Abundance and microhabitat use of *Leiopelma archeyi* in relation to land-use

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I dedicate this thesis to…

laughter, love, sun-kissed skin and rain drops, family, friendship, the night sky, and a frog sitting in the hills.

An individual *Leiopelma archeyi* posing on a *Knightia excelsa* leaf during emergence in Wharekirauponga. Photo: E.R. Hotham

Abstract

Habitat disturbance has been recognised as a significant factor contributing to biodiversity decline worldwide. In New Zealand, land-use activities on conservation land and privately-owned property have been disputed due to their potential effects on vulnerable species. Currently, there is limited information regarding the impact of land-use activities on populations of Archey's frogs (*Leiopelma archeyi*), a small ground-dwelling amphibian. Historical exploration mining in Wharekirauponga (WKP), and roading and housing-related activities in Mahakirau Forest Estate (MFE) in the Coromandel Peninsula, were the land-use activities focused on in this thesis. Disturbance from these activities included site clearance, which removed > 50% of vegetation in ca. 100 m² areas, during the 1980s, 1990s and 2010-16. My primary aims were to investigate whether these disturbances have affected the current abundance and microhabitat use of *L. archeyi*.

I surveyed 16 pairs of disturbed and undisturbed sites for emerged frogs over three consecutive nights. These sites were 10 m x 10 m. Captured frogs were photographed, measured and weighed for individual identification and recaptures noted. Vegetation of sites was characterised using reconnaissance (RECCE) plot vegetation descriptions. To predict frog presence within the 100 m² areas, microhabitat features were assessed in 1.5 m³ plots where frogs were found and randomly-selected plots where frogs were not found. A purpose-built closed-mark recapture model was developed to calculate detection probabilities that were used to estimate abundance within disturbed and undisturbed sites. This modelling incorporated a disturbance effect and habitat characteristics assumed to be important to *L. archeyi*. Vegetation composition from the RECCE data and finer habitat features were characterised using ordination techniques and coefficients of determination, both to assess how vegetation was affected by disturbance and assess whether this was a useful predictor of frog abundance and presence. The probability of finding a frog within a 1.5 m³ plot was analysed using a generalised linear model (GLM) with logit link function.

Sites disturbed by historical exploration mining, roading and housing-related activities did not have significantly lower abundance of *L. archeyi* than undisturbed sites i.e. those with no vegetation clearance after 1980. Abundance estimates were instead correlated with higher elevation and with plant species typically associated with mature forest, which were found in both disturbed and undisturbed sites. Ordination techniques used to assess vegetation composition revealed differences among sites that could be due to forest succession and replantation in disturbed sites. Mature forest species, such as tree ferns and rewarewa (*Knightia excelsa*), which were associated with higher frog abundance, also provided the substrates that frogs were most frequently found on. These plant species contribute to greater leaf litter depth, which was the only microhabitat variable that differed significantly between 1.5 m³ plots where frogs were present or absent. In comparison, sites that had been replanted with Kānuka (*Kunzea robusta)* and kauri (*Agathis australis)* did not provide substantial leaf litter.

These results do not imply that land-use activities have no immediate effect on *L. archeyi* populations. However, over the time elapsed since disturbance, frogs of various age classes likely re-colonised sites after leaf litter build-up and reached densities determined by the local habitat quality. Because the disturbances considered were on a small scale (ca. 100 m² for mining exploration, roading and housing), frogs would have been available for re-colonisation from the surrounding landscape. Abundance estimation accounting for detection probability was a valuable method to increase our understanding of the historical effects of disturbance on *L. archeyi* and to determine the habitat features that instead influence abundance. Further, this information should be used in translocation site selection and survey methodology to predict abundance and presence of frogs in other areas. Based on my results I recommend that rehabilitation of sites following disturbance should be undertaken by natural forest succession and should emphasise retention and restoration of leaf litter.

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Chapter 1

General introduction

An individual *Leiopelma archeyi* climbing a tree fern (*Cyathea dealbata)* at Mahakirau Forest Estate. Photo: E. Hotham

1.1 Habitat disturbance

Habitat disturbance is arguably one of the greatest threats to species survival and to the future of biodiversity worldwide (McNeely et al. 1990; UNEP-WCMC, IUCN & NGS 2018). 'Habitat', as defined by Hall, Krausman and Morrison (1997), is "the resources and conditions present in an area that produce occupancy - including survival and reproduction - by a given organism". Habitats that maximize the organism's individual fitness, thus its lifetime reproductive success, will contribute the most to future generations if ecological restraints, such as predation, are not limiting factors (Johnson 2007; Mathewson & Morrison 2015). Habitat disturbance occurs when an event changes the conditions or constrains the resources required for occupancy, thus, changing the quality of the habitat (Hall, Krausman & Morrison 1997; White & Pickett 1985; Johnson 2007). Disturbance can occur from natural events, such as tree fall or competition, or events caused by humans, such as disease or clearcutting, and usually results in habitat loss for some species. Changes to resources and/or conditions are often temporary and few habitats are destroyed entirely through disturbance (Laurence 2010). This temporary change can affect species on a variety of levels because habitat use can vary by age, sex, and in time and space (Morrison, Block & Verner 1991).

Spatial scale is important to consider in investigations of habitat use because the effects from disturbance events depend on the scale and resolution of the study (Wien, Van Horne & Rotenberry 1987; Steele 1992). Johnson (1980) called these scales 'orders'. The broadest scale, referred to as *First-order selection,* is the selection of the physical or geographical range of a species. *Second-order selection* dictates the home range of an individual within the first-order scale. *Third-order selection* is the finer scaled habitat features that individuals use within the home range. Finally, the *Fourth-order selection* is the acquirement of these resources (Johnson 1980; Ash 1996). The term "macrohabitat" is generally associated with Johnson's *first order* of habitat selection, and "microhabitat" refers to the finer habitat features in the *second*, *third* and *fourth orders*, with these associations species and site specific (Hall, Krausman & Morrison 1997). Which of Johnson's orders are used to observe a population's habitat use influences the interpretation of data, and thus, management strategies drawn from the conclusions of such observations (Babbit, Veysey & Tanner 2010).

Habitat disturbance events are likely to become more common with the combined impacts of the increased human population, which is projected to reach 9.8 billion by 2050, and the effects of climate change (United Nations, Department of Economic and Social Affairs 2017). The need to continue acquiring and producing resources to fuel this growth creates tension between conserving biodiversity and having to modify ecosystems that produce optimal habitat (Fardell et al. 2018). Currently, the total global percentages of terrestrial and marine areas protected from human modification are 15.2% and 7.4% respectively (*UNEP-WCMC*, *ICUN* & *NGS* 2020). Outside these protected areas, species and ecosystems are still being modified at rates that are beyond their capacity to withstand change (*UNEP-WCMC*, *ICUN* & *NGS* 2018). However, depending on the nature of the disturbance, species may also benefit, or be unaffected, by changes in their habitat (Ash 1996; Brown & Hutchings1997; Hamer & Hill 2000). An example of biodiversity benefiting from disturbance events was seen in the increase of native annuals after fire disturbance in Australia (Hester & Hobbs (1992). An increase in species richness following large-scale disturbance is not uncommon, with disturbance events often major sources of variation in biological communities (Grime 1973; Connell 1978; Denslow 1980). Furthermore, disturbance events are often temporary, with successional changes occurring after appropriate time intervals, modifying and restoring resources and conditions and promoting occupancy and species distribution within that area over time (Denslow 1980; Hamer & Hill 2000). For this reason, disturbances can play a central role in structuring plant and animal communities depending on the type and spatial context of the disturbance (Jonsson & Essen 1998).

The protection of biodiversity, however, can generally best be done through the protection of habitats (McNeely et al. 1990). In theory, this concept is easily implemented. But in a world driven by economic markets and resource exploitation, the protection of habitats is not always practical. Additionally, the protection of areas often arises as a reactive response to the loss of biodiversity (McNeely et al. 1990). This seldom changes the social and economic pressures threatening these areas, with actions such as mitigation or off-setting not always based on current ecological science or community involvement (Calvet, Napoleone & Salles 2015). Corruption, loop holes in policies and the change in governments also contribute to uncertainty that such areas remain under protection (Smith & Walpole 2005). Conservation strategies must therefore look to integrate the views from various disciplines, such as from the social sciences, to ensure the upmost protection is held for biodiversity.

This research relates to the conflict between resource use and biodiversity conservation throughout New Zealand. For over 150 years, minerals, such as gold, have been important resources for the New Zealand economy (Nathan 2006). In 2018, the gross domestic product (GDP) from mining and exploration in New Zealand contributed $2.2 billion or 1% of the national GDP (Infometrics 2019). These activities can occur on public conservation land under the Crown Minerals Act 1991 (Ministry of Business, Innovation and Employment 1991). The history of habitat disturbance from the mining sector and the conflict between conservation land use and economic gain provides an ideal opportunity to integrate social and ecological practises.

1.2 Biodiversity declines in New Zealand

1.2.1 Agents of decline

New Zealand has a history of human-induced disturbances which has generally resulted in loss of native biodiversity. This loss of biodiversity has been severe for a number of reasons. New Zealand was the last major archipelago of islands to be colonised by humans and this allowed for an extended period of evolution of plant and animal species in the absence of terrestrial mammalian predators (Davidson 1984; Diamond 1990). This biota was extensively altered after human colonisation. The arrival of Polynesians between about 1280-1300 AD led to the burning of forests, introduction of kiore (*Rattus exulans)*, and the exploitation of large birds such as moa (Davidson 1984; King 1984; McGlone 1989; Wilmshurst & Higham 2004). European settlement followed some 300 years later and accelerated the trend of native species decline by habitat loss/disturbance, the introduction of exotic plants and animals, and disease (Hobbs 2000).

1.2.2 Habitat loss and modification

In New Zealand, the burning of indigenous forest by early Polynesian inhabitants caused the reduction in native forest cover from 78% to 53% (King 1984). A further 27% reduction of native forest cover has occurred following European colonisation (Ministry for the Environment & Stats NZ 2018). Destruction of vegetation from activities such as fire can lead to other changes in the ecosystem including the loss of organic material in soils (Fernandez, Cabaneiro & Carballas 1996; Certini 2005), soil instability resulting in erosion (McGlone 1983), changes in microclimate (Ash 1995; Murcia 1995) and alteration in floristic composition (Naveh 1975; Denslow 1980; Cammeraat & Imeson 1998). Moreover, coastal, lowland and wetland ecosystems have also been heavily impacted by human-caused disturbances and continue to decline in extent (Ministry for the Environment & Stats NZ 2018). Just over 50% of the land area in New Zealand is now modified for human activities, such as urbanisation, agricultural production and exotic forestry plantations (Ministry for the Environment & Stats NZ 2018).

As of 2010, 33.4% of the total land area in New Zealand was under protection (Ministry for the Environment 2010). The distribution of these areas reflects the economic value of the land, with protected areas skewed towards hilly, mountainous landscapes that are less desirable for agricultural and forestry practises (Clout & Saunders 1995). Furthermore, the remaining native forest in lowland areas consists of small, fragmented patches (Clout & Saunders 1995; Craig et al. 2000). Ewers (2004) demonstrated that these patches have complex, irregular shapes, and noted that the effects of habitat fragmentation can take many decades to become apparent over Johnson's (1980) orders. On Stephens island (Takapourewa) in Cook Strait, forest cover disappeared from browsing by sheep and cattle. This caused fragmented forest patches that were vulnerable to strong winds and has been linked to the range reduction of native frogs (*Leiopelma hamitoni*) due to habitat loss (Newman, Crook & Imboden 1978). At a macro scale, immigration and emigration between (sub-) populations can be hindered by fragmentation, leading to smaller populations and increased inbreeding (Caughley 1994; Harrison & Bruna 1999). At a microscale, such effects can include reduced food availability; an increase in exotic plant species; disease prevalence, alterations in microclimate and susceptibility to edge effects (Saunders, Hobbs, & Margules 1991; Murcia 1995; Harrison & Bruna 1999; Hutchison 2008).

Human-induced modification can also benefit species diversity in plant communities and can have long-term positive effects for animal species when modification is managed with a range of ecosystem services in mind (Denslow 1980; Clout & Gaze 1984; Spitzer, Novotny, Tonner & Leps 1993). An apparent example of bridging the gap between resource use and biodiversity conservation is the positive response of the New Zealand bush kārearea (*Falco novaeseelandiae ferox*) to exotic pine plantations. Kārearea are an At Risk- Recovering species in the Department of Conservation Threat Classification System, with habitat destruction a key factor contributing to their conservation status (Lawerence 2002; Robertson et al. 2017). These birds of prey have been discovered breeding in exotic pine plantations and are more resilient to modified landscapes than initially suspected (Stewart & Hyde 2004; Thomas, Minot, Holland 2010). The forestry and logging industry contribute $1.74 billion to New Zealand's economy annually and pine plantations have a potential role in mitigating effects of historical deforestation (Zurita & Bellocq 2010; Ministry for the Environment & Stats NZ 2019). The management of pine plantations to support biodiversity and kārearea populations in the absence of indigenous forest is therefore beneficial for the conservation of the species and also allows forestry companies to meet Forestry Stewardship Council (FSC) certification and improve their public image (Pawson, Ecroyd, Seaton, Shaw & Brockerhoff 2010). Connections from integrating systems will influence the maintenance of ecosystem health, human well-being, and in the long run, the sector itself and the economy (Guerry 2005; Tallis & Polasky 2009).

1.2.3 Introduced predators and competitors

Predation and competition are ecological constraints that strongly influence an animals' behaviour, resource use and fitness (Johnson 1980; Olsson, Brown & Smith 2002). These constraints can be short- or long-term selective pressures, shaping the habitat available to that animal throughout that period (Clark & Shutler 1999).

Prior to the arrival of humans, the only land mammals in New Zealand were bats (King 1990). The absence of mammalian predators and competitors influenced the evolution of New Zealand's flora and fauna (Clout & Saunders 1995). One such effect resulted in other animal groups evolving to become functional equivalents of mammals or evolving traits such as longevity, low reproduction rates and freeze tactics, leading to the vulnerability of many species after the arrival of humans (King 1984; Diamond 1990). The introduction of mammals, in particular, has transformed ecosystems and landscapes by reducing vegetation density and altering vegetation composition from selective browsing (King 1990; Wardle et al. 2001). The browsing of native biota from herbivores has also created habitat suitable for introduced plant species to colonise, posing a further threat to indigenous plant communities (Craig et al. 2000). Predator-free off-shore islands and fenced sanctuaries have played an important role in indigenous species survival by offering refuge from the drastic effects of introduced mammalian predators and competitors.

1.2.4 Disease

An additional hypothesis in New Zealand's biodiversity decline is the impact of emerging disease (Tompkins & Jakob-Hoff 2011). Having evolved in isolation, New Zealand native species can lack defences against introduced diseases, such as avian malaria and Chytridiomycosis (Bell et al. 2004; Tompkins & Jakob-Hoff 2011). The lack of diversity and species richness in host communities can also increase and alter the frequency of infection and disease (Oppliger et al. 1998; Price et al. 2014). Furthermore, the change in environmental conditions can cause an animal stress and if the individual cannot adapt or immune systems are suspectable, it can lead to both temporary and long-term physiological changes for that individual (Milton & Lutz 2003). Conservation managers need to consider disease as a potential cause of population decline (Tompkins & Jakob-Hoff 2011).

1.3 New Zealand Native Frogs: *Leiopelma*

Endemic New Zealand frogs have long been isolated and are among the most unique amphibian species in the world (Fleming 1975; Worthy 1987a). The endemic frogs in New Zealand belong to the genus *Leiopelma* (Anura: Leiopelmatidae) and are part of New Zealand's "archaic" fauna that originated from Gondwana (Fleming 1975). Extant species of *Leiopelma* include two terrestrial and morphologically similar taxa: *L. archeyi* and *L. hamitoni (L. pakeka* was synonymised with L. *hamitoni* by Easton 2018)*,* and one semi-aquatic species, *L. hochstetteri* (King et al. 2009; Easton 2018). Extinct *Leiopelma* include *L. auroraensis, L. markhami* and *L. waitomoensis,* with the first two being osteologically similar to *L. hochstetteri*, and the latter to *L. hamitoni* (Worthy 1987a; Easton 2018).

Extant *Leiopelma* species are small, with snout-vent-length (SVL) ranging from up to 40 mm for the smallest species, *L. archeyi*, to 51 mm for *L. hamitoni*, the largest species (Worthy 1987a; Bell 1978; Bishop et al. 2013). They are carnivorous, eating a range of invertebrates such as beetles and mites (Stephenson & Stephenson 1956; Bell 1978; Shaw, Skerratt, Daglish & Bishop 2012). All three *Leiopelma* species are generally nocturnal. They are terrestrial breeders, with egg clutches laid under stones, logs, or vegetation (Bell 1978). *L. archeyi* display parental care, with tailed froglets developing on the male's back, conversely *L. hochstetteri* larvae are aquatic without close association to parents (Bell 1978; Bell 1985a). All three species are sit-and-wait predators that display "freeze" tactics when threatened and are cryptically-coloured in predominantly shades of brown and green (Bell 1978; Thurley & Bell 1994). The frogs lack certain middle ear structures and external eardrums that are characteristic of modern frogs, with *Leiopelma* not known to vocalize in a social context, although they have been observed to vocalise when in distress or to startle predators (Bell 1978). Evidence suggests *L. hamitoni* communicate through chemical signals and show strong site fidelity (Bell 1978; Newman 1990; Lee & Waldman 2002; Waldman & Bishop 2004).

The extinctions of *L. auroraensis, L. markhami,* and *L. waitomoensis* and the New Zealand threat classification of extant *Leiopelma* coincide with habitat loss after human settlement and predation from kiore (Table 1) (Worthy 1987; Bell 1994). The primary agent of recent declines in *Leiopelma* include mammalian predation and disease (Thurley & Bell 1994; Bell et al. 2004; Bishop et al. 2013). but have not been conclusively demonstrated as threats to *Leiopelma*, as stated in the New Zealand Native Frog Recovery Plan 2013-2018 (Bishop et al. 2013). Population declines for *Leiopelma* can have huge implications for the overall survival of the species due to the current isolation and size of populations. Additionally, the slow maturity (3-4 years) of the species and their reliance on environmental cues for breeding and low clutch sizes (2- 19 eggs), can result in lower lifetime productivity in high predation or stressful environments (Stephenson & Stephenson 1957; Bell 1978; King et al. 2009; B.D Bell *pers. comm*.).

Habitat modification is regarded as an ongoing threat to *Leiopelma* species (Bishop et al. 2013). Amphibians are highly sensitive to changes in their environments for several reasons, a key factor is their semi-permeable skin. Habitat modification impacts microclimates and ecosystem processes that are essential for amphibian survival and reproduction (Pough et al. 1987; Ash 1996; Krishnamurthy 2003). *Leiopelma* are particularly vulnerable to habitat loss and modification because they occupy discrete home ranges and depend on particular microclimates (Stephenson & Stephenson 1956; Bell 1978; Cree 1989; Thurley & Bell 1994; Ramirez 2017). They are also a relatively immobile species and therefore cannot easily relocate when their home ranges are adversely affected (Essner et al. 2010; Ramirez 2017). For example, severe modification of *L. hamiltoni* habitat on Stephens Island (Takapourewa), with the clearance of indigenous vegetation thought to have contributed to confining the population to a boulder bank (Bell 1985b). Reduction in indigenous forest cover also occurred on Maud Island, with remaining *L. hamitoni* populations occurring in forest remnants on the island (Bell 1985b). Furthermore, habitat loss has contributed to the fragmentation of populations of *L. hochstetteri* on the mainland, with isolation shown to cause smaller, cytogenetically distinct populations that are at risk of potential inbreeding (Green 1994; Easton 2018). Lastly, habitat disturbance from mining in southern Coromandel has been highlighted as an activity that could impact *L. archeyi* populations (Bishop et al. 2013; Burns et al. 2018).

Leiopelma evolved in the absence of mammalian predators. Their immobility, cryptic colouration and lack of vocalisation could have helped them evade native predators such as the extinct laughing owl (*Sceloglaux albifacies*) but is less beneficial against introduced mammalian species with highly developed olfactory receptors such as rats (*Rattus* spp.) and pigs (*Sus scrofa*) (Bell 2010). *L. archeyi* and *L. hochstetteri* co-occur with mammalian predators on the mainland (Bell 1985b; Thurley & Bell 1994). *L. hamitoni* are restricted to rat-free islands (Bell 1985b; Bishop et al. 2013). Evidence of predation from rats has been observed on the mainland, with remains of *L. archeyi* displaying bite marks characteristic of the rodent (Thurley & Bell 1994). The remains of *L. archeyi* in the stomach contents of an introduced frog, *Litoria aurea,* was also examined (Thurley & Bell 1994). In a study on the microhabitat of *L. archeyi* in Whareorino forest, Ramirez (2017) found that frogs in rat-controlled grids were more likely to utilise the soil, leaf litter and ferns. In comparison, grids not controlled for rats had frogs more likely to be above ground level (Ramirez 2017). These results suggest *L. archeyi* select different microhabitats in the presence of rats, possibly allowing them to co-occur these predators (Ramirez 2017).

L. archeyi populations have also been impacted by disease (Bell et al. 2004). Chytridiomycosis (disease caused by chytrid fungus) is suspected to have contributed to a population crash in *L. archeyi* on the Coromandel Peninsula between 1996-2001 (Bell et al. 2004). Chytrid fungus has also been detected in the *L. archeyi* Whareorino population and in introduced *Litoria* species (Bishop et al. 2009). Laboratory research has demonstrated, however, that all three *Leiopelma* species can eliminate and be treated for chytrid, so there is still uncertainty surrounding the population decline (Bishop et al. 2009). Furthermore, the Coromandel Peninsula population of *L. archeyi* has since stabilised (Bishop et al. 2013), with infected individuals persisting in the wild (Bishop et al. 2009). Chytrid fungus has not been detected in the other *Leiopelma* species (Moreno, Aguayo & Brunton 2011; Bishop et al. 2013), but new amphibian diseases pose a significant threat to native frogs should they reach New Zealand (Bishop et al. 2013).

With the growing human population in New Zealand, climate change, and continued mammalian predation, research is required to ensure management of existing and future *Leiopelma* populations. This is a difficult task when the appreciation of *Leiopelma* is restricted (Bishop et al. 2013), and funding towards frog conservation and research in New Zealand is limited.

Table 1 Threat classifications of *Leiopelma* species by the New Zealand Threat Classification System (2018) and the IUCN (International Union for Conservation of Nature). *Note: *Leiopelma Hamiltoni* is still recognised as a separate species to *L. pakeka* by the IUCN, thus is included separately in this table

Leiopelma Species	**New Zealand Threat Classification System**	**IUCN Red List Category**
L. archeyi	At Risk – Declining	Critically Endangered (IUCN 2017)
L. hochstetteri	At Risk – Declining	Least Concern (IUCN 2015)
L. hamiltoni*	Threatened- Nationally Vulnerable	Vulnerable (IUCN 2015)
L. pakeka	Taxonomically Indistinctive	Vulnerable (IUCN 2015)
L. auroraensis	Extinct	Extinct
L. markhami	Extinct	Extinct
L. waitomoensis	Extinct	Extinct

1.3.1 Global trends

Research presented at the first World Congress of Herpetology (WCH) Conference in 1989 indicated that many amphibian populations were experiencing declines (Blaustein & Wake 1990; Blaustein 1994). Approximately 41% of amphibian species are threatened and causes of population decline observed in *Leiopelma* populations (habitat loss and modification, predation, and disease) are also affecting amphibian species globally (Blaustein 1994; Pechmann & Wilbur 1994; Stuart et al. 2004; IUCN 2014).

Often referred to as environmental indicators, amphibian species are important contributors to the trophic dynamics of both terrestrial and aquatic ecosystems (Blaustein & Wake, 1990; Graeter 2005). This is largely due to their roles as predators, prey and herbivores, and their abundance in these roles, with a loss in amphibian populations affecting other species that they eat or eat them (Blaustein & Wake 1990). The joint interaction of these biotic relationships with abiotic factors are the primary drivers of species distribution, especially for ectotherms, which rely heavily on abiotic conditions for survival (Farallo & Miles 2016).

The significance of amphibian declines has been disputed, with natural fluctuation observed in amphibian populations and caution surrounding short-term studies that did not account for these population trends (Blaustein & Wake 1990; Blaustein 1994; Marsh 2001). What is not disputed, however, is that the human population is causing major modifications to amphibian habitats. More research is therefore needed on the potential threats these activities could pose to amphibian populations, regardless if there is an overall species decline or not.

1.3.2 New Zealand Native Frog Recovery Plan 2013-2018

The key agent(s) of decline for *Leiopelma* are not well understood, with recovery actions focusing on managing threats that are considered most likely to impact populations (Bishop et al. 2013). Key information is required to increase our understanding in native frog behaviour and microhabitat requirements (*Action 16.2*) and how land use activities, such as mining, may impact on these requirements (*Action 14.9*) (Bishop et al. 2013). Without this knowledge, translocations, habitat restoration, and recommendations on land use activities are hindered, thus, the group regard these actions as “essential” and “high” respectively (Bishop et al. 2013).

1.4 Study species: *Leiopelma archeyi*

Leiopelma archeyi (Figure 1.1) is the world’s most evolutionary distinct and Globally Endangered (EDGE) amphibian species (ZSL 2012). Natural populations occur within a 600 hectare area of Whareorino Forest and in scattered populations throughout the Coromandel Peninsula, New Zealand (Figure 1.2). *Leiopelma archeyi* occurs sympathrically throughout both the Coromandel and Whareorino Forest with *L. hochstetteri* (Stephenson & Stephenson 1956; Bell 1978; Thurley & bell 1994; Bishop et al. 2013). The total population size of *L. archeyi* is estimated to be 5000-20000 individuals (Bishop et al. 2013).

Leiopelma archeyi are the least nocturnal of the *Leiopelma* species (Cree 1989; Bell 1978). During the day, individuals retreat under logs, rocks and leaf litter/ fronds or in other refuges (e.g., hollow tree ferns, vegetation) (Bell 1978; Ramirez 2017; J.T. Cisternas *pers. comm.*). Emergence from retreat sites is strongly correlated with humidity, rainfall and wetness of vegetation (Cree 1989; Ramirez 2017). Cree (1989) found individuals could rehydrate rapidly from wet foliage, such as *Freycinetia banksii*, and similar numbers of frogs emerged on wet nights during both summer and winter. Emerged frogs have been observed climbing tree trunks, stems of shrubs over 2 m, and sitting on foliage and leaf litter (Stephenson & Stephenson 1956; Bell 1978; Cree 1989; Ramirez 2017). Nightly movements of *L. archeyi* ranged, on average, between 0.5 and 1.5 m in Whareorino Forest, with larger frogs moving further (Ramirez 2017).

Leiopelma archeyi lay eggs in moist, sheltered areas, such as under logs, with partial tadpole development taking place within eggs (Stephenson & Stephenson 1956; Bell 1985). Males guard the eggs and care for hatched froglets for several weeks until metamorphosis is near complete (Bell 1978). Maturity is reached after 3-4 years, with adult frogs observed reaching ages of ≤ 37 years (Bell 1978; B.D. Bell *pers. comm.*). *Leiopelma archeyi* cannot be sexed on external morphology, except for greater body size in females than males and if eggs are visible through the skin on the female’s abdomen (Bell 1978). Distinct black patterns on the dorsal, ventral and flanks allow for identification to the individual level.

Initial management of *L. archeyi* was focused on statutory advocacy and legal habitat protection (Newman et al. 2009; Bishop et al. 2013). Since the discovery of chytridiomycosis, research and management efforts have increased (Bishop et al. 2013). From 2001, *L. archeyi* populations have stabilised and are no longer in decline (Newman et al. 2009; Bishop et al. 2013). However, the species is still considered ‘At Risk’ (Table 1), with concerns raised over continued predation from introduced mammalian and amphibian species, proximity of populations to land use activities and the lack of populations on predator-free islands (Newman et al. 2009).

Figure 1.1 An individual *L. archeyi* emerged during nocturnal surveys at Mahakirau Forest Estate. Photo: E. Hotham

Figure 1.2 Current distribution of extant *L. archeyi.* Accessed and modified from google.com/maps in May 2019, NZ map from google.com/images, May 2019.

1.4.1 Habitat disturbance: Land use activities

As mentioned above, the impact of land use activities on *L. archeyi* is not well understood. There is concern surrounding the Coromandel Peninsula population in regards to mining activities, with scrutiny placed on this sector by their involvement in habitat disturbance in conservation land.

Minerals, including gold, silver and petroleum, are valuable national assets. The mining of such minerals is an industry that has been a major contributor to New Zealand's economic development and growth since the arrival of European settlers (Christie & Barker 2013). Over the past 25 years the mining industry in New Zealand has grown strongly, with mineral extraction having the potential to increase the national GDP by between 1.3% and 3.4% (Christie & Barker 2013). The effects of this growth also include additional income generated in regions from employment (Basu et al. 2015). Growth is largely driven by rising demand from consumers, with these minerals used in mobile phones, construction, wiring and appliances, and is essential for the equipment required to generate sustainable forms of energy, e.g. wind turbines (World Bank 2017). On the other hand, extraction and processing of minerals is associated with various economic, environmental and social issues (Azapagic 2004). These issues include effects of habitat disturbance, such as forest clearance, on plants and animals; mortality of animal species; effects on water quality from dischargers or spills; noise and vibration; and economic impacts to some regions after the completion of mineral extraction (Muduli & Barve 2011).

Within the past few decades there has been a strong push for corporations, particularly those perceived in a negative light, to incorporate sustainable development in their business models (Azapagic 2004). This approach comes in the form of social responsibility in recognising the needs of everyone; effective environmental protection; prudent use of natural resources; and the maintenance of high and stable levels of economic growth and employment (Jenkins & Yakovleva 2004). Corporate social and environmental disclosure has also grown considerably, with Annual Reports required by legislation (Jenkins & Yakovleva 2004; Muduli & Barve 2011). Furthermore, increased awareness of environmental impacts and the personal ethical of individuals in corporations should help minimise adverse effects of resource extraction.

In New Zealand, to prospect, explore, or mine a Crown owned mineral a permit must be granted (Ministry of Business, Innovation, and Employment 2019). Further, an Access Agreement is required from the Department of Conservation (DOC) for mining on public conservation land. However, continued mining and exploration on conservation land has led to social and ecological conflicts in some areas.

Habitat disturbance from past roading and housing was also explored in this thesis. The construction industry does not get as much scrutiny as the mining sector, especially in the Coromandel. However, similar to mining, the development of roads and housing is driven by demand from consumers and can have adverse effects on plants and animals. Reports on the environmental effects of a roading development is required by Council, but how these reports are followed through depends on the Council and DOC.

1.5 Thesis outline

1.5.1 Objectives of this study

The main aim of this thesis is to investigate whether human-induced habitat disturbance impacts the abundance and microhabitat use of *L. archeyi*. Questions to be addressed are:

1. What habitat characteristics affect *L. archeyi* abundance within survey sites?
2. Does historical disturbance from exploration mining, housing-related activities or roading affect habitat characteristics and abundance of *L. archeyi*?
3. Is microhabitat use selected due to physiological constraints or behaviour responses?
4. Are there intrinsic (age class) factors influencing microhabitat selection?

1.5.2 Study area

This study was carried out in two areas within the Coromandel Peninsula, New Zealand, Wharekirauponga (**WKP**) catchment (38°17’51.8”S, 175°49’18.2”E) and Mahakirau Forest Estate (**MFE**) (36°50’20.9”S, 175°31’45.9”E) (Figure 1.3). *Leiopelma archeyi* has been recorded in WKP (although size or distribution of population is unknown) and was chosen because of the various time scales of disturbance, the presence of frogs and the type of disturbance. This (sub-) population is also recognised as the southern-most *L. archeyi* population on the Coromandel Peninsula. Similarly, MFE had a known (sub-) population of *L. archeyi*. MFE was chosen because the area differed in the disturbance type and in topography from WKP.

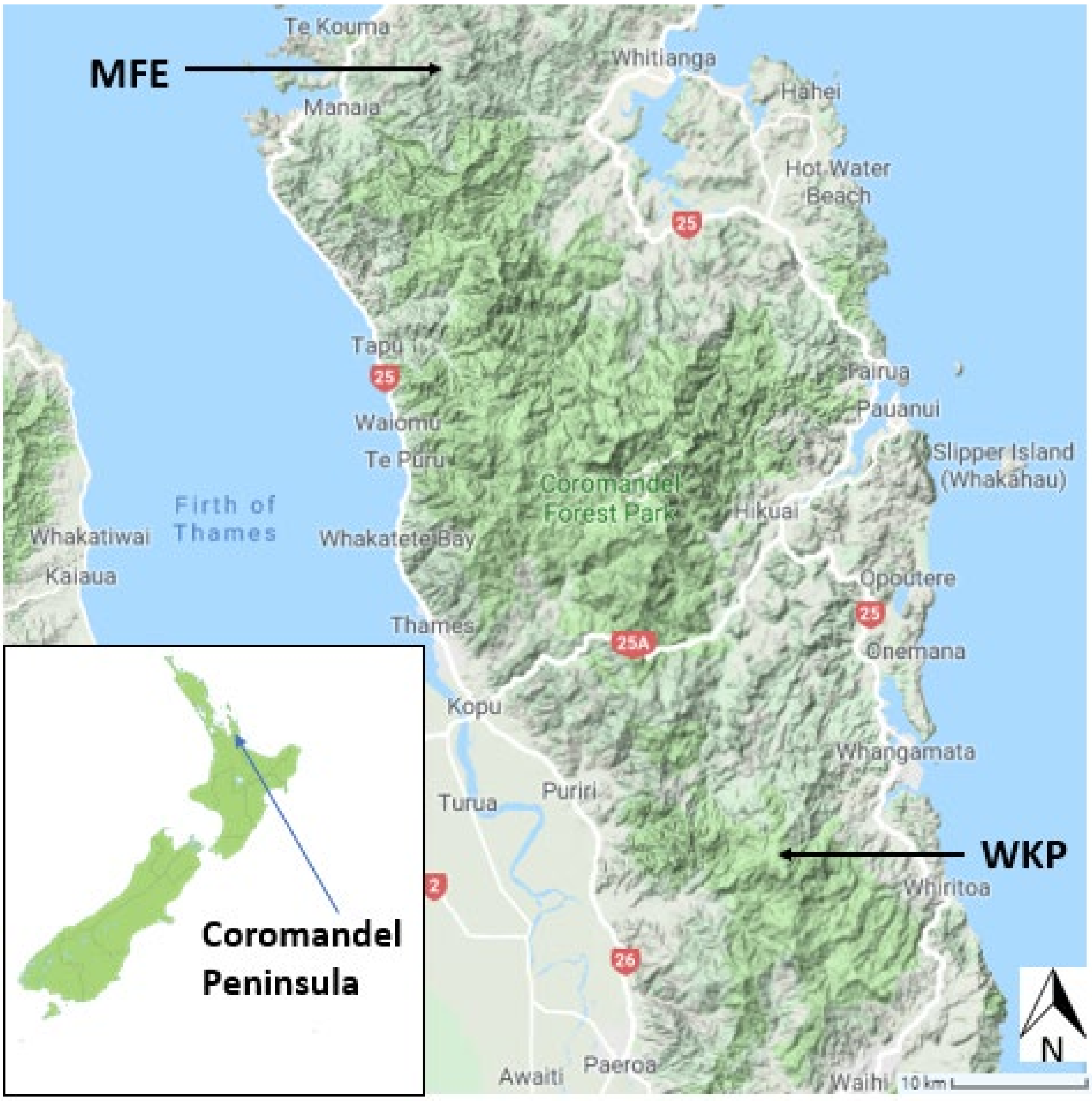

Figure 1.3 Coromandel Peninsula in the North Island of New Zealand (NZ) (inset). The blue circle indicates Wharekirauponga (WKP) and the orange circle Mahakirau Forest Estate (MFE). The darker green on the map indicates forested areas. Accessed from google.com/maps on August 2019, NZ map from google.com/images, August 2019.

1.5.2.1 Wharekirauponga

Wharekirauponga (WKP) is located within the Coromandel Forest Park, a public conservation area managed by the Department of Conservation (DOC) with limited predator control applied when funding is available (a 1080 poison aerial drop occurred in 2017, with no follow-up control currently scheduled). WKP has a history of disturbance, including logging kauri (*Agathis australis)* and *Pinus radiata* prior to the 1980s. Vegetation in the lower catchment of the WKP area is largely regenerated forest including species such as *Kunzea robusta*, *Cyathea dealbata* and *Knightia excelsa*, reflecting this period of earlier disturbance (Figure 1.4). The WKP area was prospected for gold and from the 1980s onwards patches (approx. 10 m x 10 m) of vegetation were cleared for exploration sites or other mining activity. *Leiopelma archeyi* and *L. hochstetteri* occur sympathrically throughout WKP.

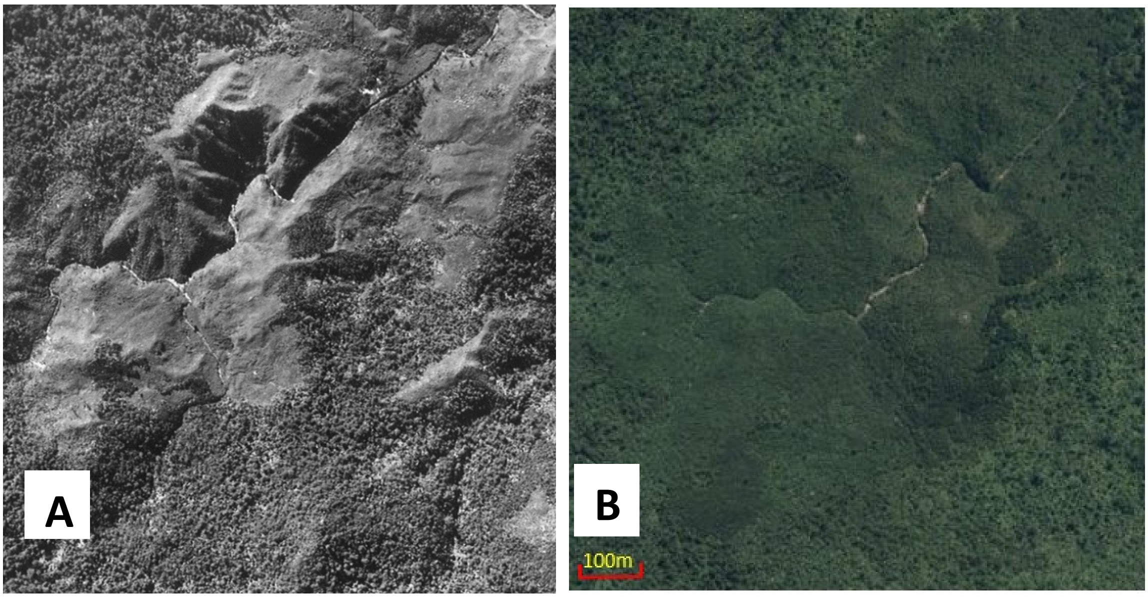

Figure 1.4 A: Aerial photograph of WKP taken in 1948, showing the extent of vegetation clearance (OceanaGold Ltd 2019). **B:** Aerial photograph of WKP taken during 2012-2013, accessed from data.linz.govt, showing vegetation regeneration.

This study focused on historical exploration mining sites (1980s, 1990s and 2010-16) and the effect this activity had on the habitat use of *L. archeyi*. The continued exploration at WKP and interests in mining activities on the Coromandel Peninsula might be better managed if the effect of exploration on *L. archeyi* is better understood.

Exploration mining is required to locate and define a particular economically mineable commodity in a mineral province (Christie & Barker 2013). Once the mineral has been found, exploration begins by selecting an area to investigate based on an assessment of geological history and past mining activity (Christie & Barker 2013). Geophysical, geochemical and geological methods have been developed to assist with the investigation of prospects, including the use of drills that collect core samples that are examined for mineral composition (Christie & Barker 2013). The selection of sites from which to drill for exploration of veins was chosen based on location and spatial orientation of favourable geological targets at WKP (Newmont 2012).

Historical exploration sites in this study were chosen based on site availability and access. The period between 2000 and 2010 was not included as minimal vegetation disturbance occurred during this time at WKP, so no pairs were available to survey (C. Stewart *pers. comm, 2018*). Sites explored from the 1980s and 1990s were unlikely to have required flora and fauna surveys prior to vegetation removal (S. Randall *pers. comm 2018*). Further, vegetation disturbance outside the proposed exploration area is likely to have occurred from activities such as roading (L. Torckler *pers. comm. 2018*). Two sites used in this study from the 1980s were replanted with *K. robusta* and *A. australis*. However, flora and fauna surveys, including *L. archeyi* surveys, were completed from 2010-2016, and equipment was placed within the cleared sites via helicopter to avoid additional vegetation loss. Proposed exploration sites from 2010-2016 were at least 20 m from a water course, not exceeding 150 m^2, relatively flat and free of mature trees to minimise vegetation disturbance. Four sites from this period had deliberately been replanted with *K. robusta* and *A. australis*.

1.5.2.1 Mahakirau Forest Estate

Mahakirau Forest Estate (MFE) comprises almost 600 hectares, divided into 24 privately owned properties. A stoat trapping programme was established in 2001, with rat and possum baiting implemented in 2007 and 2008. Predator control, however, is not carried out on all the privately-owned properties. MFE also has a history of disturbance, including kauri logging, and from the 1990s patches of vegetation were cleared for farming, housing-activites and roading areas. The focus for this study was on sites that had been cleared for past roading construction or during building construction (housing) activities, although no sites had been physically built on. Housing-related activities include areas used for material storage, machine parking and gardens. Roading sites were more severe in terms of disturbance, with continued use over an extended period of time in comparison to housing sites that had less vegetation clearance (still over 50%) and were used over a shorter timeframe. Roading sites were no longer used as roads during this study period and never had tarseal. The 2010-16 sites were closer to areas that were still used by people, such as a house, and one site had a pathway through it.

1.5.3 Chapter outline

The chapters are laid out as continued research chapters. This format was chosen to reduce repetition when methodology was the same.

Chapter 1 is thesis introductory chapter.

Chapter 2 addresses the impact of historical exploration, roading and housing-related activites disturbance on *L. archeyi* abundance, accounting for variation in detection probability, and investigates habitat selection in disturbed and undisturbed sites. This chapter is important in addressing how land use activity impacts the abundance of *L. archeyi* and gathers information on the species and habitat characteristics that are relevant for future monitoring and population management.

Chapter 3 focuses on the microhabitat selection of *L. archeyi* and whether microhabitat use differs from the microhabitat availability within sites at WKP and MFE. This study increases our understanding of the suitability of habitats for *L. archeyi* to establishment or maintain populations in the future.

Chapter 4 is a summary of the results and conclusions of each chapter. Finally, I discuss the implications for future management of populations within the Coromandel Peninsula and offer suggestions for future research to increase our understanding of *L. archeyi's* habitat use and ecological drivers.

Chapter 2

Abundance of *Leiopelma archeyi* in relation to disturbance caused by land-use

An individual *Leiopelma archeyi* captured during a nocturnal survey. Photo: E. Hotham

2.1 Introduction

Habitat degradation and loss from land use activities is a primary case of decline in amphibian populations worldwide (Blaustein & Wake 1995; Blaustein et al. 1994; Stuart et al. 2004). Habitat loss can negatively affect populations and this has been shown to be through changes in the conditions required for breeding and survival (Hall et al. 1997; Ash 1997). Such changes have knock on effects through trophic chains, predator-prey relationships and in the dispersal of individuals (Findlay & Houlahan 1997; Houlahan & Findlay 2003; Crawford & Semlitsch 2008). Habitat degradation and loss is largely fuelled by the needs and demands of the growing human population (McNeely et al. 1990). But biological systems have a limit and will not sustain the current rate of consumption (McNeely et al. 1990). Conservation management decisions therefore need to balance these impacts with economic objectives and sustainable resource use.

Amphibians are particularly susceptible to habitat changes because they are generally slow-moving and small-bodied, making them unlikely to disperse great distance when exposed to adverse effects (Pough et al. 1987; Ash 1997; Gibbs 1998). Their sensitivity to the microclimate also increases vulnerability, such as the risk of desiccation or inducing stress (Findlay & Houlahan 1997; Krishnamurthy 2003). An example of microclimate sensitivity is shown in salamander populations during timber harvesting, with modification to soil moisture, temperature and humidity causing detrimental effects on individuals (Petranka, Elderidge & Haley 1993). The demand for resources, such as timber, is unlikely to significantly decline in the foreseeable future. Understanding how amphibians utilise and select the resources and conditions within a given landscape is therefore important in the management of populations and in the development of conservation plans to mitigate the effect of habitat changes (Petranka, Elderidge & Haley 1993; Ash 1997; Hero & Morrison 2004; Crawford & Semlitsch 2008).

It has been acknowledged in the National Frog Recovery Plan that land use activities and habitat disturbance are possible threats and agents of decline to *Leiopelma* species in New Zealand (Bishop et al. 2013). Currently, the habitat requirements of *Leiopelma* are largely unknown. In the past, management plans have focused on mitigating for disease, but plans are in need of revision in the changing landscape.

Leiopelma archeyi, the smallest of the *Leiopelma* species, populate an area of Whareorino Forest and are scattered throughout the Coromandel Peninsula, New Zealand (Bell 1978). Their lack of vocal chorus and nocturnal emergence cause difficulty for monitoring, but their colouration is unique to each individual, allowing identification of individuals (Bell 1978; Thurley & Bell 1994). Semi-permeable skin is a contributing factor to the correlation of emergence with humidity, rainfall and wetness of vegetation (Cree 1989; Ramirez 2017). Emerged frogs have been observed climbing tree trunks, stems of shrubs over 2 m, and sitting on foliage and leaf litter (Stephenson & Stephenson 1956; Bell 1978; Cree 1989; Ramirez 2017). Average recorded nightly movements of individual *L. archeyi* ranged between 0.5 and 1.5 m in Whareorino Forest, with larger frogs moving further (Ramirez 2017). Maturity is reached after 3-4 years, with adult frogs observed reaching ages up to 37 years (Bell 1978; *B.D. Bell pers. comm.* 2018).

As a ground dwelling amphibian, *L. archeyi* could be more susceptible to changes to the resources and conditions present in the environment. *Leiopelma archeyi* are thought to be particularly vulnerable because they occupy discrete home ranges and depend on particular microclimates to reduce the chance of desiccation (Stephenson & Stephenson 1956; Bell 1978; Cree 1989; Thurley & Bell 1994; Ramirez 2017). And therefore, resources and conditions that affect temperature and moisture within areas determine the availability of habitats, such as areas with high humidity, for *L. archeyi* (Pough et al. 1987). Land use activities that remove quality habitat, for example canopy cover that then causes a reduction in moisture through reduced leaf litter, may affect the abundance and demographics of frogs. *Leiopelma archeyi* have shown sufficient resilience to survive severe habitat disturbance in the past, including kauri logging, disease and mammalian predation (Bell, Carver, Mitchell & Pledger 2004). It is unknown, however, if these past disturbances have impacted or continue to impact, current populations.

The mining industry is a major contributor to New Zealand's economy, but this often comes at a cost to the environment (Christie & Barker 2013). Exploration mining, the process before gold and silver extraction, can disturb habitats by the complete removal of vegetation and associated substrates, such as woody debris and litter, from an area over a prolonged time. Vibrations, constant light and noise pollution immitted by drills are also factors associated with exploration. As the human population expands, increased pressure is also put-upon decision makers to approve the clearance of forest to make way for roading and housing. Like exploration mining, building new roads and homes involves the disturbance of habitats by the removal of vegetation and associated substrates. It is important to measure these effects of habitat disturbance on vulnerable species, like *L. archeyi*, to understand how species react and whether they can persist during and after these land-use activities. From this information, decision makers can then be informed of the best conservation management plans to assist vulnerable species.

The historical disturbance from exploration mining, roading and housing-related activities on the Coromandel Peninsula were investigated in this study to determine the effects on current *L. archeyi* abundance. Mining activities from the 1980s, 1990s and 2010-16 are regarded as historical mining. Roading and housing-related activities from the 1990s and 2010-2016 are also regarded as historical activities. Investigation of the demographics of individuals within these age categories was also an important consideration because measures of density, reproduction and survival provide important information regarding habitat quality over time (Johnson 2007).

2.1.1 Research questions

1. What habitat characteristics (elevation, vegetation) affect *L. archeyi* abundance within survey sites?
2. Does historical disturbance from exploration mining, roading or housing-related activities affect resources and conditions within sites? Does this affect the abundance of *L. archeyi*?
3. Does the effect of historical disturbance on habitat features influence demographics within study sites?
4. What effects the detection probability of *L. archeyi* within sites?

Objectives of managing wildlife usually involve managing the environment (Sweeny and Henderson 1986). The information gathered and analysed in this research will increase our understanding on the habitat requirements of *L. archeyi*. Such information is important for translocations and future management of populations when exposed to land-use activities.

2.2 Methods

2.2.1 Sampling design

Field sampling was carried out in two forests on the Coromandel Peninsula, New Zealand, in Wharekirauponga (WKP) catchment (38°17’51.8”S, 175°49’18.2”E) and Mahakirau Forest Estate (MFE) (36°50’20.9”S, 175°31’45.9”E). Both WKP and MFE have undisturbed and disturbed areas in each (Figure 2.1). WKP has a history of mining exploration and MFE was subdivided into housing lots in the 1990s. Within WKP and MFE, pairs of 100 m² survey sites were selected. Each pair consisted of a disturbed site (D) and an adjacent undisturbed site (U) (Figure 2.1; Appendix 1a & 1b). WKP had 12 pairs of sites and MFE had 4 pairs. There were more pairs at WKP because of the number of separate and available disturbed sites and the significance of this area for both frog conservation and exploration mining (Bishop et al. 2013). These pairs were all within 315,000 m² area of the WKP catchment and surrounding ridges and encompasses an area of 110,000 m² in MFE. Data were collected between 14 November 2018 and 20 March 2019.

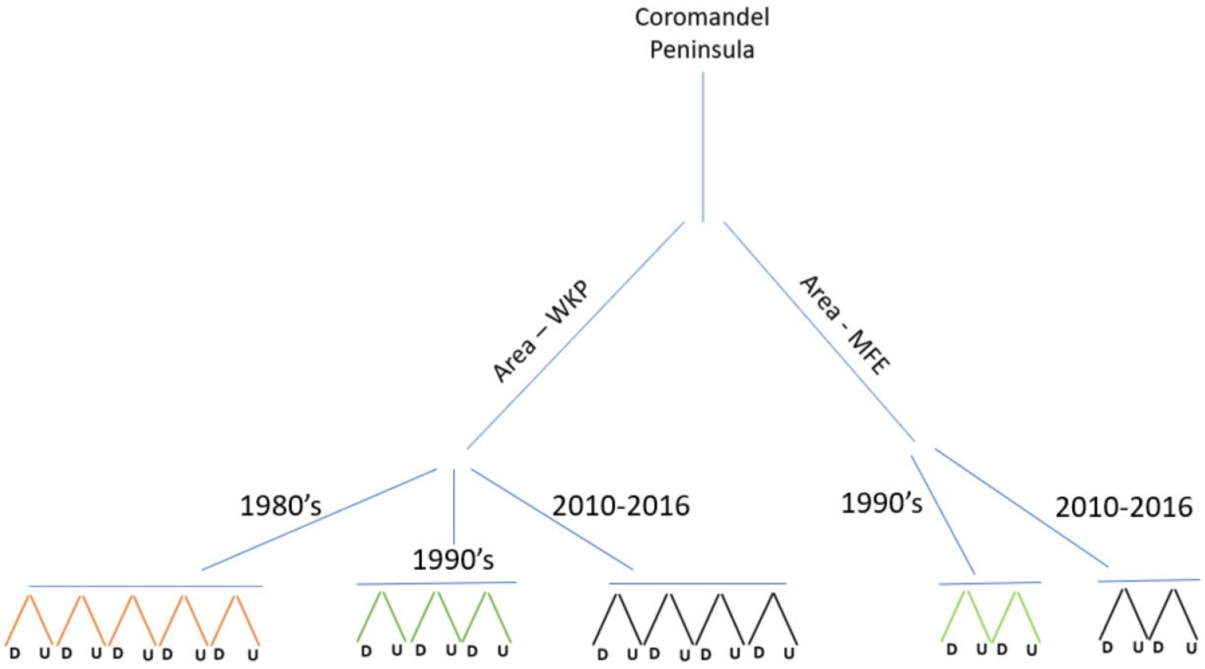

Figure 2.1 Sampling design to assess the effect of disturbance on abundance of *Leiopelma archeyi***.** The disturbed (D) and undisturbed (U) sites are within two study areas on the Coromandel Peninsula. Disturbed sites are grouped into “Years of disturbance”.

Locations of past exploration sites at WKP were obtained from OceanaGold Ltd (43 Moresby Ave, Waihi), and additional disturbed site locations at MFE were provided by Sara Smerdon, a resident with knowledge of the area. Sites were classed as disturbed if > 50% of vegetation had previously been cleared for either mining exploration (WKP) or roading and housing-related activities (MFE) at any time after 1980.

Paired sites were separated by a minimum distance of 20 m, but no more than 100 m to ensure physiography and orientation remained comparable. Disturbed sites were selected first, and then matched with an undisturbed site with respect to elevation, aspect and when relevant, distance to a body of water. No disturbed or undisturbed sites were known to contain frogs immediately prior to site selection. Undisturbed sites have had no significant vegetation clearance after 1980; however, it is very likely that even undisturbed sites have been disturbed by human activity at some stage in the remote past due to pre-1980 mining activity in WKP and farming practises in MFE.

Disturbed sites were put into categories of 'Years since disturbance' (Figure 2.1; Appendix 1 a & 1b), with these categories chosen based on their significance to *L. archeyi's* life cycle and site availability. The period between 2000 and 2010 was not included in this study as minimal vegetation disturbance occurred during this time at WKP, so no pairs were available to survey (C. Stewart *pers. comm, 2018*).

Five disturbed sites at WKP (two from the 1980s, three from 2010-16) had been replanted with *Kunzea robusta* and/or *Agathis australis* by OceanaGold Ltd (previously Newmont Mining) because of consent requirements to restore habitat after exploration activities. At MFE, disturbed sites had been left to regenerate after clearance, although a pathway through Site 14D has continued to be used by the local residents.

The size of each site was chosen to be 100 m² in reference to the mean distances travelled per night of *L. archeyi* (1.0 – 3.0 m) to ensure movement out of the site was less likely, the scale of disturbance events, and the survey effort required within a restricted time period (Thompson, White & Gowan 1998; Ramirez 2017). Most sites were squares, where possible (10 m x 10 m). Sites 14D and 14U were 8 m x 12 m due to the proximity to site 14D of ongoing human disturbance (gravel driveway). Sites were set up by marking the perimeter with flagging tape for ease of delimitation during nocturnal surveys.

2.2.2 Field methods

Frog surveys

One to two pairs of sites were surveyed each night between the hours of 20:00 and 07:00 when frogs are most active (Cree 1989; Ramirez 2018). A site from each disturbance category and the paired undisturbed site was surveyed in November, December and February. Unfavourable conditions in January limited surveys, with only one pair from the 1980s surveyed. March was also too dry to survey extensively, with one pair from the 1980s and one pair from 2010-16 surveyed.

Leiopelma archeyi were counted within sample sites over 33 nights. This sampling period spanned spring to autumn and included the end of the breeding season (November), brooding season (December), and non-mating (March) of *L. archeyi* (Bell 1978). Sites were surveyed at least 24 h after the perimeter had been flagged (excluding four sites due to time limitations) to minimise the influence of human interference on frog counts.

Surveys involved searching for emerged frogs rather than lifting rocks or logs and so had less potential for habitat destruction and disruption to animals (Scott & Woodward 1994). However, up to two dead fern fronds, if present, were lifted as my personal observations from prior experience is that fronds are favoured substrates for *L. archeyi* and are easily replaced with minimal risk of crushing unseen frogs. Surveys were only conducted on nights with temperature > 14°C and humidity > 85% to avoid nights likely to have low frog emergence (Bell 1978; Cree 1989; Ramirez 2017).

Each site was surveyed over three consecutive nights, using closed mark-recapture methods (Scott & Woodward 1994; Lettink & Armstrong 2003). Three survey nights were recommended by the Department of Conservation (DOC) Frog Recovery Group to Oceana Gold Ltd for *L. archeyi* surveys. Six survey sites had the third night of surveying two weeks after initial survey nights due to dry weather conditions. The time and abiotic conditions, including moon phase, temperature, relative humidity, cloud cover, and precipitation ('none', 'light', or 'heavy') were recorded at the start and end of each survey, consistent with previous surveys for *L. archeyi* (Scott & Woodward 1994; Babbitt, Veyser & Tanner 2010). Vegetation wetness during the surveys was recorded as 'dry', 'moist', or 'wet' because wetness of vegetation did differ at times from precipitation (Cree 1989). A *Kestrel 3000* and a *Kestrel 5000 Pocket Weather Meters* were hung 1.5 m off the ground within each site to record both temperature and humidity at the beginning and end of each survey. As defined by Cree (1989), "moist" vegetation was "only slightly wet, or wet in some patches of the site and dry in others". "Wet vegetation" was recorded when the vegetation and leaf litter were saturated throughout the site.

Surveys of each pair of sites were conducted in teams of 2-3 surveyors. The ground and vegetation up to eye level (1.5 m) were visually searched during these surveys for emerged *L. archeyi*. Over the 3 consecutive nights, the direction of walking within each site changed to also ensure the site was completely surveyed and to minimise heterogeneity in detection probability among individuals (Figure 2.2). Each site within a pair was surveyed at different times over the 3 nights; on night 1 we surveyed the disturbed site first, on night 2 we surveyed the undisturbed site first, and on night 3 a coin toss was used to determine which site was to be surveyed first. This reduced potential bias due to human error (e.g., more alert at the start of the night). Constant search effort was attempted, but the time spent in each site necessarily varied according to vegetation density and complexity, number of frogs processed, and topography.

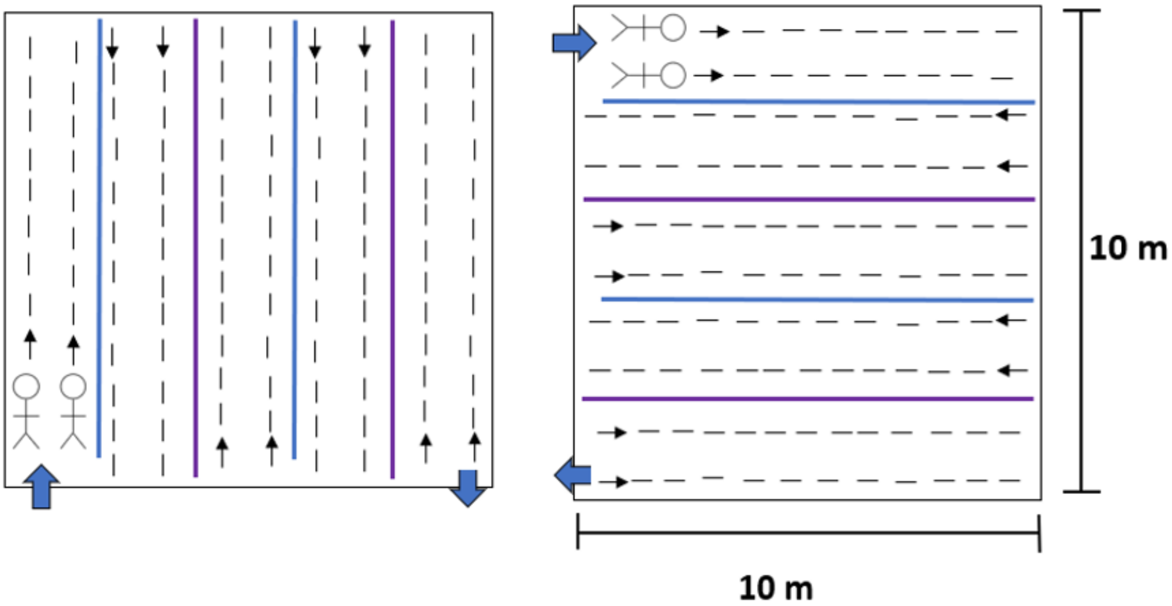

Figure 2.2 Survey design for visual encounters of individual *L. archeyi*. Each site was surveyed over three nights, with the direction of walking throughout the site changing between nights to increase the likelihood of finding a new frog. The direction of walking is indicated by arrows and broken lines. Purple and blue lines represent ropes used within the site that reduced disorientation, minimised heterogeneity in detection probability and ensured site area was completely surveyed. Ropes were removed by pulling delicately from outside the site.

Frog data collection

Each frog was photographed on the substrate it was found on e.g., on an *Astelia trinervia* leaf (Figure 2.3.A). Additionally, its location was marked using a Garmin *GPSMAP 64st* GPS. Researchers wearing powder-free nitrile gloves captured frogs individually and placed each frog into its own pre-numbered clean ziplock bag for immediate processing, with frogs assigned a number in order of capture (Figure 2.3.B & Figure 2.3.C). While the frog was in the bag, snout-to-vent length (SVL) was measured using digital callipers (Figure 2.3.D), and the frogs were weighed using a spring balance scale calibrated for the weight of the bag. Age-class classifications were grouped as the following < 18 mm SVL juveniles, 18 - < 24 mm SVL for sub-adults, and > 24 mm SVL for adults (Whitaker & Alspach 1999; Easton 2015). In order to identify individual frogs, any peculiarities were noted, and close-up photographs were taken to capture unique markings.

The substrate the frog was found on was noted and height above ground (zero was recorded for on the ground) recorded. The percent of vegetation cover within 10 cm vertically above the frogs was estimated over an area the size of the frog. Air temperature and relative humidity (RA) at each frog capture location was measured using a *Kestrel 3000* weather meter. Time of capture was recorded. The captured frog was left inside the bag and pegged off the ground to a tree until the site was surveyed for that one night. This avoided recapture or trampling of frogs (Figure 2.3.E). No frog was left inside a bag for more than 2 hours. The frogs did not appear to experience any discomfort from prolonged capture. A small marker tag and flagging tape with the number associated with each individual frog was placed in the capture location for future vegetation surveys (Figure 2.3.F).

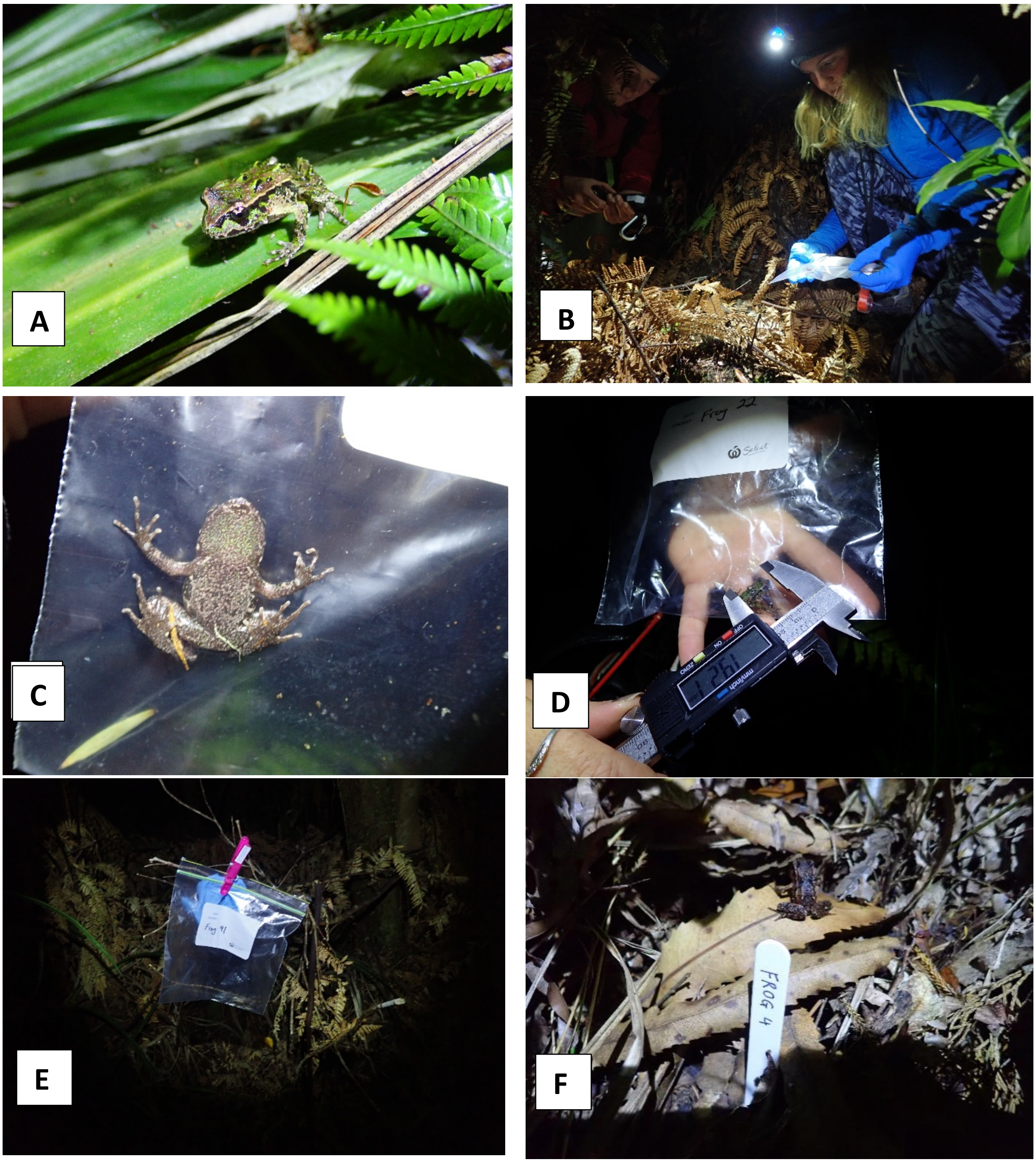

Figure 2.3 A: An emerged *L. archeyi* on an *Astelia* leaf; **B:** *L. archeyi* being captured and location of frog marked with a GPS; **C:** Ventral photograph of an individual *L. archeyi* inside a ziplock bag; **D:** Snout-to-vent (SVL) length of *L. archeyi* being measured with digital callipers to 0.1 mm; **E:** In a numbered ziplock bag an individual *L. archeyi* waits to be released after being processed; **F:** A released individual near its marker stake.

Habitat characteristics

To investigate the habitat characteristics potentially affecting *L. archeyi* abundance, reconnaissance plot vegetation descriptions (RECCEs) (Allen & McLennan 1983; Allen 1992) were compiled. RECCEs were completed from January - March 2019 after the completion of frog surveys. Vegetation surveys occurred during the day (Table 2.4). Cover was estimated for all the species or taxa in each site in six standard height tiers (>25 m, 12-25 m, 5-12 m, 2-5 m, 0.3-2 m, 0.3 m) and one epiphytic class (Allen & McLennan 1983). Cover was taken as the species' foliage shadow at solar zenith in each tier (Redpath & Rapson 2015), and assigned to one of six cover-abundance classes, ranked from 1-6 were used (<1%, 1-5%, 6-25%, 26-50%, 51-76%, 76-100%) for each tier height (Allen & McLennan 1983). Tree species were identified using the New Zealand Plant Conservation Network website (NZPCN) (NZPCN 2019) to delimit nomenclature (accessed June 2019).

RECCE descriptions were used to derive two further vegetation variables possibly relevant to frog habitat quality: the average canopy height of the dominant vegetation (estimated to the nearest metre) and the canopy cover above 1.35 m (visually estimated by the proportion of sky blocked out by vegetation; Allen & McLennan 1983). Site variables recorded included elevation, physiography (as ridge, face, gully, terrace or hillside), and drainage were also included in the site descriptions, but the latter two were not included in the analysis because majority of the sites were on hillsides with good drainage.

2.2.3 Analysis

Frog abundance estimates

Variation in *L. archeyi* abundance among sites within WKP and MFE either together or separately was estimated to establish whether variation in abundance was associated with disturbance and habitat characteristics.

In most cases, counts of individuals within each site will be less than the true number present, and the degree of underestimation will vary with weather conditions and other factors. It is therefore important to measure detection probability which can be estimated from repeated encounters of individually identifiable *L. archeyi*. Previous studies on *L. archeyi* have shown that individuals typically move between 1.5 m - 3 m throughout the night and go back to the same refuge, or in close proximity to that refuge, each night (Cree 1989; Ramirez 2017). A closed mark-recapture model was used to estimate frog abundance within sites because it was assumed over three consecutive survey nights it would be unlikely that birth, death, immigration and emigration would occur within a site.

Data were analysed using purpose-built closed mark-recapture models fitted in OpenBUGS (version 3.2.3) (Spiegelhalter, Thomas, Best & Lunn 2014) using Markov Chain Monte Carlo (MCMC) methods (Appendix 2). OpenBUGS was used because the site design was complex and fewer pairs were surveyed than anticipated, so a flexible modelling approach was required. For more on modelling mark-recapture processes in OpenBUGS refer to McCarthy (2007), Link and Barker (2010) and Kery and Schaub (2012).

Under these models, the number of newly found and recaptured frogs detected on night *j* on site *i* are assumed to be sampled from binomial distributions based on the total numbers present at the site and the capture and recapture probabilities for each night, i.e.:

> *u[i,j] ~ dbin(c[i,j],U[i,j])*
> *m[i,j] ~ dbin(p[i,j],M[i,j])*

where *u[i,j]* is the number of new frogs captured in numbered order, *m[i,j]* is the number of recaptures, *U[i,j]* is the number of frogs on the site that have not yet been captured, *M[i,j]* is the number of frogs captured to date, *p[i,j]* is the probability of a new frog being captured, and *c[i,j]* is the probability of a frog being recaptured. On the first night:

```
U[i,1] <- N[i,j]
M[i,j+1] <- 0
```

where *N[i,j]* is the number of frogs on the site. On each subsequent night they are adjusted as follows:

```
U[i,j+1] <- U[i,j]-u[i,j]
M[i,j+1] <- M[i,j]+u[i,j]
```

I expected that the capture and recapture probabilities might be affected by:

- temperature
- humidity
- the effect of capture on subsequent recapture probability, e.g., did capturing and handling affect *L. archeyi's* behaviour with this effect reducing the probability of emergence, and therefore a recapture, over the following survey nights

Capture and recapture probabilities were therefore modelled as:

```
logit(c[i,j]) <- a.p+b.T*T[i,j]+b.H*H[i,j]+re.t.p[night[i,j]]
logit(p[i,j]) <- logit(c[i,j])+b.B
```

where *a.p* is the intercept, *T* and *H* are the temperature and humidity, *b.T* and *b.H* are the effect of these variables on detection probability, *b.B* is the effect of capture on subsequent detection probability, and *re.t.p* is the nightly random effect on detection probability.

The number of frogs on each site was taken to be sampled from a Poisson distribution, i.e.:

```
N[i] ~ mu[i]
```

where mu[i] is the expected number of frogs. An unconstrained model was run first to show patterns among sites of detection and abundance probabilities without explanatory variables used to explain these patterns. This process ensured the subsequent models fit the data I used. I then wished to assess whether abundance was affected by disturbance while accounting for potential variation due to area (WKP vs MFE) and finer-scale spatial variation. I therefore modelled the expected abundance as:

```
log(mu[i]) <-a.mu+b.dist*dist[i]+b.dist90*dist90[i]+b.dist10*dist10[i]+b.area*area[i]+re.pair[pair[i]]
```

where *b.dist* is the overall effect of disturbance and accounts for sites disturbed during the 1980s, *b.dist90* and *b.dist10* allow for potential differences due to the age of the disturbance (1990 and 2010-16), *b.area* is the effect of the area (WKP vs MFE), and re.pair is a random effect accounting for residual variation among pairs.

To assess whether the numbers of frogs varied according to vegetation and other habitat characteristics within sites, expected abundance was also modelled as:

```
log(mu[i]) <- a.mu+b.pca1*pca1[i]+b.pca2*pca2[i]+b.ele*ele[i]+b.canper*std.canper[i]
        +b.domveg*domveg[i]+re.pair[pair[i]]
```

where *b.pca1* and *b.pca2* is the effect of vegetation composition (see Section on Vegetation analysis for an explanation of these parameters), *b.ele* is the effect of elevation, *b.canper* is the effect of canopy cover above 1.35 m, and *b.domveg* is the effect of the tallest dominant vegetation. The explanatory variables were standardised prior to analysis to allow for easier interpretation of effect sizes.

The model had uninformative priors (normal distributions with mean 0 and precision 0.1 for main parameters) and was run in two chains for 41000 samples, with the first 500 samples discarded as burn-in.

Habitat characteristics

Temperatures and other characteristics of the environment were averaged over the survey period.

Vegetation composition at sites was characterised using ordination techniques and coefficient of determination, to assess how vegetation was affected by disturbance and whether this was a useful predictor of frog abundance.

For each species the maximum cover category over all tiers was linearised in respect to the midpoint of each cover class by square-root transformation. Sample sites were arranged along a gradient of similarity with respect to vegetation composition using Principal Components Analysis (PCA) in CANOCO, Version 4.55 (Ter Braak & Smilauer 2002), and a plot produced of the location of each species in the top two dimensions of ordination space was produced. Site locations in ordination space were summarised by plotting mean and standard deviations of each site for both areas and for the different disturbance histories in each area.

L. archeyi abundance and habitat interactions

The pattern of the vegetation composition was further explored by categorising the species and taxa into functional groups such as might affect the behaviour of frogs, whose phytotaxonomic skills are unknown (Appendix 4).

To determine if the separate categories differed in the sites and habitat suitability for frogs, plants were sorted into functional groups based on the characteristics according to the species' NZPCN description (NZPCN 2019). The functional groups included:

- *Tree ferns* - fern species with "trunks" that bear a large crown of fronds.

- *Ground ferns* and *climbing ferns* - grouped together because these species occupy similar habitats and can often be both or either ground dwelling or climbers.

- *Nest* – rosette-forming species, including *Blechnum discolor* and *B. fluviatile*.

- *Low growing monocot* - Low growing species that are loose tussock forming, with upright to strongly curved and distinctly dropping leaves.

- *Monocot tuft* included species such as *Astelia solandri* and *Gahnia setifolia* that had the leaf's furrow open upwards and leaves rather stiffly erect.

- Sedges and grasses were grouped together into *monocot low growing* due to their lax morphology.
- *Schoenus tendo* is classed as a 'sedge' by NZPCN description, but was placed separately into *Restiad* due to the circular, narrow culms forming densely interwoven tangles that were unlike

other species in the sedge structural class

- Epiphytic species were split into four functional groups; *Epiphyte* - species which grew on other plants; *Climbers* - which included the woody vines (*Metrosideros* spp.); *Epiphyte vines* – non-woody stems that climb the trunks of trees; and *Epiphyte nest*- leaf open upwards forming a water-holding container in the centre of the plant.

- *Moss* and *lichens* were grouped together due to their small stature growing close to the ground, and often forming dense cushions or mats.

- Shrubs were split into two functional groups: *Shrub* and *Dry shrub*. *Shrub* was used for a woody plant which is smaller than a tree and has several main stems arising at or near the ground, with *Dry shrub* containing species which have small leaves (< 30 mm)

- *Small tree < 12 m* incorporated tree species which rarely grew over 12 m.

- *Tree* was used for woody species which commonly grew over 12 m.

- *Palm-like* incorporated palm species (*Rhopalostylis sapida*).

- *Herbs/ Low growing* included small herbs and low growing species.

For this analysis, the average maximum cover values for all species within each functional group was used. Analysis of the functional group data was otherwise the same as for the species' cover data. In addition, the difference between the disturbed and undisturbed sites in 2-dimensional ordination space the ordination axes was scaled by the percent of variance explained by each axis, sing the equation:

$\sqrt{(\text{disturbed site on axis 1} - \text{undisturbed site axis 1})^2 * \% \text{ variance on axis 1} + (\text{disturbed site on axis 2} - \text{undisturbed site axis 2})^2 * \% \text{ variance on axis 2}}$

The scaled distances were then graphed against the difference in frog abundance between disturbed and undisturbed sites to correlate with the frog abundance estimates, as these vegetational differences were not included in the modelling.

2.3 Results

2.3.1 Frog captures

A total of 176 individual *L. archeyi* were found from November 2018 to March 2019. Twenty-six of the 176 frogs were found at Mahakirau Forest Estate (MFE). *Leiopelma archeyi* were found within both disturbed and undisturbed sites and ranged in frequency of capture over the age categories (Table 2.1). There were 29 *L. archeyi* recaptures. In addition, 28 *L. archeyi* were found outside the sampling sites and were excluded from analysis.

Table 2.1: *Leiopelma archeyi* capture totals in disturbed and undisturbed sites and average number per site within each disturbance category. Wharekirauponga (WKP) had a total of 12 disturbed sites and 12 undisturbed sites. Mahakirau Forest Estate (MFE) had four disturbed sites and four undisturbed sites.

Area	**Wharekirauponga (WKP)**		**Mahakirau Forest Estate (MFE)**	
	Disturbed sites	Undisturbed sites	Disturbed sites	Undisturbed sites
Total frogs found	66	84	18	8
Number of frogs found per site	5.5	7	4.5	2
Number of frogs found per 1980s site	4.6	3.4	N/A	N/A
Number of frogs found per 1990s site	7.6	6.3	2	0
Number of frogs found per 2010-2016 site	5	4.5	8.5	4

2.3.2 *L. archeyi* abundance estimates

Disturbed sites on average at both WKP and MFE had higher estimates of *L. archeyi* abundance overall (Figure 2.4). Disturbed sites from the 1980s was estimated to have a higher abundance of *L. archeyi* than paired undisturbed sites. Disturbed sites from 2010-2016 had lower estimates of *L. archeyi* abundance than in their paired undisturbed sites at WKP. MFE had higher abundance estimates in disturbed sites. Estimated *L. archeyi* abundance ranged from 0 to 25 frogs over the 32 sites as expected. This range was not entirely caused by disruption from disturbance activities as sites varied in other habitat characteristics unrelated to disturbance. The error bars for each pair of sites did however have large ranges and overlap (Figure 2.4). WKP and MFE also differed in abundance estimates, although this is likely caused by lack of sites at MFE instead of the disturbance types (Figure 2.4, Table 2.2).

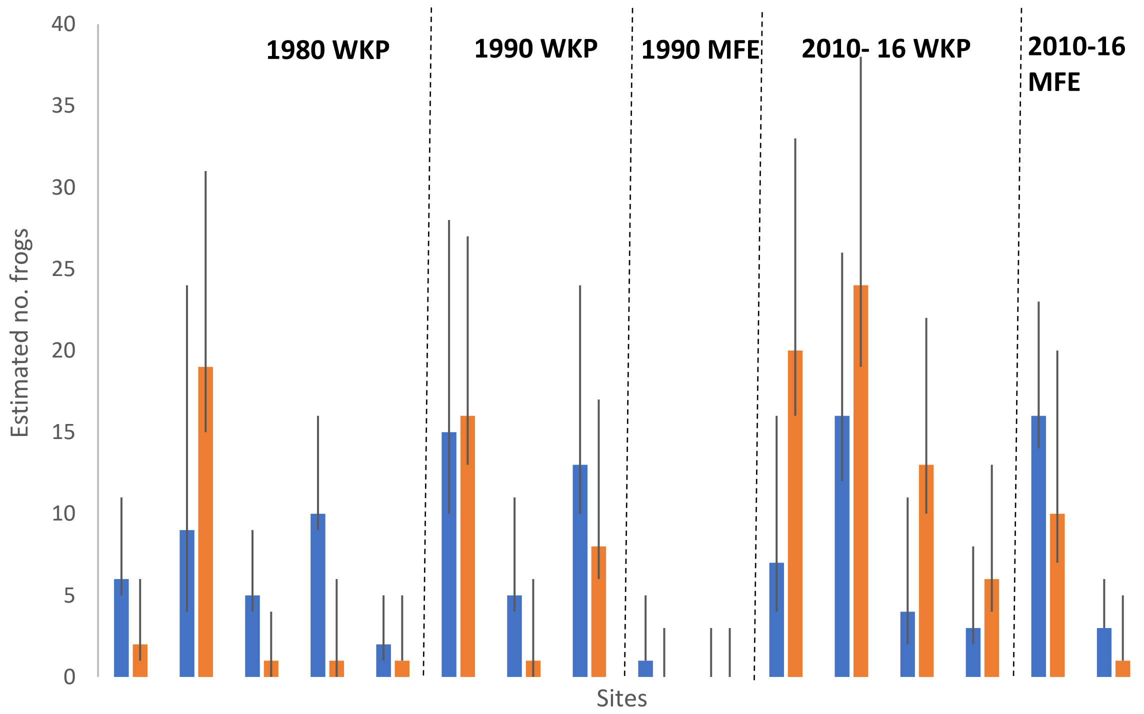

Figure 2.4 Estimated and 95% credible intervals for frog abundance within sites at WKP and MFE when modelled in relation to the effects of area (WKP vs. MFE) and disturbance. Estimates for disturbed (blue bars) and undisturbed sites (orange bars), with errors bars showing 95% credible limits. Very similar estimates are obtained when abundance is modelled in relation to vegetation and habitat characteristics.

Based on abundance parameters shown in Table 2.2, on average there is estimated to be 6.5 frogs within undisturbed sites in WKP, 7.9 at sites disturbed in the 1980s, 8.1 for sites disturbed in the 1990s, and 4.6 for sites disturbed in the 2010s. However, these differences are not significant, as the 95% credible intervals for the relevant effects (*b.dist, b.90, b.10*) all overlap zero.

Frog abundance at MFE was estimated to be 37% as high at WKP (based on parameter *b.area*). However, this is not a significant difference between the 95% credible interval for *b.area* overlaps zero (Table 2.2).

The effect of capture (*b.B*) on individual *L. archeyi* had a negative response on detection probability with a 10% chance of recapturing a frog over the following survey nights at each site. The probability of detecting a previously undetected frog (obtained by back-transforming parameter a.p) was estimated to be 0.32 (Table 2.2). This means that on average about 32% of frogs at a site on the first night were detected and 68% by the end of the third night. Temperature and humidity did not have a significant effect on detection probability in the model, with 95% credible intervals overlapping zero (Table 2.2).

Table 2.2 Means and credible limits (CL) for the parameters used to model the effect of area and disturbance on *L. archeyi* abundance and the effect that temperature, humidity and capture has on detection within the 32 sites at WKP and MFE. A logit function was used to form linear relationships by dividing the number of frogs found by the number of frogs known to be on the site, but not sampled in any one night, with the logit then back-transformed so conditional effects can be interpreted.

Parameter	Meaning	Mean	SD	2.5% CL	Median	97.5% CL
a.mu	Intercept: log(*N*) at average undisturbed site at WKP or MFE	1.87	0.41	1.04	1.88	2.66
b.dist	Overall effect of disturbance and accounts for sites disturbed during 1980s	0.20	0.30	-0.39	0.19	0.80
b.90	Effect of disturbance during 1990s on abundance estimates	0.02	0.41	-0.78	0.02	0.82
b.10	Effect of disturbance during 2010-16 on abundance estimates	-0.55	0.37	-1.29	-0.55	0.17
b.area	Effect of the area (WKP vs MFE) on abundance estimates	-1.00	0.74	-2.55	-0.99	0.43
s.pair	Random effect accounting for residual variation among pairs	1.15	0.32	0.68	1.01	1.91
a.p	Intercept: log (*N*) for capture probability	-0.76	0.36	-1.55	-0.74	-0.10
b.B	Effect of capture on subsequent detection probability	-1.47	0.46	-2.35	-1.47	-0.52
b.H	Effect of humidity on detection probability	0.19	0.16	-0.12	0.20	0.50
b.T	Effect of temperature on detection probability	-0.05	0.14	-0.32	-0.06	0.23

2.3.3 Habitat difference

Differences in the resources and conditions present between sites and pairs were not only caused by exploration mining, roading or housing-related disturbances (Table 2.3). Abundance estimates of *L. archeyi* within sites was likely associated with these differences in the habitat.

Site elevation ranged throughout WKP and MFE, with 272 m the average elevation. The highest and lowest elevations surveyed overall was 448 m and 149 m, respectively (Table 2.3). Both these extreme ends of the range in elevation had frogs in high numbers (>7).

There was also variation in the mean temperature and humidity between pairs throughout the five months of surveying (Table 2.3). This range in abiotic conditions did not deter *L. archeyi* emergence, with frogs recorded over a range of humidity (< 85.3% - 100%) and temperatures (9.0°C – 18.5 °). Fewer frogs (<4), however, emerged when humidity was lower (<88 %) while in comparison temperature was not shown to have the same effect on emergence. Less variation was seen among disturbed and undisturbed sites within a pair, likely caused by the proximately of the sites and the consecutive surveying methodology (Table 2.3).

Drought conditions were experienced from January through to March, with pairs 14 and 15 particularly dry. There were 96 surveys (32 sites surveyed over 3 nights), with 16 surveys conducted in rain, 33 when vegetation was wet and 47 surveys when vegetation was dry.

Factors affecting the distribution and abundance of plant species within these sites include abiotic conditions, elevation, disturbance age and type and site maintenance after the disturbance (Figure 2.5). A total of 95 plant taxa were identified within sites at WKP and over the 8 sites surveyed at MFE, a total of 60 plant taxa were identified. The dominate height of plant species and the canopy cover above 1.35 m also varied between sites and pairs (Table 2.3). On average, disturbed sites had a lower height in dominant vegetation (9.7 m) than undisturbed sites (13.9 m) and a lower percent of canopy cover above 1.35 m (51.1 %) than undisturbed sites (81.2%) overall.

Table 2.3: *L. archeyi* abundance and habitat characteristics in disturbed and undisturbed sites within pairs categorised by age of disturbance at Wharekirauponga (WKP) and Mahakirau Forest Estate (MFE).

	Variables	**Disturbed Site**	**Undisturbed site**
Pair 1 - 1980	Total no. frogs	5	1
WKP	Mean SVL	27.31	23.70
	Elevation	212	211
	Mean temperature nocturnal surveys	9.2	9.0
	Mean humidity nocturnal surveys	95.7	97.6
	Canopy cover above 1.35 m (%)	40	85
	Average top height vegetation (m)	12	12
Pair 2 - 1980	Total no. frogs	4	15
WKP	Mean SVL	28.28	23.88
	Elevation	217	214
	Mean temperature nocturnal surveys	17.8	17.7
	Mean humidity nocturnal surveys	93.6	94.0
	Canopy cover above 1.35 m (%)	70	60
	Average top height vegetation (m)	10	14
Pair 3 - 1980	Total no. frogs	4	0
WKP	Mean SVL	23.51	0
	Elevation	N/A	N/A
	Mean temperature nocturnal surveys	15.7	16.2
	Mean humidity nocturnal surveys	94.9	95.2
	Canopy cover above 1.35 m (%)	25	75
	Average top height vegetation (m)	7.5	14
Pair 4 - 1980	Total no. frogs	9	0
WKP	Mean SVL	25.95	0
	Elevation	222	225
	Mean temperature nocturnal surveys	14.5	14.3
	Mean humidity nocturnal surveys	97.7	98.1
	Canopy cover above 1.35 m (%)	40	85
	Average top height vegetation (m)	8	13
Pair 5 - 1980	Total no. frogs	1	1
WKP	Mean SVL	N/A	22.2

	Elevation	200	190
	Mean temperature nocturnal surveys	16.8	16.9
	Mean humidity nocturnal surveys	90.9	90.6
	Canopy cover above 1.35 m (%)	40	50
	Average top height vegetation (m)	6	10
Pair 6 - 1990	Total no. frogs	10	13
WKP	Mean SVL	19.57	20.64
	Elevation	152	149
	Mean temperature nocturnal surveys	16.7	16.3
	Mean humidity nocturnal surveys	94	96.8
	Canopy cover above 1.35 m (%)	60	70
	Average top height vegetation (m)	8	9
Pair 7 - 1990	Total no. frogs	3	0
WKP	Mean SVL	21.33	0
	Elevation	261	N/A
	Mean temperature nocturnal surveys	15.7	15.2
	Mean humidity nocturnal surveys	87.6	90.6
	Canopy cover above 1.35 m (%)	95	95
	Average top height vegetation (m)	6	8
Pair 8 - 1990	Total no. frogs	10	6
WKP	Mean SVL	25.32	27.95
	Elevation	213	211
	Mean temperature nocturnal surveys	10	9.4
	Mean humidity nocturnal surveys	97.2	97.6
	Canopy cover above 1.35 m (%)	45	85
	Average top height vegetation (m)	14	12
Pair 9 – 2010-16	Total no. frogs	4	16
WKP	Mean SVL	26.12	25.6
	Elevation	252	244
	Mean temperature nocturnal surveys	16.5	16.2
	Mean humidity nocturnal surveys	93.2	94.5
	Canopy cover above 1.35 m (%)	50	90
	Average top height vegetation (m)	4	14
Pair 10 - 2010-16	Total no. frogs	12	18
WKP	Mean SVL	24.19	22
	Elevation	239	N/A
	Mean temperature nocturnal surveys	16.3	14.2
	Mean humidity nocturnal surveys	98.2	96.8
	Canopy cover above 1.35 m (%)	40	95
	Average top height vegetation (m)	15	17
Pair 11 - 2010-16	Total no. frogs	2	10
WKP	Mean SVL	28.55	26.43
	Elevation	259	268
	Mean temperature nocturnal surveys	16.9	16.7
	Mean humidity nocturnal surveys	96.9	96.5
	Canopy cover above 1.35 m (%)	50	80
	Average top height vegetation (m)	2	10
Pair 12 - 2010-16	Total no. frogs	2	4
WKP	Mean SVL	28.75	29.00
	Elevation	254	247
	Mean temperature nocturnal surveys	12.8	13.2
	Mean humidity nocturnal surveys	91.1	88.6
	Canopy cover above 1.35 m (%)	20	90
	Average top height vegetation (m)	11	9
Pair 13 – 2010-16	Total no. frogs	14	7

MFE	Mean SVL	26.62	22.93
	Elevation	N/A	448
	Mean temperature nocturnal surveys	15.1	15.1
	Mean humidity nocturnal surveys	98.9	98.2
	Canopy cover above 1.35 m (%)	N/A	N/A
	Average top height vegetation (m)	12	20
Pair 14 - 2010-16	Total no. frogs	3	1
MFE	Mean SVL	31.02	26.22
	Elevation	312	312
	Mean temperature nocturnal surveys	16.1	15.7
	Mean humidity nocturnal surveys	93.8	97.3
	Canopy cover above 1.35 m (%)	N/A	N/A
	Average top height vegetation (m)	18	25
Pair 15 - 1990	Total no. frogs	1	0
MFE	Mean SVL	32.68	0
	Elevation	317	303
	Mean temperature nocturnal surveys	17.3	16.5
	Mean humidity nocturnal surveys	85.3	91.8
	Canopy cover above 1.35 m (%)	60	90
	Average top height vegetation (m)	12	12
Pair 16 - 1990	Total no. frogs	0	0
MFE	Mean SVL	0	0
	Elevation	286	277
	Mean temperature nocturnal surveys	18.5	18.4
	Mean humidity nocturnal surveys	85.2	83.3
	Canopy cover above 1.35 m (%)	90	96
	Average top height vegetation (m)	13	22

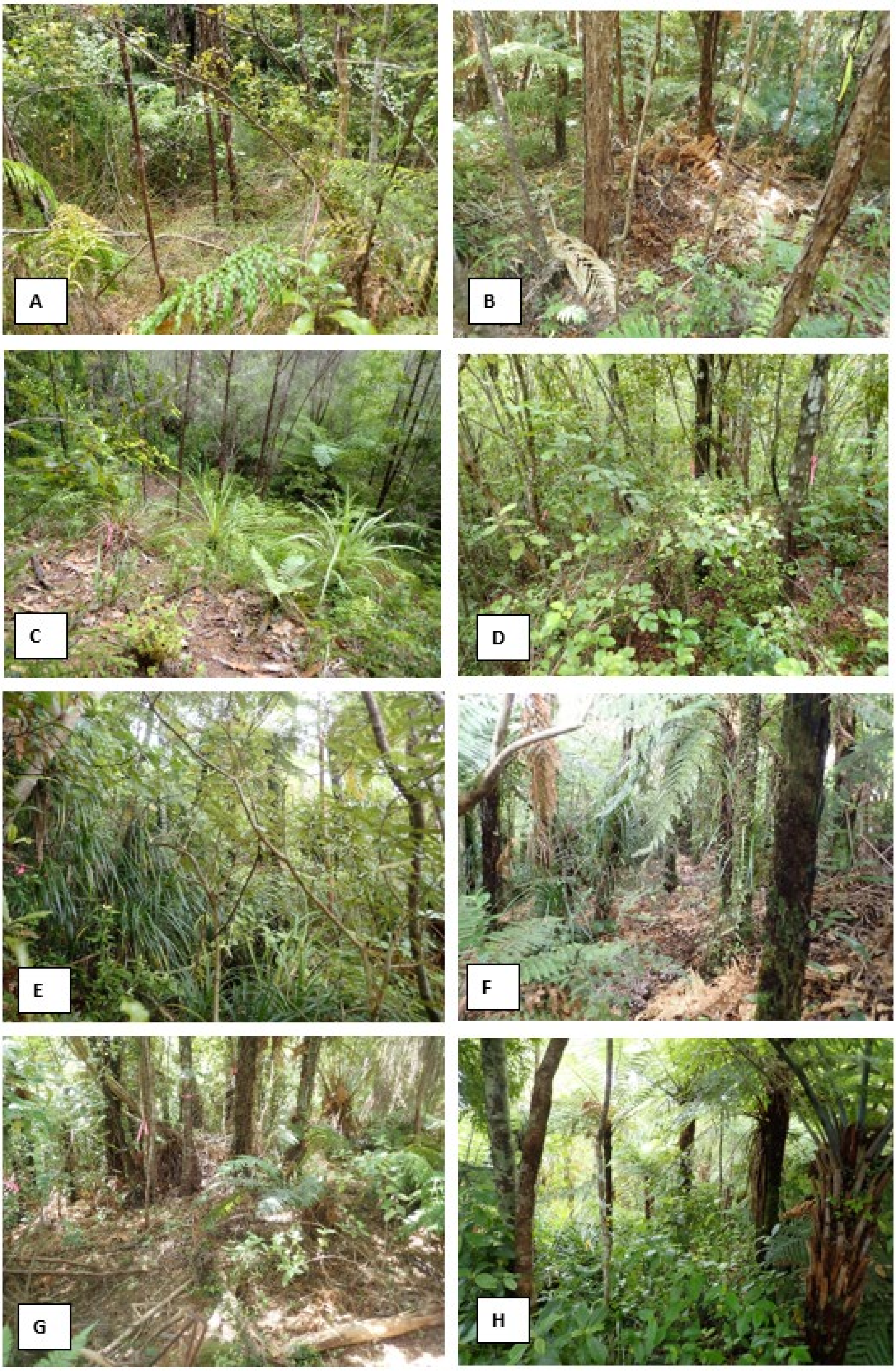

Figure 2.5 A: 1980s disturbed site at WKP; **B:** 1990s disturbed site at WKP; **C:** 2010-16 disturbed site at WKP; **D:** Undisturbed site at WKP; **E:** Undisturbed at MFE; **F:** 1990s disturbed site at MFE **G:** 1990s disturbed site at MFE; **H:** 2010-16 disturbed site at MFE.

2.3.4 Vegetation characteristics

Comparison of vegetation characteristics gave support that plant species differed in various degrees within WKP and MFE, between disturbed and undisturbed sites and time since disturbance (Figure 2.6).

In the PCA, axes 1 and 2 explain 33% and 16% of the variance in the data respectively. Axis 1 was positively associated with forest species such as *Cyathea dealbata*, mature trees species such as *Kunzea robusta*, *Weinmannia silvicola*, and *Knightia excelsa*, and negatively related to a range of species associated with early succession such as ground ferns and tufted herbs (Figure 2.6, Appendix 3). The second axis is more of a disturbance gradient, with mature forest lower down, and seral forest at the top of the axis (Figure 2.6, Appendix 3).

There is no overlap between the two areas sampled (Figure 2.6 and Appendix 3). The sites within WKP had a stronger association with tree species commonly seen in mature forests, such as *W. silvicola* and *Phyllocladus trichomanoides*, as well as *Schoenus tendo* which is associated with regenerating *Agathis australis* or *K. robusta*. Sites within MFE had a higher cover of *Beilschmiedia tawa* and *Rhopalostylis sapida*, as well as tree ferns and understory species, including *Hedycarya arborea* and *Geniostoma ligustrifolium.*

Disturbed and undisturbed sites within WKP and MFE show a small degree of separation (Figure 2.6). Undisturbed sites were all located slightly lower down on Axis 2 than the disturbed sites, so they have higher abundance of tree ferns, *Dicksonia squarrosa* and *C. dealbata*, and *Freycinetia banksii*, and lower levels of *S. tendo* and *Blechnum vulcanicum*. However, the standard deviations of disturbed and undisturbed sites overlap within both areas suggesting there is a significance difference in vegetation characteristics, but not one with a low p-value (Figure 2.6).

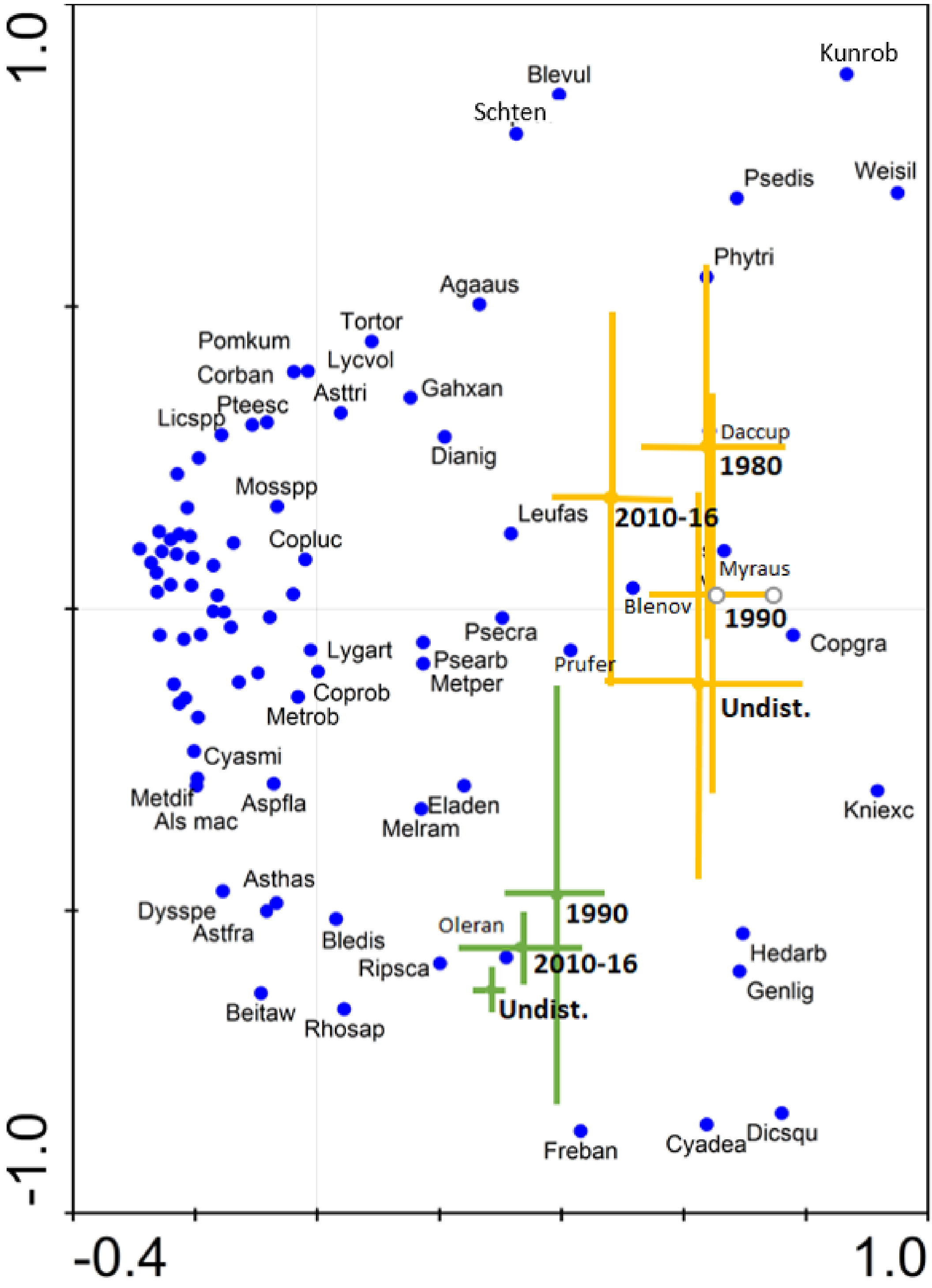

Figure 2.6 Unscaled PCA biplot of the maximum cover values from the RECCE tier data from the vegetation in each of the sampled sites. Means and standard deviations are presented for the locations in ordination space of the undisturbed sites and sites in the three disturbance periods at WKP (yellow) and MFE (green). Codes are the first 3 letters of the genus and first 3 of the species for all the named species, and as groups for other taxa – see Appendix 4 for a full list of codes. Species codes were removed for the clustered species on the mid left of the diagram due to inability to distinguish overlapping codes.

The variance explained by Axis 1 and Axis 2 for the functional group data is 38% and 26%, respectively. In comparison to Figure 2.6, the biplot shows WKP is more associated with restiads and dry shrubs, while MFE associates with epiphytes, tree ferns and nest forming species (Figure 2.7). Disturbed sites are more associated with low ground covers (mosses and lichens), while the undisturbed sites associate with abundance of trees in particular. There are differences on the disturbance categories, with sites disturbed during the 1980s at WKP more associated with restiads in comparison to the other periods, while later disturbances appear less severe or closer to undisturbed forest. However, the overlapping standard deviations indicate that these differences are not strong and the maturity of species within groups is not apparent in this figure (Figure 2.7).

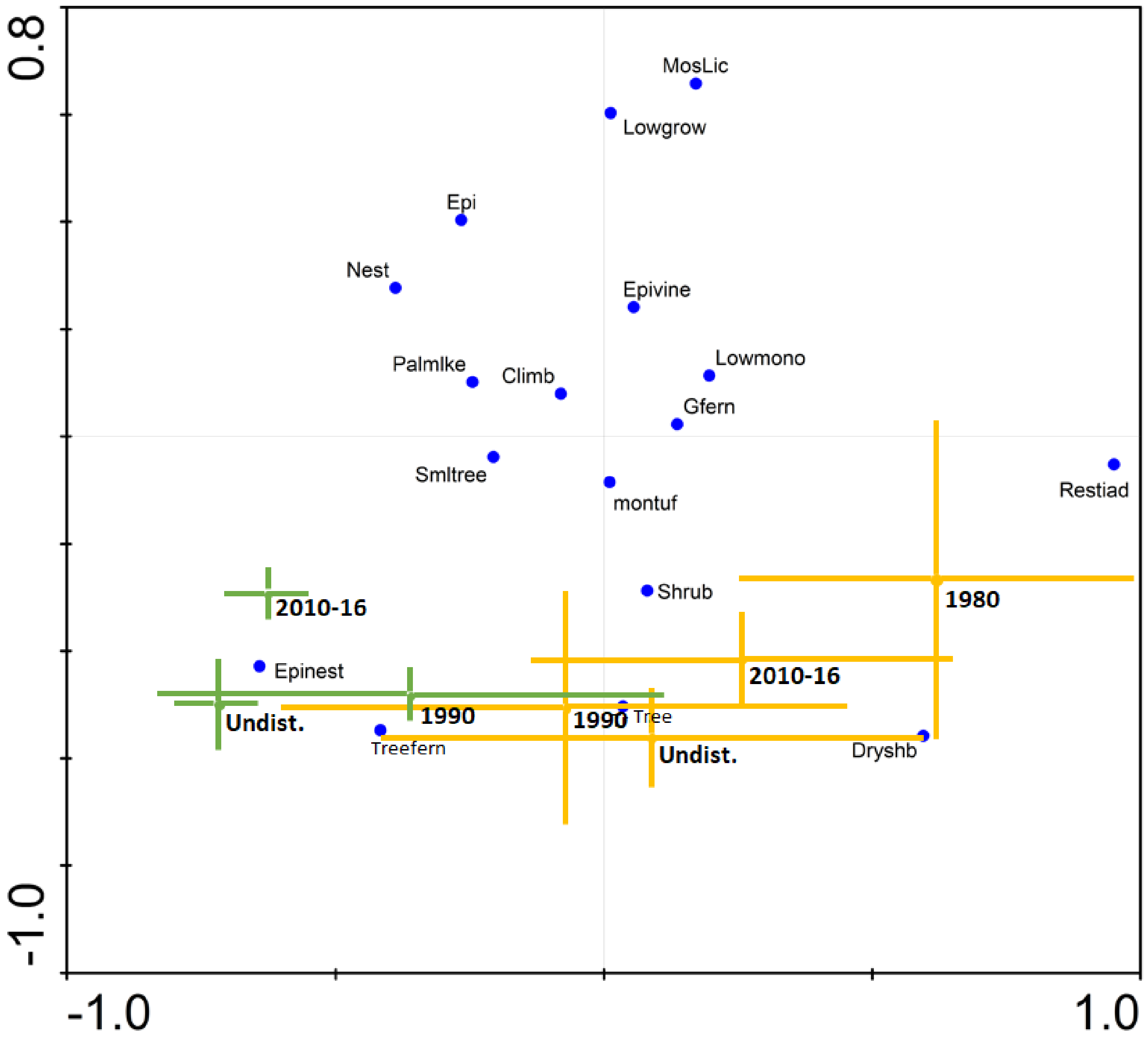

Figure 2.7 Unscaled PCA biplot of the means and standard deviations from the disturbance periods and undisturbed sites at WKP (yellow) and MFE (green) plotted with the functional groups derived from the maximum cover values from the RECCE tier data (Appendix 4).

2.3.5 Relationships between habitat and *L. archeyi* abundance

Estimated *L. archeyi* abundance within sites was positively correlated with elevation and vegetation type as summarised by PCA1 (Table 2.4).

The probability of detecting a previously undetected frog was 0.31 in the model incorporating vegetation and other habitat characteristics (Table 2.4).

Table 2.4 Means and credible limits (CL) for the parameters used to model the effect of vegetation and habitat characteristics on frog abundance within 32 sites at WKP and MFE. A logit function was used to form linear relationships by dividing the number of frogs found by the number of frogs not found which have then been back-transformed so conditional effects can be interpreted.

Parameters	Meaning	Mean	SD	2.5% CL	Median	97.5% CL
a.mu	Intercept: log(*N*) at average undisturbed site at	1.42	0.31	0.80	1.42	2.02
b.pca1	Effect of pca1 on abundance	1.25	0.40	0.50	1.23	2.11
b.pca2	Effect of pca2 on abundance	-0.17	0.15	-0.48	-0.17	0.12
b.ele	Effect of elevation on abundance	0.70	0.36	0.03	0.69	1.44
b.canper	Effect of canopy cover above 1.35 m on abundance estimates	-0.31	0.29	-0.91	-0.30	0.25
b.domveg	Effect of dominate vegetation on abundance	-0.13	0.29	-0.72	-0.13	0.42
s.pair	Random effect accounting for residual variation among pairs	1.13	0.27	0.71	1.01	1.76
a.p	Intercept: log (*N*) for capture	-0.75	0.37	-1.55	-0.73	-0.11

Scaling the distances between the pairs of disturbed and undisturbed sites by the axis eigenvalues and plotting these against the differences in frog abundance between the sites showed the regression line to be non-significant (Figure 2.8).

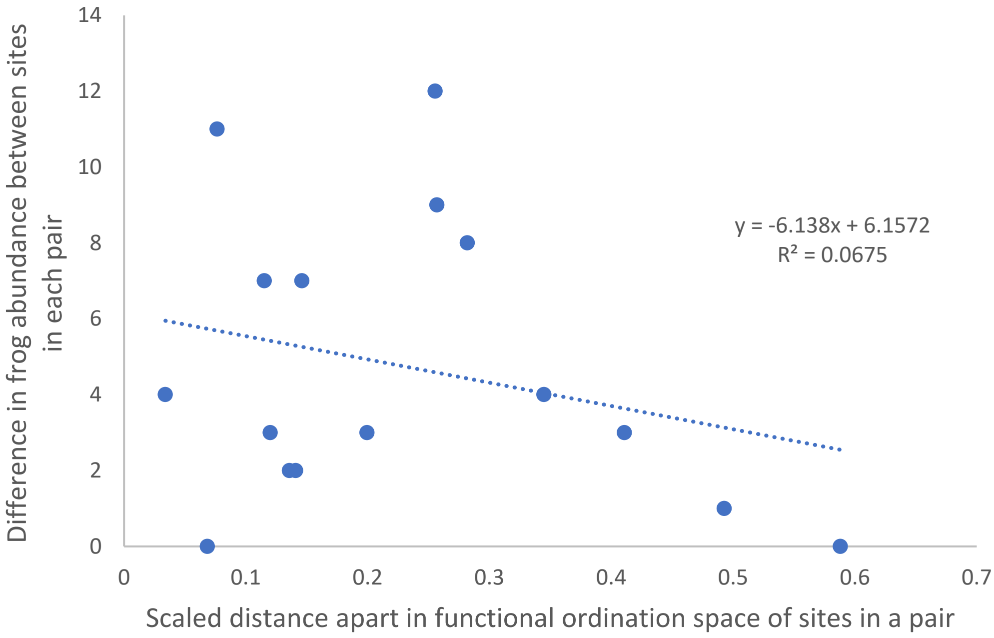

Figure 2.8 The difference in frog abundance between a pair of disturbed and undisturbed sites plotted against the difference between the pair in their scaled functional types in PCA space.

2.3.6 *L. archeyi* demographics

It was hypothesised that trends would be observed in the age structure of *L. archeyi* within disturbance categories. These expectations were somewhat matched with observed data (Figure 2.9). As predicted, *L. archeyi* in disturbed sites from the 1980s and 2010-2016 at WKP ranged in age class, with greater abundance of adult frogs found (Figure 2.9). Disturbed sites from the 1990s and undisturbed sites ranged more evenly over the age classes, excluding undisturbed sites from 2010-2016 that had a higher density of sub-adult and adult frogs (Figure 2.9).

At MFE, there was also a higher number of adult *L archeyi* in 2010-16 disturbed sites (Figure 2.9). Undisturbed sites from 2010-16 showed more of a range in age class.

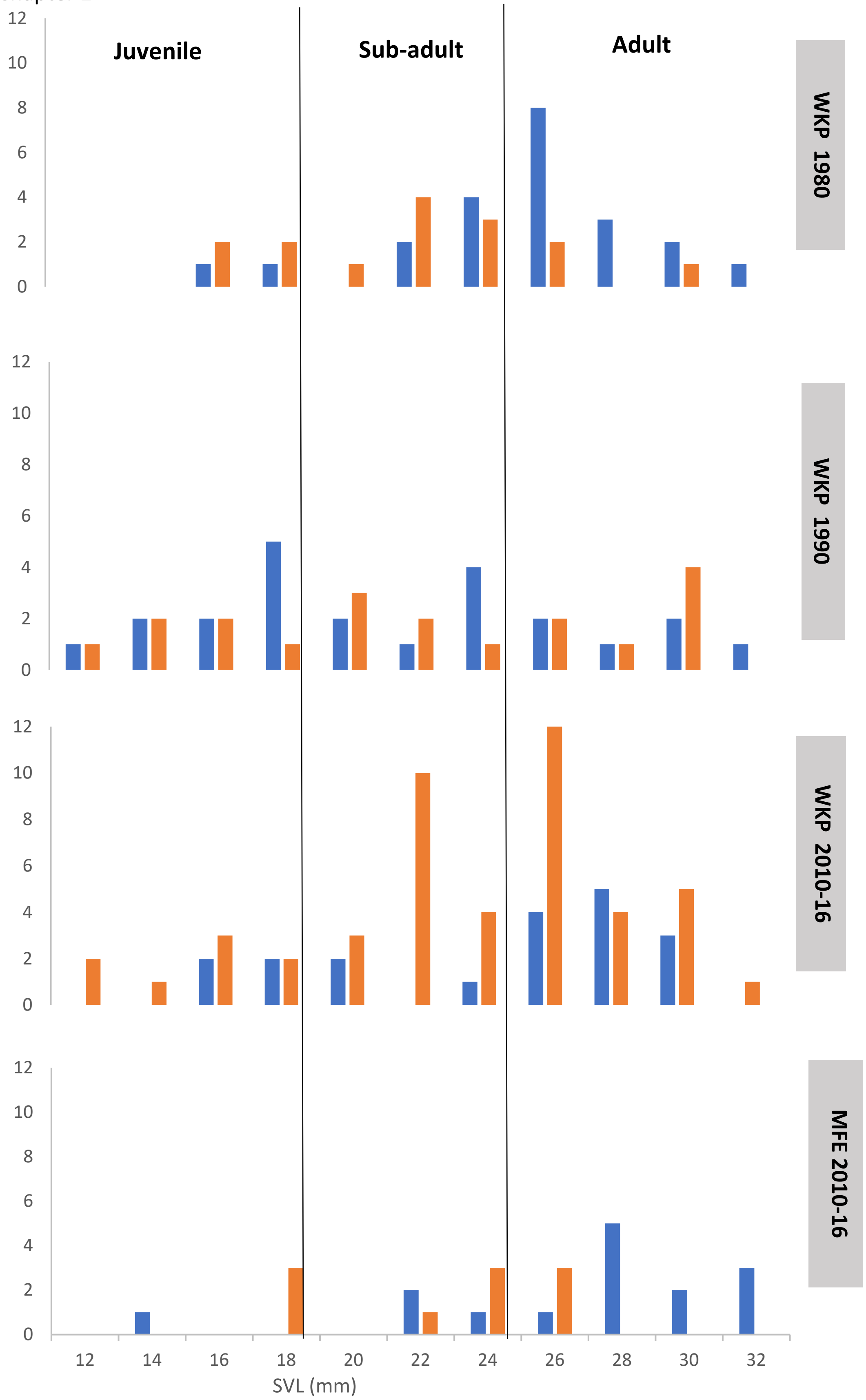

Figure 2.9 Number of *L. archeyi* found at WKP (top) and MFE (bottom) within each age class (Juvenile snout-vent-length (SVL) < 18.0 mm; Sub-adult SVL > 18.01 – < 24.0 mm; Adult SVL > 24.01 mm) in sites disturbed during 1990, 1980 and 2010-2016 (blue) and in the paired undisturbed sites (orange). WKP Number of sites 1980 = 5; Number of sites 1990 = 3; Number of sites 2010-16 = 4. MFE Number of sites 2010-16 = 2.

2.4 Discussion

2.4.1 Habitat features promoting *Leiopelma archeyi* abundance

Habitat features correlated with *L. archeyi* abundance include higher elevation and vegetation composition, including forest species and mature tree species. Both features likely determine habitat selection of *L. archeyi* at the home range scale (*second-order selection* in Johnson's 1980 hierarchy).

Increased *L. archeyi* abundance at higher elevation can be attributed to increased rainfall and humidity and a reduction in predator numbers (Duellman & Trueb 1994; Chappell 2013). Terrestrial amphibians require habitat with high levels of moisture for respiratory and osmoregulatory functions, and this is thought to often limit their habitat to higher elevations with adequate humidity and rainfall (Duellman & Trueb 1994; Spotila et al. 1992; Hillyard 1999). Elevation greater than 450 m has previously been associated with a higher abundance of *L. archeyi* than elevations below this level at other surveys sites on the Coromandel and in Whareorino forest (Bell 1978; Cree 1989; Thurley 1996). Contrary to these previous findings, elevations at WKP and MFE did not exceed 450 m, yet *L. archeyi* were still present in high numbers. This indicates that individuals are found at lower elevations but favoured higher elevations within these areas likely due to preferred climatic conditions.

Particular plant species were also habitat features associated with higher *L. archeyi* abundance thought to be through their contribution to the leaf litter and habitat use for *L. archeyi* during emergence. Tree species connected to higher abundance of frogs, such as *Knightia excelsa*, have leaves larger than the body size of a juvenile frog (> 18 mm), allowing shelter or emergence positions to individuals. The leaves also have relatively slow decomposition, causing build-up on the forest floor and trapping moisture between layers that individuals use to prevent desiccation (*Chapter 3*). Forest species include tree ferns, such as *Cyathea dealbata*, that also contribute to the leaf litter and therefore increased moisture rates on the forest floor. Tree ferns were also recognised as valuable habitat features during emergence as *L. archeyi* were frequently observed climbing or in the crowns of the plants. The crown of tree ferns offer shelter from fallen litter, moisture and rehydration. Trunks of tree ferns are probably easier to climb than those of trees, with frond stumps observed as perching spots and aiding in climbing by acting as grip points. The prominence of these plant species is consistent with previous studies reporting on the association between *L. archeyi* abundance and vegetation types in the Coromandel and Whareorino areas (Cree 1989; Thurley 1996; Ramirez 2017).

2.4.2 Disturbed sites vs. Undisturbed sites

The pattern shown in the vegetation characteristics indicated tentative differences between disturbed and undisturbed sites, although *L. archeyi* were present in both site types. Undisturbed sites had a greater association with forest species overall, including *Dicksonia squarrosa*, *C. dealbata* and *Freycinetia banksii*. In comparison, disturbed sites had a stronger relationship with mature tree species, including *Kunzea robusta*, *Agathis australis* and *Phyllocladus trichomanoides.* In disturbed sites these species were expected as *K. robusta* is a recolonising species after disturbance, *P. trichomanoides* is also common in secondary growth and grows in association with *A. australis*, and *A. australis* has been replanted in five sites following exploration. *Kunzea robusta* and *P. trichomanoides* do not only occur after human-induced disturbance, but also after natural disturbances such as tree falls (Brockerhoff, Ecroyd, Leckie & Kimberley 2003). Exploration mining, roading and housing-related activities therefore provided favourable conditions for these species to regenerate. As mentioned above, forest species and plants typically associated with mature forest are associated with *L. archeyi* abundance through their role in the ecosystem. Therefore, the fact that these species are found to some extent at both disturbed and undisturbed sites suggests that there is appropriate habitat used by *L. archeyi* at both types of sites.

Climatic conditions recorded in the field during surveys did not differ between the disturbed and undisturbed sites within each pair, so these data were not analysed further. The differences are likely due to the close proximity of the sites, the size of the sites, and the nocturnal timing of the measurements. Both temperature and humidity, however, are likely to be much more variable between pairs during the heat of the day (Hardwick et al. 2015), especially given that the disturbed sites had consistently lower canopy heights (by 4.1 m) and canopy covers (by 30%) than the undisturbed sites. These sites are likely to have drier soils that reduce the vegetation species able to revegetate sites and could affect the daily movements and refuge selection of *L. archeyi.* It is important to consider the possibility that disturbed sites in general could be drier, as this could affect *L. archeyi* behaviour in their response to the risk of dehydration. If different resources, such as logs or tufted plants, are selected by *L.* archeyi to mitigate for a drier habitat, management plans need to account for this. Further investigation is required on the day-time behaviour of *L. archeyi* before conclusions can be made.

2.4.3 The effect historical disturbance during the 1980s, 1990s and 2010-16 has on current habitat characteristics and frog abundance

There was some tendency for *L. archeyi* abundance to be lower at the most recently disturbed (2010-16) sites but this difference was not significant.

Exploration mining requires the removal of all the vegetation within an area of 10 x 10 m^2 for a drill rig. After the removal of the drill rig, sites at WKP were either left to revegetate or were partially replanted with *K. robusta* and *A. australis.* All three age categories slightly differed in vegetation composition. This is not uncommon because the succession or rate of recovery following disturbance depends on the nature of the disturbance, the severity, and the impact of the prevailing environment (Sarmiento, Llambi, Escalona & Marquez, 2003; Brown, Mark, Kershaw & Dickinson, 2006; Warren & Buttner 2008). Between the decades, exploration mining techniques likely evolved, and the level of disturbance is expected to have been different between the 1980s, 1990s and 2010-16. Further, time since disturbance was predicted to influence abundance because succession is a process that requires time and it has been shown that *L. archeyi* is associated with mature forest. Fewer frogs were therefore estimated to be in 2010-16 sites.

Several possible explanations exist for the lower abundance estimates of frogs in 2010-16 disturbed sites at WKP. First, and most importantly, this tentative difference at WKP is due to chance. Climatic conditions during surveys, such as precipitation, influenced emergence, observer error effected percent of frogs found, and unknown variables are among such explanations.

Secondly, there has been no research, to date, examining the effect of drill rigs on the behaviour of *Leiopelma*. It is unlikely noise from exploration activities affect the frogs as they do not have external ear drums (Stephenson 1951). However, vibrations and the constant light emitted from rigs could act as a deterrent to frogs in a certain radius and have lasting effects within the two years post drilling. A follow-up research project from this study would be an opportunity to explore this hypothesis.

Following on, a third feasible explanation is the replantation of sites with *K. robusta* and *A. australis* did not promote occupancy in the short term. Both plant species have relatively small leaves (< 35 mm) and *A. australis* litter has extremely slow decomposition rates impacting on moisture levels in the litter (Enright & Ogdon 1987; Wyse, Wilmshurst, Burns & Perry 2018). The presence of leaf litter has been shown in other terrestrial amphibian studies as an important habitat feature. For example, terrestrial Plethodontid salamanders recolonized sites after 4-6 years post disturbance once litter has reformed and based linear regressions it was estimated that after 20-24 years salamander numbers in these sites will equal or exceed numbers on forested plots (Ash 1997). If litter dryness affects abundance, then the reformation of a moist litter layer could be dictating the time-frame of *L. archeyi* re-establishment in this study (Ash 1997). *Schoenus tendo*, a reed species favoured by frogs when present in sites was not in great abundance in comparison to 1980s replanted sites, causing a further reduction in habitat quality. *Leiopelma archeyi* were also observed in the least disturbed areas in the replanted sites where leaf litter was deeper and low growing tufted plants were present, increasing moisture levels and available refuge sites for frogs. Sites disturbed in the 1990s had a greater abundance of forest species, while in comparison sites from the 1980s had a greater abundance of plant species associated with mature forest. These results indicate frogs utilise different resources for survival and reproduction and abiotic and biotic conditions possibly become suitable in disturbed sites, only after a minimum period of a decade. Allowing sites to naturally regenerate after disturbance could therefore have a greater benefit for *L. archeyi* abundance.

It is difficult to make the same conclusions regarding *L. archeyi* abundance in sites at MFE due to the small sample size and the environmental conditions during nocturnal surveys. Sites disturbed by roading during the 1990s at MFE were surveyed in drier conditions. The humidity was above 80% for all surveys, but the leaf litter was drier during the MFE surveys due to a period of drought. Through modelling, I accounted for the effect that such differences in temperature and humidity might have on detection probability. Roading disturbance had a prolonged and more destructive effect on sites than housing-related activities due to the continued use of the site over an extended period and the volume of vegetation removal required in these sites. Plant species typically associated with mature forest, such as *Elaeocarpus dentatus*, were associated with 1990s disturbed sites, as expected, due to the longer regeneration period and the drier environment at lower elevations. Forest species, including *C. dealbata* and *F. banksii*, were mostly found in 2010-16 disturbed sites. These species were reflective of the environment where higher elevations at MFE had increased humidity from the low cloud cover. Favourable habitat features, such as higher humidity and mature plants, at increased elevations likely has a greater influence on *L. archeyi* abundance at MFE than the effect of historical disturbance.

To conclude, although there was no statistical significance difference in abundance between the time periods, there were obvious differences in individual sites that contributed to higher abundance and indicated habitat preference of *L. archeyi*. How a site was managed during and after disturbance has shown to have a key role in abundance estimates in the future.

2.4.4 Historical disturbance effects on *L. archeyi* demographics

Understanding effects of habitat disturbance on population demographics may lead to better predictions about the effects of land use activities on individuals. The behaviour and habitat use of *L. archeyi* in disturbed and undisturbed areas is not well understood. Therefore, movement and dispersal patterns are also largely unknown. Graphing the SVL data shows a difference in demographics between disturbed and undisturbed sites. The similarities in vegetation between 1990s sites and undisturbed sites, and 1980 and 2010-16 disturbed sites at WKP, could explain differences in demographic structure among these sites. In a study on plethodontid salamanders, recently-disturbed sites usually contained adults, indicating juveniles and sub-adults did not have the ability to withstand the marginal moisture conditions in the thin and dry leaf litter within disturbed sites (Ash 1997). *Leiopelma archeyi* juveniles have also been associated with deep leaf litter and microhabitats that provided cover (Ramirez 2017). As mentioned above, the replanting of *K. robusta* and *A. australis* in 1980s and 2010-16 disturbed sites at WKP is likely to have impacted leaf litter moisture and the regeneration of ground-dwelling plant species. This likely has led to habitat of low quality for juvenile frogs. Sites at MFE and undisturbed sites, 1990s disturbed sites and unplanted 1980s sites at WKP had a greater abundance of plant species that produced deeper leaf litter and vegetation that provided ground cover for individuals. The 2010-16 disturbed sites that were not replanted had a wider range of age classes, suggesting the ability of *L. archeyi* to survive this type of disturbance is reasonably high at both WKP and MFE if resources and conditions are adequate.

2.4.5 Disturbance activities

Exploration mining at WKP and roading and housing-related activities at MFE did not result in significantly lower abundance estimates of *L. archeyi*. It is difficult to compare the effects from exploration mining, roading or housing disturbance on *L. archeyi* abundance because there were fewer sites surveyed at MFE, leading to low statistical power in the abundance model. The low sample sizes can easily result in spurious conclusions that do not adequately reflect *L. archeyi* habitat use or the quality of habitat within an area (Anderson et al. 2001). In addition, because of this low sample size at MFE, an interaction term to assess any differences in effects of disturbance between the areas was not appropriate. Unconstrained estimates also did not give any indication that the two disturbance types reflected a different pattern. Future research on different disturbance types will add weight to the possible effects on the habitat use of *L. archeyi*.

This study does not conclude exploration mining, roading or housing-related activities have no effect on *L. archeyi*. This research is based on the impact of historical disturbance on the present-day abundance of frogs and it can be speculated that immediate effects from land-use activities will negatively affect frogs.

Between the 1980s and 2016, the nature of the exploration process changed as regulations tightened. Exploration mining during the 1980s and 1990s was less focused on avoiding ecological impacts than at present, with sites chosen based on ease of access and mineral position. Qualified ecologists were not present during clearance and vegetation was not checked for species such as amphibians or geckos. During site clearance it is very likely that detrimental effects, including tramping, occurred within the exploration footprint. In comparison, tighter protocols within access agreements were in place during 2010-16, with sites chosen in respect to physiography, density of mature forest and potential frog refugia (Newmont 2012). Qualified ecologists surveyed sites before vegetation clearance and were present during the removal of trees. Despite these conditions decreasing the likelihood of adverse effects on *L. archeyi,* the removal of vegetation and quality habitat will not favour *L. archeyi* abundance in the interim. Further, cleared vegetation was placed in other areas of the forest, causing secondary habitat disturbance that possibly affected frogs in these areas by damaging refugia and crushing individuals.

A similar pattern of vegetation removal is thought to have occurred at MFE. Vegetation clearance operations during the 1990s had less regard to ecological impacts, while 2010-16 clearance was overseen by a local resident with ecological experience and an interest in *L. archeyi*. In the literature, the effects of land-use activities in forests may cause physiological stress from landscape fragmentation, influence host-parasite interactions and the persistence of regional metapopulations (Gibbs 1998; McKenzie 2007; Janin, Lena & Joly 2011). The small-scale (10 m x 10 m^2) of vegetation clearance is likely not large enough to have caused many of the effects seen in large scale fragmentation studies. However, it is important to note that *L. archeyi* populations are presumed to be prone to wide-scale fragmentation owing to the spatial and temporal dynamic nature of amphibians (Gibbs 1998).

Over a decade after disturbance, *L. archeyi* abundance in sites reflected abundances in undisturbed sites presumably due to the limited size of the disturbance. The resulting open canopy and lack of understory following disturbance, whether natural or human-induced, will not promote abundance for a species that are at risk of desiccation. As noted in populations of *Mixophyes iteratus,* the initial period after disturbance before forest regeneration could not be tolerated by the amphibians due to the lack of wetter forest (Lemckert 1998). Once regeneration commenced and depth litter increased, *M. iteratus* returned to the area (Lemckert 1998). A similar relationship between *L. archeyi* and forest generation is likely to occur and results from *Chapter 3* indicate that alternation of the vegetation composition may not be a problem as individuals utilised various substrates during emergence. Additionally, the scale of disturbed sites is thought to resemble natural tree fall in forests.

2.2.6 Detection probability

Amphibians can be particularly difficult to survey as they are often cryptic and require certain abiotic conditions for emergence (Blaustein 1994). It is therefore assumed that during a survey not all individuals within the area will be found. In this study, the probability of detecting a previously undetected frog was estimated to be 32% for a one-night search. Consequently, over three nights of surveying, it was estimated that 68% of *L. archeyi* in a site would be detected. Detection probabilities are expected to increase if surveys are more intensive i.e., diurnal and nocturnal. During subsequent surveys, the detection of *L. archeyi* was also influenced by previous capture as indicated by the 10% recapture probability estimate.

The degree of stress experienced by the frogs is difficult to determine, but it can be assumed handling and bagging individuals causes some level of distress. There are likely additional factors not considered in this study that influence emergence of *L. archeyi*, such as predator avoidance or food requirements that future research could address.

Predator abundance within the two areas was also not considered in this study due to time restraints, although predator avoidance is expected to have affected *L. archeyi* habitat use during emergence. Future research on these variables effecting the Coromandel *L. archeyi* population could be extremely informative for survey methodology.

2.4.7 Conclusion

The aim of this chapter was to address what habitat characteristics could be driving *L. archeyi* abundance, and whether land use activities affected the resources and conditions within sites. At the scale of this study, results indicate that the abundance of *L. archeyi* is partly in response to the species' relationship with plant species typically associated with mature forest and higher elevation. Historical disturbance impacted the vegetation characteristics present in disturbed and undisturbed sites, but this did not have significant effects on *L. archeyi* abundance in the present. I therefore recommended allowing sites to naturally regenerate after a disturbance activity, or if consent conditions require replanting, I suggest that tree ferns or other species that contribute to leaf litter depth and moisture would promote *L. archeyi* return to sites.

During the process of exploration mining, roading or housing-related activities, it is presumed negative effects on individuals will occur through the loss in resources or due to the activity itself. As the human population continues to grow and demand for resources increase, the effect of land-use activities on the habitat use of species requires further understanding to mitigate for these possible adverse effects.

Chapter 3

Microhabitat selection of *Leiopelma archeyi* in Wharekirauponga and Mahakirau Forest estate

An individual *Leiopelma archeyi* emerged on a dead fern frond at Wharekirauponga. Photo: E. Hotham

3.1 Introduction

Organisms are not typically distributed randomly in their environments. Instead, as a result of natural selection, they tend to choose habitat characteristics that are most favourable to them (Southwood 1977; Clark & Shutler 1999). It is important to recognise that this selection is a hierarchical process. Selection is exercised over scales from the geographical range of a species, deemed *first-order selection*, to the home ranges, or *second-order selection*, as seen in *Chapter 2* (Johnson 1980). *Third-order selection* is the habitat use within the home range and finally, *fourth-order selection* is the acquisition of resources at that site (Johnson 1980). "Microhabitat" refers to the finer habitat features in the second, third and fourth orders, and these associations are species- and site-specific (Johnson 1980; Hall, Krausman & Morrison 1997).

The microhabitat requirements for ectotherms are structured by physiological constraints (Duellman & Trueb 1994; Bell 1978; Cree 1989; Graeter 2005; Ash 1997). A primary physiological feature of amphibians is their semi permeable skin (Duellman & Trueb 1994). Abiotic and vegetative characteristics that affect temperature and humidity are important factors in determining the microclimate and microhabitats available (Pough et al. 1987). A moderate to warm, moist environment is required to persist for terrestrial amphibians, and the animals rely on behavioural changes to regulate evaporative water loss to lessen their susceptibility to desiccation (Duellman & Trueb 1994). Cree (1989), for example, recorded *L. archeyi* emerged during dry periods, but most individuals disappeared back into refuges within an hour. *L. archeyi* are likely displaying behavioural responses to undesirable climatic conditions. The second constraint on the habitat use of amphibians is that some species are nocturnal (Bell 1978; Farallo & Miles 2016; Ramirez 2017). This allows for the avoidance of higher daytime temperatures and lower atmospheric humidity (Duellman & Trueb 1994). Further, any active thermoregulation utilised must involve exploiting certain microhabitats (Farallo and Miles 2016). An advantage to amphibians is that they can utilize microhabitat refugia, such as leaf litter and cover objects. However, specific habitat types are required at different life stages for species persistence (Graeter 2005; Farallo & Miles 2016).

Leiopelma archeyi are a k-selected species, meaning they have high parental investment, low dispersal and a long generation time (Stephenson & Stephenson 1957; Bell 1978). Rocks, logs and vegetation are used as refuge sites during the day (Bell 1978; Ramirez 2017). Adult *L. archeyi* do not exceed 41 mm snout-vent-length (SVL), with sub-adult SVL 18–24 mm and juvenile SVL < 18 mm (Bell 1978; Whittaker & Alspach 1999). *L. archeyi* are the smallest of the New Zealand *Leiopelma* species, with microhabitat selection during activity periods likely reflecting their small surface area and susceptibility to desiccation (Bell 1978; Ramirez 2017). Ramirez (2017) demonstrated *L. archeyi* likely have small home ranges, however each age class utilizes an array of microhabitats. Adult frogs are avid climbers and younger individuals more likely to be in the leaf litter (Ramirez 2017). The use of vegetative species by the frogs is thought to reduce dehydration and increase cover from mammalian predators (Cree 1989; Thurley & Bell 1994). Further, individuals tracked during their activity period when on the surface were found to select microhabitats differently from those available (Ramirez 2017). As Ramirez (2017) highlights, the study of species' microhabitat use is important in the conservation management of the species as basic ecological interactions need to be understood before recommendations can be explored.

3.1.1 Study aims and research questions

Gathering data on the microhabitat use of *L. archeyi* will assist in decisions surrounding translocations, captive housing and in the effective management of their environment to sustain populations. The objective of this study was to build on from *Chapter 2* on *L. archeyi's* microhabitat selection on the Coromandel Peninsula. Locations previously surveyed for *L. archeyi* in the Coromandel differ in topography, elevation and microhabitat features to the focal areas in this study. Therefore, the information gathered from this research will provide a greater insight into the conditions used during the emergence of *L. archeyi* from spring through to autumn in these areas of the Coromandel Peninsula.

Due to their semi permeable skin, it is expected that *L. archeyi* will preferentially select microhabitat types that offer protection from desiccation. I therefore collected data on microhabitats where *L. archeyi* were found and compared microhabitat characteristics to random plots where frogs were not found. Questions addressed in the Chapter include:

1. Do *L. archeyi* select specific microhabitat in response to overall vegetation composition?
2. Do *L. archeyi* select specific microhabitat in response to specific features expected to affect desiccation, such as leaf litter depth, logs or stones?
3. Is microhabitat selection different between age class?

The methods section which follows are at times repeated from *Chapter 2* or will refer to sections in *Chapter 2* to reduce repetition.

3.2 Methods

3.2.1 Sampling design

Field sampling was carried out in two forests on the Coromandel Peninsula, New Zealand; Wharekirauponga (WKP) catchment (38°17’51.8”S, 175°49’18.2”E) and Mahakirau Forest Estate (MFE) (36°50’20.9”S, 175°31’45.9”E). Within WKP and MFE, pairs of 100 m² survey sites were selected.

Site selection and pair-wise methodology is explained in section **2.2.1 Sampling design** in **Chapter 2**. In summary, pairs consisted of a disturbed site (D) and an adjacent undisturbed site (U). Sites were classed as disturbed if > 50% of vegetation had previously been cleared for either mining exploration (WKP), roading (MFE) or housing-related activities (MFE) at any time after 1980. Disturbed sites were grouped into years since disturbance (Appendix 1a & 1b). Locations of past exploration sites at WKP were obtained from OceanaGold Ltd (43 Moresby Ave, Waihi), and additional disturbed site locations at MFE were provided by Sara Smerdon, a resident with knowledge of the area. A disturbed and undisturbed site in each pair were both surveyed each night over 3 consecutive nights.

Habitat selection can be exercised at different scales (Johnson 1980). To investigate whether microhabitat selection by *Leiopelma archeyi* was driven by physiological constraints at a finer scale, additional data was collected within sites after nocturnal frog surveys. Plot resolution (3.375 m³) was at Johnson’s (1980) third (usage of various habitat components) and fourth orders (procurement of resources) of selection (Ramirez 2017). Microhabitat data collection methods are described below.

Data were collected between 14 November 2018 and 20 March 2019.

3.2.2 Field methods

Frog surveys (repeat of 2.2.2 Field methods)

One to two pairs were surveyed each night between the hours of 20:00 and 07:00 when frogs are most active (Cree 1989; Ramirez 2018). The sampling period spanned spring to autumn. This period included the end of the breeding season (November), brooding season (December), and non-mating (March) of *L. archeyi* (Bell 1978).

In order to minimise habitat destruction and disruption to animals, surveying was limited to identifying emerged frogs rather than lifting rocks or logs (Scott & Woodward 1994). The exception was in the presence of two dead fern fronds. From personal observations during prior experience, fronds are a favoured substrate for *L. archeyi* during emergence and in refuge. The lifting of two fronds reduced the risk of crushing unseen frogs and minimised the chance of finding a frog in refuge. The ground and vegetation up to 1.5 m were visually searched for frogs.

Frog data collection

Each frog was photographed (without flash) on the substrate it was found on e.g., on an *Astelia trinervia* leaf (Figure 3.1.A). Additionally, its location was marked using a Garmin *GPSMAP 64st* GPS. Wearing powder-free nitrile gloves, frogs were captured and placed it in a pre-numbered clean ziplock bag for immediate processing, with frogs assigned a number in order of capture (Figure 3.1.B & Figure 3.1.C). While the frog was in the bag, snout-to-vent length (SVL) was measured using digital callipers (Figure 3.1.D) and the frogs were weighed using a spring balance scale calibrated for the weight of the bag. In order to identify individual frogs, any peculiarities were noted, and close-up photographs were taken to capture unique markings. This process lasted between 5 – 10 minutes.

Air temperature and relative humidity (RA) at each frog capture location was measured using a *Kestrel 3000* weather meter. Time of capture was recorded. The captured frog was left inside the bag and pegged off the ground to a tree until the site was surveyed for that one night. This avoided recapture or trampling of frogs (Figure 3.1.E). No frog was left inside a bag for more than 2 hours. The frogs did not appear to experience any discomfort from prolonged capture.

Observed microhabitat use

In order to investigate the microhabitat use of emerged *L. archeyi*, observations were made during nocturnal surveys. The substrate the frog was found on was noted and height above ground (zero was recorded for on the ground) recorded. Cover is an important factor for species that require moist conditions to prevent desiccation. The percent of vegetation cover within 10 cm vertically above the frog was therefore visually estimated over an area the size of that individual frog.

A small marker tag and flagging tape with the number associated with each individual frog was placed in the capture location for future vegetation surveys (Figure 3.1.F).

Figure 3.1 A: An emerged *L. archeyi* found during a nocturnal site survey; **B**: Capturing an individual frog; **C**: Individual *L. archeyi* were held in bags for Snout-vent-length (SVL) and weight measurements; **D**: SVL measurement; **E:** Frog identification at location of capture; **F**: Stake in the precise location of where an individual was found during nocturnal surveys.

Microhabitat availability

It is hypothesised that amphibians select resources due to physiological constraints (Pough et al. 1987; Duellman & Trueb 1994; Ash 1997). The vegetative characteristics were further explored to determine if *L. archeyi* presence could be predicted by these microhabitat features.

Areas where *L. archeyi* were found were compared to areas where no frogs were found (Figure 3.2. A & B). Areas, referred to hereafter as 'plots' were inside the 100 m² sites. Plots were 1.5 m x 1.5 m x 1.5 m (Figure 3.3). This resolution was chosen based on the nightly movement patterns of *L. archeyi* and the likelihood that the plot would contain habitat characteristics associated with emergence and refuge sites (Ramirez 2017).

The number of frog plots per site were < 10. This could include recaptures and was chosen due to time restraints and site availability. Each site had 5 random plots, regardless if any frogs had been located elsewhere within that site. Five was an optimal number for adequately characterising microhabitat features not used by *L. archeyi* at the time of capture, given time pressures. The random plots were found by using a random number generator app (*Random UX*). The numbers generated in the app were used to determine the location along a tape measure e.g., 8 and 5 would translate to 8 m along one side of the site and 5 m into the site. Random plots did not overlap with the frog plots or previous random plots selected, i.e. overlapping plots were rejected and replaced. Plots were marked out temporarily using string. A total of 160 random plots and 155 frog plots (315 total plots) were sampled.

Figure 3.2 A: Microhabitat frog plot. The white stake that the plot was situation around has the assigned number for the captured frog. **B:** Random plot. No frog over the three survey nights was found within this area.

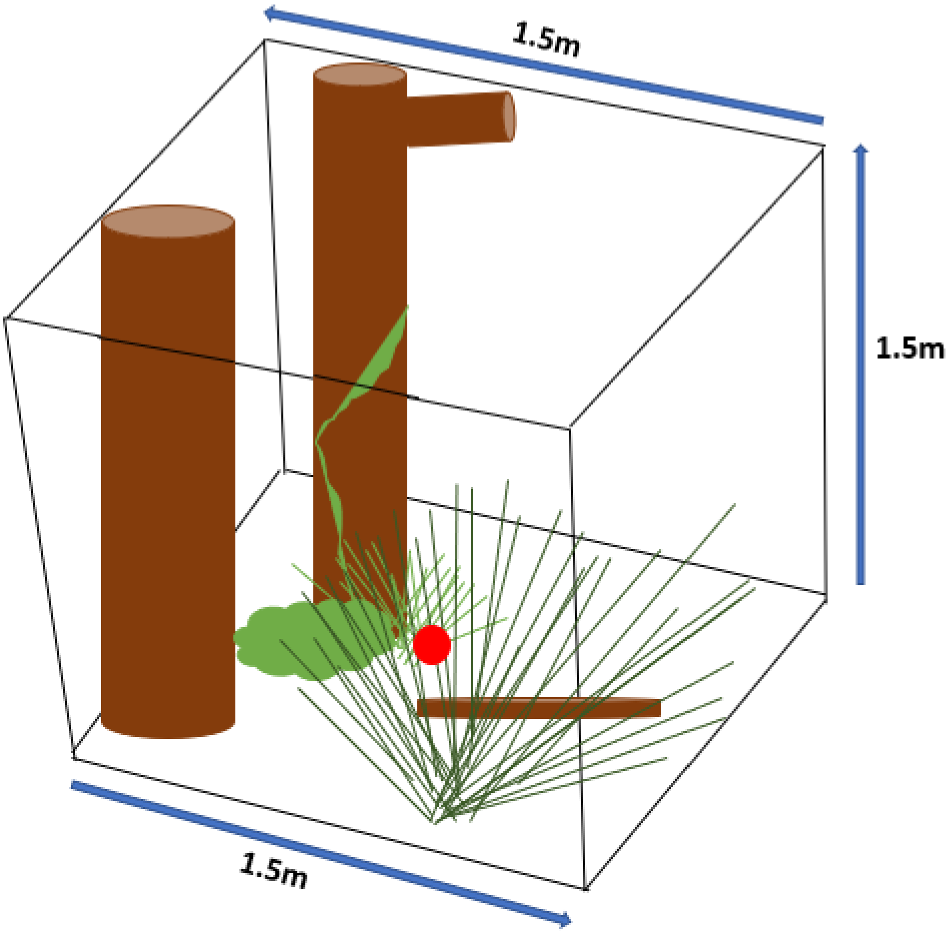

Figure 3.3 An example of a 3.375 m^3 plot (1.5 m x 1.5 m x 1.5 m). The red circle indicates either the position of the emerged frog or where the random generated numbers intersected. Substrates within the plot were assigned into microhabitat types.

Microhabitat types

Ecologically relevant environmental data for *L. archeyi* was collected in order to understand microhabitat use. This data selection reflected the physiological requirements of the amphibians and methodology from previous studies on *L. archeyi* emergence (Cree 1989; Thurley 1996; Ramirez 2017).

The percent of the total area of sky vertically above each plot was estimated by the shadow from the canopy cover at solar zenith (Redpath & Rapson 2015). A higher percent of sky above plots indicates less canopy. Canopy density affects the leaf litter depth, causing changes to moisture availability on the forest floor (Suggitt et al. 2011). Further, more sky means an increase in sun exposure and possibly more air flow, which may increase the risk of desiccation to *L. archeyi*.

Leaf litter holds moisture, an important condition required for species with semi-permeable skin (Duellman & Trueb 1994). Leaf litter has been recognised as a substrate utilized by *L. archeyi* in Whareorino Forest (Ramirez 2017). An average depth of leaf litter was measured (± 1 mm) by three points in each plot from soil level. Dead fern fronds were counted in leaf litter measurements.

Microhabitat types were categorized. Substrates were placed into microhabitat types based on substrate characteristics and the species NZPCN description (NZPCN 2019) (Table 3.1). I recorded the approximate volume of these substrates within each 3.375 m³ plot. I initially calculated volumes as proportions, i.e. so they added to 1. To convert these to actual volumes, six plots were completely cleared of organic material and weighed. The volume proportions estimated in the field were then plotted against the actual measured volumes, and the estimated coefficients used to convert the proportions to approximate volumes.

Table 3.1 Microhabitat types found inside plots in (WKP) and (MFE) (modified from Ramirez 2017).

Microhabitat type	**Code used in analysis**	**Description**
Tree ferns	*Tferns*	Tree ferns with trunks that bear a large crown of fronds. (e.g. *Cyathea dealbata*)
Bare	*Bare*	Exposed soil and rocks of all sizes
Epiphyte	*Epiph*	Grows on the surface of other plants (e.g., *Metrosideros carminea*)
Sedges	*Sedge*	Loose tussock forming species, with upright to strongly curved and distinctly dropping leaves. Includes grasses. (e.g., *Uncinia uncinate, Gahnia setifolia*)
Restiad	*Restiad*	Restiads (e.g., *Schoenus tendo*)
Freycinetia banksii	*Freban*	*Freycinetia banksii* (Kiekie)
Seedling	*Seedling*	Seedling and small plants <2 Diameter at Breast Height (DBH)
Debris	*Debris*	Fallen woody material not attached to a tree (e.g., branches, twigs, logs)
Tree	*Tree*	Trees > 2 DBH (e.g., *Weinmannia silvicola*)
Leaf litter	*Litter*	Dead leaves on ground layer
Moss and Lichens	*Moss*	Moss and lichen species
Dead fern fronds	*DFF*	Dead fern fronds from tree ferns (e.g., *Cyathea dealbata fronds*)
Ground ferns	*Gfern*	Ferns on the forest floor (e.g., *Blechnum novae-zelandiae, Asplenium bulbiferum*)

3.2.3 Data analysis

Microhabitat characteristics

To assess whether vegetation characteristics was a useful predictor of frog presence and to evaluate the availability of substrates, microhabitat types within plots were characterised using ordination techniques and coefficient of determination.

Microhabitat types were linearised in respect to the midpoint of each cover class by square-root transformation. In order to explain the variation between microhabitat types, sample plots were arranged along a gradient of similarity with respect to microhabitat type using Principal Components Analysis (PCA) in CANOCO, Version 4.55 (Ter Braak & Smilauer 2002). PCA1 and PCA2 were used to generate two variables that captured the variation in microhabitat type between plots and whether frog presence was correlated. Plot locations in ordination space were summarised by plotting mean and standard deviations of random plots and frog plots at both areas.

Frog presence

Using the software R version 3.6.0 (R Core Team 2017), overall habitat features, and specific factors expected to influence microclimate, such as leaf litter, were analysed to determine if such variables could predict frog presence.

The probability of finding a frog within a microhabitat plot was predicted using a generalised linear model (GLM) with logit link function. The depth leaf litter, percent of sky above plots, and vegetation characteristics (PCA1 and PCA2) were used as separate predictors of frog presence and significance was tested at $P < 0.05$ level.

3.3 Results

3.3.1 Frog captures

A total of 176 individual *L. archeyi* were found from November 2018 to March 2019. Frog captures at MFE included 26 (14.7%) individuals of this total. There were 29 *L. archeyi* recaptures altogether at WKP and MFE.

3.3.2 Predicting frog presence through microhabitat characteristics

The only microhabitat type to influence frog presence was depth of leaf litter (Table 3.2; Figure 3.4). This indicates that leaf litter is an important habitat feature utilised by *L. archeyi* during emergence.

Statistically, microhabitat types plotted to get PCA1 and PCA2 (**Section 3.3.4**) and the percent of sky above plots had no significant effect on frog presence (Table 3.2).

Table 3.2 Summary of habitat characteristics in plots with associated *P - values* thought to influence *L. archeyi* microhabitat selection in WKP and MFE. Significant P values are highlighted in bold.

Microhabitat features	Estimate	SE	P value
Veg1	0.01	0.13	0.92
Veg2	-0.10	0.11	0.36
Leaf litter depth (cm)	0.19	0.06	**0.004**
Percent sky above plot	-0.00	0.004	0.63

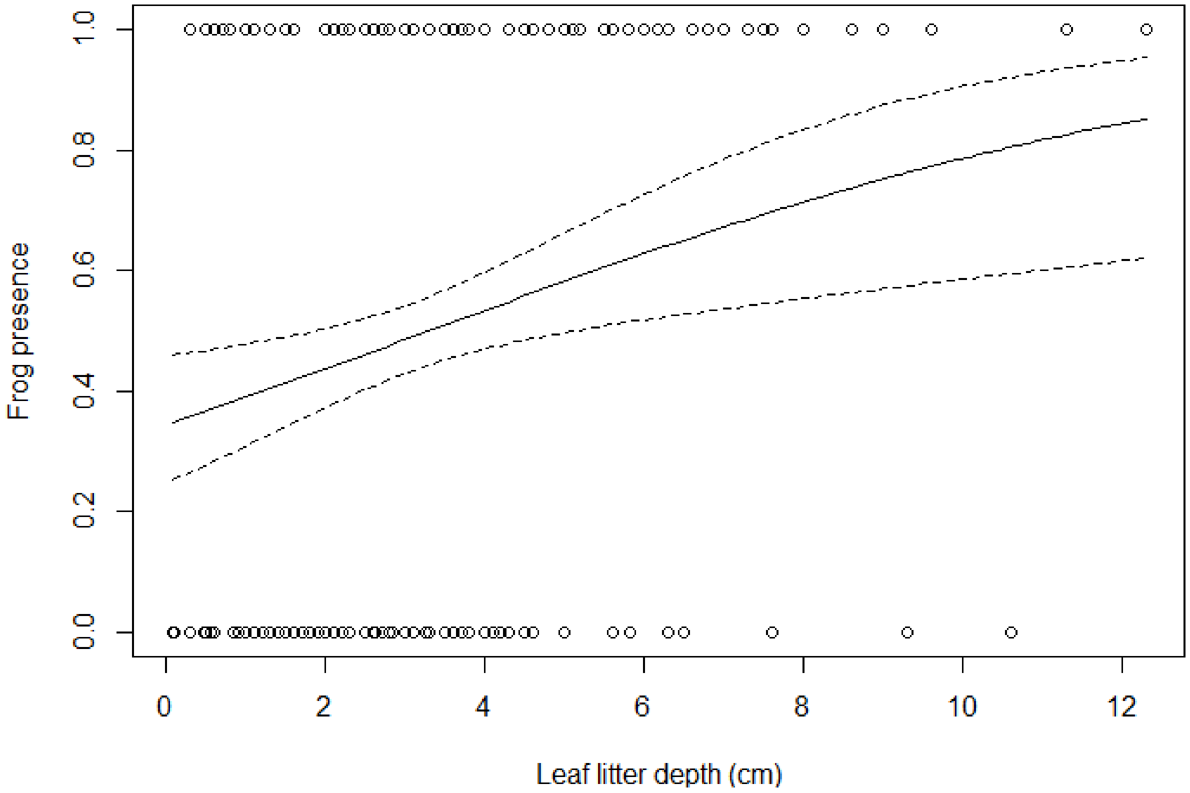

Figure 3.4 Modelled relationship between *L. archeyi* presence and depth leaf litter (black line) pooled for Mahakirau Forest estate and Wharekirauponga (dashed lines are 95% credible intervals).

3.3.3 Observed microhabitat use

From observational data, emerged frogs were found on dead fern fronds (DFF) and leaf litter (Litter) during surveys (Figure 3.5; Figure 3.6). These were the most frequently used microhabitats types for all three age classes, but sub-adult and adult *L. archeyi* used a greater range of microhabitat types in comparison to juvenile frogs (Figure 3.5; Figure 3.7).

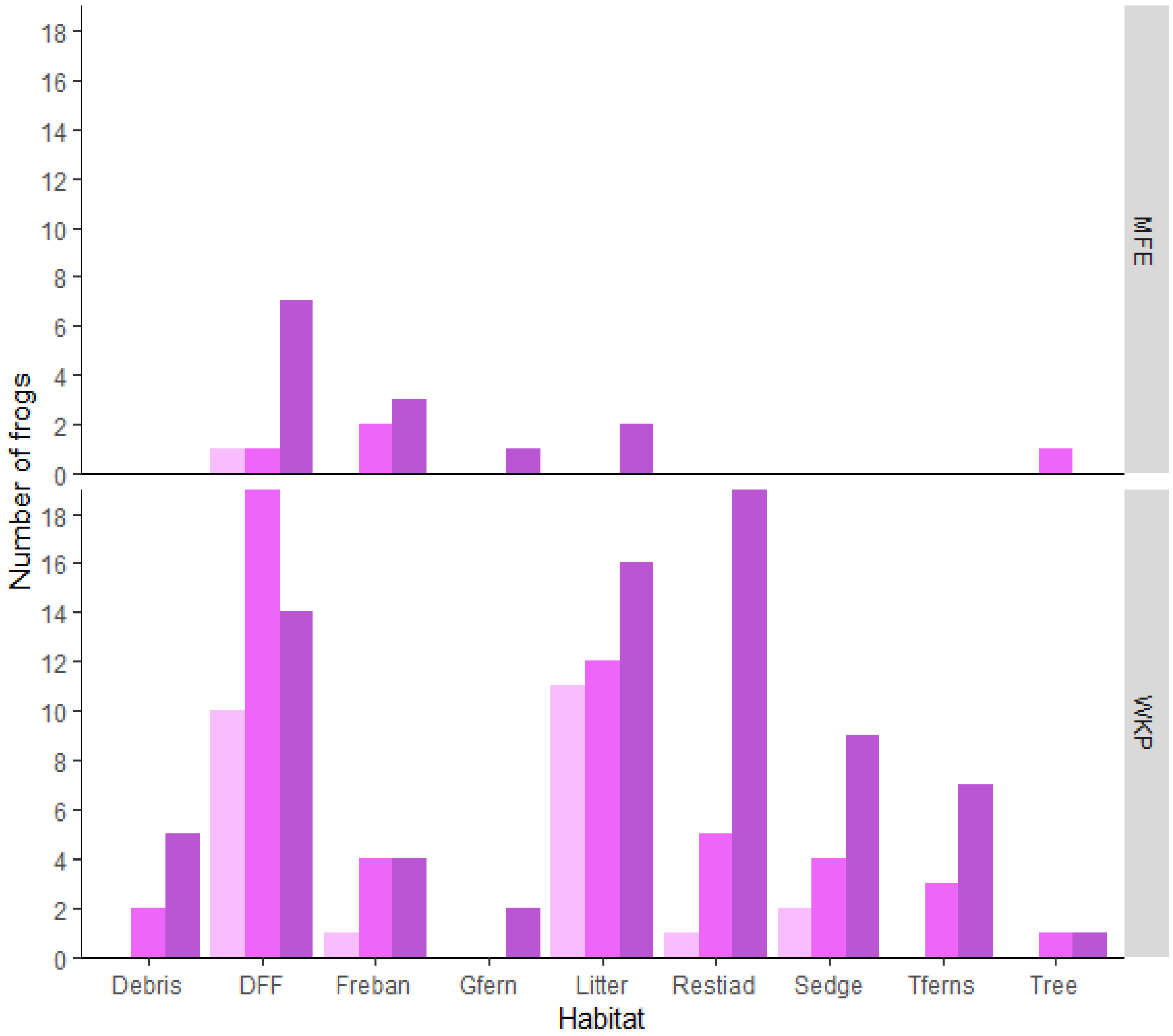

Figure 3.5 Number of *L. archeyi* found on each microhabitat type during nocturnal surveys at Mahakirau Forest Estate (MFE) and Wharekirauponga (WKP). Microhabitat types are explained in **Table 3.1.** Light pink bars represent juvenile *L. archeyi*, violet bars represent sub-adults, and purple bars represent adults.

Figure 3.6 An individual *L. archeyi* emerged on woody debris and leaf litter during a nocturnal survey at Wharekirauponga.

Figure 3.7 Two adult *L. archeyi* found during nocturnal surveys hanging onto *Schoenus tendo* (left) and climbing *Astelia trinervia* (*right*).

When pooling MFE and WKP, there was an indicative trend between height above the ground (H.A.G) (cm) climbed by individual *L. archeyi* and snout-vent-length (SVL) (mm) (Figure 3.8). The trend of H.A.G and SVL was suggestive that frogs with greater SVL were more likely found at greater heights. *Leiopelma archeyi* climbed vegetation, either in the presence or absence of rain, but from observation individuals were more likely to be found above the ground during precipitation events or if vegetation was wet. Vegetation climbed over 100 cm by *L. archeyi* included *Cyathea dealbata*, *Dicksonia squarrosa*, *Weinmannia silvicola* and *Freycinetia banksii.*

The highest proportion of *L. archeyi* were found on the ground among the leaf litter (0 – 10 cm) at both WKP and MFE (Figure 3.9; Figure 3.10).

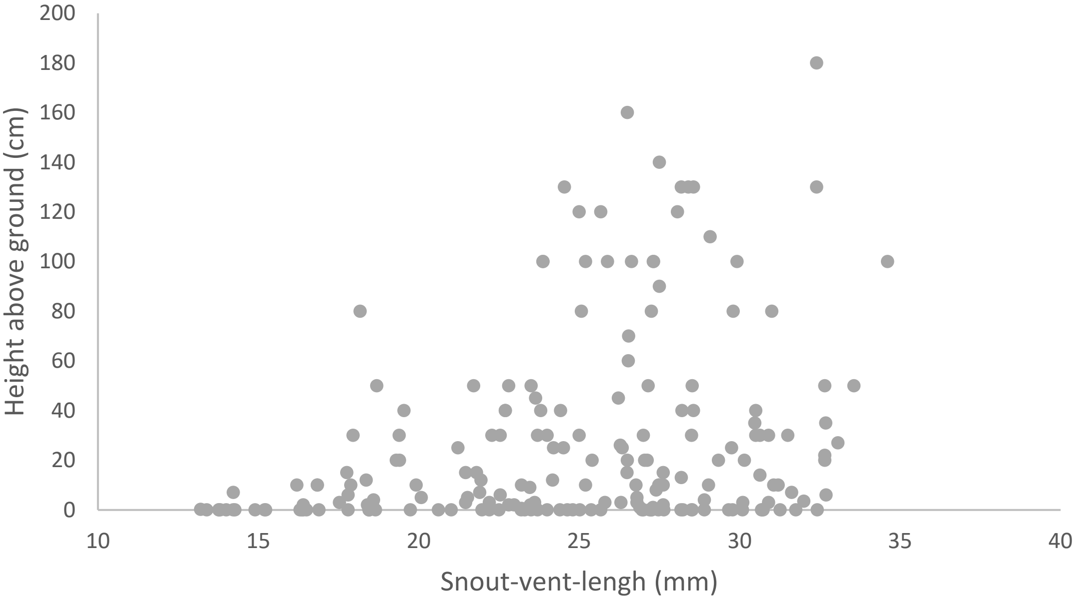

Figure 3.8 Snout-vent-length (SVL) (mm) of individual *L. archeyi* and the height above the ground (cm) they were found at during nocturnal surveys. Data from WKP and MFE were pooled due to the small sample size at the latter.

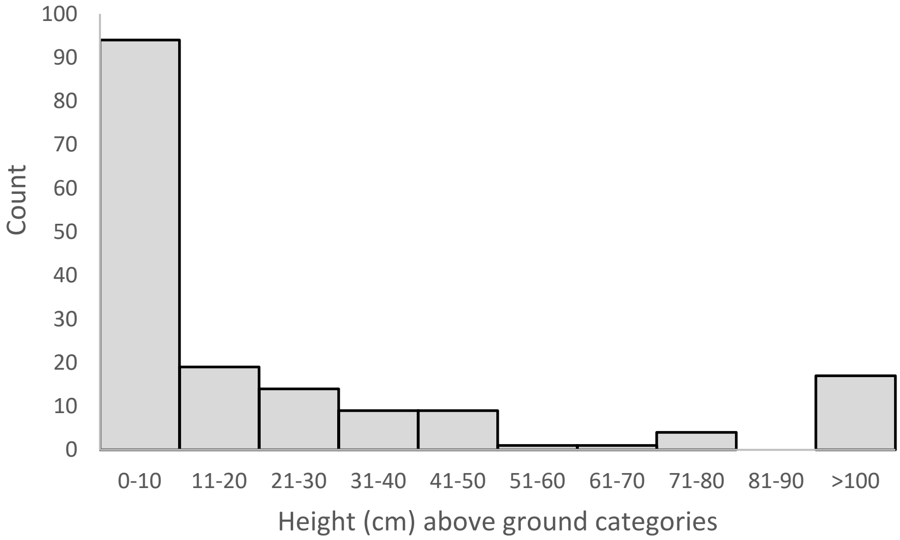

Figure 3.9 Counts of *L. archeyi* found at given height classes above the ground (H.A.G) (cm) at WKP.

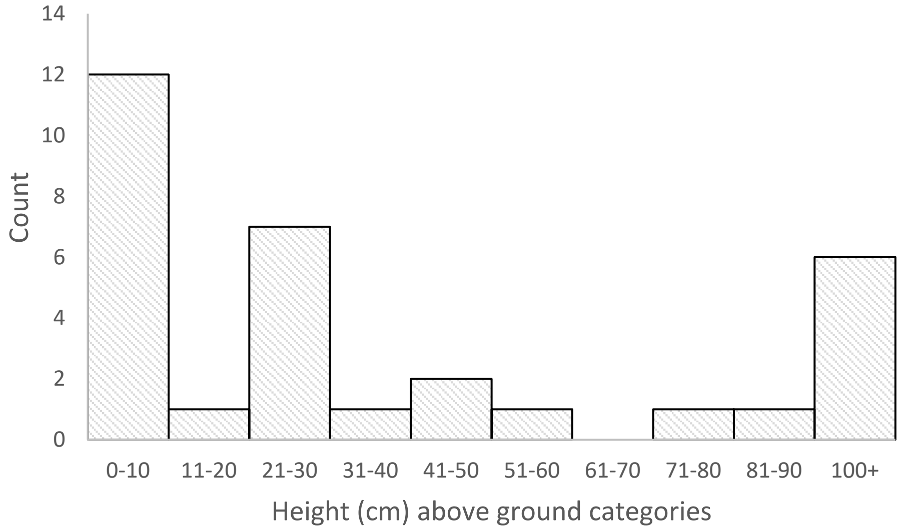

Figure 3.10 Counts of *L. archeyi* found at given height classes above ground (H.A.G) (cm) at MFE.

Leiopelma archeyi was more often found in locations that did not provide cover 10 cm vertically above an individual (Figure 3.11). Individuals not under cover were observed sitting out or 'basking' in the rain. WKP and MFE showed a similar trend with more individuals found in locations not providing cover (Figure 3.11). However, these results could be due to uncovered individuals being easier to find rather than a preference by frogs for uncovered sites.

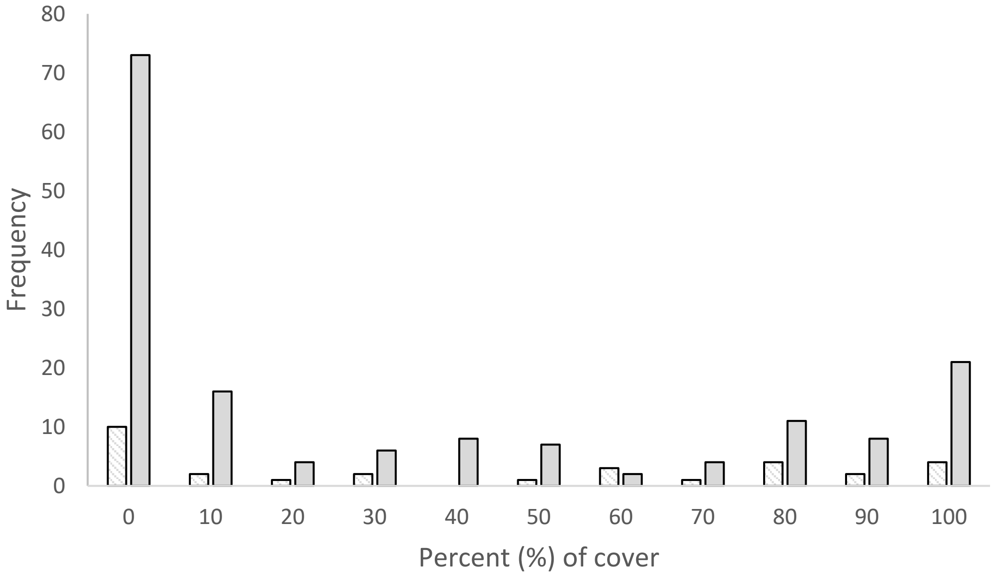

Figure 3.11 Frequency of the percent of cover from vegetation 10 cm vertically above individual *L. archeyi* at MFE (striped bars) and WKP (grey bars).

3.3.4 Microhabitat availability versus Use

A range in microhabitat types was seen in both random plots and frog plots, indicating available resources for *L. archeyi* use within both plot types.

PCA1 and PCA2 explain 28% and 12% of the variance among plots respectively. PCA1 was positively associated with tree ferns such as *C. dealbata*, and dead fern fronds (Figure 3.12). PCA1 was negatively related to seedlings and sedges. PCA2 was more associated with ground ferns (Gfern) and restiads Figure 3.12).

The overlapping standard deviations in PCA scores between random plots and frog plots indicate that there is no apparent overall difference in microhabitat types (Figure 3.13). Frog plots had a greater abundance of dead fern fronds and tree ferns in comparison to random plots, when areas were compared separately. Frog plots at WKP also had a greater proportion of restiads in comparison random plots and plots at MFE (Figure 3.13).

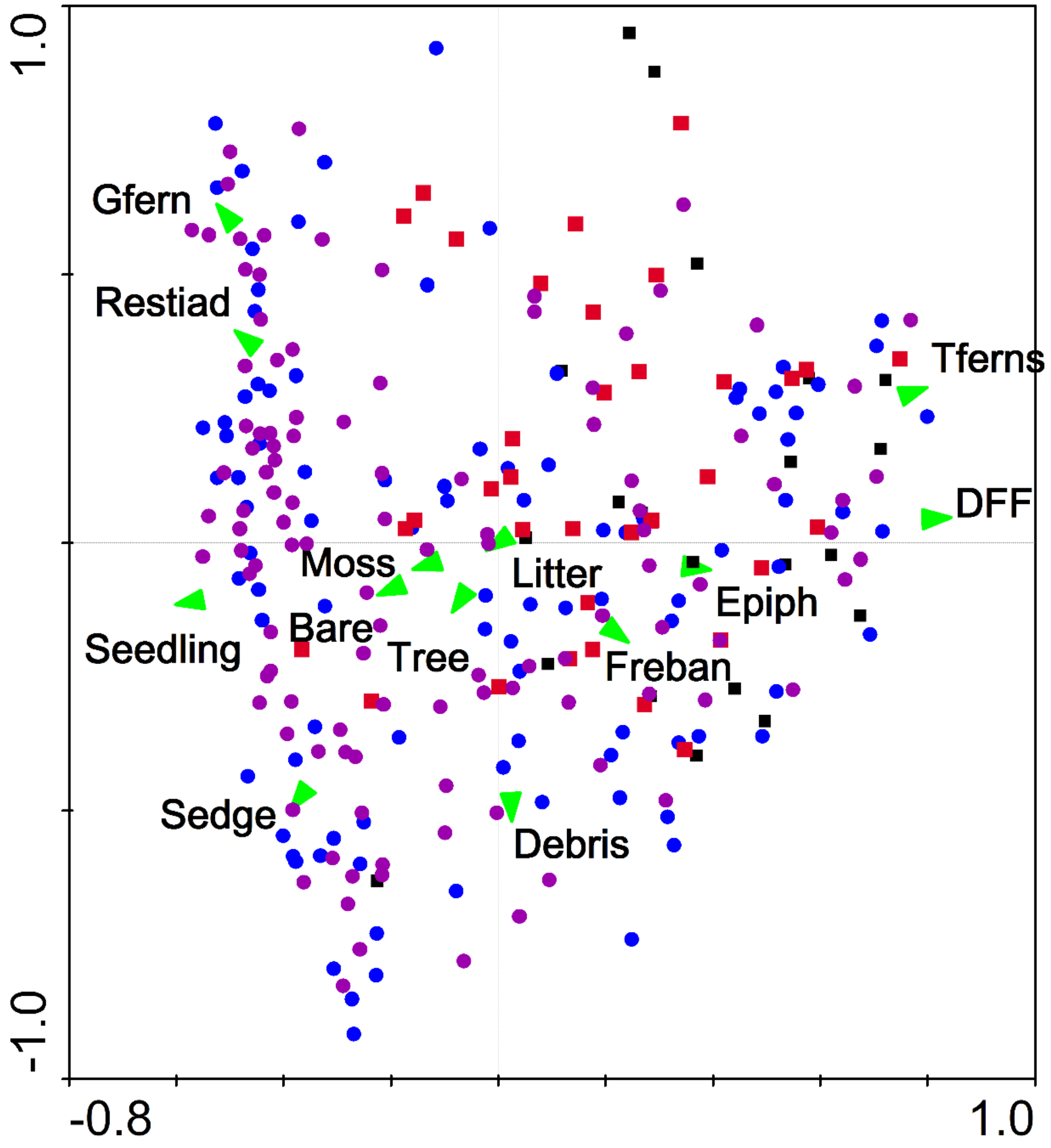

Figure 3.12 Unscaled PCA biplot of the microhabitat types (**Table 3.1**) within frog plots and random plots at WKP and MFE. Purple circle – WKP random plot; blue circle – WKP frog plot; black square – MFE frog plot; maroon square – MFE random plot.

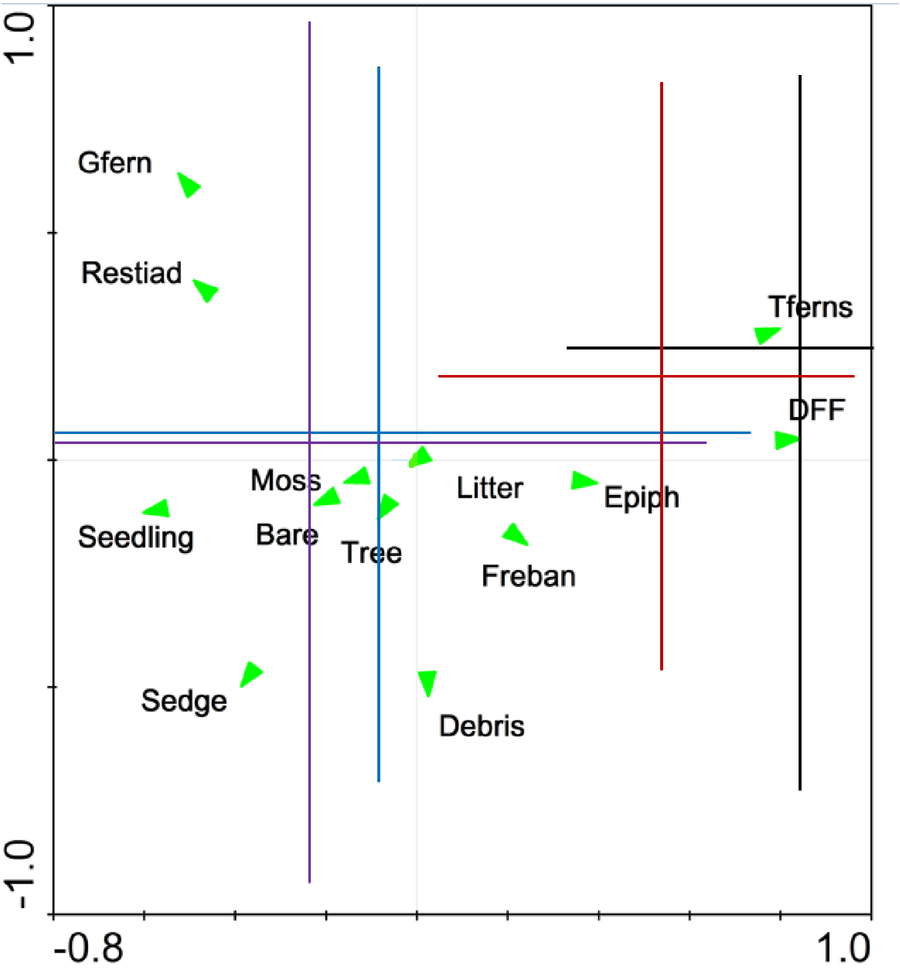

Figure 3.13 Unscaled PCA biplot of the means and standard deviations from the WKP frog plots (Blue lines) and random plots (purple lines) and MFE frog plots (black lines) and random plots (maroon lines) plotted with the microhabitat types. See **Table 3.1** for description of microhabitat types.

3.4 Discussion

This study adds to previous research demonstrating a range of microhabitat types were used by *L. archeyi* during nocturnal emergence (Bell 1978; Cree 1989; Thurley 1996; Ramirez 2017). However, specific habitats were sought out and frog presence was associated with leaf litter depth.

As discussed in *Chapter 2*, *L. archeyi* abundance was correlated with higher elevation and plant species associated with mature forest. These plant species often had vegetative characteristics that affect conditions and resources on the forest floor that are important in determining finer scale microclimates and microhabitats available to forest-dwelling amphibians such as *L. archeyi* (Pough et al. 1986). Leaf litter depth was identified in this study as an important habitat type that predicted frog presence. Leaf litter depth is associated with certain forest species, particularly *Cyathea* and *Dicksonia* spp. (tree ferns) and *Knightia excelsa*. Shedding of tree fern fronds created a large volume of litter on the forest floor, and this litter was used by individual *L. archeyi* during emergence and in refuge. Dead frond layers retain moisture, an important condition required by amphibians (Duellman & Trueb 1994). Furthermore, fronds have a large surface area in comparison to other tree leaves, such as those from *Kunzea robusta*, and are light in weight. These characteristics of tree fern fronds allow *L. archeyi* easy escape from predators as frogs can hide between layers. In previous studies on *L. archeyi* dead fern fronds have not been recognised as an important microhabitat type to the same degree as in my research. This is likely attributed to the different habitat types available in WKP and MFE in comparison to Whareorino Forest and Tapu where majority of habitat surveys for *L. archeyi* have occurred (Thurley & Bell 1994; Thurley 1996; Ramirez 2017; B.D Bell *pers. comm*). I further hypothesise that dead fern fronds are not only used during emergence but are diurnal refuge sites in the absence of rocks. Future research could address these questions.

Knightia excelsa, a mature tree species, was also important in leaf litter composition and could explain why this species tended to be found in sites with higher frog abundance (*Chapter 2*). Dead leaves from *K. excelsa* have resistant tissue that slows decomposition rates, increasing depth of leaf litter on the forest floor (Enright & Ogden 1987). Similar to fern fronds but to a lesser extent due to surface area, *K. excelsa* leaves on the forest floor create moist, penetrable layers (Quinn, Burrell & Parkyn 2000). Further, dead *K. excelsa* leaves were observed stuck in other vegetation, such as between restiad culms or in tree fern crowns. Emerged *L. archeyi* utilised *K. excelsa* leaves on the forest floor and on plant species for a range of activities, such as climbing, basking and it is assumed, rehydration. Additionally, Leaves on the forest floor were favoured by juvenile frogs and used to avoid capture. This was an effective behavioural response due to the ability of *L. archeyi* to camouflage among the litter. If *K. excelsa* leaves and tree ferns aid in the survival of individuals, particularly juveniles, then it is expected that sites (disturbed or undisturbed) will have greater abundance estimates of frogs in comparison to sites without these species.

The PCA analysis in *Chapter 2* was useful for predicting abundance at a greater scale but not for distinguishing areas preferred by frogs at the finer scale. Individuals utilised a range of substrates, as shown in the PCA biplots and other than leaf litter depth, the microhabitat variables were not statistically significant predictors of *L. archeyi* presence. However, in my field observations restiads and tree ferns, in addition to leaf litter, were utilised by *L. archeyi* during emergence, more so than woody debris or trees. *Schoenus tendo,* classified as a restiad, was used in response to predator avoidance and during emergence. *Schoenus tendo* has densely tangled culms that individual *L. archeyi* used to avoid capture by researchers and it is assumed, mammalian predators due to their small size and colouration allowing them to move into the plant and camouflage. In terms of behavioural responses, emerged frogs were observed without cover perching on culms. This behaviour often occurred during precipitation events. Frog microhabitat use may therefore reflect individuals seeking optimal thermoregulation, water balance maintenance or feeding opportunities, or all of the above (Duellman & Trueb 1994; Cree 1987). Furthermore*,* as discussed in *Chapter 2*, *S. tendo* is also associated with *Agathis australis* and shrub forests (Enright and Ogden 1987). *Agathis australis* typically grows in well drained soils and produces acidic and very slow decomposing leaf litter that is likely not ideal for an amphibian that requires moist habitat (Enright and Ogden 1987). Shrub forests at WKP were largely comprised of *K. robusta*, a species also attributed to well drained, dry soils and additionally have small leaf sizes (> 28 mm) (NZPCN 2019). For a species that displays freeze tactics or burrowing when threatened, small leaf size and dry soil makes it difficult to avoid predation. In the absence of substantial leaf litter depth, *S. tendo* is therefore likely favoured by *L. archeyi* as it provides cover, moisture from its densely tangle culms and emergence opportunities. Previous surveys on the habitat use of *L. archeyi* in Whareorino and Mt. Moehau have not indicated *S. tendo* as an important resource. This is likely due to the habitat requirements of *S. tendo*, with *A. australis* absent from Whareorino and the dry environment for growth not present on Mt. Moehau, on the Coromandel Peninsula. However, *L. archeyi* has been found on a reed species, *Juncus effusus,* at Whareorino*,* indicating their complex structure is similar, and that might be what frogs are choosing (Thurley 1996).

These results are similar to those previously recorded on the microhabitat use of *L. archeyi* in Whareorino Forest, with individuals using more than one type of microhabitat substrate during emergence (Thurley 1996; Ramirez 2017). Although I did not record data on the nightly activity of individual frogs, I did record the substrates frogs were found on. These substrates reflected the plant species identified in *Chapter 2* as drivers in frog abundance and included *Freycinetia banksii*, tree ferns and restiads, among others. Substrates in sites ranged, as did use between individuals, indicating *L. archeyi* within (sub-) populations used a range of resources during emergence, as also seen in the PCA analysis. On Coromandel Peninsula, *L. archeyi* had previously been predominantly found under logs and stones that provide moisture, and on trees and *F. banksii* (Stephenson & Stephenson 1957; Bell 1978; Cree 1989; Personal observation). In the absence of stones at WKP and MFE, dead fern fronds and leaf litter probably act as the equivalent by providing moist refuge, although *L. archeyi* were frequently observed on *F. banksii*. However, the use of trees was not as prevalent. When trees were used during emergence, individuals were observed in the branch forks, possibly as a method to capture prey (Cree 1989). Leaf litter was not a predominate substrate compared to other studies, but the use of leaf litter was recorded when frogs were observed for longer periods of time during emergence (Ramirez 2017). In general accordance to other research, juvenile *L. archeyi* were more often found on the ground (Cree 1989; Ramirez 2017). Lastly, while *L. archeyi* tended to be observed without cover 10 cm vertically above individuals, this result may be more indicative of observer bias than behavioural evidence.

Microhabitat selection is a response to morphological structures of the frog, physiological processes, and behavioural responses (Duellman & Trueb 1994). It is important to distinguish between primary and secondary factors influencing microhabitat selection (Heatwolfe 1962). Plant cover was likely a secondary influence at a greater scale in that *L. archeyi* did not directly associate with trees at a microscale, but instead the increased leaf litter from plant species had a greater impact on the presence of individuals, as discussed in *Chapter 2* (Heatwolfe 1962). The vast majority of water loss in terrestrial amphibians is evaporation from the skin. Rehydration through the skin may occur from free water or from substrates (Duellman & Trueb 1994). Not only does leaf litter, including dead fern fronds, provide cover that helps stop the frogs and substrate from drying as rapidly, but also provides cover from climatic conditions and predators. These factors could explain why this microhabitat type was so highly used in this study and numerous others involving forest amphibians (Heatwolfe 1962; Pough et al. 1987; Ash 1997; Lemckert 1999; Ramirez 2017). The importance of leaf litter has also been investigated in the re-population of sites by *Plethodon cinereus* (Pough et al. 1987). As leaf litter depth was reduced, forage above ground occurred less frequently by the salamanders due to the risk of desiccation in this lungless species (Pough et al. 1987). *Leiopelma archeyi* on Mt. Moehau have also been observed to rapidly rehydrate from wet foliage, and that microhabitat selection reflected behaviours in response to climatic conditions (Cree 1989). As mentioned above, future research into the use of leaf litter as a diurnal refuge would increase our understanding of the microhabitat type at WKP and MFE.

Feeding requirements and predator avoidance of *L. archeyi* are likely to affect microhabitat use but was not explored in through this research. *Litoria aurea* and *Rattus spp.* have been observed preying on *L. archeyi* in other studies, although habitat selection was not thoroughly investigated (Thurley & Bell 1994). Additionally, stomach contents from pigs (*Sus scrofa)* have revealed *Leiopelma hochstetteri* remains in areas *L. archeyi* also populate (Bishop et al. 2013; *Pers. comm*). Frog proximity to *S. tendo* and deep leaf litter is no accident, and their choice of these resources maybe because they can escape predators easily.

3.4.1 Conclusion

A key question in conservation biology is what determines species distribution and presence (Farallo and Miles 2016). A species microhabitat use can buffer individuals from climatic conditions and allow them to persist in locations that would otherwise result in decreased performance (Farallo 2017). Limited information on the ecology and biology of *L. archeyi* makes it difficult to assess how habitat characteristics could affect individuals (Lemckert 1999). Such information on the frog's habitat use, and therefore its physiological requirements and behavioural responses, is therefore important in the management of the species (Bell & bell 1994). As discussed in *Chapter 2*, elevation and vegetation types correspond with *L. archeyi* abundance among sites and at a finer scale, presence within sites is correlated with leaf litter depth associated with these plant species. It can be said with relative confidence that a reduction in leaf litter depth, such as from intensive habitat disturbance and canopy removal, will have adverse effects on the species.

Chapter 4

General Discussion

An individual *Leiopelma archeyi* emerged on woody debris at Wharekirauponga. Photo: K. Muchna

'Habitat' is defined as "the resources and conditions present in an area that produce occupancy – including survival and reproduction – by a given organism" (Hall, Krausman & Morrison 1997). Disturbance to these resources and conditions is one of the greatest threats to species survival and has contributed to the threatened classification status of 41% of amphibians (McNeely et al. 1990; IUCN, 2019). In New Zealand, disturbance activities from humans, such as uncontrolled burning, have reduced the native forest cover to 26%. This reduction has affected the distribution of native frog species, including *Leiopelma archeyi*. For the effective management of remaining populations of *L. archeyi*, key questions need to be addressed. These include the microhabitat use of *L. archeyi* and how land use activities may impact the microhabitat use and abundance of frogs. This chapter concludes the results of a study aimed at providing information on such questions.

The pertinent land use activities thought to affect *L. archeyi* abundance included historical exploration mining, roading and housing-related activities. Spatial and time scales are important to consider when investigating the habitat use and requirements of species to understand how disturbance events, such as exploration mining or roading, impact individuals and populations (Wien, Van Horne & Rotenberry 1987; Steele 1992). Site clearance, which removed > 50% of vegetation from ca. 100 m² areas, occurred during the 1980s, 1990s and 2016 in Wharekirauponga (WKP) and the latter two periods in Mahakirau Forest Estate (MFE). Resource use was investigated at *second order* selection (Johnson 1980), or within the home range of *L. archeyi*. Habitat features associated with abundance in 100 m² areas was also explored. *Leiopelma archeyi* are difficult to detect due to their small size, emergence behaviour and colouration. However, their individual markings and restricted nightly movements was appropriate for a closed-mark recapture model. In *Chapter 2*, survey methodology consisted of three consecutive nights per site searching for emerged frogs. For analysing these field data, a purpose built closed-mark recapture model was developed in OpenBUGS. The probability of detecting a previously undetected frog was estimated to be 32% per night, meaning that by the end of the third night of surveying approximately 68% of the frogs at a site would be found. Detection probabilities allow for the estimation of abundance within sites and was important in this study to determine the effect of disturbance activities on *L. archeyi.*

Historical disturbance from exploration mining, roading and housing-related activities during the 1980s, 1990s and 2010-16 was not significantly associated with *L. archeyi* abundance within sites over the scale or time period considered. Tentative results were detected in the vegetation composition after disturbance, but successional changes had occurred over the time scale resulting in little impact on *L. archeyi* abundance. As shown by the mark-recapture model and PCA biplots in *Chapter 2*, abundance estimates were instead correlated with higher elevation and plant species typically associated with mature forest, which were found in both disturbed and undisturbed sites. Over the time elapsed since disturbance, frogs of various age class probably re-colonised sites and reached densities determined by the local habitat quality. Amphibians require habitats with high levels of moisture for respiratory and osmoregulatory functions (Duellman & Trueb 1994; Spotila et al. 1992; Hillyard 1999). It is therefore predictable that more frogs were found at higher elevations because there is higher humidity and rainfall and has been associated with *L. archeyi* habitat use in other studies (Bell 1978; Thurley 1996). Plant species associated with higher frog abundance, including *Cyathea dealbata* and *Knightia excelsa*, are thought to provide increased moisture on the forest floor through leaf litter depth. There was a tentative indication that *L. archeyi* abundance was lower in 2010-16 disturbed sites, but this was not significant. One explanation for the possibly lower abundance in these recently-disturbed sites was that replantation of *Agathis australis* and *Kunzea robusta* limited leaf litter build-up and forest floor moisture, leading to conditions not favoured by *L. archeyi* (*Chapter 2* & *Chapter 3*). Leaving sites to naturally regenerate may therefore result in forest composition more favourable to frogs.

In *Chapter 3*, the finer-scale habitat use during emergence was investigated. The vegetation PCA analysis that effectively modelled vegetation composition in 100 m^2 sites in *Chapter 2* was not as informative at a 1.5 m^3 scale in *Chapter 3* because *L. archeyi* were found utilising a range of substrates. Other results in *Chapter 3* however were consistent with *Chapter 2*. Through the use of a generalised linear model (GLM) with logit link function, the presence of a frog within a site was shown to correlate with depth of leaf litter. *Leiopelma archeyi* selected areas with deep leaf litter over a 1.5 m^3 scale, and in a 100 m^2 area vegetation species correlated with higher abundance of frogs had leaf characteristics, such as slow decomposition, that contributed to the leaf litter. Although disturbance was not a factor explored in predicting frog presence at a 1.5 m^3 scale, leaf litter will be almost absent immediately after vegetation clearing and frogs are only likely to reappear after it returns to a substantial depth. Based on my results I recommend that rehabilitation of sites should be undertaken by natural forest succession and should emphasise retention and restoration of leaf litter.

It is promising to observe that *L. archeyi* in the Coromandel used a range of microhabitats and appear to have been resilient to the historical disturbances studied. However, this does not mean that land-use activities have no effect on *L. archeyi* populations. In this case the disturbances considered were on a small scale (ca. 100 m^2 for mining exploration, roading and housing), and while this probably had an immediate effect on *L. archeyi* in the disturbed areas, recolonization from the wider landscape means there has been no detectable effect on the time-scale considered. Larger-scale habitat disturbances are likely to negatively affect *L. archeyi* populations, such as through habitat fragmentation. Surveys for *L. archeyi* prior to habitat clearance, careful removal of vegetation from areas and erected fences to stop dispersal back into sites during human activity is recommended to prevent immediate harm to frogs. Future studies on the effect of individuals during exploration mining would be beneficial to assess the effects of such work, including from drill vibrations. Further, the future study on the effects of different types and levels of habitat disturbance would also be beneficial, e.g. vegetation removal vs. litter disturbance.

Abundance estimates modelled from the detection probabilities were valuable for understanding the habitat features affecting *L. archeyi* and for examining the association between abundance and disturbance. To obtain more precise estimates, sites could have been surveyed over additional nights. However, this was decided against due to limited survey time available and disturbance to the habitat. It was also shown through the closed-mark recapture modelling that handling of frogs, and perhaps the effect of photographing individuals, reduced subsequent detection, with only a 10% recapture rate. The surveying was completed over too few nights (3) to detect how long this behavioural effect lasted. This effect is an important point to highlight because it suggests that capture is causing some stress. Frogs should be handled as little as possible or not handled at all to reduce possible stress, with photographs taken instead, although photography as a stressor also needs further study. Abundance can be estimated without finding all the frogs, but given the estimated detection probability of 32%, many nights of surveying would be required to be confident that frogs are absent from a site. I conclude that three nights of surveying a 10 m x 10 m site during appropriate weather conditions was adequate to model the abundance of frogs within a 100 m^2 site and did not cause extensive damage to the habitat or *L. archeyi*. Site methodology was adopted from recommendations from the Frog Recovery Group to Oceana Gold Ltd. This study developed further on those recommendations by providing a method on how to measure abundance, detection probability and prediction of *L. archeyi* presence, providing guidance for future monitoring.

This study does not imply that exploration mining, roading or housing-related disturbances have no effect on *L. archeyi* abundance and microhabitat use. Land-use activities are expected to have some immediate adverse effects on *L. archeyi*. However, due to the re-colonisation of frogs and vegetation succession in sites, such associations were not apparent over the time period or scale considered in this study. Small changes after disturbances, such as leaving sites to naturally revegetate, are likely to have positive effects on abundance. Effective communication and involvement between conservationists and land managers can therefore reduce the impacts on vulnerable amphibian species in New Zealand.

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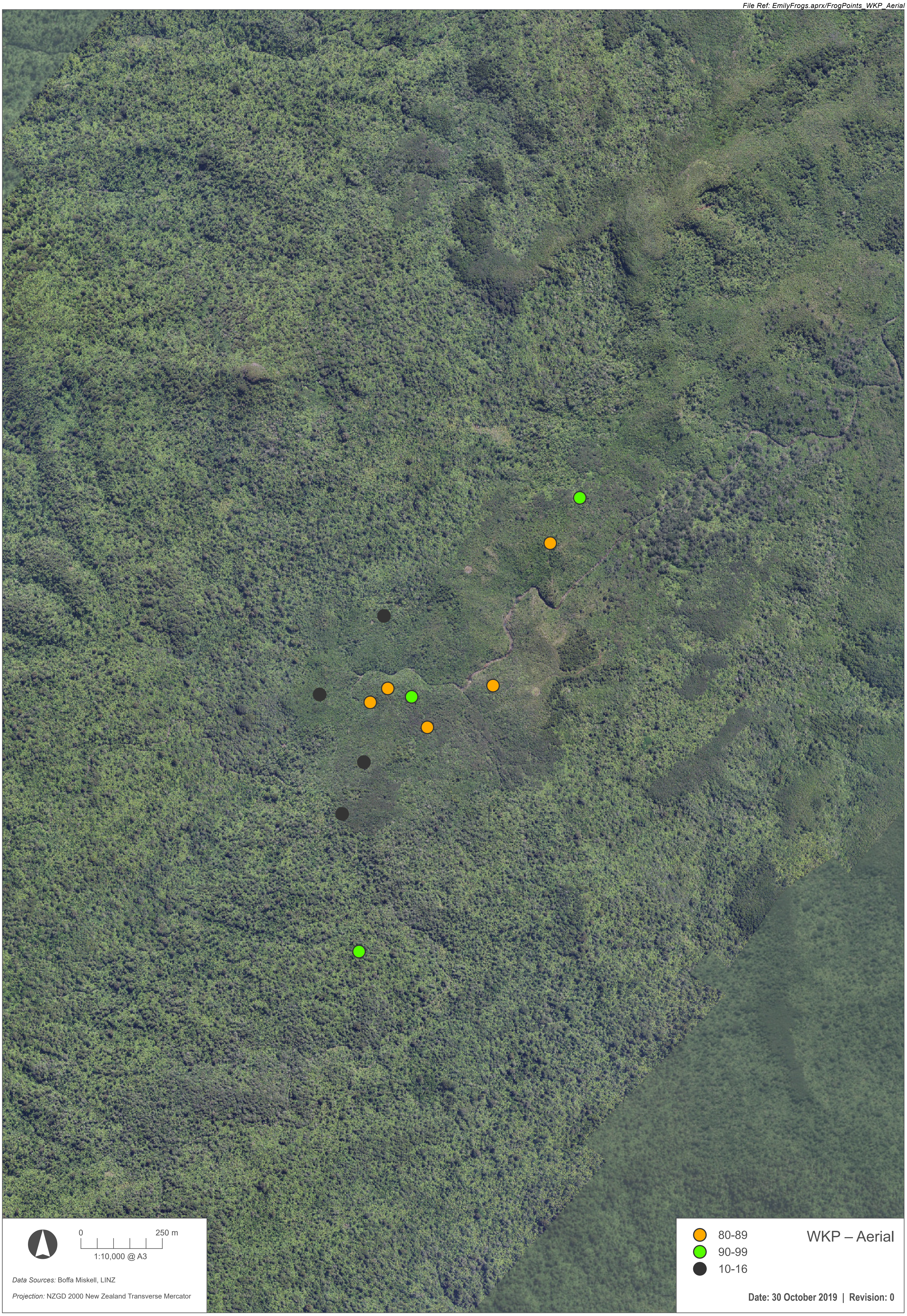
Appendix

Appendix 1a. WKP

Map 1. Aerial map indicating where 1980s (orange circles), 1990s (green circles) and 2010-16 (black circles) historical exploration mining sites were at WKP. Location of historical disturbed sites was provided by Oceana Gold Ltd. Undisturbed sites were 20 m from its paired disturbed site, but not shown on this map.

File Ref: EmilyFrogs.aprx/FrogPoints_WKP_Aerial



- 🟠 80-89
- 🟢 90-99
- ⚫ 10-16

WKP – Aerial

Data Sources: Boffa Miskell, LINZ

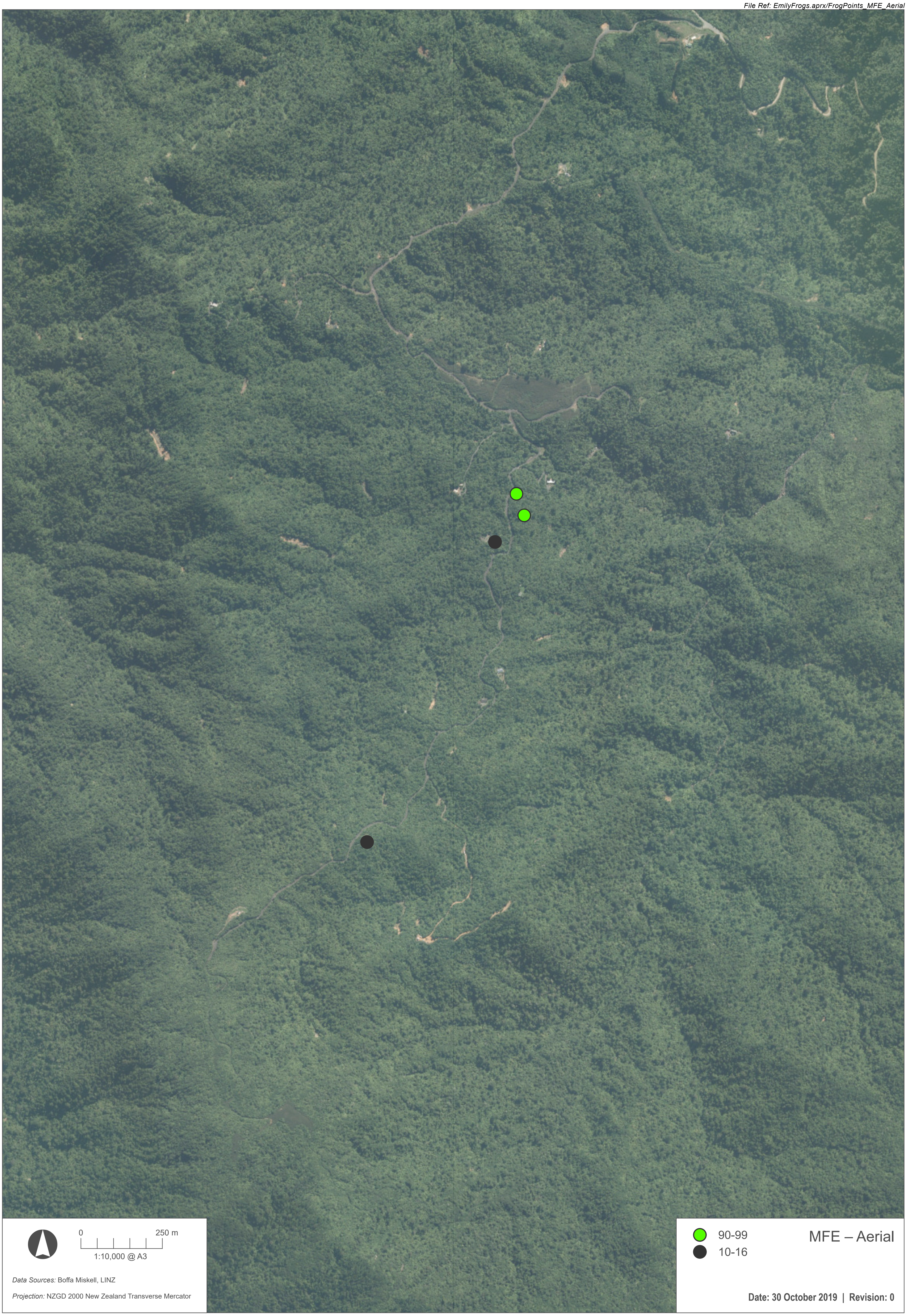
Projection: NZGD 2000 New Zealand Transverse Mercator

Date: 30 October 2019 | Revision: 0

Appendix 1b. MFE

Map 2. Aerial map indicating where 1990s (green circles) and 2010-16 (black circles) historical roading and housing sites were at MFE. Location of historical disturbed sites was provided by Sara Smerdon. Undisturbed sites were 20 m from its paired disturbed site, but not shown on this map.

File Ref: EmilyFrogs.aprx/FrogPoints_MFE_Aerial



🟢 90-99
⚫ 10-16

MFE – Aerial

Data Sources: Boffa Miskell, LINZ

Projection: NZGD 2000 New Zealand Transverse Mercator

Date: 30 October 2019 | Revision: 0

Appendix 2 Modelling code for frog abundance estimates

To estimate abundance within sites, data were analysed using purpose-built closed mark-recapture models fitted in OpenBUGS (version 3.2.3) (Spiegelhalter, Thomas, Best & Lunn 2014) using Markov Chain Monte Carlo (MCMC) methods. Co-authored with Doug Armstrong.

```
Model { # for unconstrained estimates for each site
        a.p ~ dnorm(0,1)                        # intercept of logit of detection probability (p)
        b.B ~ dnorm(0,1) I(,0)    # negative effect of capture on detection probability
        b.T ~ dnorm(0,0.1)                      # effect of temperature on detection prob.
        b.H ~ dnorm(0,0.1)                      # effect of humidity on detection prob.
        s.t.p ~ dunif(0,1)
        tau.t.p <- pow(s.t.p,-2)

        for (t in 1:n.nights) {
                re.t.p[t] ~ dnorm(0, tau.t.p)    # assign nightly random effect on detection probability
        }

        for (i in 1:n.sites) {

                f0[i] ~ dnegbin(0.1,1)                  # prior for no. undetected frogs on plot
                N[i] <- f0[i]+sum(u[i,])                # no. frogs on plot

                U[i,1] <- N[i]                          # initially all individuals are unmarked
                M[i,1] <- 0                             # and no individuals are marked

                for (j in 1:3) {                # for each sampling occasion
                        std.T[i,j] <- (T[i,j]-mean(T[]))/sd(T[])
                        std.H[i,j] <- (H[i,j]-mean(H[]))/sd(H[])
                        logit(c[i,j]) <- a.p+re.t.p[night[i,j]]+b.T*std.T[i,j]+b.H*std.H[i,j] # calc. prob of
first capture
                        logit(p[i,j]) <- logit(c[i,j])+b.B
                                # calc. prob of recapture
                        u[i,j] ~ dbin(c[i,j],U[i,j])            # sample no. new found from no. unmarked
present
                        m[i,j] ~ dbin(p[i,j],M[i,j])            # sample no. marked found from no. marked
present
                        U[i,j+1] <- U[i,j]-u[i,j]
                        M[i,j+1] <- M[i,j]+u[i,j]
                }
        }
        logit(p.ave) <- a.p                             # average detection prob. for unmarked frog
        logit(r.ave) <- a.p+b.B                 # average detection prob. for marked frog

}

Initial values
list(
N=c(4,2,10,6,1,5,3,1,7,14,18,12,10,13,1,1,1,0,9,0,0,0,10,2,15,4,4,0,16,4,4,0), # number caught
b.area=0, b.dist=0, b.1990s=0, b.2010s=0
)

Model { # for modelling effective of disturbance and area

        # Priors for detection probability
        a.p ~ dnorm(0,0.1)                      # intercept of logit of detection probability (p)
        b.B ~ dnorm(0,0.1) #I(,0)       # effect of capture on logit detection probability
        b.T ~ dnorm(0,1)                        # effect of temperature on logit detection prob.
        b.H ~ dnorm(0,1)                        # effect of humidity on logit detection prob.
```

```
    s.t.p ~ dunif(0,1)                  # sd among nights in logit detection prob.
    tau.t.p <- pow(s.t.p,-2)

    for (t in 1:n.nights) {
        re.t.p[t] ~ dnorm(0, tau.t.p)   # assign nightly random effect on detection prob.
    }

    # Priors for frog density
    a.mu ~ dnorm(0,0.1)     # log of expected no. frogs at average undisturbed site
    b.area ~ dnorm(0,0.1)   # effect of area (WKP vs MFE) on log no. frogs
    b.dist ~ dnorm(0,0.1)   # effect of any disturbance on log no. frogs
    b.1990s ~ dnorm(0,0.1) # additional effect of 1990s disturbance
    b.2010s ~ dnorm(0,0.1) # effect of 2010s disturbance
    s.pair ~ dunif(0,10)                # sd among pairs of sites in log no. frogs
    tau.pair <- pow(s.pair,-2)

    for (i in 1:n.pairs) {
        re.pair[i] ~ dnorm(0,tau.pair)  # assign random effect to each pair of sites
    }

    # Likelihood
    for (i in 1:n.sites) {
        log(mu[i]) <-
a.mu+b.area*area[i]+b.dist*dist[i]+b.1990s*dist1990s[i]+b.2010s*dist2010s[i]+re.pair[pair[i]]
        N[i] ~ dpois(mu[i])
            # actual no. frogs on plot

        U[i,1] <- N[i]                      # initially all individuals are unmarked
        M[i,1] <- 0                         # and no individuals are marked

        for (j in 1:3) {            # for each sampling occasion
            std.T[i,j] <- (T[i,j]-mean(T[,]))/sd(T[,])
        # standardise temperature data
            std.H[i,j] <- (H[i,j]-mean(H[,]))/sd(H[,])
    # standardise humidity data
            logit(c[i,j]) <- a.p+re.t.p[night[i,j]]+b.T*std.T[i,j]+b.H*std.H[i,j] # calc. prob of
first capture
            logit(p[i,j]) <- logit(c[i,j])+b.B
                # calc. prob of recapture
            u[i,j] ~ dbin(c[i,j],U[i,j])        # sample no. new found from no. unmarked
present
            m[i,j] ~ dbin(p[i,j],M[i,j])        # sample no. marked found from no. marked
present
            U[i,j+1] <- U[i,j]-u[i,j]
            M[i,j+1] <- M[i,j]+u[i,j]
        }
    }

    # Calculations
    logit(p.ave) <- a.p                     # average detection prob. for unmarked frog
    logit(r.ave) <- a.p+b.B         # average detection prob. for marked frog
    intercept <- exp(a.mu)          # expected no. frogs at average undisturbed site
    dist.effect <- exp(b.dist)              # effect of disturbance on mean number of
frogs
}
```

Initial values

```
list(
N=c(4,2,10,6,1,5,3,1,7,14,18,12,10,13,1,1,1,0,9,0,0,0,10,2,15,4,4,0,16,4,4,0), # number frogs caught
```

```
b.pca1=0, b.pca2=0, b.ele=0, b.canper=0, b.domveg=0, s.site=0.1
)

list(
N=c(4,2,10,6,1,5,3,1,7,14,18,12,10,13,1,1,1,0,9,0,0,0,10,2,15,4,4,0,16,4,4,0), # number frogs caught
b.pca1=-1, b.pca2=-1, b.ele=-1, b.canper=-1, b.domveg=-1, s.site=0.1
)

list(
N=c(4,2,10,6,1,5,3,1,7,14,18,12,10,13,1,1,1,0,9,0,0,0,10,2,15,4,4,0,16,4,4,0), # number frogs caught
b.pca1=1, b.pca2=1, b.ele=1, b.canper=1, b.domveg=1, s.site=0.1
)


Model { # For modelling effect of SITE CHARACTERISTICS

        # Priors for detection probability
        a.p ~ dnorm(0,0.1)                      # intercept of logit of detection probability (p)
        b.B ~ dnorm(0,0.1) #I(,0)       # negative effect of capture on detection probability
        b.T ~ dnorm(0,0.1)                      # effect of temperature on logit detection prob.
        b.H ~ dnorm(0,0.1)                      # effect of humidity on logit detection prob.
        s.t.p ~ dunif(0,1)                      # sd among nights in logit detection prob.
        tau.t.p <- pow(s.t.p,-2)

        for (t in 1:n.nights) {
                re.t.p[t] ~ dnorm(0, tau.t.p)   # assign nightly random effect on detection prob.
        }

        # Priors for frog density
        a.mu ~ dnorm(0,0.1)     # log of expected no. frogs at average undisturbed site
        s.site ~ dunif(0,10)                    # residual sd among sites in log no. frogs
        tau.site <- pow(s.site,-2)
        b.pca1 ~ dnorm(0,0.1)           # effect of PCA1 on log no. frogs
        b.pca2 ~ dnorm(0,0.1)           # effect of PCA2 on log no. frogs
        b.ele ~ dnorm(0,0.1)                    # effect of site elevation on log no. frogs
        b.canper ~ dnorm(0,0.1)# effect of % canopy > 1.35 m on log no. frogs
        b.domveg ~ dnorm(0,0.1)         # effect of average top height of dominate vegetation on log
no. frogs
        b.area ~ dnorm(0,0.1)   # effect of area (WKP vs MFE) on log no. frogs
        # Likelihood
        for (i in 1:n.sites) {
                re.site[i] ~ dnorm(0,tau.site)  # assign random effect to each sites
                # standardise all explanatory variables
                std.pca1[i] <- (pca1[i]-mean(pca1[]))/sd(pca1[])
                std.pca2[i] <- (pca2[i]-mean(pca2[]))/sd(pca1[])
                std.ele[i] <- (ele[i]-mean(ele[]))/sd(ele[])

                std.canper[i] <- (canper[i]-mean(canper[]))/sd(canper[])
                std.domveg[i] <- (domveg[i]-mean(domveg[]))/sd(domveg[])
                log(mu[i]) <-
a.mu+b.pca1*std.pca1[i]+b.pca2*std.pca2[i]+b.ele*std.ele[i]+b.canper*std.canper[i]+b.domveg*std.do
mveg[i]+re.site[i]+b.area*area[i]
                N[i] ~ dpois(mu[i])
                        # actual no. frogs on plot

                U[i,1] <- N[i]                          # initially all individuals are unmarked
                M[i,1] <- 0                             # and no individuals are marked

                for (j in 1:3) {                # for each sampling occasion
                        std.T[i,j] <- (T[i,j]-mean(T[,]))/sd(T[,])
                # standardise temperature data
```

```
            std.H[i,j] <- (H[i,j]-mean(H[,]))/sd(H[,])
    # standardise humidity data
            logit(c[i,j]) <- a.p+re.t.p[night[i,j]]+b.T*std.T[i,j]+b.H*std.H[i,j] # calc. prob of
first capture
            logit(p[i,j]) <- logit(c[i,j])+b.B
                # calc. prob of recapture
            u[i,j] ~ dbin(c[i,j],U[i,j])            # sample no. new found from no. unmarked
present
            m[i,j] ~ dbin(p[i,j],M[i,j])            # sample no. marked found from no. marked
present
            U[i,j+1] <- U[i,j]-u[i,j]
            M[i,j+1] <- M[i,j]+u[i,j]
        }
    }

    # Calculations
    logit(p.ave) <- a.p                             # average detection prob. for unmarked frog
    logit(r.ave) <- a.p+b.B                 # average detection prob. for marked frog
    intercept <- exp(a.mu)                  # expected no. frogs at average undisturbed site
    pca1.effect <- exp(b.pca1)                  # effect of pca1 on mean number of frogs
    pca2.effect <- exp(b.pca2)                  # effect of pca2 on mean number of frogs
    ele.effect <- exp(b.ele)                    # effect of elevation on mean number of frogs
    canper.effect <- exp(b.canper)          # effect of canopy cover above 1.35m on mean number of
frogs
    domveg.effect <- exp(b.domveg)              # effect of dominate vegetation height on mean
number of frogs
}




Initial values for numbers of frogs in each site
list(
N=c(4,2,10,6,1,5,3,1,7,14,18,12,10,13,1,1,1,0,9,0,0,0,10,2,15,4,4,0,16,4,4,0), # number caught
b.pca1=-1, b.pca2=-1, b.ele=-1, b.canper=-1, b.domveg=-1
)

list(
N=c(4,2,10,6,1,5,3,1,7,14,18,12,10,13,1,1,1,0,9,0,0,0,10,2,15,4,4,0,16,4,4,0), # number caught
b.pca1=1, b.pca2=1, b.ele=1, b.canper=1, b.domveg=1
)


Model { # PREVIOUS MODEL for modelling effective of disturbance AND OTHER STUFF
COMBINED BUT WITH NO AREA EFFECT ETC

    # Priors for detection probability
    a.p ~ dnorm(0,0.1)                          # intercept of logit of detection probability (p)
    b.B ~ dnorm(0,0.1) #I(,0)               # negative effect of capture on detection probability
    b.T ~ dnorm(0,1)                            # effect of temperature on detection prob.
    b.H ~ dnorm(0,1)                            # effect of humidity on detection prob.
    s.t.p ~ dunif(0,1)
    tau.t.p <- pow(s.t.p,-2)

for (t in 1:n.nights) {
        re.t.p[t] ~ dnorm(0, tau.t.p)           # assign nightly random effect on detection prob.
    }

    # Priors for frog density
    a.mu ~ dnorm(0,0.1)     # log of expected no. frogs at average undisturbed site
```

```
    b.dist ~ dnorm(0,0.1)   # effect of disturbance on log number of frogs
    s.pair ~ dunif(0,10)            # sd among pairs of sites in log number of frogs
    tau.pair <- pow(s.pair,-2)
    b.pca1 ~ dnorm(0,0.1)
    b.pca2 ~ dnorm(0,0.1)
    b.ele ~ dnorm(0,0.1)    #elevation within sites
    b.canper ~ dnorm(0,0.1)#canopy percent above 1.35m within each site
    b.domveg ~ dnorm(0,0.1)     #average top height of dominate vegetation within sites

    for (i in 1:n.pairs) {
        re.pair[i] ~ dnorm(0,tau.pair)  # assign random effect to each pair of sites
    }

    # Likelihood
    for (i in 1:n.sites) {
        std.ele[i] <- (ele[i]-mean(ele[]))/sd(ele[])        #elevation
        std.canper[i] <- (canper[i]-mean(canper[]))/sd(canper[])            #canopy
percent above 1.35m
        std.domveg[i] <- (domveg[i]-mean(domveg[]))/sd(domveg[])            #average
top height of dominate vegetation within sites

        std.pca1[i] <- (pca1[i]-mean(pca1[]))/sd(pca1[])            # pca data
        std.pca2[i] <- (pca2[i]-mean(pca2[]))/sd(pca1[])
#       log(mu[i]) <- a.mu+b.dist*dist[i]+re.pair[pair[i]]  # expected no. frogs on plot
#       log(mu[i]) <- a.mu+re.pair[pair[i]]+b.pca1*std.pca1[i]+b.pca2*std.pca2[i]
        log(mu[i]) <-
a.mu+re.pair[pair[i]]+b.dist*dist[i]+b.pca1*std.pca1[i]+b.pca2*std.pca2[i]+b.ele*std.ele[i]+b.canper*std.
canper[i]+b.domveg*std.domveg[i]
        N[i] ~ dpois(mu[i])
            # actual no. frogs on plot

        U[i,1] <- N[i]                  # initially all individuals are unmarked
        M[i,1] <- 0                     # and no individuals are marked

        for (j in 1:3) {        # for each sampling occasion
            std.T[i,j] <- (T[i,j]-mean(T[,]))/sd(T[,])
        # standardise temperature data
            std.H[i,j] <- (H[i,j]-mean(H[,]))/sd(H[,])
    # standardise humidity data
            logit(c[i,j]) <- a.p+re.t.p[night[i,j]]+b.T*std.T[i,j]+b.H*std.H[i,j] # calc. prob of
first capture
            logit(p[i,j]) <- logit(c[i,j])+b.B
                # calc. prob of recapture
            u[i,j] ~ dbin(c[i,j],U[i,j])        # sample no. new found from no. unmarked
present
            m[i,j] ~ dbin(p[i,j],M[i,j])        # sample no. marked found from no. marked
present
            U[i,j+1] <- U[i,j]-u[i,j]
            M[i,j+1] <- M[i,j]+u[i,j]
        }
    }

    # Calculations
    logit(p.ave) <- a.p                 # average detection prob. for unmarked frog
    logit(r.ave) <- a.p+b.B     # average detection prob. for marked frog
    intercept <- exp(a.mu)      # expected no. frogs at average undisturbed site
    dist.effect <- exp(b.dist)          # effect of disturbance on mean number of
frogs
    pca1.effect <- exp(b.pca1)      # effect of pca1 on mean number of frogs
    pca2.effect <- exp(b.pca2)      # effect of pca2 on mean number of frogs
```

```
        ele.effect <- exp(b.ele)                # effect of elevation on mean number of frogs
        canper.effect <- exp(b.canper)   # effect of canopy cover above 1.35m on mean number of
frogs
        domveg.effect <- exp(b.domveg)          # effect of dominate vegetation height on mean
number of frogs
}
```

Appendix 3 PCA Vegetation Biplot

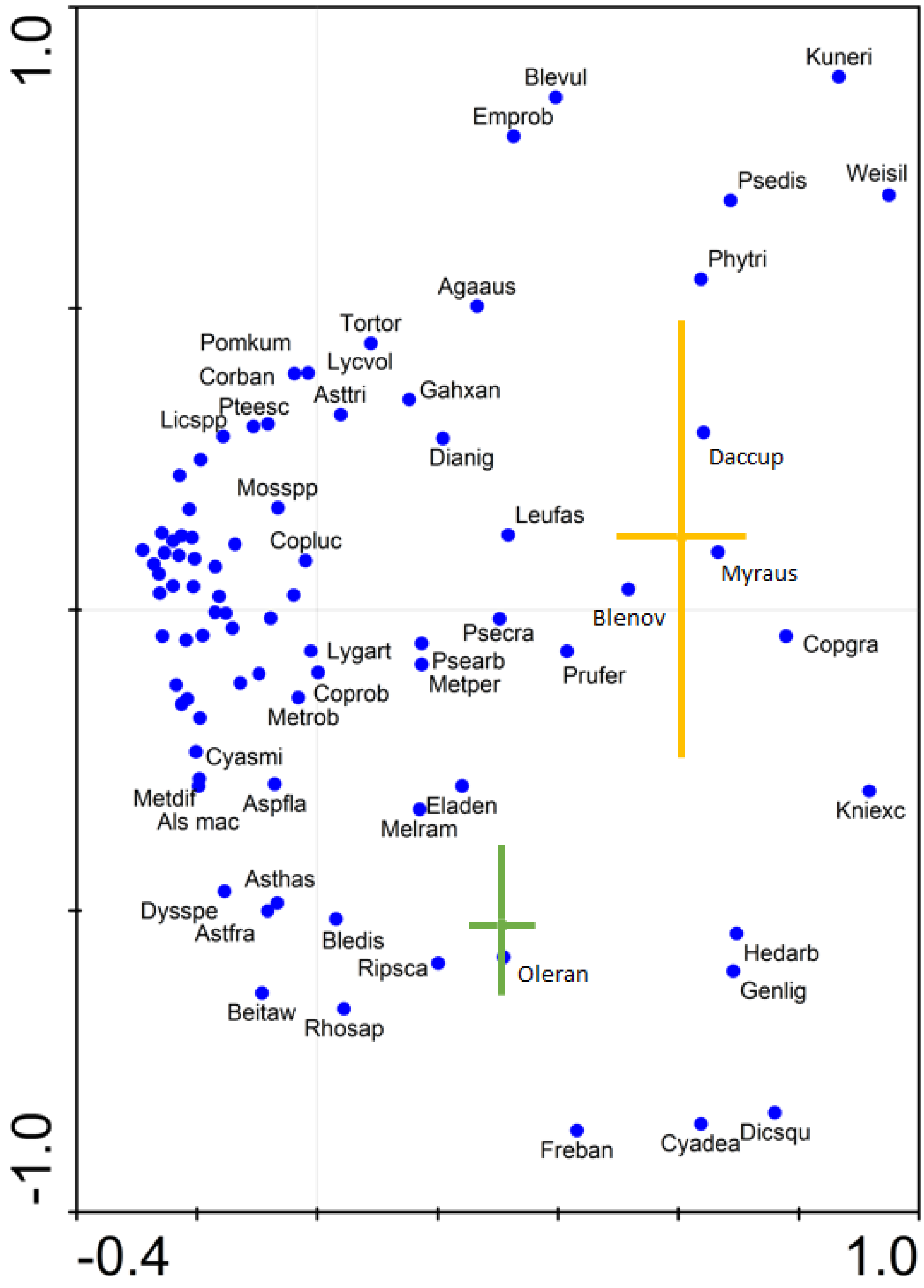


Figure 1. Unscaled PCA biplot of the means and standard deviations from the maximum cover values from the RECCE tier data for vegetation species/taxa within WKP (yellow) and MFE (green) (See Appendix 4 for full species names). Species codes were removed for the clustered species due to inability to distinguish overlapping codes.

Appendix 4 Vegetation codes and Functional groups

Table 1. Plant species present in WKP and MFE and their classification into functional groups. Note: * exotic flora species.

Scientific Name	**Functional Group**	***Six-letter code***
Adiantum cunninghamii	Ground fern/ Climbing fern	*Adicun*
Agathis australis	Tree	*Agaaus*
Alseuosmia macrophylla	Shrub	*Alsmac*
Asplenium bulbiferum	Ground fern/ Climbing fern	*Aspbul*
Asplenium flaccidum	Epiphyte	*Aspfla*
Asplenium lamprophyllum	Ground fern/ Climbing fern	*Asplam*
Asplenium oblongifolium	Ground fern/ Climbing fern	*Aspobl*
Astelia fragrans	Monocot tuft	*Astfra*
Astelia solandri	Monocot tuft	*Astsol*
Astelia hastata	Epiphyte nest	*Asthas*
Astelia trinervia	Monocot tuft	*Asttri*
Beilschmiedia tawa	Tree	*Beitaw*
Blechnum discolor	Nest	*Bledis*
Blechnum filiforme	Ground fern/ Climbing fern	*Blefil*
Blechnum fraseri	Ground fern/ Climbing fern	*Blefra*
Blechnum fluviatile	Nest	*Bleflu*
Blechnum nigrum	Ground fern/ Climbing fern	*Blenig*
Blechnum novae-zelandiae	Ground fern, Climbing fern	*Blenov*
Blechnum vulcanicum	Ground fern, Climbing fern	*Blevul*
Brachyglottis repanda	Shrub	*Brarep*
Cardamine debilis	Herb/ Low growing (<1.5 m)	*Cardeb*
Carpodetus serratus	Small tree <12 m	*Carser*
*Cirsium arvense**	Herbs/ Low growing (<1.5 m)	*Cirarv*
Cordyline australis	Palm like	*Coraus*
Cordyline banksia	Palm like	*Corban*
Coprosma arborea	Shrub	*Coparb*
Coprosma grandifolia	Shrub	*Copgra*
Coprosma lucida	Shrub	*Copluc*
Coprosma robusta	Shrub	*Coprob*
Coprosma spathulata	Shrub	*Copspa*
Ctenopteris heterophylla	Epiphyte	*Ctehet*
Cyathea cunninghamii	Tree fern	*Cyacun*
Cyathea dealbata	Tree fern	*Cyadea*
Cyathea medullaris	Tree fern	*Cyamed*
Cyathea smithii	Tree fern	*Cyasmi*
Dacrydium cupressinum	Tree	*Daccup*
Dacrydium dacrydioides	Tree	*Dacdac*
Dawsonia superba	Moss/ Lichens	*Dawsup*
Dendrobium cunninghamii	Epiphyte	*Dencun*
Dianella nigra	Monocot low growing structure	*Dianig*

Dicksonia squarrosa	Tree fern	*Dicsqu*
Dysoxylum spectabile	Tree	*Dysspe*
Elaeocarpus dentatus	Tree	*Eladen*
Empodisma robustum	Restiad	*Emprob*
Filmy fern species	Epiphyte	*Filfer*
Freycinetia banksii	Nest	*Freban*
Gahnia setifolia	Monocot tuft	*Gahset*
Gahnia xanthocarpa	Monocot tuft	*Gahxan*
Geniostoma ligustrifolium	Shrub	*Genlig*
Gleichenia dicarpa	Ground fern/ Climbing fern	*Gledic*
Griselinia littoralis	Tree	*Grilit*
Hedycarya arborea	Small tree <12 m	*Hedarb*
Ixerba brexioides	Small tree <12m	*Ixebre*
Kunzea ericoides	Dry shrub	*Kuneri*
Lastreopsis hispida	Ground fern/ Climbing fern	*Lashis*
Laurelia novae-zelandiae	Tree	*Launov*
Leptopteris hymenophylloides	Ground fern/ climbing fern	*Lephym*
Leptospermum scoparium	Dry shrub	*Lepsco*
Leucopogon fasciculatus	Dry shrub	*Leufas*
Lichen species	Moss/ Lichens	*Licspp*
Lotus pedunculatus	Herbs/Low growing (<1.5 m)	*Lotped*
Lycopodium deuterodensum	Herbs/Low growing (<1.5 m)	*Lycdeu*
Lycopodium volubile	Climber	*Lycvol*
Lygodium articulatum	Epiphyte vines	*Lygart*
Melicytus ramiflorus	Tree	*Melram*
Metrosideros carminea	Climber	*Metcar*
Metrosideros diffusa	Climber	*Metdif*
Metrosideros fulgens	Climber	*Metful*
Metrosideros perforata	Climber	*Metper*
Metrosideros robusta	Climber	*Metrob*
Microlaena avenacea	Monocot low growing structure	*Micave*
Microsorum pustulatum	Epiphyte	*Micpus*
Moss species	Moss/ Lichens	*Mosspp*
Myrsine australis	Shrub	*Myraus*
Myrsine salicina	Small tree <12 m	*Myrsal*
Nestegis lanceolata	Tree	*Neslan*
Olearia rani	Shrub	*Oleran*
Phyllocladus trichomanoides	Tree	*Phytri*
*Pinus radiata**	Tree	*Pinrad*
Piper excelsum	Shrub	*Pipexc*
Pittosporum umbellatum	Small tree <12 m	*Pitumb*
Podocarpus laetus	Tree	*Podlae*
Podocarpus totara	Tree	*Podtot*
Pomaderris kumeraho	Shrub	*Pomkum*

Prumnopitys ferruginea	Tree	*Prufer*
Prumnopitys taxifolia	Tree	*Prutax*
Pseudopanax arboreus	Shrub	*Psearb*
Pseudopanax crassifolius	Tree	*Psecra*
Pseudopanax discolor	Shrub	*Psedis*
Pseudopanax lessonii	Shrub	*Pseles*
Pterostylis banksii	Herb/ Low growing (<1.5 m)	*Pteban*
Pteridium esculentum	Ground fern/ Climbing fern	*Pteesc*
Quintinia serrata	Small tree <12 m	*Quiser*
Rhopalostylis sapida	Palm like	*Rhosap*
Ripogonum scandens	Epiphyte vines	*Ripsca*
Rubus cissoides	Epiphyte vines	*Rubcis*
*Rubus fruticosus**	Shrub	*Rubfru*
Schefflera digitata	Shrub	*Schdig*
Trifolium repens	Herb/ Low growing (<1.5 m)	*Trirep*
Tmesipteris tannensis	Epiphyte	*Tmetan*
Toronia toru	Shrub	*Tortor*
*Ulex europaeus**	Shrub	*Uleeur*
Uncinia uncinata	Monocot low growing structure	*Uncunc*
Weinmannia silvicola	Tree	*Weisil*