Long tailed cuckoo	*Eudynamys taitensis*	*Eudynamis taitensis*	NU		X	X	X	X	X	X	X	X
New Zealand owlet-nightjar	*Aegotheles novaazaezealandia*		E		X							
Kingfisher	*Todiramphus sanctus*	*Halcyon vagans*	NT		X	X	X	X	X	X	X	X

Rifleman	*Acanthistta chloris*		D		X	X	X					
Bush wren	*Xenicus longipes*		E		X	X						
Rock wren	*Xenicus gilviventris*		NE		X	X	X					
Stout-legged wren	*Pachyplichas jagmi*		E		X							
New Zealand pipit	*Anthus novaeseeandiae*		D		X	X	X	X	X	X	X	X
New Zealand fernbird	*Bowdleria punctata*		D		X	X	X	X	X	X	X	X
Whitehead	*Mohoua albicilla*		NT		X	X	X	X	X			
Grey warbler	*Gerygone igata*	*Gerygone flaviventris*	NT		X	X	X	X	X	X	X	X
New Zealand fantail	*Rhipidura fuliginosa*	*Rhipidura flabellifera*	NT		X	X	X	X	X	X	X	X
Tomtit	*Petroica macrocephala*	*Petraeca toitoi*	NT		X	X	X	X	X	X	X	X
North Island robin	*Petroica longipes*	*Petraeca longipes*	NT		X	X	X	X	X			
Silvereye *	*Zosterops lateralis*	*Zosterops dorsals*	NT	1850			X	X	X	X	X	X
Stitchbird	*Notiomystis cincta*		NV		X	X		X				
New Zealand bellbird	*Anthorrnis melanura*		NT		X	X	X	X	X			
Tui	*Prosthemadera novaeseelandiae*	*Prosthemadera novaezelandia*	NT		X	X	X	X	X	X	X	X
North Island kokako	*Callaeas wilsoni*	*Callaeas cinera*	R		X	X	X	X	X	X	X	X
North Island saddleback	*Philesturnus carunculatus*	*Creadion carunculatus*	R		X	X			X			
Huia	*Heteralocha acutirostris*		E		X	X						
North island piopio	*Turnagra tanagra*		E		X	X						
Welcome swallow *	*Hirundo noexena*		NT	1950			X				X	X
New Zealand raven	*Corvus antipodum*		E		X							
23	number of species				57	45	31	33	32		24	24	23

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Suppl. 4: Introduced mammalian predator species (Order Carnivora), following human colonisation of New Zealand.

Colonizing Society	Species introduced			Reasons of their introduction	Introduction attempt
	Family	Common Name	Species Name		
Polynesian Society	Canidae	Dog	Canis lupis	Utility	Successful
	Muridae	Kiore	Rattus exulans	Utility	Successful
European Society	Felidae	Cat	*Felix catus*	Escapees	Successful
	Muridae	Black rat	*Rattus rattus*	Stowaway	Successful
		Norway rat	*Rattus norvegicus*	Stowaway	Successful
		Mouse	*Mus musculus*	Stowaway	Successful
	Mustelidae	Ferret	*Mustela putorius*	Biological control	Successful
		Stoat	*Mustela erminea*	Biological control	Successful
		Weasel	*Mustela nivalis*	Biological control	Successful
	Sciuridae	Chipmunk	*Tamias striatus*	Stowaway	Unsuccessful
		Brown Californian squirrel	*Otospermophilus beecheyi*	Stowaway	Unsuccessful

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Chapter 4

Influence of prior human experience on invasion success of birds in New Zealand

Abstract

Throughout the history of human colonisation, fauna is frequently transported by people to locations outside their native range. The degree of human affiliation of a species can be a strong determinant of invasion success. Here, I examine population establishment of bird species that have been introduced to the Auckland Region of New Zealand. I extend this research by investigating the potential influence of the duration of human coexistence and how this may determine the time lag before establishment occurs. I highlight that introduced species with a extended period of coexistence with human society had a higher proportion of establishment success. The introduced species were from multiple continents, and it was found that a higher percentage of European species were categorised as having fast establishment success (less than ten years) compared to other species from other continents. Such results expose the potential influence of past anthropogenic filtering on the probability of an introduced species becoming successfully established.

4.1 Introduction

Since the first prehistorical translocations, the deliberate or inadvertent transport, of plant or animal organisms outside of their naturals ranges has continued to occur with the spread of human to new regions (Duncan *et al.* 2003, Boivin *et al.* 2016). For example, before humans started to introduce animal and plant species, Cyprus Island had displayed a paucity of edible plants or food animals (Vigne *et al.* 2012). However, species transported by humans have displayed varying degrees of success in establishing self-sustaining wild populations. The variation in the establishment success of invasive species is still not completely understood. The observation of a species becoming successfully established following an introduction event in novel habitats is known to be correlated with some determinants of invasion success termed 'invasiveness' characteristics, such as propagule pressure (Gray 1879, Henslow 1879, Lockwood *et al.* 2005). Thus research investigating determinants of invasion success along the different invasion stages (i.e., transport, establishment, spread, impact; Lockwood *et al.* 2005), has been able to establish the importance of propagule pressure (Lockwood *et al.* 2005, Simberloff 2009), human affiliation (Lockwood 1999, Jeschke and Strayer 2006) and other key life-history traits, such as egg mass, sexual dimorphism, maximum lifespan, breeding frequency, adult survival (Kolar and Lodge 2001, Fisher and Owens 2004, Jeschke and Strayer 2006, Sol and Maspons 2012).

The degree of affiliation that an introduced species has experienced with human populations (i.e., domestic animals, species deliberately raised as pets, food or sport and species in higher density in human settlement) is generally a strong determinant of invasion success (Lockwood 1999, Jeschke and Strayer 2006). The degree of human affiliation of a species should depend on several factors, such as the capacity of the species to adapt to humans, and its capacity to adapt to human-modified habitats and to other introduced species. Species with longer eco-evolutionary experiences, within human society and their related habitats, may have greater establishment and invasion success (Saul *et al.* 2013). Such setting lead to 'human transformed habitat legacy' during biotic interaction of the invaded area after human transformations, which may likely be decisive for the success or failure of invasion (Sih *et al.* 2011, Saul *et al.* 2013). Thus,

European species, which coevolved with European societies and their ecological disturbances, present some strong advantages for success over newly colonised habitats during the European imperialism period, known as Ecological Imperialism (Crosby 1986, Jeschke and Strayer 2005), along the two invasive stages of establishment and spread (Lockwood *et al.* 1993). This spread to new habitats has often been followed by habitat changes and alterations in response to the requirements and desires of its population, in term of ecosystems and subsistence regimes. Consequently, a species that displays a past-evolutionary history with European society and their subsistence regimes (i.e., habitat and landscape homogeneity through agriculture or urbanization) should be more successful during the establishment and spread stages of the invasion (Lockwood *et al.* 1993) in the habitat modified by this society following the same subsistence regime of their ecological inheritance (Laland and O'Brien 2001), in comparison with species inexperienced or with a shorter coexistence history with habitat modifications made by this human society (Sih *et al.* 2011, Hendry *et al.* 2011). Therefore, for understanding biological invasion, we need to consider the role of species' past historical-experiences with human society on their population establishment stage in areas they were introduced to (Blackburn *et al.* 2011).

New Zealand and its ecosystem have suffered from a large number of bird introductions (Veltman *et al.* 1996) following the arrival of European immigrants, 150 years ago (Thomson 1922). During this period, all introduction attempts (i.e., timing of introduction and propagule) were recorded by the acclimatisation societies (Thomson 1922), which consequently offers a detailed history of avian introductions in this country.

The objective of this study were to answer two specific questions: (1) Do species introduced to New Zealand from different ecological niches, differ in their degree of establishment success? (2) Does the duration of previous 'eco-evolutionary experience' of species, with human societies in general, and specifically the industrial society, explain the variation in the time-lag response for an introduced species to establish a self-sustaining population?

The first of these questions addresses the potential importance of the evolutionary history of species during the invasion process during colonisation, whereas the second question is determined by the importance of a species' past experience with human society and on the capacities of species to be more

predisposed to new habitat colonised by human and its induced habitat changes, in such ways as to favour a rapid time lag between the year of introduction in the region and the date recorded for the introduced species becoming successfully established (included population growth and range expansion of the alien species; Crooks and Soulé 1999). To answer these questions, I used historical records on introduced avifauna species from the temperate region of Auckland, in New Zealand, between 19th and 20th centuries, using two key parameters: (1) the timing of introduction and (2) the length of time to establish a self-sustaining wild population. Since the founding of the Acclimatisation Society (1867), this region has been the centre of the ambitious programme of bird importation in New Zealand (Druett 1983) and presents the most detailed record of bird introductions.

The industrial society period was selected here because it represents the major human imprint on the global environment and largely characterised the Anthropocene epoch (change of Earth's global, geological and ecological force trajectories under human activity; Steffen et al. 2011). This period has represented the exploitation of fossil energy and major landscape change with the appearance of new environmental stress (e.g., pollution, acid rain, climate change) and consequently is driving novel evolutionary pressures on biodiversity, by modifying selection pressures (Steffen *et al.* 2011, Boivin *et al.* 2016).

4.2 Materials and methods

4.2.1 Study area

The North Island of New Zealand (113,729 km^2) is part of the New Zealand biodiversity hotspot (Conservation International 2017) and represents the 14th largest island in the world. The Auckland region (4,894 km^2) is one of the nine governmental regions of the North Island. This region has attracted large populations of settlers during both Māori and European colonisations, due to its landscape and milder climatic features, which resulted in large numbers of species introductions, most notably during the two last centuries (Duncan and Young 2000). This area is also characterised larger human population (human propagule pressure) during the European settlements in New Zealand (Gisbon 1973), which have resulted in

more local landscape (Kirk 1871, Duncan and Young 2000).

4.2.2 Duration of coexistence with humans

Data on the timing of human contact in each continent was extracted from published information (Stanyon *et al.* 2009). The timing of human arrival in the continent and the country of origin for an introduced species was considered a suitable measure for the duration of its co-occurrence with human (Chapter 2). For any given species, this date was used as a proxy for the level of experience that a species has previously had with a human habitats or human-modified habitats. To establish the year of first appearance of character of the industrial society for each areas, I have extracted from published information the date of the first appearance of machines, mechanisation or use of fossil energy, following the description of Ellis (2015) in each continent. Thus I used AD 1750 for Europe, AD 1790 for North America, AD 1813 for Australia, AD 1875 for Africa and AD 1870 for Asia (Japan AD 1870, China AD 1960).

4.2.3 Introduction rate and biological data

Data on the introduction of exotic bird species to the Auckland area were collected from published information (Hutton 1869, 1871, Drummond 1906, Thomson 1922) and an online website (New Zealand Birds online 2013) (See Suppl. 5*)*. including both the date of a species' first release and the reported date of the successful establishment of a wild population in the Auckland Region if available. I excluded introduction attempts of less than 5 individual birds (Drummond 1906, Moulton and Pimm 1983, Simberloff and Boecklen 1991, Brooke *et al.* 1995, Cassey 2002, New Zealand Birds online 2013), because introduction attempts of fewer than 5 individuals are unlikely to establish a persistent population (Cassey 2002). The minimum known number of introduction and the minimum number of birds introduced for each species were extracted from Thomson (1922). Data on the reproductive potential (e.g., clutch size, number of brood) were collected from Veltman *et al.* (1996) and from the website New Zealand Birds Online (2016). To estimate the lag-phase establishment response, I used the difference between the first date of introduction and the first record of species establishment into the wild. Lag-phase response of establishment

after introduction was compared with two historical parameters, (1) the date that a species first came into contact with humans within their native range and (2) the date when human society entered the industrial age, in the native range of species that were introduced.

4.2.4 Analysis

To test my two central questions, I proceeded with my analysis along two lines. Firstly, I have examined the invasion success establishment response (presence or absence) to variables composed of two sets of chosen variable (timing of human arrival and industrialised society) and standard variables (i.e., propagule pressure, clutch size, the minimum number of individuals introduced, the number of release events, based on Veltman *et al.* 1996). I used a multivariate approach for nonparametric data to avoid the multivariate normality, using 'nonpartest' from the package npmv (1000 Permutations; Ellis *et al.* 2017). Secondly, the same test was used to explore if the variables could explain time-lagged success establishment response. Species were categorised as short and long, based on their time of establishment in the Auckland Region, using the average time-lag of 24.1 years. When significant results were observed, I used the 'ssnonpartest' function from the package npmv to determine the variable levels that caused the significance (Ellis *et al.* 2017). All tests were carried out using statistical software R 3.1.2 (© R Foundation for Statistical Computing, 2010).

4.3 Results

4.3.1 Scope of the data

Since 1861, introduction attempts for 56 exotic bird species have occurred in the Auckland region, but not all of these resulted in established populations. The size of the release flock and the number of attempts per species have been variable. For 16 species, introduction attempts of less than five individuals occurred, all of which were subsequently unsuccessful in establishing. Of the remaining 40 species (Table 4.1) that had full introduction efforts, a further 9 species that were introduced and had an appropriate group

size (i.e., > 5), failed to establish viable populations. This included the Chestnut-breasted manikin (*Lonchura castaneothorax)*, which was recorded in the region up to 55 years after the initial release but has not been recorded thereafter. The remaining 32 species (32 / 40, 80%) that were introduced were successful in establishing successful self-sustaining populations. Three species have been successfully introduced during the late twentieth century but have subsequently been eradicated throughly human control.

Based on the assumption that an introduction attempt of more than 5 birds presents a full introduction effort (see *Methods*), there is a noticeable difference in the proportion of introduced species that subsequently became established, according to their continent of origin: European, Asian, African and Australian species had an establishment success of 82% (14 / 17), 100% (5 / 5), 100% (3 / 3) and 78% (7 / 9) respectively (Table 4.1). In contrast, North American species had a lower establishment success rate (20%, 2 / 6) in the Auckland region (Figure 4.1).

Based on the data for introduced species, the average time-lag for the establishment of a successful population for all bird species released in the Auckland region was 24.1 years (±28.6 years SD) and ranged from 1 to 104 years (*K-W tes*t = 5.66, *df* =5, *p* = .34). There was an observable difference in time-lag establishment response of species in relation to its continent of origin : European (10.1 ±12.3 years SD), Asian (42 ±36.2 years SD), Australia (19.7 ± 19.7 years SD), North America (20.5 ±19.1 years SD), and Africa (64.7 ±52.3 years SD) species (Figure 4.2).

Around half of the species (46.9%) that were successfully introduced established viable populations in the Auckland region in less than 10 years (Figure 4.1). There was also no noticeable difference in the likelihood of establishment in less than 10 years for an introduced bird species according to its continent of origin: European, Asian, African, North American, and Australian species had an establishment success of 64.3% (9 / 14), 25% (1 / 4), 33.3% (1 / 3), 50% (1 / 2) and 43% (3 / 7) respectively (Figure 4.2) (X^2 = 1.06, *p* = .90).

4.3.2 Relationship between variables and response using a multivariate approach

The difference of introduction success response was significantly affected by the selected variables (Permutation test ANOVA, F $_{3,84}$ = 2.75, *p* = .022). Among the five variables considered, clutch size, time of

human contact and number of release events have been observed to show results differing significantly in establishment success. The relative effect on the whole variable chosen showed that 'time of human contact' and 'Number of release events' variables perfectly discriminate the success of establishment response of avifauna in the Auckland Region with a probability of 0.75 and 0.68 respectively, when the "clutch size" variable seems to separate well the failure of the establishment response in the region (0.78, see Table 4.1).

The time-lag response in establishment success has not displayed an evident difference effect using the criteria selected (Permutation test ANOVA, $F_{3,67} = 2.38$, $p = .068$).

Table 4.1: Relative variable effect value on response (in percentage) significant value ($p > 0.05$) are in bold.

		Time of human contact	Time of industrial society	Clutch size	Number of propagules	Number of releases
Establishment response	Fail	**25.1**	43.0	**78.1**	53.9	**32.1**
	Success	**74.9**	57.0	**21.9**	46.1	**67.9**
Time-response in the establishment success	Short (> 24.1 years)	69.7	75.8	53.8	35.4	71.2
	Long (< 24.1 years)	30.3	24.2	46.2	64.6	28.8

Table 4.2: The outcome of bird species introduced in the Auckland Region and their continent of origin (n = 41 species). Only introduction attempts of greater than 5 individuals were included. The numbers in brackets represent the number of species introductions that occurred after 1950 (See Suppl. 4, for full species lists).

Natural range	No. of species introduced presenting a full introduction effort	No. of unsuccessful species	Successful species and their time lag to establish			
			< 10 years	$10 \leq x < 20$ years	≤ 20 years	Unknown
Australia	8 (1)	2	2 (1)	1	3	
Europe	17	3	9	4	1	
North America	6	4	1		1	
Asia	3 (2)	0	(1)	1	2	(1)
Africa	3	0	1		2	
Total	37 (3)	9	13 (2)	6	9	(1)
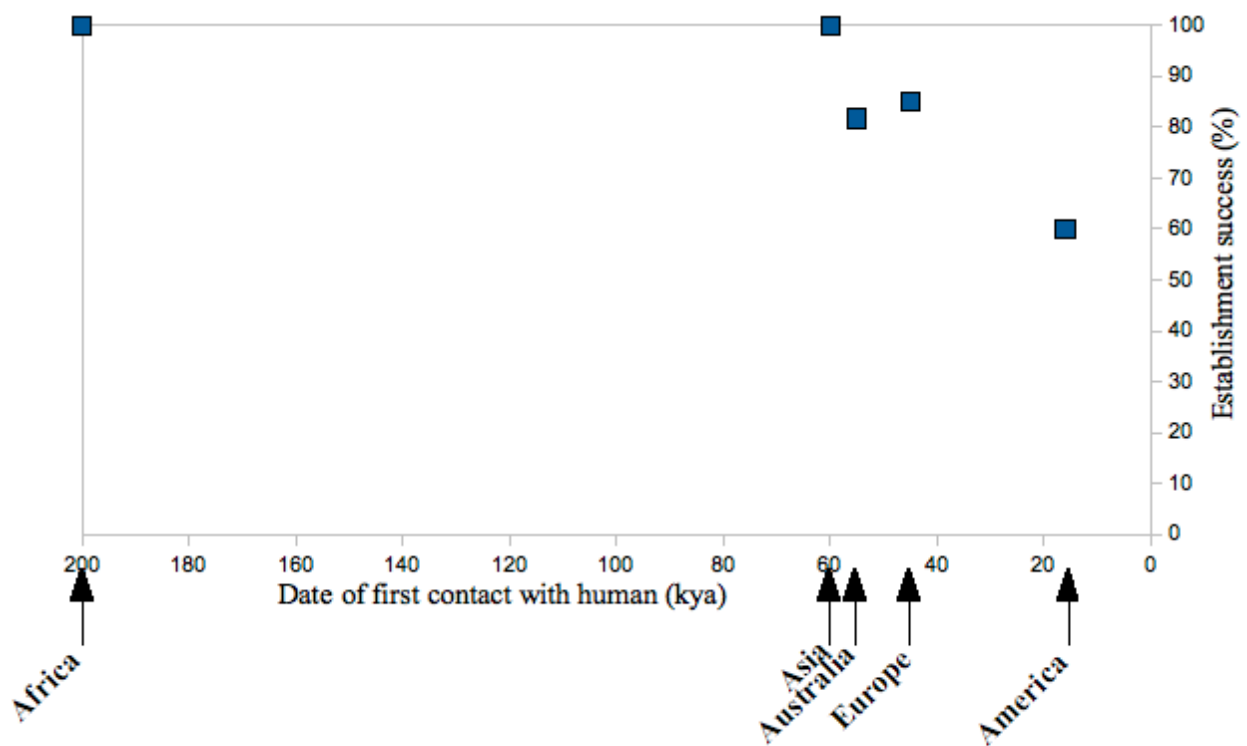
Figure 4.1: Variation in rates of successful establishment for birds introduced to the Auckland Region, depending on the continent of origin and date of first contact with humans (kya: thousands of years ago) on their respective source continent.

4.4 Discussion

Acclimatisation societies set up by European colonists during the late nineteenth century conducted the introductions of exotic species in many European colonies across the globe (Osborne 2000), including New Zealand (see Suppl. 5) to respond to economic and cultural factors in these new areas. New Zealand, and particularly the Auckland Region, has thus experienced a very high degree of flora and fauna introductions (Thomson 1922, McDowall 1994, Veltman *et al.* 1996, Duncan and Young 2000) and has hence displayed higher rates of introduction success, with notably 77.5% of birds species acclimated having been successfully introduced (31 of the 40 species). My results underlined a higher success level by the Auckland Acclimatisation Society in the introduction of bird species in the Auckland Region comparing New Zealand as a whole (20%, Veltman *et al.* 1996), with North America, where only 52.4% of European species were successfully introduced, and Europe where only 54.4% of the North American species have been able to establish a viable population (Jeschke and Strayer 2005). Such variation in introduction success between countries and areas could be explained by a difference in propagule pressure lead by the European human population (Gibson 1973), notably by divergence in their population size and density during colonisation and their establishment in the landscape or habitat (Pyšek *et al.* 2010). The massive influx of humans has led environmental changes and created habitats that increased likelihood for species to succeed during the introduction, as observed in alien plant invasions in New Zealand (Aikio *et al.* 2010). Introduction attempts in the Auckland Region have mainly occurred in the late nineteenth century, shortly after the establishment of European settlement in New Zealand. The late introduction in the area also occurred after the early stage of European settlement, from mainly illegally releases of species by members of the public (e.g., Red-vented bulbul, Rainbow lorikeet, see Suppl. 5). The analysis of the successful establishment events in the Auckland Region during this period revealed that 50% of the bird species introduced during this early stage of the European settlement originated from Europe.
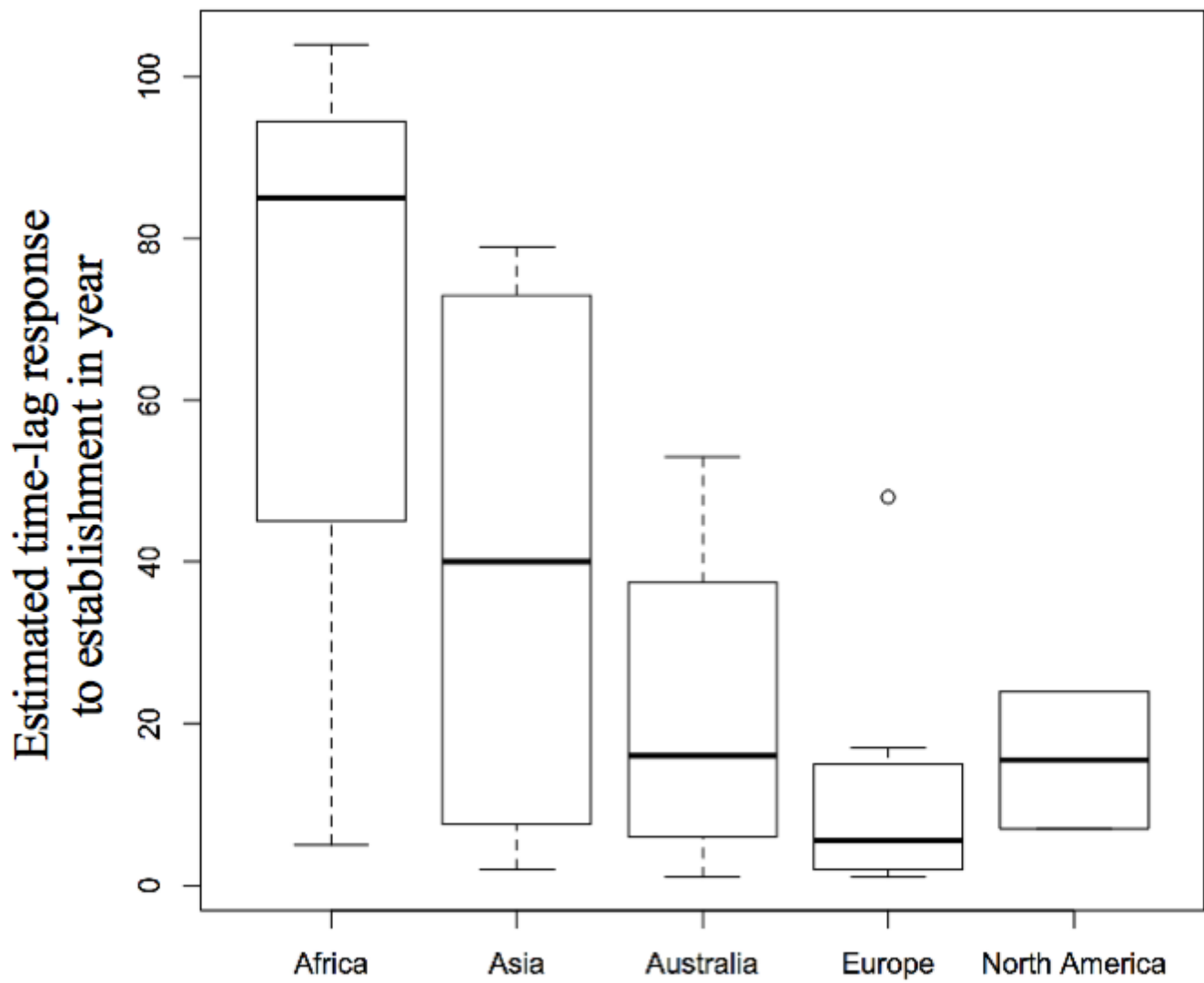
Figure 4.2: Differences in time lag establishment response among bird species introduced to the Auckland Region in relation to their continent of origin. Only those species with known introduction and establishment dates were included (n = 31 species).

My results support the first hypothesis outlined in the introduction. Human history is one of the element determinants of establishment success in Auckland Region, along with number of releases (Veltman *et al.* 1996) and clutch size (Green 1967, Cassey 2002). It is conceivable that the human history of species affects the establishment phase of the introduction by shaping and selecting key parameters. Through their evolutionary history with human society, species may be better prepared, notably via cue-response systems adapted to the human habitat transformations. Human transformation homogeneity over time provides stable and reliable environmental cues that should favour organisms with this evolutionary history to evolve optimal reaction norms or traits with higher flexibility or plasticity for species to respond to novel habitat transformations (Sih 2013). My observation reinforces previous observations (Crosby 1989, Jeschke and Strayer 2005) that European species are more likely to establish inside new regions, as per 'Imperialism dogma' (Crosby 1989). Imperialism dogma states that European species may have a higher invasion success due to their past experiences with a European society and in particular its ecological processes and environmental transformation (Crosby 1989). Here, I have demonstrated that in the Auckland Region, bird introductions tended to be more successful if the species had previously a long period of association with a human society, such as those in Europe and North America. But so far, the duration of the past-experience with human industrial society could not explain the success of the invasions and the rapidity of this process, in Auckland Region. Across the evolution of human society, industrial society has had the most marked effect on reshaping of the terrestrial biosphere (Steffen *et al.* 2007), most notably with the transformation of more than three-quarter of the terrestrial biosphere from biome to anthromes (Ellis 2010, 2013 and 2015). Despite the absence of significant result in this study, such aspects should be taken into account and tested at a larger scale in a future study because it has shown higher probability compared with a randomly chosen variable (see Table 4.1). Consequently, the finding at the Auckland Region level showed that species with a natural ecological niche in habitats transformed by human society may possess more suitable traits, potentially due to the species' evolutionary history (i.e., habitat filtering process, adaptive plasticity, optimal reaction norms). Such characteristics may allow them to cope with immediate ecological change during the establishment stage of the invasion (Sih *et al.* 2011). The approach offers substantial potential for the understanding of multiple cues involved in the invasiveness characteristics used to explain future success in

habitat colonisation of a species.

4.5 Conclusion

I have highlighted that the European exotic species introduced in the Auckland Region have had a higher rate of establishment success compared to species from other countries or areas. My findings suggest the influence of past-experience with human society may influence the potential of a species success when introduced to habitats recently colonised by humans (e.g., Sih *et al.* 2011). Indeed, my approach has highlighted the role of the duration of the past-experience with humans in introduction success across the Auckland Region but this may need to be explored at a broader level (e.g., in an island system or at country level). Further research should be conducted in order to understand the role of evolutionary history with human society in species invasions by studying how evolutionary history with humans has shaped key animal traits or behaviours. This knowledge could help to predict and produce a better understanding of species when introduced to new area.

Supplementary forms

Suppl. 5 : Avian species introduced to the Auckland area after European settlement. Exotic species introduced data for Auckland Area, including date and number of attempt, date of establishment or fail and times response.

Note – ? indicate absence of information, (+) indicates many birds introduces

References:

Thomson GM (1922) The naturalization of animals and plants in New Zealand. Cambridge University Press, Cambridge, UK.

Hutton FW (1869) On the introduction of the Pheasant into the Province of Auckland. *Transactions and Proceedings of the Royal Society of New Zealand,* **2**, 80.

Drummond J (1906) On introduced Birds. *Transactions and Proceedings of the Royal Society of New Zealand*, **39**, 227-252.

Common names	Scientific names recorded	New scientific names	Original continental niche	Date of attempt (No of bird)	Date of success establishement	Date of fail	Intentional vs accidental introduction	Number of introduction event	Time lag response between introduction and establihment	clutch size	Number of brood per season
Successful introduction											
Barbary dove	*Turtur risorius*	*Streptopelia risoria*	Africa	1867 (5)	1972		I	1	5	2	Na
Chestnut-breasted manikin	*Munia castaneithorax*	*Lonchura castaneothorax*	Australia	*1867(4) 1869(+) 1871 (510)*	1868	1922	I	1	1	5	Na
Indian peafowl	*Pavo cristatus*		Asia	1843 (+) 1860 (+)	1922		I	many	~79	6	Na
African collared dove	*Streptopelia roseogrisea*		Africa	1867-80 (+) 1970 (+)	1971		I	many	104	2	Na
Rock dove	*Columbia livia*		Europe	1860-65(+)	1922		I	many	16	1,9	7
Eastern rosella	*Platycercus eximius*		Australia	1910 (	1920		I	many	10	3	5,6
Black bird	*Turdus merula*		Europe	1865 (8), 1867 (30), 1868 (132)	1868		I	3	2	3,8	3
House sparrow	*Passer domesticus*		Europe	1861 (?), 1867 (47)	1868		I	2	7	3,9	3
Eurasian Skylark	*Alauda arvensis*		Europe	1867 (10), 1868 (52)	1873		I	2	6	3,7	3
European goldfinch	*Fringilla carduelis*	*Carduelis elegans*	Europe	1867 (11), 1871 (44)	1922		I	2	15	4,4	3
Spotted dove	*Streptopelia chinensis*		Asia	1920	1997		I	many	67	2	3
Song thrush	*Turdus musicus*	*Turdus philomelos*	Europe	1867 (30), 1868 (95)	1870		I	2	3	4,7	2
Common starling	*Sturnus vulgaris*		Europe	1865 (12), 1867 (15), 1868 (82)	1870		I	3	5	4,8	2
Common chaffinch	*Fringilla coelebs*		Europe	1864 (+), 1867(45), 1868 (68), 1969 (+)	1868		I	4	4	4,9	2
European greenfinch	*Fringilla chloris*		Europe	1865 (+), 1867 (18), 1868 (33)	1868		I	3	2	4,8	2
California quail	*Ortyx californicus*	*Callipepla california*	North America	1862 (+) 1867 (113), 1877 (9)	1869 # 1870		I	3	7	14,2	2
Yellowhammer	*Embezia citrinella*		Europe	(8), 1867(4), 1868 (5), 1869 (?), 1870 (16), 187	1906		I	4	17	4	2
Dunnock	*Accentor modularis*		Europe	1867 (1) 1868(2) 1872 (7) 1874 (19) 1875(18)	1873		I	3	1	3,4	2
Common redpoll	*Linota rufescens*	*Carduelis flammea*	Europe	1871(1) 1872(209)	1922		I	1	48	5	2
Brown quail	*Coturnix ypsilophora*		Australia	1867(4) 1869(+) 1871 (510)	1906		I	3	39	7	2
Australian magpie	*Gymnorhina tibicen*	*Cracticus tibicen*	Australia	1867 (10), 1870 (1)	1870		I	1	3	4	1
Common pheasant	*Phasianus torquatus*	*Phasianus colchicus*	Europe	1851 (7), 1856 (6), 1867 (7), 1868 (2)	1865		I	3	14	11,8	1
Rook	*Corvus frugilegus*		Europe	1869 (2) 1870 (64)	1872		I	1	2	3,6	1
Common myna	*Acridotheres tristis*		Asia	1893	1906		I	many	13	3,7	1
Sulphur-crested cockatoo	*Cacatua galerita*		Australia	late 19s (?)	1922		I	many	22 <	1,6	1
Laughing kookaburra	*Dacelo gigas*	*Dacelo novaeguineae*	Australia	1860-65(+)	1916		I	1	53	2	1
Helmeted guineafowl	*Numida meleagris*		Africa	1860s (+), 1864 (+)	1945		I	many	85	9	1
Wild turkey	*Meleagris gallopavo*		North America	1860 (+) many times()	1894		I	many	34	12	Na
sful introduction due to human controlled											
Rainbow lorikeet	*Trichoglossus haematodus*		Australia	*1990s*	1999	2014	A	many	9	2	1
Rose-ringed parakeet	*Psittacula krameri*		Asia	?	2005	?	A	many	Na	3,5	1
Red-vented bulbul	*Pycnonotus cafer*		Asia	*1952*	1954	1955	A	many	2	2,5	Na
Unsuccessful introduction											
Moutain quail	Oreortyx pictus		North America	1876(3) 1877(9) 1881(80) 1882 (+)		1915	I	2	0	9,5	1
Grey partridge	Perdix cinerea	Perdix Perdix	Europe	1867(17) 1868(20) 1871 (9)		1874	I	3	0	14,6	1
Nothern bobwhite	Ortyx virginiana	Colinus virgianus	North America	1898(200)		1909	I	1	0	13,7	1
Greater prairie chicken	Tympanuchu americanus	Tympanuchus cupido	North America	1881 (20)		1922	I	1	0	12	1
Sharp-tailed grouse	Pediocactus columbianus	Tympanuchus phasianellus	North America	1876(22)		?	I	1	0	12,3	1
Northern Lapwing	Vanellus cristatus	Vanellus vanellus	Europe	1872(36)		1909	I	1	0	3,8	1
Crested bronze wing pigeon	Ocyphaps lphotes		Australia	1883 (5) 1887 (10)		1884	I	2	0	7	1
Common bronzewing	Phaps chalcoptera		Australia	1867(6) 1869(+)		1870	I	2	0	2	2
Common linnet	*linota cannabina*	*Carduelis cannabina*	Europe	1865 (8) 1867(14) 1868(20) 1969(+)		1871	I	4	0	5	2

Chapter 5

Influence of past-human colonisation history on current traits-assemblage of birds in Anthropogenic habitats

Abstract

Human colonisation and land transformation have led to the development of anthropogenic habitats, habitats disturbed by human activity. I hypothesise that disturbances associated with human society acts as a filter on species that favours certain species traits over others. In addition, I suggest that the effect of this filter change over time, and therefore, species from ecosystems with a recent human history will share different biological characters than species with a longer co-evolutionary history with humans. This view predicts a divergence between native and introduced bio-diversity based on the extent of their evolutionary history with humans. Here, I investigated 13 biological traits of New Zealand avifauna related to breeding and general biological characters. I evaluated these traits at the community level along an anthropogenic gradient associated with the degree of habitat transformation by humans. Species groups with similar tolerances for a habitat transformation were associated with both biological traits related to habitat use and with phylogenetic history. I found that the period of coexistence with human society and the degree of anthropogenic habitat transformation influenced the types of life history traits expressed by species (e.g., sexual-size dimorphism, mass). In addition, I show that anthropogenic habitats act differentially on native and introduced avifauna. I conclude that the effects of human society and the extent of past experience with humans have played a significant role on the traits in extent species of avian communities.

5.1 Introduction

The species composition of ecological communities varies across space and time, due in large part to geographical and temporal variations in habitat properties (Jackson and Sax 2010). Some ecosystem drivers, such as environmental filtering and biotic interactions act to select species traits that match habitat characteristics (Ernst *et al.* 2012). Thus species assembly within communities has resulted from selection pressures stemming from environmental condition leading to two contrasting trends. First species colonising new habitats should exhibit traits that allow them to survive through specific habitat filters, i.e., possess similar trait to species currently extant in the community) (i.e., hierarchical landscape filters; Poff 1997, McGill *et al.* 2006). The second trend is that species with similar traits may be limited in their ability to coexist within a community, due to higher levels of interspecific competition. This trend acts to constrain the degree of species similarity within a community, leading to a phenotypic trait divergence (Bonsall *et al.* 2004). Thus environmental filtering combined with biotic (interspecific) interactions are likely to be key driving forces for equilibrium in species composition of communities (Chesson 2000, Chase and Leibold 2003, Pavoine *et al.* 2014).

Humans have transformed the ecosystems they inhabit by land transformation and resource consumption (Ellis 2011). Unlike others species, human-caused transformations have resulted in significant alteration of most ecosystems (Ellis 2011), and this has resulted in profound impacts on environmental and biodiversity structures. Such changes have dramatically modified ecosystem dynamics (Jackson and Sax 2010) and species assemblage (Blair 1996, Kark *et al.* 2007, Croci *et al.*, 2008). In many cases, such major disruptions on ecosystem dynamics have acted as 'environmental filters' for species,that is, some of them pass and others do not, leading to associated local extinctions or extirpation (Chapters 2-3). In addition, the nature of changes in habitat characteristics result from human-induced habitat modification, acts as a new selection pressures on the biological traits of organisms (Statzner *et al.* 2004). Thus the surviving species of these habitat modifications should share traits that enable suitability and adaptation for existing in human-modified habitats. This may explain in part why habitat modification, typically causes changes in species

composition in communities and their associated distribution of traits (Boivin *et al.* 2016). Therefore, anthropogenic filtering should be considered and added to the commonly known environmental filtering processes, including abiotic filters (e.g., external forces such as the physical environment), biotic filters (e.g., internal forces such as competition and resource partitioning), and stochastic processes (trait-neutral) (Hubbell 2001). During the establishment of anthropogenic habitats, anthropogenic selection pressures combined with natural selection pressures, could radically restructure local biotic communities (Pautasso *et al.* 2011).

In addition to habitat modification, species introductions have caused substantial impacts to community structure and composition (Hierro *et al.* 2005). When species are introduced to a novel environment that has been colonised by humans (Kawecki 2008, Chapter 4), species with longer evolutionary histories of being associated with humans in their native range, should cope better because these species have previously gone through selection processes favouring traits adapted to the conditions of human-altered habitats. Therefore they may be more suited to the habitats they were translocated to if the altered conditions are similar to their past environment (McMamara *et al.* 2011, Sih 2013). The duration and frequency of exposure of these species to anthropogenic-altered habitats, may affect their behavioural flexibility when colonise new locations (Sih 2013). Thus adaptive plasticity may therefore provide an advantage when introduced and exposed to a new but similarly human-modified habitat (Sih *et al.* 2011, Essl *et al.* 2015a, Chapter 4). Therefore the habitat modifications during human colonisation tend to restructure of the local community, which favour (1) introduced species with traits already better adapted to anthropogenic habitats (Chapter 3) and (2) native species with characteristics that predispose them to succeed and survive the habitat changes (Sih *et al.* 2011, Sih 2013). These criteria may provide the foundation for a framework to improve prediction of native species' response in anthropogenic change.

Newly colonised countries, such as New Zealand, offer valuable research opportunities to understand alterations to community structure following human-induced changes and human-induced filtering events. Indeed, island archipelagos such as New Zealand and Hawaii have a relatively short human history. Local species of these recently colonised areas have had little time to adjust their evolutionary trajectories that have been shaped by native communities and their native habitat (e.g., flightless birds and ground nesters

with little exposure to mammalian predators; Holdaway 1989, Duncan and Blackburn 2004). The recent colonisation of these countries by human societies has dramatically altered their local ecosystem characteristics (Duncan and Young 2000, McWethy e*t al.* 2010), thus radically changed their natural ecological characteristics (McGlone 1983, Schaniel 2001, McWethy *et al.* 2009, McWethy *et al.* 2010, Chapter 2 and 3). All human transformation of habitats has resulted in depleted soil nutrients (Davidson 1978b), increased soil erosion and a drastic reduction of native landscape types such as native forest habitats (McWethy *et al.* 2010). New Zealand native avifauna, with the long geological isolation and the short evolutionary history with humans, provides an opportunity to understand the effects of environmental and human filtering on shaping biological communities in new colonised habitat.

Since 1842 New Zealand has experienced large-scale introductions of avian species. Of the ~137 exotic bird species introduced, 34 species successfully established (Thomson 1922, Turbott 1990, Duncan *et al.* 1999, Checklist Committee 2010). The current New Zealand metacommunity are thus composed of exotic birds combined with the remnants of a native bird community that has only experienced contact with a human society and their associated impacts since 1280 (~737 years, Wilmshurst *et al.* 2011). The introduced avian species in New Zealand originate from various regions that have been associated with the human societies for a much more extended period (Duncan *et al.* 1999). The intentional introduction of birds into New Zealand started in 1842, coinciding with the arrival of European settlers (Thomson 1922, Lamb 1964). So the current avian assemblage in New Zealand has been shaped by three critical periods: First, by human induced modification of the natural ecosystem (~737 years). Second, by the competition with introduced avian species (~175 years) more experimented in the human-disturbed habitats. And third, by the new predation pressure from introduced mammalian predators.

In this study, I test three hypotheses:

(1) The pattern of avian traits human modified habitats in New Zealand converge with that of other regional assemblages in anthropogenic habitats. This is due to the uniformity of selection pressures and filtering effects across human modified habitats throughout the world, leading to the homogenisation of avian traits.

(2) More avian traits suitable for human-modified habitats should found in the non-native community than in the native community in New Zealand due to their divergent past-histories of selection on these

characteristics.

(3) New Zealand native species should possess traits divergent from those favoured by environmental filtering from anthropogenic habitats, due to a possible time-lag in their responses to environmental filtering from new habitats.

To test the above hypotheses, I ask four specific questions:

(1) How do habitat-selected traits in the New Zealand vary along with an anthropogenic habitat gradient?

(2) Do habitat-selected traits involved across the anthropogenic habitat gradient result from environmental filtering that acts independently from a phylogenetic effects?

(3) Does human habitat modification impact the evolutionary history of species and their habitat-selected traits relationship along an anthropogenic gradient?

(4) How do habitat-selected traits differ in assemblages of native and non-native species, and how do these patterns vary along the anthropogenic gradient?

5.2 Materials and methods

5.2.1 Data sources

I used the list of 76 introduced and native species terrestrial bird species, occurring on the two main islands of New Zealand (Heather and Robertson 1996, Checklist Committee 2010) including species of Gruiformes, Galliformes, Columbiformes, Falconiformes, Strigiformes, Caprimulgiformes, Cuculiformes, Psittaciformes, Passeriformes and Struthioniformes.

5.2.2 Life-history traits

For each species, I tabulated 13 traits (Table 5.1, see Appendix 2 Table 1) that potentially influence a species' tolerance to anthropogenic habitat changes. Data on life history and the ecology of each species were obtained fromDel Hoyo *et al.* 1999, Heather and Robertson 2005, New Zealand Birds online,

nzbirdsonline.org.nz.

<u>Habitat</u> categories include Forest, Open landscape, Aquatic, Shrub and Generalist (when a species was observed in 2 or more habitat categories) (classifications based on Del Hoyo *et al.* 1999; Heather and Robertson 2005; Robertson *et al.* 2007).

<u>Dietary</u> guilds are based on principal food sources consumed (i.e., herbivore, insectivore, omnivore, granivore, and carnivore).

<u>Nest types</u> are divided into two groups; nests containing large openings (i.e., cup, saucer, and platform nests) and nest being partially enclosed (i.e., cavity, burrow).

<u>Nest height</u> were divided into 4 guilds: ground (<0.5 m), medium (shrub layer to the mid-storey canopy, up to 5 m), canopy (upper forest layer >5 m), and undefined (commonly using more than one zone).

<u>Foraging strata</u> were classified into three categories, ground (<0.5 m), understory (shrub layer to canopy including aerial predation) or multiple strata (commonly using both areas).

<u>Sexual plumage dimorphism (SPD)</u> and <u>Sexual size dimorphism (SSD)</u> were assigned based on published information (Heather and Robertson 2005, Robertson *et al.* 2007, NZbirdonline).

<u>Nestling time</u> (mean number of days from laying to fledging), were separated into four groups; period of less or equal to 12 days (S), period comprised between 13 to 16 (M), period comprised between 17 to 20 (L) and the period over than 20 days (XL).

<u>Number of broods</u> was classified into two categories, species with less than two clutches per season and species with two or more clutches per season.

<u>Social structure</u> was categorised into three groups, group living (including family group) (G), pair-living (P) and solitary living (I).

traits	Type	Source and /or coding
Habitat	N	A = Aquatic, F = Forest, S= Shrub, O = Open, G = Generalist
Diet	N	H = Herbivore, I = Insectivore, C = Carnivore, G = Granivore, O = Omnivore
Foraging area	N	G = Ground, U = Understory, MS = Multiple strata
Social structure	N	I = Solitary, P = Pair, G = Group
Nest height	N	G = Ground, M = Medium, H = Canopy, U = Undefined
Nest type	N	O = Open, C = Close
Sex Plumage dimorphism (SPD)	N	A = Absence, P = Presence
Sex Size dimorphism (SSD)	N	A = Absence, P = Presence
Nestling feeding	N	A = Alone, O = One parent, B = Both parent, P = Parent and other member
Number of clutch	N	O = One clutch, M = 1 year <
Nestling times	N	S = x<12 days, M = 13≤x ≤16, L = 17≤x ≤20, XL= 20 day<x
Mass	Q	Log transformed
Clutch size	Q	Log transformed

Variable	Min-max	Coding
Human cohabitation	1-4	1 = native New Zealand bird, 2 = American bird, 3 = Australian bird, 4 = European bird
European cohabitation	1-4	1 = native New Zealand bird, 2 = Australian bird, 3 = American bird, 4 = European bird

Table 5.1: Trait used for the description of New Zealand avifauna species in mainland communities. Traits type are coded in N: Nominal, Q: Quantitative.

Parental care was classified into four categories, nestling fed by parent and other group members, by both parents, by only one parent and not fed.

Body mass and Clutch size were based on average values from published sources (New Zealand Birds online, nzbirdsonline.org.nz, Heather and Robertson 2005).

5.2.3 Species abundances

Species abundance data were extracted from the Atlas of bird distribution in New Zealand (Robertson *et al.* 2007) for 3 landscapes types:

1) *Natural Forest landscape*, composed of a complex natural systems

2) *Farmland landscape* characterised by a simplified agricultural ecosystems (Meurk and Swaffied 2000, Moller *et al.* 2008). Farmland landscape is land used principally for agriculture, horticulture and pastoral purposes. So the Farmland landscape is defined by open habitat dispersed with patches of a few buildings and often characterised by a presence of a monoculture or domination of grass-clover mixed (Meurk and Swaffied 2000)

3) *Residential landscapes* defined by Freeman and Buck (2003) as land used principally for roads, commercial, industrial and residential building purposes. Residential landscapes are defined by a rich cover of different sized buildings, small land holdings, concrete cover over soil, with a few parks and woodlands (anthropogenic habitat) (Freeman and Buck 2003).

Species abundances have been extracted from Robertson *et al.* (2007) based on surveys conducted between 1999 and 2004. Following Kennedy *et al.* (2010), based on the abundance of a species in these three habitats, I categorised each species to a habitat association as either natural (N), farmland (F), residential (R), if the average association with one habitat was at least two times greater than that with other habitat associations. Species with no specific apparent preference for any of these three habitats were classified as generalists (G) (see Appendix 2 Table 2).

5.2.4 Phylogeny

To correct for phylogenetic correlation of traits, I conducted phylogenetic controlled comparative analysis. For this analysis, I used 100 trimmed phylogenetic trees, on a subset of species selected in this study, obtained from the recently built phylogenetic tree of all extant birds species (http:// birdtree.org, Jetz *et al.* 2012). The trees selected from the subset of 76 species (Appendix 2 Figure 1) was based on the 'Hackett Backbone' (Hackett *et al.* 2008). I employed model averaging of phylogenetic distance, using Ape package (Paradis *et al.* 2004), to estimate phylogenetic signal (see Appendix 2 Figure 1).

5.2.5. Influence of human cohabitation experiences

To understand the filtering effects of human presence on biodiversity, I categorised the extent that each species experienced into three parameters of human cohabitation: i) Early human society (i.e., the time since first human contact of any kind), ii) European society (i.e., the time since first encounter with a European society), and iii) combined (the total contact score based on the sum of the two previous categories scores). Each species was assigned a score for the two first parameters from 1 (short cohabitation) to 4 (long cohabitation) (see Table 5.1). To establish the length of human cohabitation in the native species range, I used the date of the first colonisation by humans and the contact with European population for each location. To establish the effect of each variable at the community level, the mean of the species present in the community was calculated. So each community of an anthropogenic habitat has been assigned a score for each parameter: early human society, European society and combined effect (See Appendix 2 Table 3).

5.2.6. Statistical analyses

   Question 1:

I used classification decision tree analysis to assess whether species responses, across a gradient of anthropogenic habitats, shared biological traits. This provides a nonparametric method which determines the membership of each biological traits to predefined groups (i.e., the different habitats from the anthropogenic

gradient) based on a suite of characteristics using recursive data partitioning (Kennedy *et al.* 2010). I selected the final model based on a series of 1000 10-fold cross-validation, using the Gini index of impurity and prior probabilities proportional to sample size (De'ath and Fabricius 2000). Overall statistical significance of the final tree was determined based on Monte Carlo resampling (N = 1,000 randomisations, Breiman *et al.* 1993) using the package rpart (Therneau and Atkinson 1997) and caret (Kuhn 2008) in the R Statistical system (version 3.1.2, R Development Core Team 2008).

I tested the relative importance of each trait for species sensitivity to the four habitat types. First, I calculated the ability of each character to distinguish among matrix response types by the decrease in impurity attributable to the best surrogate split of each variable on the final classification tree, following Breiman *et al.* (1993). Goodness-of-fit tests were used to determine the statistical significance of each trait with the matrix response to expose any variable that may not be detected in the tree framework (McCune and Grace 2000, Maindonald and Braun 2003, Kennedy *et al.* 2010). To estimate the overall difference driving between classes and due to multicollinearity among traits, I conducted a random χ^2 test using Monte Carlo simulation (N = 1,000,000 randomisations). I examined adjusted residuals from χ^2 tests to determine classes that were driving significant overall differences as suggested by Everitt (1992). The importance of each trait for a given variable (Table 5.2) was determined by calculating the change of impurity using Gini index when each character individually was extracted for the original variable on the final decision tree (see Kennedy *et al.* 2010). Variable importance was then expressed as the change in relative magnitude of the total increase in impurity, using normalised quantiles.

Questions 2-3:

I adapted the method suggested by Pillar and Duarte (2010), on the possible influence of the environment on traits with high phylogenetic signal. Based on their analytical framework, I predicted that the level of historical experience with humans (H) would present a strongly correlate with their current traits (T), all mediated by the phylogeny (P) (model 1: H => P => T). Alternatively, phylogenetic signal and past-evolutionary experience are independent of each other and are both correlated to species traits (model 2: H => T <= P) and thus would explain the absence of trait convergence along the anthropogenic habitats.

Correlation among the human effect on these three parameters (level of historical experience with humans, H), the species composition in trait states (T) and the given phylogenetic distance (P) have been evaluated following Pillar and Duarte (2010), using the SYNCSA package (Debastiani and Pillar 2012) in R (version 3.1.2, R Development Core Team 2008).

Question 4:

To assess if there are trait more associated with introduced or native birds, I used effect sizes (Hedges'g) to evaluate the difference in trait values between introduced and native birds within trait categories. I calculated from the proportion of individuals represented for a given trait (*X*) of the trait category, derivable from Rosemberg *et al.* (2000) and Van Kleumen *et al.* (2010), the effect size (Hedges' g) as:

$$d = \frac{((\overline{X})_{introduced} - (\overline{X})_{native})}{(S)} \cdot J \qquad \textbf{(4)}$$

with S the pooled standard deviation between species status with n and J a weighting factor based on the number of species (N) per status was calculated as

$$J = 1 - \frac{3}{(4(N_{introduced} + N_{native} - 2) - 1)} \qquad \textbf{(5)}$$

A positive value of Hedges' *g* means that the introduced species had a larger value than the native bird species for this specific trait in the trait category. Each trait category may represented more than one trait. SoI calculated the effects sizes and its significance using Fisher's exact test, for each trait separately, using R (version 3.1.2, R Development Core Team 2008).

5.3. Results

Question 1:

The most parsimonious classification tree model (with the most significant prediction accuracy) includes only 2 of 13 traits, habitat and nest height (Figure 5.1), and predicts five matrix response types of New Zealand birds to the different landscape associations (with 39.4% misclassification). Based solely on habitat and nest heigh, the model correctly classified the response of 73.68% of the terrestrial avifauna of New Zealand to anthropogenic landscape gradients, and 64.7% of the bird species associated with farmland landscape (Figure 5.1). Open habitat characterised 82.35% of the bird species associated with farmland landscape, and only 64.7% of this community have nests that are low (< 0.5 m) or in the canopy (> 5 m) nests. However, species defined as generalists living in open landscapes represented only 25% of the generalist landscape community, with notably, a majority of them characterised by medium and undefined nest ranges. Bird communities associated with natural forest landscapes were further divided into two categories. The first sub-category was composed by forest specialists, which represented 42.3% of the avifauna community and 91.7% of the forest landscape specialist species in the New Zealand mainland. The second category was comprised of ground-nesting species that were found in an extensive range of habitats (e.g., generalist, aquatic and shrub habitats), but was primarily characterised by species living in the native forest landscape. Generalist landscape birds were marked by more flexibility in the habitat type selected but were mainly observed in nesting height ranking between the medium (M) and the undefined (U) stages (Figure 5.1). Residential landscape bird communities did not indicate any specific association with any of the four categories.
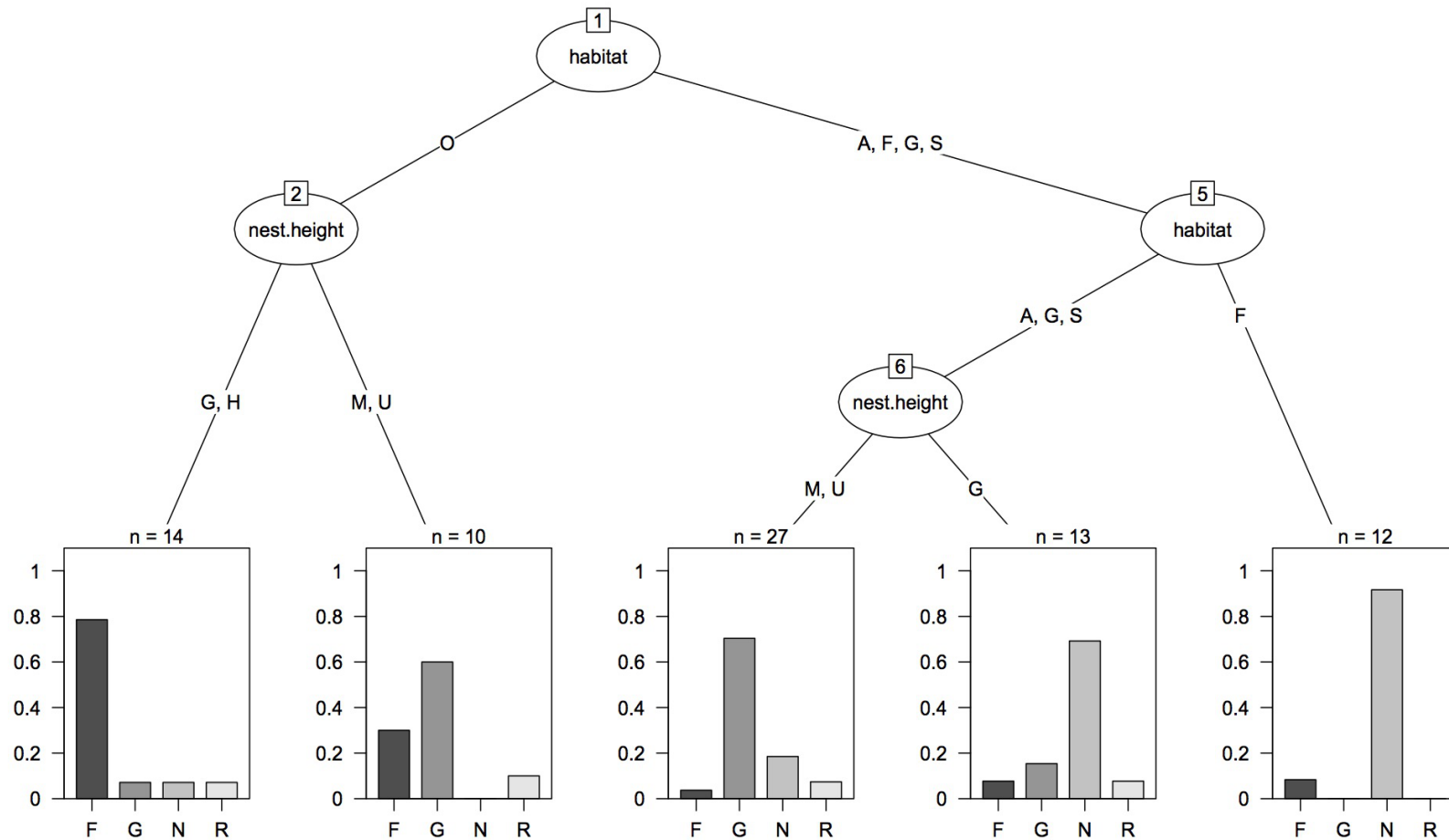
Figure 5.1: Predicted response type and the distribution of species abundance of birds based on classification tree analysis of species response to the gradient of anthropogenic landscapes in the relation of 13 traits. Species responses were categorised as (1) type F: Farmland, (2) type G: Generalist, (3) type N: natural, (4) type R: Residential. Number of species (n). Habitat and Nest height were the only traits retained in the final model, with five matrix types predicted (type F, two types G and two type N) (with 39.4% misclassification rate).

Based on variable importance from the decision tree and statistical significance from χ^2 tests, habitat and nest height were strongly associated with species responses to the anthropogenic landscape gradient (Table 5.2). Other traits such as nest type, sexual size dimorphism, nestling period and foraging area were moderate significantly predictors while sexual plumage dimorphism and the number of clutches were weak predictors. Some traits like clutch size, diet, social structure, and foraging mode showed trends, but lacked statistical significance.

Habitat

Species favouring open habitats exhibited the greatest used of farmland landscapes, with 58.3% (Figure 5.2A). In contrast, 91.7% of forest species were associated with untouched forest landscapes, and 57.1% of the generalist species were significantly found living in generalist landscapes. The anthropogenic habitat, residential landscapes, did not display any strong association with any single habitat-associated species, but rather exhibited a positive relationship with several habitat-species types, including aquatic habitat (16.7%), generalists (0.5%), and open habitat species (8.3%) but not with the species living in forest or shrub habitats (Figure 5.2A).

Nestling times

In natural forests habitats, the chick nestling periods usually did not exceed 16 days (S = 41.2% and M = 50%). In contrast, nestling period for species living in residential landscapes were shorter where the period was typically between 13 to 16 days (M = 20%) (Figure 5.2B). The chick nesting period of generalist species (Figure 5.2B) was characterised by longer nestling periods of 17 to 20 days (L = 57.1%) while those in farmland landscapes had the longest nestling periods (XL = 36.4%).

Nest height

Species using a ground nestling strategy were mostly observed in Farmland (37.0%) and Natural (40.7%) landscapes (Figure 5.2C). In contrast, 60% of the canopy nesters were species living
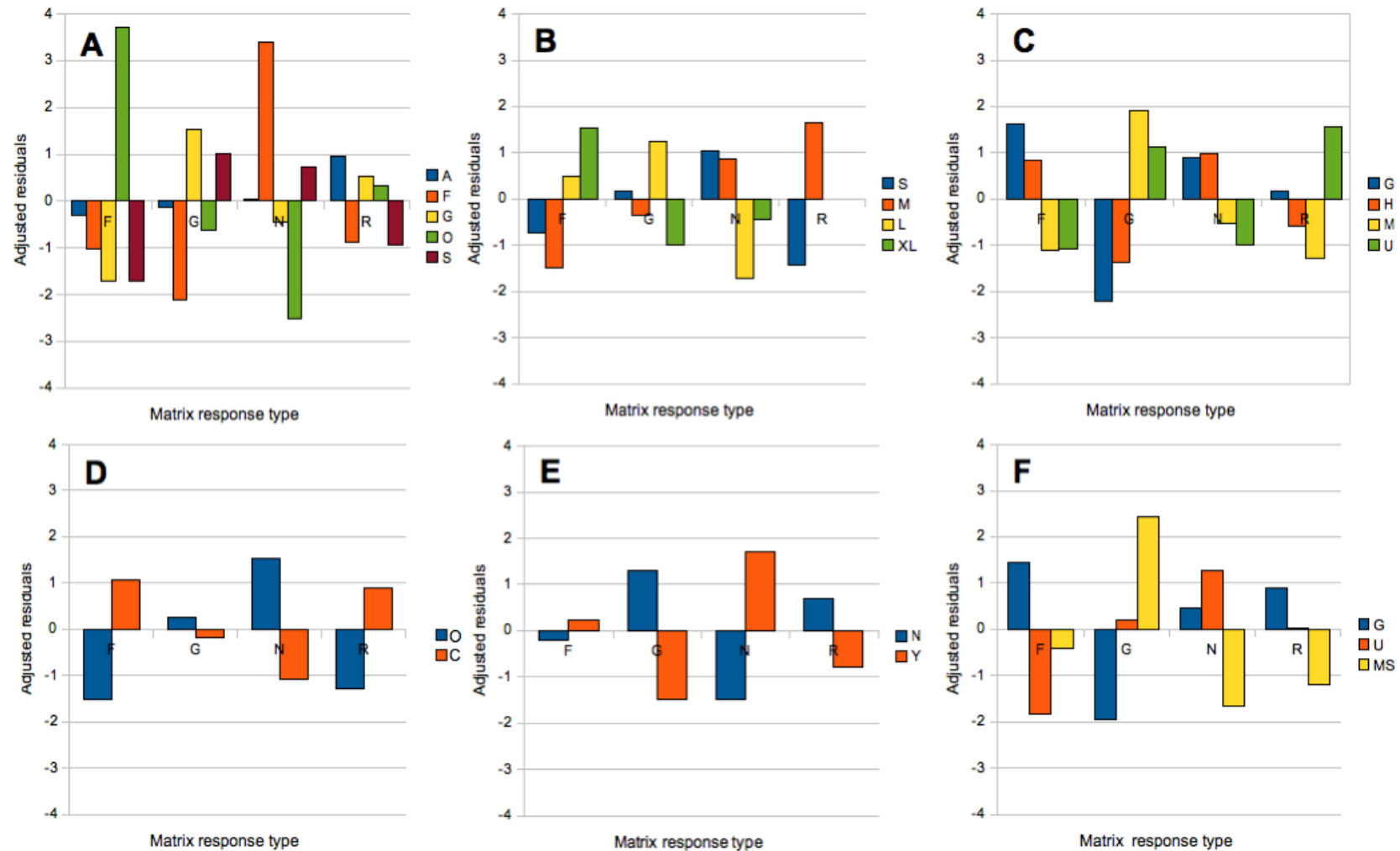
Figure 5.2: Adjusted residual of the χ^2 analyses, relating the number of resident bird species associated with each of the four habitats types along the anthropogenic gradients, in relation to key life-history variables measured: (A) habitat, (B) nestling times, (C) Nest height , (D) Nest type, (E) Size dimorphism, (F) foraging area. Each trait was grouped into the four habitat types: (1) type F: Farmland, (2) type G: Generalist, (3) type N: natural, (4) type R: Residential. The highest absolute value for each graph indicates the habitat class driving overall significant differences among matrix responses and the trait in question. Adjusted residuals with the highest absolute value indicate the class driving overall significant differences among matrix responses and the trait in question .

in native habitats. Birds species presenting medium height nesting strategy were mainly represented by species living in generalist habitats (60%). Most birds (60%) in residential habitats had an undefined nesting strategy. Species with such nesting strategies represented 15.8% of all species in the analysis, indicating a strong tendency for such species to live in human-modified areas.

Nest type

Species with closed nests were most common in natural forest landscape (52% of enclosed nesting species). In contrast, 39.2% of species with open nests were observed into the two human-dominated landscapes (i.e., farmland and residential landscapes, Figure 5.2D).

Size dimorphism

Species displaying sexual size dimorphism (SSD) were most commonly present in natural forest landscapes (51.5% of SSD species, Figure 5.2E). Whereas species without sexual size dimorphism were more frequently found in the anthropogenic habitats (79.1%), with 9.5% of species in residential landscapes, 20.9% in farmland landscapes and 48.8% in generalist landscapes.

Foraging area

Multi-strata foraging species exhibited a preference (68.2% of species) for generalist landscapes, whereas 53.3% of the understory foraging species were found in natural forest landscape (Figure 5.2F). Ground foraging species (43.6%) are present in the two anthropogenic landscapes, with 10.3% in residential landscapes and 33.3% in farmland landscape.

Q*uestion 2*

There was a significant phylogenetic signal of all traits, as indicated by trait-based distance among species (p(BF) = 0.264, p = .001). When each trait was analysed independently only 4 of the 13 traits (i.e., social structure, clutch size, plumage dimorphism and foraging area, Table 5.3) did not have a significant phylogenetic signal at the species pool level, indicating no relationship between species phylogenetic

Table 5.2: The strength of association among 13 traits with an anthropogenic gradient by New Zealand birds. (p value from a randomised χ^2 test: ***p < .001 **p < .01 |*p < .05).

Traits	Variable importance	X^2	p	
Habitat	100	50.647	**0.0000**	***
Mass #	83.00	11,3413	**0.0086**	**
Clutch size §	67.29	6,9504	0.07029	
Diet	48.64	19,1688	0.0845	
Nest height	46.60	24,7977	**0.0032**	**
Foraging area	44.68	22,0889	**0.0012**	**
Nestling times	35.54	18,0996	**0.0340**	*
Social	24.71	12,1272	0.0592	
Size dimorphism	21.66	10,1808	**0.0171**	*
Feeding	19.73	16,7548	0.0527	
Nest types	17.76	9,4366	**0.0240**	*
Plumage dimorphism	12,21	2,6787	0.4439	
Number of clutch	10,40	2,0006	0.5723	

Variable importance was based on continuous ordinal data: χ^2 test was based on the classified group (> 708 g and < 708 g).

§ Variable importance was based on continuous ordinal data: χ^2 test was based on the classified group (> 3.05 nestlings and < 3.05 nestlings).

similarities and species trait similarities. When the phylogenetic signal was analysed at the meta-community level, however, no signal was observed when all characters were considered. Considering traits individually at the meta-community level, only the variable 'mass' and 'nestling times' (respectively p(PT) = 0.999, p = .018 and p(PT) = 0.999, p = .013, see Table 5.3) had a significant relationship with community distance and the phylogenetic structure of the community. This indicates that communities that are similar in terms of phylogenetic structure are also similar in their average value of these two traits. Considering the combination of all the traits, I found a low significant matrix correlation at the species level (p(PT) = 0.264, p < .001) . However the combination of the traits at the meta-community level has resulted in a non-significant correlation (p(PX.T) = 0.7, p = .52).

Question 3:

Historical human impacts (Table 5.3)

Consider human history filtering along the anthropogenic habitat gradient, 'Sexual size dimorphism' was the only trait maximising the expression of trait convergence assembly pattern (p(TH) = 0.998, p = .017). Because sexual size dimorphism was the only trait displaying a correlation convergent, I only conducted the test of niche conservatism for this trait. I used a comparison of competing casual model, using the probability for each model for the causal relationship between level of human association, phylogenetic structure and trait convergence assembly patterns in the anthropogenic habitat of New Zealand. The probability for the model 2 (model 2: H=> T <= P) (p = .940) was higher than for model 1 (model 1: H => P => T), which appear to be the less tenable of the two models (p = .014).

Inversely 'Nestling times' explained a significant correlation between trait divergence assembly patterns and human history (p(XH, T) = 1, p = .045).

Table 5.3: Phylogenetic signal at the species pool and community levels and the correlation of trait divergence and trait-convergence assembly patterns in response to the human-induced effect along an anthropogenic gradient in New Zealand (* α = .05, ** α =.01, *** α =.001).

Traits	Species pool level p(**BF**)	Metacommunity level p(**PT**)		p(**PX.T**)	Historical filtering p(**TH**) Human history	Human colonization	European colonization	Trait-divergence assembly patterns p(**XH.T**) Human history	Human colonization	European colonization
All traits	0,2640 ***	0,7002		-1,0000	-0,8047	-0,783	-0,372	1,0000 **	1,000 *	1,000
Habitat	0,0499 *	0,4757		-1,0000	-0,6094	0,536	0,475	1,0000	-1,000	-1,000
Nest height	0,0953 ***	0,8867		1,0000	-0,8020	-0,952	-0,972	-1,0000	-1,000	-1,000
Feeding	0,3621 ***	0,7454		1,0000	-0,8419	-0,029	-0,100	1,0000	1,000	1,000
Mass	0,3036 ***	0,9989	*	1,0000 **	-0,9937	-0,805	-0,760	-1,0000	-1,000	-1,000
Clutch size	-0,0129	0,8993		0,0000	-0,8183	1,000 **	0,996 *	0,0000	-1,000	-1,000
Social	0,0354	0,0446		1,0000	0,2028	0,219	0,149	-1,0000	1,000	-1,000
Nest type	0,0800 *	0,0488		0,0000	0,1105	-0,463	-0,525	0,0000	0,000	0,000
Plumage dimorphism	0,0088	0,9228		0,0000	-0,8498	-0,687	-0,737	0,0000	0,000	0,000
Size dimorphism	0,0508 *	-0,9953		0,0000	0,9980 *	-0,901	-0,868	0,0000	1,000 *	0,000
Number of clutch	0,0750 *	-0,0215		1,0000	-0,1376	-0,903	-0,931	-1,0000	-1,000	0,000
Diet	0,0708 **	0,4632		-1,0000	-0,5981	-0,737	-0,784	1,0000	-1,000	1,000
Foraging area	0,0268	0,6253		-1,0000	-0,7414	0,114	0,043	-1,0000	-1,000	-1,000
Nestling times	0,1265 ***	0,9993	*	-1,0000	-0,9806	0,754	0,705	1,0000 *	-1,000	-1,000

Definition of abbreviation used in this table (based on Pillar and Duarte 2010)

BF: Phylogenetic signal at the species pool reporting the matrix correlation between species phylogenetic similarities and species trait similarities.

PT: Phylogenetic signal at the meta-community level reporting matrix correlation between community distance computed on phylogenetic structure and community distance.

PX.T: related *PT* matrix correlation when community trait average by communities is removed.

TH: Historical Filtering revealed by matrix correlation between community distance on traits and communities distance on historical variables "Trait convergence Assembly patterns based on Historical filtering".

XH.T: Trait -divergence assembly patterns related to TH matrix correlation when community trait average by communities is removed.

The effect of human colonisation on bird assemblages

Along the anthropogenic habitat gradient, I found that the combination of all traits maximised the correlation between trait divergence assembly pattern and human colonisation filtering [p(XH.T) = 1, p = .001]. A similar pattern was observed for 'sexual size dimorphism' [p(XH.T) = 1, p = .03] under human colonisation filtering (see Table 5.3). When the trait-convergence assembly was analysed, only clutch size had been significantly affected by the human historical filtering along the anthropogenic habitat gradient [p(TH) = 1, p = .004].

For 'clutch size', analysis of trait-convergence assemblage revealed that phylogenies and he anthropogenic habitat gradient are independently correlated with this trait (p(model 2) = .952 > p(model 1) = .388).

The effect of colonisation by Europeans on the avian community

I found that no traits have maximised the correlation of trait-divergence assembly pattern across the European colonisation filtering. However along anthropogenic habitat gradient, 'clutch size' has been a significantly affected by European colonisation filtering, with a notable correlation between trait-convergence assembly pattern to the European colonisation filtering (p(TH) =0.996, p = .02). The analysis of trait-convergence assemblage revealed that phylogeny and European colonisation filtering were independently correlated with species traits in the case of 'clutch size' (p(model 2) = .929 > p(model 1) = .378), as also observed for tests of anthropogenic habitat gradient.

Question 4:

Results indicated some variation in effect sizes among specific characters of species between the native and introduced avian communities. Six of the 13 traits were significant, indicated by trait larger to zero (Figure 5.3).
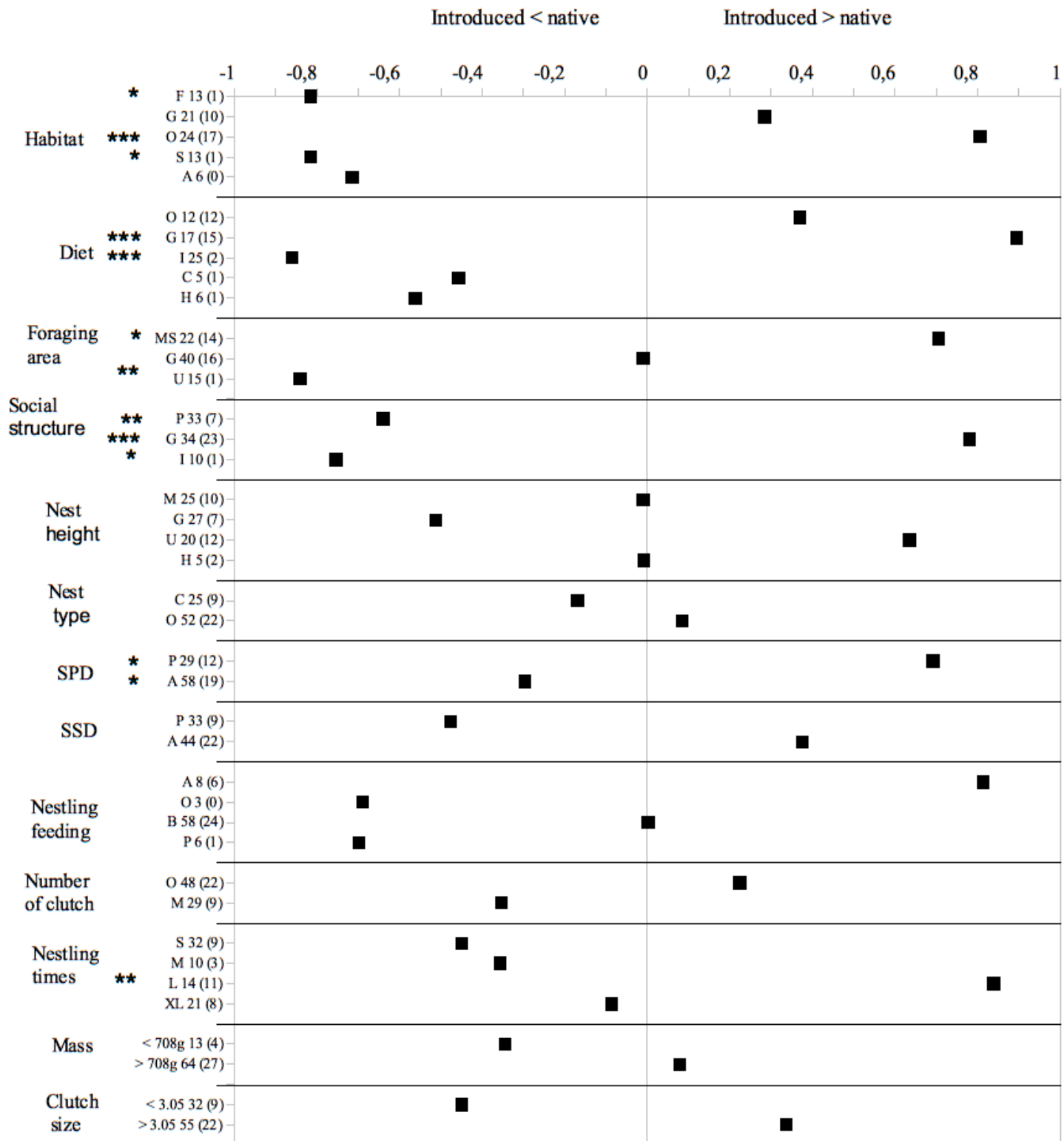
Figure 5.3: Mean effect sizes (Hedges' g) of differences between introduced and native birds species for the 13 traits . The samples sizes (i.e., number of species comparisons) and the number of introduced birds (in parentheses) are given on the left side of the graph near each trait. Positive effects sizes indicate that the introduced bird species had larger trait values than the native bird species. Mean effect size can be characterised by three levels of effect following Cohen (1988) (0.2<d<0.5 is a small effect, 0.5<d<0.8 is a medium effect and d>0.8 is a large effect). P value from Fisher exact test ***p < .001 **p < .01 *p < .05 (subcategories refers to Table 5.1).

Diet

Introduced species have two traits with positive mean effect sizes, but only having an omnivorous diet (d = 0.89, Fisher's exact test, p = 0.001) was significantly higher than for native birds (Figure 5.3). In contrast, native species have a significantly higher effect size for insectivore diet (d = 0.86, Fisher's exact test, p = .0001). Carnivorous, herbivorous and generalist diets all have a medium value, lower than zero, suggesting no difference between native and introduced species for these traits (respectively: d = 0.46, Fisher's exact test, p = .643; d = 0.56, Fisher's exact test, p = .392; d = 0.37, Fisher's exact test, p = .317).

Foraging area

For comparison of foraging area, effect sizes of understory foraging area were significantly larger than zero (d = -0.84, Fisher's exact test, p =.011), indicating native birds were more likely to use this trait (Figure 5.3). However, generalist foragers where mainly composed of introduced birds in New Zealand (d = 0.71, Fisher's exact test, p = .011).

Nest height

Medium effect size has been observed for introduced species for undefined nest height (d = 0.64, Fisher's exact test, p = .062). Similar pattern was also displayed on ground nest selection where a medium value lower than zero has exhibited with no notable effect of native species on this trait (d = 0.51, Fisher's exact test, p = .088).

Nestling times

Nestling times of introduced species (17 to 20 days) were significantly larger than zero (d=0.84, Fisher's exact test, p = .002, Figure 5.3). Other sub-categories of traits have only displayed lower comparison value between the bird characters but without notable effect.

Sexual plumage dimorphism

Introduced species have higher levels of sexual plumage dimorphism than native species, but this trend was not significant (d = 0.69, Fisher's exact test, *p* = .061; Figure 5.3). Similar observation on native birds which have displayed lower size effect in absence of sexual plumage dimorphism without also notable effect (d = 0.30, Fisher's exact test, *p* = .061).

Nest types

My results indicate that the variation in native versus introduced species communities doesn't depend on nest type (Figure 5.3; Fisher's exact test, *p* = .629).

5.4 Discussion

My analyses indicate that a simplistic model of human-modified habitats along an anthropogenic gradient is not sufficient to accurately explain recent changes in New Zealand avifauna communities. Of the 13 species traits analysed in this study, seven (i.e., habitat, mass, nest height, foraging area, nestling time, size dimorphism, nest type) were found to be potential drivers of community change along the anthropogenic gradient (see Appendix 2 Figure 2). Some of these habitat-traits relationships are compatible with previous findings in the ecological literature. For example, previous research demonstrated that trait such as foraging area differed along an urban system (e.g., Blair 1996, Kark *et al.* 2007, Hagen *et al.* 2017), whereas diet type did not (e.g., Sol *et al.* 2014). In this study, however, when species phylogenies were integrated into the analysis, only the 'foraging area' trait did not show a notable phylogenetic signal. Moreover, most of traits, at the communities' level displayed any meaningful phylogenetic signal, with the exception of 'mass' and 'nestling time'. Furthermore, across the seven traits noted above to be potential drivers of community change, 'size dimorphism' was the only one that revealed significant filtering effect from human history. When this trait was observed at the community level, it revealed that filtering effects from human history may have had an impact on the presence sexual dimorphism observed in the non-native population.

5.4.1 Anthropogenic landscape matrix filters for traits in avifauna assemblages

Anthropogenic landscape changes play an important role in shaping the traits of avian communities. Overall, different landscapes favoured communities with different trait-assemblages. Thus, the current distribution of New Zealand avifauna tends to group species around similar tolerance patterns and ecological associations. Of the 13 traits tested, 'habitat structure' and 'nest heights' were both associated with different landscape types (Figure 5.1). However, other traits (e.g., nestling time, foraging area, nest type and size dimorphism) also helped to predict variations in how bird communities respond to the four different habitat types in this study. A significant value of p(PT) reveals evidence of phylogenetic niche conservatism for 'Mass' and 'Nestling times' along the range of habitats (Wiens and Graham 2005, Pillar and Duarte 2010). Indeed, the expression of these traits in communities have been similar in their phylogenetic structure and also in their average values across the habitats (Stubbs and Wilson 2004).

Bird species associated with farmland or agricultural landscapes were characterised by a preference for open habitats, a ground foraging strategy and a more extended nesting period (> 17 days long). Farmland landscape tend to support a higher number of species that use an open nesting strategy, preferring either ground or high canopy nesting sites (Benton *et al.* 2003). Most species associated with higher nests are limited by the availability of suitable trees, often associated with forest habitats (Benton et al. 2003). Indeed, increasing nest height reduces predation risk (Martin and Badyaev 1996, Chapter 7). New Zealand farmland, which is characterised by sheep, dairy and orchard farming, has both a high diversity and high population density of natural and introduced predators (Ragg *et al.* 2000). This high predation pressure threat favours an increased nest height by using surrounding hedgerows and trees as refuge (Robinson and Sutherland 1999).

New Zealand's recent agricultural development (see Chapter 3) has led to vast open landscapes (Meurk and Swaffield 2000), that offer advantages for ground foraging birds. Open landscape is advantageous for ground foraging species due to easier detection of predators, by reducing the level of visual obstruction (Whitingham *et al.* 2006). Furthermore, the open landscapes may increase food availability, with an increase in weed seeds, grains or insects . Additionally, the agriculture intensification that has occurred with the European colonisation in New Zealand (Gibson 1973, Chapter 3) has acted as an

ecological filter via the process of biotic homogenisation (Gámez-Virués *et al.* 2015), favouring the presence of synanthropic birds (i.e., those ecologically associated with humans; Sih *et al.* 2012). The introduced avian species in open landscapes may possess an evolutionary advantage due to previous experience with such habitats (Chapter 4) and therefore already exhibiting appropriate behavioural responses and life-history traits, most notably to novel abiotic stressors and new resources (i.e., food resources like crops). Introduced avifauna will have an advantage in these new conditions, due at least in part to their past-evolutionary history with humans in similar habitats in their natural range (Sih, 2011). Traits that were found selected for in these habitats, could be the result of the difference in duration of past-experience between introduced species and native species traits (i.e., time-lagged responses; Ramalho and Hobbs 2012). However, the homogenisation of anthropogenic habitat features (biotic and abiotic) should lead to a decrease in native bird species richness due in part to the time-phase in behavioural or trait adaptations.

In this study, residential or urban landscapes supported a large assemblage of bird species that lack sexual size dimorphism, use an open nesting strategy and have an intermediate nestling period (13 to 16 days). Contrary to urban birds from other areas, New Zealand urban birds seem to display contrasting nest characteristics (i.e., open nest) to Eurasian and North American urban birds (Landcaster and Rees 1979, McLure 1989, Lim and Soghi 2000, Croci *et al.* 2008), where cavity and enclosed-nesting traits are an advantage in cities. This divergence may result from the recent development of urban areas in New Zealand within the last 175 years where green patches and in particularly remnant forests were included in the urban plan (Preston 1987). Consequently, urban avifauna may find protection in remnant forest patches (Wilson *et al.* 1988) and maintain the use of other nesting strategies. Several studies (e.g., Landcaster and Rees 1979, Clergeau *et al.* 1998, Jokimäki and Suhonen 1998, Croci *et al.* 2008, Kark *et al.* 2007) in northern hemisphere cities have found that omnivorous species have an advantage in cities due to their capacity to eat a large range of food types. However, I did not find any significant increase in omnivorous species in urban areas in New Zealand. Thus the dietary preference may not play a major role in the capacity of species in New Zealand to adapt to urban habitats, as suggested by Clergeau *et al.* (2006). Nonetheless, the capacity of species to cope in urban environments seems to be more a product of their breeding habits. Interestingly, urban avifauna appear to more commonly have intermediate nestling periods, shorter than that of species in

farmland landscapes, leading to a shorter exposure of nestlings and breeding adults to risk factorss, such as predation and human disturbance (Chapter 7). A short nestling period may therefore reflect a higher risk of nest predation (Chapter 7) that can occur in urban habitats, due to a higher density of commensal predators (i.e., rats, cat; Gillies and Clout 2003, van Heezick *et al.* 2010, Aguilar and Farnworth 2013). Indeed, previous research has highlighted that fast development of nestlings is generally associated with higher nest predation (Case 1978, Martin and Li 1992, Bosque and Bosque 1995, Martin 1995).

Generalist avian communities in New Zealand were characterised by bird species with flexible habits, such as utilising multiple-foraging areas, undefined or medium nesting location and no sexual size dimorphism. The current status of this community to have more generalised traits is likely due to their capacity to cope with a larger range of habitats. Indeed, modified habitats increase the variability of food web structure and of functional resource availability.

In contrast, bird communities associated with natural habitat landscapes were represented by forest species with shorter nestling times, higher foraging areas and ground nesting. These strategies make it difficult to cope with any habitat disturbance. The composition of the traits seem to reflect those that have been favoured by the stability and the predictability of the habitat, in contrast to the anthropogenic habitat.

5.4.2. Ecological traits and phylogenetic patterns

The phylogenetic signal differed greatly between species p(BF) and meta-community pools p(PT). By comparing the phylogenetic signal of traits from the local to the meta-community level, my results indicate that of the ten traits that had a significant phylogenetic signal at the species level, only two traits (i.e., mass and nestling time) had a significant phylogenetic signal at the metacommunity level. By using functional niche dimension analysis (Stubbs and Wilson 2004), these results suggest that the communities more similar in their phylogenetic structure (more similar ancestry) tend to display similar phenotypic trait (e.g., nestling times, mass). So these two traits may display a functional affiliation (Stubbs and Wilson 2004) and provide evidence of phylogenetic niche conservatism for the given avifauna species (Wiens and Graham 2005) without including any human effect of New Zealand avifauna across the anthropogenic habitats. The significant value of the mass trait found after fuzzy weight correction indicates the importance of mass trait

divergence inside of the New Zealand avifauna communities. This result relates the importance of species mass of a species in the avian assemblage along different a gradient of anthropogenic habitats transformation, showing notably larger mass birds in rural versus urban areas (Liker *et al.* 2008, Coetzee and Chown 2016).

5.4.3 Ecological traits and Phylogeny associated with the level of human history with species.

A species' evolutionary past has been argued to play an important role in their capacity to persist through changes (Sih *et al.* 2011, Essl *et al.* 2015a). Research on variation in life-history traits among species has highlighted the importance of trait function as an indicator of response to habitat changes (Vandewalle *et al.* 2010). Previous research thus highlights the importance of evolutionary responses to ecological disturbance, most notably in the response of habitat-related traits (Pillard and Duarte 2010, Pavoine *et al.* 2014). Important research by Cartwright *et al.* (2014) identified an influence of anthropogenic habitat exposure on life-history strategies in a wild population of Mauritius kestrel, *Falco punctatus* (i.e., shift in age-specific patterns in reproduction and survival). Here in this study, I highlighted the importance of some life-history traits in community assemblage processes along an anthropogenic gradient in New Zealand avifauna population. By analysing the trait divergence assembly pattern along different human historical gradients, I found that 'nestling times', 'all traits' and 'sexual size dimorphism' were related more to biotic interaction than from human filtering (i.e., human history, human colonisation).

In contrast, I identified that the degree of sexual-size dimorphism within avian communities the anthropogenic gradient may be related to human history. This finding supports a previous observation on the potential importance of sexual dimorphism during the introduction phase (McLain *et al.* 1999). In the New Zealand avifauna, sexual-size dimorphism may have contributed in the process of community assembly related to human history filtering. However, the energy allocated to these traits will be more sensitive to the detriment of other more adaptive traits, which may allow a better chance of survival in anthropogenic habitats.

These two results suggest that the trait convergence observed (i.e., sexual size dimorphism, nestling times) in the anthropogenic habitats has resulted from human filtering, which has tended to favour species with similar phenotypic traits. However, I am currently not able to suggest if the anthropogenic habitat has selected species with similar ecological requirements without including the past history of species community. It is likely that the previous experience and shared ancestry trends of introduced species (chapter 3) could have altered the result of trait convergence. Consequently, an analysis of the traits associated with the species previous experience with an anthropogenic habitat is needed.

5.4.4 Ecological traits associated with species history.

The question of what kinds of traits are more common among exotic birds compared to native birds in New Zealand is required for an understanding of the current community structure and the mechanisms involved in the establishment of communities structured in anthropogenic habitats and in recently colonised countries. My results demonstrated clear trait differences between native and exotic birds in New Zealand avifauna, across five of the thirteen trait categories selected: habitat, diet, foraging area, social structure, sexual plumage dimorphism and nestling times. Native species were more likely to be in forest and shrub habitats, have an insectivorous diet and use understory foraging area, reflecting it evolutionary association with forest. Before human colonisation, New Zealand was mainly cover by conifer-broadleaf forest (McGlone 1989, Chapter 3). In contrast, exotic species are more generalist in habitat, diet or foraging area. The generalist traits of introduced species may result from a trade-off between the capacity of a species to exploit a range of resources and their capability to use them (i.e., 'Jack-of-all-trades is master of none' hypothesis; MacArthur 1972, Kawecki 2008). So species presenting generalist trait will be better able to cope with environmental stochasticity, due to their broader-environmental tolerance (Sol *et al.* 2002, Kawecki 2008, Evans *et al.* 2010, Sol *et al.* 2014). Thus, generalist exotic species should be more successful in anthropogenic habitats. Indeed, generalist species may show better adaptations to a 'marginal habitats' (Kawecki 2008), especially in the case of introduced species that have already have a past-evolutionary history with anthropogenic habitats, helping them to survive in these new environments (Sih *et al.* 2011, Sol

et al. 2014). This prediction could explain the failed introductions of some species with shorter periods of human association (Cassey 2001, Chapter 4).

Sexual plumage dimorphism also differed between the two communities with more sexual plumage dimorphism present in introduced than in the native avian species. This result is not consistent with previous findings (Mclain *et al.* 1995, Mclain *et al.* 1999, Sorci *et al.* 1998, Sol *et al.* 2002), which highlighted that introduced species with plumage dimorphism have a higher rate of extinction than plumage monomorphic species. Plumage dimorphism has evolved under sexual selection and may be costly to be produced and maintained, therefore affecting adaptation and survival (Sol *et al.* 2002). However, research conducted in mainland Europe on sexual plumage dimorphism has provided no clear support of the influence of sexual selection on population trends and suggests the potential effect of human fondness for attractive bird species (Prinzing *et al.* 2002). Species that were introduced to New Zealand by the acclimatisation society (Thomson 1922, Chapter 4), were characterised by attractive species (i.e., potentially sexually selected) (Thomson 1922) and have populations that have been persevered via many introduction attempts (Chapter 4). Consequently, the prevalence of sexual dimorphism in the exotic avian community in New Zealand may just be the result of being chosen by human for introduction.

5.5 Conclusion

There are outstanding examples in the literature of the response of life-history traits to human habitat change (e.g., Cartwright *et al.* 2014, Sol *et al.* 2014). However, there is relatively little knowledge about the mechanisms of changes in community structure in countries with a more recent human history and consequently, recent human induced habitat change. My study suggests that trait composition in New Zealand habitats are the result of a complex environmental effect, but without offering a clear trait-habitat relationship. I also highlighted the potential influence of human society on some species life-history traits, suggesting the presence of a human filtering effect, acting in parallel to a more commonly known environmental filter (Pillar and Duarte 2010, Hagen *et al.* 2017). The discrepancy observed could reflect the

fact that my approach has not included a temporal perspective. Indeed the anthropogenic habitats studied were only established a maximum of 175 years ago, so some species and habitat-selected traits relationship might not have had enough time for any evolutionary adjustments to the new anthropogenic environment to occur, with the exception of introduced species that may already be more suited to the new local conditions. More research on avian populations of anthropogenic habitats is required to further understand the complexity of strategies developed to cope with anthropogenic habitats.

Acknowledgments

Chapter 6

Change in avian community structure over 26 years in an urban forest fragment remnant.

Abstract

The effects of human society development on natural landscapes have been immense, especially the more recent effects of urban development which has profoundly altered the local biota. Most previous studies on the effect of urban development on bird assemblage have been focused at large landscape scales such as geographic regions or entire country. Few studies have investigated variation in urbanisation intensity and its effect on the biodiversity of local ecological communities in countries with recent human colonisation. In this study, I analyse bird survey data collected in an urban forest fragment of Auckland, New Zealand from two different sampling periods, 1980s and 2010s, to investigate changes in avian diversity over time. Despite the continued growth of Auckland city, the forest fragment remnant and its surrounding landscape has maintained avian community structure over time. However, a change that was identified was a transition from a bird assemblage dominated by native species to the current assemblage dominated by exotic species.

6.1 Introduction

Human populations have colonised almost all of the terrestrial biosphere (Hamilton *et al.* 2009), causing drastic changes to local habitats. Most notably, humans have transformed land use and land cover (Glade 2003) and developed anthropogenic ecosystems (Ellis 2011, Ellis 2015). Such transformations have created new constraints and acted as a filter on local organisms (Croci *et al.* 2008, chapter 2), which has led to extinction or extirpation events and a reduction of biodiversity (Steadman 1995). Urban development, during human sociocultural niche construction (Ellis 2015) represented one of the major causes of habitat change (Blair 1996, Pauchard *et al.* 2006, Hagen *et al.* 2017). Throughout urban development, natural landscapes have been replaced by man-made structures in response to human needs, resulting in the remaining natural ecosystems becoming a patchwork of relic habitats within the new urban ecosystems, which are dominated by industrial and commercial infrastructure, and urban housing (Pautasso *et al.* 2011). Such nature relics often serve as sites for public use and recreational purposes, and are affected by the surrounding urban developments that shape these ecological communities in time and space (Fernandez-Juricic 2000).

The changes in habitat and species composition patterns that have been observed following urbanisation, have primarily been focused on countries with a long period of human history (usually over several centuries, > 100 years). Most notably, such research has focused on species composition patterns, the structure of nestedness within ecological communities and ecological development over time (Aldrich and Coffin 1980, Idzelis 1992, Fernandez-Juricic 2000, Chace and Walsh 2006, Clergeau *et al.* 2006). The effect of urbanisation on native and introduced biodiversity in countries recently colonised by human societies, which have undergone rapid urbanisation (Weber 1899, Gibson 1973) and the most anthropogenic habitat changes (Elmqvist *et al.* 2014) in a short period (i.e., only a few centuries, < 100 years), are poorly known. Islands like Hawaii and New Zealand have experienced one of the fastest and major shifts from their original natural status to a human dominated landscape, with the rapid city development during only one or

two centuries (Weber 1899, Gibson 1973). The fast establishment of urban impacts into the natural landscape have driven multifaceted dynamic of landscape changes through a specific trajectory across time and space driven by strongly interrelated factor like land use change, population development and cultural transformation (Ramalho and Hobbs 2012, Beichler 2015), and subsequently leading to significant changes in the natural environment and so in species composition in forest remnant patches in urban systems. The late discovery and colonisation of locations like New Zealand, have likely resulted in a different urban transition. Indeed rapid colonisation by a human society with a complex sociocultural system, and access to advanced technological and cultural knowledge (Hamilton *et al.* 2009, Ellis 2011, Ellis 2015) have produced different scale and rate of urban expansion to most northern hemisphere countries. More recently colonised lands have differed markedly from historical patterns of urban growth, and resulting in different urban ecological responses. This fact, as well as the varying biogeographical factors and geological history of New Zealand, may mean that research into ecosystem changes following urbanisation conducted at other locations may not be applicable.

New Zealand was the last significantly large land mass to be colonised by humans (Anderson 1991, Craig *et al.* 2000). The island ecosystems have observed two periods of colonisation; in AD ~ 1280 by Polynesian society (Māori) (Wilmshurst *et al.* 2008, Wilmshurst *et al.* 2011) and ~ 500 years later by European societies (mid AD 1800) (Duncan and Young 2000). So as a recent colony of the British empire, New Zealand's urban development has been strongly influenced by European technologies and cultures and in particular by English urban planning and management. A significant recommendation regarding urban planning was by the committee on Health of Towns of 1840, which recommended including public parks in urban planning for the health of the people (Preston 1987). Consequently, New Zealand's urbanisation has undergone a process of urban development through concentric and compact rings, from a relatively linear manner characteristic of European cities (Lambin *et al.* 2001, Ramalho and Hobbs 2012), through a rapid transition (ca. 170 years) characterised by highly expansive and dispersed configuration. Auckland City, one of the fastest developing cities within Australasia (Gibson 1973), has incorporated urban forest parks as part of their urban planning. Auckland Domain, the first public recreational reserve in Auckland was created in 1844 (Boffa Miskell 1993). The central location of this reserve has promoted its wide use by the public and

also for activities such acclimatisation of introduced species (Thomson 1922). Auckland Domain, with detailed historical records of its structure, composition and function as a reserve in an urban landscape (Ramalho and Hobbs 2015), provides an excellent study site to understand temporal changes in its ecology. A detailed survey of the avifauna by Gill was conducted during the 1980s, coupled with quantified habitat changes, provides the opportunity to investigate avian community change over time. In this study, I analyse the influence of surrounding landscape changes, caused by urban development on local avian community, using bird census data recorded in Auckland Domain during 1988-89 and 2014-15. I test the following hypotheses:

1) Species diversity in Auckland Domain reduce over time due to the anthropogenic pressure of the city.

2) Community composition should have changed due to a reduction of the native species community that may still express a potential temporal delay of response to urbanisation-change.

3) Community change in species diversity and composition correlates with the at a regional level.

6.2 Materials and methods

6.2.1 Study area.

Auckland Domain (75 ha, WGSB4: 174.775136, -36.859921) is a recreational reserve in the Auckland city business district (CBD), and represents 0.16% of the regions native forest cover. The reserve was originally a volcanic hill which was cleared of tall vegetation (podocarp-hardwood forest dominated by Metrosideros *spp.*, Burns *et al.* 2013) by Maori to establish gardens on the fertile soils and as a source of water and animal proteins (Auckland Museum 2005). The cone was also used as a hill fort (pã) with homes and storage shelters (Hayward 1983, Auckland Museum 2005). The hill area was abandoned by Maori population in early 19 centuries (Hayward 1983) and reverted to bracken fern, *Pteridium esculentum,* manuka, *Leptospermum scoparium* (Esler 1991, 2004). Several of the natural springs of the reserve were used as water reservoir for the city until 1875 (Boffa Miskell 1993), while others were drained and converted to

sports fields (Auckland Museum 2005). In early 1867, the site has been used by the Acclimatisation Society of Auckland for the introduction of exotic flora and fauna (Boffa Miskell 1993, Wilcox *et al.* 2004). Consequently between 1867 and 1882, the reserve has experienced the introduction and extirpation of many exotic species of flora and fauna, leading to changes in local community structure. The forest fragment of Auckland Domain currently includes a mix of native and introduced trees and shrubs shaped by Maori and European settlers, with native remnant patches among the mix (Auckland Transport 2011). The canopy is mainly composed of old exotic trees (e.g., oaks, tree privet) with some native trees (i.e., karaka, puriri and kauri) (Auckland Transport 2011). Recently, as part of the ecological restoration of the site , there has been removal of tree privets (*Ligustrum lucidum*) and others understory weeds (weed removal management, Wilcox *et al.* 2004) and replanting of native plants such as whau (*Entela arborescens*) and sedges (Wilcox et al. 2004, *pers. obs.*).

6.2.2 Landscape structure and dynamics.

To quantify change in land use and vegetation cover between the two survey periods. Spatial-temporal landscape data at Auckland Domain and its surrounding areas were collected from aerial photographs (1:8,000) from 1940, 1959, 1996 and 2015, using software from Auckland Council website (http://maps.aucklandcouncil.govt.nz/aucklandcouncilviewer/, version 1.1). Three land cover types were identified and extracted from the photographs: general forest, building (road, building) and open habitat (green patch or unbuilt area). The area of each category in the reserve and within 1 km surrounding area were measured and expressed as the percentage of cover occupied. I compared percent cover values between years to quantify the changes in habitats cover in Auckland Domain and its surrounding.

6.2.3 Weather data.

I obtained the last 53 years of annual precipitation data for the study area from a NIWA (National Institute of Water and Atmospheric Research) weather station located 16.6 km from the study site, to identify any major climatic events that might affect the avifauna of the area during this period (Wiens and

Rotenberry1981, Maron *et al.* 2005).

6.2.4 Bird surveys.

Local avian surveys

Avian diversity and abundance data from two surveys, between April 1987 and April 1988 by Gill (1989), and between April 2013 and April 2014 during this study, were used to compare changes in avian diversity in the Auckland Domain forest fragment. In 1989, the bird assemblage of Auckland Domain forest fragment was surveyed from two fixed locations (WGS84, point 1, lovers-Glades walks: 174°77'41.887", 36°85'53.557; point 2 Forest-domain walk: 174°77'64.541, 36°85'62.195) using a 5 minute point-count method (Dawson and Bull 1975, Fuller and Langslow 1984, Hartley 2012) as used by Gill (1989). Gill recorded the number and species of birds, four times monthly for 1 year during fine weather, between 0920 to 1530 h. In the modern survey, twelve to fifteen bird counts of 5 minute bird counts were conducted in each of the historical locations between April 2014 and April 2015, between 0900 to 1600 h, in order to reduced confounding factor due to the method five-minute bird counters (see Hartley 2012)

Regional bird presence

To assess the influence of regional bird communities on the avifauna of the reserve, I measured the changes in avifauna diversity at a local and regional level. The local forest bird species composition was quantified as part of the 5 minute counts during the historic and present surveys. Regional forest bird species composition was based on published data on the region during the relevant time periods (1980s: Lovegrove 1980, 2010s: Robertson *et al.* 2007).

6.2.5 Local species richness.

I evaluated species diversity by comparing measures of species richness at different time periods, and locations (Figure 6.1). I used different measures of α , β and γ diversity (Whittaker 1960, Jurasinski *et al.* 2009), where α was the monthly diversity record at the study site for each year, βd was estimated based on the difference in species turnover between months, within the survey period, and γ diversity was recorded
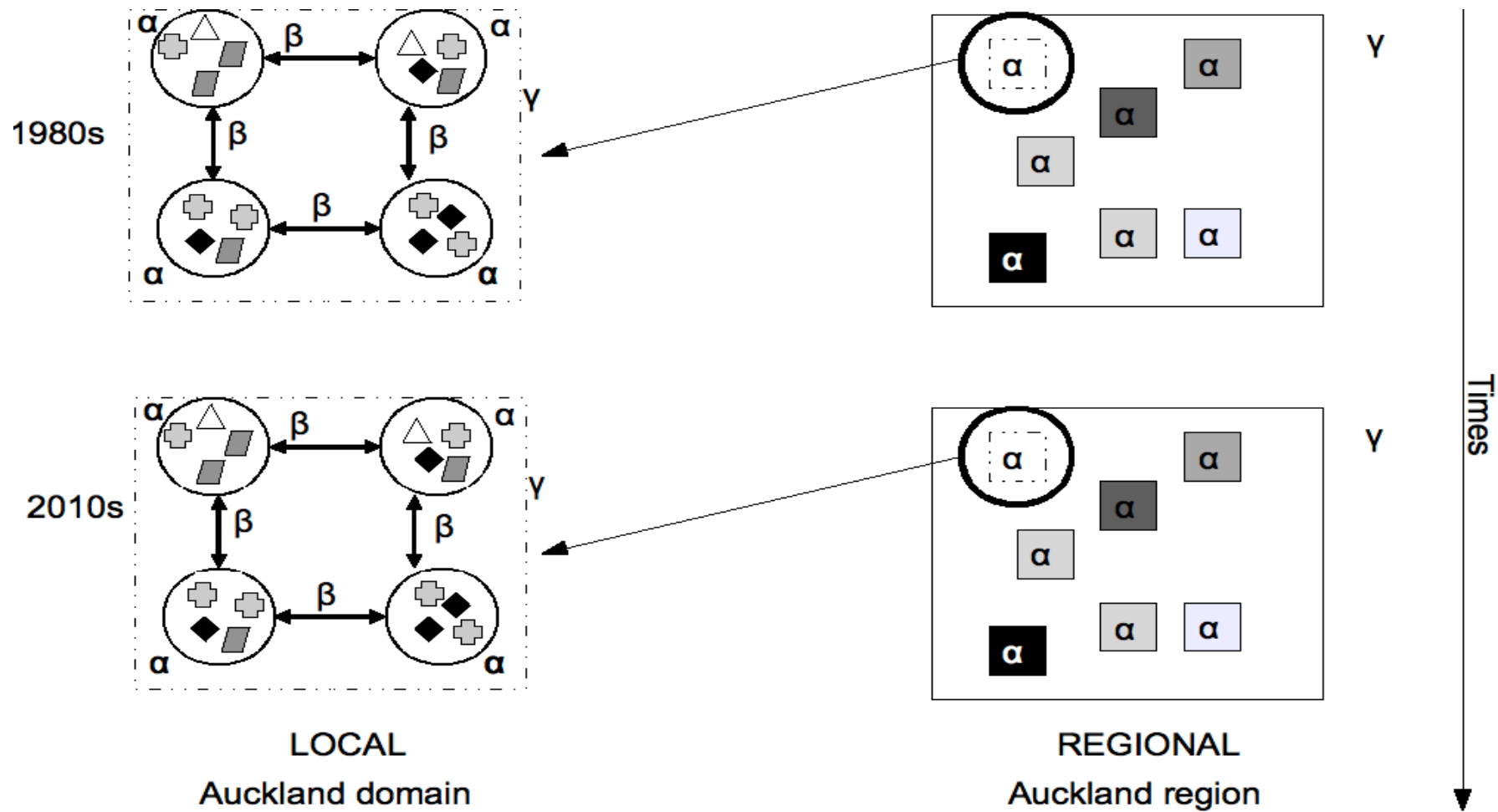
Figure 6.1: Illustration of how α, β and γ diversity were used in this study and the different scales of study they represent. At the local level, the circles (α diversity) represent variation in population abundance sampled monthly within species (different symbols to represent the different species). The pool of species found within this set defines the γ diversity at the local level. The black circles represent the subset of local diversity found at Auckland Domain within the regional scale. The square represents γ diversity at the regional scale, which includes all other available habitats in the Auckland region.

within the year sampled. *β* diversity was calculate using the additive partitioning model *βd = γ - α* (Veech et al. 2002, Jurasinski 2009). *α* diversity was calculated using Simpson's reciprocal index *(1 - D)* where *D = pi ₂*, based on the proportion (*p*) of each species (*i*) observed out of the total number observed per month. α diversity was then broken down into an Evenness (E) and Species richness (S) index (Martin *et al.* 2005). The Evenness index was calculated using *E = 1/D/S* (Martin *et al.* 2005). *S* was estimated using the total number of species present in the γ diversity.

6.2.6 Local-regional richness relationship.

I compared species diversity within Auckland Domain (local scale) to the regional scale to quantify the s regional influence on local species diversity. I used *αl* diversity, as measured from a set of year samples (local scale), and *γr* diversity, the species richness at a higher aggregation level (regional scale) (Whittaker 1960Srivastava 2002), in a partitioning model of diversity (*βp= γr / αl*). I calculated proportional *βp* diversity(local/regional), which assessed the relationship between changes at the local and regional scale (Whittaker 1960, Jurasinski *et al.* 2009), where α represents the mean of the local diversity. Local diversity was extracted from the two survey periods using γ richness for each year. The slope of these local -regional plots was estimated using (1/*βp*; Srivastava 1999).

6.2.7 Data analysis.

The average abundance of each species was calculated for each month and for each survey period. The abundance of each species was then compared between the two sampling periods, 1987-1988 and 2013-2014, using a student's paired t-test. Total, native and exotic species richness were also calculated for each month and for each year from both sampling periods, and were then compared using student's paired t-tests. Because the two survey periods were not conducted in successive years, I calculated the minimum annual turnover (minT) of species in the forest fragment using the formula (Maron *et al.* 2005):

$$minT = \frac{(A+P)}{N} \times 100 \quad \textbf{(6)}$$

where A is the number of species present during the survey period one and absent in the survey period two (i.e., number of local extinctions), *P* is the number of species found only during survey period two (i.e., number of local colonisations), and *N* is the total number of species observed during both survey periods.

To visualise bird assemblage patterns between the two survey periods, I used non-metric multidimensional scaling (NMDS) using the package "vegan" (Oksanen *et al.* 2015). To assess the difference in bird assemblage between the two survey periods, a similarity matrix among month and year was created using a Bray-Curtis index based on the mean number of each species observed per month. Gross differences between years and months were calculated with an analysis of similarity (ANOSIM in vegan package), using 5000 permutations. In addition, a similarity percentage procedure (SIMPER) was used to investigate the species contribution to the mean Bray-Curtis dissimilarity between years (a 70% cut-off value was used). All tests were performed using R (version 3.1.2 GUI, 2013).

6.3 Results

6.3.1 Landscape structure.

The landscape structure of Auckland Domain reserve remained fairly stable between 1940 and 2015 (Figure 6.2), with the reserve being predominantly covered by forest. Some changes in land cover occurred between 1959 and 1996, with a 17.8% increase in forest cover due to replanting of trees in a previously grassed area and a reduction of grass cover between 1940 and 2015. In contrast, building surface cover did not changes during this period, except in 1959 when temporary buildings of 23,377 m^2 were set up on the grass area (1946 to 1963, Titoki Street Transit Camp).

The land cover structure of the surrounding area hasn't observed any major changes (Figure 6.2), with a high proportion of building cover (86-88%) for both periods. However there has been an increase in building density, with an increase of warehouse construction (as opposed to smaller buildings) during 1940-1996 (Figure 6.2). Forest cover of the surrounding area for both periods was around 7%. There were few changes in network patterns of forest cover in the surrounding area, with all forest fragments that were present in

		1940	1959	1996	2015
	Wood cover	50.87	50.03	67.83	67.93
Reserve	Grass cover	46.05	40.43	27.18	27.08
	Building surface cover	3.08	9.54	4.99	4.99
1 km	Wood cover	7.74	6.42	7.68	7.32
surrounding	Grass cover	5.86	5.56	4.69	4.40
the woodland	Building surface cover	86.4	88.02	87.63	88.28
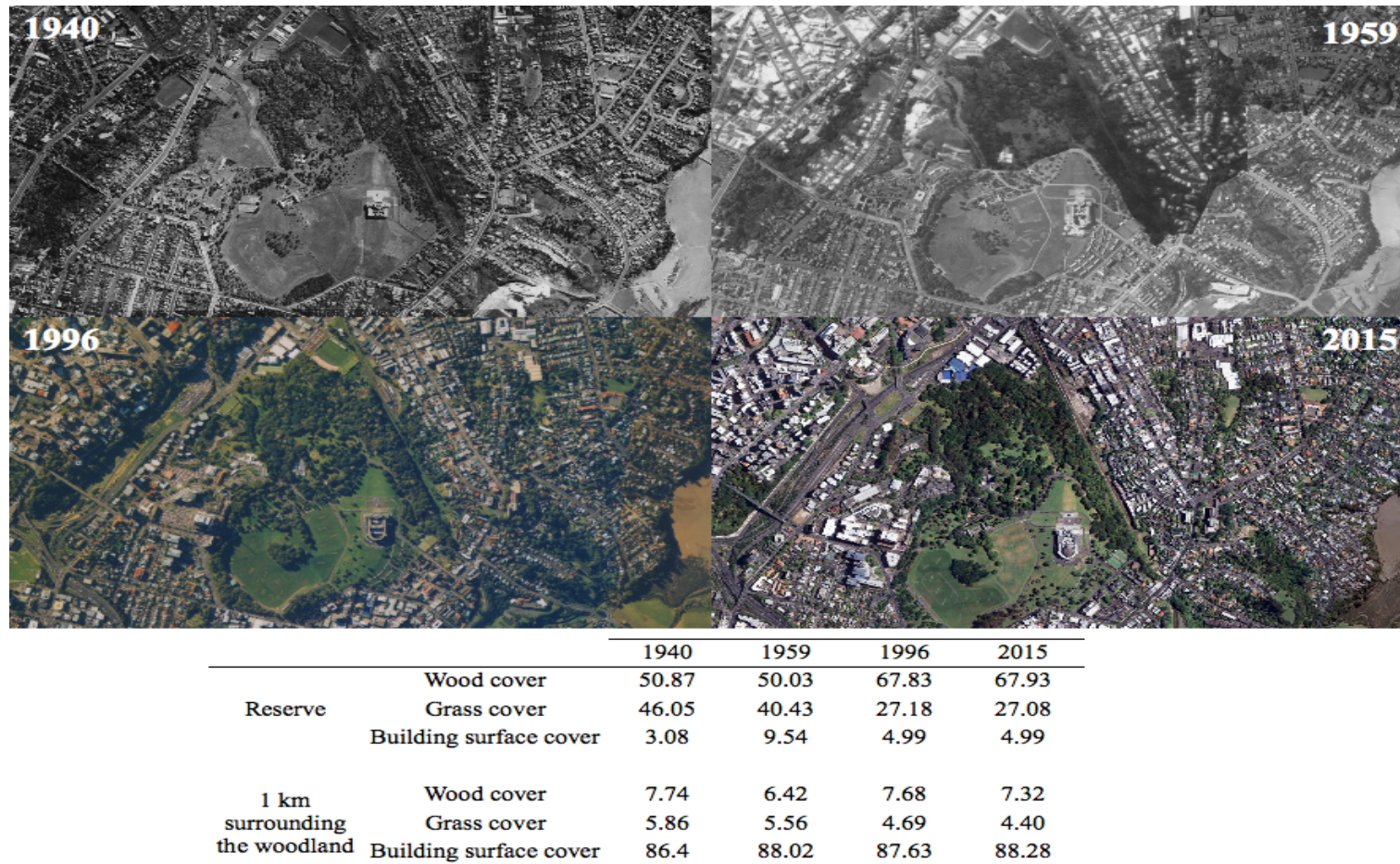
Figure 6.2: Temporal variation in land cover at Auckland Domain and surrounding areas as demonstrated by a) Aerial photographs (1:8,000, Auckland council copyright), taken at 1940, 1959, 1996 and 2015 and b) a table showing percentage changes in cover area for both the Auckland Domain and the areas immediately surrounding.

1940 still present in 2015, despite some variation in size during this period (Figure 6.2). Consequently, the surrounding area of Auckland Domain has not undergone significant variation in landscape structure and land cover between 1940 and 2015.

6.3.2 Precipitation.

The annual rain fall between April 1962 and March 2014 varied between 754.4 mm and 1504 mm, with a mean of 1111.9 mm for the 53 years (see Suppl. 6). The two surveys were done during dry conditions but not in abnormally dry years. The rainfall recorded for the first survey period was 937.4 mm, which was lower than that of the second survey period (1059.8 mm).

6.3.3. Species diversity and turnover.

Twenty-one bird species (α_{local}) were recorded in Auckland Domain for both surveys combined; 17 during the first survey (γ_{1980s}) and 18 during the second (γ_{2010s}). Two species were newly recorded in the second survey period, including 1 native species (Long-tailed Cuckoo, *Eudynamys taitensis)* and 1 exotic species (Spotted Dove, *Streptopelia chinensis*). This resulted in a small species turnover (minT= 15.8%). The mean species richness (S) was significantly different between the two sampling periods ($t_{12} = 6.76$, $p < .001$, Figure 6.3b), with fewer species recorded in survey period 1 (mean ± s.e., α_{1980s}: 10.39 ± 1.66 species) than in survey period 2 (α_{2010s}: 13.08 ± 1.49 species). The richness of native species did not differ ($t_{12} = 0$, $p = 1$, figure 6.3b) between the two surveys (period 1, α_{nat}: 5.08 ± 0.64 species, period 2, α_{nat}: 5.08 ± 0.76 species), despite a higher native species turnover (minT = 25%). In contrast, the richness of exotic species differed significantly between these two survey periods ($t_{12} = 8.57$, $p < .001$, Figure 6.3b), with species richness lower in period 1 (α_{ext}: 5.23 ± 1.48 species) than during the second period (α_{ext}: 8 ± 1.23 species) and a small species turnover (minT = 9.1%).
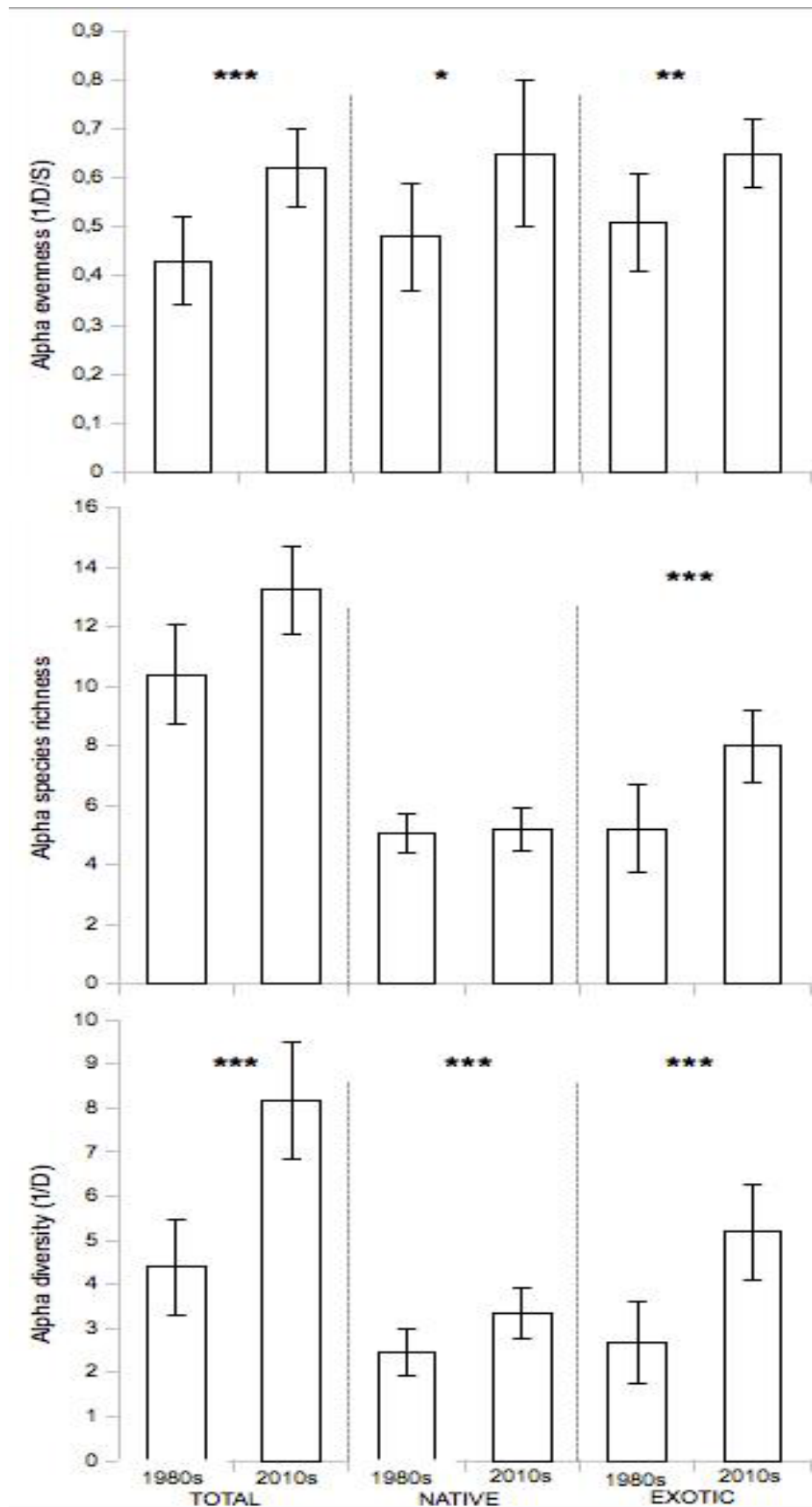
Figure 6.3: Changes in measures of diversity for total, native and exotic bird species found in Auckland Domain between survey periods (based on monthly survey data), for (a) evenness (E= 1/D/S), (b) species richness, and (c) α diversity (1/D) (* < .05, ** < .01, *** < .001).

Table 6.1: Bird species recorded with the diet and foraging area guild allocated to, and their abundance (mean no. individuals recorded per month ± SE) between survey period 1 and 2 (student's paired t-tests). Effect size is Cohen's g.

Species	Mean no. bird/month		Abundance comparison			Effect size (%)
	Survey 1987-88	Survey 2014-15	V	P	Z	
Native						
Silvereye, *Zosterops lateralis*	3.19 ± 0.97	4.22 ± 0.81	79	*	2.341	45.91
New Zealand Fantail, *Rhipidura fuliginosa*	1.42 ± 0.36	1.97 ± 1.10	69	NS		
Grey Warbler, *Gerygone igata*	0.52 ± 0.29	1.85 ± 0.89	91	***	3.180	62.36
Tui, *Prosthemadera novaeseelandiae*	0.24 ± 0.16	1.91 ± 0.87	91	***	3.180	62.36
Sacred kingfisher, *Todiramphus sanctus*	0.19 ± 0.21	0.03 ± 0.04	4	*	2.502	49.08
New Zealand pigeon, *Hemiphaga novaeseelandia*	0.02 ± 0.04	0.04± 0.05	24	NS		
Shining cuckoo, *Chrysococcyx lucidus*	0.01 ± 0.02	0	0	NS		
Long-tailed cuckoo, *Urodynamis taitensis*	0	0.003 ± 0.01	1	NS		

Introduced

Common blackbird, *Turdus merula*	1.47 ± 0.54	2.46 ± 0.86	88	**	2.970	58.25
Common Chaffinch, *Fringilla coelobs*	0.53 ± 0.50	2.00± 1.30	89	***	3.040	59.62
European song thrush, *Turdus philomelos*	0.28 ± 0.23	1.33 ± 0.71	91	***	3.180	62.36
European greenfinch, *Chloris chloris*	0.27 ± 0.36	0.20 ± 0.38	23	NS		
European goldfinch, *Carduelis carduelis*	0.09± 0.12	0.35 ± 0.49	49	*	2.261	46.31
Common starling, *Sturnus vulgaris*	0.09 ± 0.12	0.43 ± 0.55	43	NS		
House sparrow, *Passer domesticus*	0.06 ± 0.08	2.71 ± 0.93	91	***	3.180	62.36
Common myna, *Acridotheres tristis*	0.02 ± 0.04	0.36 ± 0.46	51	*	2.502	49.08
Eastern rosella, *Platycercus eximius*	0.01 ± 0.04	1.30 ± 0.94	78	**	3.148	61.73
Rock dove, *Columba livia*	0.01 ± 0.02	0.12 ± 0.30	12	NS		
Spotted dove, *Spilophelia chimensis*	0	0.13 ± 0.32	15	NS		

When all bird communities were included, α Simpsons' reciprocal index of diversity and evenness were all higher during the second survey period compare to that of the first period (t_{12} = 10.66, p < 0.001, Figure 6.3c; t_{12} = 6.11, p < .001, Figure 6.3a; respectively). Simpsons' reciprocal index (Figure 6.3c) was significantly greater during the 2010s survey for both native (t_{12} = 5.53, p < .001) and exotic community (t_{12} = 6.81, p < 0.001). Simpson's evenness (Figure 6.3a) was also significantly lower for 1980s survey for both native (t_{12} = 3.27, p = .011) and exotic community (t_{12} = 3.74, p = .003).

6.3.4. Proportion of β diversity.

The proportion of β richness showed the same trend with higher value (βp1980s38.94%) from the first survey than that of the second survey (βp2010s 27.78%), when all avifauna were considered (Figure 6.4a). However the difference is not statistically significant (Fisher Exact test, p = .134) due to a significant interaction between data of native and exotic communities. The β richness of native species have not significantly increased over time, from 27.4% (*βp1980s nat*) of the first survey to 27.57% (*βp2010s nat*) of second survey (Fisher Exact test, p = 1). In contrast, β richness of the exotic bird community has significantly decreased over time, from 47.7% (*βp1980s ext*) during the first survey to 27.3% (*βp2010s ext*) during the second survey (Fisher Exact test, p = .003).

The proportion of *β* Simpson's index of diversity was smaller in general, for both native and in exotic species, with less than 5% of γ diversity (Figure 6.4b). No significant difference was observed along the communities within the Simpson's index between the two surveys (β Simpson's index general: Fisher Exact test, p = .826; β Simpson's index native: Fisher Exact test, p = .228; β Simpson's index exotic: Fisher Exact test, p = .253, Figure 6.4b).
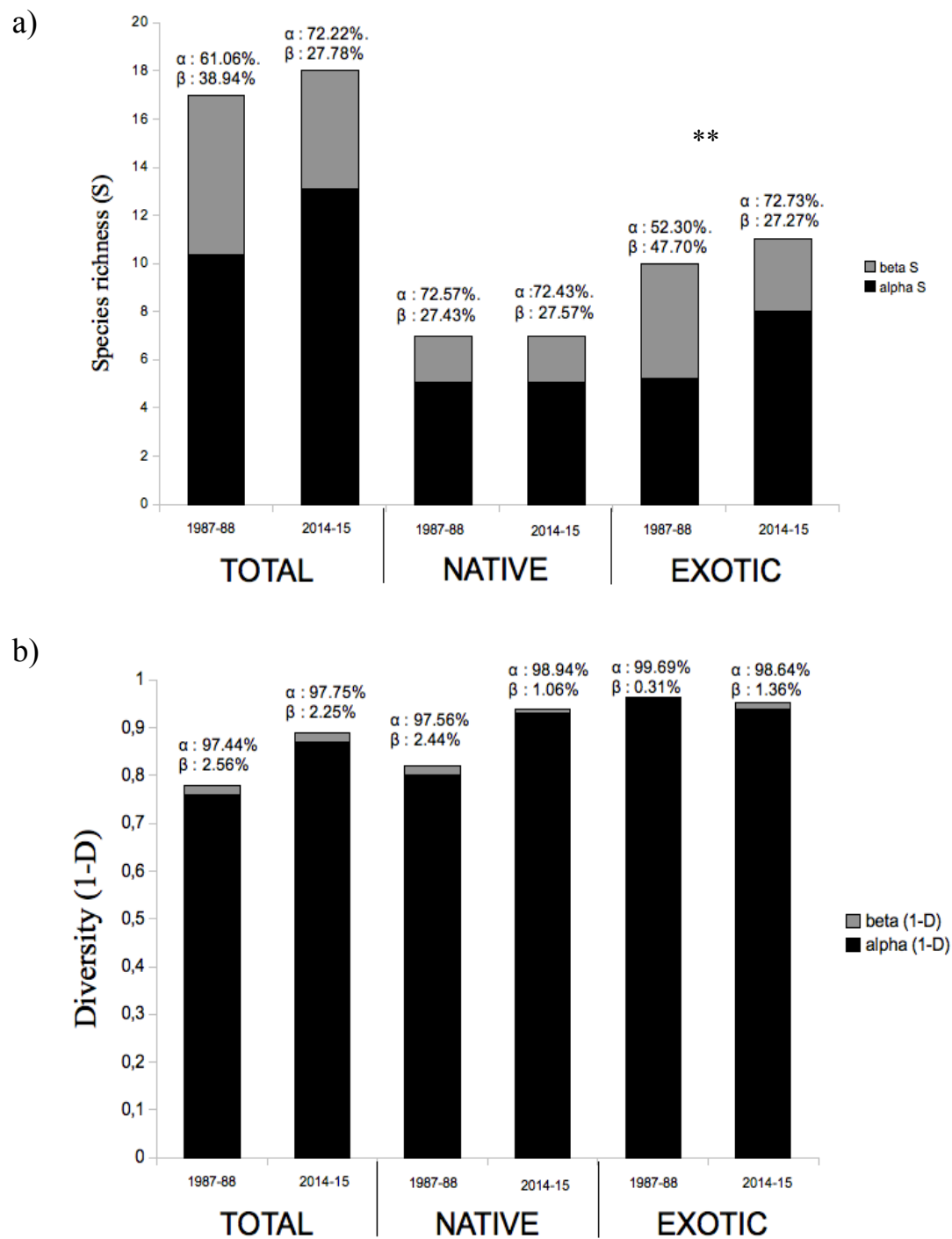
Figure 6.4: Changes in both α and β (a) richness and (b) diversity (1 - D) between survey periods, using the additive partitioning method, within the Auckland domain for total, native and exotic avifauna. γ values are represented by the total height of each bar. The proportions of γ that are α and β are given by percentages above each bar. Significant differences between time periods are represented by * <0.05, ** <0.01, *** <0.001.

6.3.5 Abundance.

Of the 21 species recorded in Auckland Domain forest fragment during the two survey periods (Table 6.1), 2 native species were recorded only once during the survey periods. These species were Shining Cuckoo, Long-tailed Cuckoo and were respectively record during the first and the second survey. During the second survey, more than twice as many birds were observed (S_{2010s}: 22.47 ±6.66 birds per month) as compared to during the first survey (S_{1980s}: 8.39 ±1.66 birds per month). Eighteen species (85.7%) have increased their abundance, with 10 species (55.6%) that significantly increased their abundance (Table 6.2). One species, sacred kingfishers, significantly decreased in abundance in the second survey periods (Table 6.1). Exotic species have generally increased in their proportion of the total species abundance during the second survey (50.32 ± 5.08%), compared to the first survey (32.86 ± 7.8%).

6.3.6 Bird assemblage.

Based on Bray-Curtis similarity indices, the avifauna composition recorded in each survey period were significantly different (ANOSIM; Global R = 0.86, p <.001). A similar pattern was observed when exotic and native species were considered separately (ANOSIM: Exotic species: Global R survey 1 = 0.96, p <.001; Native species: Global R survey 2 = 0.69, p <.001).

Eight species account for 75.8% of the total similarity between the two survey periods, including 3 native species (Tui, Silvereyes and Grey Warbler) that account for 33.3% of total similarity (Table 6.2). Only 48.2% of dissimilarity has been found between the two survey periods, mainly as the result of differences in the observed abundance between species during each survey (i.e., House Sparrow, Silvereye, Tui).

Table 6.2: Contribution (%) of species to similarities and pairwise dissimilarity between the survey periods based on Bray-Curtis similarity indices (SIMPER). (Values are only provided for species that contributed to the top 70% of similarity). [†] Native species.

Species	Similarity (% contribution)	Dissimilarity (% contribution)
House Sparrow	16.2	10.3
Silvereye [†]	14	8.9
Tui [†]	10.2	6.5
Chaffinch	9.6	6.1
Common Blackbird	9.5	6.1
Grey Warbler [†]	9.1	5.7
Eastern Rosella	7.2	4.6
Native	33.3	21.1
Exotic	42.5	27.1
Total	75.8	48

6.3.7 Proportion of local-regional diversity relationship.

Forty-six species (23 natives and 23 exotics, *βp1980s* = 0.37) were present in the forest habitats of the Auckland region in 1980s and 51 species in the 2010s (24 natives and 27 exotics, *βp2010s* = 0.39). The proportional increase in species richness between these two periods in the Domain reserve (local scale) (5.9%, 17-18 species) is consistent with that at the regional scale (10.9%, 46-51 species) (Chi-square for independence, *p* = .92 ; Figure 6.5a), suggesting that local richness was determined by regional richness. A similar pattern was exhibited for the community of exotic bird species, with a gain of 10% (10-11 species) between survey periods at the local scale and 17.4% (23-27 species) at the regional scale (Chi-square for independence, *p* = .88 ; Figure 6.5e; *βp1980s exo* = 0. 0.43 > *βp2010s nat* = 0.41).

The regional-local relationship in the native community displayed no increased between these two survey periods (0%, 7-7 species) at the local scale, in contrast to the regional level where this increased was smaller (4.3%, 23-24 species) (Chi-square for independence, *p* = .81 ; Figure 6.5c), showing a better representation of the native bird community diversity at the regional than at the local level (using beta native diversity; Figure 6.5d; *βp1980s nat*= 0.30 > *βp2010s exo* = 0.29).
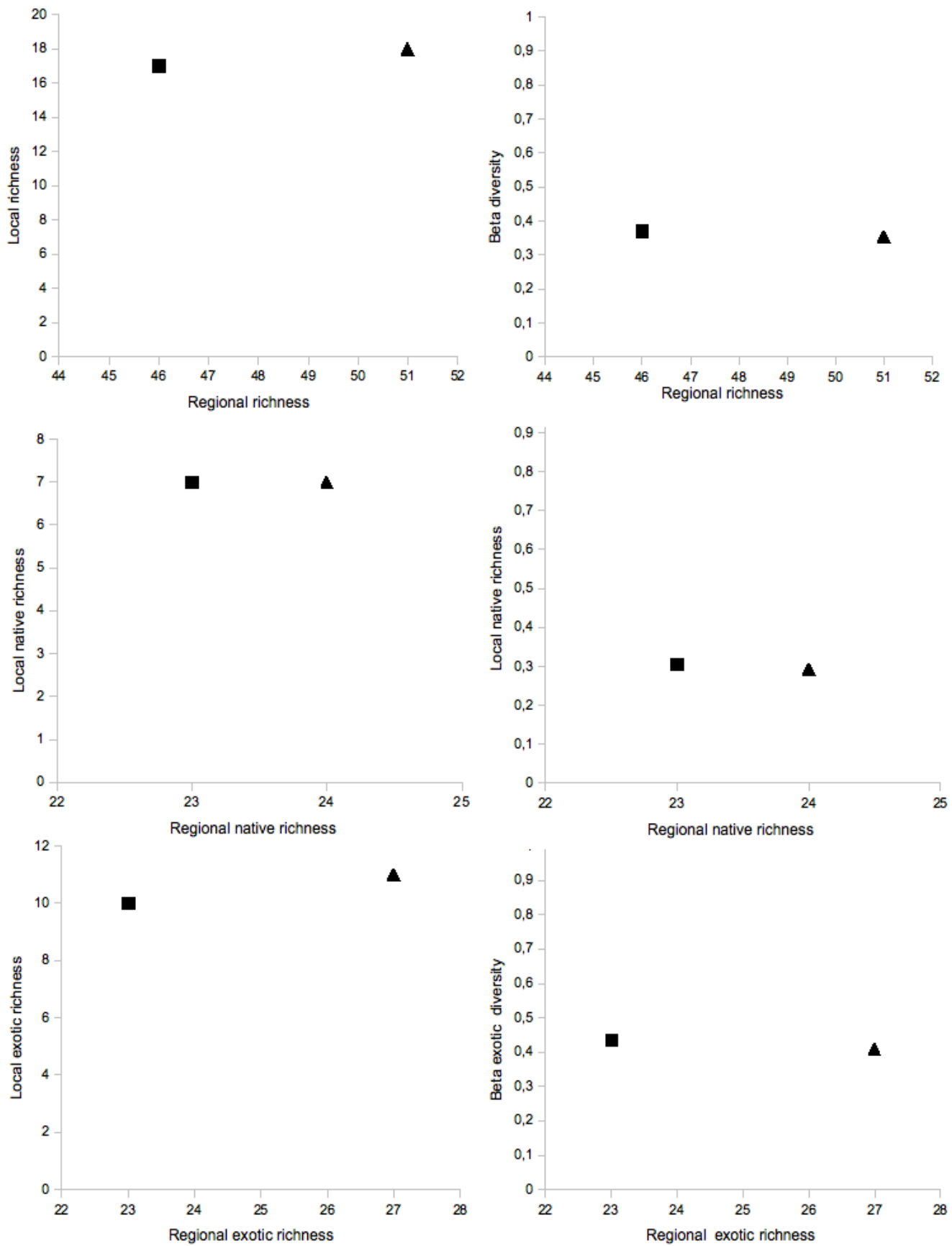
Figure 6.5: Changes in local/regional richness (a, c, e) and β /regional diversity (b, d, f) for the local (Auckland Domain) and regional (Auckland Region) avifauna pool. Figures **a)** and **b)** total bird community; **c)** and **d)** native species community; **e)** and **f)** exotic species community (■: data from 1980s, ▲: data from 2010s).

6.4 Discussion

Notwithstanding the central location in a major city and a site used for exotic species release by the acclimatisation society, in the late nineteenth century (1867s), the Auckland Domain has undergone little change in land cover and use over the 26 years between the two surveys. There was an increase of abundance in species and a small change in α diversity associated with regional change in avian biodiversity, based on five minute bird counts. However I found no important changes in α diversity in the community between survey periods.

6.4.1 Landscape structure changes.

Besides the historical changes observed in land use and cover on Auckland Domain under the presence of Maori and European, in the last 75 years, the land cover and use of the reserve have not undergone significant changes. However, vegetation structure, especially the forest fragment change since 1940 (i.e., deforestation of some area, overseas vegetation management techniques; Boffa Miskell 1993) with now presence of many large old and mature trees. Consequently, the forest fragments of the reserve now offer a higher diversity of native and exotic plant community, with 858 plants species of which 73% are introduced (Landcare Research 2011), and different successional ages of "natural" (i.e., vegetation not significantly affected by man, Cumberland 1941, Küchler 1969) and "cultural" (i.e., all vegetation altered by man directly or indirectly; Cumberland 1941, Küchler 1969) vegetation (Thomson 1922, Gardner 1981, Boffa Miskell 1993, Wilcox *et al.* 2004). In the last two decades, vegetation management by Auckland Council for improving understory cover and the removal of exotic plants (e.g., privet or other weed control) has resulted in a reduction of competition for native shrubs and ground cover plant species (see Hanula *et al.* 2009, McAlpine *et al.* 2014). These management actions have then allowed development of patches of plants with different maturity in the forest fragment and provided heterogeneity along the vertical layers (Boffa Miskell 1993), offering a large range of habitats cover type and food resource for local fauna through the ecological succession.

The surrounding landscape (within 1 km) has had no major change in land cover between 1940 and 2008. However during this period, there had been very small changes, with the replacement of grass cover by building surfaces (i.e., manufacture, commerce and residential development), mainly during the modernisation and gentrification process that occurred between 1950s and 1970s (Gu 2014). After 1970s, the surrounding landscape of the reserve had a strong intensification of buildings, primarily due to house construction due to subdivision of old residential plots (Figure 6.2; Gu 2014), which therefore caused an increase of barrier for dispersion and a decrease of garden size and buffer zone for terrestrial species. The vertical landscape structure during this period was characterised by development of higher new buildings (Gu 2014). Nonetheless, remnant forest fragment patches (7.3% of the surface cover) surrounding the reserve in the 1940s did not undergo significant transformation, which may have played an important role in the maintenance of local metapopulations throughout the urban matrix. The outcomes of this study demonstrate only a small change in landscape structure and land use in this dynamic environment, hence the absence of large effect of landscape changes on species assemblage and diversity over time. Although beyond the scope of this study, the increase of building densities within the landscape near the reserve could affect the dispersion of smaller birds along with the impact of more intense human disturbances (i.e., noise pollution and light, traffic in the park, recreational used); both known to affect bird species in forest remnants (Van der Zande *et al.* 1984, Fernández-Juricic 2000).

6.4.2 Temporal variability in avifauna community.

This study has some limitations within the bird counts survey. First, the two surveys were done by different observers using the same protocol which could provide some observer bias notably in the detection of bird population change. Often, observer differences are due to variation in ability and experience (Link and Sauer 1998, Boulinier *et al.* 1998). So during both survey observers has presented similarly experienced in conducting bird surveys, and more specifically during the second survey the observer have undertaken trial survey in other urban remnant forests before to the survey period. The high conspicuousness of avifauna in New Zealand urban forest has also reduced the likelihood of large observer effects. Second, the

sampled period could have presented as an excellent or weak year for breeding and survival, so the pattern observed and discussed is only representative. Indeed authors of numerous long-term studies worldwide have concluded that bird population tend to fluctuate on stochastic manner year to year and so represent only a picture of 'the' bird assemblage of the area (Enemar *et al.* 1984, Virkkala 1991). Nevertheless, some discussion can be drawn from the two survey periods.

The change in bird assemblage during the second survey periods was mainly due to a 2.3 fold increase in bird abundance (Table 6.1) over the 26 years. I suppose that the impact of observer differences along the two survey was probably minor compared to the magnitude of the bird assemblage differences as suggest by Maron et al. (2005). This pattern of change has also been noted in the Northern hemisphere, with a 2.4 fold increase in avian populations over 16 years in New Hampshire (Holmes *et al.* 1986) and 2.1 fold increase in a bird population in a subalpine birch forest in Lapland province in Sweden over a 20 year period (Enemar *et al.* 1984). Similar trends were recorded in other areas of the Southern hemisphere, with a 3 fold increase of bird abundance in South-eastern Australia (Maron *et al.* 2005) and 1.3 fold increase over 117 years in Wellington (Brockie and Duncan 2012 ; between 1888-89 to 2005-06). However, this study presents the first research showing a temporal variation of bird density at a small scale in an urban habitat, over a long temporal scale. Indeed previous research in urban systems investigated the effect of time on bird communities using study sites or suburbs of varying ages (in North America: Vale and Vale 1976, Savard 1978; in Europe: Huhtola 1978, Luniak 1980; in Australia: Munyenyembe *et al.* 1989). Their research findings demonstrated an increase of bird densities in relation to suburb age. Thus the increase in the number of birds observed in Auckland Domain can be partly explained by the presence of scrub and plant communities with different degrees of maturity in the forest of Auckland reserve (Boffa Miskell 1993), as well as by the absence of major environmental changes in the reserve over time. Blair (1996) suggested that management of urban parks and gardens improved the diversity and richness of the plant species, increasing resource availability for avifauna, and thereby allowing a higher bird density, which should continue to improve plant diversity and plant structural heterogeneity of the forest fragment to provide better breeding sites, refuges and food resources for local avifauna. Furthermore, the recent presence of pest-mammal control program that occurs in the reserve could also explain the increased in the bird assemblage. Innes *et*

al. (2010) highlight the significance of mammal pest-control for increasing survival of juvenile and adult native forest birds. These would offer a parsimonious explanation for the changes in bird abundance observed between the two bird surveys.

6.4.3 Response of bird assemblage.

The species richness between the two survey periods did not differ markedly, with a weak turn-over of 16% over the 26 year period, indicating that the proportion of the regional community represented within the local community (i.e., Auckland Domain) has remained consistent, so no change in the pattern of nestedness has occurred (Wright and Reeves 1992, Kaiser 2015). The species found during the first survey (1987-1988) were often recorded during the second survey (2014-2015), with the exception of Shining Cuckoo (*Chrysococcyx lucidus*), which was only sighted during the first survey (Gill 1989). Interestingly, two new specie were recorded in the later survey. One of them, the Long-tailed Cuckoo (*Urodynamis taitensis*), which is not commonly record in urban forest survey, was only recorded once during the survey in January. The reserve may have been used as a resting time, during its passage to or from its breeding location. The introduced Spotted Dove (*Streptopelia chinensis tigrina*) were also only recorded during the second survey period and was observed throughout the second survey period, showing a recent establishment of this species in Auckland. The lack of change in native assemblage composition within and between survey periods in the urban forest fragment is likely a reflection of a stable regional pool of native birds. Indeed Brown *et al.* (2001) suggested that species richness of an ecosystem may remain relatively stable over time when resources and the regional species pool are relatively large to compensate for any colonisation or extinction of species at the local level. Thus the observed increase in the exotic species richness over-time may be a result of the unsaturated character of the urban avian assemblage or the impoverishment of the local avifauna community (Pautasso *et al.* 2011), both patterns which are more prone to invasion by exotic species. The Auckland region has experienced a reduction in the native avifauna pool since the arrival of humans due to habitat clearance and the introduction of large range of exotic species. Bird species may present some survival advantage in human modified environments due to their history of coexistence with human population and anthrome (Sih *et al.* 2011, Pautasso *et al.* 2011) and establish

following introduction (Martin and Colbert 1996). Indeed, competition free situations using the concept of 'niche opportunity' (Shea and Chesson 2002) and, also from high habitat and resources tolerance, created by human-induced rapid environmental change, may contribute to human experienced invader to establish and growth a population in the invasion site. For example, the fast establishment of a spotted dove population in Auckland region since their introduction in the 1920s (nzbirdonline.com, http://www.nzbirdsonline.org.nz/) could potentially be explained by its past evolutionary experiences with human induced habitat changes and its ability to cope with these habitats using key behaviour (e.g., selfish herd geometry; Sadedin and Elgar 1998), as well as the instability of the avifauna community dynamics of Auckland region, following recent disturbance events notably due to loss of populations of native bird species. Indeed Spotted dove may have found a particular combination of biological factors, such as resource supply and availability combined with past experience and the development of key behaviours, all favour the invader potential of this species in the anthropogenic landscapes, as observed by Galbraith *et al.* (2015).

Overall bird community assemblage of the Auckland Domain appears to have not changed over-time. Indeed the results indicate that seven species accounted for 75.8% of the total similarity between the two survey periods. Of these seven species, three were natives (i.e., Grey Warbler, Silvereye and Tui) and displayed similar contribution throughout the two surveys with a total similarity of 33.3% for the native community (Table 6.3). This result suggests that these species have successfully maintained populations in habitat surrounded by urban landscapes as observed in Wellington by Mc Arthur *et al.* (2012). The dissimilarity between the surveys are primarily a function of differences in abundance between species through the survey periods (Table 6.3). The main change over time at the Auckland Domain is the switch from a bird community dominated by native birds (66.32% of native bird observed for 33.68% of Exotic bird observed by Gill during the survey 1987-88, 1989)to a mix of exotic and native (in both species number and densities, with 46.83% of native bird observed and 53.17% of Exotic bird observed in 2014-15), due to the increase of abundance of some introduced species such House sparrow, eastern rosella, common blackbird, or chaffinch (Table 6.1). Indeed these species have shown a higher similarity contribution between the two surveys with 42.5% for the exotic community. A similar trend of change in community structure was detected in Adelaide (Tait *et al.* 2005), showing adaptive qualities of exotic species to an urban

matrix. My results show that common birds found in European towns, such as *Sturnus vulgaris*, *Passer domesticus* (Clergeau *et al.* 2006), species adapted to city life, also dominated in Auckland domain. Thus, my findings highlight the current global trend (Clergeau *et al.* 2006, McKinney 2006) of similar avian community structure, independently of geographical location (Clergeau *et al.* 2006).

6.4.4 Difference in response of bird species to urbanization over-time.

My results showing no change in α diversity and richness within Auckland Domain are not consistent with other urban studies in New Zealand and on mainland forests (Pierce *et al.* 1994). Brockie and Duncan (2012)have recorded an increase of α diversity in Wellington over a 40-year period. The small gain in the richness observed in this study doesn't fully reflect the improved of richness noticed in Wellington (Brockie and Duncan 2012). However, short-time temporal variation at a local scale is unlikely to reflect absolute change at a broader scale. Consequently, to understand the population dynamics at a local scale, the correlation with the recorded population dynamics at a larger scale is needed (Virkkala 1991). For example, some native species such as Tui (*Prosthemadera novaeseelandia*), New Zealand Fantail (*Rhipidura fuliginosa*) and introduced species like Eastern Rosella (*Platycercus eximius*), European Starling (*Sturnus vulgaris*), European Goldfinch (*Carduelis carduelis*) have all presented similar patterns of change with an increased at the local level and at the national level during the period 1969-1979 and 1999-2004 (Bull *et al.* 1985, Robertson *et al.* 2007). Silvereyes (*Zosterops lateralis*) and the Grey Warbler (*Gerygone igata*) have demonstrated an inverse pattern, with a substantial increase at the study site compared to their abundance at the national level (Bull *et al.* 1985, Robertson *et al.* 2007). Based on this observation, the increase in the presence of these two native species indicate that population of these species have the capacity to survive in stable forest fragments in urban systems and the associated dynamic of changing landscape as recently observed in Tui (Froude 2006, Bell 2008). Introduced species, such House Sparrow, Song Thrush, Blackbird, common chaffinch have exhibited different population pattern of distribution change at the national and local, by increasing over time their population in Auckland Domain when at the national level no change was observed (Bull *et al.* 1985, Robertson *et al.* 2007). These species are generally described as coping with urban disturbance (Blair 1996, Kark *et al.* 2007, Croci *et al.* 2008). The numbers of individuals

of Sacred Kingfishers (*Todiramphus sanctus*) recorded in the reserve decreased, in contrast to patterns within urban reserves in Wellington (Froude 2006, Brockie and Duncan 2012, McArthur *et al.* 2015) and nationwide where the species has increased (Robertson *et al.* 2007). This decrease in urban populations and the high degree of fidelity of the species to breeding sites (Heather and Robertson 2000) suggests an effect of local activity on its abundance and may be resulted from temporary variation.

The relatively recent exposure of New Zealand avifauna to urban habitats may explain some temporal delay in responses to change of some species in urban habitats (Ramalho and Hobbs 2012). Indeed times-lagged response to a landscape structure has been estimated to be around 100 years for birds species (Brooks *et al.* 1999, Metzger *et al.* 2009).

6.4.5 Influence of regional biodiversity.

Despite the Auckland Domain representing only 0.16% of forest fragment available in the region, the avifauna community of the reserve contained ~ 37% of the regional species pool during both periods. My results highlighted that a small urban forest fragment can support a stable and substantial proportion of the regional pool of avian species. The result of *βp2010s* and βp*1980s* in my survey were low (0.37 for 1980s and 0.35 for 2010s), indicating that turnover observed previously was the dominant contributor to *β* diversity. The most likely explanation of this finding is that the composition change results mostly from species replacement (moderate turnover) than a difference in richness (small nestedness-resultant component) The results exhibited some contrasting patterns of local-regional relationship change inside of the local community. Considering the local-regional dynamics across the time, the native species community has presented a stronger relationship with minimum differentiation in the most recent survey (Figure 6.5b; βp1980s nat < βp2010s nat) with a great arrival of regional species in the local pools. In contrast, exotic species exhibited a good ratio of similitude between local and regional biodiversity (Figure 6.5f; βp2010s exo < βp1980s exo) over time due to arrival of new species at the regional level not found so far in the local pool.

6.5 Conclusion

Overall using historical and current avian community abundance data, I identified temporal variation in the dynamics of a bird community in response to urbanisation processes. Urbanisation is known to affect biodiversity (Batten 1972, Walcott 1974), leading to temporal patterns of change in community composition (Edgar and Kershaw 1994, Chouteau *et al.* 2012). However, a moderate level of development may potentially lead to an increase in species diversity (Blair 1996, Marzluff 2001). I have recorded small changes in avian community composition over 26 years period in an older forest remnant from the centre of Auckland, a city recently developed and urbanised, and I have shown an increase in species richness and abundance through time and that also correlated with the regional pool. I have also demonstrated that different community dynamic processes are occurring simultaneously for native and introduced species with an alteration in the balanced between native and exotic species in avian community structure, due to changes that have occurred in reserve over the two survey periods (e.g., weed control, introduction and control of predator...).

Further research is required to understand the biological effects of urbanisation in recently colonised habitat on communities. Information from current areas such as Auckland Domain will help to predict and consider the impact of urban sprawl on native biodiversity community over time, but more research on forests in a new suburb overtimes should offer a better understanding of community responses to urbanisation and anthropogenic constraints.

Acknowledgments

Supplementary forms

Suppl. 6: Mean annual rainfall in Auckland area during 1960-2014. Broken red line indicates the long-term annual mean
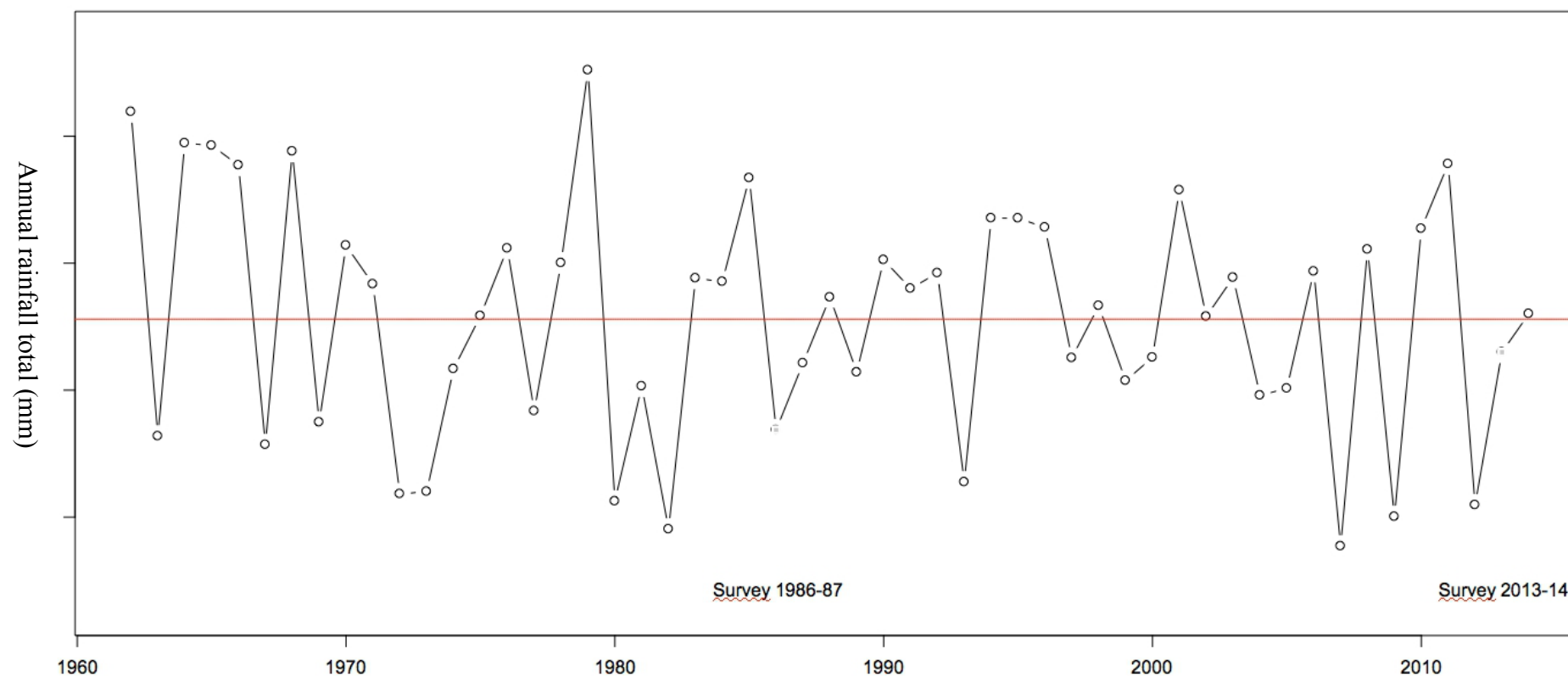
Chapter 7

Plasticity in nest site selection co-varies with length of

inhabiting human modified habitats

Abstract

Nest site selection is a parental care trait that is subject to natural selection. The nesting strategy used by species will vary, depending on type of nest predators, they are exposed to and the length of time they have coexisted. Furthermore, for natural selection to work, traits should vary within a population and the degree of phenotypic plasticity of these traits can also play an essential role in a species' ability to adapt to new selection pressures. In this study, used six passerines species with divergent patterns of evolutionary history, to explore how nest-site selection strategies differ in response to predator and human-disturbance. In particular, I tested the prediction that birds minimise the risk of disturbance, by both humans and nest predators, by using one of three alternative nest location strategies. My results showed that species exhibit divergent nest-site selection strategies related to the duration of human coexistence. Native species, which have a short history of inhabiting anthropogenic habitats, exhibited a change in the horizontal index of nest sites by nesting more towards the edge of the foliage, compared with their congeners in natural habitats. However, no changes were observed for introduced species in nest-site selection in response to anthropogenic habitats. Native species are likely to be under strong selection pressures on nest site choice in response to recent changes in predation risk due to introduction of mammal predators. Introduced species showed little change, most likely due to a longer period of coexistence with similar human-induced habitats changes, which may have influenced their degree of behavioural plasticity. Overall, the results suggest that differences in responses of nest-site selection among species are likely to be associated with their experience in both human-induced habitat changes and predator cues.

7.1 Introduction

Predation is one of the strongest selection pressures on animal traits (Martin and Briskie 2009, Ibáñez-Álamo *et al.* 2015). During their lifetime, animals will experience various critical stages when they are more vulnerable to predation events. Early development is such a stage when high predation pressures will select for 'key' morphological and behavioural traits of both parents and offspring (Martin 1995). These traits are selected to help mitigate predation risk (Ghalambor and Martin 2001, Ghalambor and Martin 2002, Fontaine and Martin 2006). For different species that experience similar predation risks, convergent evolution of behavioural traits may occur. The development of traits that best avoid predation would subsequently become an optimal strategy and become stabilised across different species within a specific environment. However, the arms race between predator and prey may result in antagonist coevolution to maintain their relative fitness advantage (where it gains a selective advantage with the most fitness benefit for the lowest cost; i.e., the red queen hypothesis; Van Valen 1973).

Human activities have resulted in multi-dimensional changes of natural habitats (Sih *et al.* 2011) that have created new evolutionary conditions (Sih *et al.* 2011, Sih *et al.* 2012) for other organisms. Human-induced rapid environmental change (HIREC) includes strong alteration of habitat structure (e.g., habitat loss, fragmentation, changes in plant communities and structure), habitat conditions (e.g., increased noise, light pollution, temperature) and biotic interactions (e.g., the introduction of 'novel enemies'; Sih *et al.* 2011, Alberti *et al.* 2017). The effects of HIREC will consequently result in novel selection pressures on the traits of organisms (Thompson and Burhans 2003, DeGregorio *et al.* 2014a, LaMamma *et al.* 2015, Ibáñez-Álamo *et al.* 2015, Alberti et al. 2017). Anthropogenic activities may alter predation patterns by deterring natural predators and/or introducing novel predators that may result in changes in prey detection strategies used by predators (e.g.,. cues used to find prey ; Sih *et al.* 2012, Selva *et al.* 2014). Such changes are likely to alter the proximate cues that prey species use for detecting the predation risk over time (Zanette *et al.* 2011, Hua *et al.* 2014), and will influence-nesting site selection outcomes to minimise disturbance from both humans and nest

predators (Beale and Monoghan 2004, Hua *et al.* 2013).

The responses of birds to HIREC vary in relation to a species' historical legacies (Essl *et al.* 2015a). Birds may move out of their original breeding territory to seek a safer breeding site, or shift the nest placement within the same breeding territory (Knight and Fitzner 1985, Hockin *et al.* 1992, Beale and Monaghan 2004)). Species with a longer history of coexisting within human-modified habitats and their associated environmental changes are likely to have evolved new nesting strategies in response to altered selective pressures (Martin and Briskie 2009, Ibáñez-Álamo *et al.* 2015, Samia *et al.* 2015). Different species experiencing similar HIREC may demonstrate behavioural shifts (Sih *et al.* 2011, Sih 2013) over time towards common anti-predator behaviours (Lowry *et al.* 2012) and method to cope with human disturbance (Beale and Monoghan 2014).

Passerine birds have been extensively used to comprehend HIREC complex interactions (Hockin *et al.* 1992). For birds, nest sites are vital to offspring success (Gotmark 1992, Martin 1993, Ibáñez-Álamo *et al.* 2015). The horizontal and vertical locations of bird nests are thought to be influenced by predation and human disturbances (Knight and Fitzner 1985, Datta and Pal 1993, Martin 1995, Beale and Monaghan 2004, Forstmeier and Weiss 2004, Yeh et al. 2007); however, our understanding of these patterns remains limited,

New Zealand avifauna have experienced a very short period of human coexistence, providing a unique system to evaluate the responses of this group to HIREC. Before human settlement, the predators of New Zealand's avifauna were predominantly avian predators, which are mainly reliant on visual cues to find prey (e.g., moreporks, Australian harriers; Remeš *et al.* 2012). Throughout the process of human settlement in New Zealand, humans have systematically denuded vegetation from the landscape, through burning and agricultural practices (McWethy *et al.* 2011), and introduced exotic wild and agrarian species (Thomson 1922). The arrival of exotic mammalian predators (e.g., Norway rat, ship rat, stoat) (O'Donnell 1996, Craig *et al.* 2000) has also introduced new predation strategies. Many of these introduced mammalian predators locate prey from the ground using acoustic or olfactory cues: techniques that native avifauna were naïve to (Remeš *et al.* 2012). This caused an asymmetric reduction in native species (Innes *et al.* 2010), with those exhibiting vulnerable life-history behaviours, particularly ground-nesting and ground-foraging species, being more susceptible to extinction (Duncan and Blackburn 2004, Steadman 2006).

European colonists also successively introduced many avian species to New Zealand during the 1860s, largely due to the establishment of an Acclimatisation Society. These introduced species that were more familiar with humans and HIREC were more successful in newly established human-modified habitats (McWethy *et al.* 2011; Innes *et al.* 2009). These introduced birds have displaced some native avian species in multiple native New Zealand ecosystems (Thomson 1922, Duncan and Young 2000, Innes *et al.* 2009). Therefore, New Zealand provides a good system to investigate how the history of coexistence with humans and their habitat disturbances affect the behavioural traits of animals inhabiting human-modified habitats.

In this study, I used six passerine species with divergent patterns of evolutionary history to explore how nest-site selection strategies differ in response to predator and human-disturbance. I examined how nest location differs across habitats that vary landscape change and levels of disturbance by humans and predators. In particular, I aim to (i) investigate variation in nest-placement strategies among species at three habitats, which vary in levels of predation and human disturbance; (ii) test if the nest-site selection by different species reflects their history of coexistence with human and mammalian predators; (iii) examine whether changes over time in nest-site selection has occurred as a response to recent changes in selection conditions, development of urban areas or mammalian predator control.
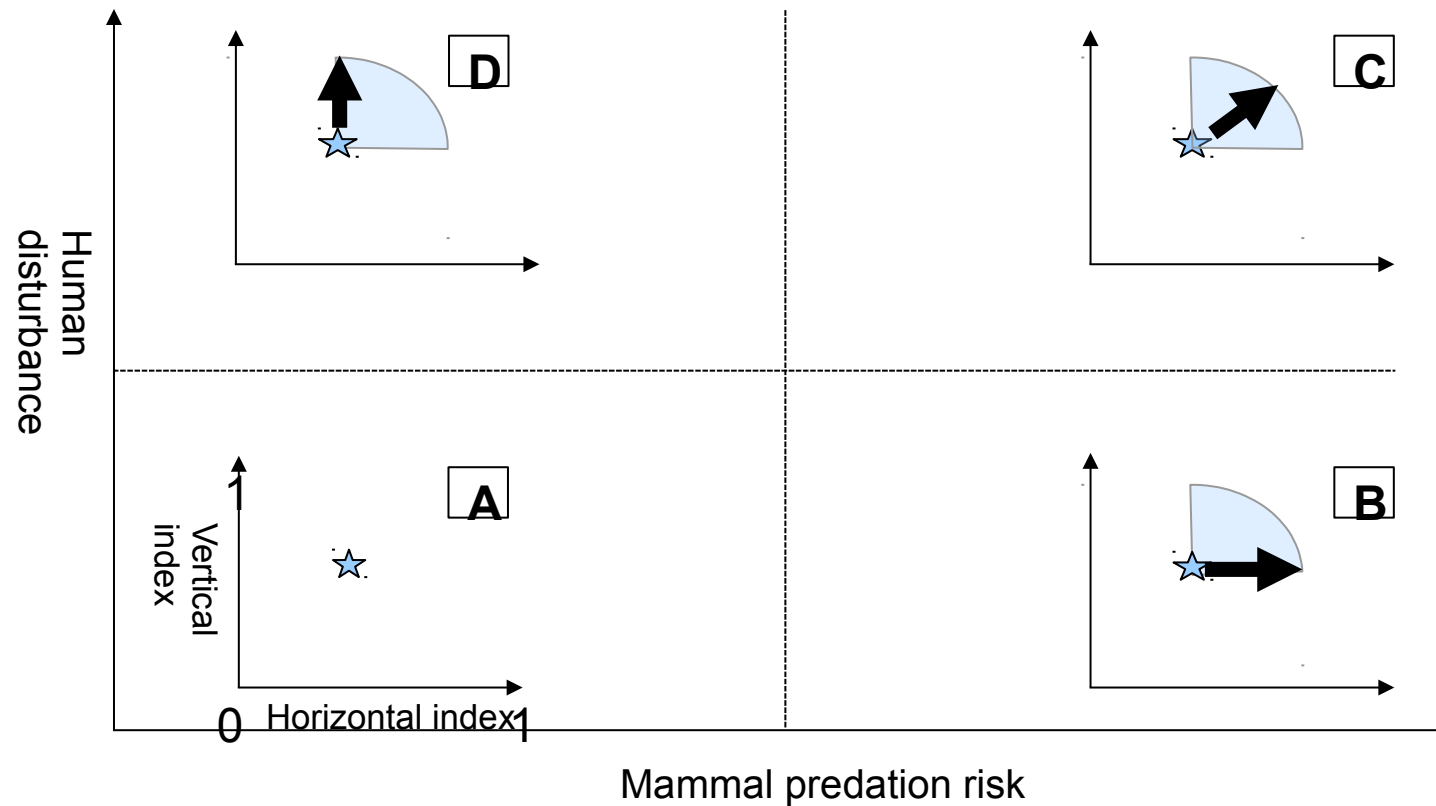
Figure 7.1: A conceptual depiction of the possible tradeoffs in nest-site selection in response to changes in the immediate risk of mammalian predation and human disturbance. Each smaller graph (A-D) represents a scenario where a shift in either predation risk or human disturbance has occurred. Graph A represents the ancestral state for native New Zealand species prior to human colonisation. The optimal-tradeoffs response (i.e., a nest-site that offers the best tradeoff between the benefits and long-term cost of avoiding predators and environmental constraints; Lima 1998b), for graph A is represented by a star. Graphs B, C and D, represent the predicted changes in nest-site location following changes in predation and human disturbance levels. The black arrow represents the best trajectory of the proximate response through phenotype plasticity (ecological time), using environmental cues. The blue quarter circles represent the fundamental niche of species nest sites.

Birds that live in habitats with high levels of human disturbance (e.g., noise pollution and artificial lights, visitation by humans and their dogs) are more likely to place their nest higher to reduce the effect of these disturbances (Ibáñez-Álamo *et al.* 2015). I therefore predict that birds will use one of two alternative nest-location strategies to minimise the risk of disturbance by humans (Figure 7.1 C, D). By contrast, species that experience an increase in levels of predation should either move their nest sites (a) higher, to decrease the probability of nest predation (Forstmeier and Weiss 2004, Yeh et al. 2007), or (b) move their nests further along the horizontal axis, limiting accessibility (Martin 1995, Fry and Keith 2004, Ramos-Lara and Cervantes 2007, Echeverry-Galvis *et al.* 2014). I therefore predict two alternative nest location strategies to minimise the risk of disturbance by a predator: a change in nest location along the horizontal axis or both horizontal and vertical axes (Figure 7.1 B, C). In contrast, bird species that live in habitats without mammalian predators or human disturbance, are more likely to select their nest-sites near the trunk and at the middle height of the tree to avoid climatic problems (e.g., wind, rain; Ramos-Lara and Cervantes 2007) and reduce visual cues for potential avian predators (Martin 1995; Figure 7.1 A).

Thus, the selection pressures imposed by different levels of human habitat modification and nest predation patterns on nest-site location may select for an optimal nest location strategy to specifically lower risk of predation (Figure 7.1 C, B) or human disturbance (Figure 7.1 D, C), or a combination of both (Figure 7.1 C), based on reliable threat information (Ibáñez-Álamo *et al.* 2015).

7.2 Materials and methods

7.2.1 The study area and experimental design.

The study was conducted from 2012 to 2014 in the North Shore district of the Auckland region (36.471°S 174,452°E), New Zealand. All study sites were characterised by mature native broadleaf-podocarp forest, varying in area from 1.74 to 113.6 ha. These sites have undergone similar histories of spatiotemporal characteristics of habitat fragmentation (Figure 7.2 A, B) and other environmental changes (Figure 7.2 C).

Three types of forest fragments were selected according to their land-use legacies (Figure 7.2 C, D): 1) rural areas dominated by farmland, 2) urban areas and 3) mammal predator-free nature reserves. The urban area and mammal predator-free nature reserve categories were also further divided into two subcategories based on the temporal patterns of landscape change (see below for details). A GIS-based habitat map of North Shore district was used to identify habitat of interest (Suppl. 7).

7.2.1.1 Rural sites (RU) **(Figure 7.1)**

In rural sites (RU), forest fragments are exposed to an agricultural matrix and associated disturbance processes (such as chemical input, soil erosion and homogenisation of biodiversity). The habitats (Suppl. 7-8) are characterised by a high density and diversity of terrestrial mammalian predators (e.g. stoat, *Mustela erminea* ; ship rat, *Rattus rattus* ; kiore, *Rattus exulans*; Australian brushtail possum, *Trichosurus vulpecula*; domestic and feral cats, *Felis catus*; ferret, *Mustela putorius furo*; weasel, *Mustela nivalis)* and avian predators (morepork, *Ninox novaeseelandia*; Australian harrier, *Circus approximans*). Local avian communities are thus exposed to intense mammalian and avian predation (predation pressure of 27%, Suppl. 9.1), as well as human disturbances (2.82 pedestrians/hour, Suppl. 9.2).
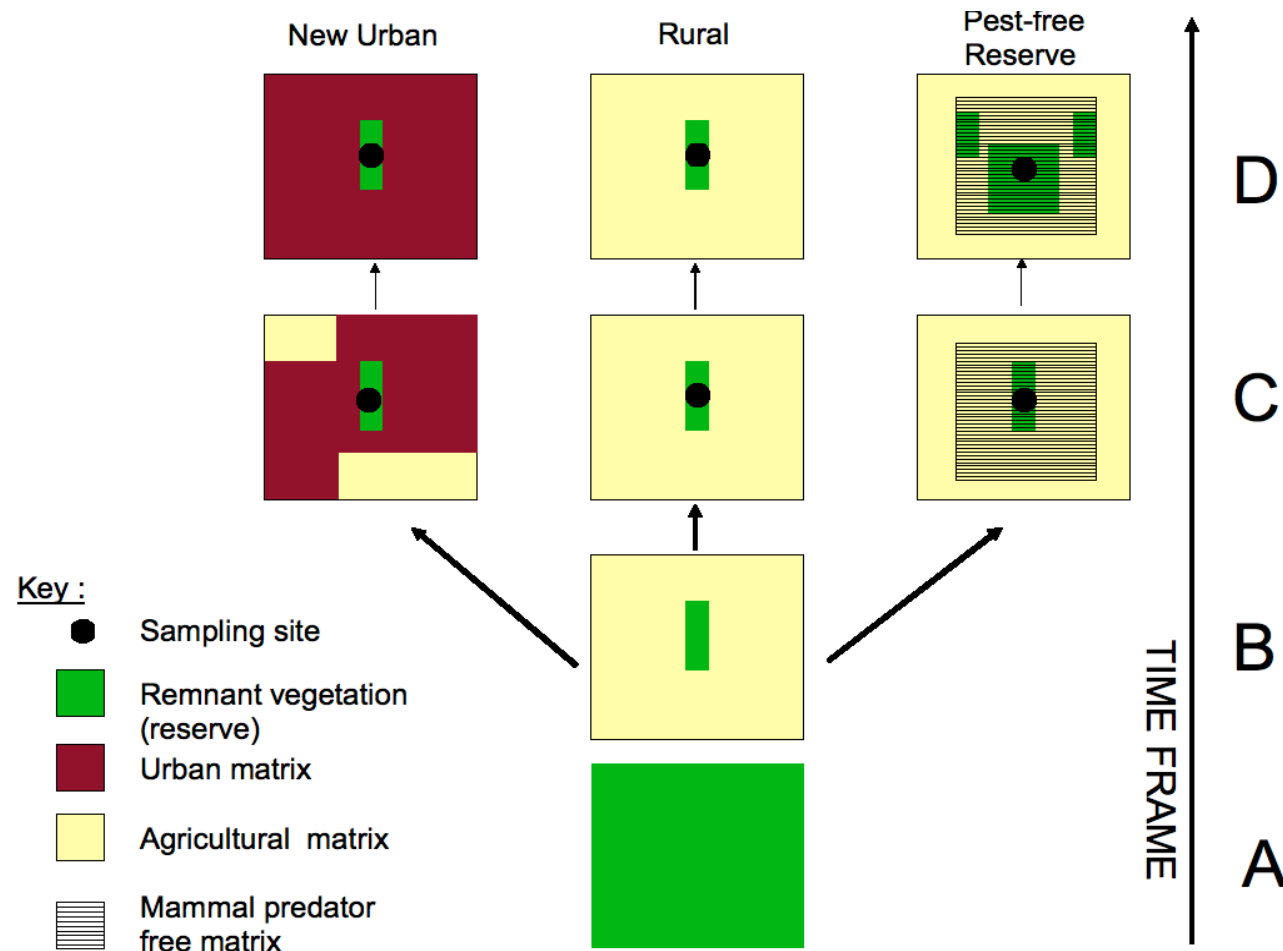
Figure 7.2: A conceptual depiction of three different scenarios of landscape change, due to temporal and spatial variation in habitat reduction and age of habitat remnants. If a 'snapshot' approach is used to assess each habitat remnant at the present time, variation due to historical factors will not be characterised. However, remnant habitats within each landscape can be defined as having an agricultural cause for fragmentation, giving the same spatial distribution, intensity of exposure (i.e., edge effect) and filtering of biodiversity, due to its sharing ancestral stage between landscape remnants. Thus, biodiversity of each habitat will share common inherited traits.

7.2.1.2 Urban sites (UB) **(Figure 7.2)**

Forest fragments in urban locations (UB, see Suppl. 7-8) are in areas that have been exposed to urban development and become part of the urban matrix, with a high density of domestic and feral cats (Anguilar and Farnworth 2013), a medium density of rats and a low density of possums (Pest-free Kapiti 2017, Suppl. 10.1). Local bird communities are exposed to both mammal and avian predation (predation pressure of 33%, Suppl. 9.1, and human-induced urban disturbances (3.78 pedestrians/hour, Suppl. 9.2), such as artificial light, noise and human presence. Urban sites are further divided into two categories: new urban habitats and old urban habitats.

New urban habitats (UBN; Figure 7.2 C) are remnant patches of native vegetation with recent exposure to urbanisation processes (< 25 years; Auckland Regional Council 2010). This landscape is characterised by a mix of urban structure and high concentration of vegetation cover. Residential areas present property with open vegetated space comprising mature gardens with large trees and shrubs (Residential III; Freeman and Buck 2003). The most common nest predators are ship rats, brushtail possums, domestic and feral cats, moreporks, swamp harriers and a low number of mustelids (Gillies and Clout 2000, Anguilar and Farnworth 2013, personal observation).

Old urban habitats (UBO; Figure 7.2 D) are characterised by highly fragmented urban forest fragments, in highly and densely built-up areas within the urban matrix, present since the early 1900s (Auckland Regional Council 2010, Suppl. 7-8.). The landscape is characterised by industrial and highly residential areas with open vegetated spaces and small gardens comprising lawn, flowerbeds and a low density of mature trees (Residential I; Freeman and Buck 2003). Nest predators are predominantly mice, ship rats, feral and domestic cats, possums, and moreporks with the occasional presence of stoats, possums, and swamp harriers (Gillies and Clout 2000, Anguilar and Farnworth 2013, Pest-free Kapiti 2017, Suppl. 10.1).

*7.2.1.3 Pest-free Reserve (NUR) (*Figure 7.2)

Remnant forests form open sanctuaries (NUR, Suppl. 7-8) that are protected from mammalian predators by a pest/predator-proof fence. Terrestrial mammalian predators (i.e., brushtail possums, cats, ferrets, stoats, weasels, ship rats, Norway rats) have been eliminated via aerial poison drops (e.g., 1080 or brodifacoum). However, three species (house mice, rabbits and hedgehogs) persist. Incursions of mammalian pests are controlled by trapping and poison (i.e., brodifacoum) in bait stations. Consequently, only avian predators (e.g., pukeko, *Porphyrio porphyrio,* morepork) were/are present at these sites (predation pressure unknown, Suppl. 9.1) and the have a lower human disturbance (1 pedestrian/hour, Suppl. 9.2). Reserve sites can be further divided into two categories: old pest-free reserves and new pest-free reserves.

Old Mammal-free Reserve (NURO; Figure 7.2D) (Tāwharanui Regional Park, 36.370°S 174.800°E): This fenced reserve has a long history of mammalian predator exclusion (since October 2004) but the area is still characterised by the presence of avian predators (TOSSI 2009). Following the mammal exclusion, this area has experienced the re-introduction of locally extinct bird species, either from natural colonisation from nearby populations, for example, the bellbird (*Anthornis melanura*), or by translocation, for example, the North Island brown kiwi *(Apteryx mantelli)*, North Island robin (*Petroica longipes*), whitehead (*Mohoua albicilla*), pāteke (*Anas chlorotis*), red-crowned kākāriki (*Cyanoramphus novaezelandiae*), saddleback (*Philesturnus rufusater*), takahē (*Porphyrio mantelli*).

New Mammal-free Reserve (NURN; Figure 7.2C) (Shakespear Regional Park, 36.608°S 174.823°E): This reserve is a remnant forest that recently, from December 2011, became a fenced mammalian predator-free sanctuary but the area is still characterised by the presence of avian predators (SOSSI 2016). Since mammal pest eradication, North Island robins were introduced by translocated, and bellbirds were self-introduced.

7.2.2. Focal species.

Six passerine species (Table 7.1) common at all study sites were chosen for this research. These species are all foliage-nesting birds with different degrees of experiences with humans and associated environmental changes, allowing us to investigate the influence of past-evolutionary experience with humans on the nest location strategy used by a species. The six passerine species represent three endemic, one naturalised and two exotic species, characterised by different nest type. Tui, the New Zealand fantail and grey warbler are common endemic passerine species in anthropogenic habitat (van Heezik *et al.* 2008, Chapter 6). The silvereye (*Zosterops lateralis*), self-introduced during the 1850s from Australia and widely distributed in New Zealand, including anthropogenic habitats (van Heezik *et al.* 2008, Chapter 6), is considered a native species that has a longer histories of encountering humans compared with endemic species due to the earlier human colonisation of Australia (~ 55,000 years ago). The song thrush and black bird were introduced from the United Kingdom in New Zealand around 1862, during the European colonisation.

7.2.3 Nest site characteristics.

Nests of focal bird species were located in each of the study habitats during their breeding season between September and March, using well-established nest-searching techniques (Martin and Geupel 1993). The nest contents were checked once, using a mirror, while the parents were absent.

After the chicks fledged, I recorded the following parameters of each nest: the height of the nest from the ground (NH), height of the tree (NT), the horizontal distance from the trunk to the edge of the supporting branch of the nest (branch length, BL), the distance from the trunk to the centre of the nest (ND), and the canopy height of the forest (CH) to the nearest metre (van Heezik *et al.* 2008).

To reduce the effect of habitat structure on NH and BD, I used two ratios to characterise the nest location:

lVertical index (VI) = nest height (NH) / tree height (NT)

lHorizontal index (HI) = distance trunk-nest(ND) / branch length (BL)

Each index value will have a value between 0 and 1 (Figure 7.1).

Table 7.1: Taxonomic status, species code, historical status(E: Endemic; N: Naturally introduced; I: Introduced) and breeding characteristics for the species used in this study.

Common name	Scientific name	Family	Species code	Status	Nest type	Long human experience	Nests measured per habitat		
							UB	RU	NUB
Tui	*Prosthemadera novaeseelandiae*	Meliphagidae	TUI	E	Woven cup	N	52	65	34
New Zealand fantail	*Rhipidura fuliginosa*	Rhipiduridae	NZF	E	Woven cup	N	74	34	16
Silvereye	*Zosterops lateralis*	Zosteropidae	SIL	N	Woven cup	Y	6	5	5
Grey warbler	*Gerygone igata*	Acanthizidae	GRW	E	Enclose dome	N	3	1	13
European song thrush	*Turdus philomelos*	Turdidae	STH	I	Woven cup	Y	39	12	9
Common blackbird	*Turdus merula*	Turdidae	BBI	I	Woven cup	Y	29	11	11

7.2.4 Statistical analyses.

All statistics were performed using R v. 3.1.2 (R Development Core Team 2014). Differences in nest location parameters (VI and HI) for each bird species among the different habitat conditions and among species within the same habitat were tested using permutational analysis of variance (PERMANOVA) (McArdle and Anderson 2001, Anderson 2001), with the function 'Adonis' from the package 'vegan'. I used metric distance matrices (i.e. Euclidian) with 999 permutations. I also performed a pairwise comparison with 999 permutations, using the function 'pairwise.perm.t.test' of the package 'RVAideMemoire'. To improve normality, nest height, tree height and distance to trunk were natural log-transformed and the vertical and horizontal indices were arcsine-transformed.

Differences in nest location parameters (VI and HI) between species with long and short history of coexisting with human were tested using a permutational student's t test due to the absence of normality of some data, using the function perm.t.test of the package RVAideMemoire.

7.3 Results

7.3.1 Nest description.

Over three breeding seasons from 2012 to 2014, data were collected from 419 [UB, RU, NUB] nests of 6 bird species at the three habitat types (Table 7.1).

7.3.2 Effect of habitat type on nest site selection.

The canopy was higher in urban reserves, 2224.18 ± 800.79 cm (n = 51), than in both the rural reserves, 1256.23 ± 624.85 cm (n = 44) and pest-free reserves, 1021.15 ± 643.5 cm (n = 52).

Figure 7.3: Changes in vertical and horizontal nest position among habitats for each study species. Scatterplots represent the positions of each nest, and show variation in the vertical and horizontal indices for each study species. Boxplots represent the median and quartiles for each index within each habitat type (U = urban reserves, blue scatter points and bars; RU = rural reserves, green scatter points and bars; NUB = pest-free reserves, red scatter points and bars). Photos of a nest of each study species accompany graphs. a) NZ fantail,b) silvereye, c) common blackbird, d) European song thrush, e) grey warbler, f) tui.
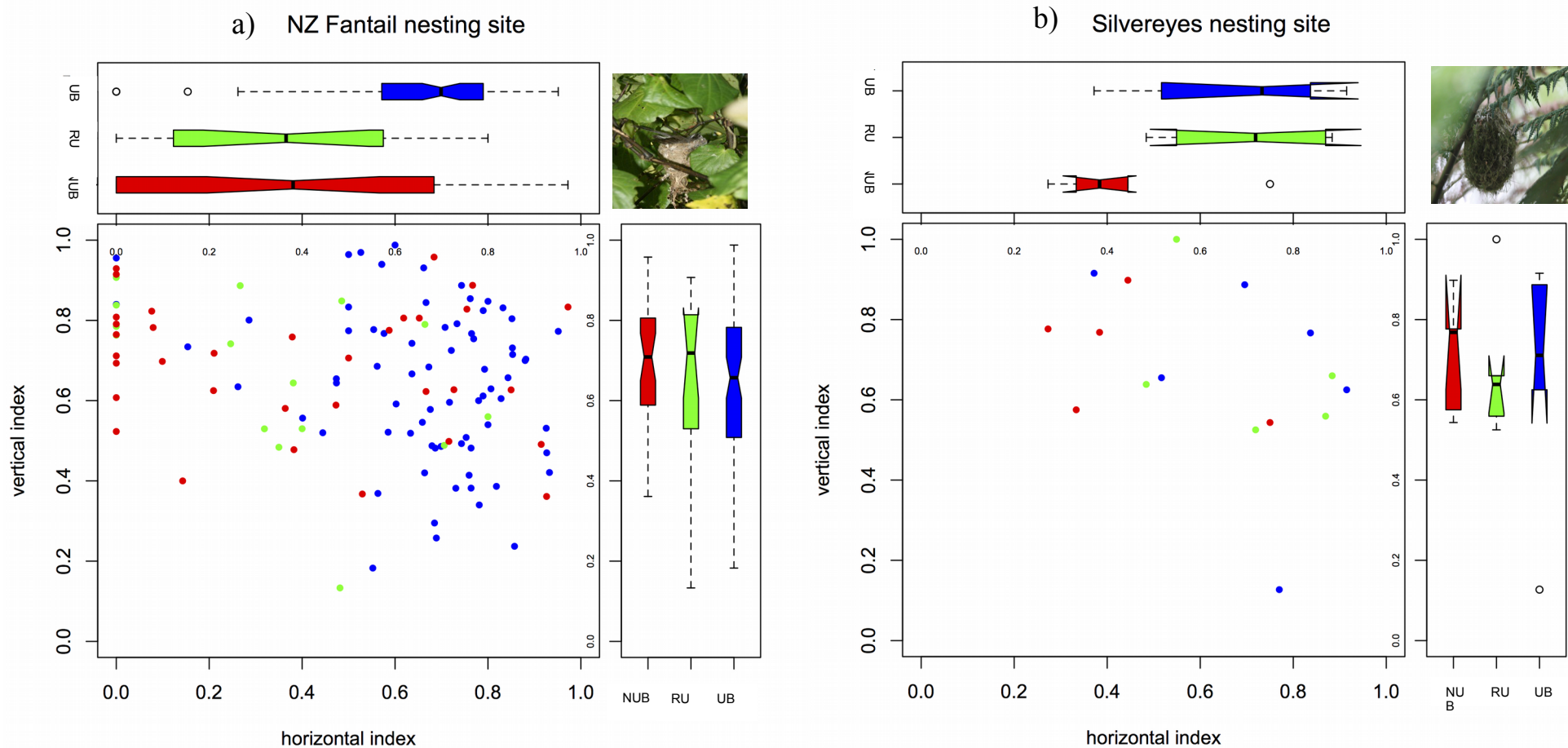
c) Blackbird nesting site
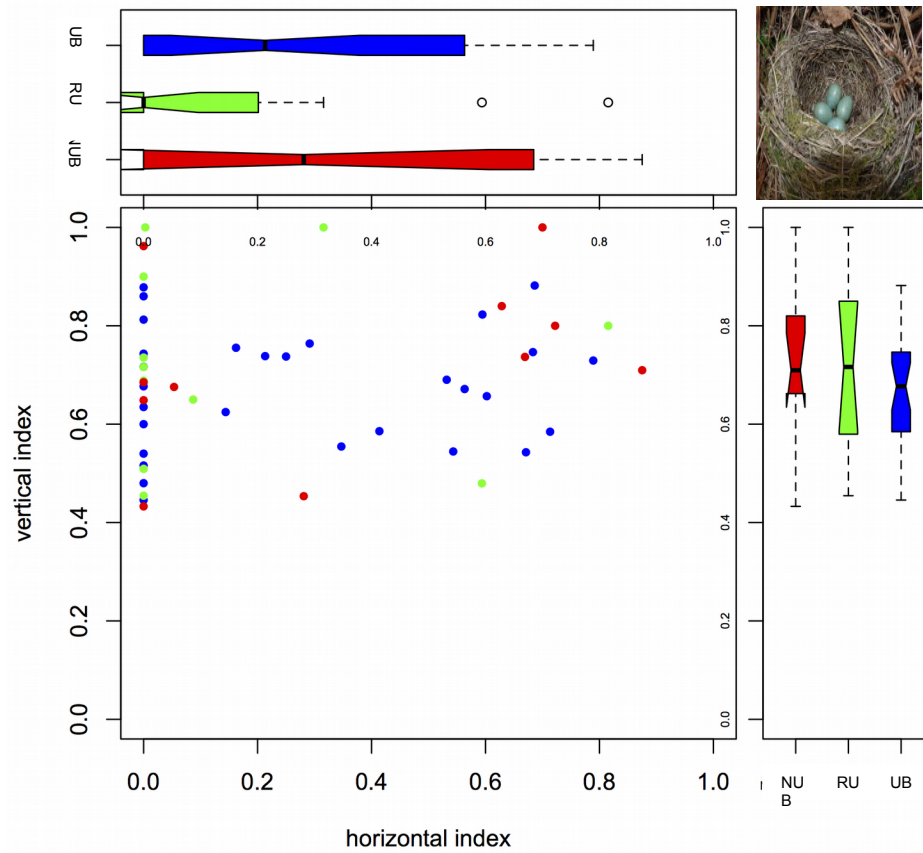
d) Songthrush nesting site
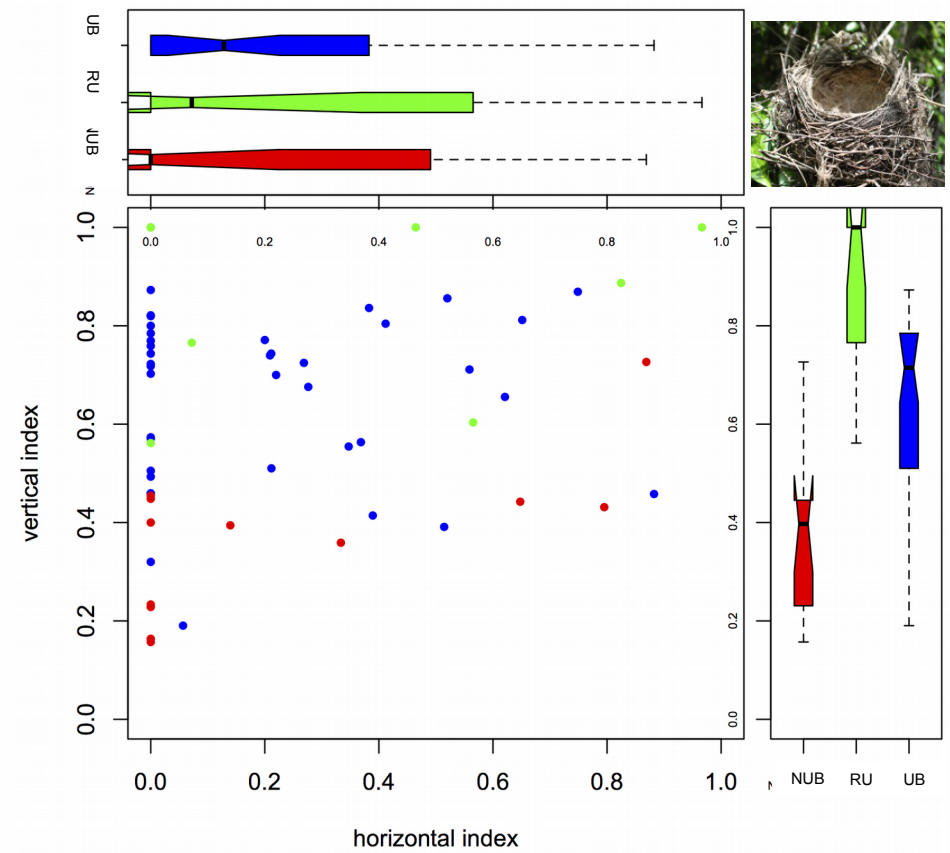
e) Grey warbler nesting site
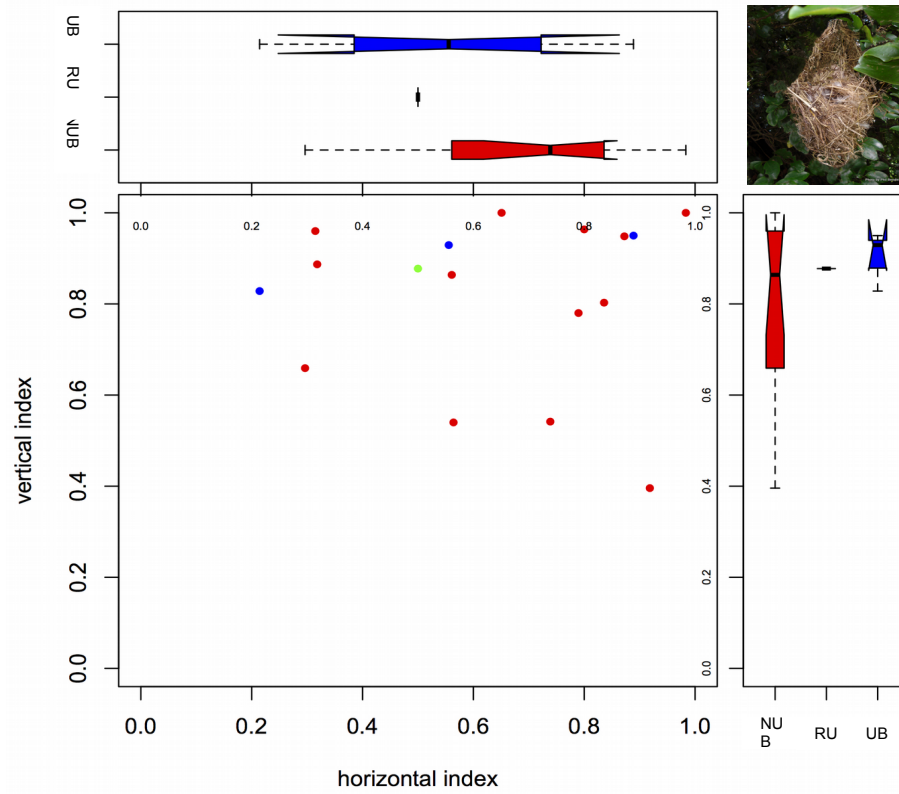
f) Tui nesting site
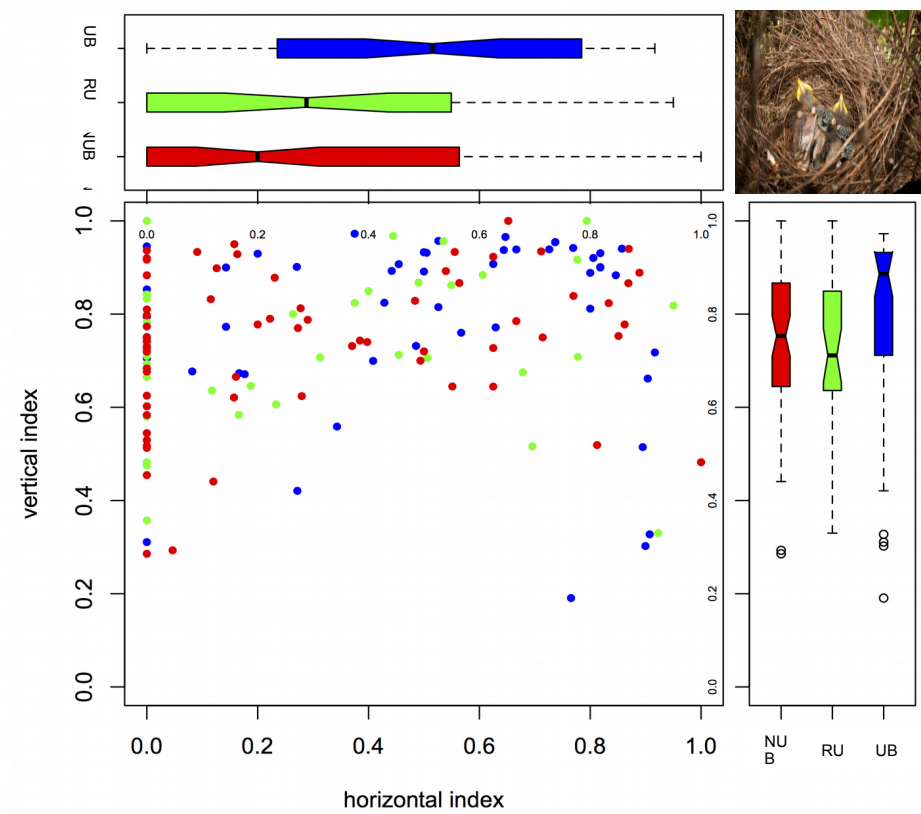
The nest location of blackbirds, silvereyes and grey warblers did not differ significantly in their location in the trees between urban, rural and pest-free reserves (BBI Figure 7.3 E, PERMANOVA: $F_{2,50}$ = 0.40, p = .86 ; SIL figure 7.3 D, PERMANOVA: $F_{2,15}$ = 1.50, p = .25; GRW Figure 7.3 A, PERMANOVA: $F_{2,16}$ = 0.82, p = .52). This suggests a lack of variation in their nest-site selection strategies across the different habitats compositions and structures. Nest-site selection of song thrushes were significantly different among the habitats (PERMANOVA: $F_{2,58}$ = 8.16, p = .001, Figure 7.3 F). The pairwise comparison on horizontal index did not suggest any differential response to habitat. However that of the vertical index suggested significant variation among all habitat types (RU vs. NUR, p = .002; UB vs. NUR, p = .002; UB vs. RU, p = .002). The nest location of some native species have presented significant variation among habitat types, such as the tui (PERMANOVA: $F_{2,151}$ = 5.86, p = .001, Figure 7.3B) and fantail (PERMANOVA: $F_{2,123}$ = 11.79, p = .001, Figure 7.3C) species. The pairwise comparison of the vertical index between habitats showed no difference for either species. In contrast to the song thrush, it was the horizontal index that showed variation between habitats, with significant variation between the urban and other habitats (pairwise comparisons: TUI: UB vs. NUR, p = .012; UB vs. RU, p = .015; NUR vs. RU, p = .722, Figure 7.3B; NZF, UB vs. NUR, p = .006; UB vs. RU, p = .454; NUR vs. RU, p = .454, Figure 7.3C).

7.3.3 History of coexistence with human and nest site selection.

At the pest-free sites, the species with a longer history of coexisting with humans displayed significantly lower vertical index than species with a shorter period of human experience (mean ± SE, long exp. species : 0.57 ± 0.24, short exp.species: 0.73 ± 0.17 ; perm.sudent's t test: t = -4.19, p = .002, Figure 7.4). In contrast, no significant differences were found between species of these two categories in urban reserves (long exp.species: 0.66 ± 0.16, short exp.species: 0.71 ± 0.21 ; perm.student's t test: t = 1.40, p = .17, Figure 7.4A) or rural reserves (long exp.species: 0.77 ± 0.20, short exp.species: 0.71 ± 0.18; perm.student's t test: t = 1.20, p = .24, Figure 7.4B). In urban habitats, species with longer human experience have lower HI values (long exp.species: 0.28 ± 0.29, short exp.species: 0.6 ± 0.25 ; perm.student's t test: t = 8.10, p = .002, Figure .4A). No difference in HI was found between these two

Figure 7.4: Differences in vertical nest position between sites with long and short-periods of human disturbance for each of the three habitat types. Graphs are for A) urban reserves, B) rural reserves and C) pest-free reserves. Graphs are boxplots with median and quartile values and with data for all 6 of the study species combined to test for overall trends in nest-location changes.
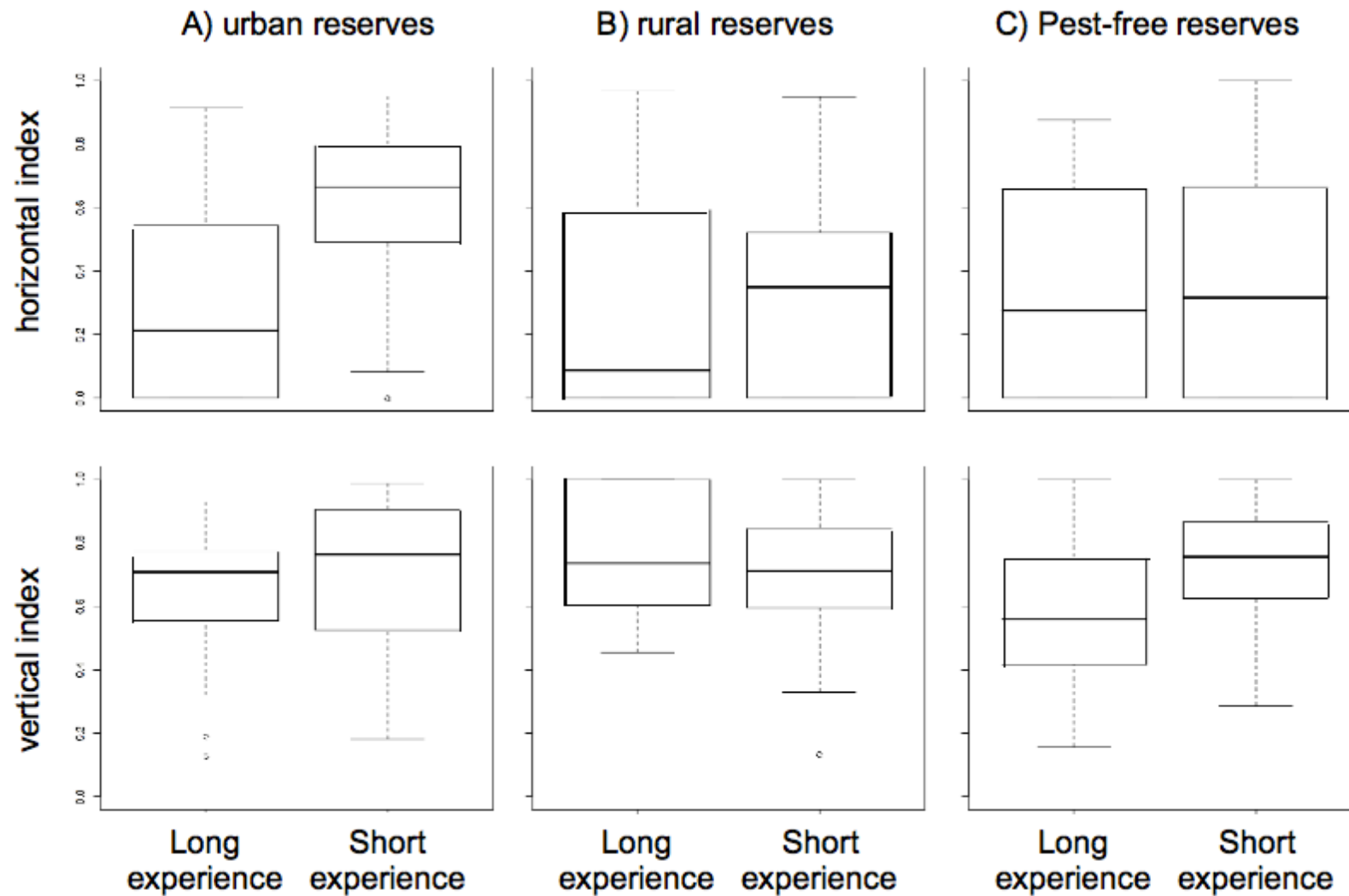
categories in other habitats (rural reserve, long exp. species: 0.33 ± 0.36, native species: 0.34 ± 0.29 ; perm.Student's t-test: $t = .12$, $p = 0.90$, Figure 6.4B; pest-free reserve, long exp. species : 0.32 ± 0.33, short exp. species : 0.38 ± 0.33; perm.Student's t test: $t = .82$, $p = 0.40$, Figure 7.4C).

7.3.4 Variation between species in nest placement.

I found different nesting strategies among species within each of the three landscapes through differences in both the vertical and horizontal indices (Figure 6.3). Song thrushes displayed significant differences in the vertical index among habitats. In contrast, blackbirds, fantails and grey warblers exhibited similar patterns in nest-site selection on both the vertical and horizontal index in rural and pest-free reserve habitats. Indeed, nest distance from the trunk (horizontal index) was significantly different between species only in the urban habitat ($F_{5/194}$, $Z=11.39$, $p < .001$), mainly due to three species, fantails, silvereyes and tui which favoured nest sites at greater distances from the trunk.

7.3.5 Time-lagged response to habitat change (urbanisation and mammal predator isolation) in nest site selection.

No significant differences were found among the four species (TUI, NZF, STH, BBI) in both VI and HI, between new and old urban sites (see Table 7.2). Only fantails displayed a significant difference in the VI between Tawharanui and Shakespear, with higher nest locations selected in the location with a longer history of mammalian pest control (Table 7.2, two-sample $t_{(11)}= 3.88$, $p < .01$). No significant differences were found in the HI (Table 7.2, two-sample $t_{(8)}= 1.47$, $p < .18$).

Table 7.2: Times-lagged responses in nest-location site in response to habitat change in urban and pest-free reserves. Differences in nest sites between recent and older reserves were evaluated using a *t* test. All values presented are means ± standard errors (sample sizes) and significant *p* values are highlighted in bold.

		Urban Reserves (UB)				Pest-free Reserves (NUR)			
		Recent (UBN)	Older (UBO)	T	*p*	Recent (NURN)	Older (NURO)	T	*p*
Tui	vertical index	0.75 (± 0.17, (10)	0.80 ± 0.20 (42)	-1.109	.284	0.79 ± 0.11 (14)	0.74 ± 0.17(51)	-0.338	.738
	horizontal index	0.40 ± 0.29 (10)	0.52 ± 0.31 (42)	-1.219	.242	0.25 ± 0.33 (14)	0.35 ± 0.32 (51)	-0.846	.407
New Zealand fantail	vertical index	0.67 ± 0.14 (22)	0.63 ± 0.21 (51)	0.449	.655	0.79 ± 0.07 (4)	0.71 ± 0.16 (30)	-3.880	**.003**
	horizontal index	0.67 ± 0.24 (22)	0.63 ± 0.16 (51)	-1.501	.143	0.56 ± 0.16 (4)	0.37 ± 0.35 (30)	1.466	.181
Common blackbird	vertical index	0.65 ± 0.17 (14)	0.70 ± 0.12 (15)	-1.268	.216				
	horizontal index	0.32 ± 0.32 (14)	0.25 ± 0.28 (15)	0.679	.503				
European song thrush	vertical index	0.67 ± 0.18(17)	0.64 ± 0.16 (21)	0.676	.504				
	horizontal index	0.25 ± 0.30 (17)	0.18 ± 0.22 (21)	0.957	.347				

7.4 Discussion

My examination of the avian nest-site locations indicates that nest-site selection differs among species, habitat type and habitat quality (in terms of predation risk and human disturbance) and length of coexistence within human-modified habitats. My results suggest that tui select nest-sites in higher trees across all habitats. Fantails showed significant changes in their preferred nest location by increasing their horizontal distance from the trunk of the tree when inhabiting urban environments. This indicates that this species is consistent with habitat modification (i.e., adaptive plasticity, Massaro *et al.* 2008, Chalfoun and Martin 2010, Hendry *et al.* 2011, Lankau *et al.* 2011).

Zanette *et al.* (2011) and Ghalambor *et al.* (2013) noted that breeding birds are sensitive to the risk of predation near nests. In birds, particularly open-nesting species, it is highly likely that ambient predation risk and human disturbances influence the choice of nest site. My observations of 5 open-cup and one enclosed cup nest species suggest different degrees of plasticity of species in nest-site selection in response to increased human disturbances or predator activities. Three of these species displayed behavioural flexibility, altering vertical nest placement in the tree (Figure 7.3 B, C, F), which is also found in other bird (Stoner 1937, Hickey 1942, Preston and Norris 1947, Ratcliffe 1962, Knight and Fitzner 1985), and along the horizontal index. These findings indicate that environmental cues, such as predation risk or human disturbance, are used by these species in nest building. Song thrushes modified nest location on the vertical index among the different habitats (Figure 7.3 F). The beneficial effect of an increase in the height of the nest in the presence of human disturbance has been reported (Stoner 1937, Hickey1942, Preston and Norris 1947, Ratcliffe 1962, Savard and Falls 1981, Knight and Fitzner 1985, Yeh *et al.* 2007). This strategy may be beneficial, as it may increase the fitness from reduced disturbance by humans (Gliwicz *et al.* 1994, Møller 2010) as mammal predation (Miller and Hobbs 2000). In contrast, tui and NZ fantail differed in their nest placement across the different habitats, by changing the relative horizontal position (horizontal index), , i.e., 'marginal habitat' (Kawecki 2008). Such a change is likely in response to predation by mammalian predators that can use the tree trunk to access the nest, as predicted (Figure 7.1 A, B, E) (Forstmeier and

Weiss 2004). However, this strategy may also incur costs and become a maladaptive response in the absence of mammalian predators, i.e., an 'ecological trap' (Misenhelter and Rotenberry 2000, see Schlaepfer *et al.* 2002). Such a shift of nest-site is likely to result in changes in nest structure, due to the changes in nest support structures (i.e., reduced branch size, increased branch flexibility; Heeman and Seymour 2011) and less stable microclimate at the nest site (i.e., increased wind speed, rain exposure; Kern 1984, Van Heezick *et al.* 2008). Also, the behavioural response of placing a nest at the periphery of the tree may cause a trade-off due to changes in vulnerability to different types of nest predators (Lima 1998a). Altering the nest site to more horizontal peripheral locations to reduce predation risk from introduced mammals may make the nest more vulnerable to avian predation due to an increase in nest visibility and access (Lima 1998a). For example, dusky warblers (*Phylloscopus fuscatus*) in Russia, that shifted their nest placement in response to predation pressure from small mammal predators (i.e., chipmunks, *Tania sibiricus*), exposed the nest and nestlings to adverse climatic conditions, avian predation and brood parasitism by cuckoos (Forstmeier and Weiss 2004). The absence of variation observed for blackbirds and silvereyes, suggests the use of different anti-predator strategies during the nesting period, such as using phenotypic plasticity of other traits (e.g., nestling duration or clutch size) (Martin and Briskie 2009, Lima 2009, Zanette *et al.* 2011, Hua *et al.* 2014, Ibáñez-Álamo *et al.* 2015) or using other anti-predator behaviours, such as nest desertion (Berger-Tal *et al.* 2010).

7.4.1. Influence of past-experience of HIREC and novel predation risk.

Predation risk represents one of the most significant selective pressures for species, particularly during the reproductive period, which can cause changes in life-history strategies. Additionally, human activities have led to changes in habitat characteristics worldwide (Ellis 2015) with habitat loss, fragmentation and an alteration of the predator-prey relationships (DeGregorio *et al.* 2014a, DeGregorio *et al.* 2014b), most notably via the introduction of new predators (Sih *et al.* 2011, Ibáñez-Álamo *et al.* 2015). As has been suggested previously (Sih *et al.* 2011, Hendry *et al.* 2011), species with past experience with HIREC will increase their ability to cope and develop a rapid evolutionary response to human-induced change and novel predators (Knight *et al.* 1987). My results showed that species could respond differently in response to

environmental cues and this response may potentially be mediated by their previous duration of coexistence with human-modified environments. In urban habitats, species differing greatly in their period of human coexistence demonstrated contrasting patterns of nest-site location in response to habitat changes (Figure 7.4). The two endemic species (tui and NZ fantail) with shorter periods of human coexistence have increased the horizontal distance of nests from the tree trunk in response to predation by mammals such as the ship rat, which is active in arboreal habitats (Knight *et al.* 1987). Thus, the absence of past cohabitation by these species with terrestrial mammalian predators may explain the divergence with other species in nest-site selection. My results suggest that the nest-site strategy used by native species is an adaptive response, based on their ability to respond to the cues of new predators (Sih *et al.* 2011, Sih 2013). The large number and variety of novel predators introduced into New Zealand by humans have necessitated a fast response of native species to perceive the new mode of nest predation, failing in such a response will risk species extirpation or extinction, which may explain the failure of some native species (e.g., stitchbird *Notiomystis cincta*, saddleback, kokako *Callaeas cinerea*) on the mainland of New Zealand. Indeed, the high density and the broad range of novel introduced predators to which native species have been exposed have influenced the speed of their behavioural innovations in anti-predator strategies (Massaro *et al.* 2008), leading to adaptive or maladaptive responses (Wong *et al.* 2007, Hendry *et al.* 2011, Sih *et al.* 2011, Sih 2013). This suggestion is notably reinforced by the response of the two native species to habitats presenting the absence of major mammalian predators, resulting in nest sites being selected near the trunk. This observation has provided the first demonstration of the capacity of bird species with recent human and mammalian predator cohabitations to distinguish the degree of novel predation risk and to adjust their nesting strategy accordingly.

The results also support the prediction that birds that have more experience with human disturbance and mammalian predation (e.g., blackbird, silvereyes) have evolved appropriate strategies to cope with predators being present (Møller 1988, Sih 2013), without shifting their nest-site strategy (e.g., see Evans *et al.* 2010). Instead, strategies such as reducing clutch size (Eggers *et al.* 2006, Zanette *et al.* 2011) and laying multiple clutches (Farnsworth and Simons 2001), in order to reduce reproductive losses from a single predation event, appear to be a more common response. Because, these species may already have optimal

(Lima 1998a) nesting-site strategies, it might be necessary to alter other life-history traits to further reduce predation risk (i.e., high rate of nest desertion). Indeed, species more familiar with the habitat type and the predation risk due to their broader experience within the habitat may gain 'private value' (Piper 2011) and thus develop a strategy in response to changes in the risk of predation and human activities in ecological time (Møller 2006, Lima 2009).

Interestingly, song thrushes, which have a long evolutionary history with mammalian predators and human-modified habitats demonstrate an adjustment of the nest-site strategy along with a vertical ratio in relation to habitat characteristics, showing a lower vertical index value in the absence of mammal predation. A possible explanation of this divergence with other species might be a founder effect, resulting from traits of the former population at the time of their first introduction attempts from the United Kingdom (~ 400 birds, Congdon and Briskie 2014), which may have inadequate nest-site habitat preference (i.e., difference in genetic basis from the core population). Congdon and Briskie (2014) have identified some differences between life-history traits of original and introduced populations, notably with a reduction of parental investment of the song thrush population in New Zealand. The reduction of investment in parental care by parents (Ghalambor *et al.* 2013) in the New Zealand population of song thrushes could explain the change in nesting strategy observed among the different habitats studied. Song thrush populations may have selected 'optimal' distances from human activity, using the 'win-stay: lose-switch' strategy with the return to use the previous nest-site location if successful, or leaving if not (Hildén 1965, Greig-Smith 1982). An observed reduction in reproductive effort (Congdon and Briskie 2014) might suggest that this species is more successful due to fitness advantages found in urban habitats (Croci *et al.* 2008). This could be because nests established near areas of human activity receive a protective benefit (Mönkkönen *et al.* 2007) against mammalian nest predators.

7.4.2. Nest site selection in similar habitats along different time scale.

Conditions among and within habitats are not uniform, leading to variation in nest-site selection over time and space. Thus, organisms are subjected to spatiotemporal heterogeneity among habitats due to change in the surrounding conditions, which may affect their life history traits and behaviours (Ibáñez-Álamo *et al.*

2015). Indeed, in heterogeneous environments, organisms will favour their optimal behavioural responses, based on their interpretation of the cues available (i.e., predation risk, human disturbance risk, abiotic risk, competition risk), to best match local conditions (The Modelling Animal Decisions group 2014). Habitats continue to change rapidly worldwide; the heterogeneity of habitats and their temporal changes will lead to a species level evolutionary response to new selection pressures, which will be conducive to behavioural adjustments of wildlife over time (e.g., timing of urbanisation of blackbirds; Evans *et al.* 2010). Research on the temporal variation of predation risk within habitats has demonstrated a fast and adaptive response by fauna (Lima 1998b, Lima and Bednekoff 1999, Hamilton and Heithaus 2001). Nevertheless, isolation from some predator guilds has resulted in lack of both predator recognition and anti-predator behaviour of local species (Blumstein and Daniel 2005, Whitwell *et al.* 2012). Urbanisation in such areas result in fauna being exposed to a high risk of such novel predators, which are often commensal to human civilisation, such as introduced mammals in New Zealand (e.g., rodents, cats; Gillies and Clout 2003). It has been suggested that animals in urban systems need a fast and adaptive response to such selection pressures (Lowry *et al.* 2012). My findings on tui and NZ fantail are consistent with previous suggestions that rapid adaptation or mechanism of adjustment influence the adaptation of native species to the recent anthropogenic changes. Interestingly, in habitat mammal predator have recently been removed, NZ fantails used nest locations with lower HI values (distance between nest and trunk), smaller trees and displayed considerably more variations in HI compared to sites with older history with mammal predators removed. The outcome of the response observed in these reserves may be explained in part by a cost-benefits approach, in terms of energy involved in the maintenance of anti-predator behaviour in the absence of a predation pressure (i.e., the energy involved in the maintenance and production of the behaviour could be saved; Dewitt *et al.* 1998, Magurran 1999) and allocates this energy to another more beneficial behaviour (i.e., nest attentiveness, thermoregulation of the nest, reproductive effort, as suggested by the risk allocation hypothesis; Lima and Bednekoff 1999).

In conclusion, my findings suggest a substantial divergence between species in their nest-site selection in response to anthropogenic habitats (i.e., urban environments) and risk of predation. Furthermore, due to the nesting period being a particularly vulnerable stage of reproduction, particularly for

open cup nesting birds, the nest-site strategy seems to present the first stage of adaptive response to HIREC (Sih 2013). This is especially true for species naive to these new habitats, which should have the greatest flexibility in nest-site location characteristics, due to little previous selection pressure and a short learning period in such habitats, to exploit anthropogenic habitats successfully. Finally, selection pressures caused by human-induced habitat transformation tend to select a more uniform strategy in nest-site location for all species within these habitats. This may favour the development of additional anti-predator strategies, such as nest defence and life-history responses (Lima 2009). It can also lead to apparent competition between human commensal species and the naive species, in terms of nest site selection (Martin 1996).

Acknowledgments

Supplementary forms

Suppl. 7: Map of New Zealand, the Auckland region with study sites: pest-free reserve (▫), rural reserve (■), new urban area (▤) and the old urban area (■).
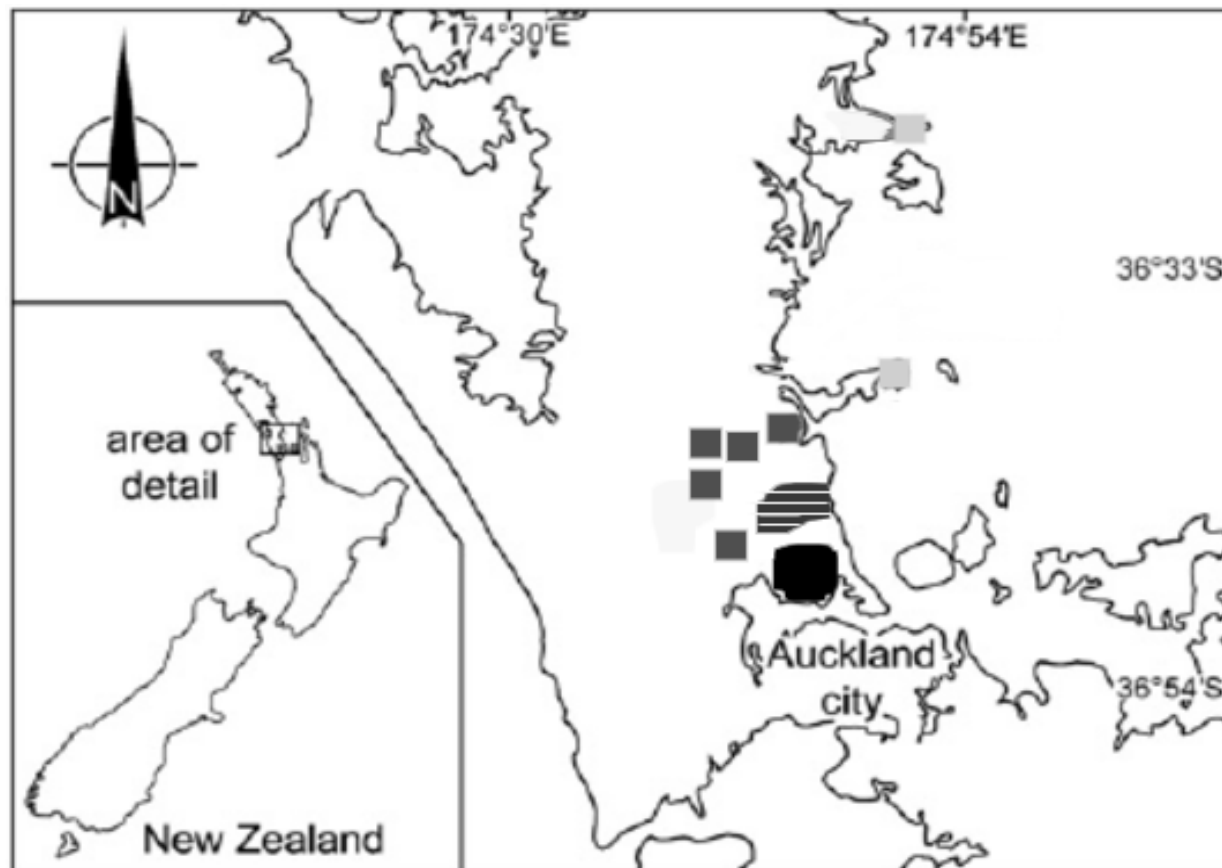
Suppl. 8: List of study site with GPS location and habitat category.

Habitat	Habitat category age	Reserve name	GIS (WGS84)		Size (ha)
			Longitude	Lattitude	
Non-urban reserve	Recent	Shakespear regional park 1	174.819	-36.603	279,5
Non-urban reserve	Recent	Shakespear regional park 2	174.826	-36.608	7,7
Non-urban reserve	Recent	Shakespear regional park 3	174.833	-36.608	16,8
Non-urban reserve	Recent	Shakespear regional park 4	174.825	-36.613	1,3
Non-urban reserve	Old	Tawharanui regional park 1	174.821	-36.372	2,25
Non-urban reserve	Old	Tawharanui regional park 2	174.830	-36.373	9,73
Non-urban reserve	Old	Tawharanui regional park 3	174.841	-36.373	58,07
Non-urban reserve	Old	Tawharanui regional park 4	174.846	-36.370	1,27
Non-urban reserve	Old	Tawharanui regional park 5	174.843	-36.370	1,55
Rural	No classified	Okura bush scenic reserve	174.712	-36.669	174
Rural	No classified	Albany scenic reserve	174.695	-36.709	37,4
Rural	No classified	Coastville scenic Reserve 1	174.656	-36.719	51,8
Rural	No classified	Coastville scenic Reserve 2	174.646	-36.711	24,3
Rural	No classified	Paremoneno scenic reserve	174.650	-36.748	96,7
Rural	No classified	Three streams reserve	174.680	-36.722	3,5
Urban	Recent	Fermhill escarpment	174.696	-36.734	32,8
Urban	Recent	Burnside escarpment	174.646	-36.738	15,8
Urban	Recent	Schnapper rock reserve	174.688	-36.755	6,6
Urban	Recent	Pin oak Reserve	174.683	-36.756	4,6
Urban	Recent	Parkhead reserve	174.697	-36.752	1,6
Urban	Recent	Torbay heights reserve	174.724	-36.701	10,3
Urban	Recent	Stredwick reserve	174.733	-36.700	4,5
Urban	Recent	Awaruku reserve	174.736	-36.696	3,3
Urban	Old	Smith Bush Scenic Reserve	174.752	-36.792	6
Urban	Old	Stancich reserve	174.742	-36.795	3,2
Urban	Old	Holland reserve	174.737	-36.791	1,5
Urban	Old	Linley reserve	174.732	-36.794	1,2
Urban	Old	Gretel scenic reserve	174.725	-36.799	0,8
Urban	Old	Birkenhead domain	174.720	-36.797	54,7
Urban	Old	Kauri glen park	174.735	-36.805	32,8
Urban	Old	Kaka street reserve	174.739	-36.800	0,3
Urban	Old	Onepoto reserve	174.753	-36.807	4,4
Urban	Old	Little shoal bay reserve	174.740	-36.814	4
Urban	Old	Le roys bush reserve	174.732	-36.813	16,3
Urban	Old	Woodcote scenic reserve	174.724	-36.788	0,6

Suppl. 9: Determination of predation pressure and human disturbance

Predation pressure

To estimate the level of predation pressure in each area, I collected the frequency of failing nest due to predation per sites based on NZ Fantail populations, using the ratio of the number of nests predated before fledging (nest was considered as predated when at least one nestling was missing) to the total number of the nest found (Table Suppl. 9.1).

	URBAN	RURAL	RESERVE
Predation Pressure	37.33%	30.43%	20%

Table Suppl. 9.1: Percentage of nests failing in NZ Fantail due to human and dog activities for each area type.

Human disturbance

In order to gauge the amount of human disturbance in forest patches, I recorded the number of pedestrians and dogs passing in each forest fragments during day times (08.00 to 19.00 hours) during 20 minutes periods (expressed as rates per hour). This procedure was repeated at least 20 times per site over the three years of experimentation and a mean per type of forest fragments was used (Table Suppl. 9.2).

	URBAN	RURAL	RESERVE
Human activity (pedestrian/hour)	3.78	2.82	1
Dog activity (ind/h)	0.88	0.49	0

Table Suppl. 9.2: Mean of human and dog activities per area.

Suppl. 10: An inventory of mammal pest in urban sites of the North shore district

Mammal surveys were conducted in 9 sites, in the North Shore district of Auckland. Tracking tunnels were set up at 50 m interval in each study area, a week before the mammal recording. On the recording day, commercially available tracking cards, re-inked in the middle, were placed and baited with peanut butter and 5 drops of sardine oil. During three days during three weeks in June 2011, tracking cards were removed in the morning, and any footprints identified, and then replaced with a new tracking card. All surveys were conducted during a rain-free period.

Hedgehog	Mouse	Cat	Rat	Stoat
29.6 ± 22.6	6.8 ± 9.3	1.2 ± 2.2	20.4 ± 16.1	3.7 ± 6.6
(7/9)	(3/9)	(1/9)	(7/9)	(1/9)

Table Suppl. 10.1: Mean percentage tracking rates ± SEM of mammal through tracking tunnel. Value in parentheses represent the number of study sites where the species was detected.

Chapter 8

General Discussion

There are three main objectives in this research:

(1) Develop a new framework to investigate the anthropogenic impact on natural habitats and biodiversity, which incorporates, the phases of human sociocultural niche construction. I explore this framework using regions with a long human colonisation history and New Zealand, a country with unique natural history and a recent human colonisation history.

(2) Test whether the life history of species influence their ability to colonise and adapt to human modified habitats.

(3) Examine the influence of species' evolutionary history with humans on its response to the anthropogenic transformation of habitats through two approaches: 1) investigate the success of the establishment of introduced species with variable histories of coevolution with human and 2) investigate the behavioural responses (nest site selection) to urbanisation by species with variable histories of co-evolution with human.

8.1 Ecological consequence of sociocultural niche construction on megafauna and importance of timeline

Analysis of the historical avian dataset suggested that the evolution of human sociocultural niche construction has two significant patterns of impact on biodiversity. A shift in human sociocultural niche construction had an effect on the rate of megafauna extinction. Furthermore, more recent sociocultural systems such as the 'industrial system' had a stronger impact leading to higher degree of extirpation or extinction in native megafauna compared to an earlier system such as a 'hunter-gatherer system'. This is, due to human population expansion and higher efficiency in habitat modification and hunting techniques in industrials societies. The case study using New Zealand as a model (Chapter 2) has shown similar patterns in the impact on megafauna: colonisation by more complex society, the European society or 'Industrial system' resulted in a faster rate of

species extinction and changes in land use through development of urban and agricultural areas.

The impact of the Polynesian 'hunter-gatherer society' on native biodiversity was more difficult to assess due to the paucity of data. When included in the longer-term trends, Polynesian society had a strong impact on forest cover and medium impact on the native avifauna extinctions. However, these first impacts on megafauna have led to the first anthropogenic selection of species and habitat transformations. Thus, the colonisation by a hunter-gatherer society had a significant impact on megafauna that often included keystone species in New Zealand, in a similar way to the late Pleistocene expansion of humans (Boivin *et al*. 2017). The diversity change in megafauna species likely led to a strong effect on ecosystem structure via altering nutrient availability and seed dispersal (Johnson 2009, Doughty *et al*. 2013, Boivin *et al*. 2017). The cumulative human activities across the transitions of the sociocultural systems have led to different anthropogenic filtering pressures that resulted in a dramatic change in biodiversity parameters such as abundance and distribution. Thus, the pattern of current biodiversity structure is strongly linked with the historical pattern of the ancient anthropogenic change of the sociocultural systems and their transition patterns. In New Zealand, which was colonised by two different human communities with different sociocultural systems, the transition between the sociocultural systems that occurred during the establishment of Europeans with a larger population and their industrial systems resulted in a stronger shift in the sociocultural niche construction. The absence of soft and smooth transitions during the regime shift between the Polynesian and European communities has resulted in an increase in the effect on the local avian biodiversity. Consequently, integration of the sociocultural systems and their historical transitions in the process of human niche construction have reshaped and influenced the evolutionary trajectories of species.

The analysis of historical datasets also showed that areas with a long history of human niche construction, such as Africa and Europe, had lower extinction and extirpation rates in their megafauna, despite the data underestimating the human impacts because the extinct species recorded in the dataset were not the only ones to suffer from human pressure. This is in contrast to New Zealand, where 700 years of human niche construction has led to a faster anthropogenic shaping of species community structure. However, these areas have shown similar cumulative human sociocultural activities, with the presence of at least three main

sociocultural systems (i.e., hunter-gatherer, agrarian, industrial). One of the major difference was the succession speed during the sociocultural niche construction, offering different transition times and a sociocultural niche construction gap (i.e., a relaxation time between the two societies, or an 'anthrosequence'). Such a period can play an important role in determining the current biodiversity assemblage pattern. Indeed, extinction rates can be compared between Hawaii and New Zealand, because they that had similar colonisation history (i.e., two waves of colonisation, by Polynesian and Europeans). Hawaii, with a longer transition period between the two human establishment stages (Polynesian: AD ~800, European: AD ~1800; Athens 1997, Burney and Burney 2003, Kirck 2007), had lower extinction rates than New Zealand (Polynesian: AD ~1300, European: AD ~1840). This observation emphasised the potential effect of the transition time of human sociocultural systems on megafauna extinction. Indeed, it is well known that species responses to environmental change may display considerable time-lag (relaxation times; see Essl *et al.* 2011) resulting from direct modification of individual fitness (see Essl *et al.* 2011). In the case of short relaxation times due to colonisation events over a shorter period, new anthropogenic changes may lead to accumulating time lags in biodiversity responses and may potentially explain some mechanisms like extinction debt. Such a pattern could help at some level to explain the higher extinction rate during the second colonisation phase (of European establishment in New Zealand). However, the time lag between the environmental changes results from human sociocultural niche construction and the expression of these impacts on biodiversity could cause some difficulties in establishing the ecological impact of human sociocultural systems and should not be under-estimated (see Essl *et al*. 2011, 2015a). The negative consequence of human sociocultural niche construction could be still under-estimated in the areas where human establishment has caused rapid and profound biodiversity changes that has driven a disequilibrium of the biodiversity (see Chapter 2). So, contemporary biodiversity in areas with recent human colonisation could still present a potential time lag in species extinction responses which could explain extirpation or extinction of current species.

Consequently, recognising the past processes that have shaped the local biodiversity would help in understanding the contemporary human impact on current and future biodiversity (Hermy and Verheyen 2007,

Metzger *et al*. 2009, Boivin *et al*. 2017). Analysis of historical data from areas of longer human colonisation history can help conservation in areas with shorter-term human history, despite the dissimilarity of the sociocultural niche transition, by enabling an assessment of potential changes to biodiversity in the long-term. Consequently, an understanding of the evolutionary history of species with human societies can help more accurate prediction of future changes in biodiversity (Essl *et al.* 2015a).

8.2 The anthropogenic habitats filtered and shaped New Zealand avifauna

Our analyses of the effect of life history traits of avian species on their adaptations in human modified habitats indicate the ecological requirements of a species to survive anthropogenic habitats. Consistent to previous findings (Donnelly and Marzluff 2004, Kowarik and Körner 2005, Croci 2007), the preferences of New Zealand native birds for forests and shrubs potentially benefit for their survival in urban systems and its associated forest remnants (Chapter 4). Through comparative analysis of the two avifauna communities, I provided evidence that life history traits of the native and exotic avifauna of New Zealand influence their habitat preferences and colonisations of anthropogenic habitats (i.e., farmland and residential areas), which is consistent with the findings of previous studies (Croci *et al.* 2008). This study highlights the first mechanism driving the difference in bird assemblages along the anthropogenic gradient in New Zealand and shows the filter effect of habitats on the avifauna assemblage through selection on life history traits. My findings indicate the importance of some life history and behavioural traits of New Zealand avian species on their capacity to cope with anthropogenic habitat modifications. For example, farmland adapters, species mainly observed in this anthropogenic habitat in New Zealand, and farmland avoider, species using other habitats preferentially, differed in habitat and nest location preferences (i.e., open vs forest, canopy nest vs ground nest). Such knowledge allows us to predict the adaptability of native species to anthropogenic habitat modification and provide guidance to conservation management of biodiversity in human modified habitats.

8.3 Importance of past-human history on avian responses to habitat modification

Through investigating the effect of the history of coevolution with human on the success of population establishment of exotic avian species in New Zealand (Chapter 3), I have demonstrated the potential effect past-human history on invasion success. Species with longer period of coexistence with human can better survive repeated episodes of human habitat modifications and sociocultural niche construction (Ellis 2015, Boivin *et al.* 2017). Such species tend to establish well and outcompete other species in the novel ecosystems (Ellis 2015) However, the small dataset available prevent making firm conclusions. Further study including a larger dataset and larger scale is needed to clarify the potential influence of past coexistence with human on invasion outcomes

I studied nest site selection of species with variable history of coexistence with humans along a gradient of urbanisation, where the degrees of human disturbance and mammalian predation vary (Chapter 6). I demonstrated that native and exotic avifauna varied in their nest site selection in response to habitat modifications, with native species exhibiting higher variability in nest site location in the horizontal index. Positive correlation has been observed between nest distance from the trunk and the degree of mammal predation for native species with shorter past history with these predators. Human niche construction in New Zealand is recent and the natural ecosystems have undergone major changes within a short time frame. While natural selection on genetic-based phenotypes requires longer periods, species that exhibited more plasticity in biological traits such as behaviour may be more successful in adapting to environmental perturbations (Kawecki 2008, Hendry *et al.* 2011), while species with a smaller degree of plasticity in its biological traits may fail to provide an adequate response and decline or become extinct (Sih *et al.* 2011). My findings support previous finding on a shift in parental behaviour of naïve species in the presence of novel predators (Massaro *et al.* 2012). These findings indicate that endemic avifauna in remnant woodland of an urban system are not

stuck in an evolutionary 'trap' in the presence of mammal predation, but show an ability to adapt to disturbance from humans and mammal predators by altering their nest site selection. Our results also show that some individual differences remain for nest site selection within a species under similar constraints, suggesting that a bird's individual experience could affect the behavioural shift observed. It remains to be determined whether the ability of the native birds to adapt to disturbance from humans and mammal predators by altering their nest site selection has altered other life history traits and population sustainability in the habitat, such as the number of offspring, as observed by Zanette *et al.* (2011). The absence of a response in nest location from some exotic species may be because of their evolutionary history with humans (e.g., the blackbird in Europe; Evans *et al.* 2010) and anthropogenic perturbations have already shaped sensory and cognitive processes controlling nest site selection behaviour. One imitation associated with this study is the potential confounding effect of factors such as predator control history at the study site and the density and type of mammal predators present.

8.4 Directions for future research

In this thesis, I investigated the ecological consequences of the establishment of human society in terms of its impact on avian biodiversity. Further research in other countries will improve our understanding of the influence of the transition time of sociocultural niche construction on the species extinction rate. Niche constructions have not been merely been a source of environmental change but also a driver of selection, which could produce new evolutionary outcomes, as suggested by Laland *et al.* (2016). So, further research is needed to explore and understand the patterning of ecological communities emerging through these sequences of succession that occurred during sociocultural niche construction. This research would offer a better understanding of the effect of human society on current biodiversity and help future conservation of biodiversity in human modified landscapes.

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Appendices

Appendix 1. Global list of extinct and extirpated megafauna by geographical region

-Table 1: Global list of extinct and extirpated megafauna in Africa

- Table 2: Global list of extinct and extirpated megafauna in Europe

- Table 3: Global list of extinct and extirpated megafauna in North America

- Table 4: Global list of extinct and extirpated megafauna in New Zealand

Table 1. Global list of extinct and extirpated megafauna in Africa

CLASS	ORDER	FAMILY	Latin name	Common name	Date considered as extinct or extirpated	Date used (BP)
MAMMALIA	CARNIVORA	FELIDAE	*Homotherium ethiopicum*	Homotherium	1500000 BP	1500000
MAMMALIA	CARNIVORA	FELIDAE	*Homotherium hadarensis*	Homotherium	1500000 BP	1500000
MAMMALIA	ARTIODACTYLA	BOVIDAE	*Pelorovis oldowaywensis*	Prodigious/monstrous sheep	800000 BP	800000
MAMMALIA	ARTIODACTYLA	BOVIDAE	*Megalotragus kattwinkeli*	Megalotragus	10000 BC	12015
MAMMALIA	ARTIODACTYLA	BOVIDAE	*Pelorovis antiquus*	Pelorovis	12000 BP	12000
MAMMALIA	CETARTIODACTYLA	BOVIDAE	*Megalotragus priscus*	Giant hartebeest	9078-8604 BP	8841
MAMMALIA	CETARTIODACTYLA	BOVIDAE	*Antidorcas bondi*	Bond's springbok	8557-8180 BP	8368
MAMMALIA	ARTIODACTYLA	GIRAFFIDAE	*sivatherium*	Shiva's beast	8000 BP	8000
MAMMALIA	CETARTIODACTYLA	BOVIDAE	*Pelorovis antiquus*	Giant long-horned buffalo	6180-4645 BP	5413
MAMMALIA	SORICOMORPHA	SORICIDAE	*Crocidura balsamifera*	Giant forest shrew	2771–2121 BP	2446
MAMMALIA	PERISSODACTYLA	EQUIDAE	*Equus africanus atlanticus*	Atlas wild ass	300	1715
MAMMALIA	RODENTIA	MURIDAE	*Malpaisomys insularis*	Lava mouse	784–1116	1065
MAMMALIA	PROBOSCIDEA	ELEPHANTIDAE	*Loxodonta africana pharaoensis*	North African elephant	1500-pre	515
MAMMALIA	CETARTIODACTYLA	BOVIDAE	*Hippotragus leucophaeus*	Bluebuck	1800	215
MAMMALIA	CARNIVORA	URSIDAE	*Ursus arctos crowtheri*	Atlas bear	1841?	174
MAMMALIA	CARNIVORA	FELIDAE	*Panthera leo melanochaitus*	Cape lion	1865	150
MAMMALIA	CETARTIODACTYLA	SUIDAE	*Phacochoerus aethiopicus aethiopicus*	Cape warthog	1871 (1896?)	144
MAMMALIA	PERISSODACTYLA	EQUIDAE	*Equus quagga quagga*	Quagga	1878	137
MAMMALIA	CHIROPTERA	VESPERTILIONIDAE	*Kerivoula africana*	Tanzanian wooly bat	1878-pre	137
MAMMALIA	RODENTIA	MURIDAE	*Leimacomys buettneri*	Togo mouse	1890	125
MAMMALIA	CETARTIODACTYLA	BOVIDAE	*Cephalophus jentinki*	Jentink's duiker	1892	123
MAMMALIA	CETARTIODACTYLA	BOVIDAE	*Eudorcas rufina*	Red gazelle	1894-pre	121
MAMMALIA	CETARTIODACTYLA	BOVIDAE	*Damaliscus selousi*	Uasin Gishu Topi	1900s?	115
MAMMALIA	AFROSORICIDA	CHRYSOCHLORIDAE	*Cryptochloris wintoni*	De Winston's golden mole	1907	108
MAMMALIA	SORICOMORPHA	SORICIDAE	*Crocidura goliath*	Goliath shrew	1908	107
MAMMALIA	PERISSODACTYLA	EQUIDAE	*Equus quagga burchellii*	Burchell's zebra	1910	105
MAMMALIA	CETARTIODACTYLA	BOVIDAE	*Kobus leche robertsi*	Roberts' lechwe	1913-after	102
MAMMALIA	ARTIODACTYLA	BOVIDAE	*Alcelaphus buselaphus buselaphus*	Bubal hartebeest	1925	90
MAMMALIA	CETARTIODACTYLA	BOVIDAE	*Alcelaphus buselaphus buselaphus*	Bubal hartebeest	1925	90
MAMMALIA	RODENTIA	MURIDAE	*Nilopegamys plumbeus*	Ethiopian amphibious rat	1928	87
MAMMALIA	CARNIVORA	VIVERRIDAE	*Genetta cristata*	Crested genet	1933	82
MAMMALIA	CARNIVORA	FELIDAE	*Leptailurus serval constantinus*	North African serval	1936 (1996?)	79
MAMMALIA	RODENTIA	NESOMYIDAE	*Dendromus vernayi*	Vernay's climbing mouse	1937	78
MAMMALIA	CETARTIODACTYLA	BOVIDAE	*Alcelaphus caama caama*	Cape red hartebeest	1940	75
MAMMALIA	CARNIVORA	FELIDAE	*Panthera leo leo*	Barbary lion	1942	73
MAMMALIA	CETARTIODACTYLA	HIPPOPOTAMIDAE	*Choeropsis liberiensis heslopi*	Niger delta pygmy hippopotamus	1945	70
MAMMALIA	CARNIVORA	VIVERRIDAE	*Genetta poensis*	King genet	1946	69
MAMMALIA	CETARTIODACTYLA	BOVIDAE	*Gazella bilkis*	Queen of Sheba's gazelle	1951	64
MAMMALIA	RODENTIA	MURIDAE	*Hybomys basilii*	Father Basilio's striped mouse	1962	53
AVES	STRUTHIONIFORMES	STRUTHIO	*Struthio camelus syriacus*	Arabian ostrich	1966	49
MAMMALIA	RODENTIA	NESOMYIDAE	*Dendromus kahuziensis*	Mount Kahuzi climbing mouse	1967	48
MAMMALIA	PERISSODACTYLA	EQUIDAE	*Equus africanus africanus*	Nubian wild ass	1970s	45
MAMMALIA	PRIMATES	CERCOPITHECIDAE	*Piliocolobus pennantii bouvieri*	Bouvier's red colobus	1970s	45
MAMMALIA	SORICOMORPHA	SORICIDAE	*Crocidura wimmeri*	Wimmer's shrew	1976	39
MAMMALIA	PRIMATES	CERCOPITHECIDAE	*Piliocolobus badius waldronae*	Miss waldron's red colobus	1978	37
MAMMALIA	CETARTIODACTYLA	BOVIDAE	*Ourebia ourebi kenyae*	Kenya oribi	1980s?	35
MAMMALIA	CETARTIODACTYLA	BOVIDAE	*Oryx dammah*	Scimitar-horned oryx	1988	27
MAMMALIA	ARTIODACTYLA	BOVIDAE	*Ourebia ourebi kenyae*	Kenya oribi	1996	19
MAMMALIA	PERISSODACTYLA	RHINOCEROTIDAE	*Diceros bicornis longipes*	Western black rhinoceros	1996	19
MAMMALIA	CARNIVORA	FELIDAE	*Panthera pardus adersi*	Zanzibar leopard	1996	19
MAMMALIA	PRIMATES	CERCOPITHECIDAE	*Cercopithecus mitis mitis*	Pluto Monkey	1997-pre	17
MAMMALIA	PRIMATES	CERCOPITHECIDAE	*Cercopithecus mitis schoutedeni*	Schouteden's blue monkey	2003-pre	12
MAMMALIA	PERISSODACTYLA	RHINOCEROTIDAE	*Diceros bicornis longipes*	Western black rhinoceros	2006-pre	9
MAMMALIA	PERISSODACTYLA	RHINOCEROTIDAE	*Ceratotherium simum cottoni*	Northern white rhinoceros	2007 (2009?)	7

Table 2. Global list of extinct and extirpated megafauna in Euope

CLASS	ORDER	FAMILY	Latin name	Common name	Date considered as extinct or extirpated	Data used
MAMMALIA	CETARTIODACTYLA	HIPPOPOTAMIDAE	*Hippopotamus creutzburgi*	Cretan dwarf hippopotamus	Late pleistocene	78000
MAMMALIA	CARNIVORA	FELIDAE	*Homotherium*	Saber-toothed cat	32000-29000 BP	30500
MAMMALIA	CARNIVORA	URSIDAE	*ursus spelaeus*	Cave bear	27500 BC	29515
MAMMALIA	CARNIVORA	HYAENIDAE	*Crocuta crocuta*	Cave hyena	11000 BC	13015
MAMMALIA	CETARTIODACTYLA	CERVIDAE	*Candiacervus cretensis*	Cretan dwarf megacerine	Late pleistocene	13015
AVES	ANSERIFORMES	ANATIDAE	*Cygnus falconeri*	Giant swan	Late pleistocene	13015
MAMMALIA	RODENTIA	GLIRIDAE	*Hypnomys mahonensis*	Minorcan giant dormouse	Holocene	12015
MAMMALIA	CARNIVORA	FELIDAE	*Panthera leo spelaea*	Cave lion	10000 BC	12015
MAMMALIA	PERISSODACTYLA	CERATOMORPHA	*Elasmotherium sibiricum*	Elasmotherium	10000 BC	12015
MAMMALIA	PERISSODACTYLA	EQUIDAE	*Equus hydruntinus*	European ass	Holocene	12015
MAMMALIA	CETARTIODACTYLA	CERVIDAE	*Megaloceros cazioti*	Caziot's deer	7650-7530 BP	7640
MAMMALIA	CETARTIODACTYLA	CERVIDAE	*Megaloceros giganteus*	Irish elk	7015 BP	7015
MAMMALIA	RODENTIA	GLIRIDAE	*Eliomys morpheus*	Balearic giant dormouse	6789-6639 BP	6714
MAMMALIA	CETARTIODACTYLA	BOVIDAE	*Myotragus balearicus*	Balearic islands cave goat	5599-5329 BP	5470
MAMMALIA	PROBOSCIDEA	ELEPHANTIDAE	*Mammuths primigenius*	Woolly mammoth	4015 BP	4015
MAMMALIA	PROBOSCIDEA	ELEPHANTIDAE	*Elephas tiliensis*	Tilos dwarf elephant	4000-3500 BP	3750
MAMMALIA	PERISSODACTYLA	RHINOCEROTIDAE	*Coelodonta anthiquitatis*	Woolly rhinoceros	3015 BP	3015
MAMMALIA	SORICOMORPHA	SORICIDAE	*Nesiotites hildalgo*	Balearic giant shrew	3030-2690 BP	2860
MAMMALIA	CARNIVORA	CANIDAE	*Canis volgensis*	Volga dog	100?	1015
MAMMALIA	PERISSODACTYLA	EQUIDAE	*Equus hydruntinus*	European wild ass	1293	715
MAMMALIA	RODENTIA	GLIRIDAE	*Eliomys wiedincitensis*	Maltese giant dormouse	1500-pre	515
MAMMALIA	CETARTIODACTYLA	BOVIDAE	*Bos primigenius*	Aurochs	1627	390
MAMMALIA	CETARTIODACTYLA	BOVIDAE	*Bison bonasus hungarorum*	Carpathian wisent	1790	215
MAMMALIA	PERISSODACTYLA	EQUIDAE	*Equus ferus ferus*	Tarpan	1820	195
MAMMALIA	CETARTIODACTYLA	BOVIDAE	*Capra pyrenaica lusitanica*	Portuguese ibex	1892	115
MAMMALIA	CETARTIODACTYLA	BOVIDAE	*Bison bonasus bonasus*	Lowland wisent	1919	95
MAMMALIA	CETARTIODACTYLA	BOVIDAE	*Bison bonasus caucasicus*	Caucasian wisent	1927	88
MAMMALIA	CARNIVORA	CANIDAE	*Canis lupus deitanus*	Spanish wolf	1930	85
AVES	CHARADRIIFORMES	HAEMATOPODIDAE	*Haematopus meadewaldoi*	Canarian oystercatcher	1940	75
MAMMALIA	CETARTIODACTYLA	CERVIDAE	*lces alces caucasicus*	Caucasian moose	Mid 1900	65
MAMMALIA	CARNIVORA	FELIDAE	*Lynx lynx sardiniae*	Sardinian lynx	1967?	48
MAMMALIA	CARNIVORA	FELIDAE	*Panthera tigris virgata*	Caspian tiger	1970	45
MAMMALIA	LAGOMORPHA	LEPORIDAE	*Lepus granatensis solisi*	Majorcan hare	1980	35
AVES	FALCONIFORMES	PHASIANIDAE	*Perdix perdix italica*	Italian grey partridge	1984	31
MAMMALIA	CETARTIODACTYLA	BOVIDAE	*Capra pyrenaica pyrenaica*	Pyrenean ibex	2000	15

Table 3. Global list of extinct and extirpated megafauna in North America

CLASS	ORDER	FAMILY	Latin name	Common name	Date considered as extinct or extirpated	Date used (BP)
MAMMALIA	CETARTIODACTYLA	BOVIDAE	*Oresamnos harringtoni*	Harrington's mountain goat	12000 BC	14015
MAMMALIA	CETARTIODACTYLA	CERVIDAE	*Cervalces scotti*	Stag-moose	12000 BC	14015
MAMMALIA	PROBOSCIDAE	ELEPHANTIDAE	*Mammuthus exilis*	Pygmy mammoth	10800-11300 BC	13065
MAMMALIA	CARNIVORA	FELIDAE	*Miracinonyx trumani*	American cheetahs	11000 BC	13015
MAMMALIA	CARNIVORA	FELIDAE	*Miracinonyx inexpectatus*		11000 BC	13015
MAMMALIA	CARNIVORA	FELIDAE	*Panthera leo atrox*	American lion	11000 BC	13015
MAMMALIA	PERISSODACTYLA	TAPIRIDAE	*Tapirus californicus*	California tapir	11000 BC	13015
MAMMALIA	ARTIODACTYLA	ANTILOCAPRIDAE	*Capromeryx minor*		11000 BC	13015
MAMMALIA	PERISSODACTYLA	TAPIRIDAE	*Tapirus copei*	Cope's tapir	11000 BC	13015
MAMMALIA	CARNIVORA	FELIDAE	*Panthera leo spelaea*	Eurasian cave lion	11000 BC	13015
MAMMALIA	RODENTIA	CASTORIDAE	*Castoroides leiseyorum*	Giant beaver	11000 BC	13015
MAMMALIA	RODENTIA	CAMELIDAE	*Castoroides ohioensis*		11000 BC	13015
MAMMALIA	PERISSODACTYLA	EQUIDAE	*Equus conversidens*	Mexican horse	11000 BC	13015
MAMMALIA	PILOSA	MEGALONYCHIDAE	*Megalonyx matthisi*		11000 BC	13015
MAMMALIA	PILOSA	MEGALONYCHIDAE	*Megalonyx wheatleyi*		11000 BC	13015
MAMMALIA	PILOSA	MEGALONYCHIDAE	*Megalonyx leptostomus*		11000 BC	13015
MAMMALIA	PILOSA	MEGALONYCHIDAE	*Megalonyx jeffersonii*		11000 BC	13015
MAMMALIA	CARNIVORA	FELIDAE	*Panthera onca augusta*	Pleistocene north American jaguar	11000 BC	13015
MAMMALIA	PILOSA	MEGATHERIIDAE	*Eremotherium laurillardi*	Panamerican ground sloth	11000 BC	13015
MAMMALIA	PILOSA	MEGATHERIIDAE	*Eremotherium eomigrans*		11000 BC	13015
MAMMALIA	PILOSA	MYLODONTIDAE	*Pramulodon harlani*		11000 BC	13015
MAMMALIA	XENARTHA	NOTHROTHERIIDAE	*Nothrotheriops shastensis*	Shasta ground sloth	11000 BC	13015
MAMMALIA	XENARTHA	NOTHROTHERIIDAE	*Nothrotheriops texanus*	Shasta ground sloth	11000 BC	13015
MAMMALIA	PERISSODACTYLA	EQUIDAE	*Equus scotti*	Scott's horse	11000 BC	13015
MAMMALIA	CETARTIODACTYLA	BOVIDAE	*Bison priscus*	Steppe wisent	11000 BC	13015
MAMMALIA	CETARTIODACTYLA	CAMELIDAE	*Hemiauchenia macrocephala*	Stilt-legged llama	11000 BC	13015
MAMMALIA	CETARTIODACTYLA	CAMELIDAE	*Hemiauchenia minima*		11000 BC	13015
MAMMALIA	CETARTIODACTYLA	CAMELIDAE	*Hemiauchenia blancoensis*		11000 BC	13015
MAMMALIA	CETARTIODACTYLA	CAMELIDAE	*Hemiauchenia vera*		11000 BC	13015
MAMMALIA	CETARTIODACTYLA	CAMELIDAE	*Hemiauchenia paradoxa*		11000 BC	13015
MAMMALIA	CETARTIODACTYLA	ANTILOCAPRIDAE	*Stockoceros onusrosagris*	Stockoceros	11000 BC	13015
MAMMALIA	CETARTIODACTYLA	ANTILOCAPRIDAE	*Stockoceros conklingi*		11000 BC	13015
MAMMALIA	CARNIVORA	URSIDAE	*Ursus maritinmus tyrannus*		11000 BC	13015
MAMMALIA	PERISSODACTYLA	TAPIRIDAE	*Tapirus merriami*		11000 BC	13015
MAMMALIA	ANSERIFORMES	CAMELIDAE	*Palaeolama mirifica*	Stout-legged llama	11000 BC	13015
MAMMALIA	PERISSODACTYLA	EQUIDAE	*Equus lambei*	Yukon horse	11000 BC	13015
AVES	CATHARTIFORMES	TERATORMITHIDAE	*Aiolornis incredibillis*	Giant condor	late pleistocene	13015
MAMMALIA	CETARTIODACTYLA	CERVIDAE	*Odocoileus lucasis*	American mountain deer	10000 BC	12015
MAMMALIA	CETARTIODACTYLA	BOVIDAE	*Bison antiquus*		10000 BC	12015
MAMMALIA	CINGULATA	GLYPTODONTIDAE	*Glyptotherium arizonae*		10000 BC	12015
MAMMALIA	CINGULATA	GLYPTODONTIDAE	*Glyptotherium cylindricum*		10000 BC	12015
MAMMALIA	CINGULATA	GLYPTODONTIDAE	*Glyptotherium floridanum*		10000 BC	12015
MAMMALIA	CINGULATA	GLYPTODONTIDAE	*Glyptotherium mexicanum*		10000 BC	12015
MAMMALIA	CINGULATA	GLYPTODONTIDAE	*Glyptotherium texanum*		10000 BC	12015
MAMMALIA	CETARTIODACTYLA	BOVIDAE	*Saiga tatarica*	Saiga antelope	10000 BC	12015
MAMMALIA	PERISSODACTYLA	EQUIDAE	*Equus occidentalis*	Western horse	10000 BC	12015
AVES	CATHARTIFORMES	TERATORMITHIDAE	*Cathartornis gracillis*		10000 BC	12015
AVES	GALLIFORMES	MELEAGRIDIDAE	*Meleagris californica*	California turkey	10000 BC	12015
MAMMALIA	CETARTIODACTYLA	BOVIDAE	*Euceratherium collinum*	Shrub-ox	9500 BC	11515
MAMMALIA	CETARTIODACTYLA	BOVIDAE	*Bootherium bombifrons*	Harlan's muskox	9000 BC	11015
MAMMALIA	CETARTIODACTYLA	TAYASSUIDAE	*Mylohyus elmorei*		8500 BC	11015
MAMMALIA	CETARTIODACTYLA	TAYASSUIDAE	*Mylohyus floridanus*		8000 BC	11015
MAMMALIA	CETARTIODACTYLA	TAYASSUIDAE	*Mylohyus fossilis*		7500 BC	11015
MAMMALIA	CETARTIODACTYLA	TAYASSUIDAE	*Mylohyus gidleyi*		7000 BC	11015
MAMMALIA	CETARTIODACTYLA	TAYASSUIDAE	*Mylohyus nasutus*	Long-nosed peccary	6500 BC	11015

Table 4. Global list of extinct and extirpated megafauna in New Zealand

CLASS	ORDER	FAMILY	Latin name	Common name	Date considered as extinct or extirpated	Date used
AVES	DINORNITHIFORMES	MEGALAPTERYGIDAE	*Megalapteryx didinus*	Upland moa	1300-1400	615
AVES	DINORNITHIFORMES	EMEIDAE	*Anomalopteryx didiformis*	Little bush moa	1300-1400	615
AVES	DINORNITHIFORMES	EMEIDAE	*Pachyomis elephantopus*	Heavy footed moa	1300-1400	615
AVES	DINORNITHIFORMES	EMEIDAE	*Emeus crassus*	Eastern moa	1300-1400	615
AVES	DINORNITHIFORMES	EMEIDAE	*Pachyomis australis*	Crested moa	1300-1400	615
AVES	DINORNITHIFORMES	EMEIDAE	*Pachuomis geranoides*	Mantel moa	1300-1400	615
AVES	DINORNITHIFORMES	EMEIDAE	*Euryapteryx curtus*	Stout legged moa	1300-1400	615
AVES	DINORNITHIFORMES	DINORNITHIDAE	*Dinornis novaezealandiae*	North Island giant moa	1300-1400	615
AVES	DINORNITHIFORMES	DINORNITHIDAE	*Dinornis robustus*	South Island giant moa	1300-1400	615
AVES	ANSERIFORMES	ANATIDAE	*Cnemiornis gracillis*	North Island goose	1300-1400	615
AVES	ANSERIFORMES	ANATIDAE	*Cnemiomis calcitrans*	South Island goose	1300-1400	615
AVES	ANSERIFORMES	ANATIDAE	*Malacorhynchus scarletti*	Scartlett's duck	1300-1400	615
AVES	ANSERIFORMES	ANATIDAE	*Oxyura vantetsi*	New Zealand blue-billed duck	1300-1400	615
AVES	ACCIPTRIFORMES	ACCIPITRIDAE	*Circus teauteensis*	Eyles' harrier	1300-1400	615
AVES	ACCIPTRIFORMES	ACCIPITRIDAE	*Aquila moorei*	Haast's eagle	1300-1400	615
AVES	GRUIFORMES	APTORNITHIDAE	*Aptomis otidiformis*	North Island adzebill	1300-1400	615
AVES	GRUIFORMES	APTORNITHIDAE	*Aptomis defossor*	South Island adzebill	1300-1400	615
AVES	GRUIFORMES	RALLIDAE	*Fulica prisca*	New Zealand coot	1300-1400	615
AVES	PASSERIFORMES	CORVIDAE	*Corvus antipodum*	New Zealand raven	1500s	465
AVES	GRUIFORMES	RALLIDAE	*Porphyrio matelli*	North Island takahe	1800	215
AVES	ANSERIFORMES	ANATIDAE	*Chenonetta finschi*	Finsch's duck	1860	155
AVES	GRUIFORMES	RALLIDAE	*Diaphorapteryx hawkinsi*	Hawkin's rail	1869	146
AVES	CICONIFORMES	ARDEIDAE	*Ixobrychus novaezelandiae*	New Zealand little bittern	1890s	120

Appendix 2. Additional supporting information for chapter 5

-**Table 1:** Complete species list and associated traits

-**Table 2:** Frequency of bird presence in each habitat (e.g., Residential, Farmland, Natural, Generalist)

-**Table 3:** Species list and human score associated

-**Figure 1:** Phylogenetic tree based on Jetz *et al.* (2012) using inter-genetic distances on a subset of 79 species

-**Figure 2:** Habitat niche breadths of New Zealand avifauna

Table 1: Complete species list and associated traits

family	Genre	Common name	latin name	TipLabel	conservation status	Anthropogenic habitat	Habitat	Diet	Foraging area	Social	Nest height	Nest Type	plumage dimorphism	Size dimorphism	feeding	number of clutch	nestling times	Mass log transformed	clutch size
Falconiformes	Accipitridae	Australian Harrier	Circus approximans	Circus_approximans	native	F	G	C	M	I	M	O	Y	Y	I	O	S	2,875	4,2
Passeriformes	Cracticidae	Australian magpie	Gymnorhina tibicen	Gymnorhina_tibicen	introduced	F	O	I	M	G	H	O	N	N	C	O	S	2,544	3,5
Galliformes	Phasianidae	Brown Quail	Synoicus ypsilophorus	Coturnix_ypsilophora	introduced	F	O	O	G	G	G	O	N	N	A	O	XL	2,000	14,5
Galliformes	Phasianidae	Chukar	Alectoris chukar	Alectoris_chukar	introduced	F	O	O	G	G	G	O	N	Y	A	O	XL	2,778	13
Passeriformes	Emberizidae	Cirl Bunting	Emberiza cirlus	Emberiza_cirlus	introduced	F	O	G	G	G	U	O	Y	N	C	O	L	1,398	3
Psittaciformes	Psittacidae	Crimson rosella	Platycercus elegans	Platycercus_elegans	introduced	F	F	G	M	G	M	C	N	N	C	O	S	2,114	5,1
Psittaciformes	Cacatuidae	Galah	Cacatua roseicapilla	Cacatua_roseicapilla	introduced	F	O	G	G	G	M	C	N	N	C	O	S	2,512	3,8
Passeriformes	Motacillidae	New Zealand Pipit	Anthus novaeseelandiae	Anthus_novaeseelandiae	native	F	O	I	G	I	G	O	N	N	C	M	L	1,521	3,5
Galliformes	Phasianidae	Peafowl	Pavo cristatus	Pavo_cristatus	introduced	F	O	O	G	P	G	O	Y	Y	A	O	XL	3,653	5
Galliformes	Phasianidae	Pheasant	Phasianus colchicus	Phasianus_colchicus	introduced	F	O	O	G	G	G	O	Y	Y	A	O	XL	3,146	9
Charadriiformes	Charadriidae	Pied oystercatcher	Haematopus ostralegus	Haematopus_ostralegus	native	F	O	I	G	P	G	O	N	N	C	O	XL	2,740	2,5
Gruiformes	Rallidae	Pukeko	Porphyrio porphyrio	Porphyrio_porphyrio	introduced	F	A	O	M	G	G	O	N	Y	A	M	XL	3,021	5
Passeriformes	Corvidae	Rook	Corvus frugilegus	Corvus_frugilegus	introduced	F	O	O	G	G	H	O	N	Y	C	O	L	2,628	3,5
Passeriformes	Alaudidae	Skylark	Alauda arvensis	Alauda_arvensis	introduced	F	O	G	G	G	G	O	N	N	C	M	XL	1,580	3,1
Charadriiformes	Charadriidae	Spur-winged plover	Vanellus miles	Vanellus_miles	native	F	O	I	G	G	G	O	N	Y	C	M	S	2,568	3,5
Galliformes	Phasianidae	Wild Turkey	Meleagris gallopavo	Meleagris_gallopavo	introduced	F	O	O	G	G	G	O	Y	Y	A	O	XL	3,903	12
Passeriformes	Emberizidae	Yellowhammer	Emberiza citrinella	Emberiza_citrinella	introduced	F	O	G	G	G	U	O	Y	N	C	O	L	1,431	4
Passeriformes	Hirundinidae	Welcome swallow	Hirundo Neoxena	Hirundo_neoxena	native	F	O	I	H	P	M	O	N	N	C	M	S	1,146	4
Gruiformes	Rallidae	Banded rail	Rallus philippensis	Gallirallus_philippensis	native	G	A	O	G	P	G	O	N	N	C	M	XL	2,230	4,75
Galliformes	Odontophoridae	California quail	Callipepla californica	Callipepla_californica	introduced	G	O	G	G	G	G	O	Y	N	A	O	XL	2,255	13
Passeriformes	Turdidae	Common blackbird	Turdus merula	Turdus_merula	introduced	G	G	O	M	P	U	O	Y	N	C	M	L	1,954	3,5
Passeriformes	Fringillidae	Common chaffinch	Fringilla coelebs	Fringilla_coelebs	introduced	G	G	G	M	G	M	O	Y	Y	C	M	L	1,342	3,64
Passeriformes	Sturnidae	Common Myna	Acridotheres tristis	Acridotheres_tristis	introduced	G	G	O	M	P	M	C	N	Y	C	O	S	2,097	4
Passeriformes	Fringillidae	Common Redpoll	Carduelis flammea	Carduelis_flammea	introduced	G	G	G	M	G	U	O	Y	N	C	O	L	1,079	4
Passeriformes	Prunellidae	Dunnock	Prunella modularis	Prunella_modularis	introduced	G	G	I	G	P	U	O	N	N	C	M	XL	1,322	3,5
Psittaciformes	Psittacidae	Eastern Rosella	Platycercus eximius	Platycercus_eximius	introduced	G	O	G	M	G	M	C	Y	N	C	O	S	2,041	5,6
Passeriformes	Fringillidae	European Goldfinch	Carduelis carduelis	Carduelis_carduelis	introduced	G	G	G	M	G	U	O	N	Y	C	O	L	1,204	4
Passeriformes	Sturnidae	European Starling	Sturnus vulgaris	Sturnus_vulgaris	introduced	G	G	O	M	G	M	C	N	N	C	O	M	1,929	4,5

Order	Family	Common name	Scientific name	Scientific_name	Status													Value1	Value2
Passeriformes	Fringillidae	EuropeanGreenfinch	Carduelis chloris	Carduelis_chloris	introduced	G	G	G	M	G	U	O	Y	N	C	O	L	1,447	4,5
Passeriformes	Acanthizidae	Grey warbler	Gerygone igata	Gerygone_igata	native	G	S	I	H	P	U	C	N	N	C	O	M	0,813	3,5
Passeriformes	Passeridae	House sparrow	Passer domesticus	Passer_domesticus	introduced	G	O	G	M	G	M	C	Y	N	C	M	L	1,477	3,8
Columbiformes	Columbidae	Kereru	Hemiphaga novaeseelandia	Hemiphaga_novaeseelandiae	native	G	S	H	H	P	M	O	N	Y	C	M	S	2,813	1
Coraciiformes	Alcedinidae	Kingfinsher	Halcyon sancta	Todiramphus_sanctus	native	G	G	C	G	P	U	C	N	N	C	O	S	1,813	5
Coraciiformes	Halcyonidae	Laughing Kookaburra	Darcelo novaeguineae	Dacelo_novaeguineae	introduced	G	S	O	M	G	M	C	N	Y	G	O	S	2,538	2,5
Strigiformes	Strigidae	Little owl	Athene noctua	Athene_noctua	introduced	G	O	C	G	I	M	C	N	N	C	O	S	2,255	3
Gruiformes	Rallidae	Marsh crake	Porzana pusilla	Porzana_pusilla	native	G	A	I	G	P	G	O	N	N	C	O	XL	1,602	5,9
Strigiformes	Strigidae	Morepork	Ninox novaeseelandia	Ninox_novaeseelandiae	native	G	S	I	M	P	M	C	N	N	I	O	S	2,243	2
Falconiformes	Falconidae	New zealand Falcon	Falco novaeseelandiae	Falco_novaeseelandiae	native	G	G	C	M	I	M	O	N	Y	I	O	S	2,477	2,8
Passeriformes	Dicruridae	New Zealand Fantail	Rhipidura fuliginosa	Rhipidura_fuliginosa	native	G	S	I	M	P	U	O	N	N	C	M	L	0,903	3,5
Columbiformes	Columbidae	Rock pigeon	Columbia livia	Columba_livia	introduced	G	O	O	G	G	U	O	N	N	C	M	S	2,602	1,9
Cuculiformes	Cuculidae	Shining cuckoo	Chrysococcyx lucidus	Chrysococcyx_lucidus	native	G	G	I	H	I	M	O	N	N		G	M	1,398	1
Passeriformes	Zosteropidae	Silvereyes	Zosterops lateralis	Zosterops_lateralis	native	G	S	O	H	G	M	O	N	N	C	M	XL	1,114	3
Passeriformes	Turdidae	Song thrush	Turdus philomelos	Turdus_philomelos	introduced	G	G	O	M	P	U	O	N	N	C	M	L	1,845	2,5
Psittaciformes	Cacatuidae	Sulfur-crested Cockatoo	Cacatua galerita	Cacatua_galerita	introduced	G	O	G	M	G	M	C	N	N	C	O	S	2,954	1,6
Passeriformes	Meliphagidae	Tui	Prosthemadera novaeseelandiae	Prosthemadera_novaeseelandiae	native	G	S	O	H	I	M	O	N	Y	C	O	S	2,079	3
Passeriformes	Pachycephalidae	Brown creeper	mohoua novaeseelandia	Mohoua_novaeseelandiae	native	N	F	O	H	I	U	O	N	Y	C	O	M	1,127	3
Passeriformes	Sylviidae	Fernbird	Megalurus punctatus	Bowdleria_punctata	native	N	A	I	G	P	G	O	N	N	C	M	M	1,544	3,5
Casuariiformes	Apterygidae	Great spotted Kiwi	Apteryx haastii	Apteryx_haastii	native	N	G	I	G	P	G	C	N	Y	C	O	XL	3,380	1
Psittaciformes	Strigopidae	Kaka	Nestor meridionalis	Nestor_meridionalis	native	N	F	G	H	G	H	C	N	Y	C	O	S	2,677	4,2
Psittaciformes	Strigopidae	Kakapo	Strigops habroptilus	Strigops_habroptila	native	N	F	H	G	I	G	C	N	Y	C	O	S	3,398	3
Psittaciformes	Strigopidae	Kea	Nestor notabilis	Nestor_notabilis	native	N	G	H	M	G	G	C	N	Y	C	O	S	3,000	4
Casuariiformes	Apterygidae	Little spotted Kiwi	Apteryx owenii	Apteryx_owenii	native	N	S	I	G	P	G	O	N	Y	C	O	XL	3,061	1,5
Cuculiformes	Cuculidae	Long tailed cuckoo	Eudynamys taitensis	Eudynamys_taitensis	native	N	S	C	M	I	M	O	N	N	G	M	S	2,097	1
Passeriformes	Pardalotidae	New Zealand Bellbird	Anthornis melanura	Anthornis_melanura	native	N	S	O	H	P	M	C	Y	Y	C	O	L	1,531	3,5
Casuariiformes	Apterygidae	North island brown kiwi	Apteryx mantelii	Callaeas_cinereus	native	N	G	I	G	P	G	C	N	Y	C	M	XL	3,301	1,5
Passeriformes	Callaeidae	North island kokako	Callaeas cinerea wilsoni -	Apteryx_australis_mantelii	native	N	F	O	H	P	H	C	N	N	C	O	S	2,367	2,3
Passeriformes	Petroicidae	North island robin	Petroica longipes	Petroica_australis_longipes	native	N	F	I	G	P	M	O	N	N	C	M	S	1,544	2,45
Passeriformes	Callaeidae	North island saddleback	Philesturnus carunculatus rufusa	Philesturnus_carunculatus	native	N	F	I	M	P	G	O	N	N	C	O	M	1,845	2,5
Passeriformes	Petroicidae	New Zealand Robin	Petroica australis	Petroica_australis	native	N	S	I	G	P	U	O	Y	N	C	M	S	1,544	2,7
Psittaciformes	Psittacidae	Red-crowned parakeet	Cyanoramphus novaezelandia	Cyanoramphus_novaezelandiae	native	N	G	G	G	G	U	C	N	Y	C	M	S	1,903	7
Passeriformes	Acanthisittidae	Rifleman	Acanthisitta chloris	Acanthisitta_chloris	native	N	F	I	H	P	M	C	Y	Y	C	O	S	0,778	3,5
Passeriformes	Acanthisittidae	Rock Wren	Xenicus gilviventris	Xenicus_gilviventris	native	N	S	O	H	P	G	C	Y		C	O	S	1,204	3,1
Casuariiformes	Apterygidae	South Brown kiwi	Apteryx australis	Apteryx_australis	native	N	G	I	G	P	G	C	N	Y	C	O	XL	3,342	1
Gruiformes	Rallidae	Spotless crake	porzana tabuensis	Porzana_tabuensis	native	N	A	I	G	P	G	O	N	N	C	O	XL	1,653	3,5
Passeriformes	Notiomystidae	Stitchbird	Notiomystis cincta	Notiomystis_cincta	native	N	F	O	H	G	M	O	Y	Y	C	M	S	1,602	4
Gruiformes	Rallidae	Tahahe	Porphyrio mantelli	Porphyrio_hochstetteri	native	N	O	H	G	G	G	O	N	N	A	O	S	3,477	2
Passeriformes	petroicidae	Tomtit	Petroica macrocephala	Petroica_macrocephala	native	N	F	I	G	P	U	O	Y	N	C	M	M	1,041	3,9
Gruiformes	Rallidae	Weka	Gallirallus australis	Gallirallus_australis	native	N	G	O	G	I	G	C	N	N	C	M	XL	3,000	3
Passeriformes	Pachycephalidae	Whitehead	Mohoua albicilla	Mohoua_albicilla	native	N	S	O	H	G	M	O	N	Y	G	O	S	1,267	3
Psittaciformes	Psittacidae	Variable oystercatcher	Cyanoramphus auriceps	Cyanoramphus_auriceps	native	N	F	I	G	P	H	C	N	Y	C	M	S	1,699	5,5
Passeriformes	Pachycephalidae	Yellowhead	Mohoua ochrocephala	Mohoua_ochrocephala	native	N	F	O	H	G	M	C	N	Y	G	O	M	1,477	3,06
Gruiformes	Rallidae	Australian coot	Fulica atra	Fulica_atra	native	N	A	H	G	G	G	O	N	Y	A	O	XL	2,756	5
Columbiformes	Columbidae	Babary dove	Streptopelia roseogrisea	Streptopelia_roseogrisea	introduced	R	O	G	G	P	U	O	N	N	C	M	M	2,146	1,5
Passeriformes	Pycnonotidae	Red-Vented Bulbul	Pycnonotus cafer	Pycnonotus_cafer	introduced	R	G	H	H	G	U	O	N	N	C	M	L	1,505	2,92
Columbiformes	Columbidae	Spotted dove	streptopelia chinensis	Stigmatopelia_chinensis	introduced	R	G	G	G	P	U	O	N	N	C	M	M	2,114	2

Table 2: Frequency of bird presence in each habitat based on Robertson et al.

Observation (2007).

TipLabel	Residencial	Farmland	natural
Circus_approximans	0,0366	0,7917	0,1717
Gymnorhina_tibicen	0,0940	0,8106	0,0954
Coturnix_ypsilophora	0,0079	0,6943	0,2978
Alectoris_chukar	0,0000	0,8462	0,1538
Emberiza_cirlus	0,1008	0,7815	0,1176
Platycercus_elegans	0,0000	1,0000	0,0000
Cacatua_roseicapilla	0,0714	0,9286	0,0000
Anthus_novaeseelandiae	0,0217	0,8228	0,1555
Pavo_cristatus	0,0496	0,9271	0,0233
Phasianus_colchicus	0,0611	0,8145	0,1244
Haematopus_ostralegus	0,0963	0,8948	0,0089
Porphyrio_porphyrio	0,0707	0,9001	0,0292
Corvus_frugilegus	0,0686	0,9272	0,0042
Alauda_arvensis	0,0346	0,9422	0,0232
Vanellus_miles	0,0783	0,9088	0,0129
Meleagris_gallopavo	0,0082	0,9824	0,0093
Emberiza_citrinella	0,0732	0,8130	0,1138
Hirundo_neoxena	0,1716	0,8284	0,0000
Gallirallus_philippensis	0,0682	0,4773	0,4545
Callipepla_californica	0,1636	0,5959	0,2405
Turdus_merula	0,1967	0,5212	0,2821
Fringilla_coelebs	0,1432	0,5454	0,3115
Acridotheres_tristis	0,2529	0,6513	0,0958
Carduelis_flammea	0,1017	0,6495	0,2488
Prunella_modularis	0,1946	0,4875	0,3179
Platycercus_eximius	0,1387	0,5582	0,3031
Carduelis_carduelis	0,1560	0,7222	0,1218
Sturnus_vulgaris	0,2220	0,7207	0,0573
Carduelis_chloris	0,1581	0,7264	0,1155
Gerygone_igata	0,1253	0,3116	0,5631
Passer_domesticus	0,2969	0,6394	0,0637
Hemiphaga_novaeseelandiae	0,1263	0,2191	0,6547
Todiramphus_sanctus	0,1239	0,6427	0,2334
Dacelo_novaeguineae	0,1333	0,6444	0,2222
Athene_noctua	0,1730	0,7827	0,0443
Porzana_pusilla	0,0020	1,0000	0,0000
Ninox_novaeseelandiae	0,1553	0,2808	0,5639
Falco_novaeseelandiae	0,0672	0,3329	0,5999
Rhipidura_fuliginosa	0,1435	0,3837	0,4728
Columba_livia	0,2901	0,6908	0,0192
Chrysococcyx_lucidus	0,1316	0,2640	0,6044
Zosterops_lateralis	0,1687	0,3667	0,4646
Turdus_philomelos	0,2166	0,5542	0,2292
Cacatua_galerita	0,1221	0,4504	0,4275
Prosthemadera_novaeseelandiae	0,1695	0,2210	0,6095
Mohoua_novaeseelandiae	0,1716	0,8284	0,0000
Bowdleria_punctata	0,0040	0,2052	0,7908
Apteryx_haastii	0,0000	0,0196	0,9804
Nestor_meridionalis	0,0557	0,0625	0,8818
Strigops_habroptila	0,0000	0,1250	0,8750
Nestor_notabilis	0,0226	0,0742	0,9032
Apteryx_owenii	0,0000	0,0357	0,9643
Eudynamys_taitensis	0,0293	0,0371	0,9337
Anthornis_melanura	0,1095	0,1477	0,7428
Callaeas_cinereus	0,0000	0,0150	0,9850
Apteryx_australis_mantelii	0,0055	0,0859	0,9086
Petroica_australis_longipes	0,0029	0,0232	0,9739
Philesturnus_carunculatus	0,0065	0,0261	0,9673
Petroica_australis	0,0029	0,0232	0,9739
Cyanoramphus_novaezelandiae	0,0269	0,0909	0,8822
Acanthisitta_chloris	0,0092	0,0351	0,9557
Xenicus_gilviventris	0,0000	0,0000	1,0000
Apteryx_australis	0,0055	0,0859	0,9086
Porzana_tabuensis	0,0000	0,1923	0,8077
Notiomystis_cincta	0,0000	0,0000	1,0000
Porphyrio_hochstetteri	0,0000	0,3835	0,6165
Petroica_macrocephala	0,0093	0,0588	0,9319
Gallirallus_australis	0,0756	0,2225	0,7019
Mohoua_albicilla	0,0107	0,0252	0,9641
Cyanoramphus_auriceps	0,0020	0,0080	0,9900
Mohoua_ochrocephala	0,0153	0,0476	0,9371
Fulica_atra	0,0041	0,0123	0,9835
Streptopelia_roseogrisea	0,6977	0,2562	0,0461
Pycnonotus_cafer	1,0000	0,0000	0,0000
Stigmatopelia_chinensis	0,6772	0,3095	0,0133
Haematopus_unicolor	0,6090	0,3276	0,0634

Table 3: Species list and human score associated

TipLabel	Human colonisation	European colonisation
Fulica_atra	3	2
Circus_approximans	1	1
Gymnorhina_tibicen	3	2
Streptopelia_roseogrisea	4	4
Gallirallus_philippensis	1	1
Petroica_traversi	1	1
Mohoua_novaeseelandiae	1	1
Coturnix_ypsilophora	3	2
Callipepla_californica	2	3
Alectoris_chukar	4	4
Emberiza_cirlus	4	4
Turdus_merula	4	4
Fringilla_coelebs	4	4
Acridotheres_tristis	4	4
Carduelis_flammea	2	3
Platycercus_elegans	3	2
Prunella_modularis	4	4
Platycercus_eximius	3	2
Carduelis_carduelis	4	4
Sturnus_vulgaris	4	4
Carduelis_chloris	4	4
Bowdleria_punctata	1	1
Cacatua_roseicapilla	3	2
Apteryx_haastii	1	1
Gerygone_igata	1	1
Passer_domesticus	4	4
Nestor_meridionalis	1	1
Strigops_habroptila	1	1
Nestor_notabilis	1	1
Hemiphaga_novaeseelandiae	1	1
Todiramphus_sanctus	1	1
Dacelo_novaeguineae	3	2
Athene_noctua	4	4
Apteryx_owenii	1	1
Eudynamys_taitensis	1	1
Porzana_pusilla	1	1
Ninox_novaeseelandiae	1	1
Anthornis_melanura	1	1
Falco_novaeseelandiae	1	1
Rhipidura_fuliginosa	1	1
Anthus_novaeseelandiae	1	1
Callaeas_cinereus	1	1
Apteryx_australis_mantelii	1	1
Petroica_australis_longipes	1	1
Philesturnus_carunculatus	1	1
Petroica_australis	1	1
Pavo_cristatus	4	4
Phasianus_colchicus	4	4
Haematopus_ostralegus	1	1
Porphyrio_porphyrio	1	1
Cyanoramphus_novaezelandiae	1	1
Pycnonotus_cafer	4	4
Acanthisitta_chloris	1	1
Columba_livia	4	4
Xenicus_gilviventris	1	1
Corvus_frugilegus	4	4
Chrysococcyx_lucidus	1	1
Zosterops_lateralis	3	2
Alauda_arvensis	4	4
Turdus_philomelos	4	4
Apteryx_australis	1	1
Porzana_tabuensis	1	1
Stigmatopelia_chinensis	4	4
Vanellus_miles	3	2
Notiomystis_cincta	1	1
Cacatua_galerita	3	2
Porphyrio_hochstetteri	1	1
Petroica_macrocephala	1	1
Prosthemadera_novaeseelandiae	1	1
Haematopus_unicolor	1	1
Gallirallus_australis	1	1
Hirundo_neoxena	3	2
Mohoua_albicilla	1	1
Meleagris_gallopavo	2	3
Cyanoramphus_auriceps	1	1
Emberiza_citrinella	4	4
Mohoua_ochrocephala	1	1

Figure 1: Phylogenetic tree based on inter-genetic distances (in blue, introduced species and in orange, native species
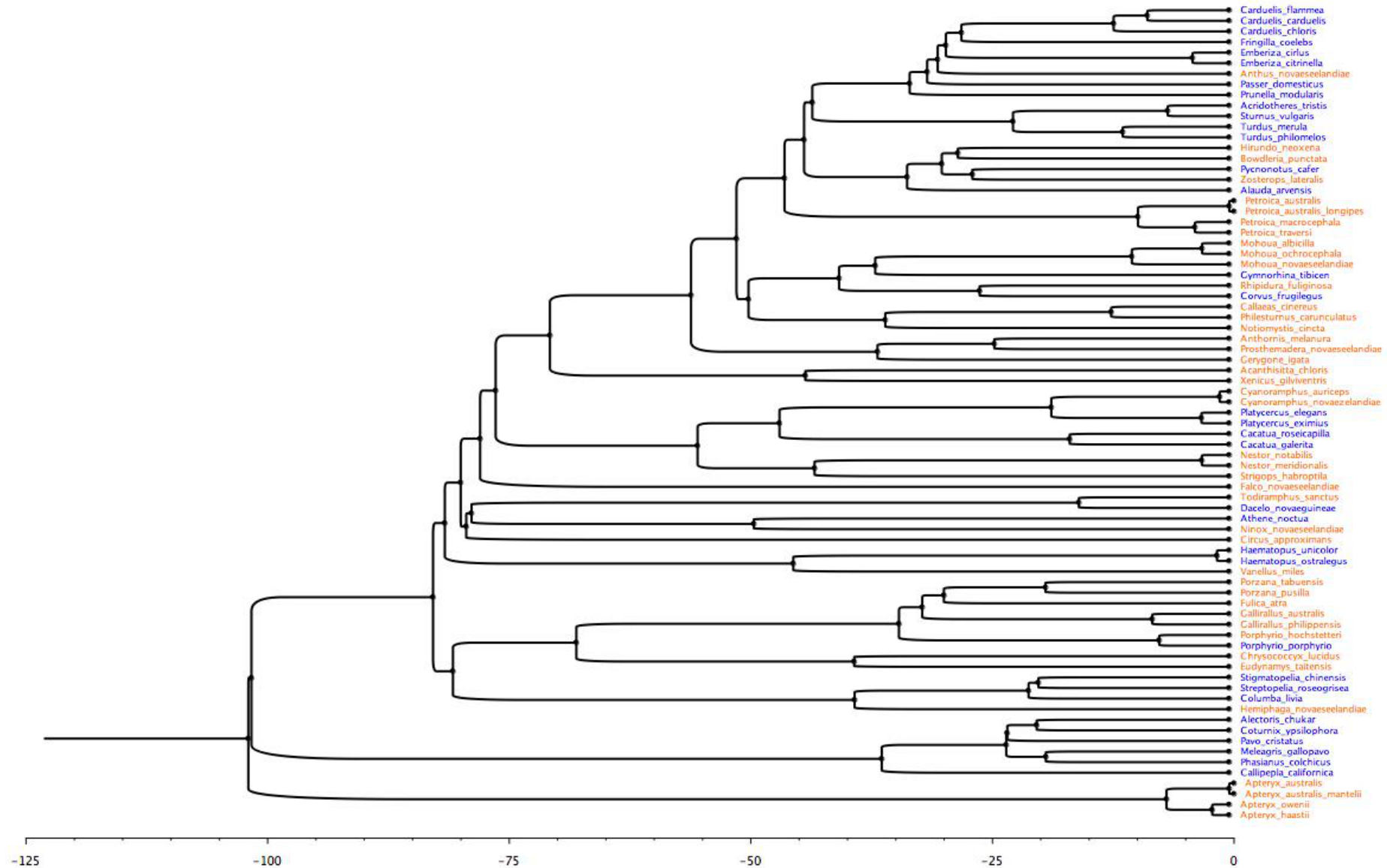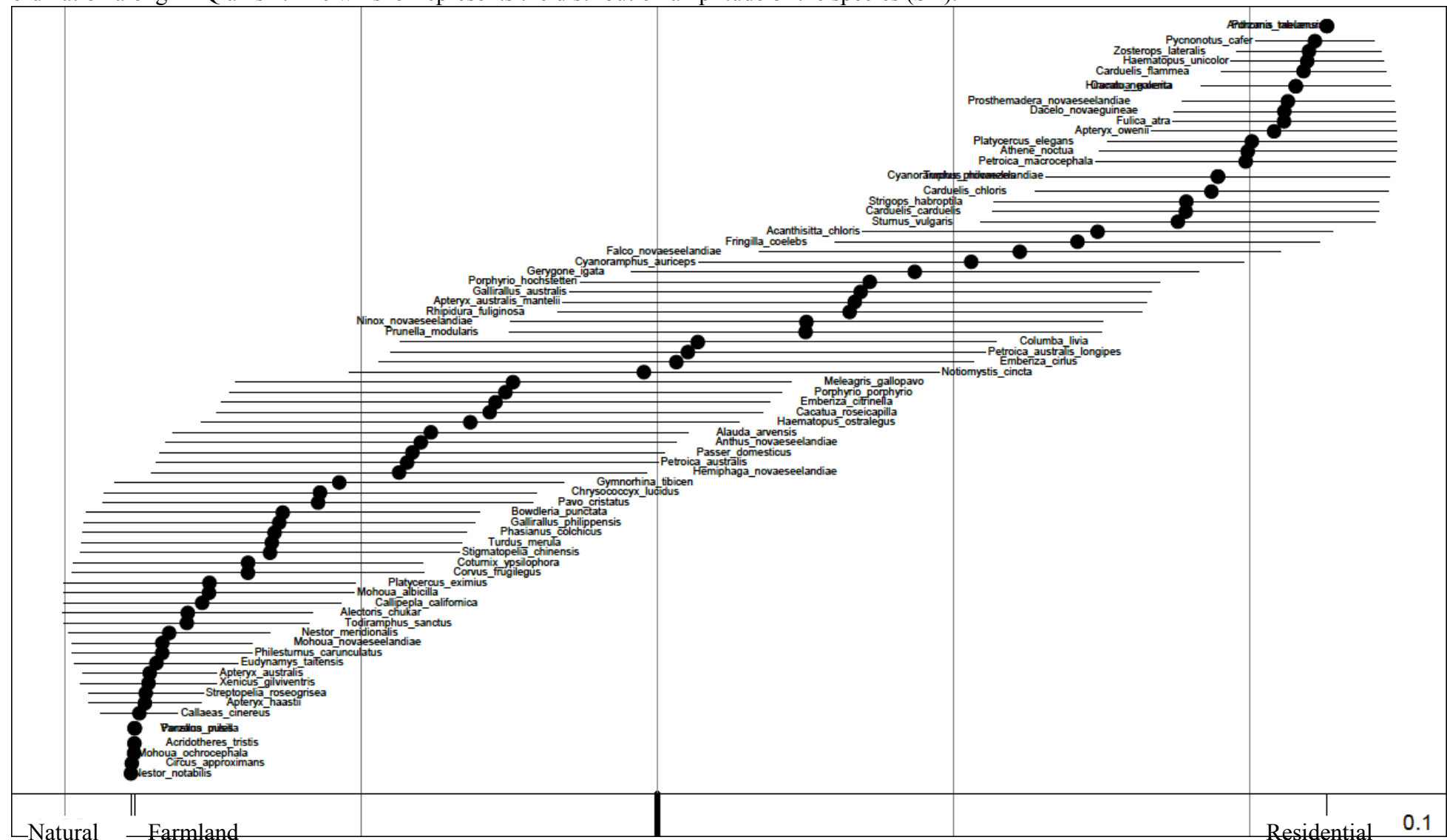
Figure 2: Habitat niche breadths of New Zealand avifauna represented as weighted average(black circle) of their occurrence at habitats based on the ordination along RLQ axis 1. The whisker represents the distribution amplitude of the species (SD).

Appendix 3. The following publications have been produced during the PhD candidature as a result

of the research presented in this thesis :

Publications

Amiot C, Hill SD, Ji W (2015) Using plumage and behavioural development to age New

Zealand fantail nestlings. *New Zealand Journal of Zoology*, **42(1)**, 35-43.

Conference presentations

Oral communication

- Amiot C, Dale J, Brunton D, Ji W (2013) Effect of nest site selection on reproductive success of
native passerine in urban woodlands. Ecotas13, 5Th joint Conference of New Zealand Ecological
Society and Ecology of Australia. Aotea centre, Auckland, New Zealand

- Amiot C, Hartley D, Ji W (2013) Nest site selection along an urban gradient by native and introduced
birds in New Zealand. Australasian society for the study of Animal Behaviour Conference. Auckland
University, Auckland, New Zealand.

- Amiot C, Dale J, Brunton D, Ji W (2011) Auckland urban woodland quality by comparison of urban
and non-urban ecosystems. New Zealand ecological society, Ecology in the Heartland, Energy events
centre, Rotorua, New Zealand.

Poster

- Amiot C, Ji W (2013) New Zealand urbanization, a new perspective for urban avifauna ecology.
SURE World conference 2013, Berlin, Germany.