

Network analysis of plant-frugivore interactions in the fragmented landscape of Tāwharanui Regional Park



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Attestation of authorship

“I hereby declare that this submission is my own work and that, to the best of my knowledge and belief, it contains no material previously published or written by another person (except where explicitly defined in the acknowledgements), nor material which to a substantial extent has been submitted for the award of any other degree or diploma of a university or other institution of higher learning.”

Signed:

Matt Funaki

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Abstract

Habitat destruction and modification is the greatest cause of biodiversity loss on the planet. Biodiversity loss has and will continue to contribute to the disruption of crucial ecological functions such as seed dispersal; the movement of a plant's genetic material by abiotic vectors such as wind or biotic vectors such as birds. Severe avian population declines are well documented in New Zealand, where avian dispersers are vital for seed dispersal for many plants. Mutualistic interactions between seed dispersing birds and fruiting plants can form large complex webs that, until recently, have impeded community level analysis. The application of network theory to these complex webs of interactions provides the necessary tools to visualise and describe their structural properties and predict the ecological consequences of network dynamics on species. In this thesis, I applied a network theory approach to describe frugivore-plant interactions across different habitats within Tāwharanui Regional park (TRP), New Zealand's first open sanctuary, 90 km north of Auckland City. I achieved this by conducting bird and fruit counts within habitat types throughout TRP. Bush interior points and bush edge points had significantly higher frugivore species richness than pasture interior points, while bush interior points supported a significantly higher number of large frugivores per point than mānuka edge points. Network analysis showed a highly modular network structure of the long-distance and short-distance potential networks, indicative of a network that is resilient to disturbance. Extinction models indicate that the extirpation of tūi and kererū, the two most connected species in the short-distance potential network, would lead to 42% of plant species losing their dispersers. To my knowledge, this is the first implementation of a predictive network model for plant-frugivore interactions. This research underscores the benefits of applying network theory as a tool for conservation managers to identify and set conservation priorities. For example, management should ensure local populations of kererū are preserved by maintaining and replanting remnant bush habitats which contain several fruiting species favoured by kererū. Their high mobility could drive the recolonization of fruiting plant species to regenerating areas which would assist restoration efforts and reduce management costs. Furthermore, this research demonstrates the efficacy of predictive networks through the novel use of co-occurrence data from field observations in combination with literature of plant-frugivore interactions.

While land modification for the purpose of acquiring natural resources (i.e., food, timber, fabrics) has occurred since the advent of human civilisation, intensive global conversion from native wildlands (e.g., forests, grasslands) to pasture and cropland has mostly occurred in the last 300 years (DeFries et al. 2004), coinciding with the rapid increase in resource consumption rates, the subsequent population growth and technological advancements (Vitousek et al. 1997, Ramankutty and Foley 1999, Foley et al. 2005). Today, approximately one third of Earth's terrestrial surface is set aside for agricultural practice (DeFries et al. 2004). Within the tropics alone, only half of the approximately 16,000,000 km² forest remains and forest loss due to land use clearing continues at a rate of 1,000,000 km² per decade (Pimm and Raven 2000).

1.1 Biodiversity loss and the consequences for ecological functions

The transformation of habitats, through the loss, fragmentation and exploitation of natural ecosystems has had devastating negative impacts on species declines and is considered the greatest cause of biodiversity loss on the planet (Vitousek et al. 1997, Pimm and Raven 2000, Foley et al. 2005). Consequently, biodiversity loss has, and will continue to, contribute to the disruption of crucial ecological functions such as pest control, pollination and seed dispersal which maintain overall ecosystem functioning and the resultant ecosystem services that benefit humans (Diaz et al. 2006).

Humans have caused approximately 25% of bird species to go extinct over the past 2000 years, mostly on islands (Vitousek et al. 1997), with the vast majority of these extinctions occurring before 1500 A.D. (~ 94%) (Sekercioglu et al. 2004). However, since the 16th century, while the number of avian extinctions may be low, extant avifauna has undergone a 25% decline in overall abundance and, for many avian functional groups, these extinction trends are expected to continue (Sekercioglu et al. 2004). Population declines and extinctions of species within functional groups such as the insectivores, nectarivores, piscivores and scavengers have concomitant negative effects on ecological functions. For example, the loss of insectivorous three-toed woodpeckers (*Picoides tridactylus*) in disturbed fragments have led to massive pest outbreaks of spruce bark beetles (Scolytidae, Coleoptera) due to a loss of pest control function provided by the woodpeckers. Consequently, unregulated bark beetle populations have caused widespread conifer losses within a couple of years (Fayt et al.

2005). Similar ecological consequences will occur for other ecological functions resulting from the population decline and loss of species from highly threatened functional groups including the pollinating nectarivores, nutrient depositing piscivores and seed dispersing frugivores (Sekercioglu et al. 2004).

1.2 Seed dispersal

Seed dispersal is the movement of a plant's seeds (its genetic material) by abiotic vectors such as wind and water, and biotic vectors including birds (Wenny et al. 2016). In the case of frugivory, birds play an important role as seed dispersers of genetic material (Sekercioglu, 2006) and connect habitat in space and time (Lundberg and Moberg 2003). Seed dispersal is a mutualistic function as both the plant and birds benefit from it. The plant's genetic material is spread across the landscape, while the fleshy pericarp provided by the plant nourishes the frugivore (Bascompte and Jordano 2014). Using the number of species involved in seed dispersal as a metric of ecological function importance, avian seed dispersal is second only to insectivory. About 40% of all bird species ($n = 4,000$) have been recorded including fruit in their diet, with one quarter of these species being highly frugivorous (i.e., > 70% diet comprised of fruit) (Wenny et al. 2016). Globally, birds disperse seeds of approximately 69,000 plants species (Wenny et al. 2016). In a review assessing the extinction threat of ten avian feeding guilds, frugivorous birds were the fourth most at-risk guild (Sekercioglu et al. 2004).

1.2.1 Ecological benefits of seed dispersal

It is hypothesised that seed dispersal by frugivores provides three distinct ecological benefits that affect the parent plant and the offspring (Howe and Miriti 2004). These benefits are not exclusive, meaning plants may use more than one of these advantages, although the value and significance of each benefit differs between plant species (Howe and Smallwood 1982). First, the "escape hypothesis" states that the transportation of seeds away from seed masses beneath the parent plant reduces the likelihood of density-dependent seed mortality by pathogens, seed predators and pest species (Janzen-Connell effects) (Harms et al. 2000, Schupp et al. 2010). Second, the "colonisation hypothesis" describes that the dispersal of seeds to forest gaps and disturbed regenerating areas allows plants to occupy and establish in uncolonised areas. This is analogous to seed dispersal and nutrient deposition functions to regenerating volcanic islands, by piscivorous seabirds (Magnusson et al. 2014). Seed dispersal to forest gaps and

regenerating areas are two critical roles provided by avian frugivores (Sekercioglu 2006) given the current deforestation trends. Finally, the “directed dispersal hypothesis” involves the non-random, concentrated dispersal of seeds to favourable sites conducive for seedling recruitment. For example, Wenny and Levey (1998) observed directed dispersal of *Ocotea endresiana* seeds within a Costa Rican neo-tropical forest. Three-wattled bellbirds (*Procnias tricarunculata*), one of five dispersers of *O. endresiana*, frequently dispersed the seeds beneath their song perches on the edge of canopy gaps. *Ocotea endresiana* seeds dispersed by three-wattled bellbirds had greater seedling survival rates as canopy gaps reduced seedling mortality by fungal pathogens, whereas seeds dispersed by the other four bird species were distributed under closed canopy sites near the parent tree (Wenny and Levey 1998). This phenomenon is not limited to the tropics. Approximately 70% of holly (*Ilex aquifolium*) and hawthorn (*Crataegus monogyna*) seeds were directly dispersed by foraging *Turdus* species to sites beneath fleshy-fruited trees within temperate forests of Northern Spain (Carlo et al. 2013).

1.3 Habitat disturbance, habitat loss and seed dispersal

The partitioning of continuous forest patches into isolated disturbed fragments due to land use change (Foley et al. 2005, Lindenmayer et al. 2008) often causes the population decline or extirpation of avian seed dispersers (Santos and Telleria 1994, Cordeiro and Howe 2003, Kirika et al. 2008, Lehouck et al. 2009, Moran et al. 2009, Uriarte et al. 2011) because smaller, fragmented forest patches—analogueous to oceanic islands—support fewer species (MacArthur and Wilson 1967, Pimm and Raven 2000). Moreover, the fragmentation of habitats into smaller isolated parcels will have a disproportionately large negative impact on dispersal-limited species with poor flight ability, as their potential to cross wide gaps and recolonise will be greatly reduced, resulting in a loss of genetic diversity for affected species (Bregman et al. 2014).

1.3.1 Consequences of frugivore loss

The loss of frugivores in small, disturbed forest fragments can have negative impacts on the recruitment success of dependent plant species (Santos and Telleria 1994, Cordeiro and Howe 2003, Kirika et al. 2008, Lehouck et al. 2009). Consequently, population declines, extirpations and changes to the spatial behavioural patterns of dispersal agents may lead to a reduction in fruit removal rates and mean seed dispersal distances of dependent plant species (Santos and Telleria 1994, Cordeiro and Howe 2003, Cramer et al. 2007, Kirika et al. 2008, Lehouck et al. 2009, Uriarte et al. 2011, Carlo et al. 2013,

McConkey and O'Farrill 2016). For example, in the Usambara mountain range of North-eastern Tanzania, fewer avian dispersers of the tropical endemic tree *Leptonychia usambarensis* were found in isolated rainforest fragments than in continuous patches. Consequently, fewer *L. usambarensis* seeds were removed within isolated fragments than in continuous forest (Cordeiro and Howe 2003). Thus, *Leptonychia* seedling densities beneath parental crowns were significantly greater within small fragments, increasing the likelihood of density-dependent seedling mortality (Howe and Miriti 2004).

Although studies have elucidated the effects of fragmentation and disturbance on frugivores of all sizes and degrees of generalisation (Cordeiro and Howe 2003, Kirika et al. 2008), larger-bodied frugivores are particularly sensitive to forest fragmentation and are at disproportionately greater risk of extinction compared to smaller-bodied frugivores, due to their naturally lower population densities, larger home ranges (Boyer 2010) and in some regions, hunting pressure (Hamann and Curio 1999, da Silva and Tabarelli 2000, Terborgh et al. 2008, Naniwadekar et al. 2015). For instance, in a North-East Indian tropical rainforest devoid of hunting and logging, large-bodied hornbill abundance within forests was 22 times greater compared to hornbill abundances within a heavily disturbed site with extensive hunting and logging pressure. Consequently, seed arrival rates of five plant species were significantly reduced in the heavily disturbed site, with three of five species completely absent from the disturbed site (Naniwadekar et al. 2015).

Large-seeded plants are at greater risk of extinction relative to small-seeded species, as they tend to be specialists, depending on a smaller suite of extant large-gaped frugivores capable of dispersing large seeds (Hamann and Curio 1999, da Silva and Tabarelli 2000, Meehan et al. 2002, Cramer et al. 2007, Moran et al. 2009, Uriarte et al. 2011). For example, within a submontane rainforest on the Philippine island of Negros, Hamann and Curio (1999) found twice as many avian dispersal agents of small-seeded plants (< 20 mm fruits) compared to large-seeded plants (> 20 mm fruits). Furthermore, in Tonga, gape width estimates of two extinct large-bodied frugivorous pigeon species (*Ducula spp.*) suggest potential avian dispersal failure of 18 large-seeded plant species with an average fruit size greater than 28 mm (the maximum gape width of the extant *Ducula pacifica*), suggesting a reason for the reduced abundance of those dependent plant species (Meehan et al. 2002).

1.4 Habitat disturbance, habitat loss and seed dispersal in New Zealand

Seed dispersal is of particular ecological significance in Australasian island ecosystems (Anderson et al. 2006, Sekercioglu 2006, Kelly et al. 2010) such as New Zealand. Given the disproportionately high percentage of New Zealand trees that are adapted for frugivorous dispersal compared to other temperate zones (Anderson et al. 2006), it is imperative to understand avian contributions to seed dispersal in order to predict and avoid the consequences of avian losses (Sekercioglu 2006). New Zealand has experienced long periods of geographical isolation, leading to high levels of endemism and niche differentiation. This has caused unique ecological features, such as a disproportionately high percentage of trees (33% of plant species), compared to a global temperate mean of 9% (Anderson et al. 2006). Moreover, 72% of tree species within New Zealand bear fleshy fruits, compared to an average northern hemisphere temperate zone range between 17–47% (Burrows 1994).

1.4.1 Land use change in New Zealand

Today, indigenous forest cover accounts for just 23% of New Zealand's total land area; an approximate 70% loss of indigenous forest within the last 800 years (Allen et al. 2013). This period of rapid deforestation largely occurred in two waves: the “initial burning period” by Polynesian settlers c. 1280 AD (McWethy et al. 2009) and a second wave of land clearance, further logging and burning following European settlement for agriculture during the mid-nineteenth century (Allen et al. 2013). Approximately 9.7 million hectares of New Zealand land area (67% of total agricultural land area) is used for sheep and beef cattle production (Morris 2013). While lowland ecosystem degradation continues due to agricultural land use intensification (Morris 2013), a disproportionately high number of legal reserves are established in montane and alpine zones; regions of pristine ecosystems that have always been unsuitable for agricultural land use (Wiser et al. 2013). On the other hand, indigenous tree cover is increasing on public land reserves due to replanting programmes and land purchase schemes. For example, pasture land no longer used for grazing has been bought by the Department of Conservation for a managed transition into successional scrublands (Allen et al. 2013). Also, the scientific reserve, Tiritiri Matangi, had volunteers plant over 280,000 native trees between 1984 and 1994, increasing the vegetation cover from just 6% to 60% within the ten year span (Galbraith and Cooper 2013).

1.4.2 Native population declines

Of the 12 frugivorous bird species extant before human colonisation, four seed dispersing species have since gone extinct, including two smaller-bodied moa of the *Eurapteryx* genus, following the arrival of Polynesian settlers (Anderson et al. 2006). A recent study by Carpenter et al. (2018) showed that moa species other than *Eurapteryx* were ineffective dispersers of fleshy-fruited large seeds. Invasive mammal predation and human hunting during the mid-nineteenth century were the likely causes of extinction for the seed dispersing huia (*Heteralocha acutirostris*) and the North Island piopio (*Turnagra tanagra*) (Anderson et al. 2006). The deliberate introduction of 14 exotic mammal species and many introduced bird species, in tandem with widespread land use change, resulted in severe population declines for native avifauna (Anderson et al. 2006, Innes et al. 2010, Allen et al. 2013). The legacy effects of population declines are still observed today. For example, frugivore species such as tūi (*Prosthemadera novaeseelandiae*) and bellbird (*Anthornis melanura*) are still absent from one or more mainland regions (Anderson et al. 2006, Innes et al. 2010).

New Zealand plants with small to medium-sized fruits (< 14 mm mean diameter) depend on a broad assemblage of dispersers, both native ($n = 9$) and introduced ($n = 4$), most notably tūi, bellbird, kererū (*Hemiphaga novaeseelandiae*), the native silvereye (*Zosterops lateralis*) and the introduced blackbird (*Turdus merula*) (Kelly et al. 2010). While all of these species are classified by Robertson et al. (2016) as “not-threatened”, kererū populations are conservation-dependent meaning that, if conservation management were to stop, kererū populations would decline and the species would accordingly be placed into a higher threat category (Townsend et al. 2008). Many of the other endemic seed dispersers have discontinuous distributions or are virtually extinct on the mainland, with the exception of mainland ecosanctuaries, also due to predation by invasive mammals and land use change (Anderson et al. 2006, Kelly et al. 2010, Wyman and Kelly 2017). For example, hihi (*Notiomystis cincta*), one of nine extant endemic seed dispersers, is deemed to be nationally vulnerable because it has a stable, but small, total population size ranging between 1000 – 5000 individuals. They too are conservation dependent. North Island Saddleback (*Philesturnus rufusater*) are considered “at risk” and recovering, with an estimated 10% increase in the population total over the next ten years. However, they are also conservation dependent and are confined within a total habitat area of less than 100,000 ha (Townsend et al. 2008, Robertson et al. 2016). Whitehead (*Mohoua*

albicilla) are also considered to be “at risk” but declining due to invasive species predation and land use change, with a predicted total population decline between 10% - 70% over the next ten years (Townsend et al. 2008, Robertson et al. 2016).

Conservation efforts have focused on widespread pest control and the establishment of mainland fenced sanctuaries such as Zealandia in Wellington, and offshore islands to preserve and increase populations of affected species (Galbraith and Cooper 2013). Moreover, kererū are now the main effective dispersal agents of large-seeded species (i.e., > 14 mm diameter) (Kelly et al. 2010) because North island kōkako populations are sparse, range restricted and highly dependent on conservation management (Townsend et al. 2008, Galbraith and Cooper 2013, Robertson et al. 2016). The elongated seed shape of New Zealand’s large-seeded plant species, a noteworthy characteristic of New Zealand’s flora (Lord 2004), suggests effective dispersal and fruit-size selection pressure of these plant species by medium-sized birds such as tūi.

It is likely that dispersal events of larger-seeded plants, such as taraire (*Beilschmiedia tarairi*) and karaka (*Corynocarpus laevigatus*), by medium-sized birds, such as tūi, do not occur frequently enough to maintain plant populations at their current levels in the absence of kererū. Moreover, in cases where plant species depend on a small number of frugivores, extirpation of even one of these dispersal agents may impact the quality, spatial scale and frequency of directed (non-random) seed dispersal events due to differences in habitat usage between extant species (Spiegel and Nathan 2007). Direct feeding observations of the medium-sized tūi (*Prosthemadera novaeseelandiae*) show that the fruits of the large-seeded karaka (*Corynocarpus laevigatus*) and pūriri (*Vitex lucens*) comprise a portion (Kelly et al. 2010) of their mostly nectarivorous diet (Murphy and Kelly 2001). However, within sites where tūi are abundant (Mt Tiger Bush, Whangarei and Wenderholm, Auckland), dispersal failure of karaka (*Corynocarpus laevigatus*) and taraire (*Beilschmiedia tarairi*) seeds, following a modelled extirpation of kererū, is predicted to significantly reduce recruitment rates (up to the 2-year-old seedling stage) of these two species by 66% and 81%, respectively, (Wotton and Kelly 2011).

Germination of most of New Zealand’s large-seeded flora is not dependent on avian ingestion (Kelly et al., 2010). However, Kelly et al. (2010) reported very low germination percentages for miro (*Prumnopitys ferruginea*), hinau (*Elaeocarpus dentatus*) and pūriri (*Vitex lucens*) after being planted in glasshouse and field sites.

Taraire (*Beilschmiedia tarairi*) were largely unaffected, with germination rates of 90% when dispersed by bird and 76% when fruits were uneaten and intact. The potential for reduced long-term plant fitness for some larger-fruited species, due to negative density-dependent seedling mortality effects and the lost capacity for long distance colonisation to new and regenerating environments, underscores the importance of maintaining dispersal mutualisms through the preservation of medium to large-bodied frugivore populations (Packer and Clay 2000, Howe and Miriti 2004, Wotton and Kelly 2011).

Initially, a meta-analysis of New Zealand plant-frugivore mutualisms, suggested a negligible role of introduced bird species as native plant dispersal agents (Kelly et al. 2006). However, using a network theory approach, Garcia et al. (2014) showed that introduced birds played a significant role in the dispersal of small and medium-sized native plants and increased plant-frugivore network generalisation in sites where native birds were rare or absent. This suggests that in disturbed sites, where native dispersal agents had been lost, generalist exotic dispersal agents that provide native plant functional redundancy, may offer conservationists an insurance buffer in preparation for native restoration efforts. For example, in Wrights Hill Recreational Reserve, an urban reserve in Wellington, New Zealand, blackbirds dispersed seeds of all eight fruiting species. Tūi were the only endemic species present in the local network and were found to interact with just five of the fruiting species (García et al. 2014).

1.5 Network analysis

Network theory presents ecologists with an analytical framework for addressing complex systems of interactions at the community level (Bascompte and Jordano 2014). The application of network theory to ecological systems provides the tools necessary to visualise, describe and predict network structural and dynamic properties. In network theory, a network is the depiction of a complex system whose components are represented by nodes. The interactions that connect these nodes and represented by links. In ecological networks, nodes represent species, individuals, or in the case of spatial networks, habitat patches. Similarly, in ecological networks, links often represent interactions between species (Bascompte and Jordano 2014). In this thesis, I focus on bipartite species interaction networks, where nodes represent species at two different trophic levels (plants and their avian frugivores), and links represent frequency of frugivory events between pairs of species.

1.5.1 Network theory before ecology

Early development of network theory occurred within physics, the social sciences and epidemiology before network perspectives were adopted by ecologists to investigate mutualisms. While the first application of network analysis was used in the study of the Königsberg bridge problem by Euler (1736), network theory was formalised by two mathematicians, Erdos and Renyi (1960). Network graphs are mathematical representations of a pairwise interactions between nodes. In random graphs there is equal importance between nodes in terms of the number of links they have. In reality, ecological networks (and other biological networks) exhibit a heterogenous degree distribution meaning the number of links differs between nodes, with many nodes having few links and few nodes having many links. For example, in a plant-frugivore network, often there are a few highly-connected generalist species that account for the majority of frugivory interactions, whereas the remainder of interactions are from the many less-well connected specialists.

The mathematical foundations of network theory has been demonstrably effective for understanding the dynamics of disease proliferation in populations (Auerbach et al. 1984, Klov Dahl 1985). Furthermore, it has been shown that a network perspective can inform vaccination programs, because like ecological networks, disease transmission networks exhibit a heterogenous degree distribution (May and Lloyd 2001, Meyers et al. 2003). The finding that network modularity was the mechanism driving an unexpected sub-exponential spread of Human Immunodeficiency Virus (HIV) has also informed disease transmission policy in Africa (Szendroi and Csanyi 2004).

1.5.2 Network theory in ecology

The first study that applied network theory to ecology focussed on mutualistic interactions of pollination and seed dispersal networks (Jordano 1987). This was followed by a period of stasis with ecological network research (Bascompte and Jordano 2014), largely due to the lack of statistical tools and computational power required for the progress and application of network analysis (Delmas et al. 2019). In the last 15 years however, further discoveries of structural properties of complex networks and the implications for network dynamics have been developed within disciplines of ecology. For example, Memmott et al. (2004) pioneered the use of extinction simulation models to predict the consequences of pollinator loss on plant

species biodiversity. Secondary extinction simulations, which determine the ecological consequences of species extinctions on their dependent mutualists, are now commonplace in network analysis and can provide conservation managers with the means to estimate the effects of species losses and prioritise conservation efforts accordingly (Dormann et al. 2008, Correa et al. 2016). Guimera and Nunes Amaral (2005) and Olesen et al. (2007) applied network theory to determine the importance and role of species within network modules (network subsets of highly connected species with little to no links with other compartments of highly connected species). While many species were peripheral species with few links within and outside their module of highly interacting species, a few species had disproportionately large impacts on the network structure and resilience. For example, some species were found to be connector species with many interactions outside of their own module. Modularity and species role analysis are tools within the network theory framework that allows researchers and conservation managers to identify the most important species within their network. Similarly, Saavedra et al. (2011) showed that the strongest contributors to the structure of mutualistic pollination networks were also those most vulnerable to extinction, whose absence reduced network persistence. Today, network theory is a rapidly expanding field due to its unique capacity to address ecological questions at the community level (Borrett et al. 2014, Delmas et al. 2019). Together, these examples above illustrate the utility of network theory as a tool for informing conservation practice and setting conservation priorities by addressing these networks at a community scale instead of the reductionist, species or species pair level approaches used in the past (Bascompte and Jordano 2014).

1.5.3 Inferring interaction networks

Within the last eight years, researchers have highlighted the difficulties of ensuring adequate sampling of ecological interactions within the field because the probability of observing most pairwise interactions even within a small network is very low (Dorado et al. 2011, Olesen et al. 2011, Morales-Castilla et al. 2015, Jordano 2016).

Consequently, authors have advocated for the use of predictive networks composed of inferred pairwise mutualist interactions to overcome this issue. A range of methodologies for predictive network analyses have been proposed for antagonistic (Gravel et al. 2013, Pearse and Altermatt 2013) and mutualistic interactions (Morales-Castilla et al. 2015). Gravel et al. (2013) implemented a body size relationship model based on log-predator size and log-prey sizes to infer marine predatory food web

interactions and showed a linear relationship between predator and prey body sizes. Each predator exhibited a feeding niche optimum, thus, a predator was inferred to feed on any prey whose size was within the 5% and 95% boundaries of the predators' feeding niche optimum. Morales-Castilla et al. (2015) incorporated a similar interaction probability models for food-webs but also highlighted the potential to utilise spatial co-occurrence data of mutualists (e.g., flowering plants and pollinators) to infer pairwise interactions. In addition to probabilistic models, predictive models can be developed with the incorporation of field data, scientific literature or functional traits (Delmas et al. 2019). However, to our knowledge, very few studies have put this into practice and none have done so for plant-frugivore interactions (Morales-Castilla et al. 2015, Delmas et al. 2019)

In sum, using a network theory approach in ecology provides researchers and conservation managers with the analytical framework required to address these complex interaction networks at the community scale. This approach uncovers the underlying structural properties of these networks and elucidates the resultant ecological implications for species within those networks. It results in metrics that allow us to compare relatively complex descriptions of community structure among multi-trophic communities across sites, fragments or habitats. Recent developments in network ecology have underscored the potential for inferring networks based on proxies including, but not limited to, functional traits and spatial co-occurrence data (Delmas et al. 2019). Given the high sampling intensity required by interaction sampling, which often leads to undersampling and an inaccurate depiction of the network's true structure, the ability to infer interaction networks will improve our capacity to manage threatened species and their biotic interactions which are the foundation for crucial ecological interactions and the ecosystem services which benefits us all.

1.6 Plan of the thesis

In this thesis I describe the avian species composition of Tāwharanui Regional park (TRP), a fenced sanctuary in the Auckland Region, and how this varies by habitat type. I use network theory to describe frugivore-plant interactions in TRP and to make recommendations for management. I achieved this by conducting bird and fruit counts within different habitat types throughout TRP to understand differences of bird and plant compositions across habitat types. Furthermore, I applied a network theory approach to investigate seed dispersal of fruiting plants by avian frugivores in TRP.

This was achieved by combining field observations of plant-frugivore interactions, spatial co-occurrence data derived from bird and plant counts, and data from the New Zealand literature on plant-frugivore interactions.

The objectives in this thesis are to answer the following questions:

- 1) *How do bird assemblages and plant communities differ among the habitat types at Tāwharanui Regional Park?*
- 2) *What is the structure and pattern of the plant-frugivore mutualistic networks within Tāwharanui Regional Park?*
- 3) *What is the state of avian seed dispersal within the fragmented pest-free landscape of Tāwharanui Regional Park?*

2.1 Study site, Tāwharanui Regional Park

Tāwharanui Regional Park (TRP), Auckland (36°22' 174°49') is a 588-ha area located on the Tokatu Peninsula, 90 km north of Auckland City, New Zealand (Figure 1).

Tāwharanui Regional Park, New Zealand's first open sanctuary, where species and ecosystem conservation, ecotourism and recreation are all prioritised and managed, is located within the Rodney Ecological district and managed by the Auckland Regional Council (Ritchie 2002). A predator-proof fence erected in 2004 preceded aerial brodifacoum poison drops which eradicated all invasive pests except mice (Ritchie 2002, Murdoch 2008). Intensive pest trapping by Auckland Council staff continues today to control mice populations and prevent reinvasions of all mustelids and rats. The Auckland Council employ professional hunters to control rabbit numbers. Tāwharanui Regional park is a mosaic of grazed pasture, wetlands, dunes and regenerating coastal lowland forest patches spread throughout the peninsula with the largest native forest fragments concentrated in the middle. The two indigenous conifers, kauri (*Agathis australis*) and rimu (*Dacrydium cupressinum*), comprise the emergent layer of the lowland forest patches and are abundant on the peninsula's hill crests. Approximately one quarter of the sanctuary (150 ha) is set aside as beef and sheep pasture land. The regenerating wetlands (actively being restored by the open sanctuary volunteers) are restricted to the western section of TRP, while the eastern tip of the peninsula, Tōkatu Point, is dominated by early-successional mānuka (*Leptospermum scoparium*) and kānuka (*Kunzea ericoides*) scrubland (Figure 1).

The literal translated meaning of Tāwharanui is “the abundant edible bracts of the kiekie vine (*Freycinetia banksii*)” (Murdoch 2008). As the translated meaning suggests, Tāwharanui was a resource-rich and strategic location for Māori, a point emphasised by the five fortification (pā) sites on the peninsula. The Tāwharanui peninsula has a long history of Māori occupation by several tribes (iwi) and sub-tribal groups (hapū) over the last few centuries including the iwi Ngai Tāhūhū from the 14th to 17th century and Ngāti Manuhiri and Ngāti Raupō up until the late 19th century (Murdoch 2008).

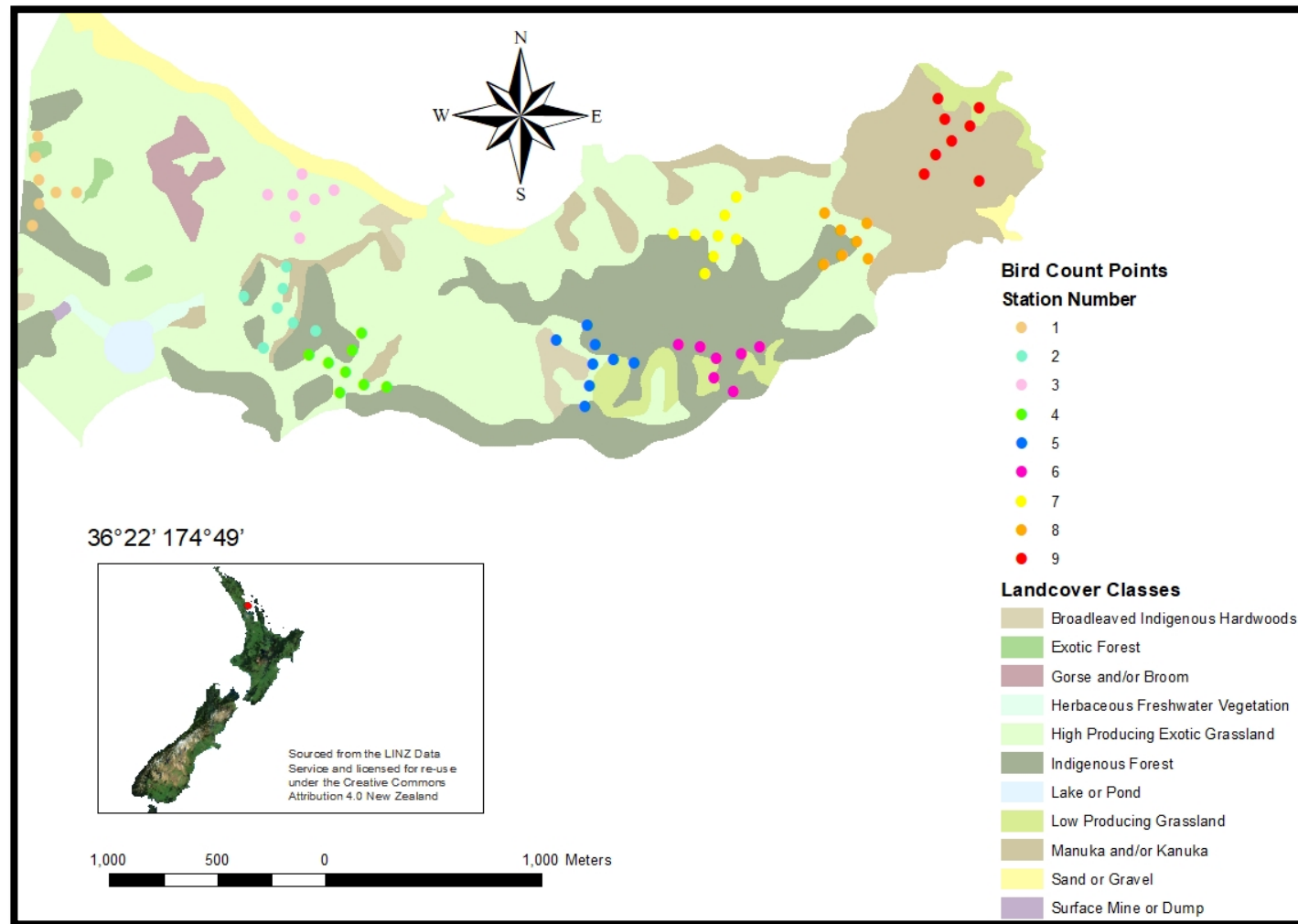


Figure 1: Tāwharanui Regional Park with New Zealand Land Cover Database (LCDB) habitat types (Landcare Research 2015). Points indicate sampling location.

2.2 Sampling station establishment

Bird and vegetation surveys, fruit counts and frugivory observations were recorded at sampling points within nine sampling stations throughout TRP. The centre sampling point of each station (i.e., the centroid point) was placed using a stratified random sampling design, to ensure adequate proportional habitat representation. Once the centre points were proportionally assigned to habitat types (mānuka, pasture and indigenous lowland forest) the nine centre points were randomly placed within the corresponding habitat using 20 equal-sized (0.6 km^2) numbered grid squares across the TRP map in ArcMap version 10.5.1 (Environmental Systems Research Institute (ESRI) 2017) and using a random-number generator to select 9 of them. The 9 selected grid squares were then further divided into 10, equal-sized numbered grid squares (0.06 km^2), with the centroid point of each station designated to the centre of the grid. Station centroids were placed no less than 400 m apart.

Each sampling station and contained up to 9 points spaced 100m apart, with point B and C, D and E, F and G and H and I placed north, east, south and west from the centre point (A), respectively (Figure 2). This station layout is an adapted version of the bird count sampling design in Mortimer and Greene (2017) which was based on the permanent plot design method by Hurst and Allen (2007). Due to the narrowness of the peninsula, a minimum distance of 100 m between point counts was selected following a preliminary field visit in January. Points were not established if they were situated on a cliff (centre points were shifted twice to avoid this) or on terrain that was too steep to access safely. Thus, not all stations contained nine points. Point coordinates were obtained in ArcGIS, saved to a handheld GPS device and marked in the field. Flagging tape was attached to surrounding fenceposts of tree branches to permanently mark point locations and assist in re-locating points during subsequent visits. Station locations were confirmed with ground truthing, a day before stations were placed to ensure that most station points could be established. A magnetic compass was used to ensure the alignment of all points in the appropriate direction and the GPS device was used to determine the approximate distances between points.

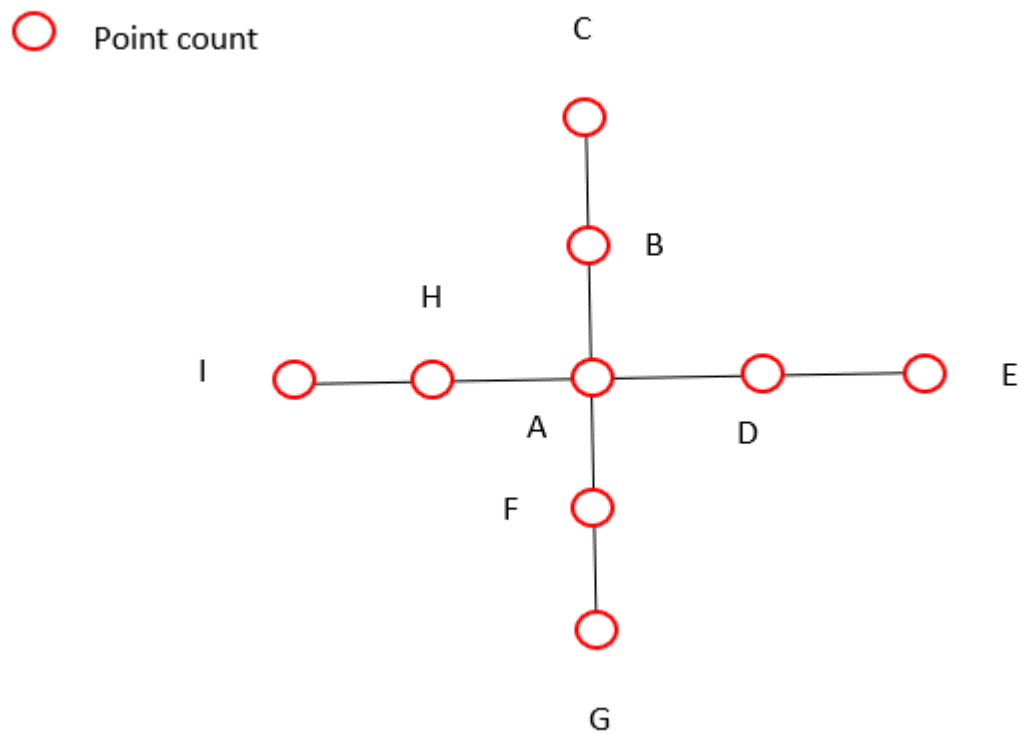


Figure 2: Point count station layout, with each point 100 m apart. Letters indicate the point count names which were always structured in a clockwise fashion.



Figure 3: Field equipment used. Five-minute bird count sheets, clipboard, Silva Ranger S Compass, Garmin Etrex GPS and Bushnell Natureview 8 ×40 Binoculars. Funaki, 2018.

2.3 Vegetation surveys

Upon setting up sampling points, I first undertook a vegetation assessment at each sample location, to determine the vegetation structure and composition of all points. These points were assessed within a circular plot of 10 m radius using a semi-qualitative plant species abundance scale within height-tiers adapted from Hurst and Allen (2007). I visually estimated the percent ground cover of each point below 1.35 m (Diameter at Breast Height, DBH) using 5 classes (V–Vascular vegetation including live tree roots, NV–Non-vascular vegetation, L–Leaf litter, dead logs and branches, ER–exposed rock and ES–exposed soil). I visually estimated the average top height of the dominant canopy species at each point. In addition, I visually estimated the percent canopy cover as the percentage of sky overhead covered by vegetation at each point. I visually estimated the height of all woody tree species at each point, classified into 6 height-tier layers (> 25 m, 12–25 m, 5–12 m, 2–5 m, 30 cm–2 m and < 30 cm), including an estimate of the total percent cover per tier.

2.4 Bird surveys

All seabirds and terrestrial birds were counted using five-minute bird count surveys, a suitable multi-species sampling method for determining relative abundances effectively, particularly within densely vegetated habitats including forests and scrublands (Bibby et al. 1992). Unlike line transects, point counts do not require full access along the sampling transect and adjacent area, meaning steep, inaccessible terrain can be avoided on the way to a point and, due to the sessile nature of the method, is suitable for detecting cryptic and quiet species (Sutherland et al. 2004). Surveys were repeated once a month for 5 months over the summer and autumn of 2018. Each sampling point was sampled between 0730–1730 once a month between early February and late June 2018, except in dangerous weather or rain, because birds are more likely to be less active during these times, i.e., reduced movement and calling. All points within a station were sampled in the same order every time based on ease of access, to reduce time between counts. However, the order that stations were sampled in was randomised by drawing the order from a hat the night before sampling occurred.

Upon arriving at each point, I waited for one minute (a settling period) and then proceeded to count all birds heard and seen for 5 minutes along with their corresponding estimated distance using 5 distance interval bands (0–15 m, 15–30 m, 31–45 m, 46–60 m and > 61 m). All observations were recorded on five-minute bird

count sheets (Department of Conservation 2018) which were customised to incorporate ground cover and canopy-height vegetation parameters (Hurst and Allen 2007) for the February sample, for vegetation composition analysis.

2.5 Fruit counts and frugivory observations

At every site visit, fruit counts were made along 100 m transects at and between sampling points of each station, to determine the availability and abundance of bird-dispersed fruits. Up to four 100 m transects were established at each sampling station, depending on the availability of surrounding non-pasture land within the 100 m radius of the site. The fruit count sampling method was adapted from García et al. (2013) and involved walking along the transect and recording all individuals of all fleshy-fruited woody tree species within 10m on either side of the transect. The semi-quantitative Fruit Abundance Index (FAI) (1–10, 11–100, 101–1000, 1001–10,000, > 10,000 fruits) of García et al. (2014) was used to estimate fruit crop size for each fruiting individual. Only ripe and near-ripe fruits were counted based on a visual qualitative assessment of ripeness (Figure 3). All FAI results were converted to mid-interval values and summed per plant species per station. Fruit count transects were conducted once per month (February to June).

Table 1: The start and end points for the 100 m fruit transects per sampling station. Letters represent bird point count locations. The number of transects per station was dependent on the proportion of surrounding forest cover.

Station number	Transect start and end point			
	1	2	3	4
1	B-C	F-G		
2	B-C	D-E	H-I	
3	A-B	A-D	D-E	A-H
4	A-B	A-F	A-H	H-I
5	A-B	B-C	D-E	F-G
6	A-D	D-E	A-H	H-I
7	A-B	A-D	F-G	H-I
8	A-F	A-H	F-G	H-I
9	A-B	A-D	F-G	H-I



Figure 4: Image of ripe and unripe drupes of taupata (*Coprosma repens*) in Tāwharanui. As only ripe fruits (red fruits) are counted, this individual received a Fruit Abundance Index (FAI) value of two (11–100 ripe fruits). Ter Huurne, 2018.



Figure 5: Image of karo (*Pittosporum crassifolium*) in Tāwharanui counted during a fruit transect. Only open capsules (capsules showing small black berries) were counted. FAI values were based on individual capsules, not on the number of seeds within, therefore this tree would receive a FAI of one (1–10 fruits). Funaki, 2018.

I conducted standardised direct observations of frugivory to determine pairwise interactions between frugivores and fruiting plants at TRP. Frugivory observation methods were adapted from García et al. (2014). Observations were conducted along the same transects used for the fruit counts because the identity and the availability and abundance of fruiting species had been quantified. Frugivory observations began immediately after a fruit transect was completed. Frugivory observation sampling involved walking slowly along each transect at a steady pace (c. 1 km/h) and searching for perched birds in trees within 10 m either side of the transect using binoculars (Bushnell Natureview 8 × 40). Once a perching bird was spotted, I recorded the number of fruits consumed per frugivory event until it was lost in the foliage or it flew away. A frugivory event was only counted if the observed bird was observed swallowing the fruit completely, confirmed using binoculars from a distance no greater than 8m. Each frugivory observation transect was sampled at least once per monthly sampling period and revisited (twice per month, 2–3 days apart) if any fleshy-fruiting individuals were recorded along the transect during the fruit count sample.

2.6 Data analysis

2.6.1 Species accumulation curves

For each sampling month ($n = 5$) bird count data in a matrix format (site × species) was imported into R (R Core Team 2017). I used the function *specaccum* from R package *vegan* 2.5-2 (Oksanen et al. 2018) to create sample-based species accumulation curves for each sample month for all sites and per habitat type (pasture, edge, bush and mānuka). I did this to evaluate whether the sampling effort was adequate for detecting all species present and for making robust estimates of avian species richness at all sampling sites and the TRP as a whole.

2.6.2 Estimating relative abundances of birds and fruit

The total relative abundance of each bird species was estimated using the summed abundance of the species seen and heard pooled across all stations and sampling dates and dividing by the pooled total abundance (across all stations and sampling dates) of all species combined. The relative abundance of each plant species was estimated by taking the sum of the midpoints of the estimated fruit abundances for each species and dividing it by the pooled total abundance of all species combined (total absolute abundance).

2.6.3 *Bray-Curtis dissimilarity ordinations for habitat- vegetation and habitat-bird composition*

I created a species composition matrix per point for plant and bird species. Using the *vegdist* function in the R package *vegan* 2.5-2. Bray-Curtis dissimilarity matrices were derived from the bird and vegetation data and used to create principal coordinate analysis ordinations to calculate and visualise the differences in vegetation and bird species composition between sites at the level of the habitat type (bush edge, bush interior, mānuka edge, mānuka interior and pasture interior). Points were coloured by habitat type.

2.6.4 *Species richness*

Generalised Linear Mixed Models (GLMMs) with a negative binomial distribution were used to investigate the effect of habitat and measured abiotic factors on bird species abundance and richness. This is the most suitable model for accounting for the overdispersion in the model errors and considering non-independent hierarchical data (Gotelli and Graves 1996). Month of sampling and sampling station were included in the model as random effects to account for pseudo-replication and non-random variation associated with month and sampling points. The GLMMs were created and analysed using the R package *lme4* (Bates et al. 2015). There were two habitat related variables included in the model and three abiotic variables. The habitat-edge variable included six levels (bush edge, bush interior, mānuka edge, mānuka interior and pasture interior) to test the effect of habitat type and edge on species richness. Percent canopy cover was included in the model because higher canopy cover was hypothesised to be a suitable proxy for habitat heterogeneity and was expected to increase the amount of habitat available for predator avoidance behaviour. The abiotic variable temperature included a six level scale (freezing < 0 °C, cold 0–5 °C, cool 6–10 °C, mild 11–15 °C, warm 16–22 °C and hot > 22 °C), while minutes of sun included the minutes of direct sunlight observed during point counts (0–5 minutes of direct sunlight per point). Wind strength included four levels (0 – leaves still, 1 – leaves rustle, 2 – leaves and branches in constant motion and 3 – trees swaying). Higher relative temperatures, low amount of direct sunlight and high wind strength were all expected to reduce avian species richness, and in the case of wind, potentially reduce the likelihood of hearing or accurately identifying bird calls. All variables were included in the final full model and significant variables were determined using the *lme4* package *drop1* ANOVA function

including the chi-squared likelihood-ratio test statistic. The R package emmeans 1.2.4 (Lenth 2018) was used to distinguish the influence of the habitat-edge type variable with numerous levels.

2.7 Analysis of the potential interaction networks

To address research objectives two and three, network analysis was used to analyse the two inferred plant-frugivore networks in TRP. Due to low detection rates and the overall undersampling of frugivory interactions, two potential plant-frugivore networks were created in R using the co-occurrence data obtained from point counts and fruit counts. These interactions were weighted by the frequency of co-occurrences between each plant-frugivore pair within the specified maximum distance, either long-distance (< 30 m) or short-distance (< 15 m), resulting in an interaction frequency for each pairwise interaction. Pairwise plant-frugivore interactions can be inferred by combining prior knowledge on traits and dispersal ecology with the co-occurrence data to estimate potential mutualisms (Ovaskainen et al. 2010, Araujo and Rozenfeld 2014, Morales-Castilla et al. 2015). The first potential network counted a potential interaction when an observed bird was within 30 m of a point with a fruiting individual present. The second network counted a potential interaction when an observed bird was within 15 m from a point with a fruiting plant individual present. Before any given interaction was permitted in the network, it was cross-referenced against a list of *a priori* plant-frugivore interactions derived from the literature on New Zealand bird-plant interactions. This allowed us to filter out previously unobserved links, thus implicitly accounting for some “forbidden links” (Bascompte and Jordano 2014, Morales-Castilla et al. 2015), i.e., ecologically impossible pairwise interactions. For example, due to a size mismatch, a silvereye is far too small to swallow the large fruits of a taraire tree, so this pairwise interaction was not permitted in the networks.

All network metric analyses and plotting functions were conducted in R (R Core Team 2017) using the network analysis packages bipartite 2.08 (Dormann et al. 2008) and tnet (Opsahl 2009) and utilised features and functions derived from community ecology R packages vegan 2.4-6 and labdsv 1.8-0 (Roberts 2016) and the formatting packages tidyverse 1.2.1 (Wickham 2017) and readxl 1.1.0 (Wickham and Bryan 2017). I visualized the network of observed interactions in matrix and bipartite graph formats using the bipartite 2.08 functions *visweb* and *plotweb*. The bipartite graph format

illustrated the relative abundances of each species using the function arguments *high.abun* and *low.abun*, for the higher (birds) and lower (plants) levels, respectively.

The species degree (the total number of species connections of a species) (Bascompte and Jordano 2007), their corresponding cumulative frequency distributions and best-fit lines for the three models (exponential, power-law and truncated power-law) were calculated and plotted for both levels using the function *degreedistr* to determine whether the inferred co-occurrence networks exhibited a broad-scale (truncated power-law) degree distribution, a commonly reported pattern within mutualistic networks with significant ecological implications, including a network's robustness to disturbance (Albert et al. 2000, Jordano et al. 2003). This broad-scale distribution results from a network with a small minority of highly connected species and many weakly-connected species.

Specialisation (d') values for each plant and bird species was calculated using the bipartite 2.08 function *dfun*, to estimate the degree of functional redundancy within the network. Low overall mean d' values for avian frugivore species within a network would suggest that the birds diets overlap, and are therefore comprised of many of the same fruit plants, thus increasing network resilience to perturbation (Correa et al. 2016). Specialisation values were also used to assess the role of each species within a network, based on the availability and interaction frequency between interacting partners from the other trophic level (Dormann 2011). Relative abundance estimates from the point count data were used, rather than the default method, which estimates abundances derived from column or row sums for higher level and lower level species, respectively. In cases where independent abundances are not included, the default method can skew the estimate of specialisation. For example, a plant whose seeds are regularly dispersed by a rare frugivore (the frugivore being a common visitor only to that plant) would incorrectly be assigned a low specialisation value (a generalist) when in reality, the plant was a specialist, which should have received a high specialisation value. I plotted the distribution of species d' values for both levels using package *ggplot2* (Wickham 2009) to investigate inter-level similarities and differences of specialisation in the two networks (Bluthgen et al. 2007).

I used the function *H2fun* to calculate the overall degree of specialisation for the entire network ($H2'$), the network-level extension of function *dfun* (Dormann 2011). To assess the statistical significance of the network specialisation ($H2'$) values of the observed

network, I used the function *vaznull* to generate 999 null models for comparison. Comparisons with null models confirm whether the structure of the potential networks is statistically more nested than null model networks of random interaction association (Gotelli and Graves 1996) as it is possible that the observed metric of interest (e.g., nestedness or modularity) is simply a product of the networks size or number of links (connectance) (Dormann et al. 2008, Fortuna et al. 2010). The *vaznull* function produces networks with a randomised number of interactions between species-pairs but fixes the number of links to ensure it is identical to the inferred networks (Vazquez et al. 2007). The algorithm produces a binary matrix that ensures all species are involved in at least one interaction. Once the number of filled cells matches the total number in the inferred network, the rest of the interactions are then randomly assigned until the connectance of the randomised matrix matches the connectance of the inferred network (Vazquez et al. 2007). Null models that fix and constrain marginal totals are prone to failing to reject the null hypothesis. In other words, they are less likely to detect significant nestedness in a network by committing a type II error (accepting the false null hypothesis) (Ulrich and Gotelli 2007). Nonetheless, they are less affected by network size compared to probabilistic null models and are less vulnerable to type I errors (falsely rejecting a true null hypothesis), recognised as a priority for interaction network null models (Ulrich and Gotelli 2007, Fortuna et al. 2010).

I analysed the degree of nestedness of the two overall inferred networks. A nested pattern arises in networks that comprise a small core of interacting generalists (the highly connected species), with specialists (the least connected species) interacting with species within the generalist core and not among themselves. This leads to an asymmetric pattern of interactions, in which a few species have the most links. For example, this occurs when a plant species is highly dependent on one frugivore for dispersal but the frugivore in question relies on multiple plant species for its food. Conversely, an asymmetric interaction may result from a frugivore that specialises on a plant species that relies on multiple frugivores for dispersal (Jordano 1987, Bascompte et al. 2003). High nestedness is a common structural feature in bipartite mutualistic networks, with direct implications for ecological function resilience, resulting from both the increased capacity for functional redundancy (attributed to the core of highly connected generalist species) and the inherent asymmetric pattern of specialisation, which supports the continued survival of specialists (Bascompte et al. 2003, Memmott et al. 2004, Bascompte et al. 2006, Bascompte and Jordano 2007). I used the bipartite

2.08 function *nested* and the function arguments *method* = “*weighted NODF*” to analyse the degree of nestedness within the network using the quantitative measure of the nestedness metric. The weighted NODF values were compared to values of 999 randomised null model networks created using the bipartite 2.08 function *vaznull*. In addition, I used the bipartite 2.08 function *nestedcontribution* to determine the nodes (species in ecological networks) that are significant contributors to network nestedness, which have been shown to be the most vulnerable to extinction in pollination networks and also within a large a non-ecological network within the clothing industry (Saavedra et al. 2011). Nestedness contributions are the *z*-scores produced from the comparison between the observed nestedness and values of nestedness from 999 probabilistic null models, derived from interaction randomisations for each bird and plant species. Thus, positive *z*-score values indicate species that actively contribute to the nestedness of the network they inhabit (Saavedra et al. 2011).

I used the bipartite 2.08 functions *ComputeModules*, *czvalues* and *plotModuleWeb* to calculate, identify and plot the presence and identity of modules (network subsets of highly connected species with little to no links with other compartments of highly connected species) (Olesen et al. 2007) in the two potential networks. The *czvalues* function produces the within-module degree and among-module connectivity value for each species of the network. These two properties define the role of each species within modules and determine the module hubs, network hubs, connector species and peripheral species within networks (Guimera and Nunes Amaral 2005). By determining the role of species within networks, conservation priorities can be established, by focusing on the species with disproportionate ecological influence. Both types of hub species have a within-module degree (*z*) above 2.5 but are differentiated based on whether they have an among-module connectivity value below 0.62 (module hubs) or above 0.62 (network hubs) (Olesen et al. 2007). Therefore, while module hubs are important connectors within their module only, network hubs are highly connected hubs for the entire network. Connector hubs have low within-module degrees ($z < 2.5$) but a high among-module connectivity ($c > 0.62$) and thus connect modules that would otherwise be isolated in their absence, whereas peripheral species have low within-module degrees ($z < 2.5$) and a low among-module connectivity ($c > 0.62$) (Olesen et al. 2007). Thus, they have few interactions either within or outside of their module. The modularity value of the potential networks was then compared to values of generated

null model networks created using the bipartite 2.08 function *vaznull* to determine the statistical significance of the metric values.

I investigated the presence of the properties of the small-world phenomenon - high clustering coefficients and short average path lengths - within the overall inferred networks (Watts and Strogatz 1998). The term “small-world” originates from the social network analysis conducted by Milgram (1967), who investigated the average number of links separating two randomly selected strangers from different states within the United States, giving rise to the now popular phrases “six degrees of separation” and “what a small world” (Bascompte and Jordano 2014). A path length is defined as the number of links in the shortest path between species, whereas a clustering- coefficient describes the degree of compartmentalisation of a network subset, whereby a high proportion of the connections of a particular node are also connected to other nodes. Essentially, the clustering coefficient is a ratio expressing the proportion of existing links between a nodes neighbours, relative to the highest possible number of links allowed within the subset (Milgram 1967, Watts and Strogatz 1998). As each species-pair within a network exhibiting both small-world properties will be closely linked, any ecological disturbance to one species can be spread throughout the network to impact other species (Bascompte and Jordano 2014). Small-world analysis was conducted on a projected one-mode network. In a projected network, using the bipartite 2.08 function *projecting_tm*, nodes are linked if they both share an interaction with a node from the other level. For example, two frugivores (e.g., kererū and tūi) are linked within the one-mode depiction of the bipartite network if they both have a plant species they interact with (e.g., cabbage tree *Cordyline australis*). I used tnet 3.0.14 (Opsahl 2009) functions *clustering_tm* and *distance_tm* to calculate the species clustering coefficients and path lengths, respectively.

Memmott et al. (2004) investigated the robustness of mutualistic plant-pollinator mutualistic networks under multiple extinction scenarios, by sequentially removing pollinator species to determine the proportion of cumulative secondary extinctions of dependent plant species. Like the network analysis tools above, secondary extinction models can be used to determine the ecological robustness of the potential seed dispersal networks, thus highlight conservation priorities for practitioners. I replicated the methods used in Memmott et al. (2004) by using the bipartite function *second.extinct* to remove one species at a time, following three different extinction

sequences: random order species removal (the null model) (Memmott et al. 2004) and two systematic removal sequences including removal of the most to least-specialised frugivore and the inverse scenario where the least specialised species are removed first. These sequences were determined by using the bipartite function *species level* and function argument *index = "degree"* (Dormann 2011) to calculate the most to least connected species within the overall network, by calculating species degrees (number of links). Although resilient to random species extinctions, networks with heterogeneous connectivity distributions (i.e., a small core of highly connected species with many weakly connected species) are susceptible to collapse, following the loss of the most connected species (Albert et al. 2000, Bascompte and Jordano 2014). On the other hand, removal of the least connected species first seeks to determine whether the least connected, and therefore the most specialised frugivores, are the rarest and consequently the most vulnerable to extinction, as reported for pollinators in plant-pollination networks (Dunne et al. 2002, Memmott et al. 2004). To see if this was the case for frugivores in the potential networks, I modelled the extinction sequence of the rarest to most abundant frugivores for comparison.

2.8 Habitat type potential networks

Finally, a loop was constructed in R using the pooled (all sample points spanning the whole sampling period) co-occurrence data to produce a potential network per habitat type and to calculate the species specialisation (d') values, cluster coefficients, weighted NODF and network specialisation ($H2'$) values for bird and plant species within these potential habitat networks, to investigate the effect of habitat type on the seed dispersal potential network structure and composition.

3.1 Bird surveys

A total of 1,958 individual birds were counted during the sampling period, comprising 34 bird species; 23 species were native and/ or endemic and 11 were introduced species (Table 2). The most abundant species overall was the endemic bellbird (*Anthornis melanura*), followed by the native pūkeko (*Porphyrio melanotus*), which were numerous in pasture points. The common myna (*Acridotheres tristis*) was the most abundant introduced species and the 11th most abundant species overall, meaning TRP was dominated by native and endemic species rather than exotic species.

Table 2: List of all bird species observed at TRP. Relative abundances of all species are given, obtained from 69 points and sampled five times, once per month between February and June. Mean gape size (mm) (Kelly et al. 2010) and mean body size (g) (Robertson and Heather 2005) are given for all fruit-eating birds.

Common name	Scientific Name	Body (g)	Gape (mm)	Relative Abundance (%)
Bellbird	<i>Anthornis melanura</i> Sparrman (1786)	30	6.5	0.255
Pūkeko	<i>Porphyrio melanotus</i> Temminck (1820)			0.213
Tūi	<i>Prosthemadera novaeseelandiae</i> Gmelin (1788)	105	9.7	0.112
Fantail	<i>Rhipidura fuliginosa</i> Sparrman (1787)			0.109
Welcome swallow	<i>Hirundo neoxena</i> Gould (1842)			0.057
Saddleback	<i>Philesturnus rufusater</i> Lesson (1828)	75	7.1	0.054
Grey warbler	<i>Gerygone igata</i> Quoy & Gaimard (1830)	6.5	5	0.030
Kererū	<i>Hemiphaga novaeseelandiae</i> Gmelin (1789)	650	14	0.020
Whitehead	<i>Mohoua albicillia</i> Lesson (1830)	27	5	0.016
Paradise shelduck	<i>Tadorna variegata</i> Gmelin (1789)			0.016
Common myna	<i>Acridotheres tristis</i> Linnaeus (1766)	125	13	0.015
Kaka	<i>Nestor meridionalis</i> Gmelin (1788)			0.012
Rosella	<i>Platycercus eximius</i> Shaw (1792)			0.011
North Island robin	<i>Petroica longipes</i> Garnot (1827)			0.011

Spur winged plover	<i>Vanellus spinosus</i> Boddaert (1783)				9.6×10^{-3}
Pied shag	<i>Phalacrocorax varius</i> Gmelin (1789)				9.1×10^{-3}
House sparrow	<i>Passer domesticus</i> Linnaeus (1758)				7.1×10^{-3}
Magpie	<i>Cracticus tibicen</i> Latham (1802)				6.6×10^{-3}
Red billed gull	<i>Chroicocephalus novaehollandiae scopulinus</i> Stephens (1826)				5.6×10^{-3}
Kingfisher	<i>Todiramphus sanctus</i> Vigors & Horsfield (1827)				4.5×10^{-3}
Takahe	<i>Porphyrio hochstetteri</i> A.B. Meyer (1883)				4.0×10^{-3}
Kahu	<i>circus approximans</i> Peale (1848)				2.5×10^{-3}
Blackbird	<i>Turdus merula</i> Linnaeus (1758)	90	9.7		1.5×10^{-3}
Goldfinch	<i>Carduelis carduelis</i> Linnaeus (1758)				1.5×10^{-3}
Silvereye	<i>Zosterops lateralis</i> Latham (1802)	13	5.1		1.5×10^{-3}
Yellowhammer	<i>Emberiza citrinella</i> Linnaeus (1758)				1.5×10^{-3}
Black backed gull	<i>Larus dominicanus</i> Lichtenstein (1823)				1.0×10^{-3}
Brown quail	<i>Coturnix ypsilophora</i> Bosc (1792)				1.0×10^{-3}
Kakariki	<i>Cyanoramphus novaezelandiae</i> Sparrman (1787)				1.0×10^{-3}
Pipit	<i>Anthus novaeseelandiae</i> Gmelin (1789)				1.0×10^{-3}
Californian quail	<i>Callipepla californica</i> Shaw (1798)				5.1×10^{-4}
Pheasant	<i>Phasianus colchicus</i> Linnaeus (1758)				5.1×10^{-4}
Song thrush	<i>Turdus philomelos</i> Brehm (1831)	70	12.2		5.1×10^{-4}
Tomtit	<i>Petroica macrocephala</i> Gmelin (1789)				5.1×10^{-4}

3.2 Avian species accumulation curves

The overall species accumulation curve for all bird species (Figure 6) showed that the total sampling effort made was adequate to estimate avian species abundance and richness. The accumulation curve approached an asymptote at the point where 58 points had been sampled. The difference between randomised avian species richness versus the expected avian species richness results using the *exact* method was small. For example, at 10 sites for the total avian species accumulation curve, the randomised species

richness was 19.88 species (± 2.51 standard deviation, SD), whereas the expected species richness was 20.31 species (± 2.66 SD). At 20 sites, the randomised species richness was 24.65 (± 2.36 SD) while the expected species richness was 24.96 species (± 2.60 SD). These patterns were also evident species accumulation curves when broken down into habitat types and months (Appendix 2, Figure 21-Figure 28) even considering small monthly differences of point count sampling intensity due to rain periods.

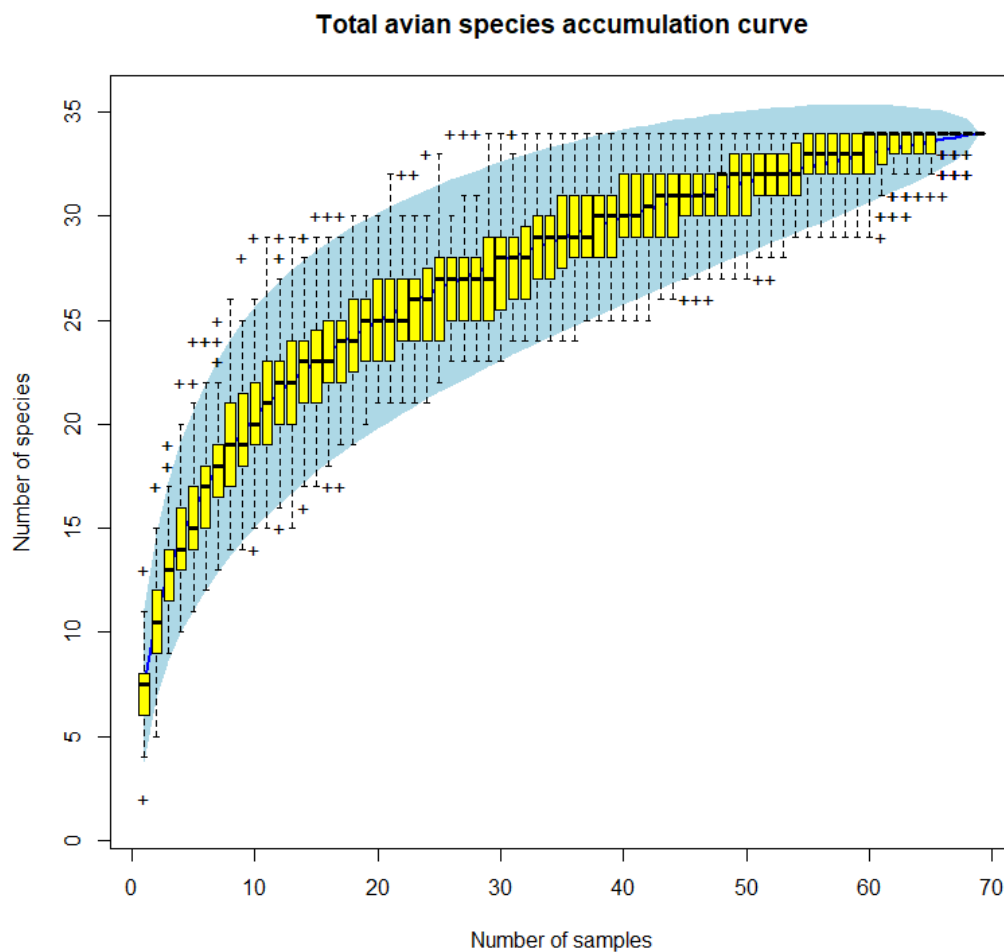


Figure 6: Total species accumulation curve for bird species sampling between February and June 2018. The blue shading indicates the range of predicted species richness values. The yellow boxplot centre line represents the median species richness per sample while the yellow boxplot represents the interquartile range, calculated from random permutations of the data. The boxplot whiskers are 1.5 times the interquartile range.

3.3 Bray-Curtis dissimilarities

Differences in plant communities at each sample point were highlighted by the principle coordinate ordinations of Bray-Curtis dissimilarity values (Figure 7). The first axis (PCO1) explained 48% of the vegetation composition variation, while the second (PCO2) explained a further 14% of the variations in plant community composition.

Points inside mānuka-dominated forest (mānuka interior points) were the most similar in composition to each other, shared compositional similarities with many mānuka edge points (points on the boundary of mānuka forest and pasture), and were concentrated at the higher end of the PCO2 axis. Mānuka edge sites were dominated by mānuka, but also included five fruiting species and typically supported many māpou (*Myrsine australis*) individuals. Mānuka interior sites were dominated by mānuka and only included a few hangehange (*Geniostoma ligustrifolium*) individuals. Bush edge and bush interior sites were quite variable regarding their vegetation composition, with several bush edge points having a similar composition to mānuka edge points. Bush edge and bush interior sites occurred at the central and lower end of the PCO2 axis. Bush edge sites supported 11 fruiting species (Appendix 1 Table 16) and were dominated by māpou and cabbage tree (*Cordyline australis*), but also included several large pūriri (*Vitex lucens*), nīkau (*Rhopalostylis sapida*), karo (*Pittosporum crassifolium*) and kawakawa (*Macropiper excelsum*). Bush interior sites supported 9 fruiting species (Appendix 1 Table 16) and were dominated by māpou, pūriri and large taraire (*Beilschmiedia tarairi*), and was also the only habitat type that contained kāraka (*Corynocarpus laevigatus*). Because there were no fruiting tree species present, all pasture sites were identical to each other.

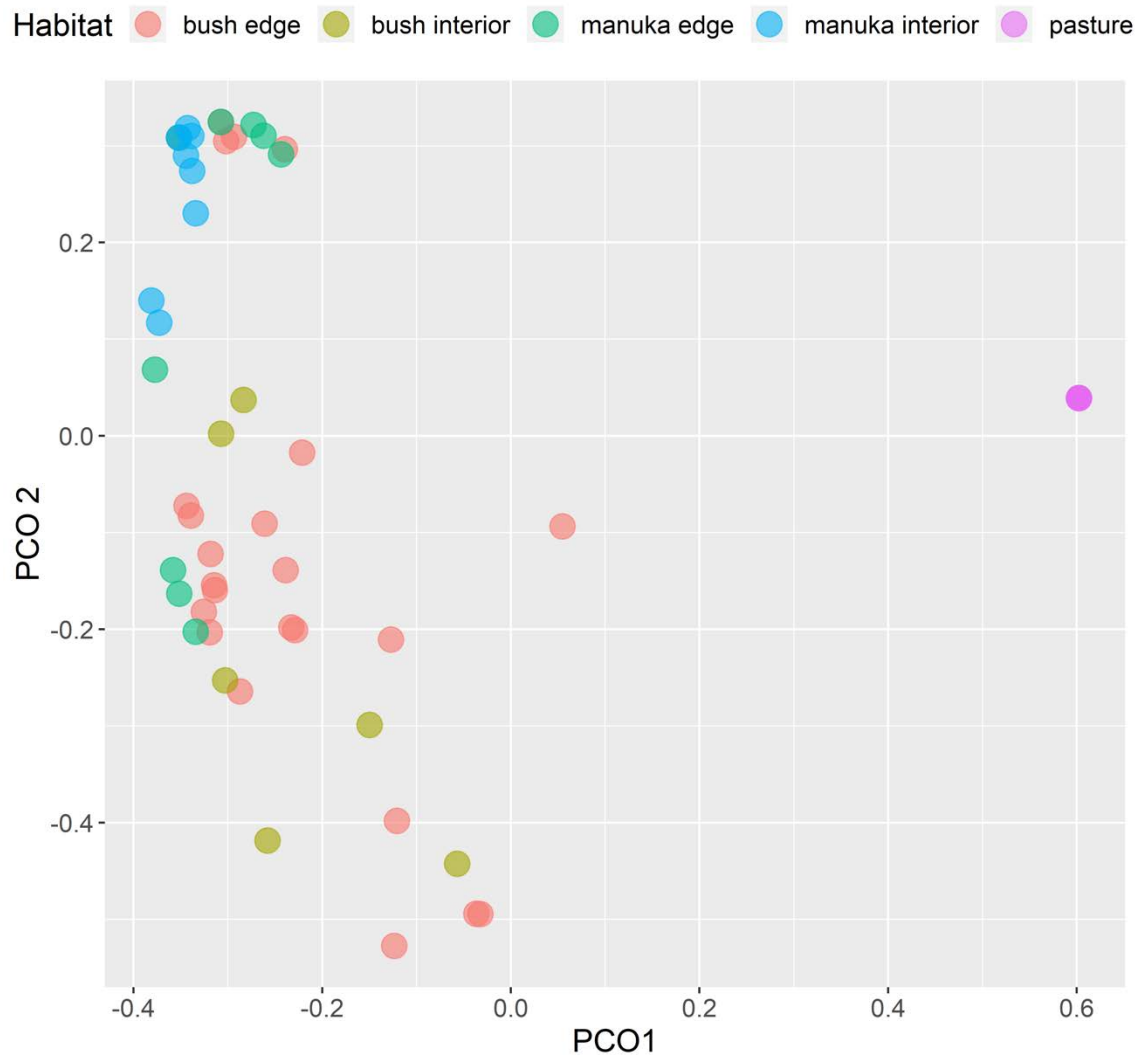


Figure 7: Principal coordinate analysis biplot of Bray-Curtis dissimilarities between sample locations, showing the differences in habitat type vegetation composition between all sampling points, with close points being more similar in vegetation composition than those separated by a greater distance.

Bray-Curtis dissimilarity ordinations of bird abundances at sample points showed that the PCO1 axis explained 35% of the bird composition variation, while PCO2 explained 10% of the bird composition variation. While plots occurring within habitat types with greater floristic richness (i.e., bush interior and edge sites) were at the higher end of the PCO1 axis, there was no distinct pattern of point distribution by habitat type visible along the PCO2 axis. Mānuka interior points were the most similar to each other, relative to other habitat types due to their very low species richness. Mānuka edge points and pasture interior points both showed a high within-group variation of bird species composition. Certain pasture interior points are located in a space along the

PCO1 axis that no other habitat type occupies indicating that certain bird species, such as paradise shelduck and spur winged plover, were unique to pasture interior points.

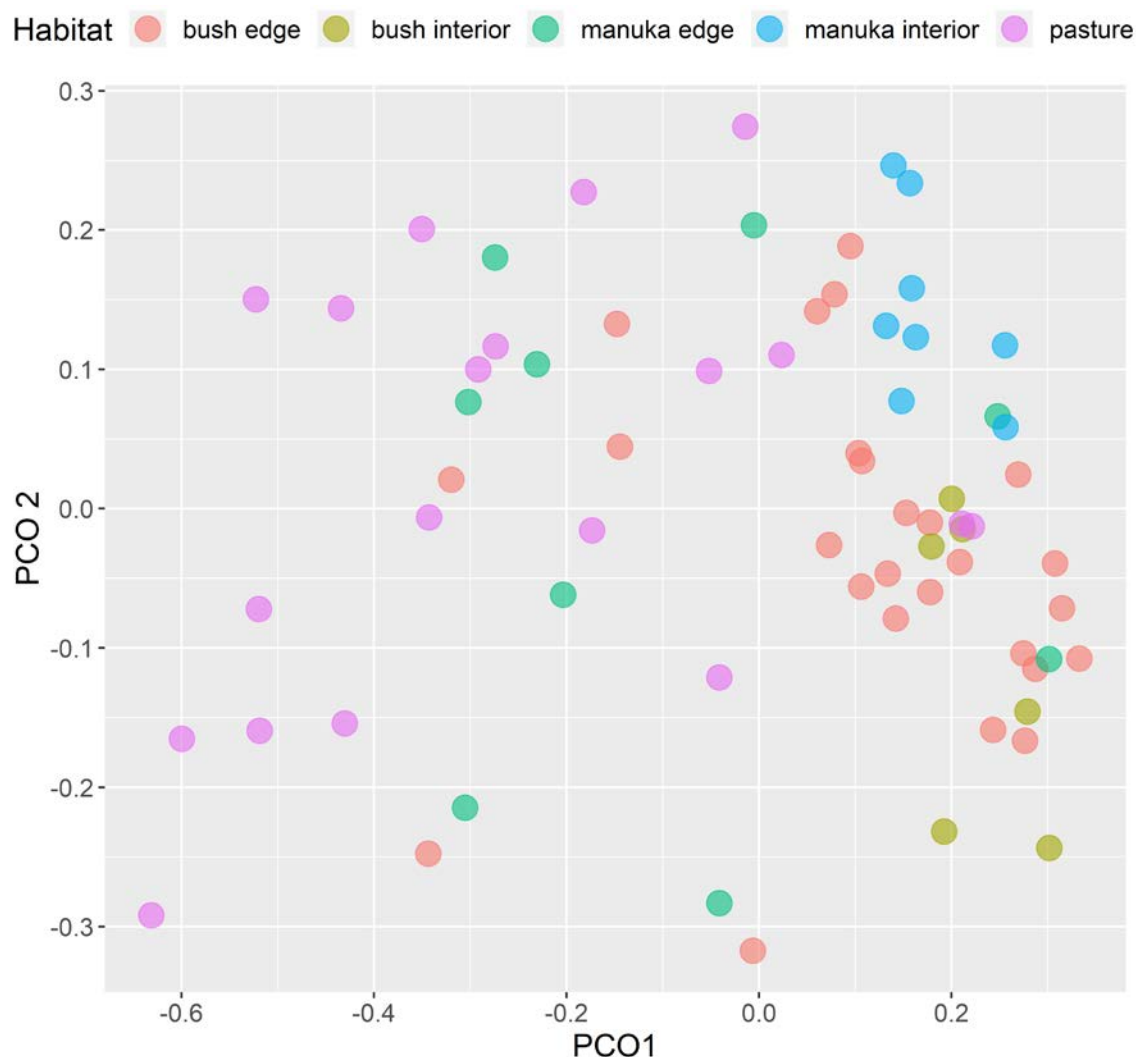


Figure 8: Principal coordinate analysis biplot of Bray Curtis dissimilarities showing the differences in habitat type bird composition between all sampling points (pooled across all times), with close points being more similar in bird composition than those separated by a greater distance.

3.4 Frugivory transects

In total, 255 fruiting individuals, of 14 bird-dispersed plant species were recorded within the fruit transects during the sampling period (Table 3) All recorded fruiting species were either native or endemic to New Zealand. Cabbage tree (*Cordyline australis*) was the species with the greatest relative fruit abundance, closely followed by māpou (*Myrsine australis*), which dominated the understory of many bush edge points. Pūriri (*Vitex lucens*) comprised 15% of the total fruit abundance and were found in bush edge and bush interior points with a couple of isolated individuals within pasture points.

Station four had the highest average fruit abundance throughout the sampling period with a mean 1,902 fruits, followed by station one with a mean 1,639 fruits (Table 3). Stations five and six, predominantly comprising bush interior and bush edge points, had a mean fruit abundance of 1,079 fruits and 973 fruits, respectively. Station two had a low fruit abundance with a mean of 126 fruits, while station nine had the lowest mean fruit abundance with a mean 55 fruits, as this station was dominated by mānuka. Station eight (transect A–F) and station five (transect F–G) contained the highest fruit abundance recorded per transect, with a mean of 5,500 fruits, both due to a singular cabbage tree (*Cordyline australis*) with a high fruit crop during the March sample. Station four (transect H–I) had the second-highest fruit abundance, with a mean of 4,411 fruits due to consistently high māpou and cabbage tree fruit yields throughout the sampling period.

Table 3: Total mean fruit abundance (mean) per station and per transect, including standard deviation (SD) and standard error (SE).

Station & transect	Mean	SD
Station 1	1,639	2381
B–C	1,625	2496
F–G	1,658	2382
Station 2	126	211
B–C	154	265
D–E	38	25
F–G	550	NA
H–I	124	239
Station 3	823	1426
A–B	813	1348
A–D	967	2013
D–E	778	1437
Station 4	1,902	2519
A–F	1,006	1918
H–I	4,411	2435
Station 5	1,079	1896
A–B	2,901	3007
B–C	862	1680
D–E	752	1516
F–G	5,500	NA
Station 6	973	1856
A–D	1,980	2647
A–H	550	NA
D–E	189	247
H–I	342	285

Station 7	773	1564
A–B	761	1593
A–D	1,216	2132
F–G	550	NA
H–I	269	266
Station 8	785	1507
A–F	5,500	NA
A–H	1,039	1817
F–G	220	285
H–I	325	258
Station 9	55	NA
F–G	55	NA

3.5 Species abundance and richness

The GLMMs of native species abundance showed strong effects of weather. Minutes of sun had a significantly positive effect on native species abundance, while wind strength had the greatest significant (negative) effect on native abundance (Table 4, Figure 9a). Habitat type had no significant effect on all native species abundance or richness. For native species richness, only wind strength had a significant negative effect (Figure 9b, Table 4).

The GLMMs of all frugivore abundance showed a strong effect of habitat type and weather. Habitat-edge type had a strong positive effect on frugivore species abundance while wind had a negative effect on frugivore abundance (Table 4, Figure 9c). Bush edge points had significantly greater frugivore abundance than pasture interior and mānuka edge points, while bush interior points had greater frugivore abundance than pasture interior points (Table 5, Figure 5). Similarly, the GLMMs of all frugivore species richness showed a strong positive effect of habitat-edge type. Bush edge points and bush interior points had significantly greater frugivore species richness than pasture interior points.

The GLMMs of small frugivore abundance showed an effect of weather. Minutes of direct sunshine during the bird count had a positive effect on small frugivore abundance (Table 4, Figure 9e). Habitat-edge type had a strong positive effect on small frugivore species abundance, with bush edge points having significantly greater small frugivore abundance than pasture interior points (Table 5, Figure 9e). Percent canopy cover per point had a significant positive effect on small frugivore species richness (Table 5 and Figure 9f). The GLMMs of small frugivore species richness found a strong positive

effect of habitat-edge type. Bush edge points and mānuka points had significantly greater small frugivore species richness than pasture interior points.

Wind strength had a significant negative effect on large frugivore abundance (Table 5, Figure 4g). Habitat-edge type had a significant effect on large frugivore abundance with bush interior points supporting a significantly higher number of large frugivores per point than mānuka edge points (Table 5, Figure 10g,). Likewise, wind strength had a significant negative effect on large frugivore species richness (Table 5, Figure 9h), while habitat-edge type had a significant effect on large frugivore species richness, with bush interior and bush edge points supporting a greater number of large frugivore species per point than pasture interior points (Table 5, Figure 10h).

Table 4: Likelihood ratio test tables of all fixed effects of all native, all frugivorous, small (body size < 75 g) frugivorous and large (body size > 75 g) frugivorous species abundance and richness. Degrees of freedom (DF) shown for each effect. Significant variables are highlighted in bold. * indicates $P < 0.05$, ** indicates $P < 0.01$ and *** indicates $P < 0.001$.

Model	Variable	DF	Likelihood ratio test
All natives abundance	Habitat + edge	4	4.75
	Temperature	1	0.07
	Sun	1	5.28*
	Wind	1	10.53**
	Canopy cover	1	0.39
All natives richness	Habitat + edge	4	3.76
	Temperature	1	0.04
	Sun	1	0.05
	Wind	1	5.66*
	Canopy cover	1	0.01
All frugivores abundance	Habitat + edge	4	27.35***
	Temperature	1	0.59
	Sun	1	1.57
	Wind	1	5.92*
	Canopy cover	1	0.02
All frugivores richness	Habitat + edge	4	18.85***
	Temperature	1	0.07
	Sun	1	0.32
	Wind	1	2.55
	Canopy cover	1	0.10
Small frugivores abundance	Habitat + edge	4	15.06**
	Temperature	1	0.55
	Sun	1	5.47*
	Wind	1	0.06

Small frugivores richness	Canopy cover	1	0.54
	Habitat + edge	4	17.13**
	Temperature	1	0.14
	Sun	1	2.90
	Wind	1	0.14
Large frugivore abundance	Canopy cover	1	4.78*
	Habitat + edge	4	19.12***
	Temperature	1	0.05
	Sun	1	0.97
	Wind	1	10.35**
Large frugivore richness	Canopy cover	1	0.48
	Habitat + edge	4	13.22*
	Temperature	1	8×10^{-4}
	Sun	1	1.54
	Wind	1	6.76**
	Canopy cover	1	0.05

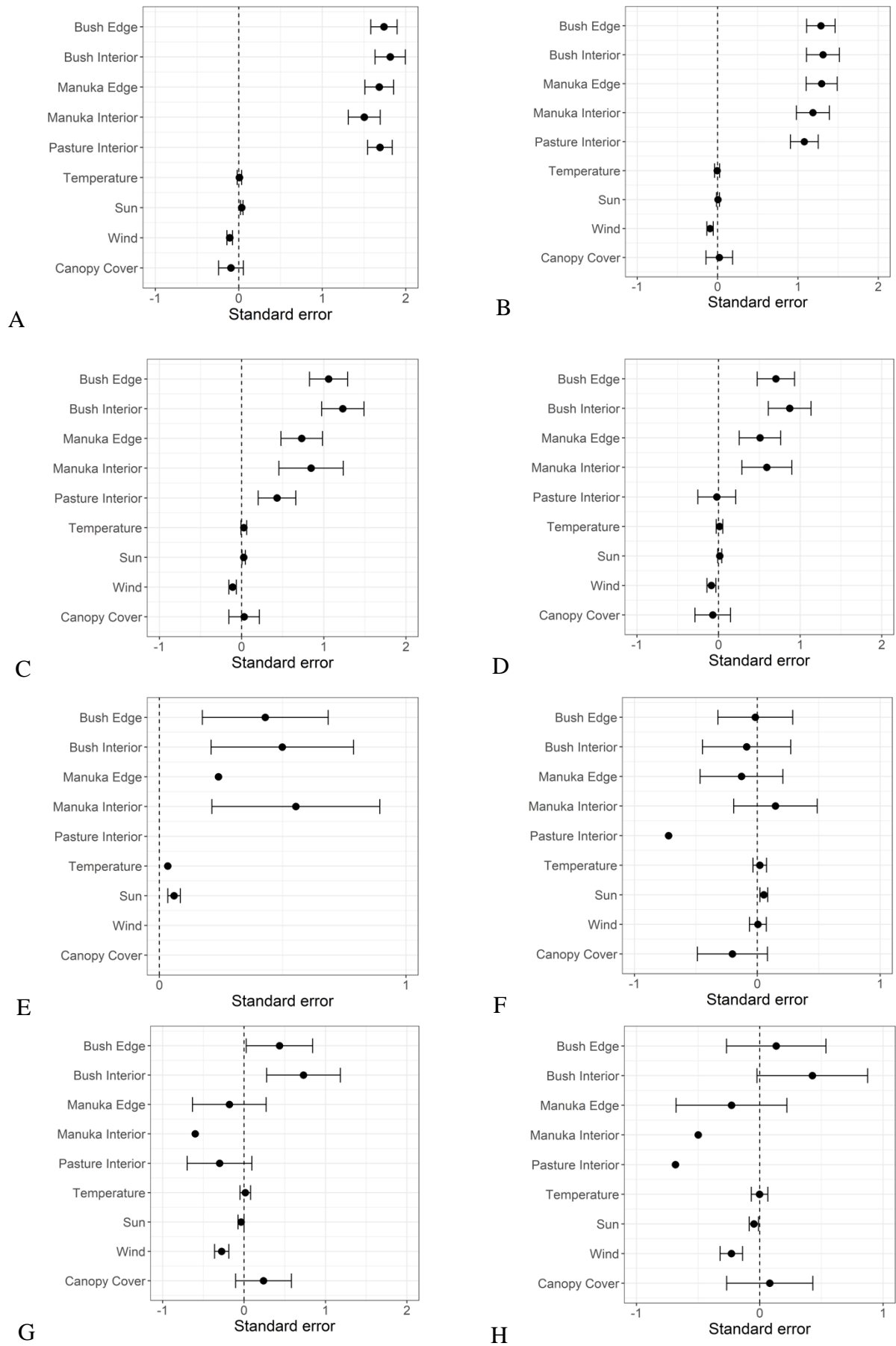


Figure 9: Coefficient plots of GLMM fixed effects and their standard errors, for: (a-b) all native species abundance and richness (c-d) all frugivore species abundance and richness (e-f) small frugivore abundance and richness (g-h) large frugivore abundance and richness.

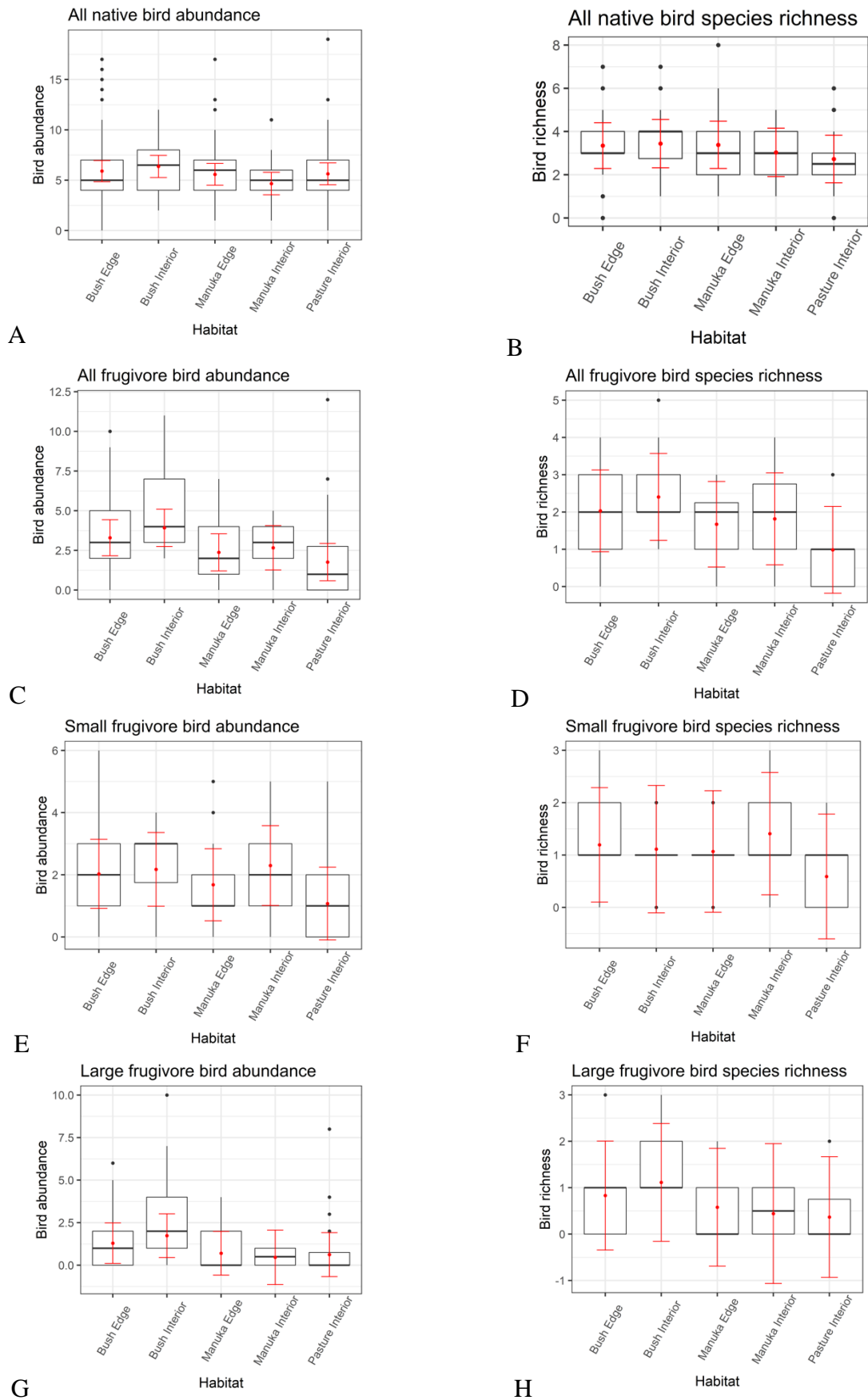


Figure 10: Observed mean bird species abundance and species richness per habitat type: (a-b) all native species abundance and richness (c-d) all frugivore species abundance and richness (e-f) small frugivore abundance and richness (g-h) large

frugivore abundance and richness. Red dots indicate the GLMM predicted mean species abundance or richness for each habitat type.

Table 5: Pairwise comparisons of the effect size (estimate) and significance (standard error, SE, and z-ratio) of each level of the habitat-edge effect on mean bird species abundance and richness GLMMs. Statistical significance indicated by asterisks, where * indicates $P < 0.05$, ** indicates $P < 0.01$ and *** indicates $P < 0.001$.

Contrasts per model	Estimate	SE	z.ratio
All frugivores abundance			
Bush Edge - Bush Interior	-0.172	0.12	-1.48
Bush Edge - Mānuka Edge	0.326	0.12	2.72
Bush Edge - Mānuka Interior	0.213	0.36	0.60
Bush Edge - Pasture Interior	0.627	0.14	4.54***
Bush Interior - Mānuka Edge	0.499	0.15	3.28**
Bush Interior - Mānuka Interior	0.386	0.37	1.06
Bush Interior - Pasture Interior	0.799	0.19	4.31***
Mānuka Edge - Mānuka Interior	-0.113	0.37	-0.31
Mānuka Edge - Pasture Interior	0.300	0.17	1.79
Mānuka Interior - Pasture Interior	0.413	0.38	1.09
All frugivore richness			
Bush Edge - Bush Interior	-0.169	0.15	-1.16
Bush Edge - Mānuka Edge	0.194	0.14	1.38
Bush Edge - Mānuka Interior	0.111	0.22	0.50
Bush Edge - Pasture Interior	0.723	0.17	4.25***
Bush Interior - Mānuka Edge	0.363	0.18	1.98
Bush Interior - Mānuka Interior	0.280	0.25	1.13
Bush Interior - Pasture Interior	0.893	0.22	3.98***
Mānuka Edge - Mānuka Interior	-0.083	0.25	-0.34
Mānuka Edge - Pasture Interior	0.529	0.20	2.67
Mānuka Interior - Pasture Interior	0.612	0.28	2.22
Small frugivores abundance			
Bush Edge - Bush Interior	-0.069	0.15	-0.45
Bush Edge - Mānuka Edge	0.189	0.14	1.32
Bush Edge - Mānuka Interior	-0.124	0.27	-0.47
Bush Edge - Pasture Interior	0.636	0.17	3.85**
Bush Interior - Mānuka Edge	0.258	0.19	1.35
Bush Interior - Mānuka Interior	-0.054	0.29	-0.19
Bush Interior - Pasture Interior	0.705	0.23	3.07
Mānuka Edge - Mānuka Interior	-0.313	0.28	-1.10
Mānuka Edge - Pasture Interior	0.447	0.20	2.26
Mānuka Interior - Pasture Interior	0.760	0.31	2.46
Small frugivores richness			
Bush Edge - Bush Interior	0.326	0.50	0.65
Bush Edge - Mānuka Edge	0.608	0.41	1.48
Bush Edge - Mānuka Interior	-0.572	0.52	-1.11
Bush Edge - Pasture Interior	1.733	0.46	3.73**
Bush Interior - Mānuka Edge	0.281	0.63	0.45
Bush Interior - Mānuka Interior	-0.898	0.66	-1.36
Bush Interior - Pasture Interior	1.407	0.68	2.06

Mānuka Edge - Mānuka Interior	-1.180	0.62	-1.91
Mānuka Edge - Pasture Interior	1.125	0.54	2.09
Mānuka Interior - Pasture Interior	2.305	0.69	3.35**
Large frugivore abundance			
Bush Edge - Bush Interior	-0.294	0.20	-1.45
Bush Edge - Mānuka Edge	0.615	0.22	2.74
Bush Edge - Mānuka Interior	1.034	0.50	2.09
Bush Edge - Pasture Interior	0.735	0.26	2.84
Bush Interior - Mānuka Edge	0.910	0.28	3.29**
Bush Interior - Mānuka Interior	1.329	0.52	2.58
Bush Interior - Pasture Interior	1.029	0.34	3.05
Mānuka Edge - Mānuka Interior	0.418	0.53	0.80
Mānuka Edge - Pasture Interior	0.119	0.31	0.38
Mānuka Interior - Pasture Interior	-0.299	0.55	-0.54
Large frugivore richness			
Bush Edge - Bush Interior	-0.292	0.21	-1.42
Bush Edge - Mānuka Edge	0.362	0.23	1.58
Bush Edge - Mānuka Interior	0.632	0.43	1.46
Bush Edge - Pasture Interior	0.817	0.28	2.92*
Bush Interior - Mānuka Edge	0.655	0.28	2.34
Bush Interior - Mānuka Interior	0.925	0.45	2.04
Bush Interior - Pasture Interior	1.110	0.35	3.13*
Mānuka Edge - Mānuka Interior	0.270	0.47	0.58
Mānuka Edge - Pasture Interior	0.454	0.33	1.36
Mānuka Interior - Pasture Interior	0.184	0.51	0.36

3.6 Field frugivory observations

There were 22 frugivory events observed in total, recorded during one sample per month between February and June. Only 18% of all unique possible pairwise interactions were observed during the sampling period. One interaction was confirmed via a fresh faecal sample obtained from a single tūi (*Prosthemadera novaeseelandiae*) during a fruit count, and compared to samples in Dr John Perrott's faecal seed collection (unpub.). Comparisons with the collection confirmed the tūi sample to be a taupata (*Coprosma repens*) seed.

In total, 218 fruits were consumed by birds during the 22 frugivory events recorded in which kererū (*Hemiphaga novaeseelandiae*) consumed 204 of the 218 fruits (94%). Kererū also consumed the most fruit in one interaction, with one individual observed consuming 143 cabbage tree fruits during a seven-minute feeding event. Furthermore, most interactions were from kererū ($n = 12$) with half of these interactions occurring with nikau palm (*Rhopalostylis sapida*). In total, 43 nikau palm fruits were consumed by kererū. Kererū was also the sole observed consumer of pūriri (*Vitex lucens*) fruits. Tūi were extreme generalists, having interactions with 5 plant species, including

hangehange (*Geniostoma ligustrifolium*), which did not have another observed disperser. Bellbird (*Anthornis melanura*) had 3 observed interactions with 2 plant species: māpou (*Myrsine australis*) and taupata (*Coprosma repens*). Saddleback (*Philesturnus rufusater*) had one interaction each with cabbage tree and māpou.

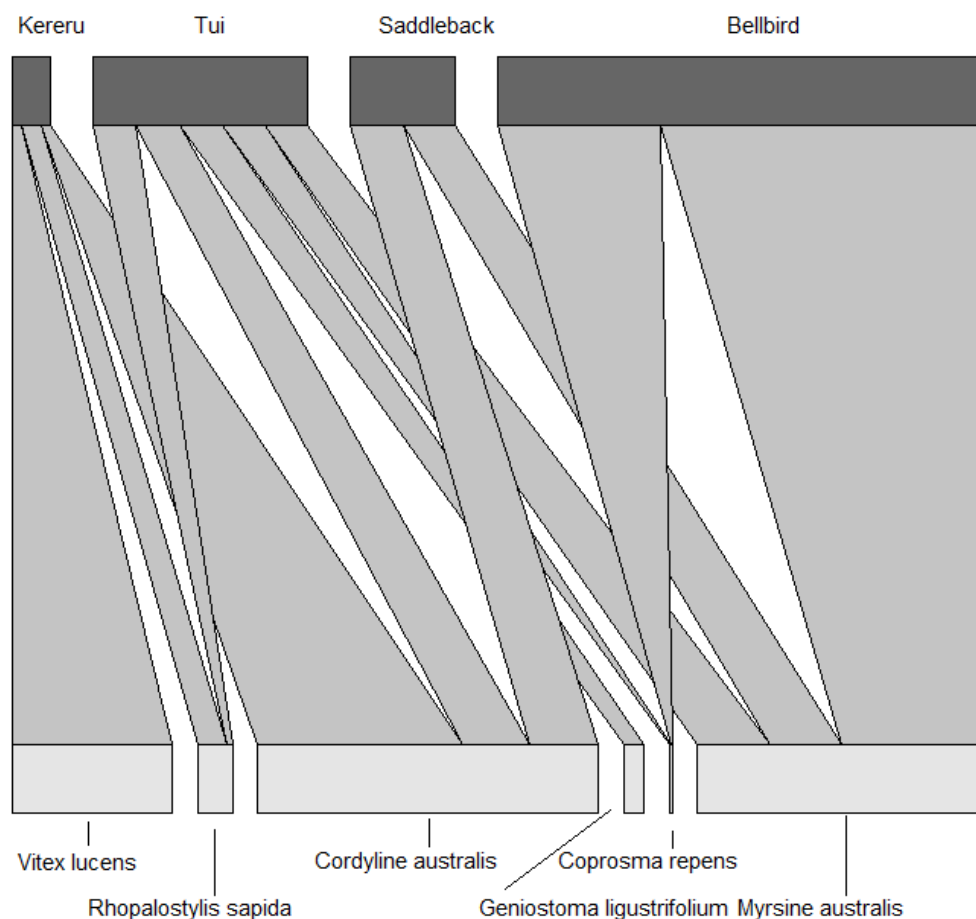


Figure 11: Bipartite graph visualising all 22 frugivory interactions (medium grey links) between bird (higher level) species represented by the dark grey squares and plant (lower level) species represented by the light grey squares of the observed network. The size of each square for both levels denotes the relative abundance of that species.

3.7 Network analysis of plant-frugivore interactions

The literature review of observed New Zealand plant-frugivore interactions showed that there were 67 possible unique plant-frugivore interactions among the bird and plant species of TRP (Table 7). In total, there were 1,201 potential pairwise interactions in the potential network using a < 30 m distance criteria, hereafter referred to as the “long-distance” (< 30 m) potential network (Figure 12 and Figure 13). In this case, a potential interaction would only be counted if a bird was detected within 30 m of a fruiting tree. Of the 126 available unique interactions in the long-distance potential network, 46 interactions were inferred using the fruit count and point count data which is 68% of the 67 unique interactions deemed possible. There were 654 potential pairwise interactions in the potential network using a < 15 m distance criteria, hereafter referred to as the “short-distance” (< 15 m) potential network (Figure 14 and Figure 15). In this case, a potential interaction would only be counted if a bird was detected within 15 m of a fruiting tree. Of the 112 available unique interactions in the short-distance potential network, 40 were inferred using the co-occurrence data and literature which is 59% of the 67 possible unique interactions.

Within the long-distance network, tūi had interactions with 12 out of a total 14 plant species, the greatest number of connections within the network (Figure 12). Only the large-seeded taraire (*Beilschmiedia tarairi*) and pūriri were not tūi-dispersed. Bellbird had very high interaction frequencies with the small-seed species including māpou (*Myrsine australis*), karo (*Pittosporum crassifolium*) and tōtara (*Podocarpus totara*). Kererū were the sole dispersers of the large-seeded taraire and pūriri (*Vitex lucens*). Saddleback interacted with 3 plant species: māpou (*Myrsine australis*), cabbage tree (*Cordyline australis*) and karamū (*Coprosma robusta*). The rest of the species within the network had very few interactions, including the predominantly insectivorous grey warbler and whitehead, and the introduced blackbird and song thrush.

For the most connected avian species within the short-distance potential network, there were no clear differences compared with the long-distance potential network, except for reduced pairwise interaction frequencies due to the shorter maximum co-occurrence distance imposed. There were several noteworthy differences between the long-distance and short-distance potential networks for the less-connected species. Although present in the long-distance potential network, blackbirds were absent from the short-distance network (Figure 15). Furthermore, whitehead had only one mutualistic link with

hangehange (*Geniostoma ligustrifolium*), whereas within the long-distance potential network, whitehead had 3 species links.

Table 6: All possible unique plant-frugivore interactions for the TRP ($n = 67$), references of each pairwise interaction and the observed interaction frequencies (column Frequency) including the total number of fruits consumed (column Fruit) for the observed plant-frugivore interactions.

Plant	Bird	Frequency	Fruit	References
<i>Beilschmiedia tarairi</i>	Kererū			Clout & Hay. 1989; Wotton. 2007
<i>Coprosma repens</i>	Bellbird	1	1	Dijkgraaf. 2002; this study
	Myna			Dijkgraaf. 2002
	Silvereye			Garcia et al. 2014
	Tūi	1	1	Garcia et al. 2014; this study
<i>Coprosma rhamnoides</i>	Bellbird			Crowe. 2009
	Kererū			Crowe. 2009
	Tūi			Crowe. 2009
<i>Coprosma robusta</i>	Bellbird			Spurr et al. 2011; Garcia et al. 2014
	Blackbird			Burrows. 1994; Dijkgraaf. 2002; Garcia et al. 2014
	Myna			Dijkgraaf. 2002
	Saddleback			Garcia et al. 2014
	Silvereye			Burrows. 1994; Garcia et al. 2014
	Song thrush			Garcia et al. 2014
	Tūi			Bergquist. 1987; Dilks. 2004; Garcia et al. 2014
	Whitehead			Garcia et al. 2014
<i>Cordyline australis</i>	Blackbird			Burrows. 1994
	Kererū	3	155	Campbell et al. 2008; this study
	Myna			Dijkgraaf. 2002
	Saddleback	1	1	this study
	Silvereye			Burrows. 1994
	Tūi	1	2	Dijkgraaf. 2002; Dilks. 2004; this study
<i>Corynocarpus laevigatus</i>	Kererū			Clout & Hay. 1989
	Tūi			Stewart. 1980
<i>Geniostoma ligustrifolium</i>	Blackbird			Stanley. 2018
	Chaffinch			Stanley. 2018
	Grey warbler			Moeed and Fitzgerald. 1982
	Silvereye			Stanley. 2018
	Tūi	1	3	this study
	Whitehead			Moeed and Fitzgerald. 1982
<i>Macropiper excelsum</i>	Blackbird			Garcia et al. 2014
	Kererū			Campbell et al. 2008; Garcia et al. 2014
	Silvereye			Garcia et al. 2014
	Song thrush			Garcia et al. 2014
	Tūi			Dilks. 2004; Garcia et al. 2014
<i>Melicytus ramiflorus</i>	Bellbird			Burrows. 1994; Garcia et al. 2014; Spurr et al. 2011
	Blackbird			Burrows. 1994; Garcia et al. 2014
	Kakariki			Garcia et al. 2014

<i>Myrsine australis</i>	Kererū			Burrows., 1994; Garcia et al., 2014
	Silvereye			Burrows., 1994; Garcia et al., 2014
	Tūi			Dilks. 2004; Garcia et al. 2014
	Whitehead			Garcia et al. 2014
	Bellbird	2	3	Spurr et al. 2011; this study
	Blackbird			Garcia et al. 2014
	Saddleback	1	1	this study
<i>Pittosporum crassifolium</i>	Silvereye			Garcia et al. 2014
	Tūi	1	1	Dilks. 2004; Garcia et al. 2014, this study
	Bellbird			Anderson et al. 2006*
	Blackbird			
	Kererū			
	Myna			
	Silvereye			
<i>Podocarpus totara</i>	Song thrush			
	Tūi			
	Bellbird			Garcia et al. 2014
	Blackbird			Garcia et al. 2014
	Kererū			Garcia et al. 2014
	Silvereye			Garcia et al. 2014
	Song thrush			Garcia et al. 2014
<i>Rhopalostylis sapida</i>	Tūi			Dilks. 2004; Garcia et al. 2014
	Blackbird			Clout & Hay. 1989; Dijkgraaf. 2002
	Kererū	6	43	Clout & Hay. 1989; Dijkgraaf. 2002; this study
	Song thrush			Clout & Hay. 1989; Dijkgraaf. 2002
	Tūi	1	1	this study
<i>Vitex lucens</i>	Kererū	3	6	Clout & Hay. 1989; this study
	Myna			Dijkgraaf. 2002

* Inferred from Anderson et al. (2006) but no references explicitly confirming pairwise interactions with karo. However, mean species gape of these species compared to mean fruit diameter of karo suggests that pairwise interactions between karo and all listed birds is possible.

Myrsine australis	99	200		27			3		
Cordyline australis	114		24	27			3	1	
Pittosporum crassifolium	51	67	7					1	1
Geniostoma ligustrifolium	86				23	13	2		
Coprosma robusta	41	62		8		1		1	
Rhopalostylis sapida	60		8						1
Coprosma rhamnoides	31	31	5						
Podocarpus totara	11	42	4				1		
Macropiper excelsum	26		9				2		
Corynocarpus laevigatus	31		5						
Melicytus ramiflorus	5	22				1			
Vitex lucens			24						
Coprosma repens	5	9						1	
Beilschmiedia tarairi			5						
	Tui	Bellbird	Kereru	Saddleback	Grey Warbler	Whitehead	Silvereye	Blackbird	Song Thrush

Figure 12: Matrix visualisation of the long-distance potential network. Filled squares indicate an inferred interaction between a bird species (bottom) and plant species (left) with the frequency of the pairwise interaction indicated in red. Shading indicates the strength of the interaction frequency. White squares indicate unrealised interactions.

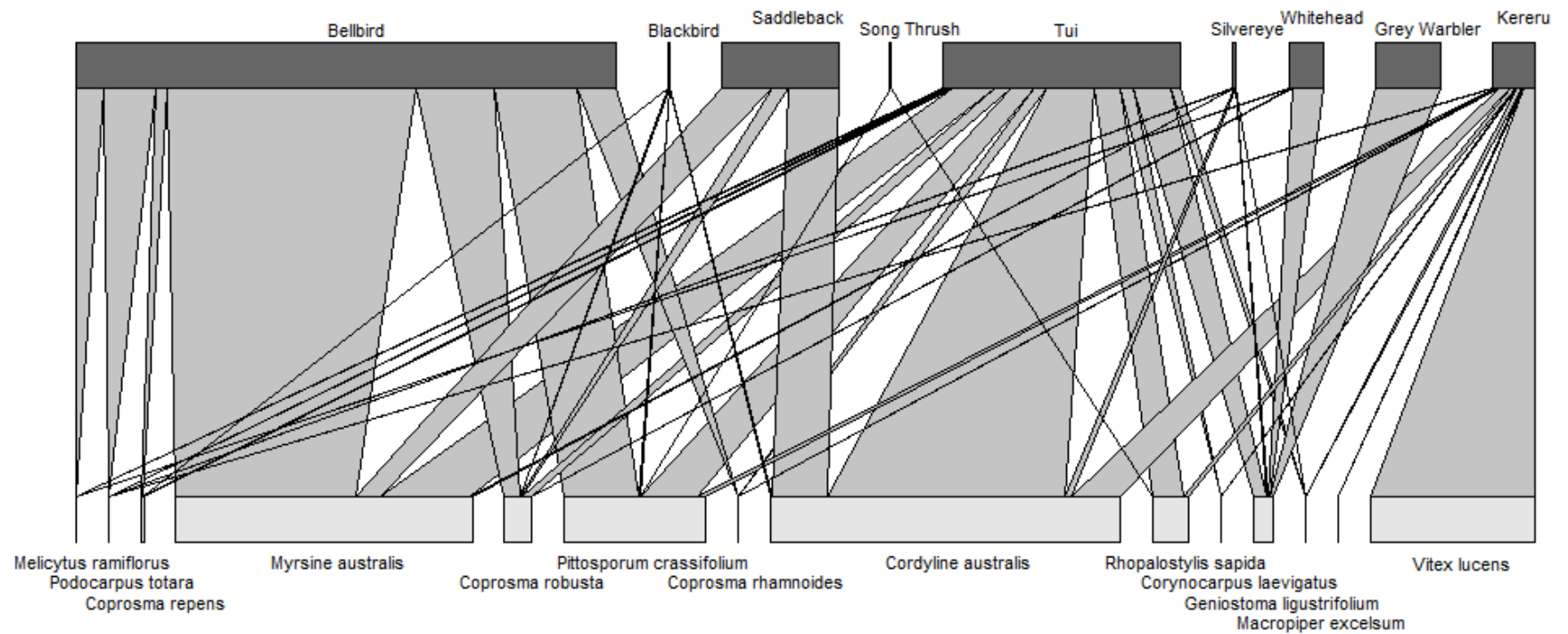


Figure 13: Bipartite graph format visualisation of all inferred interactions (medium grey links) of the long-distance potential network between bird (higher level) species represented by the dark grey squares and plant (lower level) species represented by the light grey squares of the observed network. The size of each square for both levels denotes the relative abundance of that species.

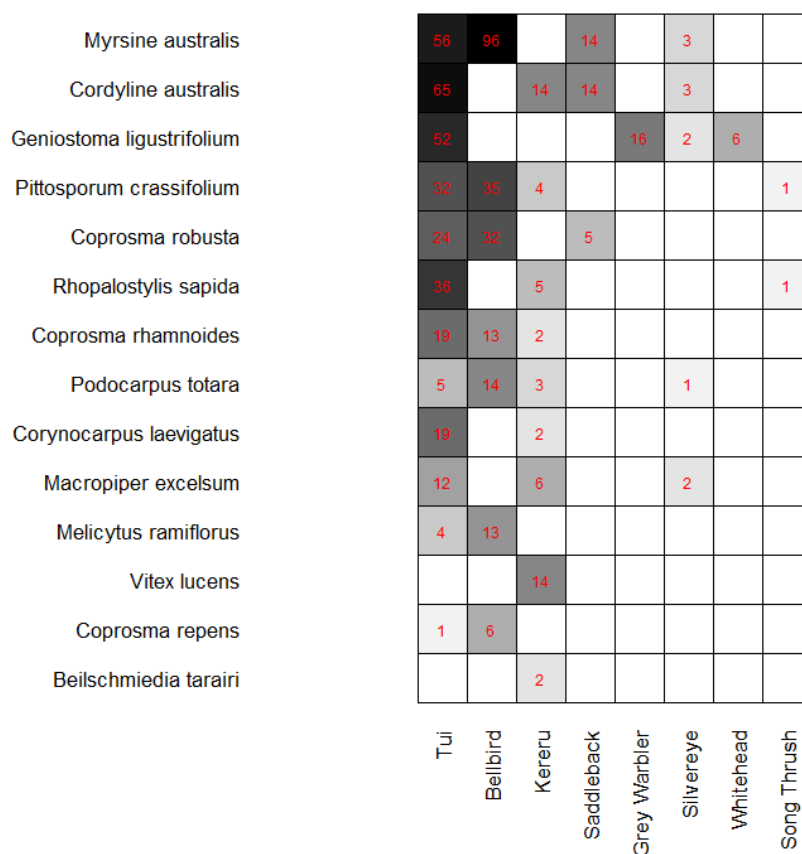


Figure 14: Matrix visualisation of the short-distance potential network. Filled squares indicate an inferred interaction between a bird species (bottom) and plant species (left) with the frequency of the pairwise interaction indicated in red. White squares indicate unrealised interactions. Shading indicates the strength of the interaction frequency.

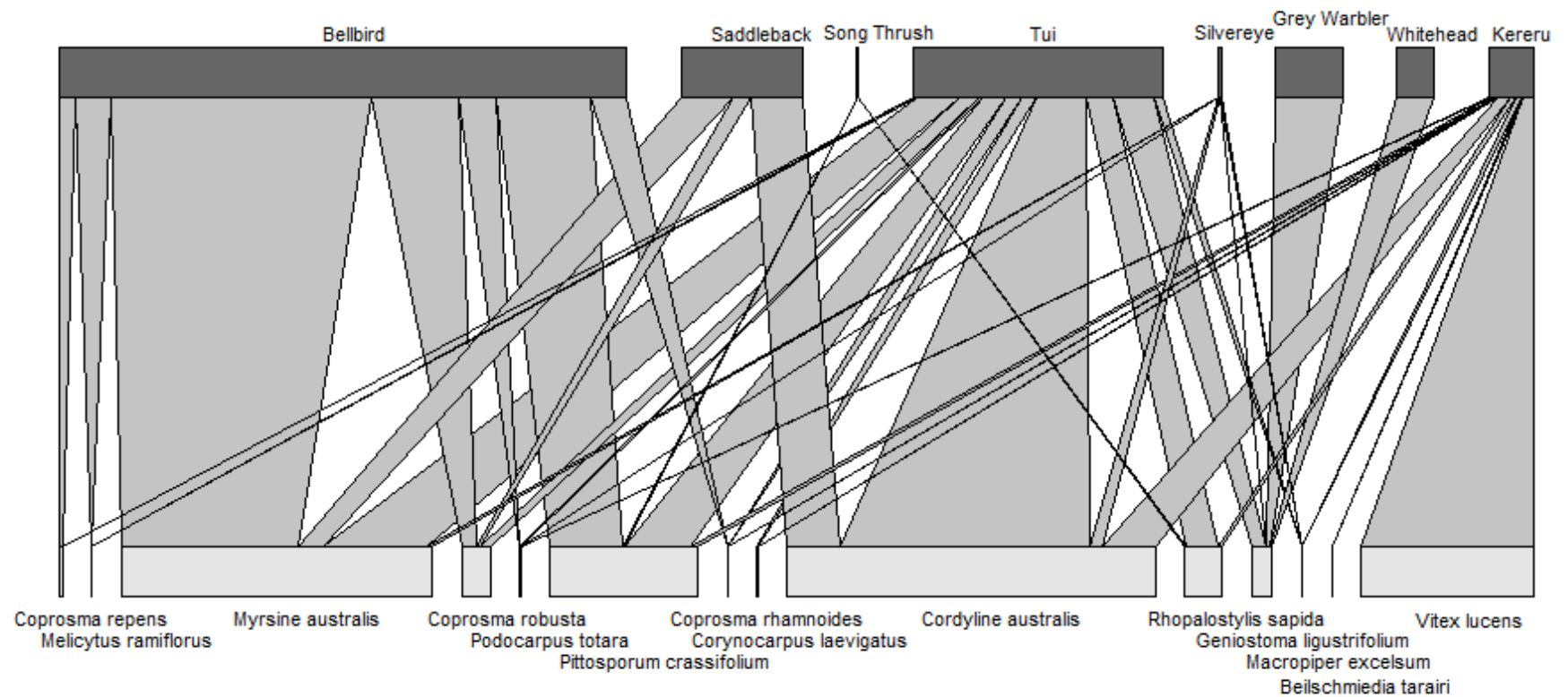


Figure 15: Bipartite graph format visualisation of all inferred interactions (medium grey links) of the short-distance potential network between bird (higher level) species represented by the dark grey squares and plant (lower level) species represented by the light grey squares of the observed network. The size of each square for both levels denotes the relative abundance of that species.

3.8 Degree distribution

I calculated the degree of the networks to infer how robust they are to disturbance. A minimum of five distinct species degree levels were required in the network, with each of the five levels comprised of n species with a specific number of links, to calculate species degree distributions. There were fewer than the five species degree levels required for the lower trophic level to accurately fit the three functions in the short-distance potential network, therefore only the long-distance potential network was used to calculate the cumulative degree distributions (Figure 16). Comparisons between the AIC values of three models suggest that both levels are best-approximated by a truncated power-law degree distribution (Table 7), leading to an extremely right-skewed distribution histogram, indicating a network comprised of many species with few links and only a few species with many links. For example, within the long-distance potential network, the most connected bird species, tūi, has a total of 12 species links, followed by kererū with a total of nine species links. Bellbird was the third most connected species with seven links. These three species comprised the minority of species with many links. The rest of the bird species within the network had a combined mean number of three species links: the majority of species with few links.

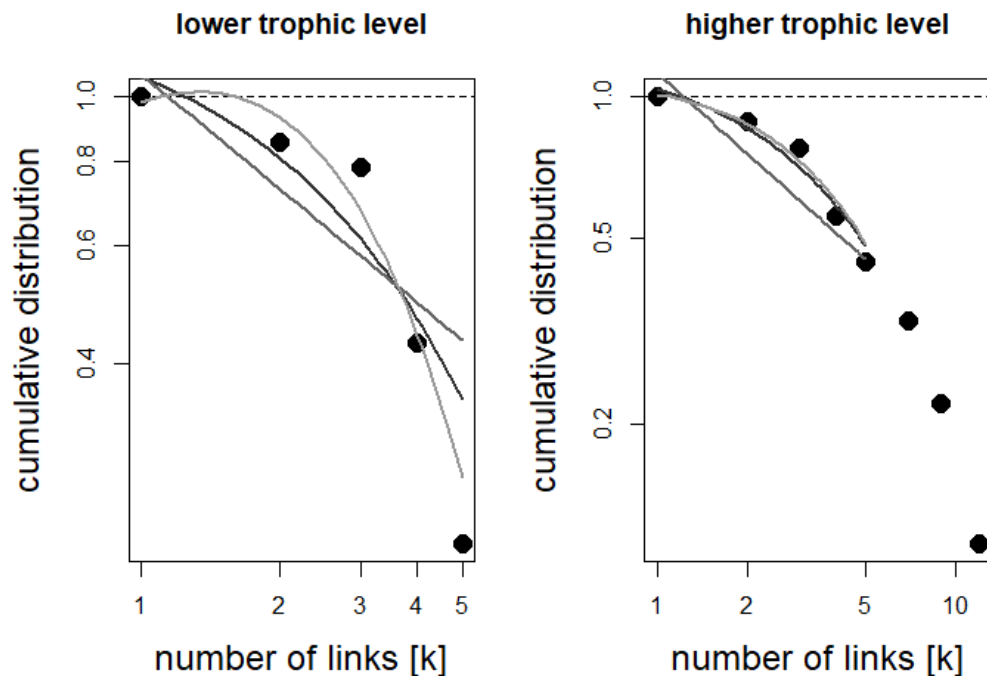


Figure 16: Cumulative degree frequency distributions of plants (lower trophic level) and birds (higher trophic level) for the long-distance potential network. Points show the distinct species degree levels with each of the levels comprised of n species with the specified number of links indicated on the x -axis. Lines indicate the model fits with the exponential, power law and truncated power law fits in black, dark grey and light grey, respectively.

Table 7: The coefficient estimates, standard errors (SE), P-values, R^2 and AIC values for the three model fits of the long-distance cumulative degree frequency distribution shown in Figure 11.

Lower Level					
Model	Estimate	SE	P-value	R^2	AIC
Truncated power law	-0.935	0.530	0.220	0.975	-5.167
Exponential	0.277	0.073	0.033	0.931	-2.185
Power law	0.567	0.215	0.078	0.851	1.438
Higher Level					
Model	Estimate	SE	P-value	R^2	AIC
Truncated power law	-0.142	0.096	0.020	0.995	-25.795
Exponential	0.192	0.012	4.61×10^{-6}	0.993	-24.875
Power law	0.564	0.102	1.47×10^{-3}	0.929	-6.088

3.9 Species specialisation (d') values

I calculated the d' values of all bird and plant species to determine species roles and to estimate the degree of functional redundancy within the two potential networks. The long-distance potential network was comprised mostly of highly generalised fruiting plant species (Figure 17a) and generalised frugivores (Figure 17c) with a mean d' of 0.148 and 0.197, respectively. Only the large-seeded species, taraire and pūriri, had d' values above 0.4 (Table 8), relatively high compared to the other species in the network. Two predominantly insectivorous birds (grey warbler and whitehead) had the highest specialisation values among birds in the long-distance potential network. Likewise, the short-distance potential network showed similar specialisation results with a mean d' of 0.150 for plant species and a mean d' of 0.202 for frugivores. Overall, both potential networks were highly generalised.

Table 8: Species specialisation (d') values for plants and birds in the long-distance ($d'3$) and short-distance potential ($d'2$) networks. Species in their respective networks are ordered from the highest to lowest degree of specialisation.

Plant species	$d'3$	Bird species	$d'3$
<i>Vitex lucens</i>	0.462	Grey warbler	0.367
<i>Beilschmiedia tarairi</i>	0.448	Whitehead	0.360
<i>Macropiper excelsum</i>	0.199	Bellbird	0.194
<i>Rhopalostylis sapida</i>	0.191	Kererū	0.189
<i>Corynocarpus laevigatus</i>	0.189	Silvereye	0.184
<i>Geniostoma ligustrifolium</i>	0.162	Blackbird	0.151
<i>Cordyline australis</i>	0.145	Song thrush	0.148
<i>Coprosma repens</i>	0.060	Tūi	0.128

<i>Coprosma rhamnoides</i>	0.045	Saddleback	0.046
<i>Melicytus ramiflorus</i>	0.040		
<i>Pittosporum crassifolium</i>	0.039		
<i>Podocarpus totara</i>	0.038		
<i>Myrsine australis</i>	0.023		
<i>Coprosma robusta</i>	0.023		
Plant species	$d'2$	Birds species	$d'2$
<i>Vitex lucens</i>	0.460	Grey warbler	0.365
<i>Beilschmiedia tarairi</i>	0.432	Whitehead	0.363
<i>Macropiper excelsum</i>	0.219	Silvereye	0.184
<i>Rhopalostylis sapida</i>	0.193	Bellbird	0.182
<i>Corynocarpus laevigatus</i>	0.191	Kererū	0.175
<i>Geniostoma ligustrifolium</i>	0.164	Song thrush	0.148
<i>Cordyline australis</i>	0.149	Tūi	0.129
<i>Coprosma rhamnoides</i>	0.057	Saddleback	0.049
<i>Podocarpus totara</i>	0.049		
<i>Pittosporum crassifolium</i>	0.045		
<i>Melicytus ramiflorus</i>	0.041		
<i>Coprosma repens</i>	0.033		
<i>Coprosma robusta</i>	0.027		
<i>Myrsine australis</i>	0.026		

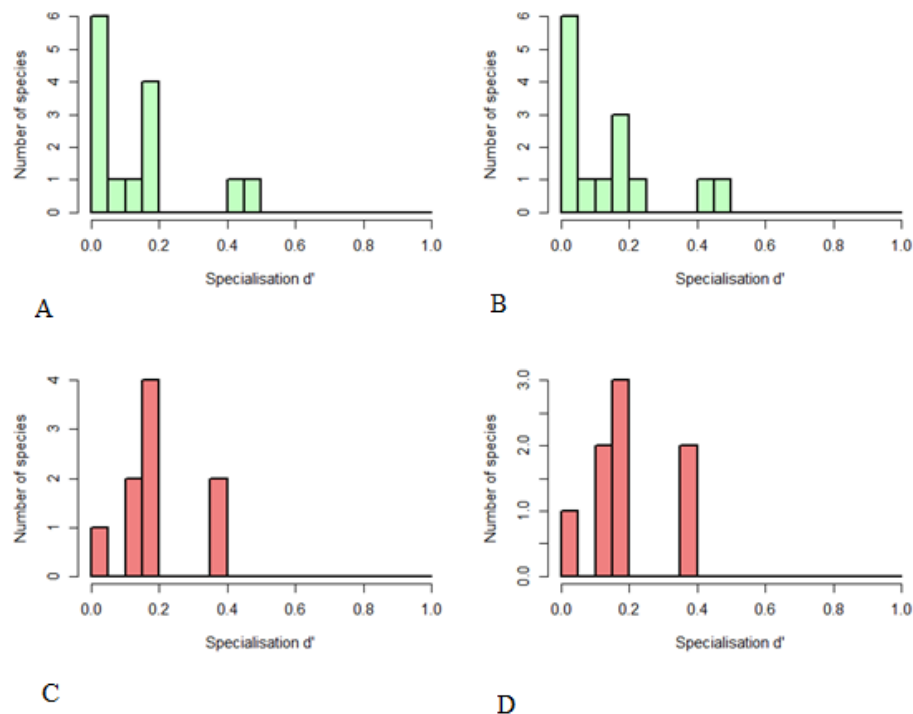


Figure 17: Distribution of plant and bird species specialisation (d') values for the long-distance and short-distance potential networks for the plant species (A, B) and bird species (C, D) in the long-distance (A, C) and short-distance (B, D) potential networks.

3.10 Network level specialisation

The network-level specialisation ($H2'$) metric describes the degree of specialisation of the network and is an index ranging from 0 (extreme specialisation) to 1 (extreme generalisation). Network-level specialisation ($H2'$) calculations returned a $H2'$ value of 0.352 for both the long-distance and short-distance inferred networks. Comparisons of the observed $H2'$ value with the *vaznull* randomisation null model $H2'$ values found that the potential network was significantly specialised ($\mu H2' = 0.136$, $P < 0.001$), and therefore not just a by-product of the network's size and connectance.

3.11 Nestedness

Nestedness is an architectural property of mutualistic networks, whose structure dictates the capacity for network robustness, functional redundancy and the persistence of specialists. The nestedness of a network ranges from low to high (0 – 100) nestedness where 0 would indicate a network that exhibits no nestedness and 100 would indicate, for example, a perfectly nested network comprised of specialist frugivores only interacting with plant species that form the subset of plants that generalist frugivores interact with. The short-distance potential network (nestedness = 35.93) was more nested than the long-distance potential network (nestedness = 30.34). However, null models confirmed that the short-distance and long-distance inferred networks were not significantly nested. In fact, the long-distance inferred network was significantly less nested than expected by chance shown by the *vaznull* (observed nestedness = 30.34, μ nestedness = 60.60, $P < .001$) model results. In addition, the *vaznull* model predicted a significantly less nested structure than expected in the short-distance potential network (observed nestedness = 35.93, μ nestedness = 57.09, $P = .003$).

3.12 Species contributions to nestedness

The species that contribute most to network nestedness are the most vulnerable to extinction and reduce the overall robustness of the network, thus nestedness contribution metrics (z -scores) provide another tool for conservation prioritisation. Tūi were the most significant avian contributors to network nestedness in the long-distance (Table 9) and short-distance (Table 10) potential networks with a z -score of 1.991 and 2.179, respectively. No other bird species in the long-distance and short-distance potential networks had positive z -scores above 1.0. The birds that contributed the least to the nested structure (i.e., species with the lowest z -scores) in the long-distance

potential network were the endemic whitehead (*Mohoua albigilla*) (Table 10) and bellbird (*Anthornis melanura*) in the short-distance potential network (Table 11). The exotic song thrush (*Turdus philomelos*) were consistent reducers of network nestedness in the long-distance and short-distance potential networks, with *z*-scores of -0.711 (Table 9) and -0.615 (Table 10) respectively. The plant species that contributed the least to the nested structure in the long-distance potential network was māhoe (*Melicytus ramiflorus*) (Table 9) and māpou (*Myrsine australis*) in the short-distance potential network (Table 10).

Table 9: Nestedness contributions per species for birds (higher level) and plants (lower level) in the long-distance potential network. (*) Biggest contributors to network nestedness; (†) Smallest contributor to network nestedness.

Higher Level	Nestedness contribution
Tūi*	2.075
Saddleback	0.488
Kererū	0.401
Blackbird	0.366
Silvereye	0.213
Grey warbler	-0.125
Bellbird	-0.288
Song thrush	-0.711
Whitehead†	-0.826
Lower Level	Nestedness contribution
Karaka (<i>Corynocarpus laevigatus</i>)*	1.857
Tōtara (<i>Podocarpus totara</i>)*	1.058
Karo (<i>Pittosporum crassifolium</i>)	1.013
Twiggy Coprosma (<i>Coprosma rhamnoides</i>)	0.735
Kawakawa (<i>Macropiper excelsum</i>)	0.691
Cabbage tree (<i>Cordyline australis</i>)	0.658
Pūriri (<i>Vitex lucens</i>)	0.537
Taraire (<i>Beilschmiedia tarairi</i>)	0.477
Nīkau (<i>Rhopalostylis sapida</i>)	-0.028
Hangehange (<i>Geniostoma ligustrifolium</i>)	-0.151
Taupata (<i>Coprosma repens</i>)	-0.219
Karamū (<i>Coprosma robusta</i>)	-0.235
Māpou (<i>Myrsine australis</i>)	-0.317
Māhoe (<i>Melicytus ramiflorus</i>)†	-0.514

Table 10: Nestedness contributions per species for birds (higher level) and plants (lower level) in the short-distance potential network. (*) Biggest contributor to network nestedness; (†) Smallest contributor to network nestedness.

Higher Level	Nestedness contribution
Tūi*	2.179
Silvereye	0.738
Kererū	0.670
Saddleback	-0.350
Grey warbler	-0.421
Whitehead	-0.432
Song thrush	-0.615
Bellbird†	-1.280
Lower Level	Nestedness contributions
Karaka (<i>Corynocarpus laevigatus</i>)*	1.197
Twiggy Coprosma (<i>Coprosma rhamnoides</i>)	0.696
Karo (<i>Pittosporum crassifolium</i>)	0.635
Kawakawa (<i>Macropiper excelsum</i>)	0.592
Tōtara (<i>Podocarpus totara</i>)	0.501
Tarairē (<i>Beilschmiedia tarairi</i>)	0.378
Māhoe (<i>Melicytus ramiflorus</i>)	0.378
Taupata (<i>Coprosma repens</i>)	0.368
Pūriri (<i>Vitex lucens</i>)	0.324
Cabbage tree (<i>Cordyline australis</i>)	0.085
Nīkau (<i>Rhopalostylis sapida</i>)	0.063
Karamū (<i>Coprosma robusta</i>)	-0.246
Hangehange (<i>Geniostoma ligustrifolium</i>)	-0.256
Māpou (<i>Myrsine australis</i>)†	-0.478

3.13 Modularity

Three modules were observed in the long-distance (Figure 18) and short-distance potential network (Figure 19) indicating the subset of bird and plant species within the network that are highly connected, with few to no links with other modules of species. Species composition within the modules differed between the long-distance and short-distance potential networks. Within the long-distance network, the endemic bellbird and introduced blackbird were the two frugivores that formed the upper left module comprised of the *Coprosma* species, māhoe, māpou, karo and tōtara (Figure 18). Kererū was the sole frugivore that formed the central module comprised of the large-seeded species, tarairē and pūriri. The module illustrated on the bottom right was the largest module within the long-distance potential network, which included tūi, the most connected frugivore, and many of the least connected species such as grey warbler and song thrush. Plants within this module included cabbage tree and the fruiting plants with

medium-sized fruits such as kāraka (*Corynocarpus laevigatus*) and nīkau (*Rhopalostylis sapida*).

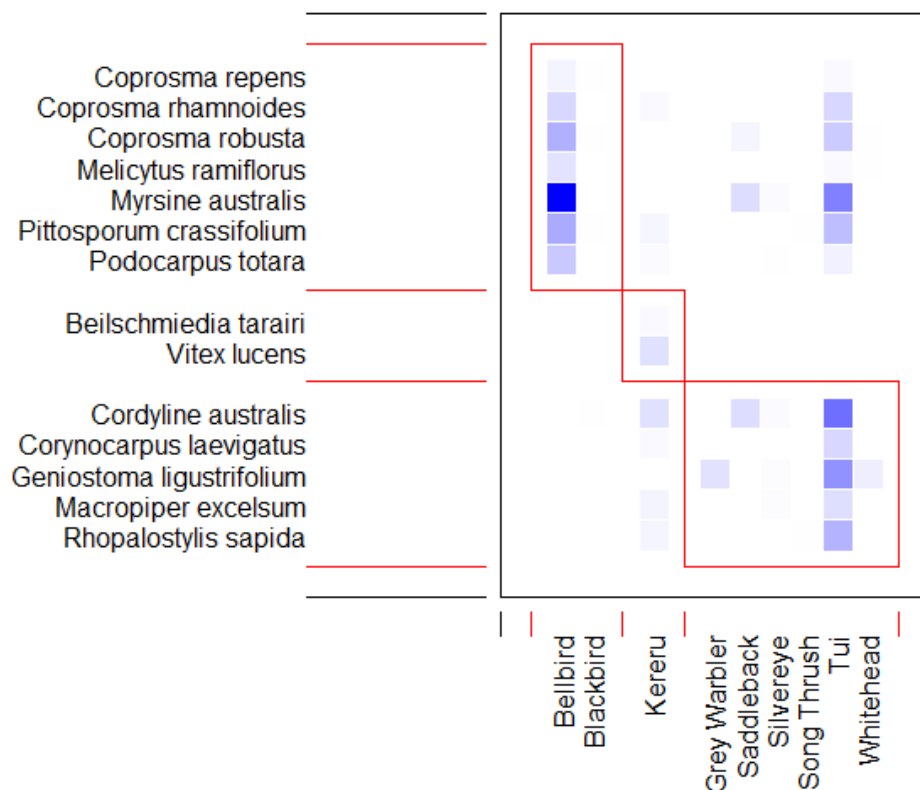


Figure 18: Modules ($n = 3$) within the long-distance potential network, indicated by species combinations within red boxes. Red lines indicate the modules of highly interacting species pairs. The colour of the squares shows the interaction frequencies of the species pairs with darker squares indicating higher interaction frequencies.

Within the short-distance network, blackbirds were absent from the network, thus bellbirds were the sole frugivore within the upper left module that, with the exception of blackbirds, was identical to the upper left module within the long-distance network. Native silvereye (*Zosterops lateralis*) and the plant kawakawa (*Macropiper excelsum*) shifted to the central module comprised of the large seeded plants and their sole disperser, kererū (Figure 19).

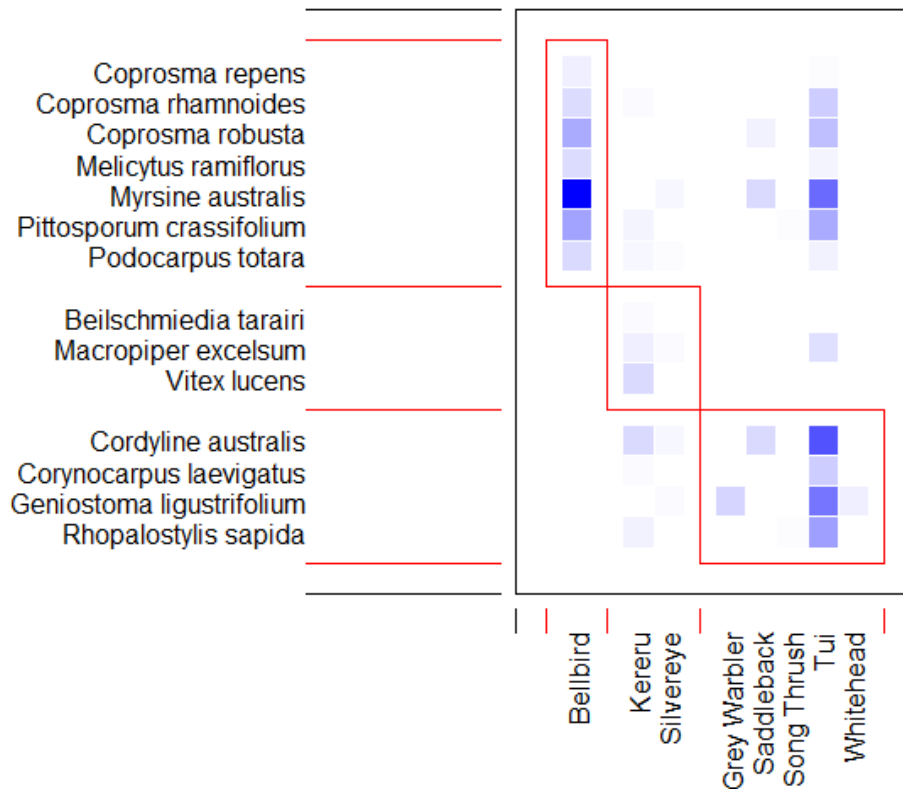


Figure 19: Modules ($n = 3$) within the short-distance potential network. Red lines indicate the modules of highly interacting species pairs. The colour of the squares shows the interaction frequencies of the species pairs with darker squares indicating higher interaction frequencies.

The within-module degree (z) and among-module connectivity (c) values of the bird and plant species for the long-distance potential network (Table 11) and short-distance potential network (Table 12) inform us of the role of each species within networks. Within the long-distance potential network, most birds were peripheral species, where most of the species links are within their module; that is, species with both a low within-module degree ($z < 2.5$) and among-module connectivity ($c < 0.62$). However, bellbird and grey warbler were ultra-peripheral species, in which all of their links were within their module ($c \leq 0.05$). Three connector species ($c \geq 0.62$), i.e., species that have many links to species within different modules, were found among the plants: *Coprosma rhamnoides*, *Pittosporum crassifolium* and *Podocarpus totara*. There were no hub species (species that are highly linked within their module, $z > 2.5$) found amongst the bird species level (Table 11).

Of the bird species in the short-distance potential network, 75% were peripheral species. Of these peripheral species, 50% of them had no links to species outside of their module (ultra-peripherals). Just two of eight species (kererū and silvereye) within the short-

distance potential network were connector species, linking modules that would otherwise be isolated. There were no hub species found amongst the bird species level. The distribution of species roles among the plant species are similar to the bird species results. Of the plant species in the short-distance potential network, 71% were peripheral species. There were four connector species within the network: *Coprosma rhamnoides*, *Myrsine australis*, *Pittosporum crassifolium* and *Podocarpus totara*. Likewise, there were no hub species within the plant species level (Table 12).

The *vaznull* randomisation null models found that the long-distance potential network (observed modularity = 0.282), and short-distance potential network (observed modularity = 0.274) were modular communities statistically more modular than expected by random chance (long-distance: μ modularity = 0.102, $P < .001$; short-distance: μ modularity = 0.075, $P < .001$).

Table 11: Within-module degree (z) and among-module connectivity (c) values for all bird and plant species in the long-distance potential network. (*) Connector species. (†) ultra-peripheral species. Species are listed in order from the highest to lowest z value. Kererū received a NA for the z value as it was the only bird species within its module.

Bird Species	z	c
Tūi	2.039	0.466
Bellbird	0.707	0
Saddleback	-0.369	0.499
Grey warbler	-0.37	0
Silvereye	-0.414	0.354
Whitehead	-0.416	0.418
Song thrush	-0.467	0.456
Blackbird	-0.707	0.123
Kererū	NA	0.447
Plant Species	z	c
Hangehange (<i>Geniostoma ligustrifolium</i>)	1.403	0
Taupata (<i>Coprosma repens</i>)	1.069	0.444
Karamū (<i>Coprosma robusta</i>)	1.069	0.48
Karo (<i>Pittosporum crassifolium</i>)*	1.069	0.64
Cabbage tree (<i>Cordyline australis</i>)	0.526	0.56
Taraire (<i>Beilschmiedia tarairi</i>)	0	0
Pūriri (<i>Vitex lucens</i>)	0	0
Kawakawa (<i>Macropiper excelsum</i>)	-0.35	0.444
Nīkau (<i>Rhopalostylis sapida</i>)	-0.35	0.444
Twiggy Coprosma (<i>Coprosma rhamnoides</i>)*	-0.801	0.666
Māhoe (<i>Melicytus ramiflorus</i>)	-0.801	0.444
Māpou (<i>Myrsine australis</i>)	-0.801	0.375
Tōtara (<i>Podocarpus totara</i>)*	-0.801	0.625
Karaka (<i>Corynocarpus laevigatus</i>)	-1.224	0.5

Table 12: Within-module degree (z) and among-module connectivity (c) values for all bird and plant species in the short-distance potential network. (*) Connector species. Species are listed in order from the highest to lowest z value. Bellbird received a NA for the z value as it was the only bird species within its module.

Bird Species	z	c
Tūi	1.788	0.541
Kererū*	0.707	0.666
Grey warbler	-0.447	0
Saddleback	-0.447	0.444
Song thrush	-0.447	0.5
Whitehead	-0.447	0
Silvereye*	-0.707	0.64
Bellbird	NA	0
Plant Species	z	c
Hangehange (<i>Geniostoma ligustrifolium</i>)	1.224	0.375
Kawakawa (<i>Macropiper excelsum</i>)	1.154	0.444
Taupata (<i>Coprosma repens</i>)	0	0.5
Twiggy coprosma (<i>Coprosma rhamnoides</i>)*	0	0.666
Karamū (<i>Coprosma robusta</i>)	0	0.444
Cabbage tree (<i>Cordyline australis</i>)	0	0.5
Māhoe (<i>Melicytus ramiflorus</i>)	0	0.5
Māpou (<i>Myrsine australis</i>)*	0	0.625
Karo (<i>Pittosporum crassifolium</i>)*	0	0.625
Tōtara (<i>Podocarpus totara</i>)*	0	0.625
Nikau (<i>Rhopalostylis sapida</i>)	0	0.444
Tarairē (<i>Beilschmiedia tarairi</i>)	-0.577	0
Pūriri (<i>Vitex lucens</i>)	-0.577	0
Karaka (<i>Corynocarpus laevigatus</i>)	-1.224	0.5

3.14 Small-world properties

The small-world properties (short network path lengths and high clustering) are two common structural features of mutualistic networks and can determine the degree to which ecological disturbances, such as diseases, can spread through the network. The average (μ) shortest path length of plant species in the long-distance and short-distance potential network was 1.28, whereas the average shortest path length of bird species differed between the inferred networks. In the long-distance potential network, the average shortest path length was 1.47. In the short-distance potential network the average shortest path length was 1.92.

Path lengths were much shorter between plants than birds, however null models showed that plant path lengths were not significantly shorter or longer than expected by chance for the long-distance (μ path length = 1.25, $P = 0.322$) or short-distance (μ path length =

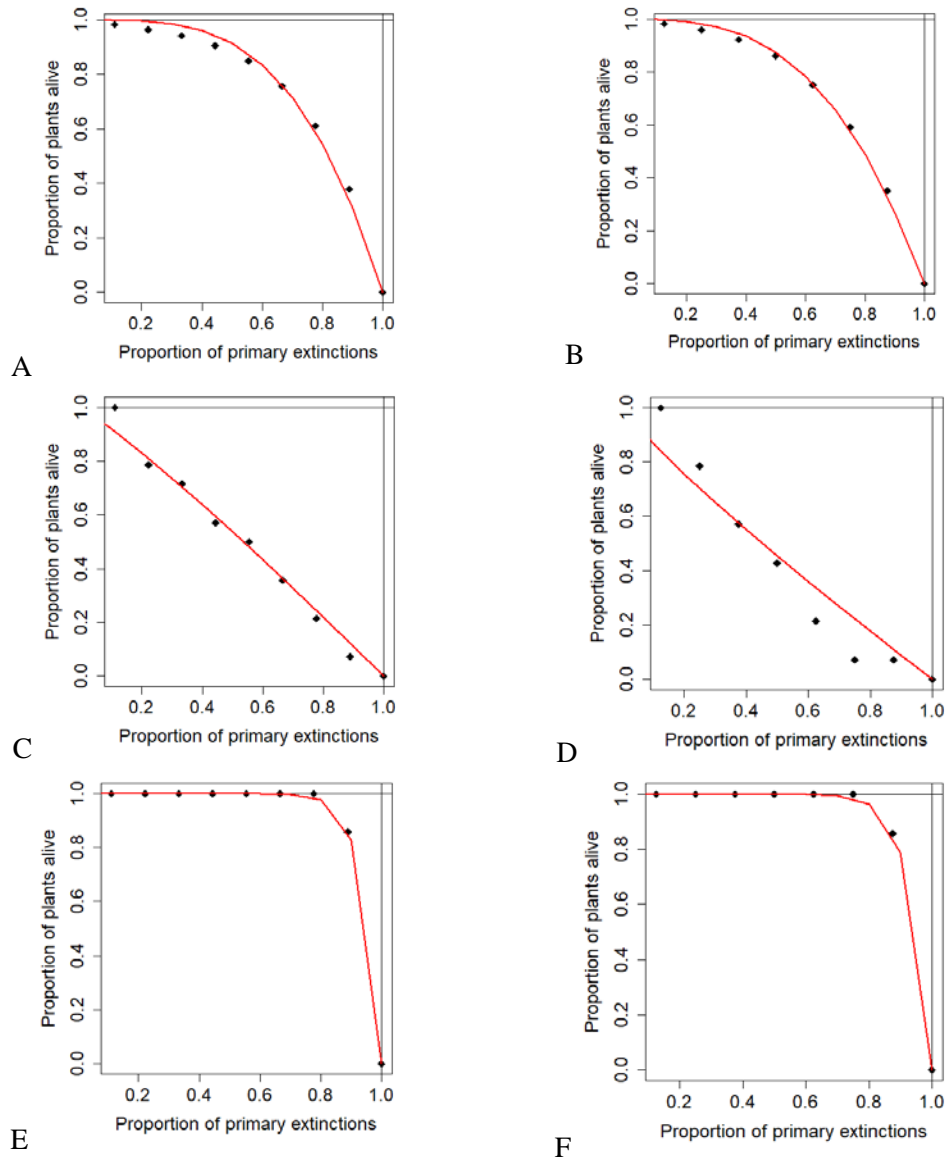
1.29, $P = 0.50$) potential networks. Null model simulations for the long-distance potential network suggest that bird path lengths are shorter than expected by chance alone (μ path length = 2.01, $P = 0.03$); however, average path lengths of birds in the short-distance potential network were not significantly shorter or longer than expected by chance (μ path length = 1.88, $P = 0.39$).

The mean clustering coefficients for the plant species and bird species in the long-distance potential network were 0.76 and 0.58, respectively. Comparisons of the observed clustering coefficient values in the long-distance potential network with null model values showed that neither the plants (μ clustering = 0.73, $P = .231$), or birds (μ clustering = 0.61, $P = .248$) within the network were significantly clustered. Similar patterns were observed in the short-distance potential network. Mean clustering coefficients for the plant species and bird species were 0.74 and 0.48, respectively. Neither the plants (μ clustering = 0.71, $P = .252$) nor birds ($\mu = 0.48$, $P = .467$) was significantly highly clustered according to null model simulations. Therefore, the long-distance and short-distance inferred networks did not exhibit the small-world properties (short average path lengths with significantly high clustering co-efficients) frequently reported in mutualistic networks.

3.15 Secondary extinction curves

Secondary extinction models of species within mutualistic networks show the robustness of the network to disturbance and highlight the potential for an ecological cascade event. The random order extinction curves for the long-distance potential network (Figure 20a) and short-distance potential network (Figure 20b) highlight the robustness of both networks to random frugivore removal. The majority of secondary extinctions of dependent plant species occurred only after 75–85% of frugivore species were removed. Similarly, systematic removal of frugivores in order of the least to most connected species prompted an even slower decline in secondary extinctions in both networks, with secondary extinctions only occurring once 90% of species were removed (Figure 20e and Figure 20f). Removal of species in order of the rarest to most abundant species in the long-distance and short-distance potential networks resulted in secondary extinctions once about 70% of frugivores were removed (Figure 20i and Figure 20j). In this case, the loss of the rarest species first would be less resilient to frugivore extinction than in a situation where the least connected species were removed first. Extirpations of the most generalised species first elicited no more than a linear secondary extinction

response of dependent plant species (Figure 20g and Figure 20h). While robust to random removal, the loss of the least connected species and the loss of the most generalised species, both networks are vulnerable to the loss of the most connected species (Figure 20c and Figure 20d). Extinction models indicate that the extirpation of tūi and kererū, the two most connected species in the short-distance potential network, would lead to 42% of plant species losing their dispersers (Figure 20d).



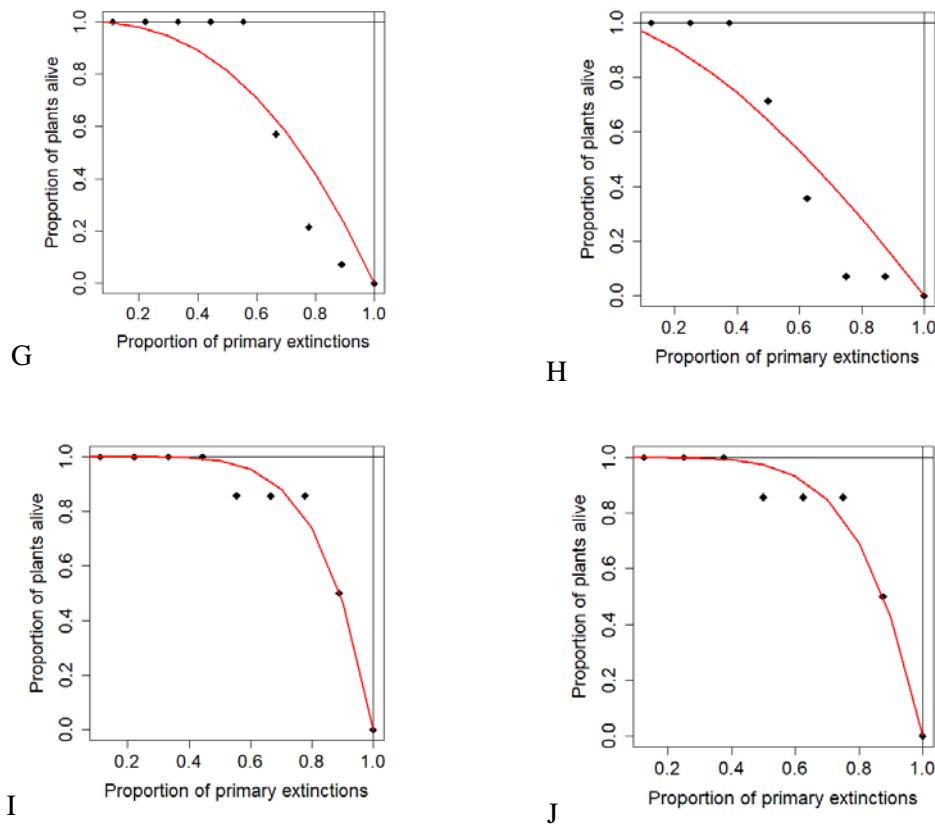


Figure 20: Cumulative secondary extinction curves following the systematic removal of: (a-b) a random order extinction sequence of bird species in the long-distance and short-distance potential network; (c-d) most to least connected bird species in the long-distance potential network; (e-f) the least to most connected bird species in the long-distance and short-distance potential network; (g-h) most to least generalised bird species in the long-distance and short-distance potential network; (i-j) most to least rarest bird species in the long-distance and short-distance potential network. Points indicate the point at which a species is removed.

3.16 Habitat type networks

Three habitat types were included in the habitat-type network metric results because pasture interior points did not support frugivores nor their dependent fruiting plants. Bird and plant species richness was greatest within the bush edge habitat network and thus had the highest mean number of links per bird and plant species compared to the other habitat types. High relative values for the bird and plant robustness metric indicated that the bush edge habitat network exhibited high resilience to ecological perturbation (Table 13). These findings were corroborated by the mean specialisation value for bush edge plants ($d' = 0.18$) and bush edge birds ($d' = 0.30$), which suggested high functional redundancy particularly for the plant trophic level.

The bush interior habitat potential network had the highest degree of network specialisation ($H2'$) and consequently the lowest degree of robustness to ecological

perturbance for the bird and plant trophic level. The mean specialisation value for bush interior plants ($d' = 0.24$) and bush edge birds ($d' = 0.32$) suggests that the bush interior potential network had relatively low functional redundancy compared to the other habitat potential networks.

While bird and plant species richness were lowest in the mānuka edge habitat network, mānuka edge habitat type had the highest network connectance and clustering coefficient for both the bird and plant trophic level. Furthermore, the mānuka edge habitat network had the lowest degree of specialisation due to a low $H2'$ value and possessed high resilience to disturbance (high robustness metric values), particularly for the plant trophic level. The mean specialisation value for mānuka edge plants ($d' = 0.13$) and mānuka edge birds ($d' = 0.25$) indicated a very high degree of functional redundancy especially for the plant trophic level.

Species specialisation (d') values indicate that the most specialised plant species available for each of the habitat type potential networks were those with the largest seeded fruits including *Vitex lucens* in the bush edge network, *Beilschmiedia tarairi* in the bush interior network and *Cordyline australis* in the mānuka edge habitat. On the other hand, small bodied frugivores comprised the most specialised species within the bush interior and bush edge habitats whereas the largest frugivore, kererū, was the most specialised species in the mānuka edge habitat (Table 14).

Table 13: Network metric values for the potential networks based on habitat type. Connectance (Conn.) represents the realised proportion of possible links within the network whereas the clustering coefficients (Cl.) represent the average clustering coefficient of the network which is derived from the the value of realised links divided by the value of possible links. The robustness index (Rob.) indicates the the resilience of the network based on the area under the extinction curve of Burgos et al. (2007). The network specialisation (H2') metric is an index which describes the degree of specialisation of the network and is an index ranging from 0 (extreme specialisation) to 1 (extreme generalisation).

Habitat	No. bird species	No. plant species	Mean bird links	Mean plant links	Conn.	Cl. birds	Cl. plants	WNODF	Rob. birds	Rob. plants	H2'
Bush edge	7	11	7.58	3.71	0.480	0.689	0.530	8.583	0.780	0.823	0.26
Bush interior	5	9	5.69	2.64	0.444	0.632	0.529	7.971	0.718	0.777	0.34
Mānuka edge	3	5	4.08	2.25	0.733	0.817	0.751	11.538	0.750	0.834	0.22

Table 14: Species specialisation (d') values for fruiting plant and bird species in the potential networks per habitat type.

Habitat type	Plant species	d'
Bush edge	Pūriri	0.580
	Hangehange	0.364
	Cabbage tree	0.252
	Nīkau	0.248
	Kawakawa	0.234
	Karamū	0.073
	Taupata	0.069
	Māpou	0.066
	Twiggy coprosma	0.054
	Karo	0.039
	Tōtara	0.039
Bush interior	Taraire	0.580
	Pūriri	0.580
	Hangehange	0.244
	Karaka	0.153
	Nīkau	0.153
	Cabbage tree	0.144
	Karamū	0.101
	Māpou	0.101
	Karo	0.092
Mānuka edge	Cabbage tree	0.522
	Taupata	0.044
	Karamū	0.044
	Māpou	0.044
	Karo	0.018
Habitat type	Bird species	d'
Bush edge	Grey warbler	0.567
	Whitehead	0.392
	Bellbird	0.333
	Saddleback	0.327
	Kererū	0.303
	Tūi	0.094
	Silvereye	0.070
Bush interior	Grey warbler	0.439
	Kererū	0.404
	Bellbird	0.397
	Saddleback	0.260
	Tūi	0.131
Mānuka edge	Kererū	0.452
	Bellbird	0.243
	Tūi	0.048

This thesis set out to answer three questions regarding: 1) the influence of habitat on bird communities (*how do bird assemblages and plant communities differ among the habitat types on Tāwharanui Regional Park?*), 2) the prediction of the network structure (*what is the structure and pattern of the plant-frugivore mutualistic networks within Tāwharanui Regional Park?*) and 3) the subsequent ecological implications for seed dispersal interactions in Tāwharanui (*what is the state of avian seed dispersal within the fragmented pest-free landscape of Tāwharanui Regional Park?*).

4.1 Sampling methodology

Overall, the bird and vegetation survey methods used to determine bird and fruiting plant species abundance, richness and composition were appropriate and applied recommended methodologies from the scientific literature, adapted for the local environment (García et al. 2014, Sutherland et al. 2004). Bird sampling was adequate and was adequate for measuring the communities as confirmed by the saturation of the overall avian species accumulation curve and the habitat type per month avian species accumulation curves (Appendix 2, Figure 21-Figure 28). However, interaction sampling (field frugivory observations) intensity was insufficient for an adequate representation of the seed dispersal network in Tāwharanui Regional Park; only 18% of possible unique pairwise interactions were observed in the field. Although timing of the sampling period was set to coincide with the peak fruiting season in New Zealand (García et al. 2014), this was likely a function of low sampling intensity. This prompted the use of potential interaction networks derived from co-occurrence data and literature of New Zealand bird-plant interactions as a supplement to field observations.

4.2 Bird species composition in habitats

Most introduced bird species (frugivorous or otherwise) at TRP were very rare, especially at the sampling stations comprised mostly of indigenous bush interior and bush edge habitat. Introduced species were typically only recorded at pasture points and points within the immediate vicinity of the commonly frequented campgrounds and public beaches. Native and endemic species comprised the top ten most abundant species, with bellbird comprising 25% of all sampled birds, followed by the ubiquitous pūkeko (21%) and tūi (11%). The endemic obligate forest species, saddleback, was the

sixth most abundant species comprising 5.4% of total counts and the endemic obligate frugivore, kererū, was the eighth most common species (2%). Introduced species, such as blackbirds (*Turdus merula*), house sparrows (*Passer domesticus*) and common myna (*Acridotheres tristis*), were present at the modified pasture points and largely absent from points within the remnant forest fragments of pest-free Tāwharanui. This is interesting considering the aggressive behaviour of common myna, although it's entirely possible that the endemic aggressive species, tūi, prevented myna intrusions into the bush interior and bush edge points.

Bird species compositions, as illustrated by the principal coordinate analyses, were not as different between pasture and other habitat types as initially expected. This was because edge habitats shared many of the species that were present at pasture points. These species tended to be generalists that can tolerate more disturbed habitats, such as pūkeko (*Porphyrio melanotus*), whereas the obligate forest species (the specialists) were restricted to the interior points, such as North Island robin (*Petroica longipes*). The influence of generalists within disturbed habitats and habitat edges has been reported in multiple types of interaction networks, such as seed-dispersal networks and food webs (Menke et al. 2012, Albrecht et al. 2013, García et al. 2014, Peralta et al. 2017). For example, García et al. (2014) found that exotic frugivore species dominated in the most disturbed habitats, thereby compensating for the loss of endemic frugivores, and consequently increasing network generalisation compared to networks with a more intact suit of endemic frugivores. Moreover, Peralta et al. (2017) found that herbivore-parasitoid food webs at habitat edges had a significantly higher abundance of generalist parasitoid species than expected by chance.

4.2.1 Bird species richness and abundance in habitats

In the GLMMs, increasing wind strength had a significantly negative effect on species abundance and richness for all native and large (body size > 75 g) frugivorous species. However, small frugivore species abundance and richness were not significantly affected by wind strength. In this study, it is not clear whether this disparity is due to behavioural differences between large and smaller frugivorous species in how they respond to strong wind, or whether it is due to sampling error because I would have been less likely to hear birds in windy conditions. Oconnor and Hicks (1980) reported significant negative correlations of wind strength and the frequencies of bird songs by tree-top singers.

Overall, bush edge points supported a significantly greater number of small and large avian frugivore individuals and species than pasture interior points. These findings are likely due to the high fruiting plant species richness and high fruit abundance within bush edge points, and the lack of fruiting species or cover and high disturbance in pasture habitat. Similarly, bush interior points supported a significantly greater number of large frugivore individuals (e.g., kererū) than mānuka points, and a significantly greater number of large frugivore species than pasture points. This likely due to the lack of large woody species within mānuka points and low fruiting species richness. The variation in plant species composition caused by differences in the presence of both the fruiting and non-fruiting plant species and relatively high number of fruiting plant species within bush interior points is a likely explanation for this result (Bregman et al. 2016).

In general, the results of the GLMMs corroborate the findings of several New Zealand studies comparing native and endemic species abundances and richness within severely modified habitats, with that of indigenous bush fragments or continuous forest. Previous research has shown that both species abundance and richness of native and endemic species tends to be lowest where habitat modification is highest (Clout and Gaze 1984, van Heezik et al. 2008, Innes et al. 2010). Similar findings have been reported in international studies (Cordeiro and Howe 2003, Kirika et al. 2008). The extent to which habitat disturbance and fragmentation affects species depends on species traits (Tylianakis and Morris 2017), such as the flight ability of affected species. Insectivores and other obligate forest species with a poor dispersal capacity, such as the saddleback or insectivorous North Island robin, are often be the most affected (Sekercioglu et al. 2002, Bregman et al. 2014). Species such as tūi, kererū and bellbirds tend to be the least affected by fragmentation, due to their ability to fly long distances to suitable foraging habitat (Bregman et al. 2014). For example, the large-bodied kererū have been recorded dispersing ingested seeds up to 1.5 km in a single flight (Wotton and Kelly 2012) and flying 33 km across the Foveaux Strait (Powlesland et al. 2011).

4.3 Field frugivory observations

Just 22 frugivory events, comprising 12 unique pairwise interactions, were recorded during the sampling period between February and June 2018. Thus, only 18% of all unique possible pairwise interactions were observed during the sampling period. Of the

67 possible unique pairwise interactions between the plants and birds recorded at the Tāwharanui sample points, 12 were observed, leaving 55 interactions that should have been possible but were not observed. It is possible that a couple of these interactions deemed possible based on the literature were actually forbidden links due to local size mismatching as the functional traits of interest— mean fruit diameter and mean bird gape width — vary between populations. However, in this study, insufficient sampling of interactions is the main issue that led to a low number of observed frugivory observations. This outcome has been reported for ecological interaction sampling, particularly for rarer species (Dorado et al. 2011, Olesen et al. 2011, Morales-Castilla et al. 2015, Jordano 2016), and hence provided the rationale for implementing potential interaction networks derived from co-occurrence data and literature of New Zealand bird-plant interactions.

Of all observed interactions, kererū consumed the most fruits during one event ($n = 143$), 94% of all confirmed swallowed fruits, were the sole disperser of the large seeded pūriri, and were responsible for just over half of the observed frugivory events. Similar findings were reported by García et al. (2014). Given their large body size, predominantly frugivorous diet and sedentary behaviour, these were unsurprising results that highlight the importance of this species within New Zealand ecosystems (Wotton and Ladley 2008, Wotton and Kelly 2011, Wotton and Kelly 2012). Tūi interacted once with several plant species of varying fruit sizes, underscoring their generalist diet (Kelly et al. 2006, Kelly et al. 2010). While Kelly et al. (2010) highlighted the capacity for tūi to disperse fruits up to 15 mm in width, nīkau fruits (fruit diameter of ~ 9.0 mm) was the largest seeded plant they were observed eating. Bellbird were observed feeding on the smaller seeded plants, māpou and taupata.

4.4 Network analysis of plant-frugivore interactions

Supplementary predictions of interactions derived from the long-distance potential network increased the number of possible unique interactions ($n = 67$) from 12 before the implementation (i.e., field observations only), to 46 following the implementation of the potential network model simulations. Whereas, supplementary predictions of interactions derived from the short-distance potential network increased the number of possible unique interactions ($n = 67$) from 12 before the implementation (i.e., field observations only), to 40 following the implementation of the potential network model simulations. As the literature of New Zealand plant-avian frugivore interactions were

“mined” in order to supplement and not replace frugivory observations, there were no false negative interactions missed. In other words, all observations that were confirmed in the field were included within the R script that created the potential networks.

Interaction predictions for tūi within the long-distance and short-distance network appear to resemble their generalist behaviour observed during field observations, but estimated that they should interact with twice as many fruiting species than observed in the field ($n = 6$); they had predicted interactions with 12 of the 14 fruiting species recorded during the sample period. Kererū and bellbird were the species with the second and third most links, respectively. Given the high abundance of tūi and bellbird, and the large body size of kererū, both potential networks highlight the effect of species abundance and large body size on interaction frequencies reported by García et al. (2014).

Low interaction frequency predictions for the endemic grey warbler and whitehead, and the introduced blackbird and song thrush, underscored their relatively low contributions to seed dispersal, most likely a consequence of their low abundances or, in the case of the endemic species, a predominantly insectivorous diet. Together, their low dispersal contribution within these potential networks, and their absence from field frugivory observations highlight the intrinsic difficulties sampling rarer species in the field (Dorado et al. 2011, Olesen et al. 2011, Morales-Castilla et al. 2015, Jordano 2016).

There were several noteworthy differences between the long-distance and short-distance potential networks for the less-connected bird species. Although present in the long-distance potential network, blackbirds were absent from the short-distance network. Furthermore, whitehead had only one mutualistic link with hangehange (*Geniostoma ligustrifolium*), whereas within the long-distance potential network, whitehead had three species links. Interaction predictions within the short-distance network resembled the long-distance potential network, with the exception of the introduced blackbird and the endemic whitehead; two of the least connected species. Blackbirds were absent from the short-distance potential network. The more restrictive maximum co-occurrence distance imposed by the short-distance potential network likely reduced false positives, i.e., the inclusion of estimated pairwise interactions that, in reality, were not happening. Therefore, more rigorous co-occurrence data, combined with the literature of plant-frugivore interactions and trait and dispersal ecology would lead to a more ecologically

precise representation of predicted dispersal mutualisms. Consequently, this would lead to more rigorous potential networks (Morales-Castilla et al. 2015).

4.4.1 Resilience of the potential networks

The bird and plants of the long-distance potential network exhibited a truncated power-law degree distribution, a characteristic property in mutualistic networks (Jordano et al. 2003, Bascompte and Jordano 2014). The truncated power-law degree distribution of the long-distance potential network suggests that the seed dispersal network would be resilient to a random loss of a species, but very vulnerable to the non-random loss of a highly connected species such as tūi, kererū or bellbird (Albert et al. 2000, Jordano et al. 2003, Bascompte and Jordano 2014). Because habitat loss and fragmentation affect species non-randomly based on their traits (Tylianakis and Morris 2017) such as body size (Larsen et al. 2005) or role within the network such as their contribution to network nestedness (specialist species interacting with more generalist species that form the core of interactions (Saavedra et al. 2011, Vidal et al. 2014, Tylianakis and Morris 2017)), highly connected species may still be at risk regardless of their high number of links, underscoring an important area of focus for conservation managers.

The most significant contributors to network nestedness also tend to be the most prone to extinction. This phenomenon has been observed in a seed dispersal network (Vidal et al. 2014), pollination networks, and also within a New York garment industry network comprised of contractor and designer firms (Saavedra et al. 2011). Applied to the Tāwharanui potential networks, tūi would therefore be the most prone to extinction as they were the most significant avian contributors to network nestedness in both the long and short-distance potential networks. Further research on this topic is required because the cause behind this phenomenon is unclear and given the high local abundance of tūi and generalist diet, this is probably ecologically unrealistic. The birds that contributed the least to the nested structure were the endemic whitehead, in the long-distance potential network, and the bellbird, in the short-distance potential network. Similar to the tūi result above, the fact that whitehead are predominantly insectivores makes it difficult to ascertain the ecological accuracy of these findings. Perhaps in the future when multilevel networks (e.g., tripartite) are possible, and several mutualistic relationship types can be considered, more ecologically accurate results can be obtained. The significant contributor to nestedness among the plant level was karaka which contributed the most in both the long-distance and short-distance potential networks.

The plant species that contributed the least to the nested structure in the short-distance potential network was māhoe and māpou (*Myrsine australis*) in the short-distance potential network. The exotic song thrush were consistent reducers of network nestedness in the long-distance and short-distance potential networks. These results indicate that tūi are important frugivores and that karaka (*Corynocarpus laevigatus*) are important fruiting plants, and that both species increase the probability of long-term persistence of plant-frugivore networks and imply that their absence would reduce the probability of long-term network persistence (Saavedra et al. 2011). Thus, if applied to conservation management, further plantings of karaka should be conducted within bush interior and bush edge habitats in order to secure long-term network stability. Saavedra et al. (2011) proposed that in addition to identifying the most extinction prone species, z-scores from nested contribution analysis could also enable an assessment of the status and impact of exotic species that are embedded within mutualistic networks. The z-scores of the introduced song thrush within the long-distance and short-distance potential networks indicate that they are one of the least vulnerable species within the networks, and therefore one of the most likely species to persist if habitat degradation and the transition to agricultural land continues. However, the current trend of increasing restoration efforts in Tāwharanui and similar offshore island and mainland ecosanctuaries suggest that the song thrush may be displaced over time.

The specialisation (d') values of the networks indicate a high amount of functional redundancy, and therefore high ecological stability, within the long-distance and short-distance potential networks. The low overall mean d' values of bird species in the potential networks showed that many frugivores serve functionally redundant roles, highlighting a high diet overlap between frugivores (Correa et al. 2016). Both the long-distance and short-distance potential networks exhibited high interaction generalisation, apart from the large-seeded taraire and pūriri in the plant level and the grey warbler and whitehead in the bird level. The high specialisation (d') of taraire and pūriri within both potential networks reflected the observation that only the large-bodied kererū has the gape width required to disperse these large fruits whole (Wotton and Ladley 2008, Wotton and Kelly 2012). Furthermore, the high specialisation of grey warbler and whitehead reflects their predominantly insectivorous diets (Innes et al. 2010), indicating that fruit makes up a small proportion of their diet due to diet-switching behaviour (Bascompte and Jordano 2014). Moreover, network-level specialisation ($H2'$) analysis of the potential networks was in line with other studies, which report high generalisation

of seed dispersal networks compared with pollination networks (Bluthgen et al. 2007, Bascompte and Jordano 2014).

4.4.4 Secondary extinction curves

The secondary extinction curve showed high network resilience following a hypothetical loss of all but the most connected species within the potential networks. These results were likely due to the heterogenous distribution of links within the potential networks (i.e., many species with few links, a few species with many links), which has been shown to increase tolerance to random species removal (Albert et al. 2000, Jordano et al. 2003). This link distribution (“degree distribution”) was confirmed to be present in the long-distance network but could only be speculated to be the degree distribution present in the short-distance potential network, due to the high demand for data. Simulated extinctions, in order of the most to least generalised species, prompted a gradual extinction response from plant species. The loss of the rarest frugivores species first would lead to more rapid plant extinctions than in a situation where the least connected species were removed first, suggesting that the least connected species aren’t necessarily the rarest. The low nestedness and relatively low network-level specialisation of the networks may have improved their overall resilience to generalist loss, a finding recently described by Correa et al. (2016). Both potential networks were highly vulnerable to the loss of the most connected species. The extirpation of tūi and kererū, the two most connected species in the short-distance potential network, would lead to 42% of plant species losing their dispersers, which would likely affect plant fitness due to decreased plant recruitment over the long-term. This result corroborates findings by several authors who have observed that the non-random removal of the most connected species in a network could subsequently lead to the collapse of that network (Albert et al. 2000, Jordano et al. 2003, Memmott et al. 2004).

4.4.5 Modularity of the potential networks

The modularity observed in the long- and short-distance potential networks suggests that if any ecological perturbations, such as disease or the extinction of a species, were to occur within a module, the modular structure of the network could act to protect the network from collapse. Modularity might restrict the disease, or the ecological consequences arising from secondary extinctions, to within the confines of the affected module, thus limiting the spread to the rest of the network (Stouffer and Bascompte 2011). Furthermore, the long- and short-distance networks were also highly connected,

compared to those found in similar studies (Fortuna et al. (2010). Fortuna et al. (2010) showed that significantly nested networks with low connectance were also significantly modular. However, in highly connected networks, these properties become mutually exclusive, with only one of these properties, nestedness or modularity, present. Therefore, in this study, the high connectance, significant modularity and low, insignificant nestedness of the networks corroborate the findings of Fortuna et al. (2010).

The within-module degree (z) and among-module connectivity (c) values indicated the predicted role of the bird and plant species within the networks. Species can be described as peripheral (species that are largely restricted to modules), ultra-peripheral (completely restricted to modules), or connector (species that connect between modules), according to their z and c values. Within the long-distance network, all frugivores were either peripheral or ultra-peripheral species. There were no other types of species roles among the frugivores, although there were three connector species among the plant level: twiggy coprosma (*Coprosma rhamnoides*), karo and tōtara. Within the short-distance network, all frugivores were peripheral species, except for kererū and silvereye, which were connector species. If these connector species were lost, modules of interacting frugivore and plant species could become isolated. On the contrary, in cases of disease, these connector species may act as vectors, spreading the disease through modules (Dupont and Olesen 2009, Stouffer and Bascompte 2011). Species roles within networks can therefore inform conservation management due to their influence on network dynamics and resilience. Conservation managers might choose to prioritise species that provide disproportionate contributions to network stability and resilience in the face of habitat degradation or disease, based on their position within the network structure (Olesen et al. 2007, Dupont and Olesen 2009, Mello et al. 2011, Stouffer and Bascompte 2011). Conservation management in Tāhwaranui should therefore ensure the preservation of kererū and silvereye, given their vital role in maintaining the high modularity of the long and short-distance networks. As highlighted above, maintaining high modularity increases network resilience to disturbance, a feature that is crucial given current global land use trends.

4.4.2 Habitat-type potential networks

The long-distance and short-distance potential networks were recalculated according to habitat type, to examine the influence of habitat on network structure. Habitat-type

potential networks showed that the bush interior had the highest degree of network specialisation ($H2'$) and the lowest degree of robustness to ecological perturbation for the bird and plant trophic levels. The high mean specialisation values for bush interior bird and plant species suggests that the bush interior potential network had relatively low functional redundancy compared to the other habitat potential networks, a finding also reported by Correa et al. (2016). The mānuka edge habitat potential network had the lowest degree of specialisation and possessed high resilience to disturbance (high robustness values). This indicates very high functional redundancy within this network subset, likely resulting from this habitat type having the highest network connectance and clustering coefficient in the bird and plant levels. These results corroborate the findings of Menke et al. (2012), who found high plant-frugivore network specialisation within the interior of a Kenyan forest, and low network specialisation within the forest edges. Similarly, García et al. (2014) found that network specialisation of seed dispersal networks in New Zealand decreased as habitat disturbance at each site increased. This was driven by the higher abundances of exotic generalists in the disturbed sites, which increased network connectance and resilience.

The most specialised plant species across all habitat types were those with the largest seeds, according to d' values, such as pūriri in the bush edge network, taraire in the bush interior network, and cabbage tree in the mānuka edge habitat. This is to be expected because only kererū would be able to effectively disperse the seeds of pūriri and taraire and were clearly the most effective dispersers of cabbage tree in mānuka edge habitats. High specialisation of large-seeded species in edge habitats has also been reported by Menke et al. (2012), who suggested that this was likely due to lower large bodied frugivore abundance at edge habitats compared to interior habitats. While this was also the case for large frugivore abundance and richness in mānuka edge habitat, there was no significant effect found in bush edge habitat. Of course, differences in findings are to be expected given the obvious difference in frugivore species composition between Tāwharanui and the Kenyan forest site in Menke et al. (2012) (i.e., frugivorous native monkeys in Kenya). Small-bodied frugivores comprised the most specialised species within the bush edge habitat whereas the largest frugivore, kererū, was the most specialised species in the mānuka edge habitat. Although, in reality plant-frugivore interactions in Tāwharanui would not be restricted to their habitat-types, subsetting the total potential networks by habitat-type provided a way to estimate the implications of

further habitat change and the implications for network structure and resilience (Tylianakis and Morris 2017).

Together, specialisation values at the network level ($H2'$) and species level (d') suggest that plant species that inhabit the forest interior, and their mutualist forest frugivores, form dispersal networks that are less generalised and have lower functional redundancy than their edge counterparts. Lower functional redundancy may lead to less of an ecological buffer against perturbances such as species loss, meaning native restoration focus by conservation management should be concentrated on these more specialised indigenous species networks.

4.4.3 Pest control and exotic bird abundance

Tāwharanui, unlike most other regions of New Zealand, contains an almost full suite of endemic frugivores due to a rigorous mammalian pest control monitoring program and species translocation program, and sufficient remnant forest habitat (Murdoch 2008). Exotic bird species were absent from almost all environments, except for the most modified patches of Tāwharanui's landscape. As a result, the endemic species such as bellbird and tūi, comprised a large proportion of the total bird abundance at Tāwharanui and were consequently the species with the most unique pairwise interactions and high interaction frequencies (Vazquez et al. 2007, García et al. 2014, Tylianakis and Morris 2017) forming the “core” of the interaction network (Bascompte and Jordano 2007). Similarly, García et al. (2014) looked at seed dispersal networks across an environmental gradient, composed of nine sites throughout New Zealand, with varying degrees of habitat disturbance. Exotics compensated for native and endemic frugivore loss by dispersing the seeds of native plants at these sites. Exotic compensation for native loss was greatest in more degraded landscapes and lowest in unmodified sites with high endemic richness (García et al. 2014). Likewise, the potential networks of Tāwharanui showed that exotic frugivores played a very minor role as seed dispersers due to the high endemic frugivore richness and high native plant species richness.

4.5 Assumptions, limitations and future research

Although the realised network was under-sampled (only 12 out of 67 possible pairwise interactions were recorded), realised interactions confirmed during frugivory observations were able to provide a useful gauge of the inferred networks' modelled prediction accuracy by highlighting interaction predictions missed by the model, but

observed in the field (Morales-Castilla et al. 2015). If this research were to be repeated, frugivory interaction sampling would include a combination of sampling methods to ensure adequate field observation of frugivory observations. Frugivory interaction sampling methods could use mist netting methods to capture birds and determine what seeds are ingesting or include phyto-centric interaction sampling (Lehouck et al. 2009, Albrecht et al. 2013, Plein et al. 2013) whereby an observer (or cameras) remains fixed in a position and records interactions of frugivores visiting the focal fruiting plant individual (Jordano 2016) being sure to determine the functional outcome of the dispersal interaction, and not just the visitation of a frugivore (Simmons et al. 2018). This method might be particularly useful within landscapes dominated by a bush-pasture matrix. In addition, the interaction sampling method described by García et al. (2014) would be used along the established walking trails within the larger indigenous forest fragments of Tāwharanui, but given the randomised placement of sampling stations in this study, the original implementation described by García et al. (2014) was not possible. Multiple sampling seasons would have accounted for the temporal dynamics of interaction networks (Olesen et al. 2008) and would have increased the number of unique pairwise interactions between birds and fruiting plants. Furthermore, some of the references used to infer New Zealand bird-plant interactions were based on frugivore visitations to fruiting plants (visitors touching the plant) as a proxy for dispersal interaction (Jordano 2016), rather than confirmed observations of fruit ingestion (Simmons et al. 2018). Thus, the functional outcomes of a couple of interactions may not be accurately quantified, thus slightly reducing the predictive power of the potential networks. Adequately sampled field observations could potentially “calibrate” predictive interaction models (Morales-Castilla et al. 2015). For example, a realised network, comprised of field observations with sufficient sampling intensity, could be compared with the inferred interactions of a potential network, to identify false negatives (realised observations that do not appear as inferred interactions within the potential network (Harvey et al. 2017).

This research used co-occurrence frequencies of possible plant-frugivore pairs as a surrogate for interaction strengths in order to build the networks (Vazquez et al. 2005). This method implements a binary or "all or nothing" approach, where possible but improbable interactions are included, disregarding varying interaction probabilities between species pairs. This approach may have overestimated the interaction strength of certain pairwise interactions, and therefore highlights the need to implement

probabilities of pairwise interaction. Moreover, species that do not, or very rarely, interact may co-occur for reasons other than food resources, and thus the probability of interaction should depend on their functional traits. I attempted to mitigate this by creating the short and long distance network as a less and more conservative estimate, respectively (Ovaskainen et al. 2010, Araujo and Rozenfeld 2014, Morales-Castilla et al. 2015). If the potential network methodology was to be implemented again, the predictive model would incorporate a probabilistic function applied to a version of the niche model (Williams and Martinez 2000) that is adapted for application to a mutualistic network (Gravel et al. 2013, Morales-Castilla et al. 2015) to account for the varying probabilities of dispersal interaction between a fruiting plant and frugivore. For example, the allometric (predator and prey body size) relationship used to predict interactions in food webs (Gravel et al. 2013) could be adapted to represent local functional trait measurements, such as frugivore gape widths and fruit diameters (Poisot et al. 2015). Such an approach could allow inferring the probability of seed dispersal interactions, resulting in a more rigorous potential network; a powerful conservation tool to predict the impact of climate change and biodiversity loss on ecological functions. Consequently, following these recommendations would allow for more accurate 1) depictions of network properties 2) predictions of ecological impacts and 3) conservation priorities (Morales-Castilla et al. 2015, Tylianakis and Morris 2017, Delmas et al. 2019).

Although the timing of the sampling period was set to synchronise with the period of highest ripe fruit availability sampling effort was limited to one season. This prevented my research from accounting for the temporal dynamics inherent within mutualistic networks (Olesen et al. 2008, Bascompte and Jordano 2014). The issue of interaction under-sampling, particularly of rarer species, are then amplified due to the non-random loss of species interactions following ecological disturbances and the ephemeral nature of rare species interactions (Dorado et al. 2011, Olesen et al. 2011, Morales-Castilla et al. 2015, Jordano 2016). For example, infrequent mutualistic interactions and interactions between specialists (species with few unique pairwise interactions) are the most likely to go extinct after an ecological perturbation (Aizen et al. 2012), meaning species that are observed to be rare during one sample season may be absent in the following season. Furthermore, in a two-year pollination network study, two thirds of unique mutualistic interactions present in the first year, were absent the following year. The rarest and most specialised species contributed to this turnover (Olesen et al. 2008).

Thus, these potential networks can be seen as a “snapshot” of seed dispersal interactions within Tāwharanui. Future research should be conducted over several seasons to assess the temporal dynamics inherent within these interaction networks.

4.7 Recommendations

The findings of this research highlight the benefits of applying a network analysis approach based on predictive mutualistic interaction networks to estimate network structure and resilience of ecological functions, such as seed dispersal or pollination. Complex ecological networks made up of many interacting species should not be reduced to individual species for the purposes of conservation. Rather, conservation managers of protected areas should apply a network analysis perspective and approach to unearth novel ecological understanding and achieve conservation objectives (Bascompte and Jordano 2014, Delmas et al. 2019), providing the recommended adaptations to the methodology implemented in this research (4.6 Future research) are adopted. The predictive network analysis approach used in this research provided ecological insights that could be useful for conservation management in Tāwharanui. For example, the short-distance potential network was highly vulnerable to the loss of tūi and kererū, which would lead to 42% of plant species within the network losing their dispersers. Furthermore, network properties showed the disproportionate influence of these two species on the network structure and resilience. Therefore, conservation management in Tāwharanui should focus efforts on preserving local populations of tūi and kererū in particular. For kererū, the maintenance and replanting of bush interior and bush edge habitat would be beneficial as these sites contain the large-seeded pūriri (*Vitex lucens*) and taraire (*Beilschmiedia taraire*) species. Kererū is the sole effective disperser of taraire in Tāwharanui, and almost everywhere else in New Zealand, due to the highly restricted range of the only other disperser, kōkako (*Callaeas wilsoni*) (Kelly et al. 2010). Kererū are also important dispersers of pūriri, a keystone species in the upper North Island, due to its long fruiting and flowering period. The proliferation of pūriri would benefit many frugivorous and nectarivorous species in Tāwharanui, including tūi. Research by Kelly et al. (2010) has shown that, based on low germination rates of intact and hand-cleaned pūriri seeds within glasshouses, kererū may be vital in maintaining pūriri plant fitness.

4.8 Conclusion

Overall, this research has highlighted the benefits of applying a network theory approach as a tool for conservation managers to identify and set conservation priorities. Furthermore, it demonstrated the efficacy of predictive networks through the novel use of co-occurrence data from field observations in combination with literature plant-frugivore interactions. Bird assemblages in Tāwharanui differed among the habitat types. Bush interior points and bush edge points had significantly higher frugivore species richness than pasture interior points, while bush interior points supported a significantly higher number of large frugivores per point than mānuka edge points. Network analysis showed a highly modular network structure of the long-distance and short-distance potential networks, indicative of a network that is resilient to disturbance. An outbreak of disease within the community, for example, would likely be restricted within the module where the disease originated, leaving other modules relatively unaffected. Structural properties of the potential networks, such as the aforementioned modularity, and the heterogeneous distribution of links within the potential networks (i.e., many species with few links, a few species with many links) suggest that the potential networks are resilient to the loss of all but the most connected frugivore species. The habitat-type potential networks underscored the impact of environmental habitat gradients on network structure and species roles and the ecological consequences for these networks in the face of persistent land use changes. Together, these results underscore the utility of implementing a predictive network analysis approach for conservation management, and emphasises the importance of avoiding further habitat loss and restoring indigenous forest ecosystems to support high frugivore species abundance and richness to ensure the maintenance of seed dispersal functioning.

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Appendix 1

Table 15: Vegetation data (including non-bird-dispersed plant species) at all bird count points. Height Tier describes the height of the species classified into 6 tiers – (Tier 1 - Emergent > 25m, Tier 2 - Canopy 12-25m, Tier 3 - Sub-canopy 5-12m, Tier 4 - Understory 2-5m, Tier 5- Shrub 30cm-2m and Tier 6 - Floor < 30cm) Cover Class describes the percent vegetation cover for each tier (< 1%, 1– 5%, 6–25%, 26–50%, 51–75%, 76–100%) Adapted from Hurst and Allen (2007).

Station	Point	Height Tier	Species	Cover Class
1	A	6	<i>pasture grasses</i>	6
1	B	5	<i>Dysoxylum spectabile</i>	2
1	B	3	<i>Rhopalostylis sapida</i>	3
1	B	3	<i>Corynocarpus laevigatus</i>	3
1	B	2	<i>Vitex lucens</i>	6
1	B	2	<i>Leptospermum scoparium</i>	6
1	C	4	<i>Leptospermum scoparium</i>	4
1	C	4	<i>Rhopalostylis sapida</i>	4
1	C	2	<i>Vitex lucens</i>	5
1	D	6	<i>pasture grasses</i>	6
1	E	6	<i>pasture grasses</i>	6
1	F	6	<i>pasture grasses</i>	6
1	G	5	<i>Geniostoma ligustrifolium</i>	3
1	G	5	<i>Myrsine australis</i>	3
1	G	3	<i>Cyathea cunninghamii</i>	4
1	G	2	<i>Leptospermum scoparium</i>	4
1	H	6	<i>pasture grasses</i>	6
2	A	6	<i>pasture grasses</i>	6
2	B	5	<i>Leptospermum scoparium</i>	2
2	C	6	<i>Macropiper excelsum</i>	3
2	C	3	<i>Myrsine australis</i>	3
2	C	3	<i>Vitex lucens</i>	3
2	C	3	<i>Leptospermum scoparium</i>	3
2	C	2	<i>Alectryon excelsus</i>	3
2	D	4	<i>Myrsine australis</i>	6
2	D	4	<i>Melicytus ramiflorus</i>	6
2	D	3	<i>Leptospermum scoparium</i>	6
2	E	4	<i>Macropiper excelsum</i>	3
2	E	3	<i>Melicytus ramiflorus</i>	3
2	E	2	<i>Rhopalostylis sapida</i>	3
2	F	6	<i>pasture grasses</i>	6
2	G	3	<i>Leptospermum scoparium</i>	3
2	H	6	<i>pasture grasses</i>	6
2	I	6	<i>Dysoxylum spectabile</i>	2
2	I	4	<i>Macropiper excelsum</i>	3

2	I	3	<i>Leptospermum scoparium</i>	3
2	I	3	<i>Myrsine australis</i>	3
3	A	5	<i>Phormium tenax</i>	2
3	A	4	<i>Leptospermum scoparium</i>	4
3	A	4	<i>Pittosporum crassifolium</i>	4
3	B	5	<i>Pittosporum crassifolium</i>	4
3	B	5	<i>Phormium tenax</i>	4
3	B	4	<i>Leptospermum scoparium</i>	3
3	D	5	<i>Phormium tenax</i>	3
3	D	4	<i>Leptospermum scoparium</i>	3
3	D	4	<i>Pittosporum crassifolium</i>	3
3	E	5	<i>Leptospermum scoparium</i>	3
3	E	5	<i>Phormium tenax</i>	3
3	E	4	<i>Pittosporum crassifolium</i>	2
3	F	6	<i>pasture grasses</i>	6
3	G	6	<i>pasture grasses</i>	6
3	H	6	<i>pasture grasses</i>	6
4	A	4	<i>Macropiper excelsum</i>	5
4	A	4	<i>Corynocarpus laevigatus</i>	5
4	A	4	<i>Pittosporum eugenoides</i>	5
4	A	3	<i>Rhopalostylis sapida</i>	4
4	A	2	<i>Vitex lucens</i>	6
4	B	3	<i>Leptospermum scoparium</i>	5
4	C	6	<i>pasture grasses</i>	6
4	D	6	<i>pasture grasses</i>	6
4	E	5	<i>Macropiper excelsum</i>	4
4	E	5	<i>Myrsine australis</i>	4
4	E	3	<i>Leptospermum scoparium</i>	5
4	F	4	<i>Macropiper excelsum</i>	4
4	F	3	<i>Vitex lucens</i>	5
4	F	3	<i>Corynocarpus laevigatus</i>	5
4	F	3	<i>Beilschmiedia tarairi</i>	5
4	H	5	<i>Phormium tenax</i>	5
4	H	5	<i>Leptospermum scoparium</i>	5
4	H	4	<i>Pittosporum crassifolium</i>	2
4	I	6	<i>Cyathea dealbata</i>	4
4	I	5	<i>Macropiper excelsum</i>	3
4	I	5	<i>Melicytus ramiflorus</i>	3
4	I	4	<i>Myrsine australis</i>	4
4	I	3	<i>Leptospermum scoparium</i>	5
5	A	6	<i>pasture grasses</i>	6
5	B	4	<i>Myrsine australis</i>	5
5	B	4	<i>Macropiper excelsum</i>	5
5	B	4	<i>Melicytus ramiflorus</i>	5
5	B	3	<i>Corynocarpus laevigatus</i>	4
5	B	3	<i>Rhopalostylis sapida</i>	4

5	B	2	<i>Vitex lucens</i>	6
5	B	2	<i>Leptospermum scoparium</i>	6
5	C	3	<i>Leptospermum scoparium</i>	3
5	C	3	<i>Melicytus ramiflorus</i>	3
5	C	2	<i>Beilschmiedia tarairi</i>	6
5	C	2	<i>Corynocarpus laevigatus</i>	6
5	C	2	<i>Rhopalostylis sapida</i>	6
5	C	2	<i>Vitex lucens</i>	6
5	D	6	<i>pasture grasses</i>	6
5	E	5	<i>Myrsine australis</i>	2
5	E	4	<i>Macropiper excelsum</i>	3
5	E	3	<i>Melicytus ramiflorus</i>	3
5	E	3	<i>Cordyline australis</i>	3
5	E	2	<i>Leptospermum scoparium</i>	4
5	F	6	<i>pasture grasses</i>	6
5	G	4	<i>Leptospermum scoparium</i>	5
5	G	4	<i>Macropiper excelsum</i>	5
5	G	4	<i>Myrsine australis</i>	5
5	G	2	<i>Cordyline australis</i>	2
5	H	6	<i>pasture grasses</i>	6
5	I	6	<i>pasture grasses</i>	6
6	A	6	<i>Geniostoma ligustrifolium</i>	2
6	A	4	<i>Myrsine australis</i>	3
6	A	3	<i>Macropiper excelsum</i>	4
6	A	3	<i>Melicytus ramiflorus</i>	4
6	A	2	<i>Leptospermum scoparium</i>	4
6	A	2	<i>Cordyline australis</i>	4
6	D	4	<i>Myrsine australis</i>	5
6	D	3	<i>Cordyline australis</i>	3
6	D	2	<i>Leptospermum scoparium</i>	4
6	E	5	<i>Myrsine australis</i>	3
6	E	4	<i>Beilschmiedia tarairi</i>	3
6	E	3	<i>Vitex lucens</i>	4
6	E	3	<i>Leptospermum scoparium</i>	4
6	F	4	<i>Leptospermum scoparium</i>	3
6	G	4	<i>Metrosideros excelsa</i>	4
6	H	5	<i>Geniostoma ligustrifolium</i>	3
6	H	5	<i>Melicytus ramiflorus</i>	3
6	H	4	<i>Myrsine australis</i>	4
6	H	3	<i>Leptospermum scoparium</i>	6
6	I	5	<i>Cordyline australis</i>	3
6	I	5	<i>Melicytus ramiflorus</i>	3
6	I	4	<i>Geniostoma ligustrifolium</i>	5
6	I	3	<i>Leptospermum scoparium</i>	5
7	A	6	<i>pasture grasses</i>	6
7	B	6	<i>pasture grasses</i>	6

7	C	6	<i>pasture grasses</i>	6
7	D	4	<i>Myrsine australis</i>	4
7	D	2	<i>Melicytus ramiflorus</i>	4
			<i>Phyllocladus</i>	
7	D	2	<i>trichomanoides</i>	4
7	D	2	<i>Podocarpus totara</i>	4
7	D	2	<i>Cordyline australis</i>	4
7	D	2	<i>Leptospermum scoparium</i>	4
7	D	1	<i>Agathis australis</i>	6
7	E	5	<i>Podocarpus totara</i>	2
7	E	4	<i>Myrsine australis</i>	5
7	E	2	<i>Leptospermum scoparium</i>	5
7	F	6	<i>pasture grasses</i>	6
7	G	6	<i>Geniostoma ligustrifolium</i>	2
7	G	5	<i>Myrsine australis</i>	2
7	G	2	<i>Knightia excelsa</i>	3
7	G	2	<i>Leptospermum scoparium</i>	4
			<i>Phyllocladus</i>	
7	G	1	<i>trichomanoides</i>	6
7	G	1	<i>Agathis australis</i>	6
7	H	4	<i>Myrsine australis</i>	5
7	H	3	<i>Vitex lucens</i>	5
7	I	3	<i>Myrsine australis</i>	5
8	A	5	<i>Phormium tenax</i>	3
8	A	5	<i>Myrsine australis</i>	3
8	A	3	<i>Podocarpus totara</i>	4
8	A	3	<i>Cordyline australis</i>	4
8	B	3	<i>Leptospermum scoparium</i>	5
8	D	6	<i>pasture grasses</i>	6
8	F	5	<i>Macropiper excelsum</i>	4
8	F	4	<i>Myrsine australis</i>	5
8	F	3	<i>Leptospermum scoparium</i>	5
8	G	5	<i>Myrsine australis</i>	3
8	G	3	<i>Leptospermum scoparium</i>	4
8	H	5	<i>Macropiper excelsum</i>	2
8	H	4	<i>Myrsine australis</i>	2
8	H	4	<i>Melicytus ramiflorus</i>	2
8	H	4	<i>Prumnopitys ferruginea</i>	4
8	H	3	<i>Podocarpus totara</i>	3
8	H	3	<i>Cordyline australis</i>	3
8	H	3	<i>Dacrycarpus dacrydioides</i>	3
8	H	2	<i>Leptospermum scoparium</i>	3
8	I	6	<i>pasture grasses</i>	6
9	A	5	<i>Myrsine australis</i>	2
9	A	4	<i>Leptospermum scoparium</i>	5

Table 16: Fruiting plant species per habitat type.

Habitat type	Plant species
Bush edge	Cabbage tree (<i>Cordyline australis</i>)
	Hangehange (<i>Geniostoma ligustrifolium</i>)
	Karamū (<i>Coprosma robusta</i>)
	Karo (<i>Pittosporum crassifolium</i>)
	Kawakawa (<i>Macropiper excelsum</i>)
	Māpou (<i>Myrsine australis</i>)
	Nīkau (<i>Rhopalostylis sapida</i>)
	Pūriri (<i>Vitex lucens</i>)
	Taupata (<i>Coprosma lucens</i>)
	Tōtara (<i>Podocarpus totara</i>)
	Twiggy Coprosma (<i>Coprosma rhamnoides</i>)
Bush interior	Cabbage tree (<i>Cordyline australis</i>)
	Hangehange (<i>Geniostoma ligustrifolium</i>)
	Karaka (<i>Corynocarpus laevigatus</i>)
	Karamū (<i>Coprosma robusta</i>)
	Karo (<i>Pittosporum crassifolium</i>)
	Māpou (<i>Myrsine australis</i>)
	Nīkau (<i>Rhopalostylis sapida</i>)
	Pūriri (<i>Vitex lucens</i>)
	Tarairi (<i>Beilschmiedia tarairi</i>)
Mānuka edge	Cabbage tree (<i>Cordyline australis</i>)
	Karamū (<i>Coprosma robusta</i>)
	Karo (<i>Pittosporum crassifolium</i>)
	Māpou (<i>Myrsine australis</i>)
	Taupata (<i>Coprosma lucens</i>)

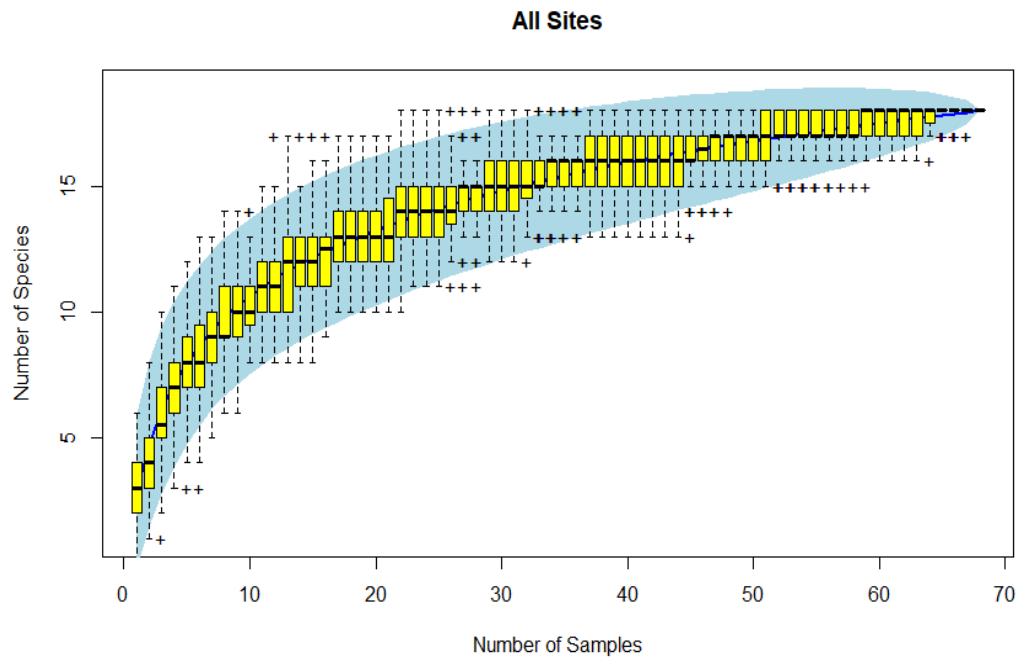


Figure 21: Total avian species accumulation curves for February. The blue shading indicates the range of predicted species richness values. The yellow boxplot centre line represents the median species richness per sample while the yellow boxplot represents the interquartile range, calculated from random permutations of the data. The boxplot whiskers are 1.5 times the interquartile range.

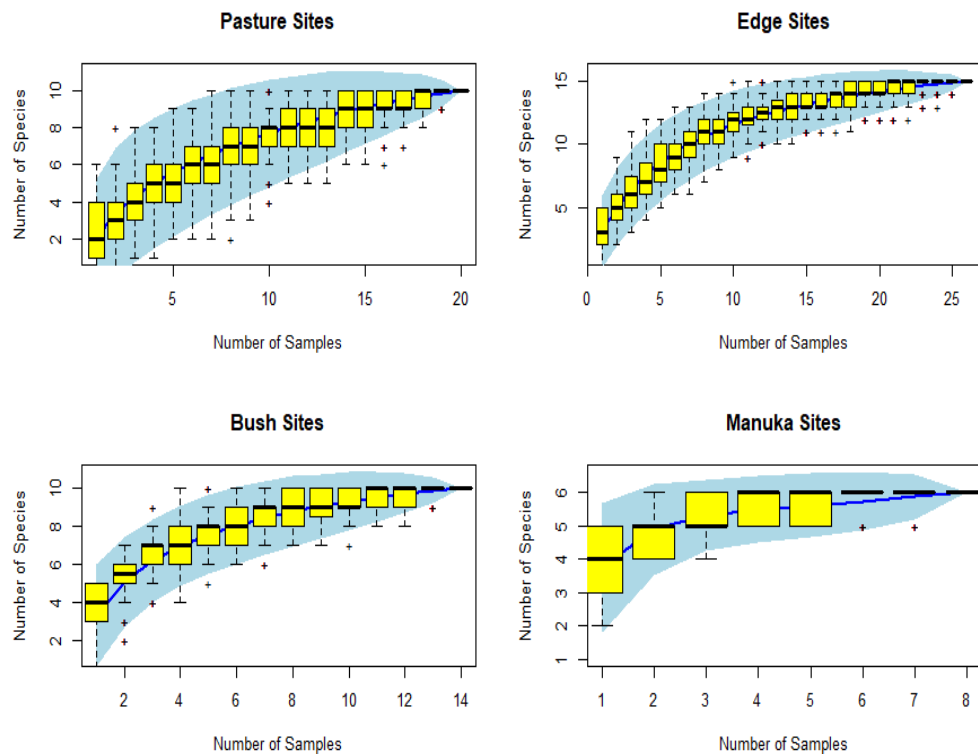


Figure 22: Avian species accumulation curves per habitat type for February. The blue shading indicates the range of predicted species richness values. The yellow boxplot centre line represents the median species richness per sample while the yellow boxplot represents the interquartile range, calculated from random permutations of the data. The boxplot whiskers are 1.5 times the interquartile range.

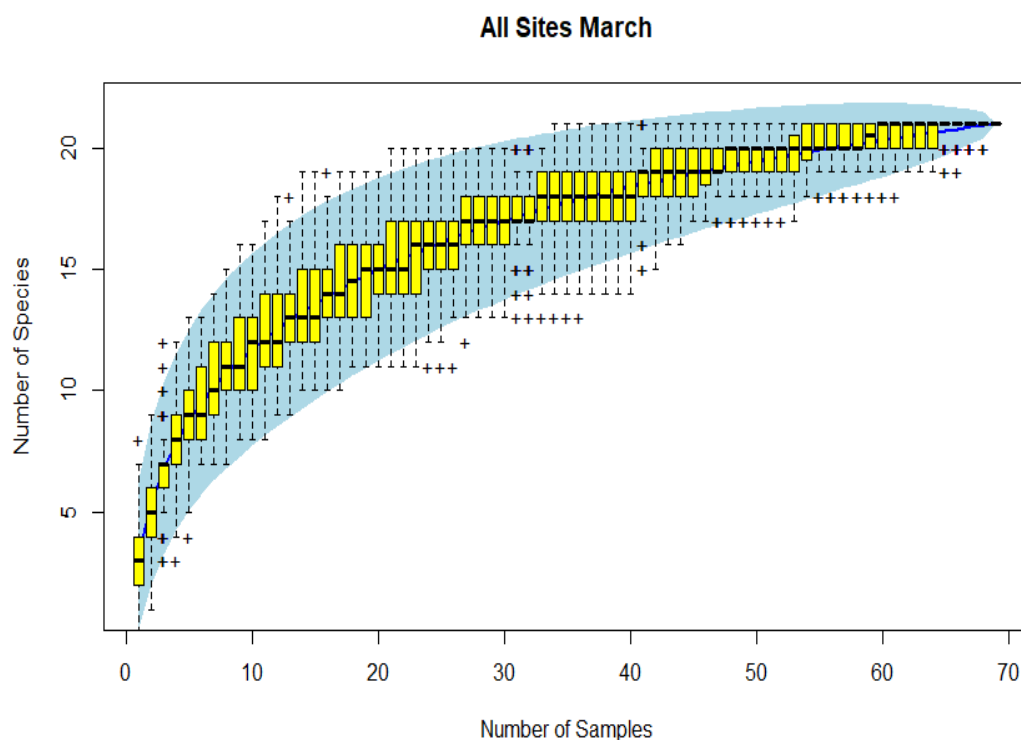


Figure 23: Total avian species accumulation curves for March. The blue shading indicates the range of predicted species richness values. The yellow boxplot centre line represents the median species richness per sample while the yellow boxplot represents the interquartile range, calculated from random permutations of the data. The boxplot whiskers are 1.5 times the interquartile range.

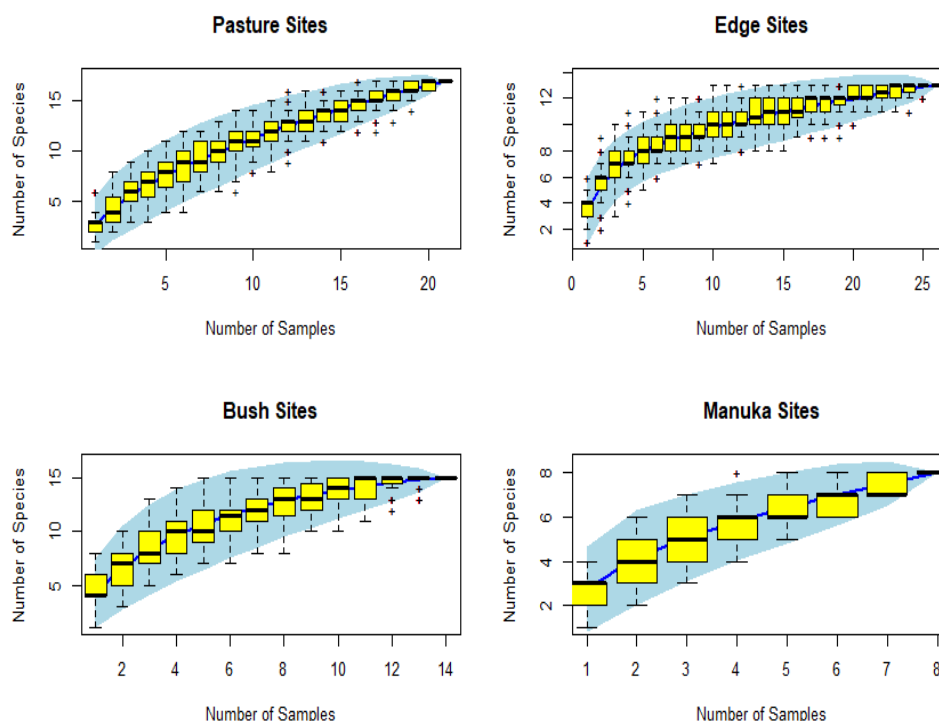


Figure 24: Avian species accumulation curves per habitat type for March. The blue shading indicates the range of predicted species richness values. The yellow boxplot centre line represents the median species richness per sample while the yellow boxplot represents the interquartile range, calculated from random permutations of the data. The boxplot whiskers are 1.5 times the interquartile range.

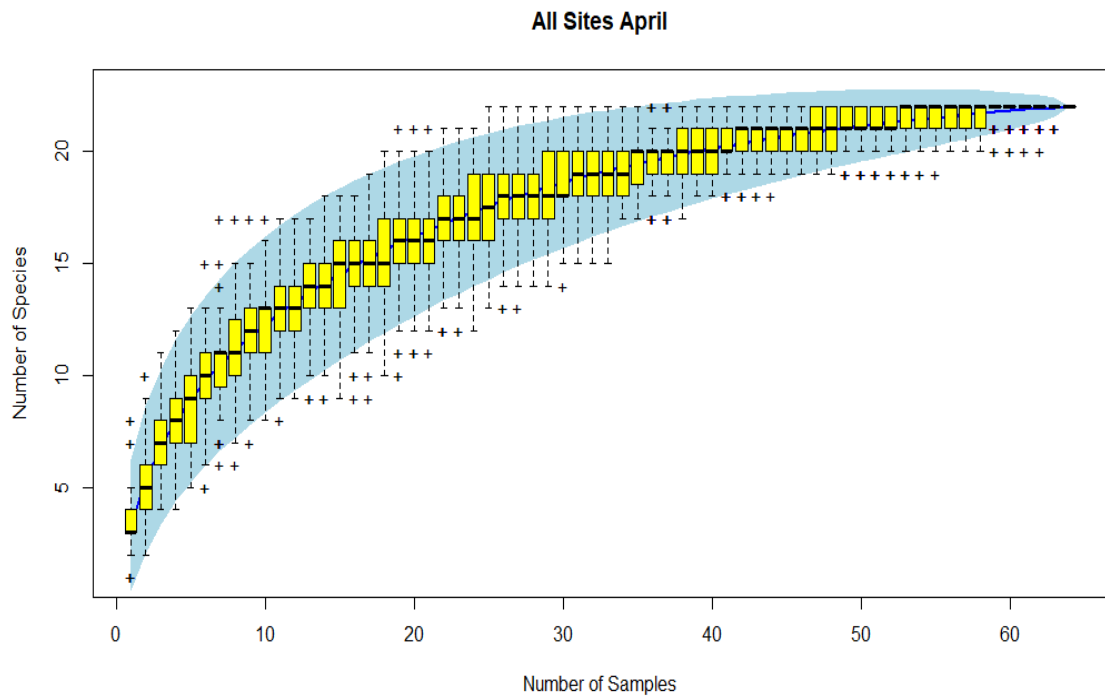


Figure 25: Total avian species accumulation curves for April. The blue shading indicates the range of predicted species richness values. The yellow boxplot centre line represents the median species richness per sample while the yellow boxplot represents the interquartile range, calculated from random permutations of the data. The boxplot whiskers are 1.5 times the interquartile range.

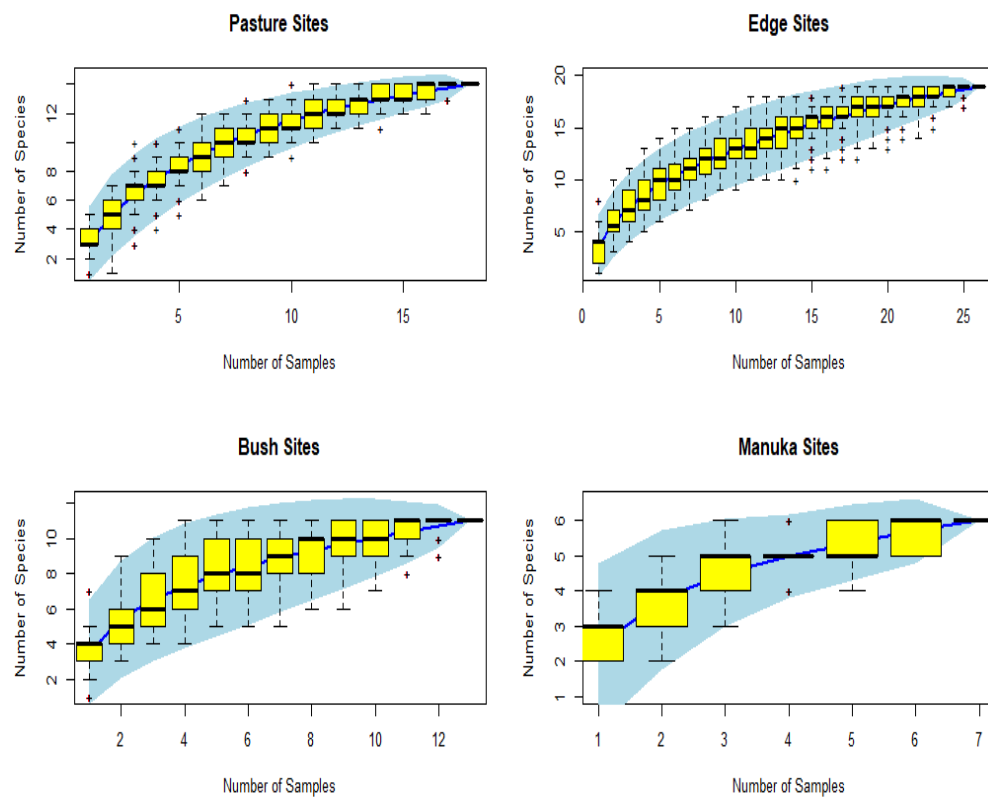


Figure 26: Avian species accumulation curves per habitat type for April. The blue shading indicates the range of predicted species richness values. The yellow boxplot centre line represents the median species richness per sample while the yellow boxplot represents the interquartile range, calculated from random permutations of the data. The boxplot whiskers are 1.5 times the interquartile range.

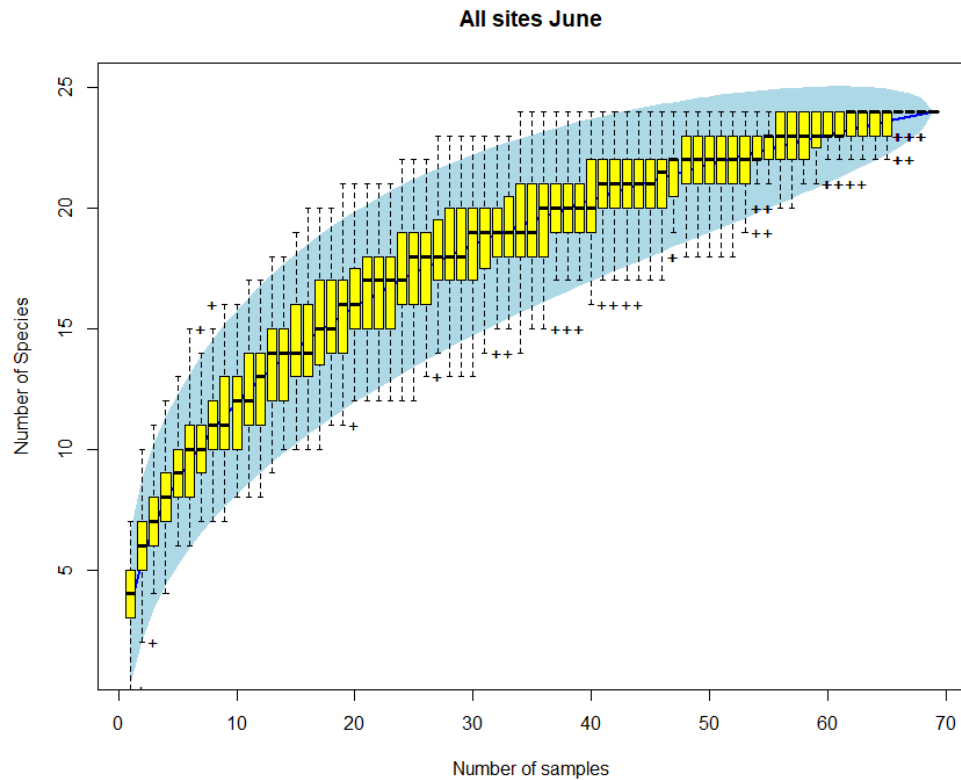


Figure 27: Total avian species accumulation curves for June. The blue shading indicates the range of predicted species richness values. The yellow boxplot centre line represents the median species richness per sample while the yellow boxplot represents the interquartile range, calculated from random permutations of the data. The boxplot whiskers are 1.5 times the interquartile range.

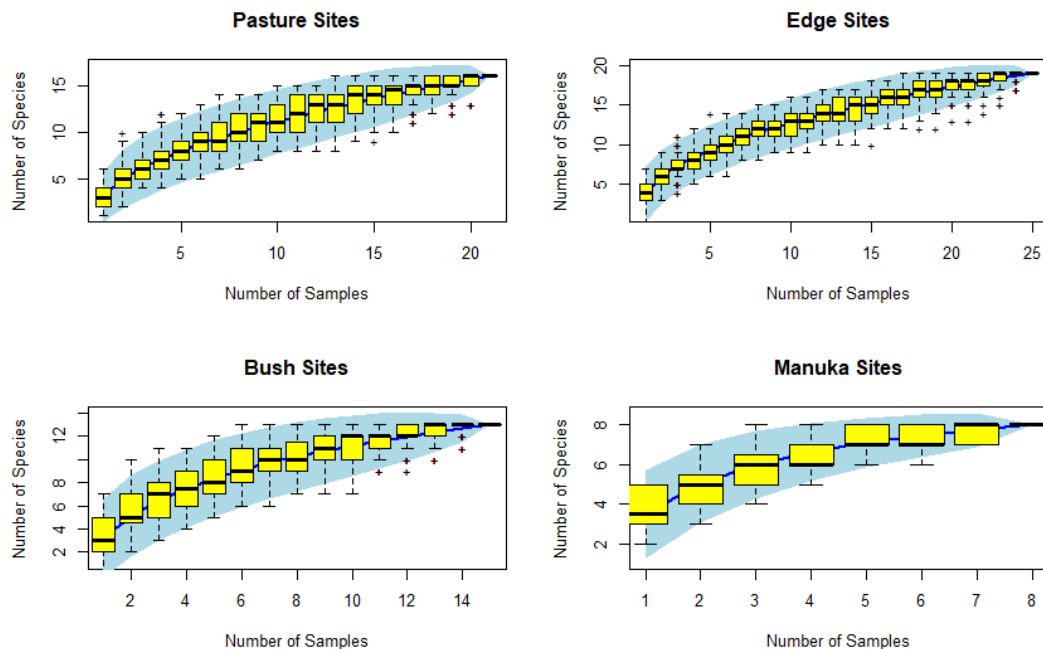


Figure 28: Avian species accumulation curves per habitat type for June. The blue shading indicates the range of predicted species richness values. The yellow boxplot centre line represents the median species richness per sample while the yellow boxplot represents the interquartile range, calculated from random permutations of the data. The boxplot whiskers are 1.5 times the interquartile range.