Plant-frugivore interactions in an urbanised landscape

Carolina Lara Mendoza

A thesis submitted in fulfilment of the requirements for the degree of

Doctor of Philosophy in Biological Sciences

University of Auckland

March 2019

Abstract

Urbanisation is one of the most rapid alterations of natural ecosystems, causing negative biodiversity impacts and potentially disrupting critical mutualistic interactions between species, like those between plants and their seed dispersers (frugivores). Most of what we currently know about the impacts of fragmentation on mutualistic networks comes from studies in agricultural landscapes rather than urban areas. Moreover, few studies have attempted to link network structure with associated ecosystem functions and combine this with other evidence of successful dispersal (i.e. seedling recruitment). In addition, network studies are limited by how data are collected as this may introduce biases in our interpretation of network structure.

In this thesis, I investigated the impacts of altered landscape composition on plant-frugivore networks at forest fragments within and urbanised landscape and their outcomes: fruit consumption and seedling recruitment. This thesis consists of three main components. First, using a multi-level path model informed by direct observations from birds feeding on fruit, I investigated the link between landscape variables, changes in plant-frugivore network structure and the effects of those network changes on fruit consumption. I found that plant species had fewer frugivore partners in fragments surrounded by high urbanisation, and that fruit consumption was greater for plant species that had more frugivore partners and high complementarity in frugivore partner use. Overall, I showed that the negative effects of urbanisation on fruit consumption are not direct, but instead mediated through changes to plant-frugivore network structure. Second, I investigated how two different methods that are frequently used to sample plant-frugivore interactions generate different network properties, and provided a novel approach for combining data from these two methods by using a single link currency. I showed how any decision to use one method in isolation could strongly bias interpretation of network structure. Lastly, I estimated spatial patterns of genetic variation in tōtara (*Podocarpus totara*) using adult trees and seedlings collected at several forest fragments within an urban landscape, and determined long-distance recruitment using parentage analysis. I found higher genetic relatedness within fragments, resembling a source-sink pattern for parental trees and offspring, resulting from long-distance recruitment.

This research contributes to our understanding of the impacts of fragmented landscapes on plant-frugivore mutualistic networks, by linking those networks to an ecological function. Furthermore, it highlights the importance of improved management and conservation of species interactions and forest fragments in urban areas that maintain plant populations and ensure persistence of species and their interactions.

Acknowledgements

Doing this PhD and writing this thesis has been, by far, the hardest thing I've ever done. I don't recall having cried so much and having felt this tired before. The end of this journey isn't as I envisioned it 15 years ago, when I decided I wanted to do a PhD. However, I've been lucky enough to have landed here and met incredible people along the way and without their help and contributions, I couldn't have accomplished this milestone. Many others have been there right from the start, supporting me from afar.

Firstly, I'd like to thank the Auckland Council and the Department of Conservation for granting the necessary permits to conduct this research. Also, I thank the mana whenua of our study area for their engagement with my project on their traditional lands, particularly the kaitiaki of Ngati Te Ata, Manuhiri Kaitiaki Charitable Trust, Te Kawerau and Ngai Tai Ki Tāmaki.

I couldn't have accomplished this project without support from the George Mason Scholarship in Biological Sciences and the scholarship from the Consejo Nacional de Ciencia y Tecnología (México). Financial support from the Nigel Barlow Fund, the New Zealand Ecological Society (NZES), the JS Watson Trust Grant from Forest and Bird New Zealand and the Faculty Research Development Fund (FRDF) from the University of Auckland enabled me to carry out my experiments.

This project involved a lot of work in the field and in the lab, to which many amazing people contributed. Many volunteers selflessly spent long hours in the field helping mist-netting, thank you guys! Particularly, thank you Kade, for always been a great companion in the field and for being so patient with the endless setting-up of seed traps and making cages. Theo, Dion and Rob, thanks for sharing your vast knowledge of New Zealand plants with me and for all the time you spent in the field counting fruits and setting up transects. Special thanks to Ewen Cameron, Colin Webb, Trevor James and Mike Wilcox for their help identifying seeds in faecal samples. Sandra, I'm forever grateful for having had the privilege of working with you and for your help catching, banding and collecting poo from all those birds. Thanks for always making sure that, no matter how busy days were, I had a quick rest and food. Manon, your enthusiasm,

positivity and high spirits carried me through those long months collecting tōtara samples and processing them in the lab, I cannot thank you enough for being such an amazing field assistant and friend!

To the Ecology Ngātahi and Tāmaki crew, thanks for introducing me to the concept of 'morning tea' and 'shared lunch' and for those long chats in the tea room, which helped stay grounded and to know that there is more to life than the PhD. Carola, thanks for our long morning conversations back when I started my PhD and for being such an awesome friend. Souad, thanks for always keeping an eye on me and how I was doing, your support and friendship have help me stay sane during these crazy PhD days. Anna, Jess and Alice, I still have a lot to learn from you, my friends. I admire your strength and the way you've overcome hardships, you're amazing!

Completing this project wouldn't have been possible if I hadn't had the support and guidance of my four amazing supervisors and advisers: Margaret, Jason, Karine and Anna. Margaret, when I sent you that e-mail five years ago asking if you wanted to be my supervisor, I had no idea what I was getting myself into. I'm deeply thankful for you not only being a supervisor, but also a friend and for always looking after me. My favourite part of this project was mist-netting and I loved our long days in the field, drinking tea, eating biscuits, having a good chat about life while waiting for birds to land in the nets. You have been amazing throughout this long journey, both academically and personally. Jason, I still remember when Margaret mentioned you as a potential co-supervisor, I had no idea who you were (sorry), but soon I realised how lucky I was to have you as part of my team. Your incredible patience at answering all my questions, no matter how silly they were, enabled me to understand more about the fascinating world of ecological networks and null models. It has been a pleasure and a privilege having you as a mentor and working with you. Karine, you trusted me since the start of this project, assuring me I was going to be alright despite my little knowledge of genetics and molecular biology. Thanks for putting up with my constant questions about how to process tōtara samples and for allowing me to use your lab space for doing so. Anna, I really enjoyed learning parentage analysis under your guidance. You have an incredible ability to make all the molecular stuff sound easy! Your kindness and positivity helped me stay calm when things

weren't working. I really appreciate all the time you devoted to my tōtara project and all the feedback you provided to make it possible.

José, amiguito, gracias por siempre tener tiempo para vernos, para llamarnos, para darme consejos, pero sobre todo para escucharme. Me llena de alegría ser tu amiga y poder compartir momentos personales tan bonitos a lado de Panda y ahora de Mikel. Gracias por haberme rescatado ese día que llegué a Auckland, hace cuatro años. Gaby, Emmanuel, Ale y Patrick, ha sido un placer coincidir con ustedes en este camino y contar con su apoyo, sin importar donde nos encontremos. Baco, hermano, agradezco a la vida caprichosa que se empeña en ponernos en el mismo lado del mundo desde hace 12 años para seguir compartiendo nuestras aventuras, ahora en un plano un poquito más 'serio'. Mony, adoro nuestros interminables mensajes de voz; has formado parte fundamental en mi nueva vida kiwi y estaré eternamente agradecida por ser tu amiga. Sofía, bebé, ¿qué te puedo decir que no sepas ya? Gracias, nuevamente, por siempre estar presente, a la hora que sea y por el medio que sea. Te amo.

Amada familia, Papito, Mamita, Ale, China, José y Titi, son de las mejores cosas que la vida me ha concedido y nunca podré agradecerles lo suficiente por tanto que me han dado. Después de tantos años, no me acostumbro a estar lejos de ustedes, la mitad de mi corazón sigue en México y nunca se irá. Gracias por apoyarme siempre en todas mis locuras, jamás habría sido capaz de lograr todo esto sin su amor, constante apoyo y palabras de aliento. ¡Soy la más afortunada de tener a la mejor familia del mundo! Seguiremos celebrando la vida, en la distancia pero siempre presentes de mente y corazón.

My whānau, Maree, John, Beth and Amanda, you have supported me in many ways (providing a home, Sunday roasts, painful massages), through this journey and since I joined your family three years ago. You opened your hearts to me, embraced me and my Latinness and made me feel part of your family. I never imagined I could feel at home in a country other than Mexico, but it has happened! New Zealand feels like home now.

Jamie, I couldn't have achieved any of this if it hadn't been for your support, kindness, patience, love and stats/writing advice through these years. You are the best and we are the best team! Thanks for not letting me skip any workout sessions (only a few when I was too tired), cooking

the best meals, driving me around, because you know I don’t like driving (and not complaining too much about it), being such a great husband, believing in me and for never let me give up. I can’t wait to start our next adventure!

Contents

School of Graduate Studies
AskAuckland Central
Alfred Nathan House
The University of Auckland
Tel: +64 9 373 7599 ext 81321
Email: postgradinfo@auckland.ac.nz

Co-Authorship Form

This form is to accompany the submission of any PhD that contains published or unpublished co-authored work. **Please include one copy of this form for each co-authored work**. Completed forms should be included in all copies of your thesis submitted for examination and library deposit (including digital deposit), following your thesis Acknowledgements. Co-authored works may be included in a thesis if the candidate has written all or the majority of the text and had their contribution confirmed by all co-authors as not less than 65%.

Please indicate the chapter/section/pages of this thesis that are extracted from a co-authored work and give the title and publication details or details of submission of the co-authored work. Chapter 3 - Different sampling methods generate complementary plant-frugivore networks. Submitted to Journal of Animal Ecology.

Nature of contribution by PhD candidate	Conceptual development of the study. Carried out data collection, analysed the data, wrote the paper.
Extent of contribution by PhD candidate (%)	80%

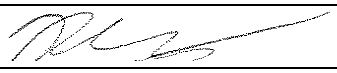
CO-AUTHORS

Name	Nature of Contribution
Jason M. Tylianakis	Conceptual development of the study. Advised on data analyses. Contributed to editing the paper.
Jamie R. Stavert	Helped analyse data. Contributed to editing the paper.
Margaret C. Stanley	Conceptual development of the study. Helped collecting data. Contributed to editing the paper.

Certification by Co-Authors

The undersigned hereby certify that:

- the above statement correctly reflects the nature and extent of the PhD candidate's contribution to this work, and the nature of the contribution of each of the co-authors; and
- that the candidate wrote all or the majority of the text.

Name	Signature	Date
Jason M. Tylianakis		10 February 2019
Jamie R. Stavert		11 February 2019
Margaret C. Stanley		11 February 2019

Chapter 1 - General Introduction

1.1 Plant-frugivore mutualistic interactions

The most important ecological processes are mediated by species interactions and unveiling the complexity of these interactions in their community context - who interacts with whom - is important to draw valid conclusions about ecological and evolutionary processes (Bascompte & Jordano, 2007; Ings et al., 2009; Strauss & Irwin, 2004). Positive species interactions, such as mutualisms, have received increasing attention in recent years due to their importance in the structuring and maintenance of ecological communities (McCann et al., 1998; Okuyama & Holland, 2008; Stachowicz, 2001). Mutualisms are a type of interaction that benefits both species partners by providing a 'service' each partner cannot provide for itself, and receiving some 'reward' in return (Bronstein, 1994). One of the most well-studied mutualisms is that between fleshy-fruited plants and animals that disperse their seeds, where animals get a food reward (fruit) for this service (Bronstein, 1994). Frugivorous birds (hereafter referred to as *frugivores*) are the most common seed dispersers, feeding on fleshy fruits and depositing (via excretion or regurgitation) the seeds away from the parental plant (Anderson et al., 2006; Herrera, 2002; Jordano & Schupp, 2000). Therefore, the study of plant-frugivore mutualistic interactions and their consequences for individual plant fitness (Rodríguez-Rodríguez et al., 2017) has become crucial for understanding ecological systems, and for their management and conservation (Bronstein et al., 2006; Valiente-Banuet et al., 2015), particularly in fragmented habitats.

1.1.1 Seed dispersal

Seed dispersal is a key process driving the structure, composition and regeneration of plant communities (Howe & Miriti, 2004). Therefore, plant-frugivore mutualistic interactions, where frugivores disperse seeds, are pivotal elements for understanding the dynamics of complex ecological systems and ecosystem functioning (Bascompte, Jordano, & Olesen, 2006; Kissling & Schleuning, 2015). Fleshy-fruited seed dispersal depends, firstly, on the interaction between a mobile animal and a sessile plant, from which seeds will be removed, followed by the interaction of that animal with the environment through seed deposition (Schupp, 1993; Wheelwright & Orians, 1982; Zamora, 2000). However, the locations in which seeds are

deposited are diffuse and vary in suitability for seedling establishment (Howe & Smallwood, 1982). Therefore, seed dispersal is a process that controls the long-term dynamics of plant communities and has a direct influence on vegetation structure and recovery (Howe & Miriti, 2004; Wang & Smith, 2002). Because of the important role seed dispersal plays in supporting biodiversity, this ecological function is considered an ecosystem service contributing to human well-being through the provisioning of natural resources at no cost (Forget et al., 2011; Kremen, 2005). Seed dispersal via frugivory confers advantages, such as: a) avoiding disproportionate mortality near the parent plant (Connell, 1971; Janzen, 1970), b) colonising disturbed sites (Howe & Smallwood, 1982; Traveset et al., 2014), c) locating sites suitable for germination with high probabilities of survival (Wenny, 2001), and d) range expansion.

Although seeds can be dispersed by a variety of abiotic (i.e. wind, water) modes, the role animals play as seed dispersers for *ca*. 60-80% of all plant species is crucial (Levey et al., 2002; Wang & Smith, 2002). In fact, in many temperate ecosystems, the frequency of species with fleshy fruits and vertebrate frugivore dispersal is high, between 27-60%, of which avian frugivores are the main dispersers (Anderson et al., 2006; Kelly et al., 2010; Willson et al., 1990). Fleshy fruits are therefore considered a highly effective dispersal mode for plants (Lord, 1999). The proportion of fleshy-fruited species correlates with moisture availability but also with other factors such as latitude, soil nutrients and succession (Willson et al., 1989). Benefits for vertebrate-dispersed seeds over abiotic dispersal may include enhanced germination following gut passage, and directed dispersal (Wenny, 2001). Directed dispersal refers to the disproportionate arrival of seeds to sites that are favourable for survival (Howe & Smallwood, 1982).

Understanding the ecology and evolution of seed dispersal requires viewing this mutualistic interaction as a process that consists of having an immediate effect on seed dispersal effectiveness, as well as a delayed effect expressed after the interaction has ended (Schupp et al., 2017). Schupp's (1993) framework (revisited in Schupp et al. 2010; 2017) disentangles the different components of seed dispersal effectiveness:

1) *Measure of the outcomes of an interaction* - Effectiveness of a mutualistic interaction between two partners is defined as the number of new adults of a partner produced by the

activity of the other partner. In this sense, effectiveness is based on the measured number of adults recruited (addition of new individuals to a population) or estimated from population growth rate, both having evolutionary and demographic implications (Schupp et al., 2017).

2) *Seed dispersal effectiveness consists of two components* - A quantitative component and a qualitative component (Schupp, 1993).
    a. *The quantitative component* of effectiveness refers to the number of immediate outcomes, that is, the number of fruits consumed (Schupp et al., 2010).
    b. *The qualitative component* of effectiveness includes the post-dispersal prospects for plant establishment (quality of treatment in frugivore mouth and gut, and quality of seed deposition) and recruitment (Schupp et al., 2010).

Schupp's (1993) framework assumes that the number of seeds handled by a frugivore is a function of the number of fruits consumed per visit and the number of visits. Thus, infrequent plant visitors that remove a large number of fruits per visit could prove to be effective dispersers (Fedriani & Delibes, 2009; Schupp et al., 2010). However, dispersal effectiveness can be strongly associated with frugivore behaviour. For example, fruit handling can affect the probability of seeds being moved away from the parental tree and the colonization of new sites (Traveset et al., 2014). While most frugivores are legitimate dispersers that process fleshy fruits by swallowing entire fruits and defecating/regurgitating viable seeds, cheating can occur in the mutualism, whereby either seeds are destroyed (seed predators) or fruit pulp is removed without seeds being dispersed (pulp peckers) (Snow & Snow, 1988; González-Varo, 2010; Simmons et al., 2018). Increasing time spent in fruiting trees results in more seeds being eaten, and therefore increases the number of seeds dispersed away from the tree source (Wotton & Kelly, 2012). There is also some evidence that suggests time spent in a tree increases with increasing frugivore body mass (Wotton & Kelly, 2012). A clear example of this is kererū, a highly sedentary New Zealand pigeon that can disperse 66-87% of ingested seeds away from the parental tree (Wotton & Kelly, 2012).

Differential movement patterns of dispersers also influences seed dispersal effectiveness. Jordano et al., (2007) found in southern Spain that avian frugivores were the main dispersers

of a small tree species, but seeds were generally dispersed over short distances compared to dispersal of seeds over hundreds of metres by mammals. Similar results have been found for differences between seed dispersal by mammals versus avian frugivores in northern Spain, where *Turdus* species dispersed seeds to microhabitats while mammals deposited seeds in less suitable open areas (Martínez, García, & Obeso, 2008). Wenny & Levey (1998) also demonstrated directed dispersal by bellbirds in Costa Rican rainforests, whereby bellbirds predictably dispersed seeds primarily under song perches in canopy gaps, resulting in higher seedling survival associated with the increased light and lower rates of fungal infections compared to seeds dispersed by other species under the canopy. In sum, there are differences among species in the quality of dispersal they provide and plants may benefit by having a range of species dispersing their seeds, as each species will perform different roles (Jordano et al., 2007; Wheelwright & Orians, 1982).

1.1.2 Long-distance seed dispersal

The movements of frugivores determine spatial aspects of seed deposition, germination and seedling establishment, and in doing so influence plant population and community dynamics (Jordano et al., 2011). Thus, frugivores are regarded as mobile links, dispersing seed across the landscape, which is critical for maintaining genetic diversity of plant populations (Kremen et al., 2007; Lundberg & Moberg, 2003). Although most seed dispersal events are short-distance (less than 100 m; Cain et al., 2000), the rarer long-distance events are the most important dispersal events for determining genetic structure and range expansion rates (Nathan & Muller-Landau, 2000). Therefore, it is important to link the movement of seeds away from the parental plant to its demographic consequences, that is, the establishment of a new adult plant (Lavabre et al., 2014; Schupp et al., 2017).

Evaluating long-distance seed dispersal has been hampered by the difficulty of measuring and quantifying this process (Hardesty et al., 2006; He et al., 2010). Most attempts at measuring seed dispersal prior to the seedling establishment phase have used observational approaches of fruit removal rates by frugivore dispersers and gut passage time, or seed rain data collected using seed traps (Bullock, Shea, & Skarpaas, 2006; Clark, Poulsen, & Parker, 2001; Holbrook & Smith, 2000; Martínez & García, 2017). Another issue with measuring long-distance dispersal is determining the threshold over which dispersal is considered long-distance. Any

threshold chosen to determine what reflects long-distance events must be case-specific (Cain et al., 2000) and based on dispersal attributes, spatial structure and scale of the system studied (Nathan et al., 2003).

Parentage analysis is another approach which has been used to evaluate seed dispersal genetically (Cain et al., 2000; Harrison et al., 2013; Jones et al., 2005), partially solving the long-standing problem of assessing long-distance seed dispersal. Parentage analyses use genetic markers to document dispersal events, providing a relatively direct measure of dispersal. The disadvantage of these methods is that the population of interest must be exhaustively sampled so that all potential parents have equal chance of identification (Cain et al., 2000; Jones et al., 2010). Genotyping endocarps (maternally inherited) from dispersed seeds has contributed to our understanding of seed dispersal in temperate forest systems and the genetic consequences of this process (Godoy & Jordano, 2001; González-Varo et al., 2017; Jordano et al., 2007). Yet, some seeds and their maternally inherited endocarp are short-lived, which makes this approach unworkable for these species (but see Karubian et al., 2010). Only seedling establishment and recruitment contributes to functional genetic connectivity between populations, and fully closes the seed dispersal loop (Luque et al., 2012; Wang & Smith, 2002). Therefore, to provide robust understanding of long-distance seed dispersal (i.e., the genetic relationships between seedlings and adult trees across space), evaluation of genetic relationships between seedlings and adult trees is required, rather than simply assessing the genetics of endocarps in dispersed seeds (Hardesty et al., 2006; Ismail et al., 2017).

1.1.3 Frugivory and seed dispersal in New Zealand

Within the New Zealand flora, fleshy-fruited plants are well represented, and comprise 72% of all tree species, with 17-47% at comparable northern latitudes (Burrows, 1994; Lord et al., 2002). Because New Zealand lacks non-volant native mammals, all the fleshy-fruited species can be considered to be bird, bat or reptile dispersed (Anderson et al., 2006; Arkins et al., 1999; Whitaker, 1987). Fleshy fruits in New Zealand are represented by fruits from native species, such as puriri (*Vitex lucens*) and hangehange (*Geniostoma ligustrifolium*) or fleshy cones, such as tōtara (*Podocarpus totara*) and kahikatea (*Dacrycarpus dacrydioides*). Additionally, several introduced fruiting plant species, such as climbing asparagus (*Asparagus scandens*), inkweed (*Phytolacca octandra*) and woolly nightshade (*Solanum mauritianum*), have successfully

established and spread as weeds (Howell, 2008; Stanley & Bassett, 2014). Fleshy fruits from both native and introduced species are consumed by native birds that act as legitimate dispersers, with tūī (*Prosthemadera novaeseelandiae*) and kererū (*Hemiphaga novaeseelandiae*), among the most important species (Clout & Hay, 1989). However, since the 19th century, New Zealand has experienced the extinction and severe decline of effective bird dispersers due to habitat loss and introduced mammal predators (Holdaway, 1989; Innes et al., 2010). At the same time as endemic birds were declining and extensive landscape changes were underway, the frugivorous silvereye (*Zosterops lateralis*) arrived from Australia during the 1850s and established, and as such (not a directly human-mediated introduction), was classified as a native (Keast, 1974). The recruitment of large-fruited plant species is particularly threatened in New Zealand given the disproportionate loss of large-bodied frugivores and their interactions (Hansen & Galetti, 2009). In highly modified landscapes, introduced bird species such the European blackbird (*Turdus merula*), song thrush (*Turdus philomelos*) and starling (*Sturnus vulgaris*) contribute to the dispersal of both native and introduced plant species (Kelly et al., 2010; MacFarlane et al., 2015; Williams, 2006).

1.1.4 Fragmentation and its consequences on plant-frugivore mutualisms

Fragmentation of habitat threatens not only biodiversity but also species mutualistic interactions and their essential ecosystem functions (Hanski, 2015; Tylianakis & Morris, 2017; Valiente-Banuet et al., 2015). Because seed dispersal is one of those pivotal ecosystem functions, particular attention has been paid to this function and its components, and how they are affected by fragmentation (Cordeiro & Howe, 2003; Emer et al., 2018; Uriarte et al., 2011). In fact, seed dispersal is tightly related to the concept of plant metapopulations, defined as spatially disjoined populations linked by dispersal (Cain et al., 2000; Hanski & Gilpin, 1991).

Overall, fragmentation increases discontinuity in spatial patterns of resource availability, affecting species' fitness and disrupting connectivity between fragments in metapopulations (Hagen et al., 2012; Hanski, 1998). Additionally, fragmentation of natural habitat also leaves plant populations susceptible to the effects of reduced gene flow (Bacles et al., 2006). Other effects of fragmentation include: an increase in the number of fragments, a decrease in fragment size and an increase in fragment isolation (Fahrig, 2003). Yet, remnant fragments can hold a significant fraction of biodiversity (Beca et al., 2017; Emer et al., 2018; Sfair et al., 2016).

Plant-frugivore interactions play a central role in assessing the consequences of fragmentation on biodiversity (Hagen et al., 2012). Such interactions may be spatially structured in accordance with variation in local frugivore assemblages (Jordano, 1994). For example, the dispersal of fleshy-fruited plants may decline in fragmented areas if legitimate dispersers are scarce or if seed predators become more abundant (Cordeiro & Howe, 2003; Moran et al., 2009; Pejchar et al., 2008). Other aspects to consider are the frequency, distance and direction of post-feeding movements of frugivores, which determine gene flow within, and between, plant populations (García, Jordano, & Godoy, 2007; Sasal & Morales, 2013) particularly in fragmented landscapes, where such movements are crucial to allow gene flow among isolated populations (Trakhtenbrot et al., 2005). Large frugivores have been shown to be particularly sensitive to fragmentation (Hansen & Galetti, 2009; Uriarte et al., 2011), decreasing the probability of long-distance seed dispersal of large fleshy-fruited plants (Pizo & dos Santos, 2011; Spiegel & Nathan, 2007). Although the effects of fragmentation on biodiversity depend on species traits, characteristics of the fragments and the surrounding matrix are important (Fahrig, 2003; González-Varo, 2010). Most studies of fragmentation effects on plant-frugivore interactions have been done within an agricultural matrix (García et al., 2007; González-Varo et al., 2017) and only recently has the focus shifted to how urbanisation affects such interactions.

1.1.5 Urbanisation

Urbanisation is one of the most rapid alterations of natural ecosystems, causing an important impact on biodiversity and ecosystem services (Aronson et al., 2014). Generalisations about traits associated with species declines in response to urbanisation are mainly based on presence or abundance (Batáry et al., 2018; Crooks et al., 2004; McKinney, 2008) and more recently the effects of urbanisation on phylogenetic diversity of birds has been explored (Sol et al., 2017). Despite the relevance of plant-frugivore interactions, the effects of urbanisation on those interactions remains poorly studied to date (but see Cruz et al., 2013; Rodewald et al., 2014). However, the negative effects of urbanisation on frugivore communities are also likely to strongly affect plant-frugivore interaction networks.

1.2 Plant-frugivore mutualistic interaction networks

Ecological networks are representations of sets of ecological objects (plants/frugivores) that have the potential to interact with one another (Bascompte, 2009). Using a network approach to study plant-frugivore mutualisms has allowed ecologists to evaluate network-level properties while also assessing functional roles of species (Heleno et al., 2014). Networks focus on the interactions between species, specifically on the number and composition of the species interacting (nodes), and on the abundance, magnitude and distribution of interactions between the nodes (links; García, 2016). Plant-frugivore networks can be described by interaction matrices, within which fruiting plant species (P nodes) are represented in columns and disperser species (A nodes) in rows, where interactions between each A and P nodes are the links (Jordano, 2016). Furthermore, interaction network matrices can be categorised into qualitative networks (binary or unweighted networks) and quantitative networks (weighted networks that reflect the intensity of interactions) (Gu et al., 2015). Network structure has important implications for the coexistence and stability of species through space and time (Bascompte & Jordano, 2007). Thus, network structural elements can strongly influence how networks respond to environmental changes such as habitat loss, climate change and invasive species (Tylianakis & Morris, 2017).

1.2.1 Structural properties of plant-frugivore networks

Studies from different ecological communities, some of them including frugivores, have demonstrated the existence of generalities in the structure of seed dispersal networks (e. g. Bascompte & Jordano, 2007, 2014; Jordano, 1987). Three main structural properties characterise plant-frugivore networks. The first is high interaction heterogeneity, where networks are typically composed of a core of species that are highly connected, while the remaining species are on the periphery of the network with few interactions (García, 2016; Jordano, Bascompte, & Olesen, 2003). The second property is the significant nestedness and modularity in the organisation of the interaction matrix (Bascompte et al., 2003). Nestedness implies that within the network, plant and frugivore species interacting with specialists are a proper subset of the species interacting with generalists (Tylianakis et al., 2010). Modules are subsets of a given network in which plant and frugivore species interact frequently with one another, but little with other species outside the module (Olesen et al., 2007; Schleuning et al.,

2014b). The third property that characterises seed dispersal networks is the frequent occurrence of asymmetries in the level of specialisation between paired species (Bascompte et al., 2006; Vázquez & Aizen, 2004). These three structural properties have important consequences for ecological and evolutionary processes (Vázquez et al., 2009). For example, a nested organisation makes networks highly vulnerable to the extinction of species that have many links, but robust to the extinction of species that have few links (Memmott et al., 2004). However, it is unknown whether different sampling methods for plant-frugivore interactions generate different network properties. If this were the case, it could lead to misinterpretation of network structure and related ecological processes. Furthermore, most of what we currently know about plant-frugivore networks comes from studies that have only used direct observations of birds feeding on fruit to sample such interactions (Schleuning et al., 2012).

1.2.2 Sampling interactions in plant-frugivore networks

Sampling species interactions to create networks becomes challenging when there are sampling biases in the number of partner species detected, number of links recorded and the estimation of network properties (Banašek-Richter et al., 2004; Blüthgen et al., 2008; Chacoff et al., 2012; Fründ et al., 2015; Nielsen & Bascompte, 2007; Olesen et al., 2011). Field sampling simply records the presence of two species that are interacting with each other. For instance, Snow and Snow (1988) considered a bird touching a plant to be an interaction. What we regard as an interaction will determine our interpretation of network properties. Different forms of plant-frugivore interactions have been used in networks to date, including: feeding observations, visitation, and presence of seeds in faecal samples (Jordano, 2016). Data on the number of seeds transported and quality of seed dispersal are difficult to assess (see 'long-distance seed dispersal' section), so instead, researchers often use frequency of visits as a surrogate of plant dependence on frugivore visitors (Vázquez et al., 2005). The disadvantage of this approach is that, although informative in terms of identifying which species are interacting with each other, it fails to account for dispersal effectiveness by not recording fruit or seed consumption (Brodie et al., 2009; Simmons et al., 2018).

Direct observations of birds interacting with specific fruiting plants (a phyto-centric approach) is a typical sampling method for obtaining bird visitation frequency and the number of fruits consumed (Donoso et al., 2017; García et al., 2014; Kelly et al., 2010; Olesen et al., 2011).

Direct sampling through identification of seeds transported by birds (a zoo-centric approach), via faeces obtained from captured birds, is less frequently used (González-Castro et al., 2015; Heleno et al., 2013). Plant-frugivore networks constructed using a phyto-centric approach are likely to result in large A:P ratios and only detect common plant-frugivore interactions (Jordano, 2016). Rare interactions are often detected using a zoo-centric approach, but this is also limited given biases in species-specific catchability of birds, particularly large bird species, species with low mobility, and canopy specialists (Costa Cruz et al., 2013; Pardieck & Waide, 1992). A way to deal with these biases would be to combine sampling approaches, although this has only been done for pollination networks (Bosch et al., 2009), which found that the addition of data collected using different sampling methods resulted in critical structural changes in plant-pollinator networks. To date, no study has attempted to use a combination of methods for sampling plant-frugivore networks.

1.2.3 Linking plant-frugivore mutualistic networks to ecosystem functioning

The positive relationship between animal biodiversity and stability of ecosystem function has been widely accepted (Cardinale et al., 2012; Ives & Carpenter, 2007). The biodiversity-ecosystem functioning (B-EF) relationship is determined by three characteristics – processes, properties and their maintenance (Naeem & Wright, 2003). Processes and properties are determined by the number and type of organisms and their interactions and how these are sustained over space and time (Loreau et al., 2001). Species richness and functional performance typically begins linearly and asymptotes at moderate richness levels (Hooper et al., 2005) and complex animal assemblages have stronger and more stable responses to disturbances and biodiversity loss (Duffy, 2003).

There are three underpinning mechanisms that explain the positive B-EF relationship: selection (or sampling) effects, complementarity and interspecific facilitation (Cardinale et al., 2002; Reiss et al., 2009). In the first mechanism, selection effects, the probability of functionally effective species occurring in a community increases with species richness (Loreau et al., 2001; Tilman et al., 1997). In small-scale B-EF experiments, the probability of including a functionally effective species increases with species richness and that could explain the driving of the positive richness-function relationship (Cardinale et al., 2011). In this way, the prevalence of selection effects could be an artefact of small-scale experiments and may not

be likely to occur in real-world ecosystems. The second mechanism that explains the positive B-EF relationship is complementarity. Species are functionally complementary when they occupy different portions of the functional niche space, so their contribution determines community-level function. Thus, where species are complementary, community-level function is higher when species occur in combination, in comparison to any one species acting in isolation (Loreau et al., 2001). Complementarity also results from reduced competition through niche partitioning (or resource partitioning); if species use different resources, or the same resources but at different times and locations, there would be more total resources available to be used by the community (Blüthgen & Klein, 2011; Hooper et al., 2005). Evidence of the positive effects of resource partitioning on trophic functions has been shown via theoretical modelling and small-scale experiments (Finke & Snyder, 2008; Poisot et al., 2013), but how these effects prevail in real-world ecosystems still remains understudied (but see Donoso et al., 2017; García et al., 2018; Peralta et al., 2014; Tylianakis, 2008). In plant-frugivore communities, complementarity can be measured at the species scale, thus providing information on the fitness of each species. Several mechanisms can explain complementarity from the frugivore's point of view, which has been the focus of most previous studies in the field (Donoso et al., 2017; García et al., 2018). Temporal complementarity occurs when frugivores feed on fruits from different plant species during the day, or over different seasons, which is important for plants that set fruit for long periods (Blüthgen & Klein, 2011). Frugivores that differ in diet, movement and phenology generate a rich and spatially heterogeneous seed rain (Bueno et al., 2013; Jordano et al., 2007). The other, less explored, mechanism of complementarity is from the plants' perspective. Seasonal complementarity can play a role for plants that flower over longer periods and it may occur when different frugivore species of a certain plant forage at different times of the day (Blüthgen & Klein, 2011).

The third, less explored, mechanism by which biodiversity enhances the performance of biodiversity is interspecific facilitation (Cardinale et al., 2002). Facilitation between species has been demonstrated in a stream mesocosm, where the increased topographical complexity of the benthic habitats altered patterns of near-bed flow such that the feeding success of individuals was enhanced (Cardinale et al., 2002). Although these findings have broad applications on marine and freshwater habitats, facilitation effects could also be observed in

terrestrial ecosystems, where fluxes of energy and matter can be influenced by biophysical complexity (Jones et al., 1997).

Most B-EF research has focused on functions that involve one trophic level (e.g. plant biomass; Balvanera et al., 2006). In contrast, frugivory is a mutualistic function that involves multiple trophic levels (Schleuning et al., 2015). Consequently, it has been recently recognised that plant-frugivore mutualistic networks provide a useful tool for understanding the actual contribution of individual species and diverse ecological communities to ecosystem functions (García, Donoso, & Rodríguez-Pérez, 2018; Schleuning, Fründ, & García, 2015; Thompson et al., 2012), although the link between such functions and B-EF is still little understood. Furthermore, the link between fragmentation and its effects on plant-frugivore networks and their function remains in its infancy.

1.3 Research aims

The overarching aim of this PhD thesis is to understand how habitat fragmentation affects plant-frugivore interaction networks and plant recruitment. Most of what we know about the impacts of fragmentation on ecological networks comes from studies in agricultural landscapes and there is a real need for studies of the impacts of fragmentation on plant-frugivore networks in urban areas. This thesis has a specific focus on how changes in plant-frugivore networks produced by fragmentation translate into changes in function, and how the choice of methods to sample plant-frugivore interactions influences interpretation of network structure. I asked the following key research questions: 1) How does altered landscape composition, particularly urbanisation, affect the structure of plant-frugivore mutualistic networks? 2) How do the effects of altered landscape composition on network structure influence fruit consumption? 3) How does the choice of sampling method affect the comprehensiveness of plant-frugivore networks? 4) Does habitat fragmentation inhibit plant recruitment in urban areas?

1.4 Thesis outline

This thesis consists of three data chapters (Chapter 2-4) that can be read as standalone research papers. The final chapter (Chapter 5) provides a synthesis of the results from this study with potential future research avenues. I have aimed to give the best possible continuity between

chapters throughout this thesis, but because all chapters are encompassed within the broader themes of plant-frugivore mutualistic networks and fragmentation, some repetition between chapters will be apparent.

Chapter 2 investigates the effects of landscape composition variables, particularly urbanisation, on plant-frugivore networks and subsequently, the effects on fruit consumption, using a multi-level path model informed by direct observations. I investigate this by linking several landscape variables to changes in network structure and their effects on the ecosystem process of frugivory. I predicted that networks in fragments surrounded by lower levels of urbanisation would have plants that were visited by a greater number of bird species, and that fruit consumption would be higher. Further, I expected that plant species in fragments surrounded by higher urbanisation would have low complementarity in frugivore resource use (niche partitioning in frugivore partners), resulting in reduced fruit consumption.

Chapter 3 provides a comparative analysis of different methods that are frequently used to sample plant-frugivore interactions, direct observations and analysis of faecal samples. I also present a novel approach for combining data from these two methods by using the number of seeds consumed as a single link currency. I use a null model approach to test how sampling effort influences network structure for the two sampling methods and a combined sampling approach. I expected that different sampling methods would detect complementary interaction subsets from the wider plant-frugivore networks. I also predicted that direct observations would capture a greater number of frugivore species relative to plant species and the opposite for analysis of faecal samples. Thus, I expected that a combination of these sampling methods would provide a more comprehensive representation of plant-frugivore interactions.

Chapter 4 investigates spatial patterns of genetic variation and long-distance recruitment of a bird-dispersed tree native to New Zealand, tōtara (*Podocarpus totara*). Based upon a survey of adult trees and seedlings collected at four urban forest fragments, I estimate long-distance seedling recruitment using parentage analysis through single nucleotide polymorphisms (SNPs). I expected that tōtara individuals from the same forest fragments would be highly related, but this high relatedness would also be evident among fragments, indicating within-population long-distance seed dispersal and seedling recruitment. Lastly, I predicted that across

fragments, long-distance recruitment would occur given the high mobility of frugivores consuming and dispersing tōtara seeds.

Chapter 5 provides a synthesis and discussion of results from all chapters. It also highlights the significance and contribution of this thesis and provides recommendations for future research avenues.

Chapter 2 - Urbanisation alters plant-frugivore networks and reduces fruit consumption

Abstract

Human modification of the biosphere is causing unprecedented global biodiversity loss, consequently disrupting mutualistic interactions and threatening ecosystem functioning. Mutualistic interactions between plants and frugivores are essential for the ecosystem function of seed dispersal, however, we currently have a poor understanding of how alteration to plant-frugivore network structure, moderated by landscape composition changes, affect frugivory. I sampled plant-frugivore interactions along an urbanisation gradient within a highly fragmented landscape in Auckland, Aotearoa-New Zealand. Urbanisation dramatically alters the composition of natural ecosystems across landscapes, and is therefore likely to have far-reaching impacts on plant-frugivore networks and frugivory function. Here, I linked network structure (frugivore richness per plant species and plant complementarity) to the ecosystem function of frugivory. I measured important aspects of landscape composition (fragment size, urbanisation and proportion of surrounding indigenous forest). I then determined (*i*) How landscape composition affected plant-frugivore network structure and frugivore abundance and (*ii*) How the resulting changes to plant-frugivore network structure and frugivore abundance affected fruit consumption. I found that plant species had fewer frugivore partners in fragments surrounded by high urbanisation. Furthermore, fruit consumption was greater for plant species that had more bird frugivore partners and high complementarity in frugivore partner use. Overall, urbanisation negatively affected fruit consumption by reducing the number of frugivore species interacting with each plant species. I show that the effects of urbanisation on fruit consumption are not direct, but instead mediated through changes to plant-frugivore network structure. My findings suggest that for plants to maximise fruit consumption, there is a trade-off between having a distinct frugivore niche (high complementarity) and retaining many frugivore partners. Thus, conserving and restoring frugivore biodiversity in urban areas is critical, provided that even small changes to frugivore biodiversity can strongly alter frugivory in species-poor urban landscapes.

Publication status: Not yet published. This chapter will be submitted to *Journal of Applied Ecology*.

2.1 Introduction

Biodiversity is important for the provisioning of ecosystem functions, whereby increased biodiversity often enhances the performance and stability of ecosystem functioning (Cardinale et al., 2011; Loreau et al., 2001). However, human modification of the biosphere is causing global biodiversity loss at an unprecedented rate, threatening the functioning of many ecosystems (Pereira et al., 2010). Destruction and degradation of natural habitat is the leading cause of global biodiversity decline and subsequently, the loss of critical mutualistic interactions between species (Tylianakis et al., 2008; Valiente-Banuet et al., 2015). Urbanisation (complex process driven by an increase in human density) causes rapid and drastic alteration of natural ecosystems, resulting in the reduction of biodiversity and associated ecosystem functioning (Aronson et al., 2014; McDonnell & Pickett, 1993). However, despite general understanding of human-driven biodiversity decline and the biodiversity-ecosystem functioning (B-EF) relationship, we have poor understanding of how human-moderated changes to plant-animal networks affect ecosystem functioning (Peralta et al., 2014; Tylianakis et al., 2007).

Fruit consumption by animals is a critical ecosystem function because it leads to seed dispersal and plant recruitment (Schupp et al., 2010). Birds are the most important group of frugivores worldwide and form complex mutualistic networks with the plant species whose seeds they disperse (García, 2016). Recent studies show that human-moderated disturbances, such as urbanisation, can have a variety of impacts on bird communities, altering species' relative abundances, diversity and life history trait composition (McKinney, 2008; Moran et al., 2009; Sol et al., 2017). Considering these community-level changes, urbanisation is also likely to alter the architecture of plant-bird interactions that result in seed dispersal. Indeed, previous studies have shown that as urbanisation increases, plant-bird networks become more nested, less compartmentalised and dominated by strong interactions between fewer species (Rodewald et al., 2014). Similarly, habitat restoration has been shown to increase seed dispersal network size and the number of interactions between species (Ribeiro da Silva et al. 2015).
Few studies have attempted to link network structure with associated ecosystem functions (García et al., 2018). In host-parasitoid networks, parasitism rate increases with network connectance (e.g., Gagic et al., 2011; Montoya, Rodríguez, & Hawkins, 2003) and in plant-

pollinator networks, habitat restoration increased the diversity of plant-pollinator interactions, which resulted in higher fruit production (Kaiser-Bunbury et al. 2017). However, the relationship between network structure and frugivory function in plant-frugivore networks is poorly understood. Previous studies indicate that seed dispersal increases with frugivore richness, suggesting frugivore biodiversity is important for maintaining plant recruitment (i.e., García & Martínez, 2012; Pejchar et al., 2008), but these studies do not link network structure with frugivory function. Changes to frugivore abundance may also be important for driving fruit consumption, particularly in urbanised landscapes because the relative abundances of some species often increase with urbanisation (e.g., urban exploiters) (Palomino & Carrascal, 2007; Sandström et al., 2006). However, trophic complementarity (originality of a species' role in a food web, relative to others; Poisot et al., 2013) is more likely to drive ecosystem functioning in multi-trophic systems (Peralta et al., 2014).

I am not aware of any other study that has linked urbanisation with changes to plant-frugivore network structure and subsequently, fruit consumption. Thus, I sampled plant-frugivore networks, along a gradient of urbanisation and linked network structure to the ecosystem function of frugivory. I concentrated on frugivory, the quantitative component of seed dispersal, on which the qualitative stages of transport and plant establishment depend (Nathan & Muller-Landau, 2000). Specifically, I focused on two questions: (*i*) How do human-moderated changes to landscape composition affect plant-frugivore network structure and frugivore abundance? and (*ii*) How do changes in plant-frugivore network structure and frugivore abundance, resulting from altered landscape composition, affect fruit consumption? Fragmentation of natural ecosystems by urbanisation is likely to alter network structure through the destruction and modification of natural habitat (Albrecht et al., 2007; Rodewald et al., 2014). I predicted that plant species in fragments surrounded by less urbanisation would have a greater number of frugivore partners. Where plants had a greater number of frugivore partners, I expected fruit consumption to be higher, as more frugivore partners should promote higher resource (fruit) consumption rate. Next, I predicted that plant species in fragments surrounded by higher urbanisation would primarily have generalist bird frugivores, and thus have low complementarity in frugivore resource use (i.e., high overlap in frugivore partners among plant species). I expected increased complementarity among plant species to result in higher fruit consumption, due to greater frugivore fidelity. I measured niche complementarity

from the plant's perspective, as I was specifically interested in linking complementarity to frugivory. Finally, I predicted that urbanisation would not alter total frugivore abundance, as there would be winner and loser species and, thus, fruit consumption would depend on changes to plant-frugivore interactions rather than frugivore abundance.

2.2 Methods

2.2.1 Study system

My study area was within the fragmented forest native to the northern and western Auckland region of New Zealand (Figure 1). In this region, only 13% of native forest from the original 93% pre-human New Zealand forest cover remains (Ewers et al., 2006) and most of the remaining forest fragments are less than 10 hectares (Wilcox, 2012). Approximately 12% of New Zealand's native plant species produce fleshy fruits (Lord et al., 2002). These species include puriri (*Vitex lucens*) and hangehange (*Geniostoma ligustrifolium*) and other species that produce fleshy cones, such as tōtara (*Podocarpus totara*). Additionally, introduced fruiting plant species, such as climbing asparagus (*Asparagus scandens*) and woolly nightshade (*Solanum mauritianum*), have successfully established in forest fragments as weeds. Fleshy fruits from both native and introduced species are consumed by native birds (hereafter referred to as *frugivores*) that act as legitimate dispersers, e.g., silvereye (*Zosterops lateralis*), tūī (*Prosthemadera novaeseelandiae*) and kererū (*Hemiphaga novaeseelandiae*) (Clout & Hay, 1989). However, since the 19th century, New Zealand has experienced the extinction and severe decline of many effective bird dispersers, due to habitat loss and introduced mammal predators (Innes et al., 2010). Recruitment of large-fruited plant species is particularly threatened due to the disproportionate loss of large-bodied frugivores and their interactions (Hansen & Galetti, 2009). The large-bodied native pigeon, kererū (*H. novaeseelandiae*), is the most important disperser for large seeded species such as tawa (*Bielschmiedia tawa*) (Kelly et al., 2010). In highly modified landscapes, introduced bird species such as the European blackbird (*Turdus merula*), song thrush (*Turdus philomelos*) and starling (*Sturnus vulgaris*) disperse both native and introduced plant species (Kelly et al., 2010; Williams, 2006).

I sampled 13 different fragments ranging between 0.5-17 ha in size (Table A1, Appendix A), across the Auckland region. These fragments were chosen as they met the following criteria: (*i*) similar native forest structure, as determined by the New Zealand Land Cover Data Base v.4.1 (Land Resource Information Systems); (*ii*) located on public land (for logistical reasons); and (*iii*) primarily surrounded by an urban matrix. One of these fragments was Shakespear Regional Park, a predator free sanctuary with mature and secondary-growth forest, where many endangered bird species have been reintroduced.

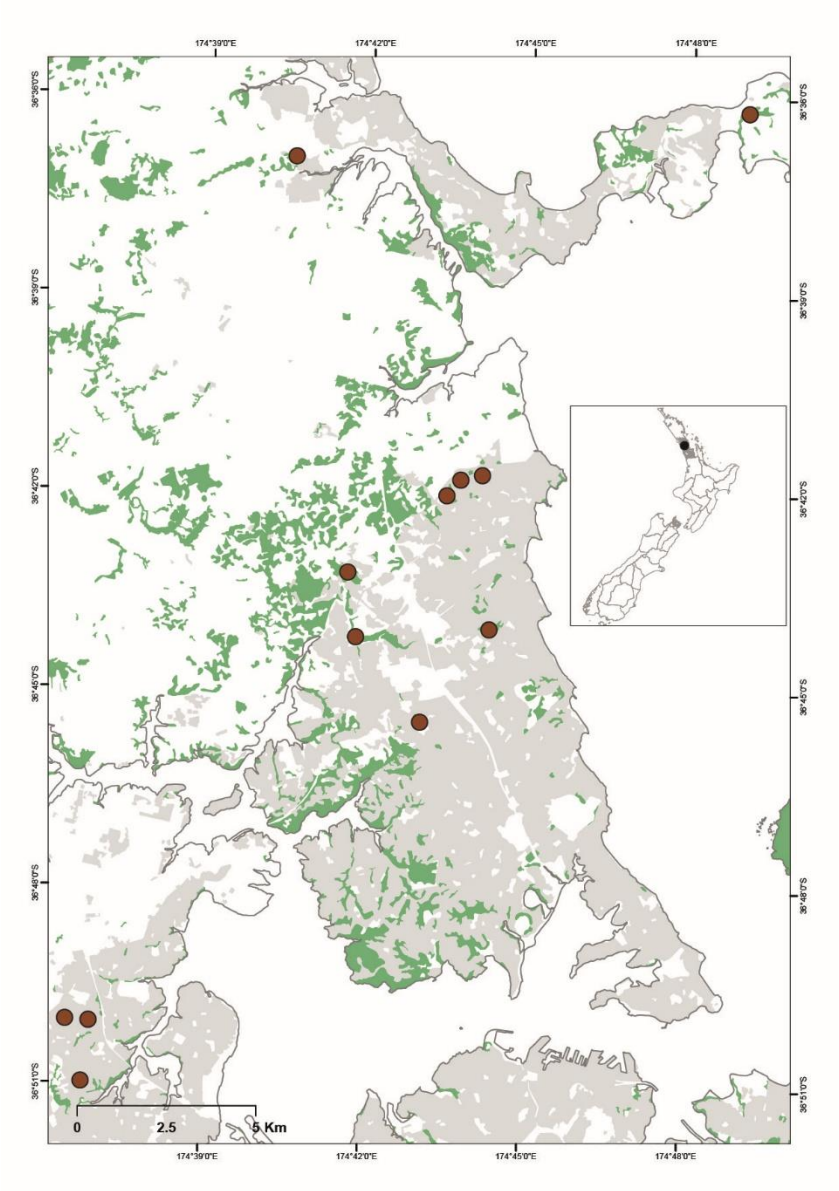


Figure 1. Location of study fragments (brown circles) and New Zealand Land Cover Data Base v.4.1 (Land Resource Information Systems) land-cover categories, showing areas dominated by buildings (grey) and indigenous forests (green). Insert indicates sampling region within New Zealand.

2.2.2 Frugivore sampling

At each study site, I established multiple transects to conduct bird censuses in three austral seasons; autumn (March-April) 2016 and 2017, and summer (January-February) 2017. In small fragments (< 4 ha), I used one 150 m transect, while in medium (> 4 to < 8 ha) and large fragments (> 8 ha), I used three 150 m transects. The purpose of having greater sampling effort in large fragments was to better resolve these larger networks and my analyses further accounted for differences in network size (Emer et al., 2018; Martensen et al., 2008). In fragments with more than one transect, I separated transects by a 50 m gap. I performed bird censuses every 4 days at each site between 08:00 and 13:00 (total of 12-36 censuses per site), when conditions were dry and wind speed was below 20 km/h. During a census, each 150 m transect was walked at a constant speed for 10 mins. All birds heard and seen within a 10 m wide band each side of the transect were recorded, which ensured detectability in the dense forest. To avoid recording the same individual bird more than once, I did not record individuals moving ahead of the observer after they were recorded on either side of the transect. For data analyses, I only included the abundance of bird species that I recorded consuming fruit, and censuses were pooled in sites with more than one sampling transect.

2.2.3 Plant-frugivore interactions

I sampled plant-frugivore interactions in each fragment. Surveys were conducted immediately after completing bird censuses (12-36 rounds per site). I observed birds consuming fruit by walking each individual 150 m transect at a slow pace (transect surveys took 12 min when no birds were seen). However, if a bird was detected, the watch was stopped, the bird was followed until it moved out of visual range and the survey was then resumed. For each survey, once a bird was detected within 5 m of either side of the sampling transect, I observed its behaviour using 8 x 42 binoculars until I could no longer see it (*sensu* García et al., 2014). Each observation of a bird swallowing fruit was considered an interaction event and the number of fruits consumed during each interaction was recorded. Events in which a bird discarded seeds or ate only the pulp of larger fruits were not recorded.

2.2.4 Landscape composition analysis

I measured three landscape composition variables related to habitat fragmentation: 1) habitat fragment size; 2) area of urban land within the landscape surrounding each study site

(urbanisation); and 3) proportion of indigenous forest habitat surrounding each fragment. I used the New Zealand Land Cover Data Base v.4.1 (Land Resource Information Systems) containing the most recent thematic classification of New Zealand's land use cover. I analysed these data using ArcGIS 10.3.1 (ESRI, 2011) and used the Spatial Analyst tool to calculate the total area occupied by my different landscape variables at a 2,000 m radius, since this scale is appropriate for evaluating effects of surrounding habitat on birds (Deconchat et al., 2009). Two main land use classes were detected within my study area; urban areas and indigenous forests. I considered urbanisation as the percentage of buildings surrounding each study fragment. Proportion of forest habitat surrounding fragments is an important measure of fragment isolation and is directly related to biodiversity loss (Bender et al., 2003; Fahrig, 2003). Collinearity among all fragment metrics was low, as indicated by variance inflation factor values (Table A2, Appendix A).

2.2.5 Network structural analyses

For each of my 13 study sites, I pooled plant-frugivore interaction data across all three seasons. I then calculated two species-level metrics, frugivore richness per plant species, and functional complementarity, which implies functions from several species are necessary for increasing overall functional performance. I created interaction matrices by summing the number of interactions between each plant and frugivore pair, at each site. First, I measured frugivore richness per plant species at each site, to test whether frugivore species richness (likely to be influenced by landscape changes) promoted fruit consumption. A link represented the presence of one or more interaction(s) between a plant and frugivore species. Next, I calculated functional complementarity for each plant species, in each network, by computing dissimilarity matrices using the Jaccard dissimilarity measure (Legendre & Legendre, 1998) for each plant species pair with the "vegdist" function in the *vegan* package (Oksanen et al., 2017). I then calculated the average dissimilarly value for each plant species, which provided a measure of complementarity in frugivore use between plant species. Thus, higher average dissimilarity values indicated higher complementarity in frugivore use for a given plant species, compared with other plant species in the network. I computed niche complementarity from the plant's perspective, as I was interested in linking this directly to frugivory, which is important for plant reproductive success.

Because network size can influence different measures of network structure, I scaled observed values of frugivore richness per plant species and functional complementarity by values obtained from a null distribution for a network of that size. First, I randomized the interaction matrix using a null model. In this null model ('type II' null model; Bascompte et al., 2003), the probability of each cell being occupied is the average of the probabilities of occupancy of its row and column. Biologically, this means that the probability of selecting a particular interaction is proportional to the level of generalisation (degree) of both the frugivore and plant species (Bascompte et al., 2003). Then, for each network (site), I ran 9999 iterations of the null model and calculated frugivore richness per plant species and functional complementarity as outlined above, for each of these null networks. To give a standardised measure of these metrics, I subtracted the mean value of the null distribution from the observed values and divided this value by the standard deviation from the null model distribution.

Finally, I constructed a site-by-species interaction matrix, according to the degree of urbanisation (Figure A1, Appendix A). In this matrix, pairwise plant-frugivore interactions were the upper-level component of the network and each study site was the lower-level component. Matrix cells were filled with the frequency of each unique plant-frugivore interaction at each site. I visualised this matrix using the "visweb" function in the *bipartite* package (Dormann et al., 2008).

2.2.6 Statistical analyses

To investigate the effects of landscape composition on plant-frugivore network structure and frugivore abundance and, consequently, fruit consumption, I used a series of linear models and generalised linear mixed effects models (GLMMs). These models comprised components of a larger hypothesis of causal pathways. Thus, to test whether these hypothesised pathways (which included variables at different scales) were congruent with my observed data, I presented my models in the form of a multi-level path model, fitted using the "piecewiseSEM" function in the *piecewiseSEM* package (Lefcheck, 2016) (Figure 2; Table 1). We used standardised regression coefficients (scaled by the mean and variance) so that coefficients were comparative across variables.

First, for the paths connecting frugivore richness per plant species with landscape variables, I used a linear mixed effects model (LMM) with the "lmer" function in the *lme4* package (Bates et al., 2015). For this model, frugivore richness per plant species (standardised as described above) was the response variable and landscape composition variables (fragment size, urbanisation and proportion of forest habitat surrounding fragments) were the fixed effects. Site identity, transect number nested within site and plant species were included as random effects, allowing me to test the effect of the covariates on fruit consumption for each species, grouped within each transect and site. Similarly, for the paths connecting complementarity with landscape variables, I used an LMM with complementarity as the response variable and the landscape variables listed above, along with the frugivore richness per plant species, as fixed effects. Frugivore richness per plant species was added as a fixed effect as this was identified as a significant path in Shipley's goodness of fit test (Lefcheck, 2016). I included site identity, transect number nested within site and plant species as random effects. For the paths connecting frugivore abundance with the landscape variables listed above, I used a simple linear model. Finally, to determine the significance of paths connecting fruit consumption with network structure, I used a generalised linear mixed effects model (GLMM) with a Poisson distribution and a log link function with the "glmer" function in the *lme4* package. The number of fruits consumed for each plant species at each site was the response variable and standardised complementarity, frugivore richness per plant species and frugivore abundance were included as fixed effects. I also included landscape variables (fragment size, urbanisation and proportion of forest habitat) as fixed effects to identify any direct effects of these variables on fruit consumption. Site identity, transect number nested within site and plant species were included as random effects. In addition to calculating direct effects of landscape variables, network structure, and frugivore abundance on fruit consumption, I calculated indirect effects of those variables, as the product of paths linking variables, and total effects as the sum of direct effects plus indirect effects (Table 1). I tested for covariance between fixed effects in all models using the "vif" function in the *car* package (Fox et al., 2016). Variance inflation factor values were low (< 2.1) in all models (Table A2, Appendix A). I validated all fitted models by examining the distribution of residuals plotted against fitted values (Crawley, 2002; Zuur et al., 2009). I tested for over-dispersion in the Poisson fruit consumption model and found no evidence of over-dispersion. Finally, I evaluated the SEM goodness of fit using Fisher's C statistic compared with a chi-squared distribution. I reported standardised coefficients for paths in the

final SEM (Lefcheck, 2016) along with conditional R^2 values for mixed effects models (Nakagawa & Schielzeth, 2013) and marginal R^2 values for simple linear models. All statistical analyses were conducted in R version 3.5.1 (R Development Core Team, 2017).

2.3 Results

Across my 13 study sites I recorded 28 unique interactions (links) between eight bird species and 16 plant species (Table A3, Appendix A). Overall, I recorded 125 plant-bird interactions and the consumption of 487 fruit. Two native bird species, tūī (*P. novaeseelandiae*) and silvereye (*Z. lateralis*), accounted for 85% of all fruit consumption across sites. In addition, 56% of fruits consumed were from three native plant species, karamu (*Coprosma robusta*), māpau (*Myrsine australis*), and mahoe (*Melicytus ramiflorus*). Although they were less frequent frugivores, blackbird (*T. merula*) and song thrush (*T. philomelos*) consumed fruit across the urbanisation gradient. Consumption of large fruit such as tawa (*B. tawa*) and puriri (*V. lucens*) by kererū (*H. novaeseelandiae*) occurred frequently in fragments surrounded by less urbanisation, but did not occur in fragments surrounded by high levels of urbanisation. Across study sites, total frugivore abundance ranged from 70 to 222 birds per site.

My structural equation model (SEM) was a good fit for the data based on the chi-square goodness-of-fit test (Fisher's C = 4.55; df = 4; $P = 0.337$). The total effect of urbanisation on fruit consumption was negative (-0.10 + 0.02 = -0.08). From the landscape composition variables that I included in the SEM, urbanisation had a direct negative effect on frugivore richness per plant species (standardised $\beta = -0.55 \pm 0.20$; $P = 0.023$; Figure 2 and Figure 3) and an indirect positive effect on functional complementarity (Figure 2) via the negative effect of the frugivore richness per plant species on functional complementarity (-0.55 x -0.17 = 0.10).

Further, urbanisation had an indirect negative effect on fruit consumption via frugivore richness per plant species (-0.55 x 0.18 = -0.10) and a positive effect through functional complementarity, which was negatively affected by frugivore richness per plant species (-0.55 x -0.17 x 0.24 = 0.02). Urbanisation had no effect on frugivore abundance, and frugivore abundance did not affect fruit consumption (Table 1). In addition, I found no evidence of the other landscape composition variables (fragment size and proportion of forest habitat

surrounding fragments) affecting network metrics or fruit consumption directly (Figure 2; Table 1).

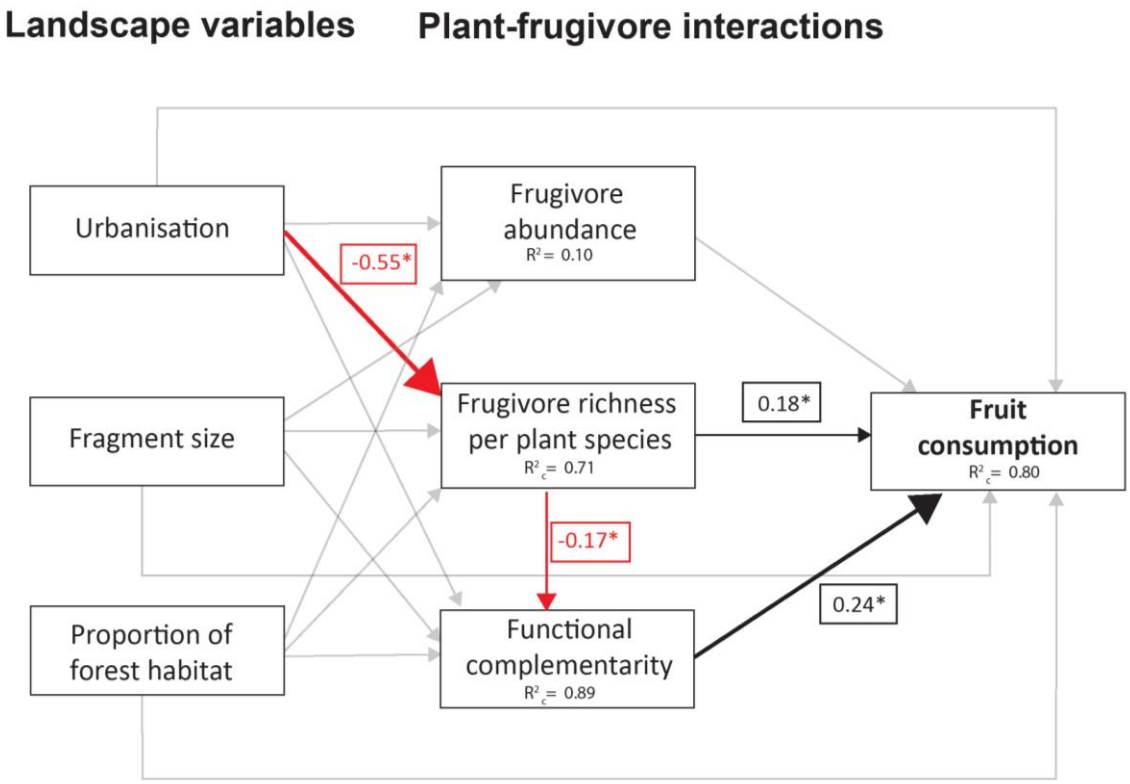


Figure 2. Structural equation model (SEM) showing relationships among fragmentation, plant-frugivore network structure, and fruit consumption. Measured variables are represented in boxes. Arrows represent unidirectional relationships among variables. Black arrows indicate significant positive relationships and red arrows are significant negative relationships. Arrows for non-significant paths are light grey ($P \geq 0.05$). The thickness of the significant paths is scaled based on the magnitude of the standardised regression coefficient, indicated next to the paths $*P < 0.05$. Component model R^2 values are shown in response variable boxes (conditional R^2_c based on the variance of both the fixed and random effects is shown for frugivore richness per plant species, functional complementarity, and fruit consumption).

Table 1. Standardised model estimates (β) for the effect of each predictor variable on model response variables along with corresponding standard errors and *P*-values. Grey rows indicate statistically significant effect paths (see Figure 2).

Predictor	Response	Estimate (β)	Standard error	*P*-value
Functional complementarity	Fruit consumption	0.24	0.11	0.026
Frugivore richness per plant species	Fruit consumption	0.18	0.09	0.044
Fragment size	Fruit consumption	-0.25	0.15	0.095
Frugivore abundance	Fruit consumption	-0.10	0.13	0.427
Proportion of forest habitat	Fruit consumption	0.11	0.17	0.522
Urbanisation	Fruit consumption	-0.07	0.14	0.598
Urbanisation	Frugivore richness per plant species	-0.55	0.20	0.023
Proportion of forest habitat	Frugivore richness per plant species	-0.20	0.21	0.367
Fragment size	Frugivore richness per plant species	0.17	0.21	0.458
Frugivore richness per plant species	Functional complementarity	-0.17	0.08	0.047
Fragment size	Functional complementarity	-0.27	0.23	0.284
Proportion of forest habitat	Functional complementarity	-0.06	0.25	0.815
Urbanisation	Functional complementarity	0.20	0.22	0.394
Proportion of forest habitat	Frugivore abundance	0.34	0.43	0.443
Urbanisation	Frugivore abundance	0.03	0.39	0.949
Fragment size	Frugivore abundance	-0.27	0.36	0.472

Functional complementarity (standardised $\beta = 0.24 \pm 0.11$; $P = 0.026$; Figure 2 and Figure 4a) and frugivore richness per plant species (standardised $\beta = 0.18 \pm 0.09$; $P = 0.044$; Figure 2 and

Figure 4b) both had positive direct effects on fruit consumption. However, frugivore richness per plant species also had a direct negative effect on functional complementarity (standardised β = -0.17 ± 0.08; P = 0.047; Figure 2), thus plant species with many interaction partners were more likely to share those partners with other plant species. Consequently, frugivore richness per plant species had a negative indirect effect on fruit consumption through its negative effect on functional complementarity (-0.17 x 0.24 = -0.04). When direct and indirect effects were combined, frugivore richness per plant species had an overall positive effect on fruit consumption (0.18 + -0.04 = 0.13).

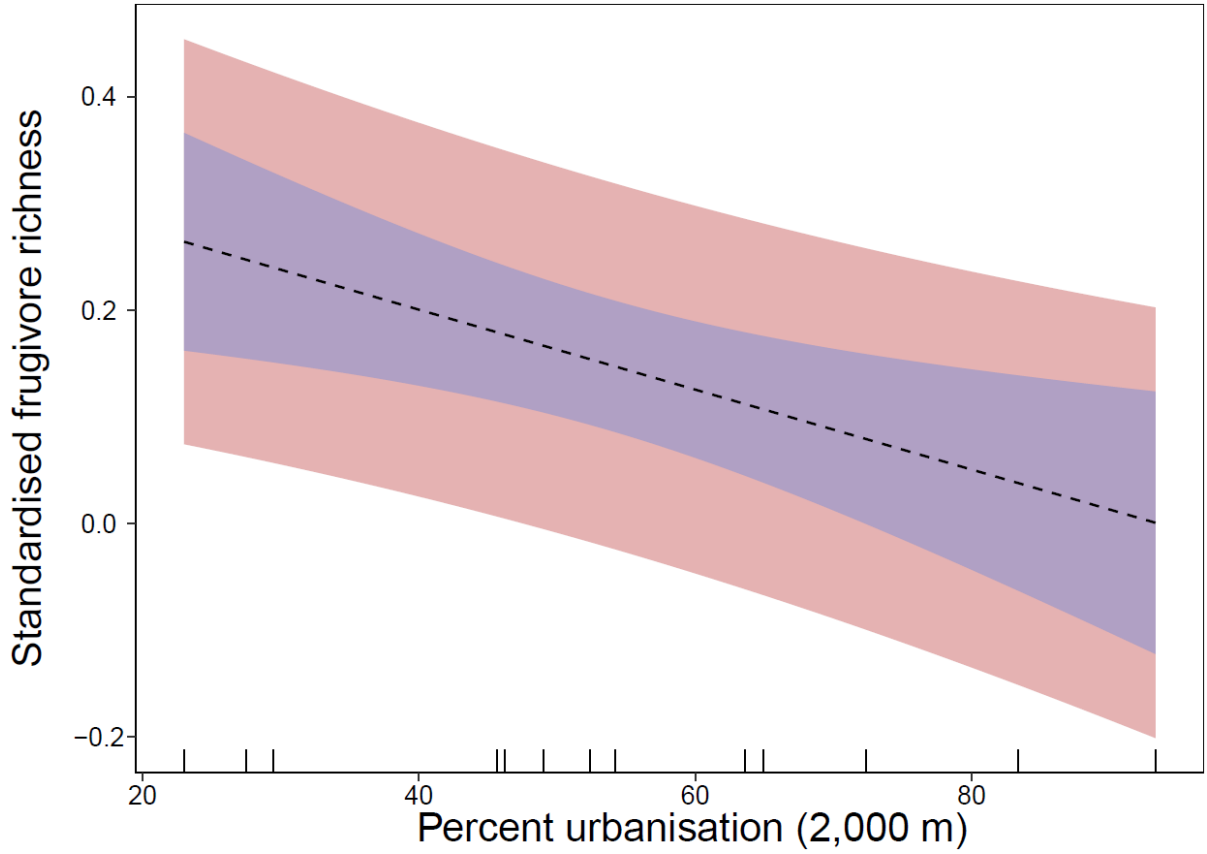


Figure 3. Model estimate for the effect of urbanisation on frugivore richness per plant species (standardised by network size). The purple band surrounding the model estimate denotes the confidence interval (±SE) accounting for the fixed effect variance and the red band is the confidence interval (±SE) accounting for both the fixed and random effects. Vertical lines on the x-axis denote the distribution and frequency of the urbanisation data.

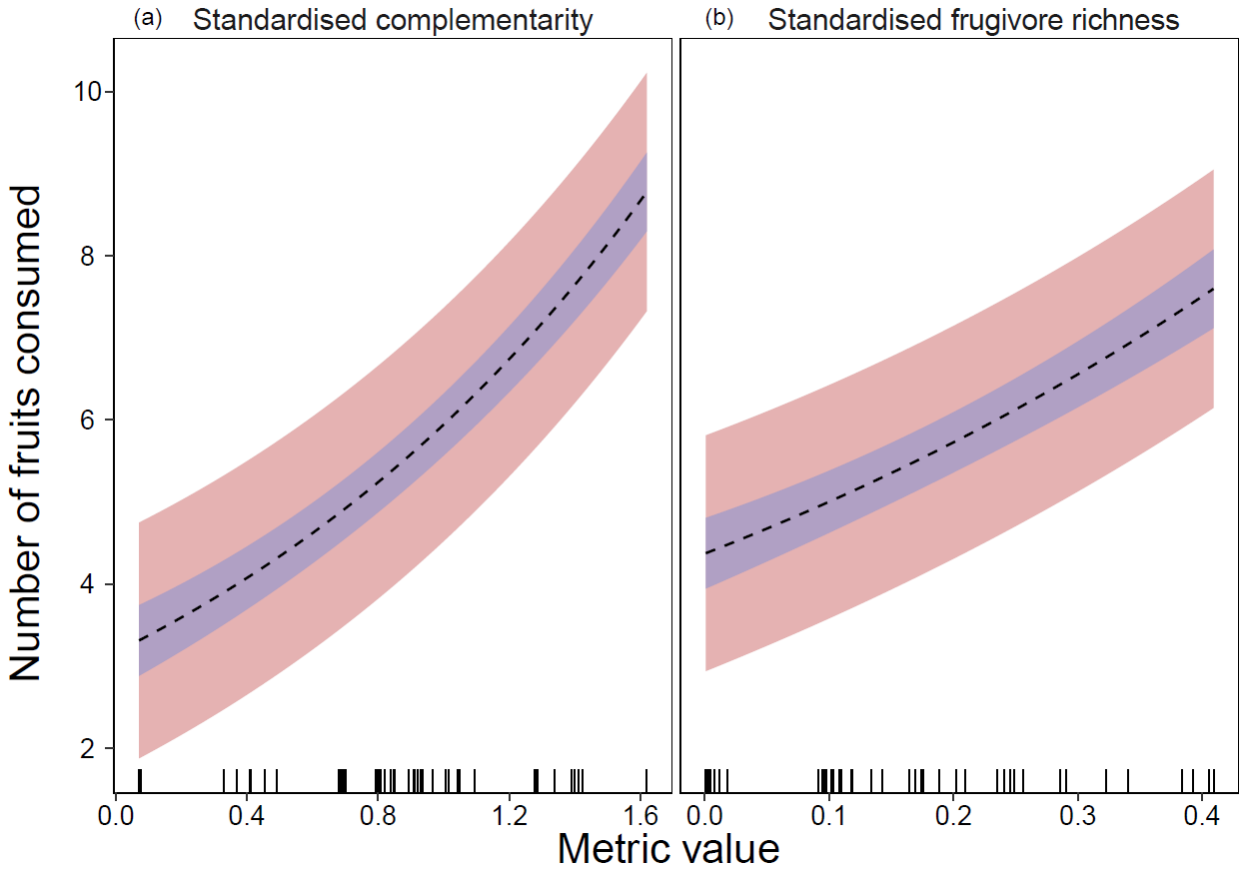


Figure 4. Model estimated average effect of (a) complementarity and (b) the frugivore richness per plant species (both standardised by network size) on fruit consumption across all plant species and sites. The purple band surrounding the model estimate denotes the confidence interval (±SE) accounting for the fixed effect variance and the red band is the confidence interval (±SE) accounting for both the fixed and random effects. Vertical lines on the x-axis denote the distribution and frequency of the complementarity and frugivore richness data.

2.4 Discussion

Here, I investigated how variation in landscape composition through urbanisation alter plant-frugivore network structure and consequently, fruit consumption. I found that one aspect of landscape composition, the degree of urbanisation surrounding habitat fragments, caused important variation in plant-frugivore interactions, which consequently drove variation in fruit consumption. Specifically, plant species in habitat fragments surrounded by less urbanisation had a greater richness of frugivore partners, which resulted in higher fruit consumption. Given the depauperate frugivore fauna in my study system, this finding is particularly important, as I show even small variation in frugivore partner richness can alter frugivory rate.

I found that urbanisation had a strong negative effect on the richness of frugivore partners interacting with plant species in habitat fragments. Urbanisation negatively affects biodiversity in a myriad of ways, being the structural simplification of vegetation one of the stronger effects, promoting the loss of species diversity (McKinney, 2008). Simplified vegetation structure also reduces the availability of stepping-stones, likely having a negative impact on many frugivore species that require habitat to move across the landscape and access resources (Graham, 2001). Neither fragment size nor proportion of natural forest habitat surrounding fragments influenced plant-frugivore interactions or fruit consumption. Previous studies have shown that landscape-level habitat connectivity and habitat availability are more important than habitat fragment characteristics for determining bird community composition and functional richness (Martensen et al., 2008). Furthermore, urbanisation is likely to influence invasive predator abundance, and predation by invasive mammals has been shown to reduce frugivore richness in forest fragments (Innes et al., 2010; Russell & Stanley, 2018). For example, kererū (*H. novaeseelandiae*) and tūī (P. *novaeseelandiae*) were more abundant in areas with predator control programs (mainly rats and possums), but maintaining or increasing forest cover was suggested as more important for conserving frugivore communities, especially in highly modified landscapes (Ruffell & Didham 2017). Indeed, I found that the predator free sanctuary, Shakespear Regional Park, not only had the highest frugivore abundance of all my study fragments, but also harboured interactions between kererū (*H. novaeseelandiae*) and tawa (*B. tawa*), found in no other fragment, suggesting that predator control positively impacted frugivore abundance and promoted plant-frugivore unique interactions. Another factor

associated with urbanisation, human-generated noise, could also reduce frugivore richness and future studies should explore this factor (Arévalo & Kimberly, 2011).

Importantly, richness of frugivore partners increased fruit consumption, likely because a greater number of interaction partners increases resource consumption rate. Several studies have experimentally tested the effects of frugivore diversity on fruit consumption, finding that frugivore richness enhanced fruit consumption in fragmented forests (Cordeiro & Howe, 2003; Menezes et al., 2016). For the first time, I have shown the link between increased richness of frugivore partners and increased fruit consumption in an urbanised landscape. Higher frugivore partner richness is also likely to increase complementarity in a variety of functional niche dimensions that are important for driving fruit consumption (Blüthgen & Klein, 2011; Díaz & Cabido, 2001). Seasonal complementarity, for example, can be important for plant species that fruit across extended periods, which is typical of temperate systems such as my study system (Blüthgen & Klein, 2011). Seasonal complementarity in frugivory is particularly important for enhancing fruit consumption because plant species have varying fruiting phenologies, and therefore require frugivores at different times of the year (Blüthgen & Klein, 2011). For example, karamu (*C. robusta*) produces fruit across multiple seasons, thus requiring frugivory throughout the year, whereas hangehange (*G. ligustrifolium*) fruits for a short distinct period (Williams & Karl, 1996). Architectural complementarity could also enhance fruit consumption whereby different bird species forage at different heights (e.g., close to the ground vs. canopy), ensuring fruit is consumed across all strata (O'Donnell & Dilks, 1994).

In addition to frugivore richness, complementarity in frugivore resource use among plant species (i.e., the degree of dissimilarity in frugivore partners among plant species) positively affected fruit consumption. In other words, plant species that shared fewer frugivores with other plant species (i.e., that had high complementarity) had greater fruit consumption rates compared with species that shared many frugivore partners. Previous studies on resource use complementarity have focused on the frugivores' perspective, finding that frugivore species with complementary rather than redundant seed dispersal roles are more effective, which translates to greater plant recruitment (García et al., 2018; Rother et al., 2016). Yet, I focused on complementarity from the plant's perspective, because I was interested in directly linking plant-frugivore use complementarity to frugivory function, which is essential for seed dispersal

and ultimately plant recruitment. Complementarity in frugivore use of plant species is likely linked to seedling recruitment, because where different bird species consume fruits (Cordeiro & Howe, 2003), seeds from different species should reach different microhabitats, reducing interspecific competition and facilitating increased seedling establishment (Bueno et al., 2013; Russo & Augspurger, 2004). Importantly, I calculated complementarity at the species, rather than the community, level, which enabled me to distinguish the effects of complementarity on fruit consumption for each plant species. Thus, my approach extends on previous studies that measure complementarity at the community level and link complementarity to function (e.g., Peralta et al., 2014).

Interestingly, I found that increased frugivore richness reduced frugivore use complementarity thereby indirectly reducing fruit consumption. This is likely due to the relatively depauperate frugivore fauna in my system, especially compared to continental ecosystems (Kaiser-Bunbury et al., 2010), and it is thus inevitable that plant species visited by many frugivore species will share a substantial proportion of those with other species in the community. As a result, my findings suggest that for a plant species to maximise fruit consumption it requires many different frugivore partners, and to share few of those partners with other plant species in the community.

Contrary to my predictions, urbanisation had an indirect positive effect on complementarity, because frugivore richness decreased with increased urbanisation, which resulted in lower frugivore partner sharing between plant species. Thus, there is a clear trade-off between having many frugivore partners and sharing those partners with other plant species in a community. This trade-off possibly explains why other measures of interaction partner richness (e.g., connectance at the network-level) can produce variable B-EF relationships (Tylianakis & Morris, 2017). Therefore, the trade-off between having high frugivore richness and high complementarity for maximising frugivory function is complex, especially when considering selective pressures of partner choice, which are shaped by co-evolutionary processes (Blüthgen et al., 2007). In New Zealand's urban landscape, recent invasions of plant and bird species have likely dissolved many co-evolutionary plant-bird mutualisms. In particular, invasive bird species are often generalists, and have likely reduced complementarity in my study system (Traveset & Richardson, 2006; Williams, 2006).

Finally, I found that urbanisation had no influence on frugivore abundance, which reflects previous findings showing lack of change in frugivore abundance with habitat fragmentation (González-Varo, 2010). However, this previous study also showed that fragmentation did not affect composition of the frugivore guild. My results indicate that despite not altering overall frugivore abundance, urbanisation can strongly alter the richness of frugivore consuming fruits from different plant species. Interestingly, both frequent (e.g., tūī *P. novaeseelandiae* and silvereye *Z. lateralis*) and infrequent (e.g., kererū *H. novaeseelandiae*) frugivores were present in fragments across my urbanisation gradient, suggesting most frugivores in my system tolerate varying levels of urbanisation. However, some interactions, such as those between kererū (*H. novaeseelandiae*) and tawa (*B. tawa*), were absent in fragments surrounded by high urbanisation, because these plant species were not present (Clout & Hay, 1989; Kelly et al., 2010). These findings highlight the need to look beyond community composition and instead focus on specific interactions between plants and frugivores that are essential for ecosystem functioning.

2.5 Conclusion

In sum, I show that urbanisation negatively effects fruit consumption, by altering both the richness and complementarity of interactions between plants and frugivores. Importantly, for the first time, I identify key mechanisms linking changes in landscape composition to plant-frugivore network structure and ultimately, frugivory function. My findings suggest that land managers of urban environments should target the conservation and restoration of key plant-frugivore interactions, rather than the conservation of single frugivore or plant species, to maintain and/or enhance frugivory function. I suggest that mitigating the drivers of frugivore biodiversity loss in urban areas, through maintaining and increasing native vegetation cover, is critical for conserving and enhancing frugivory function.

Chapter 3 - Different sampling methods generate complementary plant-frugivore networks

Abstract

Plant-frugivore networks are typically sampled by direct observations of birds consuming fruit. A less frequently used method is the identification of seeds in faeces deposited by captured birds. However, these methods are rarely used in combination to sample networks, despite both approaches having inherent biases. Thus, it remains unclear whether method choice influences the conclusions of studies. For the first time, I tested whether direct observations and faecal samples from mist-netted birds provide redundant versus complementary plant-frugivore network information, and propose a new approach for combining data generated from these methods. I sampled plant-frugivore interactions at six urban forest fragments in Auckland, Aotearoa-New Zealand, over multiple seasons, and compared networks generated from: (*i*) direct observations of fruit consumption by birds (focal sampling); (*ii*) identification of seeds in faecal samples deposited by captured birds (mist-netting), and (*iii*) a combination of these methods by weighting interactions with a single link currency. I found that most plant-frugivore interactions were not shared between methods. I detected a higher plant to bird species ratio and more plant species overall with mist-netting compared with focal sampling. Both methods indicated that plants depended more on their bird partners than vice-versa, but this dependency was stronger for mist-netting. At the species level, mist-netting detected more links per bird species, but there were no differences between methods for plants. Across sample sizes, I found that different methods produced different network metric values, and the degree of difference and point at which each metric asymptoted varied between methods. Combined data generated networks with properties that were mostly intermediate between sampling methods, and this was consistent across sample sizes. I demonstrate that both focal sampling and mist-netting methods have inherent biases that can mislead interpretation of network properties if either method is used in isolation. Importantly, interactions recorded by the respective methods are not a subset of one another and produce different network rankings in terms of various structural measures. Therefore, although mist-netting requires greater researcher resource

investment, I recommend combining focal sampling and mist-netting methods, where possible, to give more comprehensive representation of plant-frugivore networks.

Publication status: Submitted to *Journal of Animal Ecology*.

3.1 Introduction

The study of plant-animal mutualistic interactions is central to understanding the ecological processes that drive ecosystem functions (Ings et al., 2009; Vázquez et al., 2009). Consequently, defining the architecture of mutualistic networks and how they respond to anthropogenic disturbances, such as habitat loss, is crucial for informing decisions aimed at protecting biodiversity and maintaining ecosystem function (Bascompte & Jordano, 2007; Valiente-Banuet et al., 2015; Tylianakis & Morris, 2017). Plant-frugivore networks have been the focus of many recent studies (e.g. Costa et al., 2016; Costa Cruz et al., 2013; García, 2016; Heleno et al., 2014) as frugivory, and subsequent seed deposition processes, facilitate the coexistence of species (Wright, 2002).

Currently, various data collection methods are used to construct plant-frugivore interaction networks and test hypotheses, with no general consensus on which method is best (Jordano, 2016). It is unknown if different sampling methods generate differences in plant-frugivore network properties, but if this were the case it could lead to misinterpretation of network structure and related ecological processes. Direct observations of birds consuming fruits, a phyto-centric approach (hereafter referred to as *focal sampling*), is the most commonly used method for measuring bird visitation frequency and fruit consumption rate to construct interaction networks (Donoso et al., 2017; García et al., 2014; Kelly et al., 2010; Olesen et al., 2011). Sampling of seed dispersal by the identification of seeds contained in faeces deposited by captured birds, a zoo-centric approach (hereafter referred to as *mist-netting*), is less frequently used to construct interaction networks as it requires greater researcher resource investment. Although the use of faecal sample analysis has recently increased, only 37% of published plant-frugivore networks are constructed using this method (Costa Cruz et al., 2013; González-Castro et al., 2015; Heleno et al., 2012; Schleuning et al., 2012).

Unlike for plant-pollinator networks (Bosch et al., 2009), no study has attempted to construct plant-frugivore networks using a combination of sampling methods. This is primarily due to difficulties reconciling methodology and logistical constraints around sampling. The major difficulty in combining plant-frugivore network data generated from different sampling methods is identifying a link currency common to both methods (Olesen et al., 2011). Specifically, for weighted interactions, the link currency for focal sampling is the number of fruits consumed, whereas for mist-netting it is the number of seeds consumed. Furthermore, there are stark differences in research resource inputs; focal sampling requires few resources, whereas mist-netting requires substantial material and labour resources, animal ethics approvals and wildlife handling permits. Both methods require proficiency in the identification of bird species and plant species or their seeds.

Given that current knowledge of plant-frugivore networks is primarily based on data generated from focal sampling, it is critical to determine how different sampling methods affect interpretation of plant-frugivore network structure (Bascompte et al., 2006; Blüthgen et al., 2007; Jordano, 2016). It is unknown if any single method representatively captures interactions in plant-frugivore networks, or if they are each biased towards detecting a subset of interactions. For example, observational approaches are likely biased toward detecting common interactions and may fail to detect rare interactions. Further, networks generated from focal sampling often have high animal to plant ratios (Jordano, 2016). In contrast, mist-netting is likely better at detecting rare interactions, but biased by variation in the catchability of different bird species. For example, large bird species are often more difficult to catch, as are species with low mobility or those that prefer the forest canopy (Pagen et al., 2002).

Here, I evaluate how the use of focal sampling versus mist-netting methods affects interpretation of plant-frugivore network structure. Importantly, I provide a solution for combining data generated from multiple methods to give greater network representation. I sampled plant-frugivore interactions using both focal sampling and mist-netting methods and compared plant-frugivore networks generated from each sampling method, and by combining methods. Specifically, I address the following questions: (*i*) Do focal sampling and mist-netting methods detect different sets of plant-frugivore interactions? (*ii*) Do focal sampling and mist-netting methods generate plant-frugivore networks with different structures? and (*iii*) How does

sampling effort affect the networks obtained by focal sampling, mist-netting and a combination of these methods? I expected that different sampling methods would detect complementary interaction subsets from the wider plant-frugivore network. Specifically, I predicted that focal sampling would capture a greater number of bird species relative to plant species and the opposite for mist-netting. Finally, I expected that a combination of these methods would provide a more comprehensive representation of plant-frugivore networks.

3.2 Methods

3.2.1 Study system

My study area was within a fragmented landscape in northwest Auckland, Aotearoa-New Zealand, where forest fragments mostly represent the remaining 13% of native forest cover in Auckland, which was > 90% before human arrival (Ewers et al., 2006). Most forest fragments in my study area were less than 10 hectares and are on private land. Fragments were dominated by native canopy tree species, such as kahikatea (*Dacrycarpus dacrydioides)*, kauri (*Agathis australis*), tōtara (*Podocarpus totara*) and puriri (*Vitex lucens*). Common understory shrubs included fleshy-fruited hangehange (*Geniostoma ligustrifolium*), mapou (*Myrsine australis*), karamu (*Coprosma robusta*), and shining karamu (*Coprosma lucida*). Introduced fruiting plant species, such as climbing asparagus (*Asparagus scandens*), inkweed (*Phytolacca octandra*) and woolly nightshade (*Solanum mauritianum*), have successfully established as weeds. Approximately 12% of New Zealand's native plants produce fleshy fruits (Lord et al., 2002), which are consumed and dispersed by common native birds such as silvereye (*Zosterops lateralis*), tūī (*Prosthemadera novaeseelandiae*) and kererū (*Hemiphaga novaeseelandiae*) (Clout & Hay, 1989). However, since the 19th century, New Zealand has experienced the extinction and severe decline of effective bird seed dispersers due to habitat loss and mammal predators (Holdaway, 1989; Innes et al., 2010). In highly modified landscapes, introduced bird species, such as the European blackbird (*Turdus merula*), song thrush (*Turdus philomelos*) and starling (*Sturnus vulgaris*), disperse seeds of native and introduced plants (Kelly et al., 2010; MacFarlane et al., 2015; Williams, 2006). I sampled six different forest fragments of various sizes (0.5-13 ha) (Table B1, Appendix B) across the north-western Auckland region. These

fragments were selected to meet the following criteria: (*i*) have similar native forest structure; (*ii*) located on public land; and (*iii*) surrounded by an urban matrix.

3.2.2 Plant-frugivore interactions

I sampled plant-frugivore interactions in each fragment throughout three austral seasons; autumn (March-April) 2016, summer (January-February) 2017, and the following autumn (March-April) 2017 using two different methods: direct observations of bird fruit consumption (focal sampling) and analysis of faecal samples obtained from mist-netted birds (mist-netting).

3.2.3 Focal sampling

I walked a fixed transect at each site to observe birds consuming fruit. This resulted in 12 surveys for small fragments and 36 surveys in medium and large fragments, over a two-week period for each season. In small fragments (< 4 ha), I sampled one 150 m transect, whereas in medium (> 4 to < 8 ha) and large (> 8 ha) fragments I sampled three 150 m transects, which were separated by 50 m. The purpose of having greater sampling effort in large fragments was to better resolve these larger networks (Emer et al., 2018; Martensen et al., 2008). Further, I included a site level random effect (see 'statistical analyses' section) in models, so that comparisons of network metrics between methods were made within sites, thus controlling for unequal sampling effort among sites. I walked each individual transect at a slow pace and surveyed for approximately 12 min. When a bird was detected within 5 m of either side of the transect, I observed its behaviour using 8 x 42 binoculars until it was no longer visible (*sensu* García et al., 2014). Each time a bird swallowed a fruit it was recorded as one interaction. Events where birds discarded seeds or only consumed the pulp were not considered interactions. I used the number of fruits consumed, rather than the number of feeding visits to a plant to measure interaction rate, as I was interested in measuring the immediate outcome of the interaction (fruit consumption) from the plants' perspective (Schupp et al., 2010, 2017).

3.2.4 Mist-netting

I mist-netted at each site from 0800h to 1500h at the beginning of each field season, prior to focal sampling. Three 38 mm mesh nets (3 m high) were used in small fragments (total net area = 45 m^2), while four nets were used in medium and large fragments (total net area = 81 m^2). I used different numbers of mist-nets to account for site size and to have greater sampling effort

in large fragments, to better resolve these larger networks. However, analyses involved comparisons within sites (as explained above), thus accounting for unequal sampling effort. Where possible, I altered net location within fragments for each sampling round, although I used the same locations for some nets when open spaces for appropriate placement were limited. I checked nets every 10–15 mins. When birds were captured, they were immediately extracted and placed into cloth bags for 15 mins to allow them to defecate. I then collected faeces in plastic vials and stored them in a refrigerator. Seeds in faecal samples were later identified to species level using a seed reference collection. I considered one plant-frugivore interaction as a single seed in a faecal sample.

3.2.5 Sampling method comparisons

To test how network structure differed between focal observation and mist-netting methods or their combination, I generated interaction matrices for each site with all plant-frugivore interactions recorded from both sampling methods. I used the number of seeds consumed for each unique plant-frugivore interaction at each site, which provided a common link currency across both methods (Olesen et al., 2011). For mist-netting, these data were obtained by counting individual seeds for each plant species in faecal samples (as outlined above). However, for focal observations I could only record the number of fruits consumed per interaction event. Therefore, I converted fruit consumption to seed consumption by multiplying the number of fruits consumed by the mean number of seeds per fruit based on the literature (see Table B3, Appendix B).

3.2.6 Network structure

For each of my six study sites, I pooled plant-frugivore interaction data (i.e. seed consumption) across all three seasons. Thus, for each site I constructed one plant-frugivore interaction matrix, which contained the summed number of interactions for each plant-frugivore species pair. Using these matrices I calculated three sets of metrics to characterise network structure (García et al., 2014). The first set described network level properties: *connectance* (proportion of realised links divided by the number of potential links), *number of bird species*, *number of plant species*, *interaction strength asymmetry* (ISA; a weighted measure of the difference in dependence of bird species on plant species versus dependence of plant species on bird species), and *interaction evenness* (similarity between weights of different plant-frugivore

interactions). The second set consisted of group-level (bird species versus plant species) metrics: *generality* (weighted average of the number of links per bird species), and *vulnerability* (weighted average of the number of links per plant species). The last set included one species-level metric: *species degree* (the sum of unique links per bird or plant species). All metrics were calculated using the *bipartite* package (Dormann et al., 2016).

3.2.7 Statistical analyses

Do focal sampling and mist-netting methods detect different sets of plant-frugivore interactions?

I first tested whether interactions present in focal samples comprised a subset of the interactions (*sensu* Aizen, Sabatino, & Tylianakis, 2012) present in mist-netting samples. Interactions from both methods were pooled by season and site and were arranged in a binary (presence-absence) matrix, with rows representing the different methods and columns identifying unique interactions. I then calculated nestedness of these matrices (focal sampling interactions within mist-netting and vice-versa) using the nestedness metric based on overlap and decreasing fill (NODF) implemented as the "nestednodf" function in the *vegan* package (Oksanen et al., 2017).

Next, I tested whether the composition of plant-frugivore interactions differed for focal sampling versus mist-netting methods using a PERMANOVA analysis (Anderson & Walsh, 2013) with the "adonis2" function in the *vegan* package, using the Bray-Curtis measure of dissimilarity (Faith et al., 1987). Here I used the presence or absence of an interaction in the matrix, as I was only interested in the ability of the metrics to detect unique pairwise interactions, rather than their frequency (which is addressed within the network analyses). The PERMANOVA *P*-value for the pseudo-F statistic was based on 9,999 permutations. To visualise differences in the composition of plant-frugivore interactions between focal sampling versus mist-netting methods, I performed an nMDS ordination with a Bray-Curtis measure of dissimilarity (Faith et al., 1987) using the "metaMDS" function in the *vegan* package.

Do focal sampling and mist-netting methods generate plant-frugivore networks with different structures?

I used two approaches to determine whether different methods generated different network structures. First, I determined if there was a correlation between network metric values generated by focal sampling versus mist-netting at each study site using Spearman's rank correlation and Pearson's correlation. I first used Pearson's correlation to determine whether the differences among sites (including their magnitude) were correlated between the two methods. As a second step, I used Spearman's correlation to determine whether the two methods at least ranked the sites in the same order, even if the magnitudes of differences were not consistent among methods. Second, to test whether metric values generated by focal sampling versus mist-netting differed, I used generalised linear mixed effects models (GLMMs) with the "glmmTMB" function in the *glmmTMB* package (Brooks et al., 2017). I created separate GLMMs for each network metric and applied a distribution that provided the best model fit for each metric (Table B7, Appendix B). In each model, network metric values were the response variable and method (categorical: focal sampling or mist-netting) was the fixed effect. I included site as a random effect, so that differences in metrics generated by different methods were compared within sites. For some metrics, the response was log+1 transformed to meet the assumptions of normality and residual homoscedasticity.

For *species degree* I also used two different approaches to test for differences between sampling methods. First, I calculated the number of links (i.e. *species degree*) for each bird and plant species at each sampling site. Then, I determined if there was a correlation between *species degree* generated by focal sampling versus mist-netting at each site using a GLMM with a Poisson distribution and log link function. I used two models, one for birds and one for plants, with *species degree* for focal sampling as the response and species degree for mist-netting as the fixed effect. I included site and species as crossed random effects to identify the correlation between methods independent of site (because *species degree* could vary with network size) and species identity. Second, to determine if there were differences in *species degree* for plants and birds generated from focal sampling versus mist-netting methods, I used GLMMs with a Poisson distribution and a log link function. I ran two models, one for birds and one for plants, with species degree as the response variable and sampling method (focal sampling or mist-netting) as the fixed effect. Site and species identity were included as crossed

random effects. I tested for overdispersion and data were not over-dispersed. All GLMMs were validated by examining the distribution of residuals plotted against fitted values (Crawley, 2002; Zuur et al., 2009).

How does sampling effort affect the networks obtained by focal sampling, mist-netting and a combination of these methods?

To test whether the influence of sampling intensity on network structure differed for focal sampling, mist-netting and combined methods, I used a null model approach. This allowed me to assess the rate at which different methods converged on a given network structure. First, I took random samples, with replacement, of one to 1,000 (at intervals of 1) plant-frugivore interactions (seeds consumed) from focal sampling, mist-netting or combined sampling methods at each site and repeated this 100 times. In my null model, the probability of selecting an interaction was proportional to the frequency of that interaction in the sampled data, so that more frequent interactions had a higher probability of being sampled (Magrach et al., 2018; Vázquez & Aizen, 2004). Next, I took each of these 100,000 random samples of interactions and converted them to matrices, wherein the number of interactions (number of seeds consumed) was summed for each plant-frugivore species combination. For each matrix, I then calculated the following network metrics: *connectance*, *number of bird species*, *number of plant species*, *interaction strength asymmetry* (ISA), *generality*, *vulnerability* and *interaction evenness*, using the "networklevel" function in the *bipartite* package (Dormann et al., 2016). Finally, I calculated mean network metric values for each method, at each site, at each level of sample size of interactions (1-1000). To visualise this simulation, I plotted the number of interactions against network metric values. All statistical analyses were conducted in R version 3.2.4 (R Development Core Team, 2017).

3.3 Results

Using focal sampling, I recorded the consumption of 173 fruits across seven bird species and nine plant species, which equated to the consumption of 808 seeds. With mist-netting, I recorded 8,309 seeds in faeces across six bird species and 22 plant species.

3.3.1 Do focal sampling and mist-netting methods detect different sets of plant-frugivore interactions?

Focal sampling and mist-netting methods generated networks that contained different species and interactions (Figure B1, Appendix B). Specifically, interactions in networks generated by focal sampling were not a subset of networks generated by mist-netting, nor were the interactions from mist-netting a subset of the interactions from focal sampling (Table B4, Appendix B). I recorded 17 unique interactions with focal sampling and 36 unique interactions with mist-netting, and only eight of these interactions were shared between the different methods. This resulted in clear differences in interaction composition between methods (R^2 = 0.27; Pseudo F_1 = 3.75; P = 0.004; Figure B2, Appendix B).

3.3.2 Do focal sampling and mist-netting methods generate plant-frugivore networks with different structures?

Overall, there were no significant correlations (Pearson's or Spearman's) between sampling methods for network-level and group-level metrics (Figure 1; Table B5, Appendix B). However, the absence of correlation in metric values between methods might have been due to my relatively low statistical power (N = 6 networks). Three out of the seven metrics that I measured differed significantly between methods (Figure 1). Together these results indicate that not only did the two sampling methods not always give similar values for networks metrics, but also that there were no associations in the rank order of network metric values (determined by the Spearman rank correlation) across networks. Specifically, networks generated from mist-netting had more plant species and, on average, had more plant species interacting with each bird species (*generality*). However, the number of bird species, and the number of bird species interacting with each plant species (*vulnerability*), did not differ between methods. Values for *interaction strength asymmetry* (ISA) were negative for both methods, indicating that each plant species tended to be consumed by few bird species. However, networks generated from mist-netting had lower values of ISA compared with focal sampling, due to the low bird to plant species ratio recorded via mist-netting. Values for *connectance* and *interaction evenness* did not differ between sampling approaches (Figure 1).

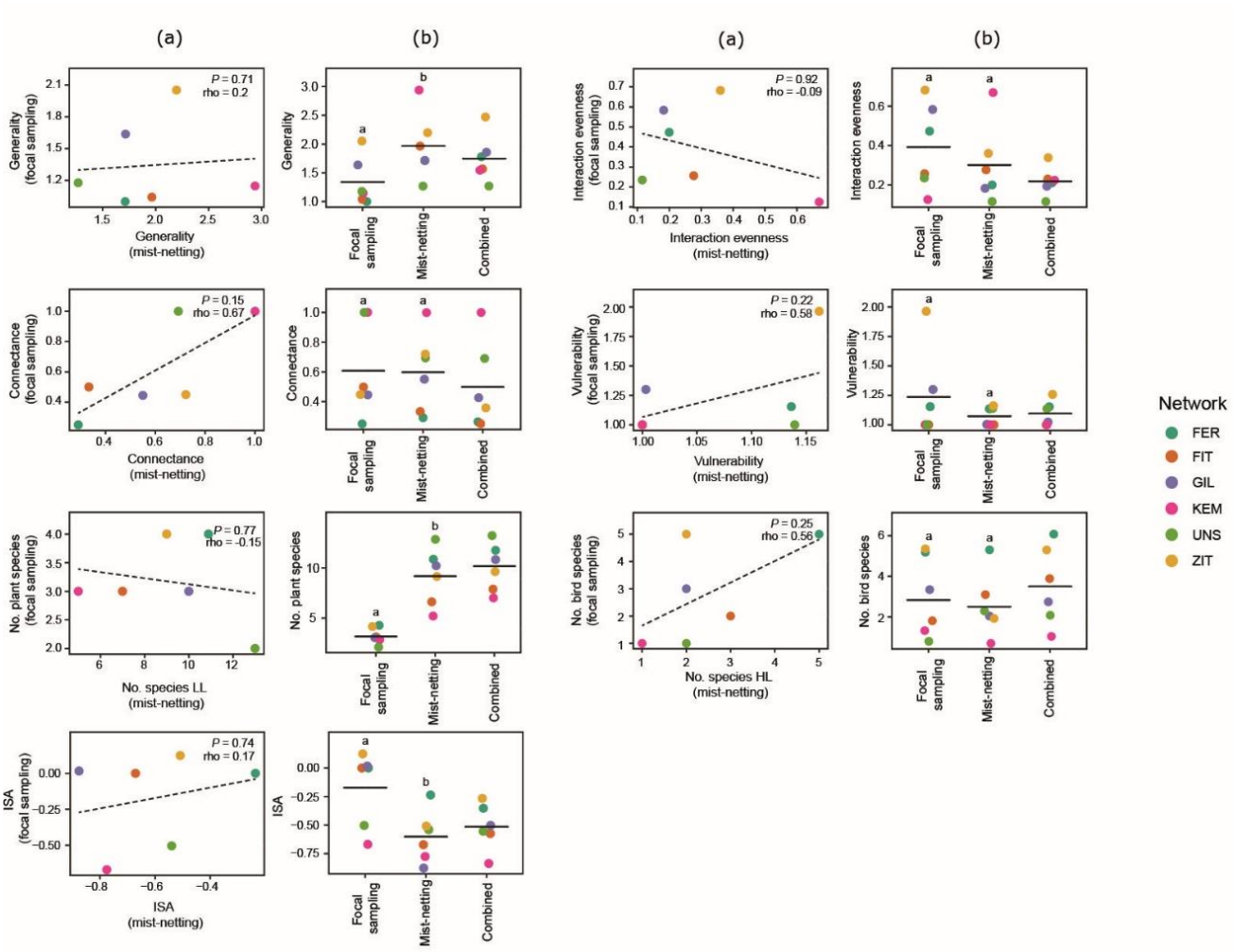


Figure 1. Spearman's rank correlations (a) and differences in network and group-level metric values generated from focal sampling and mist-netting methods (b) as determined by generalised linear mixed effect models. There are no correlations between methods for all metrics (all *P*-values > 0.05). Metric values for the combined sampling method are given, but no statistical testing was done on this group.

Finally, there was a positive association (slope = 0.11 ± 0.04; z = 2.37; P = 0.017) between focal sampling and mist-netting for the number of links per bird species (*degree*) but there was no association between methods for plants (Figure 2a). Further, the number of links per species for birds differed significantly between methods, as mist-netting detected more interaction partners compared with focal observations (Figure 2b).

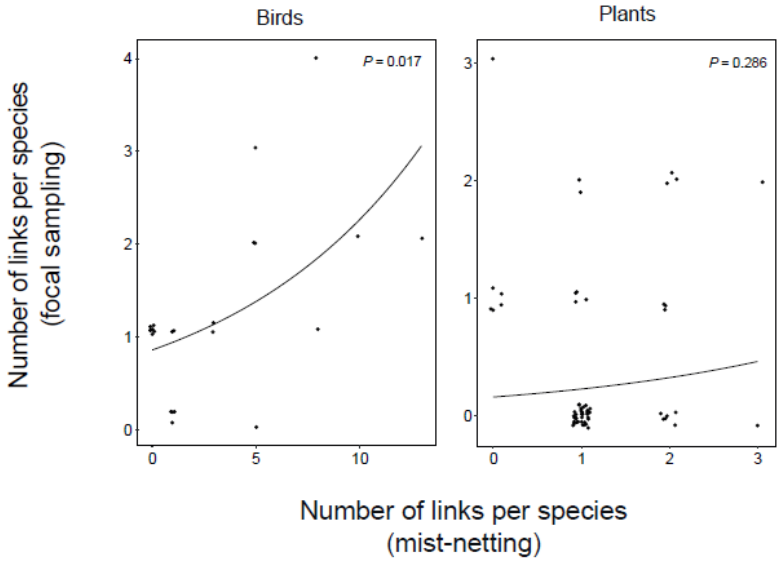


Figure 2a. Association between methods for number of links per species (*species degree*) for birds and plants. There is a positive association (P = 0.017) for the number of links per bird species but not for the number of links per plant species.

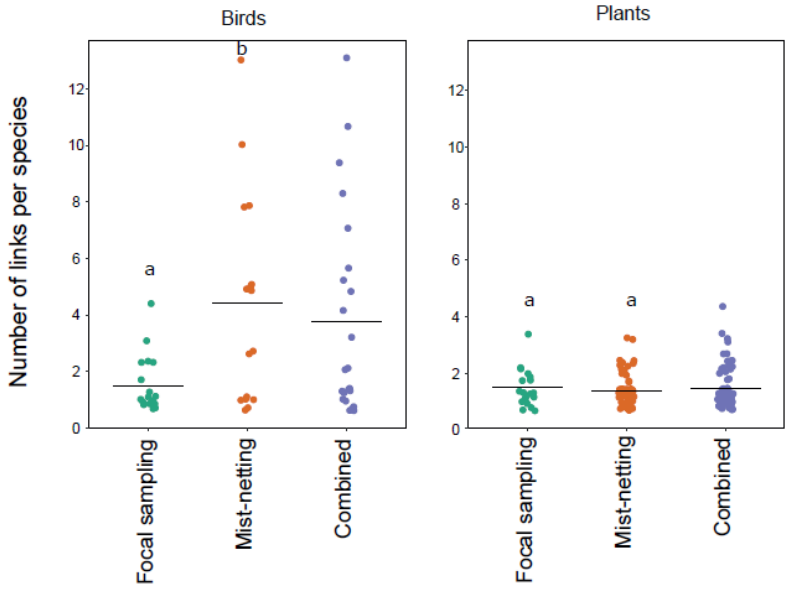


Figure 2b. Number of links per species (*species degree*) values for plants and birds for focal sampling, mist-netting and combined sampling methods, and black horizontal lines indicate the mean. Differences in metric values are denoted by different letters. Values for the combined sampling method are given, but no statistical testing was done on this group.

3.3.3 How does sampling effort affect the networks obtained by focal sampling, mist-netting and a combination of these methods?

My null model revealed that different sampling methods generated different metric values with increasing sample size (Figure 3). For example, values for *interaction evenness*, *interaction strength asymmetry* (ISA), and *vulnerability* calculated from mist-netting data and the combined sampling approach were more similar across sample sizes (except for *interaction evenness* and *generality* at one site: KEM). Mist-netting also captured more plant species (as described above), so saturated more slowly than focal sampling, while combined approaches had higher total plant richness but saturated at a similar rate.

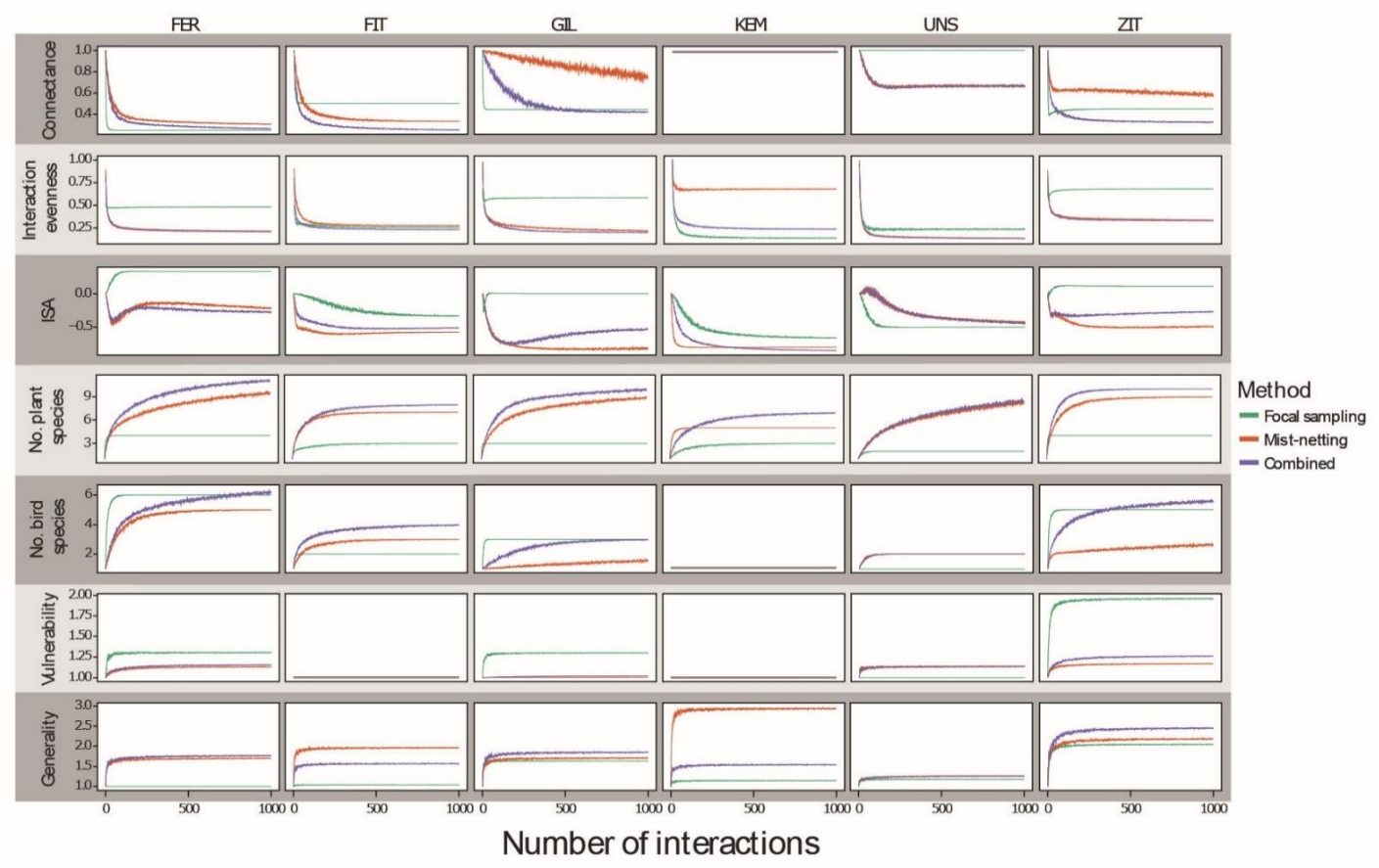


Figure 3. Network and group-level metric values for different study sites generated from random networks for 1 to 1000 plant-frugivore interactions. Different colours denote different sampling methods. Solid lines represent the mean across 100 random networks (iterations).

This indicates that mist-netting detected a greater number of rare plant-frugivore interactions. Across sites, *connectance*, *interaction evenness*, *number of plant species*, and *interaction strength asymmetry* (ISA) asymptoted more rapidly for focal sampling compared with mist-netting and combined methods. The asymptote for the *number of bird species* varied between methods, whereas *generality* and *vulnerability* asymptoted at approximately the same point. For *interaction strength asymmetry*, *number of plant species* and *generality*, differences in saturation curves between the different methods remained constant across sample sizes.

3.4 Discussion

For the first time, I show that different methods for sampling plant-frugivore networks provide different and complementary information about network structure. Specifically, most pairwise interactions identified by the two methods were unique to each sampling method, and there were clear biases in the interactions that each method detected. I found that across sample sizes, the two methods produced different metric values, but the degree of difference and point at which each metric asymptoted varied between methods. If the value of network metrics had consistently deviated by a fixed amount across the two methods, then studies comparing sites would still capture the same effects with different methods, just at different magnitudes. However, my finding that even the rank order of sites was not correlated for the two methods suggests that hypothesis tests (using sites as replicates) would be biased by the sampling method used.

Importantly, only a few of the plant-frugivore interactions that I recorded were detected by both methods. For example, some species recorded using focal sampling (e.g., kererū *H. novaeseelandiae*, a large endemic pigeon) were not recorded using mist-netting, while other species recorded using mist-netting (i.e., grey warbler, *Gerygone igata*), were not recorded in focal observations. This is probably because larger bird species are more conspicuous, while smaller species are easier to capture in mist-nets (Pagen et al., 2002). In contrast to birds, I detected more plant species with mist-netting (e.g., invasive woolly nightshade; Japanese honeysuckle, *Lonicera japonica;* and native cabbage tree, *Cordyline australis*). This can be due to not all plant species recorded with mist-netting being present along the focal sampling transects, and birds most likely feeding outside study fragments, thus recording more rare

interactions with mist-netting than with focal sampling. Also, via mist-netting I sampled everything a bird ate since its last defecation while focal sampling captured a very short feeding timescale.

Although I detected more plant species with mist-netting, this did not result in consistent differences in *connectance* between sampling methods, because I also detected more interactions (links) per species with mist-netting. Additionally, in networks constructed with mist-netting data, bird species showed stronger generalisation than plants, whereas the opposite occurred in networks constructed with data from focal observations where birds showed lower generalisation. This was likely driven by the greater number of plant species present (and therefore a higher upper limit of interaction partners for birds) in mist-netting networks. In contrast, with both methods, I found a similar number of bird species interacting with each plant species (*vulnerability*), probably because both methods detected a similar number of bird species. Interactions from focal sampling networks were almost symmetrical, as indicated by *interaction strength asymmetry* (ISA) values close to zero. This is because the number of links per plant and bird species (*degree*) was relatively equal. My focal sampling ISA values are consistent with another study (González-Castro, Traveset, & Nogales 2012), which found that avian seed dispersal networks on islands were typically highly symmetric due to low species richness and high specialisation. However, González-Castro et al. (2012) used mist-netting, rather than focal observations and sampled networks on Mediterranean islands smaller than the North Island of New Zealand. In contrast, I found that mist-netting networks were highly asymmetric, wherein plant species displayed high dependence on their bird dispersers, reflecting the greater number of links per bird species compared with plant species. This difference in ISA values generated by mist-netting could be because González-Castro et al. (2012) only sampled native species, whereas I sampled both native and introduced species. Generally speaking, plant-frugivore networks tend to be highly asymmetric, whereby plant species depend on a single or few animal species (Schleuning et al., 2014a). These general network patterns facilitate the coexistence of mutualistic species and stability of communities (Bascompte et al., 2006; Jordano, 2016), suggesting that networks generated by focal sampling would be interpreted as being more vulnerable to disturbances compared with mist-netting networks. At the species-level, although I detected a positive association between methods for the number of links per bird species, I found a greater number of plant partners for birds with

mist-netting. Most bird species are highly mobile and feed on plant species outside of focal observation transects, which explains why I detected many more plant species with mist-netting.

From the null models constructed to understand how sample size influences estimated network structure, I found that metrics for focal sampling networks tended to asymptote earlier than mist-netting or combined-methods networks with increasing sample size. This indicates that mist-netting tended to capture rare interactions more frequently. Consequently, networks generated from combined methods were often more similar to those generated from mist-netting than focal observations. Combined with my finding that the composition of interactions differed between the two methods, this indicates that different methods clearly detect different sets of plant-frugivore interactions. Thus, I show that a combination of data from focal observations and mist-netting methods provides a more comprehensive representation of plant-frugivore network structure than either method alone, reflecting findings from a previous study on plant-pollinator networks (Bosch et al., 2009).

It is important to consider the limitations and biases inherent to different sampling methods when interpreting network patterns. I have shown that focal sampling was biased towards detecting common interactions constrained within the immediate sampling area, and thus failed to detect rare interactions. For example, focal sampling tended to detect frequent plant-frugivore interactions such as silvereye consuming hangehange (*G. ligustrifolium*) and tūī (*P. novaeseelandiae*) consuming karamu (*C. robusta*), rather than rare interactions, such as primarily insectivorous fantail (*Rhipidura fuliginosa*) consuming mingimingi (*Leucopogon fasciculatus*) fruit. Focal sampling could also be biased by what researchers define as interactions. In this study, I considered an observation of a bird swallowing a fruit as an interaction event, thus capturing the dispersal mutualism via seed consumption. Caution should be taken for cases where bird visitation frequency, but not actual fruit consumption, is considered an interaction because visitation does not necessarily indicate seed dispersal (Simmons et al., 2018). Data from studies that use focal sampling and consider visitation events as interactions are unlikely to accurately reflect plant-frugivore interactions and consequently, seed dispersal. Focal sampling can also be subject to potential biases emerging from differences in species' detectability through the year (Bibby et al., 2000). Despite the biases, focal sampling

requires relatively few resources (e.g. does not require bird handling permits or ethical considerations), although advanced species identification skills are needed.

Although I found that mist-netting was more effective at detecting rare interactions, it was biased by differences in the catchability of bird species. For example, silvereyes accounted for almost 60% of all interactions detected by mist-netting, whereas some species recorded in focal observations (e.g., kererū, *H. novaeseelandiae*) were never captured in mist-nets. Large and/or inactive species that prefer the forest canopy are often more difficult to catch than small and highly active species (Biro & Dingemanse, 2009; Pagen et al., 2002). Moreover, some network patterns that I detected with mist-netting (i.e., high bird species generalism and plant dependency on birds) could have been influenced by the aggregation of data from several seasons (Vázquez & Aizen, 2003), favouring abundant and generalised species over rare ones, exacerbating asymmetric specialisation (Blüthgen et al., 2008; Vázquez & Aizen, 2004; Woodward et al., 2005). Although I found that mist-netting was more effective at detecting rare interactions, it is labour-intensive and requires a high level of expertise, appropriate permits and ethical considerations.

3.5 Conclusion

In summary, I show that focal sampling and mist-netting methods provide complementary information about plant-frugivore interaction networks and suggest a standardised link currency (i.e. seeds consumed) for combined data collected using these two approaches. The decision to use either focal sampling or mist-netting could strongly bias researcher interpretation of network structure. Accordingly, I suggest that focal sampling and mist-netting methods be treated as complementary, and that a combination of these approaches should be used where possible. Where it is only possible to use one sampling method, researchers should apply cautious interpretation of the data and discuss potential biases.

Chapter 4 - Genetic evidence of long-distance recruitment of a podocarp (*Podocarpus totara*) in a fragmented landscape

Abstract

Habitat fragmentation is likely to have negative consequences for tree species recruitment and source-sink dynamics among populations, due to changes in plant-disperser interactions and subsequent bird movement. Long-distance recruitment among forest fragments determines plant species persistence in fragmented landscapes, but data on the occurrence of this process remains scarce at a landscape scale. I investigated spatial patterns of genetic variation and long-distance recruitment for tōtara (*Podocarpus totara*), a bird-dispersed tree, at four fragments within a fragmented mixed broadleaf forest in northern Auckland, Aotearoa-New Zealand. Based upon collection of leaf material from adult trees and seedlings, I estimated long-distance recruitment among fragments using parentage analysis through single nucleotide polymorphisms. I estimated pairwise relatedness between 273 tōtara individuals and average relatedness within fragments. I then assessed first-degree relationships between individuals. I found no association between genetic and geographic structure among fragments, indicating high connectivity across the landscape. However, I found higher relatedness within fragments and a source-sink pattern. Finally, my estimates found that long-distance recruitment events for tōtara are not rare. My results provide the first insights into genetic relatedness and long-distance recruitment in tōtara within a fragmented landscape. I highlight the importance of birds as mobile links shaping the spatial and genetic structure of tōtara populations, by actively dispersing tōtara seeds between fragments. Also, I emphasise the need to conserve not only larger forest fragments in urbanised areas that are sources for tōtara, but also fragments that act as sinks for seeds, promoting seedling recruitment.

Publication status: Not yet published. This chapter will be submitted to *Biological Conservation*.

4.1 Introduction

The recruitment of new individuals is a vital step in plant population dynamics and is directly influenced by seed dispersal processes (Lavabre et al., 2014). Seed dispersal controls the long-term dynamics of plant communities and establishes the template for regeneration in natural plant populations (Howe & Miriti, 2004; Wang & Smith, 2002). Patterns of seed dispersal also influence genetic structure, and the spatial distribution of future generations (Nathan & Muller-Landau, 2000). In temperate ecosystems, the frequency of species with fleshy fruits requiring dispersal by vertebrate frugivores is high, varying between 27-60% (Willson et al., 1989, 1990). Frugivorous birds are the most common vertebrate seed dispersers, feeding on fleshy fruits and subsequently depositing seeds (via excretion or regurgitation) away from the parental sources (Anderson et al., 2006; Clout & Hay, 1989; Jordano & Schupp, 2000; Kelly et al., 2010).

Changes in plant-bird disperser interactions and reduction in bird movement due to habitat fragmentation are likely to alter seed dispersal outcomes with potentially negative consequences for tree species recruitment (Gillies et al., 2011; Robertson & Radford, 2009; Uriarte et al., 2011). A reduction in seed dispersal in the landscape may lead to population declines and potentially biodiversity loss, and it also may alter source-sink dynamics among populations, in which ensembles of individuals in sink habitats are maintained by continuous immigration from source habitats (Ibáñez et al., 2014; McConkey et al., 2012; Pulliam, 1988). Similarly, reduced seed dispersal might reduce gene flow causing the decline of genetic diversity and loss of fitness in plant populations (Auffret et al., 2017). Thus, it becomes crucial to understand the effectiveness of the seed dispersal process, i.e. the establishment of a new adult plant, along with the distance from its parental tree, for determining long-distance dispersal (Lavabre et al., 2014; Schupp et al., 2017). However, evaluating the effectiveness of seed dispersal has been hampered by the difficulty of measuring this process (Hardesty et al., 2006). Most attempts to measure seed dispersal prior to seedling establishment have used observational approaches, such as fruit removal rates by frugivore dispersers, gut passage rates, recording immediate distances birds move away from the parent plant following feeding bouts, or seed rain (Bullock et al., 2006; Clark et al., 2001; Holbrook & Smith, 2000; Martínez & García, 2017; Stanley & Lill, 2002). These approaches can fail to capture the frequency of rare

long-distance dispersal events, which play an important role both ecologically and evolutionarily (Nathan et al., 2003, 2008). Despite the well-established importance of long-distance seed dispersal, studies on this process at a landscape scale are still rare, mainly due to the difficulties in detecting and quantifying these events (He et al., 2010).

Molecular techniques are increasingly being used to evaluate seed dispersal through parentage analysis, solving the long-standing problem of assessing long-distance dispersal (Cain et al., 2000; Harrison et al., 2013; Jones et al., 2005). Parentage analysis methods use genetic markers to document contemporary dispersal events (Jones et al., 2010), providing a relatively direct measure of dispersal, with the disadvantage that the population of interest must be exhaustively sampled so that all potential parents have equal chance of identification (Cain et al., 2000). From an ecological point of view, only seed dispersal, then germination followed by seedling establishment (recruitment) contributes to functional genetic connectivity between populations (Luque et al., 2012). Thus, it is important to evaluate long-distance seed dispersal at the seedling stage (hereafter *long-distance recruitment*) to broaden our understanding of the spatial relationships between trees and their established offspring (Hardesty et al., 2006; Ismail et al., 2017). This is particularly important, as most previous attention has been given to fruit consumption and seed dispersal, with much less emphasis on seedling establishment and subsequent survival (Hobbs & Yates, 2003; Simmons et al., 2018).

In this study, I used single nucleotide polymorphisms (SNPs) to study genetic variation and effective dispersal; specifically, seedling recruitment distances from parents and each individual's relatedness in a naturally occurring fragmented population of a bird-dispersed tree, tōtara (*Podocarpus totara*) G. Benn. Ex D. Don (Podocarpaceae). The study area is highly fragmented due to increasing urbanisation, and there is no clear information about the spatial distribution of tōtara trees before recent human occupation. I focussed on two main questions: (*i*) What is the spatial pattern of genetic variation in tōtara? and (*ii*) What is the frequency of long-distance tōtara seedling recruitment? Specifically, I expected that while tōtara individuals within the forest fragments I studied would be highly related compared with individuals in different fragments isolated by an urban matrix, there would also be evidence of less-frequent high relatedness values between fragments, representing within-population long-distance seedling dispersal and recruitment. I also predicted that among fragments, I would observe a

source-sink relationship, where sinks would receive seeds from other fragments via long-distance dispersal.

4.2 Methods

4.2.1 Study system

The forest fragments I used were mixed broadleaf, semi-mature (80-130 years old) forest within an urban matrix in northern Auckland, Aotearoa-New Zealand (Figure 1), where only 13% of native forest from the original 93% pre-human New Zealand forest cover remains (Ewers et al., 2006). Native vegetation in the Auckland urban region has been substantially altered since 1840 (post-European settlement), and by 1985, 21% of native plant species recorded in 1871 were locally extinct (Duncan & Young, 2010). In the remaining forest, approximately 25% of native tree and shrub genera and c. 12% of their species produce fleshy fruits (Lord et al., 2002), such as puriri (*Vitex lucens*), or fleshy female cones, such as my study species, tōtara (*Podocarpus totara*). My study fragments included old-growth tōtara forests. Tōtara is one of the most important native coniferous trees (up to 30 m high; 2 m diameter at breast high [DBH]) of conservation interest and economic value in New Zealand (Bergin, 2000; Simpson, 2017). This species also has significant cultural value for Māori and is a taonga species (treasured entity) (Craig et al., 2012; Simpson, 2017). Extensive historical use of tōtara for timber has resulted in few remaining fragments of old-growth tōtara forests that have slowly started to recover after being legally protected by the New Zealand Government (Bergin, 2000; Farjon, 2013). Tōtara is a dioecious species and its seed ripens between March and May but can be found throughout the year (Bergin, 2000; Beveridge, 1964). This species is frequently visited by large native frugivorous birds like kererū (*Hemiphaga novaeseelandiae*) and tūī (*Prosthemadera novaeseelandiae*), but also by the small silvereye (*Zosterops lateralis*) as well as exotic bird species such as the European blackbird (*Turdus merula*) that act as legitimate dispersers of tōtara seeds (Beveridge, 1964; Dawson & Lucas, 2012; MacFarlane et al., 2015; Williams, 2006). As part of a larger study, I corroborated previous results of visitation surveys through analysing plant-bird disperser networks constructed using direct observations and analysis of faecal samples within this study system (Chapter 2 and 3). I did not record interactions with larger birds such as kererū (*H. novaeseelandiae*), but I cannot exclude

dispersal by those species. However, I can assume from these observations that most seed dispersal in the study system is almost exclusively carried out by tūī (*P. novaeseelandiae*) and silvereye (*Z. lateralis*).

4.2.2 Sampling

Surveying and mapping tōtara at fragments

I initially collected leaf tissue from 352 tōtara trees (122 females, 10 adults of unknown sex and 220 seedlings) within six fragments ranging in size from 4-2,000 ha (Table C1, Appendix C) from October 2016 to January 2017. The fragments were chosen to fulfil the following criteria: (*i*) similar native forest structure determined by the New Zealand Land Cover Database v.4.1 (Land Resource Information Systems); (*ii*) located on public land (for logistical reasons); and (*iii*) surrounded by an urban matrix. At three fragments (UNS, GIL, SAD), I surveyed and mapped all tōtara adult trees and seedlings. Due to logistical constraints, at the largest fragment (FER; 13.5 ha; Fig. 1) surveying and mapping was only conducted in the western portion of the fragment. During a pilot study, random surveying and mapping of a subsample of tōtara adults and seedlings was conducted in two other fragments in west and north Auckland, however, these samples were not further analysed due to financial constraints (for details see Table C1, Appendix C).

DNA sampling

Leaf tissue (ca. 10 cm end-branch) was collected from the canopy layer of those adult tōtara trees. Sexual maturity in tōtara is reached at about 20 years of age, when the trees reach a height between 6-8 m (Bergin, 2016). Therefore, I decided to use 5 m height as a threshold to differentiate adult trees from seedlings. All those trees higher than 5 m were considered as adults (potential parents) (Bergin, 2016). Where possible, I also collected leaf tissue from each seedling (< 5m height) in each of the four fragments (UNS, GIL, SAD and western portion of FER). In areas where more than five seedlings were close together (less than 1 m separation) I sampled tissue at random from one seedling in every three (*sensu* Hardesty et al., 2006). In addition, I collected tissue from all female trees within a 200 m urban buffer zone around each fragment. I used this buffer zone to increase the likelihood of determining the parentage of seedlings in each fragment that may have been derived from parents located outside the study

area (Hardesty et al., 2006). Secateurs were used to collect the sample and were cleaned using Trigene disinfectant after each use to prevent cross-contamination. Where possible, individuals were sexed as female by the presence of fruit (swollen, red receptacles) on the tree (using binoculars where necessary) or directly underneath the canopy. When an adult could not be sexed, it was considered as of 'unknown sex'. For those trees for which the canopy could not be reached, and fruit could not be seen with binoculars, professional tree climbers collected the samples.

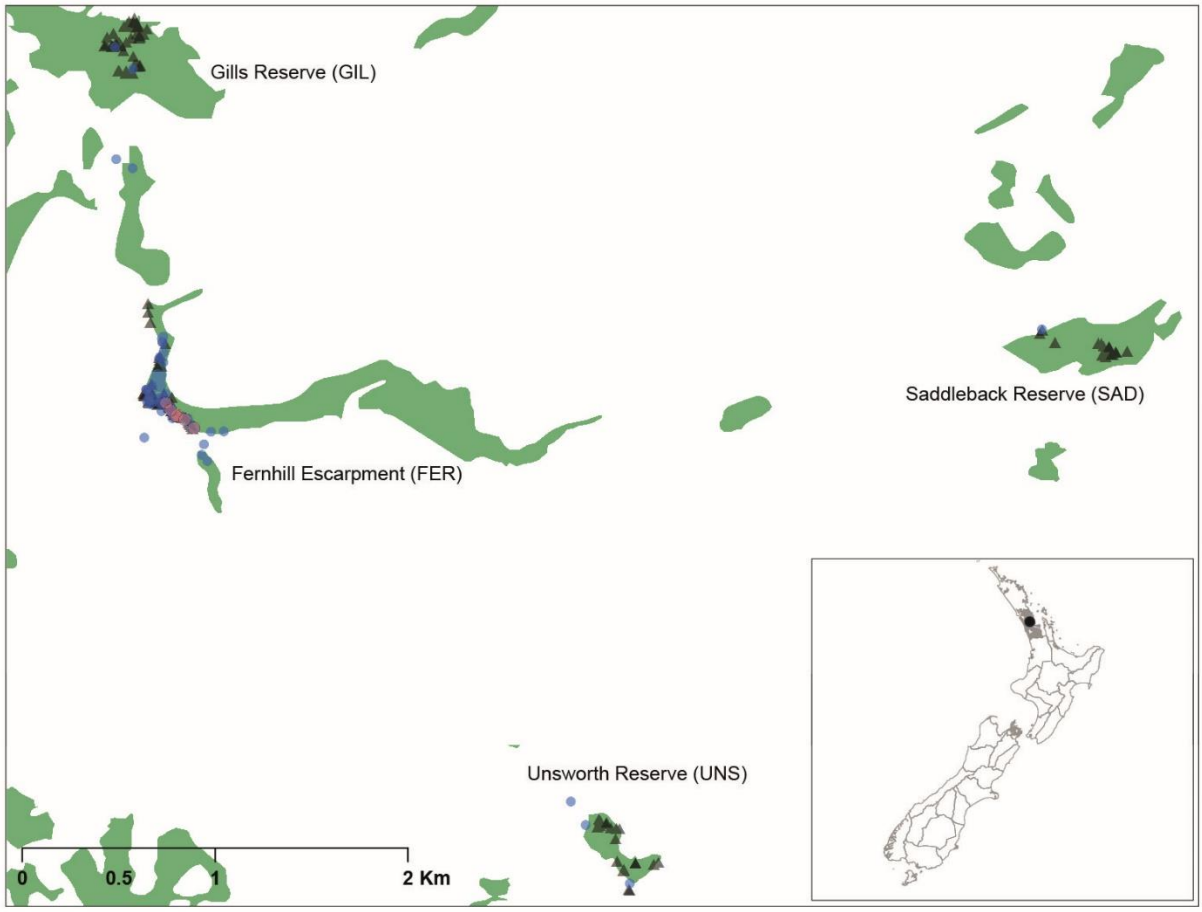


Figure 1. Spatial location of genotyped tōtara seedlings (triangles), female reproductive trees (blue circles), and genetically assigned mothers (pink circles). Areas dominated by indigenous forests are indicated in green. All tōtara present at GIL, UNS and SAD were sampled. Only tōtara present in the western portion of FER were sampled. Insert indicates sampling region within New Zealand. The distance between the four study sites ranged from 1,245 m to 4,238 m (median = 3,069 m).

In the field, I kept leaf tissue in individual sealed plastic bags to prevent DNA contamination, with a wet tissue inside to avoid moisture loss. After arrival at the laboratory, samples were frozen in liquid nitrogen and stored at -80˚C prior to DNA extraction. Due to financial constraints, 288 individuals from the four fragments (UNS, GIL, SAD and western portion of FER) and their buffer areas (Figure 1; Table C1, Appendix C) were used for the analysis, which included 107 reproductive females, 10 reproductive adults of unknown sex, and 171 seedlings.

For each individual, high molecular weight DNA was extracted from 100 mg of leaf tissue using a standard CTAB protocol (Doyle & Doyle, 1987). A genotyping by sequencing (GBS) approach was employed in order to reduce genome complexity prior to next generation sequencing (Elshire et al., 2011). The GBS library preparation protocol using an ApeK1 restriction enzyme digest was first optimised for the tōtara genome on a subset of individuals as described by Elshire et al. (2011). Following optimisation, GBS libraries were prepared for 286 individuals. The GBS libraries from 95 individuals were pooled to make the final three pooled libraries. The quantity and quality checks of the individual and pooled libraries were performed by a Qubit Fluorometer and a Fragment analyser, respectively. The three pooled libraries were dried down and sent to the commercial sequencing facility at the Australian Genome Research Facility (AGRF). The pooled libraries were sequenced on three lanes of an Illumina HiSeq2500 using single-end sequencing chemistry. The three sequencing lanes yielded a total of 795,672,214 reads, providing 2,762,750 reads per individual.

Following sequencing, the Stacks (Catchen et al., 2011, 2013) pipeline was used to demultiplex and assemble sequences, generate consensus loci and identify and genotype SNPs. Reads were first demultiplexed in stacks separately for each sequencing lane using the process_radtags command. Stacks was then used to filter the demultiplexed reads in two steps: first a sliding window approach was used to remove all reads where the average score within a sliding window of 10% of the read length fell below 15 (-q -w 0.1 -s 15), and secondly, reads with an uncalled base were also removed (-c option). Reads were further filtered using the kmer_filter program to remove reads that contained very rare (--rare) or very abundant (--abundant) kmers, indicating these reads are likely from repetitive regions of the genome or contain errors. Next, filtered reads were then assembled *de novo* and SNPs detected using Stacks. Loci were assembled per individual using the ustacks program, with the Deleveraging algorithm enabled

(-d) to help resolve over-merged tags. A catalogue of loci across individuals was assembled using cstacks, with two mismatches allowed when merging loci in the catalogue (-n 2), resulting in a total of 954,133 loci. Individual reads were matched back to this catalog using sstacks. The populations program was then used to create a plink-style output file of SNPs, with all individuals assigned to the same population, and SNPs filtered so that SNPs were present in at least 75% of individuals (-r 0.75), individuals had to have at least ten reads mapping to the locus (-m 10), and heterozygosity at the locus did not exceed 75% (--max_obs_het 0.75). A total of 686 SNPs were detected. SNPs were then filtered in plink (Purcell et al., 2007) to exclude all those with minor allele frequency <0.05, with 211 SNPs remaining after filtering.

4.2.3 Genetic analyses

Individuals with very low numbers of sequence reads after quality control were removed from the dataset (N = 15), leaving 273 individuals for analysis. All analyses included 211 loci. I calculated pairwise relatedness between every pair of individuals, as estimated by the triadic likelihood estimator (Wang, 2007), using the software COANCESTRY v.1.0.1.8 (Wang, 2011). I then used the software COLONY v2.0.6.4 (Jones & Wang, 2010; Wang, 2013; Wang & Santure, 2009) to identify putative first-degree relationships between 97 mothers, 8 unknown adults (assigned as fathers), and 168 seedlings. COLONY uses a full likelihood approach to determine whether the relationships between individuals are offspring-parent, full-sibling, half-sibling, or unrelated. It also assigns all those related individuals into clusters based on the genetic differentiation between individuals. Reproductive female individuals were assigned as putative mothers, reproductive individuals of unknown sex were assigned as putative fathers, and seedlings were assigned as putative offspring. I assumed a polygamous mating system for diploid organisms. The prior probability that the true parent was present in the sample was considered in the assignment of offspring-parent pairs, with the proportion of candidate fathers set to 0.2, and the proportion of candidate females set to 0.9. A weak prior of 1 was set for sibship size. Allelic frequencies were determined from the data set and it considered inbreeding. All results were based on three long runs with the combined full likelihood and pair likelihood score analysis method, with high precision to maximise the accuracy of assignments. This approach accounts for genotyping error at each locus of each sampled individual when estimating the likelihood of a particular family cluster, and with error rates of

1% per locus assumed in the analysis. I combined information from COLONY with the pairwise relatedness coefficients to determine the most likely relationships between individuals.

4.2.4 Landscape analyses

I calculated geographic distances (m) between every pair of individuals across all fragments using the "point distance" tool in ArcGIS 10.3.1 (ESRI, 2011).

4.2.5 Statistical analyses

What is the spatial pattern of genetic variation in tōtara?

To evaluate the relationship between geographic distance and genetic divergence, I used a Mantel test (Diniz-Filho et al., 2013; Mantel, 1967) calculated with the "mantel" function in the *vegan* package (Oksanen et al., 2017). I built matrices of genetic distances among all individuals as estimated by COANCESTRY, as well as geographic distance matrices among these individuals. I then correlated these two matrices. Values for the Mantel test close to 1 indicate that an increase in geographic distance between individuals is correlated with an increase in genetic distance between these individuals. Values close to -1 indicate the opposite pattern, and values close to zero indicate that there is no relationship between matrices (Diniz-Filho et al., 2013). I also calculated the mean pairwise relatedness from each tōtara individual to all other individuals from the same fragment to evaluate if there was higher relatedness of individuals within fragments than among fragments. All statistical analyses were conducted in R version 3.4.3 (R Development Core Team, 2017).

What is the frequency of long-distance tōtara seedling recruitment?

I analysed long-distance recruitment using two different approaches for data obtained from COLONY. First, I used the putative first-degree offspring-mother relationships to determine the distances of recruitment events. Only those dispersal events > 100m were included, because such distance necessarily involves vertebrate dispersers and represent long-distance recruitment (Cain et al., 2000). Second, I used the family cluster data to map all individuals belonging to a cluster and measured the geographic distance between individuals from those clusters to determine if any long-distance recruitment was observed.

4.3 Results

Average relatedness between tōtara individuals (N= 273) across the four forest fragments was 0.25, indicating an overall high level of relatedness. Relatedness values for individual pairs ranged from 0 to 0.88. Only 1,892 pairs (5% of all individual pairs) had relatedness values of 0.50 or more (Figure C1). The median of the geographic distance between all individual tree pairs was 1,720 m and the maximum distance was 4,948 m (Figure C2).

I found that only 12 offspring-mother relationships were supported by COLONY (Table 1), as obtained at the end of the computation ("best [ML] configuration" file). No offspring-father relationships were found. Results ("fullsib dyad and probability" file in COLONY) showed 498 full-sibling relationships (68% of all possible sibling relationships) with probabilities higher than 0.50 (Table C2, Appendix C). Additionally, the best configuration of related individual clusters that gave the maximum likelihood in COLONY consisted of 13 family clusters (Table C3, Appendix C). Given low support values on three clusters (probabilities less than 0.50), only 10 clusters, containing 65 offspring and four mothers, were used for analysis of long-distance seedling recruitment.

Table 1. Tōtara offspring-mother relationship with strong support from COLONY and COANCESTRY analysis.

Case	Offspring ID	Site	Mother ID	Site	Probability (COLONY)	Relatedness (COANCESTRY)	Dispersal distance (m)
1	TUM-19	UNS	TR-F34	FER	1	0.557	2,756.04
2	TUC-4	UNS	TR-F34	FER	1	0.541	2,744.56
3	TUC-3	UNS	TR-F34	FER	1	0.640	2,738.16
4	TGC-16	GIL	TR-F34	FER	1	0.580	1,810.70
5	TFM-21	FER	TR-F18	FER	0.508	0.574	403.87
6	TFM-13	FER	TMF-6	FER	0.964	0.562	305.18
7	TCF-29	FER	TR-F39	FER	0.997	0.631	143.51
8	TCF-14	FER	TR-F52	FER	0.853	0.522	116.92
9	TR-F44	FER	TR-F34	FER	1	0.486	85.32
10	TCF-23	FER	TMF-6	FER	1	0.495	70.64
11	TCF-22	FER	TFC-46	FER	1	0.558	37.37
12	TR-F61	FER	TR-F36	FER	0.948	0.653	8.55

Long-distance (> 100 m) recruitments are highlighted in grey.

4.3.1 What is the spatial pattern of genetic variation in tōtara?

I found a non-significant association between genetic distance and geographic distance (Mantel correlation = -0.19; *P* = >0.05; Figure 2) indicating high connectivity across the landscape between forest fragments. When I analysed the mean pairwise relatedness of each tōtara individual to all other individuals in the same fragment, I found that, on average, only tōtara individuals within FER were highly related, whereas individuals in the rest of the fragments showed low relatedness to others in the same fragment (Figure 3).

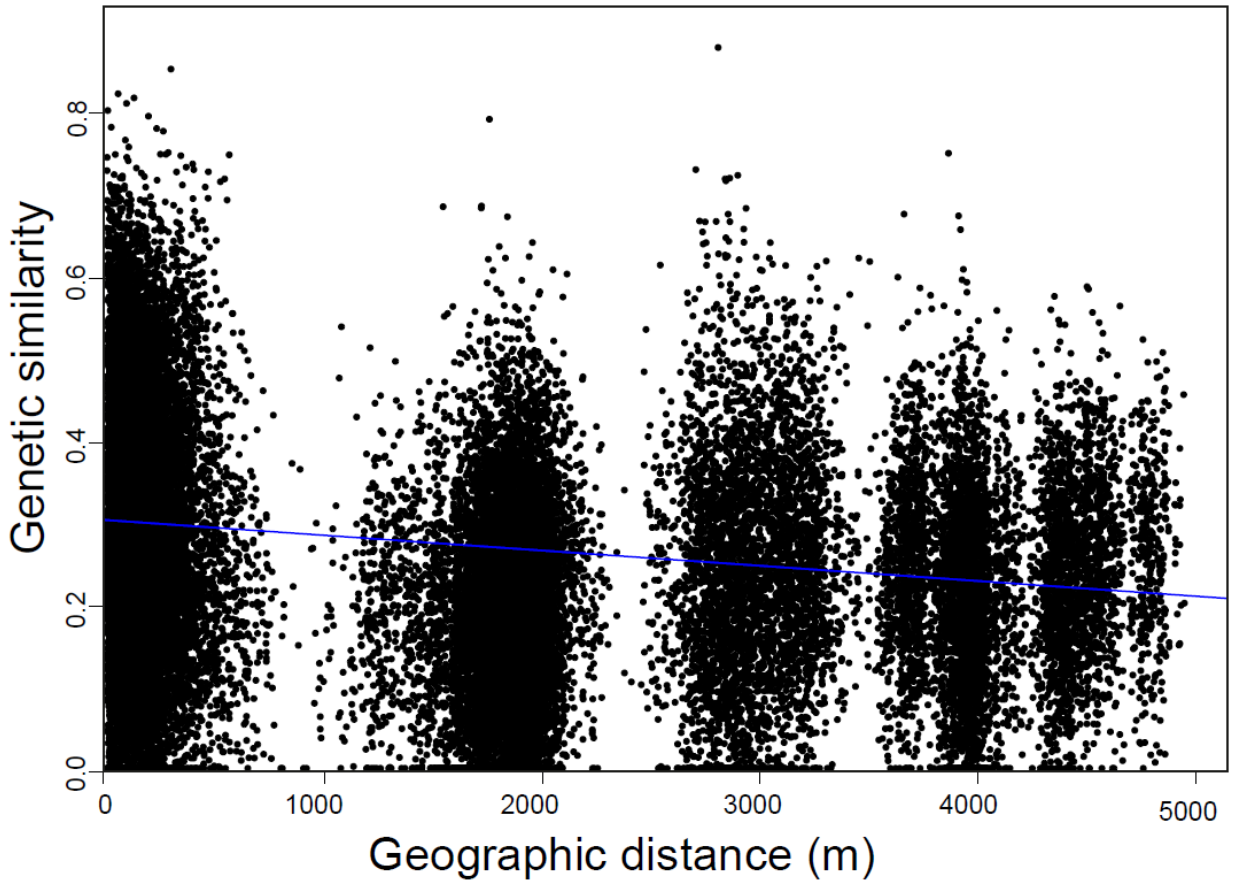


Figure 2. Relationship between pairwise genetic distances and geographic distances (*r* = -0.19, *P* = >0.05) for all sampled tōtara individuals at four forest fragments in Auckland.

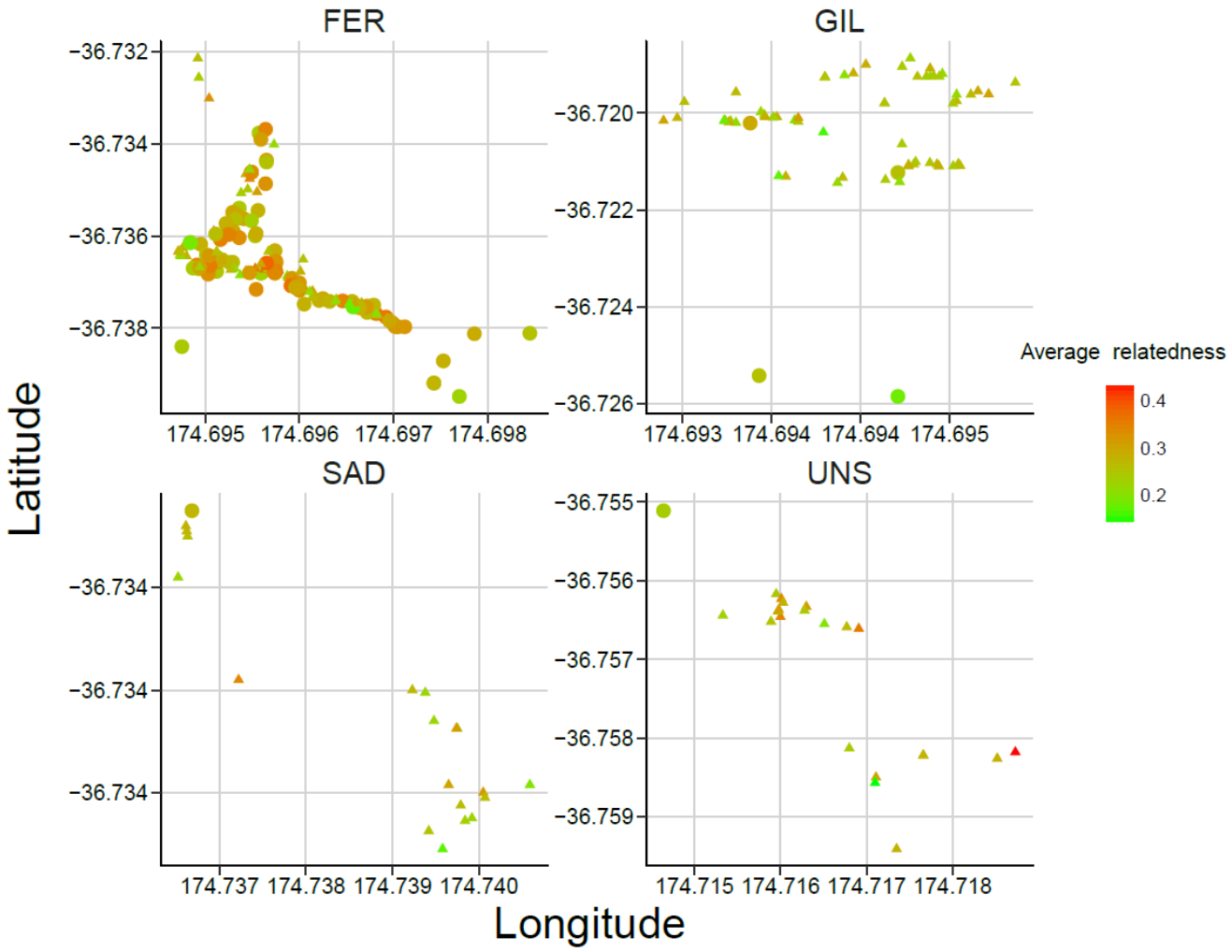


Figure 3. Mean pairwise relatedness of each tōtara individual to all other individuals in each fragment. Red points indicate those individuals that are on average highly related (> 0.3) to others within the same fragment, while green points indicate individuals that are less related (<0.2). Circles indicate female reproductive trees and triangles indicate seedlings.

4.3.2 What is the frequency of long-distance tōtara seedling recruitment?

Of the total 12 offspring-mother relationships, I found evidence of eight long-distance (> 100 m) seedling recruitment events (Table 1), with a median of recruitment distance of 403 m. In all eight cases of long-distance dispersal, the tōtara mother samples were all collected within the same fragment (FER). In four cases (cases 1-4), offspring were collected from fragments (UNS And GIL) other than FER, while in the remaining four cases, long-distance dispersal

occurred within the FER fragment, suggesting that all individual seedlings sampled in this study originated from within this fragment.

Likewise, I found evidence of long-distance seedling recruitment in six tōtara family clusters (Figures 4 and 5). For these clusters, the median of pairwise geographic distances was 4,052 m (cluster 4); 2,760 m (cluster 5); 143.51 m (cluster 7); 2,741 m (cluster 8); 1,730 m (cluster 9) and 1,956 m (cluster 10). For all clusters except one (cluster 3), I found that individuals occurred in multiple fragments. For detailed pairwise distances among individual of each family cluster refer to Table C4, Appendix C.

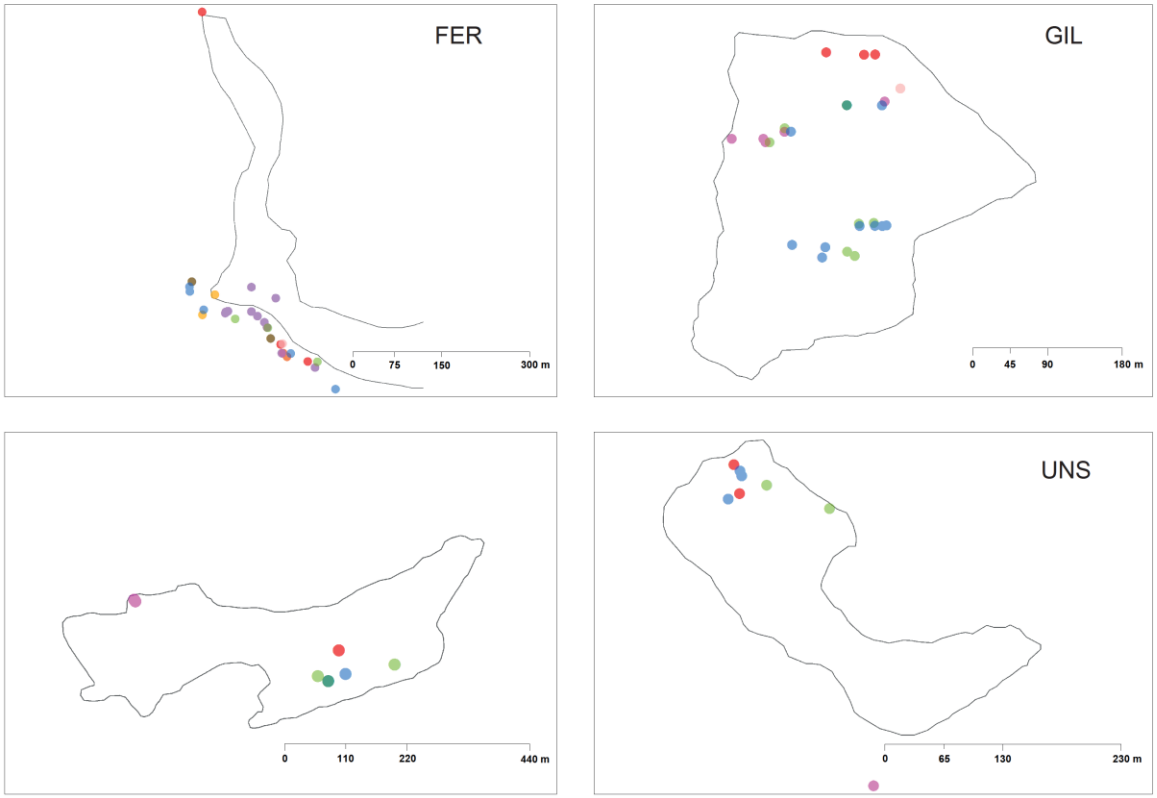


Figure 4. Spatial location of tōtara family clusters used for analyses. Individuals of the same coloured circle belong to the same cluster.

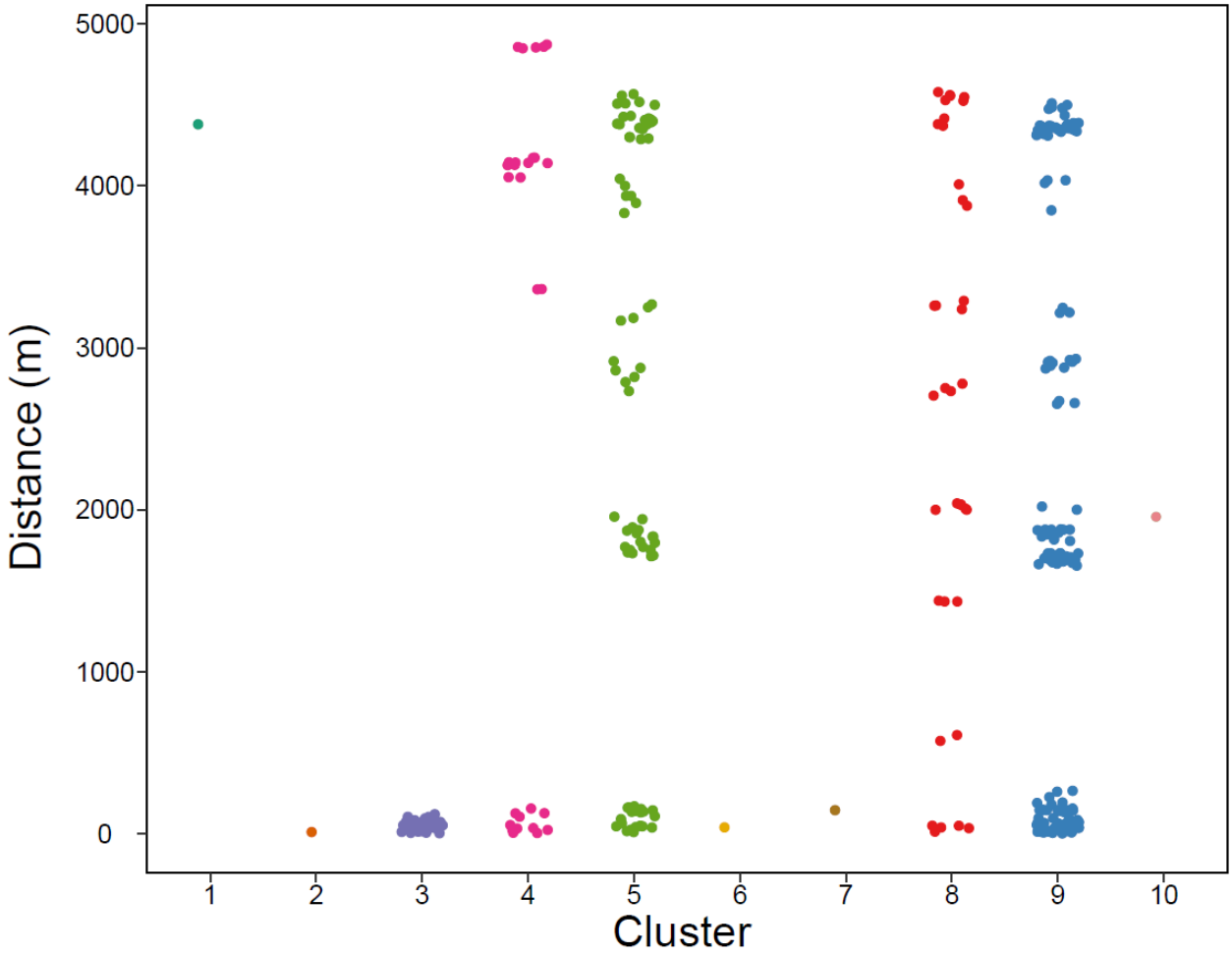


Figure 5. Geographic distance between tōtara individuals from each family cluster.

4.4 Discussion

I investigated long-distance seed dispersal and recruitment of tōtara across a fragmented landscape, through the spatial analysis of genetic variation. Seed dispersal impacts the maintenance of genetic diversity among plant populations (Hardesty et al., 2006), but has a larger impact at the local scale by creating fine-scale genetic structure (Rico & Wagner, 2016). I found no association between genetic and geographic structure in tōtara across the four tōtara populations studied, demonstrating high connectivity across the landscape. This level of connectivity is likely to vary temporally, but it is clear that ongoing gene migration connects the tōtara populations I studied. Another important consideration is that the sampled tōtara populations once belonged to a continuous native forest (before human occupation) in Auckland (Ewers et al., 2006), likely with extensive gene flow within the population.

Therefore, remaining tōtara individuals would share similar genetic structure, revealed in this study as a single genetic population with no pattern of increasing genetic diversity with increased distance.

Analysis of individual relatedness within fragments revealed that, in accordance with my predictions, the average genetic relatedness of tōtara within fragments was higher than among fragments. However, this pattern was driven by the high relatedness values within the FER fragment, with other fragments having relatively low average relatedness between individuals. This pattern can be an indication that tōtara subpopulations belong to a larger population, as discussed above, with the urban matrix not necessarily acting as a dispersal barrier. Further, dispersal from other fragments not sampled or individual adult tōtara within the urban matrix could explain those cases of low relatedness of individuals. In a similar study using parentage analysis, Ismail et al. (2017) also detected long-distance recruitment events in a fragmented landscape. However, the distance between fragments in their landscape was so large that the dispersal distances of up to 200 m were still not enough to connect the fragmented plant populations (Ismail et al., 2017).

There has been an increasing concern that indirect measures of gene flow (as given by relatedness values) reflect historical connectivity and are unlikely to capture contemporary landscape changes (Auffret et al., 2017; Epps & Keyghobadi, 2015; Holderegger et al., 2010). Thus, direct approaches such as parentage analyses reveal how gene flow is related to the current landscape (Auffret et al., 2017; Jones et al., 2010). Using this genetic technique, I found evidence of contemporary long-distance tōtara recruitment. From the pool of 273 individuals sampled across fragments, I was able to assign only 12 seedlings in my study to their maternal parent. From these assignments, eight were cases of long-distance (>100 m) recruitment. The 93% (N = 155) of unassigned seedlings could have had mothers outside of the study fragments or there could have been some sort of genotyping error (see below). However, I have enough evidence to confirm that effective seed dispersal of tōtara is occurring across the fragmented urban landscape I studied. Moreover, I have provided compelling evidence that long-distance recruitment of tōtara is not a rare event; also supported by the high proportion of full-sibling relationships across fragments found in this study. My findings are consistent with prior evidence on vertebrate-dispersed species suggesting that long-distance movements account for

a significant number of dispersal events, particularly when large-bodied frugivores act as seed dispersers in fragmented landscapes (García et al., 2007; González-Varo et al., 2017; Ismail et al., 2017). This is given by the positive relationship between avian frugivore body mass and estimated seed dispersal distance (Wotton & Kelly, 2012). In a previous study (Chapter 2) I found that most fruit consumption interactions with tōtara occurred with tūī (*P. novaeseelandiae*) and silvereye (*Z. lateralis*). These species are common, mobile and habitat generalists, which may explain why I found high genetic relatedness between fragments. Although it has been demonstrated that silvereye (*Z. lateralis*) have the potential of flying up to 12 km given their flight velocity and mean gut passage time (Stansbury, 2001), it is also true that seed dispersal is primarily determined by frugivore home ranges and seed gut passage rates are of minor importance (Santamaría et al., 2007). Therefore, it is likely that most short-distance recruitment events can be attributed to silvereye (*Z. lateralis*) and long-distance recruitment events to tūī (*P. novaeseelandiae*), indicating that tūī (*P. novaeseelandiae*) are playing a major role dispersing seeds between fragments. This is because silvereye (*Z. lateralis*) are small and primarily disperse seeds over short distances, whereas tūī (*P. novaeseelandiae*) are larger and have been recorded frequently dispersing seeds over long distances (up to 35 km in a day) farther from the source trees (van Heezik et al., 2008; Wotton & McAlpine, 2015). The detection of long-distance recruitment events are clear evidence of landscape connectivity, at least at the scale of this study. It has been demonstrated that stepping-stones in urbanised landscapes (e.g. living fences, planted trees present in parks and gardens, and shrub cover) are important for providing connectivity and enhancing bird movement (Beninde et al., 2015; Rudd et al., 2002; Sekercioglu et al., 2007). Although I did not measure stepping-stones in the urban matrix surrounding the study fragments, it is likely that their presence is allowing birds to move through the urban matrix, without this matrix representing a barrier, as discussed above. Another important aspect to note is that tōtara is a light-demanding coloniser with a remarkable capacity to regenerate on disturbed sites, provided there is a nearby seed source and birds to disperse their seeds (Wilcox, 2012). Although I have demonstrated that tōtara can be effectively dispersed in a fragmented urban landscapes, there are other variables, such as soil conditions and nutrients, that are also likely to influence tōtara colonisation of specific fragments.

COLONY assigned some tōtara individuals into family clusters, and apart from one of these clusters, I found that individuals from the same clusters occurred in multiple fragments. These results, along with the evidence of long-distance recruitment and relatedness within fragments, indicate inter-fragment dispersal. In this sense, it is possible that this process could be enhanced by habitat fragmentation. Birds feeding in small fragments are likely to be regularly moving between fragments in the landscape, regardless of the type of habitat matrix surrounding them, as food resources at any one site become scarce (Bacles et al., 2004; Uriarte et al., 2011). Further, I can corroborate that habitat fragmentation has not isolated tōtara individuals in a highly urbanised landscape. Females located in FER (92%) produced all of the long-distance recruitment events, resembling a source-sink recruitment pattern (Pulliam, 1988), where FER is acting as a source and the rest of the fragments are sinks. This pattern had been previously observed by Aldrich & Hamrick (1998) in fragmented landscapes, where adult trees of *Symphonia globulifera* (bat-dispersed) in pasture produced most of the seedlings in a remnant forest. They also concluded that the removal of the source by intensified land-use, was likely to yield demographic failure. My results suggest that the maintenance of effective seed dispersal for tōtara will depend on the conservation of both source and sink tōtara populations and the fragments in which they are found, but also on the conservation of their main bird dispersers. Of particular importance is that one fragment (FER) was the source of all long-distance recruitment events, and should therefore be prioritised for biodiversity management.

Although I have demonstrated long-distance tōtara recruitment and gene flow across a fragmented landscape, some caveats around genotyping should be considered. First, my estimates of recruitment are conservative owing to the potential false assignment in the parentage results given that the species might have quite high inbreeding. However, I would not expect any kind of bias in the assignment for offspring near or far from the parent tree. Further, if this bias was present and prevalent, I would have expected very high assignment rates of offspring to mothers, which did not occur. Given that some of the offspring were assigned mothers in different fragments, it is very unlikely that all of these offspring have been falsely assigned, particularly because such a small number were assigned a parent at all. Thus, I can be confident in the main finding of this chapter that long-distance recruitment of tōtara is not rare.

The second caveat of my analysis is that SNP filtering to ensure SNP presence in at least 75% of individuals resulted in only 211 SNPs. Although I do not have an estimate of the genome size, the small number of SNPs detected suggests that the genome is large (likely as a result of genome duplications, as is common in plants) and that the sequencing depth per individual may not have been high enough to capture the genome-wide diversity using a GBS approach. However, while some of my estimates of relatedness may become more precise with more markers, there is no bias in the missing data, so I have not systematically under or overestimated the relatedness values between pairs of tōtara individuals for particular fragments or between particular fragments. Therefore, more data would be unlikely to change my results, although it might just help refine the exact relatedness values further (i.e. reduce variation).

4.5 Conclusion

Long-distance recruitment events for tōtara in a fragmented landscape are not rare and seeds are being dispersed among fragments. Disruption of seed dispersal in fragmented landscapes has been found to be a major constraint for maintaining viable plant populations (Christmas et al., 2016). However, I have demonstrated that tōtara is highly connected across a fragmented landscape in an urban environment, with effective seed dispersal functioning between fragments. My results highlight the importance of birds as mobile links shaping the spatial and genetic structure of plant populations in fragmented landscapes and indicate that an urban matrix does not always create barriers for dispersal. It is critical for land managers to recognise the functional importance of even small forest fragments in urban landscapes, and in particular, to identify and protect fragments that act as sources and sinks for tōtara seed dispersal, promoting seedling recruitment. Coupling ongoing demographic surveys with improved parentage analyses techniques will enable us to determine the extent to which habitat fragmentation alters plant-frugivore interactions and modifies plant recruitment in highly-modified landscapes.

Chapter 5 - General Discussion

5.1 Key findings

The study of plant-animal mutualistic interactions is crucial to understanding the ecological processes that drive ecosystem functions. However, few studies have attempted to link network structure with associated ecosystem functions and then combine this with evidence of successful seed dispersal (i.e., seedling recruitment) (Ings et al., 2009; Simmons et al., 2018). In this thesis, I focused on plant-frugivore interactions and the consequences of habitat fragmentation on frugivory and seedling recruitment. I also investigated how different methods of sampling plant-frugivore interactions produce biases in the interpretation of network structure. Here, I demonstrated that urbanisation had an overall negative effect on fruit consumption, which was mediated by changes to plant-frugivore network structure (Figure 5.1). I focused on fruit consumption, the quantitative component of seed dispersal, which drives post-seed dispersal processes, such as seedling establishment. Importantly, I found that plant species had fewer frugivore partners in habitat fragments surrounded by high urbanisation. Furthermore, fruit consumption was greater for plant species that had high complementarity in frugivore partner use (Chapter 2).

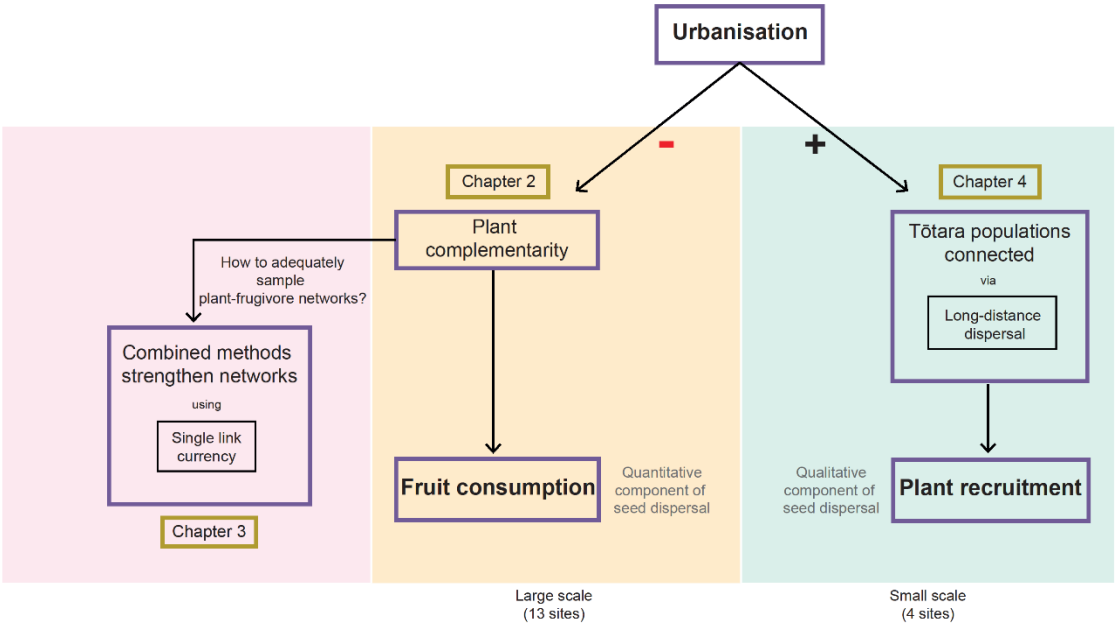


Figure 5.1 Summary diagram of my key findings from each data chapter.

My findings in Chapter 2 were based on plant-frugivore interactions, which I recorded using direct observations of birds consuming fruit. For the purposes of my study, using a combination of methods (focal sampling and mist-netting) to sample plant-frugivore interactions across the 13 study sites (Chapter 2) was both financially and logistically unattainable. However, this chapter raised the question of whether using one method to sample plant-frugivore interactions biases results towards certain set of interactions. Accordingly, I then investigated whether different sampling methods generate plant-frugivore networks with different structures. Indeed, I demonstrated that different network sampling methods produced plant-frugivore networks with different structures (Chapter 3), and that combining data from both methods provides a more comprehensive representation of network structure (Figure 5.1). In this chapter, I developed an approach for combining weighted plant-frugivore network data, which uses the number of seeds consumed as the standardised single link currency, thus measuring the true dispersal mutualism through seed consumption. This is an important contribution to the field and will progress future research on plant-frugivore networks.

The ultimate outcome of interactions between plants and frugivores is seedling establishment. Thus, in my final data chapter (Chapter 4), I provide evidence of long-distance seedling recruitment, using tōtara (*Podocarpus totara*) as a model species (Figure 5.1). Specifically, I found that higher genetic relatedness within habitat fragments, which resembled a source-sink pattern of parental trees and offspring. However, I also found relatively high relatedness among individuals located in different fragments, which suggests that urbanisation does not necessarily impede bird movement and consequently, seed dispersal.

5.2 Effects of the urban matrix on fruit consumption and seedling recruitment

5.2.1 Spatial scale

Species distribution patterns and interactions between species can vary with the spatial scale of observation and thus, different principles might apply at different spatial scales (Chase & Leibold, 2002; Levin, 1992). Other important factors to consider within spatial scales include how populations and habitats are defined and what ecosystem functions are measured (Leibold

et al., 2004; Tilman, 1994). Here, I regarded each forest fragment as a discrete area of habitat, containing both plant and frugivore populations. Given contemporary landscape changes, due to anthropogenic modification of natural habitat and environmental change, local populations do not always have discrete boundaries and different species may respond to disturbances at different spatial scales (Leibold et al., 2004). Thus, I used different scales (Figure 5.2) to assess two different aspects of seed dispersal: fruit consumption (Chapter 2) and seedling recruitment (Chapter 4).

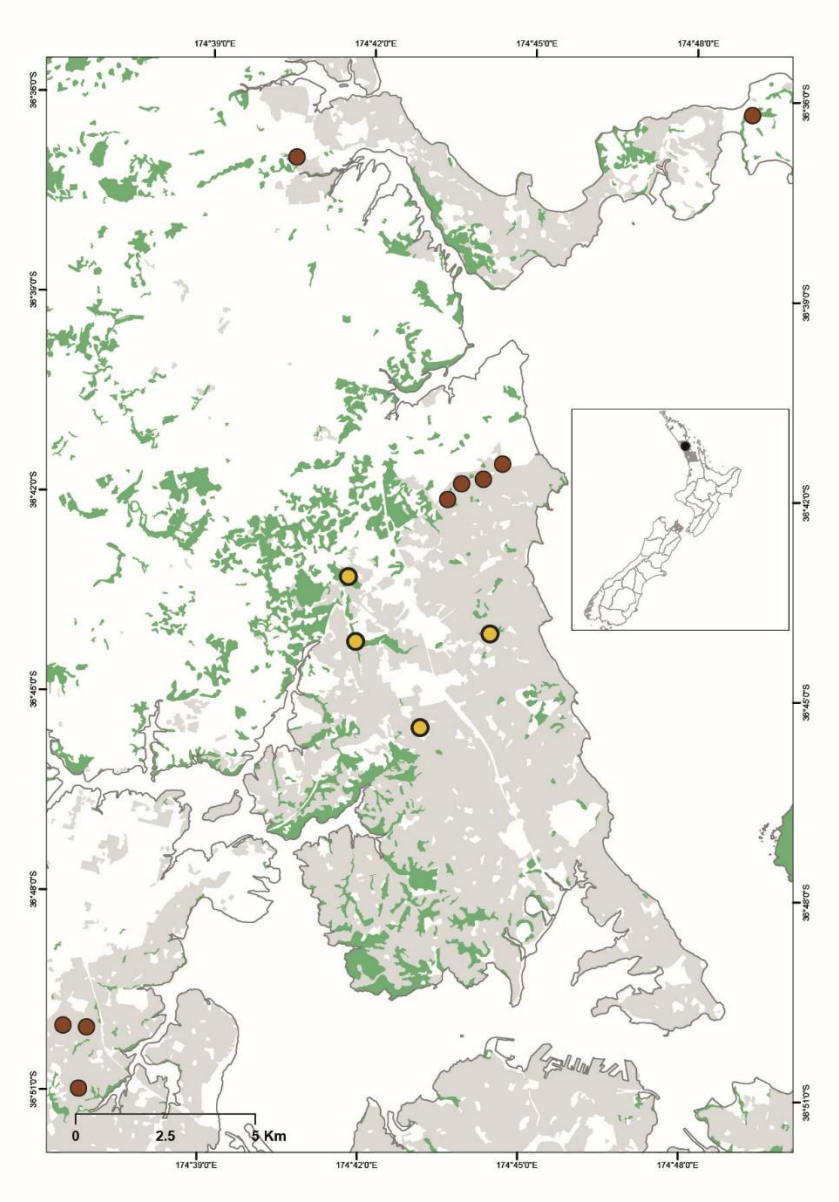


Figure 5.2 Scale of the study area in my thesis. Circles are the 13 study sites used for Chapter 2; yellow circles are those sites used for Chapter 4. Areas dominated by buildings are indicated in grey and indigenous forests are in green.

In Chapter 2, I used data collected from 13 sites across northern Auckland (median distance among fragments = 12,609 m) and found that urbanisation negatively affected fruit consumption via changes in plant-frugivore networks, potentially because highly urbanised areas were acting as barriers to frugivore movement, therefore impeding some interactions (Carbó-Ramírez & Zuria, 2011; Ikin et al., 2013). However, in Chapter 4, I found evidence of high genetic relatedness in tōtara populations across fragments, suggesting that urbanisation is not necessarily hindering frugivore movement and dispersal of tōtara seeds. However, this could also be an artefact of the relatively smaller scale of this experiment (four fragments, median of distance among fragments = 3,069 m), or because there are sufficient stepping-stones for frugivore movement within this landscape. Additionally, in Chapter 2, I found that tūī and silvereye were the main dispersers of tōtara seeds. These species are common, mobile and habitat generalists, which may explain why I found high genetic relatedness between fragments.

Auckland's northern suburbs, where I sampled tōtara adults and seedlings, are richly endowed with native forest fragments, and the restoration and maintenance of stepping-stones connecting fragments has been a management focus of these forest areas (Wilcox, 2012). Although, on average, fragments in which I sampled tōtara (Chapter 4) are surrounded by high levels of urbanisation (73%), the residential areas where these fragments are located are 'leafier' and it is likely that residential gardens are facilitating frugivore movement (acting as stepping-stones) and thus, dispersal of tōtara seeds between fragments. In contrast, where I sampled plant-frugivore interactions at a larger scale (Chapter 2), fragments were surrounded by less urbanisation on average (mean = 52%), yet urbanisation still had a negative effect on fruit consumption. This may indicate that as spatial scale increases, spatial variation in resource supply rates decreases (i.e., the availability of stepping-stones and food resources becomes scarce and dispersing through the matrix becomes harder for frugivores with increasing spatial scale) (Shurin et al., 2004). However, frugivores that use sparsely distributed or clumped resources are likely to forage over larger spatial scales, compared with species using abundant resources, particularly if those resources are critical rather than substitutable (O'Neill et al., 1988). Therefore, different movement patterns and resource use by frugivore species will determine their contribution to fruit consumption, seed dispersal and ultimately, seedling recruitment in urbanised landscapes. Moving forward, investigating species-specific foraging

behaviour will give a more mechanistic understanding of seed dispersal patterns across landscapes.

5.2.2 Source-sink relationships in plant populations

The source-sink pattern that I detected in tōtara populations (Chapter 4) indicates that different populations are subject to different abiotic conditions (e.g., suitable soil, nutrient availability). However, these populations are sufficiently connected so that dispersal results in a source-sink pattern (Leibold et al., 2004; Mouquet & Loreau, 2003). Nevertheless, seedling recruitment studies should carefully consider spatial scale, because recruitment distances at large scales may be insufficient to effectively connect plant populations in different fragments (Ismail et al., 2017).

While the focus of Chapter 4 was on the recruitment and genetic connectivity of tōtara, it is unclear how generalizable these results are to other plant species. Moreover, rapid adaptation of tōtara to changing environmental conditions may have allowed this species to flourish in urbanised landscapes, which might not be the case for plant species that are less adaptable to anthropogenic disturbances (Simpson, 2017). Importantly, in my study, the source fragment for tōtara contained most tōtara adults across all fragments, but few seedlings. This could indicate that soil conditions may have been altered due to anthropogenic disturbances after the now mature trees established, thus inhibiting establishment of new seedlings. Furthermore, factors other than abiotic soil conditions and competition with adults can determine seedling success (e.g., seed predation and seedling herbivory) (Crawley, 1985; Wenny, 2001). For example, in most plant species, fitness declines consistently as herbivory increases (Lee et al., 2010). Therefore, browsing by invasive mammal herbivores, such as the Australian brushtail possum (*Trichosurus vulpecula*), poses a major threat to many New Zealand native trees (Lee et al., 2010). Further studies on long-distance seedling recruitment in other native New Zealand plants are required to assess genetic connectivity across fragments. We also need to investigate the interaction between long-distance seed dispersal and the effects of soil and herbivory by introduced mammals on seedling recruitment. Thus, I suggest targeting plant species that are likely to be dispersal-limited (e.g., tawa, *Beilschmiedia tawa*), due to the decline and loss of key seed dispersers.

5.3 Sampling effects on interpretation of network structure

I found that plant species received higher fruit consumption when they were visited by frugivore species that were different from those used by other plant species in the community. From a seed dispersal perspective, fruit consumption by a wide variety of frugivores that have a range of behaviours, would mean that seeds could reach a wider variety of microhabitats (Bueno et al., 2013; Russo & Augspurger, 2004). However, it is important to consider that my findings were based on plant-frugivore interactions sampled using the traditional method of focal observations of birds feeding on fruit (Chapter 2). An accurate estimation of network structure is crucial to understanding within and between system network variation and the associated ecological implications (Henriksen et al., 2018). The use of one sampling method in isolation may produce data that does not comprehensively explain network responses to disturbances, such as urbanisation. These biases could influence decisions about what plant-frugivore interactions are important to conserve for maintaining ecosystem functioning. However, in Chapter 3, I found that the number of frugivore species consuming fruit from each plant species (which was also one of my main predictor variables in Chapter 2) did not differ between networks generated from mist-netting and focal observations. This suggests that although I used focal observations to sample plant-frugivore interactions in Chapter 2, my key finding (that urbanisation negatively affects fruit consumption by altering frugivore richness and complementarity) is likely to have been similar if I had used a combination of sampling methods.

The influence of sampling effects has been previously demonstrated for plant-pollinator networks (Bosch et al., 2009). Specifically, pollinator surveys that were conducted on focal plants provided insufficient information on flower visitation, especially for rare pollinator species. As a result, network data generated from floral visitation surveys often contains many pollinators interacting with single plant species (extreme specialists), which contrasts to the widely accepted view that plant-pollinator networks typically comprise many generalists species (Bosch et al., 2009; Vázquez & Aizen, 2004). The addition of pollen data from pollinators collected during surveys on focal plants can reveal many new interactions and this results in important networks structural changes (i.e., increased nestedness and modularity) (Bosch et al., 2009). However, most of what we currently know about plant-frugivore networks

globally comes from networks generated from studies that use only one method for sampling interactions (Schleuning et al., 2012). Such networks tend to be highly asymmetric, indicating high robustness against random species extinctions (Bascompte & Jordano, 2007; Schleuning et al., 2014a). Thus, interpretation of global plant-frugivore network structure could be biased by the choice of method. In Chapter 3, I show that networks generated from focal sampling were highly symmetric, likely due to my species-poor system, and thus these networks would be interpreted as being more vulnerable to disturbances.

One key challenge of combining different sampling methods is finding a common link currency that captures the true seed dispersal mutualism (Simmons et al., 2018). In my study, I used the number of seeds consumed from each plant species by different bird species as the standard link currency (Chapter 3). Using the number of seeds consumed is a functionally meaningful measure of the plant-frugivore mutualism, particularly from the plant's perspective. Thus, it allows researchers to combine the two methods in a functionally meaningful way.

5.4 Restoring and conserving plant-frugivore interactions

To date, most generalisations about traits that drive species' responses to urbanisation are based on studies that investigate the change in abundance of just a few species (Brown & Graham, 2015). Thus, there is a real need to move beyond the single-species conservation and/or trait approach to an approach focused on the conservation of communities and associated functions across landscapes (Tylianakis et al., 2010). This would be best achieved by conserving forest fragments (native habitat fragments) that are critical for the survival of species, interactions between species, and ultimately ecosystem functions (i.e., fruit consumption and seedling recruitment) (Valiente-Banuet et al., 2015). Thus, I encourage researchers and land managers to identify species that are important in plant-frugivore networks (i.e., frugivores that frequently consume and disperse seeds of different plant species across the urban matrix), to prioritise the conservation of ecosystem functions, rather than simply aiming to protect individual species. Conservation programs that target key plant-frugivore interactions, or frugivore species whose roles in networks are disproportionately important, will help to preserve ecosystem functions across landscapes. Further, using a habitat-species network approach (species as the upper trophic level and sites as the lower trophic level; Marini et al.,

2018) for applied decision-making could be a powerful tool for prioritising the conservation of forest fragments, species and their interactions.

5.4.1 Increasing native vegetation cover in urban areas

Vegetation restoration is commonly undertaken to reverse the impacts of habitat loss and/or habitat degradation (McCann, 2007). In plant-pollinator networks, habitat restoration (through removal of exotic shrubs) not only increased pollinator species richness but also native plant fruit production (Kaiser-Bunbury et al., 2017). Furthermore, another study on seed dispersal showed that habitat restoration increased network complexity over time (Ribeiro da Silva et al., 2015).

The dependence of many forest plant species on frugivores for seed dispersal has prompted suggestions that planting fleshy-fruited species in restoration projects may enhance attractiveness of the restored sites and thus, facilitate further colonisation and establishment of plants through increased seed dispersal (Norton, 1991). Increasing native vegetation cover in the urban matrix, specifically planting native fleshy-fruited species in both private gardens and parks, is likely to restore or enhance seed dispersal function. Plants' frugivore partners and complementarity in frugivore partner use would be likely to increase, thereby increasing fruit consumption. The creation of stepping-stones or corridors via connected residential gardens may also facilitate frugivore movement across the wider landscape, allowing these species to better access patchy resources (Graham, 2001). Aside from providing important fruit food resources, restored vegetation can provide nest sites and other food resources, such as nectar, to frugivores (Reay & Norton, 1999).

One advantage of urban landscapes is that they often have high resource heterogeneity, especially compared with agricultural areas where resources are much more homogenous (Dunford & Freemark, 2005). Habitat heterogeneity often facilitates greater community stability and niche availability (Shurin et al., 2004; Tylianakis, 2008). Increasing resource heterogeneity through increased vegetation cover in urban areas would be beneficial for frugivores, their interactions with plants and the functions associated with these mutualisms.

5.4.2 Increasing predator control in urban areas

In addition to increasing native vegetation cover in urban areas, I suggest focussing on other aspects of urbanisation that may alter plant-frugivore networks. Predation on bird frugivores by introduced mammals could be an important driver of changes to plant-frugivore networks in urban landscapes. Indeed, it has been demonstrated that predator control leads to an increase in the abundance of some frugivore species (Ruffell & Didham, 2017). For example, 17 years after eradication of invasive mammals in Zealandia, a predator free sanctuary in the North Island of New Zealand, tūī abundance increased dramatically. Yet, silvereye, a recent colonist in New Zealand, have not benefited from the eradication of introduced mammals (Miskelly, 2018). In fact, silvereye numbers have progressively declined in Zealandia, potentially due to competition with endemic bird species (Innes et al., 2010). I found that silvereye accounted for 49% of all fruit consumption across my study sites (Chapter 2), so increased mammal predator control could have implications for seed dispersal in urban forest fragments if it causes silvereye numbers to decline. Thus, I suggest rigorous monitoring of plant-frugivore interactions before, during and after predator control to assess whether increases in endemic bird species' abundances compensate for potential reduced fruit consumption by silvereye.

Although urban green spaces are sometimes viewed as a panacea for biodiversity conservation and management, urban areas can threaten native biodiversity (Goddard et al., 2010). For example, urbanisation can accelerate the transmission of wildlife diseases, and gardens are often home to the domestic cat (*Felis catus*), which is a major predator of many native frugivores (Bradley & Altizer, 2007; Galbraith et al., 2017; Goddard et al., 2010). In New Zealand, domestic cats prey on a variety of native bird species, which have not evolved defences against mammal predators (Medina et al., 2011). Research on how domestic cat predation in New Zealand affects frugivorous birds and consequently, seed dispersal, is required to inform management and minimise impact (van Heezik et al., 2010; Wood et al., 2016).

5.5 Future directions

5.5.1 Integrating ecological and evolutionary mechanisms that determine plant-frugivore interactions

Trait-based approaches are widely used in ecology, because traits are often more strongly associated with ecosystem functions, compared to conventional biodiversity measures, such as species richness (Gagic et al., 2015). In plant-frugivore assemblages, different frugivore species are likely to disperse seeds at different distances within the urban matrix (Wotton & Kelly, 2012). The morphological match between fleshy-fruits and frugivores is a generalised and well-studied driver of plant-frugivore interactions (González-Castro et al., 2015; Jordano et al., 2003; Wotton & Kelly, 2012). Behavioural traits, such as frugivore fruit preference and foraging patterns, may also play a key role in determining interaction occurrence and frequency (Burns, 2013; García et al., 2014), along with species-specific responses to anthropogenic disturbances (McConkey et al., 2012). Further, filtering traits (traits that determine the probability of concurrence, such as migration), along with morphological matching and behavioural traits, are likely determined by species phylogenies (García, 2016). Thus, we need to develop a framework that integrates the ecological and evolutionary mechanisms that determine the occurrence of plant-frugivore interactions and how this may be eroded by urbanisation (Aizen et al., 2016; Bartomeus et al., 2016).

5.5.2 Evaluating the role of invasive plant species in plant-frugivore networks

Seed dispersal is not only important for the regeneration of native plant communities but it can also facilitate the spread of invasive plant species, therefore disrupting ecosystem functioning (García et al., 2014; Traveset & Richardson, 2014). Most of what we currently know in New Zealand about the role of introduced species in plant-frugivore networks comes from studies that have focused on the role of introduced frugivores, rather than the role of introduced plants (Burns, 2012; García et al., 2014; MacFarlane et al., 2015; Williams, 2006). I suggest continuing to expand the quantification of seed dispersal function in naturally occurring plant-frugivore assemblages, where both native and introduced plant species are dispersed, to assess how network structure is altered by the presence of introduced plant species.

5.6 Conclusion

My study has demonstrated that at the community level, urbanisation negatively affects fruit consumption by frugivores, which is mediated by changes in plant-frugivore network structure. However, beyond fruit consumption and seed dispersal, we must also consider plant recruitment to close the seed dispersal loop, which is required for long-term plant population regeneration, particularly in fragmented landscapes. Thus, I present evidence of long-distance recruitment for a native New Zealand fleshy-fruited tree species, and highlight the importance of birds as mobile links shaping plant populations, both spatially and genetically. Further, I show that at smaller scales (i.e., among neighbouring fragments), urbanisation does not necessarily exert negative impacts on seedling recruitment. In addition, for the first time, I show that the choice of method to sample plant-frugivore interactions alters interpretation of network structure. Thus, combining data generated from different methods, and using seed consumption as a standardised link currency, provides a more complete representation of plant-frugivore networks in a functionally meaningful way. My study contributes to our understanding of the impacts of habitat fragmentation on mutualistic networks by linking changes to network structure with ecosystem function. In addition, my findings illustrate the importance of integrating concepts and analytical approaches from distinct fields (i.e., network theory and genetics) to develop a more comprehensive understanding of the factors that determine seed dispersal in heterogeneous landscapes. I emphasise the importance of focusing on the conservation of species interactions, by better managing forest fragments in urban areas, to maintain the ecosystem function of seed dispersal.

References

Aizen, M. A., Gleiser, G., Sabatino, M., Gilarranz, L. J., Bascompte, J., & Verdú, M. (2016). The Phylogenetic Structure of Plant-Pollinator Networks Increases With Habitat Size and Isolation. *Ecology Letters*, *19*(1), 29–36. https://doi.org/10.1111/ele.12539

Aizen, M. A., Sabatino, M., & Tylianakis, J. M. (2012). Specialization and Rarity Predict Nonrandom Loss of Interactions from Mutualistic Networks. *Science*, *335*(March), 1486–1489. https://doi.org/10.1016/0024-4937(90)90045-3

Albrecht, M., Duelli, P., Schmid, B., & Müller, C. B. (2007). Interaction Diversity Within Quatified Insect Food Webs in Restored and Adjacent Intensively Managed Meadows. *Journal of Animal Ecology*, *76*(5), 1015–1025. https://doi.org/10.1111/j.1365-2656.2007.01264x

Aldrich, P. R., & Hamrick, J. L. (1998). Reproductive Dominance of Pasture Trees in a Fragmented Tropical Forest Mosaic. *Science*, *281*(5373), 103–105. https://doi.org/10.1126/science.281.5373.103

Anderson, M. J., & Walsh, D. C. (2013). PERMANOVA, ANOSIM, and the Mantel Test in the Face of Heterogeneous Dispersions: What Null Hypothesis Are You Testing? *Ecological Monographs*, *83*, 557–574.

Anderson, S. H., Kelly, D., Robertson, A. W., Ladley, J. J., & Innes, J. G. (2006). Birds as Pollinators and Dispersers: A Case Study From New Zealand. *Acta Zoologica Sinica*, *52*, 112–115.

Arévalo, J. E., & Kimberly, N. (2011). Traffic Noise Affects Forest Bird Species in a Protected Tropical Forest. *Revista de Biología Tropical*, *59*, 969–980.

Arkins, A. M., Winnington, A. P., Anderson, S., & Clout, M. N. (1999). Diet and Nectarivorous Foraging Behaviour of the Short-Tailed Bat (Mystacina tuberculata). *Journal of Zoology*, *247*(2), 183–187. https://doi.org/10.1017/S095283699900206X

Aronson, M. F. J., La Sorte, F. A., Nilon, C. H., Katti, M., Goddard, M. A., Lepczyk, C. A., … Winter, M. (2014). A Global Analysis of the Impacts of Urbanization on Bird and Plant Diversity Reveals Key Anthropogenic Drivers. *Proceedings of the Royal Society B: Biological Sciences*, *281*(1780), 20133330–20133330. https://doi.org/10.1098/rspb.2013.3330

Auffret, A. G., Rico, Y., Bullock, J. M., Hooftman, D. A. P., Pakeman, R. J., Soons, M. B., … Cousins, S. A. O. (2017). Plant Functional Connectivity – Integrating Landscape

Structure and Effective Dispersal. *Journal of Ecology*, *105*(6), 1648–1656. https://doi.org/10.1111/1365-2745.12742

Bacles, C. F. E., Lowe, A. J., & Ennos, R. A. (2004). Genetic Effects of Chronic Habitat Fragmentation on Tree Species: The Case of Sorbus aucuparia in a Deforested Scottish Landscape. *Molecular Ecology*, *13*(3), 573–584. https://doi.org/10.1046/j.1365-294X.2004.02093.x

Bacles, C. F. E., Lowe, A. J., & Ennos, R. A. (2006). Effective Seed Dispersal Across a Fragmented Landscape. *Science*, *311*(February), 2006.

Balvanera, P., Pfisterer, A. B., Buchmann, N., He, J. S., Nakashizuka, T., Raffaelli, D., & Schmid, B. (2006). Quantifying the Evidence for Biodiversity Effects on Ecosystem Functioning and Services. *Ecology Letters*, *9*(10), 1146–1156. https://doi.org/10.1111/j.1461-0248.2006.00963.x

Banašek-Richter, C., Cattin, M. F., & Bersier, L. F. (2004). Sampling Effects and the Robustness of Quantitative and Qualitative Food-Web Descriptors. *Journal of Theoretical Biology*, *226*(1), 23–32. https://doi.org/10.1016/S0022-5193(03)00305-9

Bartomeus, I., Gravel, D., Tylianakis, J. M., Aizen, M. A., Dickie, I. A., & Bernard-Verdier, M. (2016). A Common Framework for Identifying Linkage Rules Across Different Types of Interactions. *Functional Ecology*, *30*(12), 1894–1903. https://doi.org/10.1111/1365-2435.12666

Bascompte, J. (2009). Pushing Networks to the Limit. *Science*, *325*(July), 24–27. https://doi.org/10.1126/science.1170749

Bascompte, J., & Jordano, P. (2007). Plant-Animal Mutualistic Networks: The Architecture of Biodiversity. *Annual Review of Ecology, Evolution, and Systematics*, *38*(1), 567–593. https://doi.org/10.1146/annurev.ecolsys.38.091206.095818

Bascompte, J., & Jordano, P. (2014). *Mutualistic Networks*. (S. A. Levin & H. S. Horn, Eds.). Princeton University Press.

Bascompte, J., Jordano, P., Melian, C. J., & Olesen, J. M. (2003). The Nested Assembly of Plant-Animal Mutualistic Networks. *Proceedings of the National Academy of Sciences*, *100*(16), 9383–9387. https://doi.org/10.1073/pnas.1633576100

Bascompte, J., Jordano, P., & Olesen, J. M. (2006). Asymmetric Coevolutionary Networks Facilitate Biodiversity Maintenance. *Science*, *431*(2006), 431–433. https://doi.org/10.1126/science.1123412

Batáry, P., Kurucz, K., Suarez-Rubio, M., & Chamberlain, D. E. (2018). Non-Linearities in Bird Responses Across Urbanization Gradients: A Meta-Analysis. *Global Change Biology*, *24*(3), 1046–1054. https://doi.org/10.1111/gcb.13964

Bates, D., Maechler, M., & Bolker, B. M. (2015). *lme4: Linear Mixed-effects Models Using S4 Classes*.

Beca, G., Vancine, M. H., Carvalho, C. S., Pedrosa, F., Alves, R. S. C., Buscariol, D., … Galetti, M. (2017). High Mammal Species Turnover in Forest Patches Immersed in Biofuel Plantations. *Biological Conservation*, *210*, 352–359. https://doi.org/10.1016/j.biocon.2017.02.033

Bender, D. J., Tischendorf, L., & Fahrig, L. (2003). Using Patch Isolation Metrics to Predict Animal Movement in Binary Landscapes. *Landscape Ecology*, *18*(1), 17–39. https://doi.org/10.1023/A:1022937226820

Beninde, J., Veith, M., & Hochkirch, A. (2015). Biodiversity in Cities Needs Space: a Meta-Analysis of Factors Determining Intra-Urban Biodiversity Variation. *Ecology Letters*, *18*, 581–592. https://doi.org/10.1111/ele.12427

Bergin, D. O. (2000). Current Knowledge Relevant to Management of Podocarpus totara for Timber. *New Zealand Journal of Botany*, *38*(3), 343–359. https://doi.org/10.1080/0028825X.2000.9512687

Bergin, D. O. (2016). *Personal Communication*.

Beveridge, A. E. (1964). Dispersal and Destruction of Seed in Central North Island Podocarp Forest. *Proceedings of the New Zealand Ecological Society*, *11*, 48–55.

Bibby, C. J., Burgess, N. D., & Hill, D. A. (2000). *Bird Census Techniques* (2nd Edition). San Diego, California: London : Academic.

Biro, P. A., & Dingemanse, N. J. (2009). Sampling Biases Resulting from Animal Personality. *Trends in Ecology and Evolution*, *24*(2), 66–67. https://doi.org/10.1016/j.tree.2008.10.004

Blüthgen, N., Fründ, J., Vázquez, D. P., & Menzel, F. (2008). What Do Interaction Network Metrics Tell Us About Specialization and Biological Traits? *Ecology*, *89*(12), 3387–3399.

Blüthgen, N., & Klein, A. (2011). Functional Complementarity and Specialisation: The role of Biodiversity in Plant-Pollinator Interactions. *Basic and Applied Ecology*, *12*, 282–291. https://doi.org/10.1016/j.baae.2010.11.001

Blüthgen, N., Menzel, F., Hovestadt, T., Fiala, B., & Blüthgen, N. (2007). Specialization, Constraints, and Conflicting Interests in Mutualistic Networks. *Current Biology*, *17*, 341–346. https://doi.org/10.1016/j.cub.2006.12.039

Bosch, J., Martín González, A. M., Rodrigo, A., & Navarro, D. (2009). Plant-Pollinator Networks: Adding the Pollinator's Perspective. *Ecology Letters*, *12*(5), 409–419. https://doi.org/10.1111/j.1461-0248.2009.01296.x

Bradley, C. A., & Altizer, S. (2007). Urbanization and the Ecology of Wildlife Diseases. *Trends in Ecology and Evolution*, *22*(2), 95–102. https://doi.org/10.1016/j.tree.2006.11.001

Brodie, J. F., Helmy, O. E., Brockelman, W. Y., & Maron, J. L. (2009). Functional Differences Within a Guild of Tropical Mammalian Frugivores. *Ecology*, *90*(3), 688–698. https://doi.org/10.1890/08-0111.1

Bronstein, J. L. (1994). Our Current Understanding of Mutualism. *Quarterly Review of Biology*, *69*(1), 31–51.

Bronstein, J. L., Alarcón, R., & Geber, M. (2006). The Evolution of Plant-Insect Mutualisms. *New Phytologist*, *172*(3), 412–428. https://doi.org/10.1111/j.1469-8137.2006.01864.x

Brooks, M. E., Kristensen, K., van Benthem, K. J., Magnusson, A., Berg, C. W., Nielsen, A., … Bolker, B. M. (2017). glmmTMB Balances Speed and Flexibility Among Packages for Zero-inflated Generalized Linear Mixed Modeling. *The R Journal*, *9*(2), 378–400.

Brown, L. M., & Graham, C. H. (2015). Demography, Traits and Vulnerability to Urbanization: Can We Make Generalizations? *Journal of Applied Ecology*, *52*(6), 1455–1464. https://doi.org/10.1111/1365-2664.12521

Bueno, R. S., Guevara, R., Ribeiro, M. C., Culot, L., Bufalo, F. S., & Galetti, M. (2013). Functional Redundancy and Complementarities of Seed Dispersal by the Last Neotropical Megafrugivores. *PLoS ONE*, *8*(2). https://doi.org/10.1371/journal.pone.0056252

Bullock, J. M., Shea, K., & Skarpaas, O. (2006). Measuring Plant Dispersal: an Introduction to Field Methods and Experimental Design. *Plant Ecology*, *186*, 217–234. https://doi.org/10.1007/s11258-006-9124-5

Burns, K. C. (2012). Are Introduced Birds Unimportant Mutualists? A Case Study of Frugivory in European Blackbirds (Turdus merula). *New Zealand Journal of Ecology*, *36*(2), 171–176.

Burns, K. C. (2013). What Causes Size Coupling in Fruit-Frugivore Interaction Webs? *Ecology*, *96*(3), 603–610.

Burrows, C. J. (1994). The Seeds Always Know Best. *New Zealand Journal of Botany*, *32*(3), 349–363. https://doi.org/10.1080/0028825X.1994.10410478

Cain, M. L., Milligan, B. G., & Strand, A. E. (2000). Long-Distance Seed Dispersal in Plant Populations. *American Journal of Botany*, *87*(9), 1217–1227.

Carbó-Ramírez, P., & Zuria, I. (2011). The Value of Small Urban Greenspaces for Birds in a Mexican City. *Landscape and Urban Planning*, *100*(3), 213–222. https://doi.org/10.1016/j.landurbplan.2010.12.008

Cardinale, B. J., Duffy, J. E., Gonzalez, A., Hooper, D. U., Perrings, C., Venail, P., … Naeem, S. (2012). Biodiversity Loss and its Impact on Humanity. *Nature*, *486*(7401), 59–67. https://doi.org/10.1038/nature11148

Cardinale, B. J., Matulich, K. L., Hooper, D. U., Byrnes, J. E., Duffy, E., Gamfeldt, L., … Gonzalez, A. (2011). The Functional Role of Producer Diversity in Ecosystems. *American Journal of Botany*, *98*(3), 572–592. https://doi.org/10.3732/ajb.1000364

Cardinale, B. J., Palmer, M. A., & Collins, S. L. (2002). Species Diversity Enhances Ecosystem Functioning Through Interspecific Facilitation. *Nature*, *415*(January), 4–7.

Catchen, J. M., Amores, A., Hohenlohe, P., Cresko, W., & Postlethwait, J. H. (2011). Stacks: Building and Genotyping Loci De Novo From Short-Read Sequences. *Genes|Genomes|Genetics*, *1*(3), 171–182. https://doi.org/10.1534/g3.111.000240

Catchen, J. M., Hohenlohe, P. A., Bassham, S., Amores, A., & Cresko, W. A. (2013). Stacks: An Analysis Tool Set for Population Genomics. *Molecular Ecology*, *22*(11), 3124–3140. https://doi.org/10.1111/mec.12354

Chacoff, N. P., Vázquez, D. P., Lomáscolo, S. B., Stevani, E. L., Dorado, J., & Padrón, B. (2012). Evaluating Sampling Completeness in a Desert Plant-Pollinator Network. *Journal of Animal Ecology*, *81*(1), 190–200. https://doi.org/10.1111/j.1365-2656.2011.01883.x

Chase, J. M., & Leibold, M. A. (2002). Spatial Scale Dictates the Productivity-Biodiversity Relationship. *Nature*, *416*(6879), 427–430. https://doi.org/10.1038/416427a

Christmas, M. J., Breed, M. F., & Lowe, A. J. (2016). Constraints to and Conservation Implications for Climate Change Adaptation in Plants. *Conservation Genetics*, *17*(2), 305–320. https://doi.org/10.1007/s10592-015-0782-5

Clark, C. J., Poulsen, J. R., & Parker, V. T. (2001). The Role of Arboreal Seed Dispersal Groups on the Seed Rain of a Lowland Tropical Forest. *Biotropica*, *33*(4), 606–620. https://doi.org/10.1111/j.1744-7429.2001.tb00219.x

Clout, M. N., & Hay, J. R. (1989). The Importance of Birds as Browsers, Pollinators and Seed Dispersers in New Zealand Forests. *New Zealand Journal of Ecology*, 27–33.

Connell, J. H. (1971). On the Role of Natural Enemies in Preventing Competitive Exclusion in Some Marine Mammals and Forest Trees. In P. J. den Boer & G. R. Gradwell (Eds.), *Dynamics of Populations* (pp. 298–312). Wageningen: Centre for Agricultural Publishing and Documentation.

Cordeiro, N. J., & Howe, H. F. (2003). Forest Fragmentation Severs Mutualism Between Seed Dispersers and an Endemic African Tree. *Proceedings of the National Academy of Sciences*, *100*(24), 14052–14056. https://doi.org/10.1073/pnas.2331023100

Costa, J. M., da Silva, L. P., Ramos, J. A., & Heleno, R. H. (2016). Sampling Completeness in Seed Dispersal Networks: When Enough is Enough. *Basic and Applied Ecology*, *17*(2), 155–164. https://doi.org/10.1016/j.baae.2015.09.008

Costa Cruz, J., Ramos, J. A., da Silva, L. P., Tenreiro, P. Q., & Heleno, R. H. (2013). Seed Dispersal Networks in an Urban Novel Ecosystem, 887–897. https://doi.org/10.1007/s10342-013-0722-1

Cowan, P. E. (1992). Analysis of the Characteristics of Fruit Eaten by Possums, Trichosurus vulpecula, in New Zealand. *New Zealand Journal of Zoology*, *19*(1–2), 45–52. https://doi.org/10.1080/03014223.1992.10423250

Craig, R., Taonui, R., & Wild, S. (2012). The Concept of Taonga in Māori Culture: Insights for Accounting. *Accounting, Auditing and Accountability Journal*, *25*(6), 1025–1047. https://doi.org/10.1108/09513571211250233

Crawley, M. J. (1985). Reduction of Oak Fecundity by Low-Density Herbivore Populations. *Nature*, *314*, 556–557. https://doi.org/10.1038/316507a0

Crawley, M. J. (2002). *Statistical Computing: an Introduction to Data Analysis Using S-Plus.* (1st Edition.). Wiley-Blackwell.

Crooks, K. R., Suarez, A. V., & Bolger, D. T. (2004). Avian Assemblages Along a Gradient of Urbanization in a Highly Fragmented Landscape. *Biological Conservation*, *115*(3), 451–462. https://doi.org/10.1016/S0006-3207(03)00162-9

Cruz, J. C., Ramos, J. A., da Silva, L. P., Tenreiro, P. Q., & Heleno, R. H. (2013). Seed Dispersal Networks in an Urban Novel Ecosystem. *European Journal of Forest Research*, *132*, 887–897. https://doi.org/10.1007/s10342-013-0722-1

Dawson, J., & Lucas, R. (2012). *Field Guide to New Zealand´s Native Trees*. Craig Potton Publishing.

Deconchat, M., Brockerhoff, E. G., & Barbaro, L. (2009). Effects of Surrounding Landscape Composition on the Conservation Value of Native and Exotic Habitats for Native Forest Birds. *Forest Ecology and Management*, *258*(SUPPL.), 196–204. https://doi.org/10.1016/j.foreco.2009.08.003

Diniz-Filho, J. A. F., Soares, T. N., Lima, J. S., Dobrovolski, R., Landeiro, V. L., Telles, M. P. de C., … Bini, L. M. (2013). Mantel Test in Population Genetics. *Genetics and Molecular Biology*, *36*(4), 475–485. https://doi.org/10.1590/S1415-47572013000400002

Díaz, S., & Cabido, M. (2001). Vive la Différence: Plant Functional Diversity Matters to Ecosystem Processes. *Trends in Ecology & Evolution*, *16*(11), 646–655. https://doi.org/10.1016/S0169-5347(01)02283-2

Donoso, I., García, D., Martínez, D., Tylianakis, J. M., & Stouffer, D. B. (2017). Complementary Effects of Species Abundances and Ecological Neighborhood on the Occurrence of Fruit-Frugivore Interactions. *Frontiers in Ecology and Evolution*, *5*(November), 1–12. https://doi.org/10.3389/fevo.2017.00133

Dormann, C. F., Fründ, J., & Gruber, B. (2016). bipartite. R package version 2.4-5.

Dormann, C. F., Gruber, B., & Fründ, J. (2008). Introducing the bipartite Package : Analysing Ecological Networks, *8*(October), 8–11.

Doyle, J. J., & Doyle, J. L. (1987). A Rapid DNA Isolation Procedure for Small Quantities of Fresh Leaf Tissue. *Phytochemical Bulletin*, *19*, 11–15.

Duffy, J. E. (2003). Biodiversity Loss, Trophic Skew and Ecosystem Functioning. *Ecology Letters*, *6*(8), 680–687. https://doi.org/10.1046/j.1461-0248.2003.00494.x

Duncan, R. P., & Young, J. R. (2010). Determinants of Plant Extinction and Rarity 145 Years After European Settlement of Auckland, New Zealand. *Ecology*, *81*(11), 3048–3061.

Dunford, W., & Freemark, K. (2005). Matrix Matters: Effects of Surrounding Land Uses on Forest Birds Near Ottawa, Canada. *Landscape Ecology*, *20*(5), 497–511. https://doi.org/10.1007/s10980-004-5650-5

Elshire, R. J., Glaubitz, J. C., Sun, Q., Poland, J. A., Kawamoto, K., Buckler, E. S., & Mitchell, S. E. (2011). A Robust, Simple Genotyping-by-Sequencing (GBS) Approach for High Diversity Species. *PLoS ONE*, *6*(5), 1–10. https://doi.org/10.1371/journal.pone.0019379

Emer, C., Galetti, M., Pizo, M. A., Guimarães, P. R., Moraes, S., Piratelli, A., & Jordano, P. (2018). Seed-dispersal Interactions in Fragmented Landscapes - A Metanetwork Approach. *Ecology Letters*. https://doi.org/10.1111/ele.12909

Epps, C. W., & Keyghobadi, N. (2015). Landscape Genetics in a Changing World: Disentangling Historical and Contemporary Influences and Inferring Change. *Molecular Ecology*, *24*(24), 6021–6040. https://doi.org/10.1111/mec.13454

ESRI. (2011). ArcGIS desktop: release 10. Redlands, CA: Environmental Systems Research Institute.

Ewers, R. M., Kliskey, A. D., Walker, S., Rutledge, D., Harding, J. S., & Didham, R. K. (2006). Past and Future Trajectories of Forest Loss in New Zealand. *Biological Conservation*, *133*, 312–325. https://doi.org/10.1016/j.biocon.2006.06.018

Fahrig, L. (2003). Effects of Habitat Fragmentation on Biodiversity. *Annual Review of Ecology, Evolution, and Systematics*, *34*(1), 487–515. https://doi.org/10.1146/annurev.ecolsys.34.011802.132419

Faith, D. P., Minchin, P. R., & Belbin, L. (1987). Compositional Dissimilarity as a Robust Measure of Ecological Distance. *Vegetatio*, *69*, 57–68.

Farjon, A. (2013). *Podocarpus totara. The IUCN Red List of Threatened Species 2013*.

Fedriani, J. M., & Delibes, M. (2009). Seed Dispersal in the Iberian Pear, Pyrus bourgaeana : A Role for Infrequent Mutualists. *Écoscience*, *16*(3), 311–321. https://doi.org/10.2980/16-3-3253

Finke, D. L., & Snyder, W. E. (2008). Niche Increases Resource Partitioning by Diverse Communities Exploitation. *Science*, *321*(5895), 1488–1490. https://doi.org/10.1126/science.1160854

Forget, P. M., Jordano, P., Lambert, J. E., Böhning-Gaese, K., Traveset, A., & Wright, S. J. (2011). Frugivores and Seed Dispersal (1985-2010); the "Seeds" Dispersed, Established and Matured. *Acta Oecologica*, *37*(6), 517–520. https://doi.org/10.1016/j.actao.2011.09.008

Fox, J., Weisberg, S., Adler, D., Bates, D., Baud-Bovy, G., Ellison, S., … Graves, S. (2016). *Package "car."*

Fründ, J., McCann, K. S., & Williams, N. M. (2015). Sampling Bias is a Challenge for Quantifying Specialization and Network Structure: Lessons from a Quantitative Niche Model. *Oikos*, *125*, 502–513.

Gagic, V., Bartomeus, I., Jonsson, T., Taylor, A., Winqvist, C., Fischer, C., … Bommarco, R. (2015). Functional Identity and Diversity of Animals Predict Ecosystem Functioning Better Than Species-Based Indices. *Proceedings of the Royal Society B: Biological Sciences*, *282*(1801). https://doi.org/10.1098/rspb.2014.2620

Gagic, V., Tscharntke, T., Dormann, C. F., Gruber, B., Wilstermann, A., & Thies, C. (2011). Food Web Structure and Biocontrol in a Four-Trophic Level System Across a Landscape Complexity Gradient. *Proceedings of the Royal Society B: Biological Sciences*, *278*(1720), 2946–2953. https://doi.org/10.1098/rspb.2010.2645

Galbraith, J. A., Stanley, M. C., Jones, D. N., & Beggs, J. R. (2017). Experimental Feeding Regime Influences Urban Bird Disease Dynamics. *Journal of Avian Biology*, *48*(5), 700–713. https://doi.org/10.1111/jav.01076

García, C., Jordano, P., & Godoy, J. A. (2007). Contemporary Pollen and Seed Dispersal in a Prunus mahaleb Population: Patterns in Distance and Direction. *Molecular Ecology*, *16*, 1947–1955. https://doi.org/10.1111/j.1365-294X.2006.03126.x

García, D. (2016). Birds in Ecological Networks: Insights from Bird-Plant Mutualistic Interactions. *Ardeola*, *63*(1), 151–180. https://doi.org/10.13157/arla.63.1.2016.rp7

García, D., Donoso, I., & Rodríguez-Pérez, J. (2018). Frugivore Biodiversity and Complementarity in Interaction Networks Matter for Seed Dispersal Function Plot Description. *Functional Ecology*. https://doi.org/10.1111/1365-2435.13213

García, D., & Martínez, D. (2012). Species Richness Matters for the Quality of Ecosystem Services: a Test Using Seed Dispersal by Frugivorous Birds. *Proceedings of the Royal Society B: Biological Sciences*, 3106–3113. https://doi.org/10.1098/rspb.2012.0175

García, D., Martínez, D., Stouffer, D. B., & Tylianakis, J. M. (2014). Exotic Birds Increase Generalization and Compensate for Native Bird Decline in Plant-Frugivore Assemblages. *Journal of Animal Ecology*, *83*, 1441–1450. https://doi.org/10.1111/1365-2656.12237

Gillies, C. S., Beyer, H. L., & St. Clair, C. C. (2011). Fine-Scale Movement Decisions of Tropical Forest Birds in a Fragmented Landscape. *Ecological Applications*, *21*(3), 944–954.

Goddard, M. A., Dougill, A. J., & Benton, T. G. (2010). Scaling Up From Gardens: Biodiversity Conservation in Urban Environments. *Trends in Ecology and Evolution*, *25*(2), 90–98. https://doi.org/10.1016/j.tree.2009.07.016

Godoy, J. A., & Jordano, P. (2001). Seed Dispersal by Animals: Exact Identification of Source Trees With Endocarp DNA Microsatellites. *Molecular Ecology*, *10*, 2275–2283.

González-Castro, A., Traveset, A., & Nogales, M. (2012). Seed Dispersal Interactions in the Mediterranean Region: Contrasting Patterns Between Islands and Mainland. *Journal of Biogeography*, *39*(11), 1938–1947. https://doi.org/10.1111/j.1365-2699.2012.02693.x

González-Castro, A., Yang, S., Nogales, M., & Carlo, T. A. (2015). Relative Importance of Phenotypic Trait Matching and Species' Abundances in Determining Plant - Avian Seed Dispersal Interactions in a Small Insular Community. *AoB PLANTS*, *7*(1), 1–10. https://doi.org/10.1093/aobpla/plv017

González-Varo, J. P. (2010). Fragmentation, Habitat Composition and the Dispersal/Predation Balance in Interactions Between the Mediterranean Myrtle and Avian Frugivores. *Ecography*, *33*(May 2009), 185–197. https://doi.org/10.1111/j.1600-0587.2009.06021.x

González-Varo, J. P., Carvalho, C. S., Arroyo, J. M., & Jordano, P. (2017). Unravelling Seed Dispersal Through Fragmented Landscapes: Frugivore Species Operate Unevenly as Mobile Links. *Molecular Ecology*, *26*(16), 4309–4321. https://doi.org/10.1111/mec.14181

Graham, C. H. (2001). Factors Influencing Movement Patterns of Keel-Billed Toucans in a Fragmented Tropical Landscape in Southern Mexico. *Conservation Biology*, *15*(6), 1789–1798. https://doi.org/10.1046/j.1523-1739.2001.00070.x

Gu, H., Goodale, E., & Chen, J. (2015). Emerging Directions in the Study of the Ecology and Evolution of Plant-Animal Mutualistic Networks: a Review. *Zoological Research*, *36*(1), 1–7. https://doi.org/10.13918/j.issn.2095-8137.2015.2.65

Hagen, M., Kissling, W. D., Rasmussen, C., Aguiar, M. A. M. De, Brown, L. E., Carstensen, D. W., … Olesen, J. M. (2012). Biodiversity , Species Interactions and Ecological Networks in a Fragmented World. *Global Change in Multispecies Systems*, *46*, 89–210. https://doi.org/10.1016/B978-0-12-396992-7.00002-2

Hansen, D. M., & Galetti, M. (2009). The Forgotten Megafauna. *Science*, *324*(April), 2–3. https://doi.org/10.1126/science.1172393

Hanski, I. (1998). Metapopulation Dynamics. *Nature*, *396*(November), 41–49.

Hanski, I. (2015). Habitat Fragmentation and Species Richness. *Journal of Biogeography*, *42*(5), 989–993. https://doi.org/10.1111/jbi.12478

Hanski, I., & Gilpin, M. (1991). Metapopulation dynamics: a Brief History and Conceptual Domain. *Biological Journal of the Linnean Society*, *42*, 3–16.

Hardesty, B. D., Hubbell, S. P., & Bermingham, E. (2006). Genetic Evidence of Frequent Long-distance Recruitment in a Vertebrate-Dispersed Tree. *Ecology Letters*, *9*(5), 516–525. https://doi.org/10.1111/j.1461-0248.2006.00897.x

Harrison, H. B., Saenz-Agudelo, P., Planes, S., Jones, G. P., & Berumen, M. L. (2013). Relative Accuracy of Three Common Methods of Parentage Analysis in Natural Populations. *Molecular Ecology*, *22*(4), 1158–1170. https://doi.org/10.1111/mec.12138

He, T., Lamont, B. B., Krauss, S. L., & Enright, N. J. (2010). Genetic Connectivity and Inter-Population Seed Dispersal of Banksia hookeriana at the Landscape Scale. *Annals of Botany*, *106*, 457–466. https://doi.org/10.1093/aob/mcq140

Heleno, R. H., García, C., Jordano, P., Traveset, A., Gomez, J. M., Bluthgen, N., … Olesen, J. M. (2014). Ecological Networks: Delving into the Architecture of Biodiversity. *Biology Letters*, *10*(1), 20131000–20131000. https://doi.org/10.1098/rsbl.2013.1000

Heleno, R. H., Olesen, J. M., Nogales, M., Vargas, P., & Traveset, A. (2012). Seed Dispersal Networks in the Galápagos and the Consequences of Alien Plant Invasions. *Proceedings B*, *280*. https://doi.org/10.1098/rspb.2012.2112

Heleno, R. H., Olesen, J. M., Nogales, M., Vargas, P., & Traveset, A. (2013). Seed Dispersal Networks in the Galápagos and the Consequences of Alien Plant Invasions. *Proceedings of the Royal Society, Biological Sciences*, (November 2012).

Henriksen, M. V., Chapple, D. G., Chown, S. L., & McGeoch, M. A. (2018). The Effect of Network Size and Sampling Completeness in Depauperate Networks. *Journal of Animal Ecology*, 0–3. https://doi.org/10.1111/1365-2656.12912

Herrera, C. M. (2002). Seed Disperal by Vertebrates. In C. M. Herrera & O. Pellmyr (Eds.), *Plant-Animal Interactions: and Evolutionary Approach* (pp. 185–208). Blackwell, Oxford.

Hobbs, R. J., & Yates, C. J. (2003). Impacts of Ecosystem Fragmentation on Plant Populations: Generalising the Idiosyncratic. *Australian Journal of Botany*, *51*(5), 471–488. https://doi.org/10.1071/BT03037

Holbrook, K. M., & Smith, T. B. (2000). Seed Dispersal and Movement Patterns in Two Species of Ceratogymna hornbills in a West African Tropical lowland forest. *Oecologia*, *125*(2), 249–257. https://doi.org/10.1007/s004420000445

Holdaway, R. N. (1989). New Zealand's Pre-Human Avifauna and its Vulnerability. *New Zealand Journal of Ecology*, *12*, 11–25.

Holderegger, R., Buehler, D., Gugerli, F., & Manel, S. (2010). Landscape Genetics of Plants. *Trends in Plant Science*, *15*(12), 675–683. https://doi.org/10.1016/j.tplants.2010.09.002

Hooper, D. U., Chapin, F. S., Ewel, J. J., Hector, A., Inchausti, P., Lavorel, S., … Wardle, D. A. (2005). Effects of Biodiversity on Ecosystem Functioning: A Consensus of Current Knowledge. *Ecological Monographs*, *75*(1), 3–35. https://doi.org/10.1890/04-0922

Howe, H. F., & Miriti, M. N. (2004). When Seed Dispersal Matters. *BioScience*, *54*(7), 651–660.

Howe, H. F., & Smallwood, J. (1982). Ecology of Seed Dispersal. *Annual Review of Ecology, Evolution, and Systematics*, *13*, 201–228.

Howell, C. (2008). *Consolidated List of Environmental Weeds in New Zealand*. Wellington.

Ibáñez, I., Katz, D. S. W., Peltier, D., Wolf, S. M., & Connor Barrie, B. T. (2014). Assessing the Integrated Effects of Landscape Fragmentation on Plants and Plant Communities: The Challenge of Multiprocess-Multiresponse Dynamics. *Journal of Ecology*, *102*(4), 882–895. https://doi.org/10.1111/1365-2745.12223

Ikin, K., Beaty, R. M., Lindenmayer, D. B., Knight, E., Fischer, J., & Manning, A. D. (2013). Pocket Parks in a Compact City: How Do Birds Respond to Increasing Residential Density? *Landscape Ecology*, *28*(1), 45–56. https://doi.org/10.1007/s10980-012-9811-7

Ings, T. C., Montoya, J. M., Bascompte, J., Blüthgen, N., Brown, L., Dormann, C. F., … Woodward, G. (2009). Ecological Networks - Beyond Food Webs. *Journal of Animal Ecology*, *78*(1), 253–269. https://doi.org/10.1111/j.1365-2656.2008.01460.x

Innes, J., Kelly, D., Overton, J. M., & Gillies, C. (2010). Predation and Other Factors Currently Limiting New Zealand Forest Birds. *New Zealand Journal of Ecology*, *34*(1), 86–114.

Ismail, S. A., Ghazoul, J., Ravikanth, G., Kushalappa, C. G., Uma Shaanker, R., & Kettle, C. J. (2017). Evaluating Realized Seed Dispersal Across Fragmented Tropical Landscapes: a Two-Fold Approach Using Parentage Analysis and the Neighbourhood Model. *New Phytologist*, *214*(3), 1307–1316. https://doi.org/10.1111/nph.14427

Ives, A. R., & Carpenter, S. R. (2007). Stability and Diversity of Ecosystems. *Science*, *317*(5834), 58–62. https://doi.org/10.1126/science.1133258

Janzen, D. H. (1970). Herbivores and the Number of Tree Species in Tropical Forests. *The American Naturalist*, *104*, 501–528.

Jones, A. G., Small, C. M., Paczolt, K. A., & Ratterman, N. L. (2010). A Practical Guide to Methods of Parentage Analysis. *Molecular Ecology Resources*, *10*, 6–30. https://doi.org/10.1111/j.1755-0998.2009.02778.x

Jones, C. G., Lawron, J. H., & Shachak, M. (1997). Positive and Negative Effects of Organisms as Physical Ecosystem Engineers. *Ecology*, *78*(7), 1946–1957. https://doi.org/10.1890/0012-9658(1997)078[1946:PANEOO]2.0.CO;2

Jones, G. P., Planes, S., & Thorrold, S. R. (2005). Coral Reef Fish Larvae Settle Close to Home. *Current Biology*, *15*(14), 1314–1318. https://doi.org/10.1016/j.cub.2005.06.061

Jones, O. R., & Wang, J. (2010). COLONY: A Program for Parentage and Sibship Inference from Multilocus Genotype Data. *Molecular Ecology Resources*, *10*(3), 551–555. https://doi.org/10.1111/j.1755-0998.2009.02787.x

Jordano, P. (1987). Patterns of Mutualistic Interactions in Pollination and Seed Dispersal: Connectance, Dependence Asymmetries, and Coevolution. *The American Naturalist*, *129*(5), 657–677.

Jordano, P. (1994). Spatial and Temporal Variation in the Avian-Frugivore Assemblage of Prunus mahaleb: Patterns and Consequences. *Oikos*, *71*(3), 479–491.

Jordano, P. (2016). Sampling Networks of Ecological Interactions. *Functional Ecology*, *30*(12), 1883–1893. https://doi.org/10.1111/1365-2435.12763

Jordano, P., Bascompte, J., & Olesen, J. M. (2003). Invariant Properties in Coevolutionary Networks of Plant-Animal Interactions. *Ecology Letters*, 69–81.

Jordano, P., Forget, P.-M., Lambert, J. E., Bohning-Gaese, K., Traveset, A., & Wright, S. J. (2011). Frugivores and Seed Dispersal: Mechanisms and Consequences for Biodiversity of a Key Ecological Interaction. *Biology Letters*, *7*(3), 321–323. https://doi.org/10.1098/rsbl.2010.0986

Jordano, P., García, C., Godoy, J. A., & García-Castaño, J. L. (2007). Differential Contribution of Frugivores to Complex Seed Dispersal Patterns. *Proceedings of the National Academy of Sciences*, *104*(9), 3278–3282.

Jordano, P., & Schupp, E. W. (2000). Seed Disperser Effectiveness : the Quantity Component and Patterns of Seed Rain for Prunus Mahaleb. *Ecological Monographs*, *70*(October 1998), 591–615.

Kaiser-Bunbury, C. N., Mougal, J., Whittington, A. E., Valentin, T., Gabriel, R., Olesen, J. M., & Blüthgen, N. (2017). Ecosystem Restoration Strengthens Pollination Network Resilience and Function. *Nature*, *542*(7640), 223–227. https://doi.org/10.1038/nature21071

Kaiser-Bunbury, C. N., Traveset, A., & Hansen, D. M. (2010). Conservation and Restoration of Plant-Animal Mutualisms on Oceanic Islands. *Perspectives in Plant Ecology, Evolution and Systematics*, *12*(2), 131–143. https://doi.org/10.1016/j.ppees.2009.10.002

Karubian, J., Sork, V. L., Roorda, T., Durães, R., & Smith, T. B. (2010). Destination-Based Seed Dispersal Homogenizes Genetic Structure of a Tropical Palm. *Molecular Ecology*, *19*(8), 1745–1753. https://doi.org/10.1111/j.1365-294X.2010.04600.x

Keast, A. (1974). Races, Colonisation and Migration in the Silvereye. *Avidata: The Journal of the Avicultural Society of New South Wales*, *1*(2).

Kelly, D., Ladley, J. J., Robertson, A. W., Anderson, S. H., Wotton, D. M., & Wiser, S. K. (2010). Mutualisms with the Wreckage of an Avifauna: the Status of Bird Pollination and Fruit-Dispersal in New Zealand. *New Zealand Journal Of Ecology*, *34*(1), 86–114.

Kissling, W. D., & Schleuning, M. (2015). Multispecies Interactions Across Trophic Levels at Macroscales: Retrospective and Future Directions. *Ecography*, *38*(4), 346–357. https://doi.org/10.1111/ecog.00819

Kremen, C. (2005). Managing Ecosystem Services: What Do We Need to Know About Their Ecology? *Ecology Letters*, *8*(5), 468–479. https://doi.org/10.1111/j.1461-0248.2005.00751.x

Kremen, C., Williams, N. M., Aizen, M. A., Gemmill-Herren, B., LeBuhn, G., Minckley, R., … Ricketts, T. H. (2007). Pollination and Other Ecosystem Services Produced by Mobile Organisms: A conceptual Framework for the Effects of Land-Use Change. *Ecology Letters*, *10*(4), 299–314. https://doi.org/10.1111/j.1461-0248.2007.01018.x

Lavabre, J. E., Stouffer, D. B., Sanz, R., & Bascompte, J. (2014). Seed Dispersal in Heterogeneous Landscapes: Linking Field Observations with Spatially Explicit Models. *Oikos*, (March), 1–10. https://doi.org/10.1111/oik.01155

Lee, W. G., Wood, J. R., & Rogers, G. M. (2010). Legacy of Avian-Dominated Plant-Herbivore Systems in New Zealand. *New Zealand Journal of Ecology*, *34*(1), 28–47.

Lefcheck, J. S. (2016). piecewiseSEM: Piecewise Structural Equation Modelling in R for Ecology, Evolution, and Systematics. *Methods in Ecology and Evolution*, *7*(5), 573–579. https://doi.org/10.1111/2041-210X.12512

Legendre, P., & Legendre, L. (1998). *Numerical Ecology* (2nd Edition). Elsevier, Amsterdam.

Leibold, M. A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J. M., Hoopes, M. F., … Gonzalez, A. (2004). The Metacommunity Concept: A Framework for Multi-Scale Community Ecology. *Ecology Letters*, *7*(7), 601–613. https://doi.org/10.1111/j.1461-0248.2004.00608.x

Levey, D. J., Silva, W. R., & Galetti, M. (Eds.). (2002). *Seed Dispersal and Frugivory: Ecology, Evolution and Conservation*. Wallingford, UK: CAB International.

Levin, S. A. (1992). The Problem of Pattern and Scale in Ecology. *Ecology*, *73*(6), 1943–1967. https://doi.org/https://doi.org/10.2307/1941447

Lord, J. M. (1999). Fleshy-Fruitedness in the New Zealand Flora, *Journal of Biogeography*, *26*(6), 1249–1253.

Lord, J. M., Markey, A. S., & Marshall, J. (2002). Have Frugivores Influenced the Evolution of Fruit Traits in New Zealand? *Seed Dispersal and Frugivory: Ecology, Evolution and Conservation*, 55–68. https://doi.org/10.1079/9780851995250.0055

Loreau, M., Naeem, S., Inchausti, P., Bengtsson, J., Grime, J. P., Hector, A., … Wardle, D. A. (2001). Biodiversity and Ecosystem Functioning: Current Knowledge and Future Challenges. *Science*, *294*(October), 804–808.

Lundberg, J., & Moberg, F. (2003). Mobile Link Organisms and Ecosystem Functioning: Implications for Ecosystem Resilience and Management. *Ecosystems*, *6*(1), 87–98. https://doi.org/10.1007/s10021-002-0150-4

Luque, S., Saura, S., & Fortin, M.-J. (2012). Landscape Connectivity Analysis for Conservation: Insights from Combining New Methods with Ecological and Genetic Data. *Landscape Ecology*, *27*(2), 153–157. https://doi.org/10.1007/s10980-011-9700-5

MacFadyen, S., Gibson, R., Polaszek, A., Morris, R. J., Craze, P. G., Planqué, R., … Memmott, J. (2009). Do Differences in Food Web Structure Between Organic and Conventional Farms Affect the Ecosystem Service of Pest Control? *Ecology Letters*, *12*(3), 229–238. https://doi.org/10.1111/j.1461-0248.2008.01279.x

MacFarlane, A. E. T., Kelly, D., & Briskie, J. V. (2015). Introduced Blackbirds and Song Thrushes: Useful Substitutes for Lost Mid-Sized Native Frugivores, or Weed Vectors? *New Zealand Journal of Ecology*, *40*(1). https://doi.org/10.20417/nzjecol.40.9

Magrach, A., Holzschuh, A., Bartomeus, I., Riedinger, V., Roberts, S. P. M., Rundlöf, M., … Vilà, M. (2018). Plant–Pollinator Networks in Semi-Natural Grasslands are Resistant to the Loss of Pollinators During Blooming of Mass-Flowering Crops. *Ecography*, *41*(1), 62–74. https://doi.org/10.1111/ecog.02847

Mantel, N. (1967). The Detection of Disease Clustering and a Generalized Regression Approach. *Cancer Research*, *27*(2), 209–220. https://doi.org/10.1038/214637b0

Marini, L. Bartomeus, I., Rader, R., Lami, F. (2018). Species-Habitat Networks: Bridging Applied Ecology and Network Theory. *Open Science Framework, 21 May 2018*, 1 – 22. https://dx.doi.org/10.1101/326041

Martensen, A. C., Pimentel, R. G., & Metzger, J. P. (2008). Relative Effects of Fragment Size and Connectivity on Bird Community in the Atlantic Rain Forest: Implications for Conservation. *Biological Conservation*, *1*. https://doi.org/10.1016/j.biocon.2008.06.008

Martínez, D., & García, D. (2017). Role of Avian Seed Dispersers in Tree Recruitment in Woodland Pastures. *Ecosystems*, *20*(3), 616–629. https://doi.org/10.1007/s10021-016-0043-6

Martínez, I., García, D., & Obeso, J. R. (2008). Differential Seed Dispersal Patterns Generated by a Common Assemblage of Vertebrate Frugivores in Three Fleshy-Fruited Trees. *Écoscience*, *15*(2), 189–199. https://doi.org/10.2980/15-2-3096

McCann, K. (2007). Protecting Biostructure. *Nature*, *446*(7131), 29. https://doi.org/10.1038/446029a

McCann, K., Hastings, A., & Huxel, G. R. (1998). Weak Trophic Interactions and the Balance of Nature. *Nature*, *395*(6704), 794–798. https://doi.org/10.1038/27427

McConkey, K. R., Prasad, S., Corlett, R. T., Campos-Arceiz, A., Brodie, J. F., Rogers, H., & Santamaria, L. (2012). Seed Dispersal in Changing Landscapes. *Biological Conservation*, *146*(1), 1–13. https://doi.org/10.1016/j.biocon.2011.09.018

McDonnell, M. J., & Pickett, S. T. A. (Eds.). (1993). *Humans as Components of Ecosystems: Subtle Human Effects and the Ecology of Populated Areas*. New York: Springer-Verlga.

McKinney, M. L. (2008). Effects of Urbanization on Species Richness: A Review of Plants and Animals. *Urban Ecosystems*, *11*(2), 161–176. https://doi.org/10.1007/s11252-007-0045-4

Medina, F. M., Bonnaud, E., Vidal, E., Tershy, B. R., Zavaleta, E. S., Josh Donlan, C., … Nogales, M. (2011). A Global Review of the Impacts of Invasive Cats on Island Endangered Vertebrates. *Global Change Biology*, *17*(11), 3503–3510. https://doi.org/10.1111/j.1365-2486.2011.02464.x

Memmott, J., Waser, N. M., & Price, M. V. (2004). Tolerance of Pollination Networks to Species Extinctions. *Proceedings of the Royal Society B: Biological Sciences*, *271*(1557), 2605–2611. https://doi.org/10.1098/rspb.2004.2909

Menezes, I., Cazetta, E., Morante-Filho, J. C., & Faria, D. (2016). Forest Cover and Bird Diversity: Drivers of Fruit Consumption in Forest Interiors in the Atlantic Forest of Southern Bahia, Brazil. *Tropical Conservation Science*, *9*(91), 549–562. https://doi.org/10.1177/194008291600900128

Miskelly, C. M. (2018). Changes in the Forest Bird Community of an Urban Sanctuary in Response to Pest Mammal Eradications and Endemic Bird Reintroductions. *Notornis*, *65*, 132–151.

Montoya, J. M., Rodríguez, M. A., & Hawkins, B. A. (2003). Food Web Complexity and Higher-Trophic Level Ecosystem Services. *Ecology Letters*, *6*(May 1972), 587–593. https://doi.org/10.1046/j.1461-0248.2003.00469.x

Moran, C., Catterall, C. P., & Kanowski, J. (2009). Reduced Dispersal of Native Plant Species as a Consequence of the Reduced Abundance of Frugivore Species in Fragmented Rainforest. *Biological Conservation*, *142*(3), 541–552. https://doi.org/10.1016/j.biocon.2008.11.006

Mouquet, N., & Loreau, M. (2003). Community Patterns in Source-Sink Metacommunities. *The American Naturalist*, *162*(5), 544–557. https://doi.org/10.1086/378857

Naeem, S., & Wright, J. P. (2003). Disentangling Biodiversity Effects on Ecosystem Functioning: Deriving Solutions to a Seemingly Insormountable Problem. *Ecology Letters*, *6*, 567–579. https://doi.org/10.1046/j.1461-0248.2003.00471.x

Nakagawa, S., & Schielzeth, H. (2013). A General and Simple Method for Obtaining R2 from Generalized Linear Mixed-Effects Models. *Methods in Ecology and Evolution*, *4*(2), 133–142. https://doi.org/10.1111/j.2041-210x.2012.00261.x

Nathan, R., & Muller-Landau, H. C. (2000). Spatial Patterns of Seed Dispersal, their Determinants and Consequences for Recruitment. *Trends in Ecology & Evolution*, *15*(7), 278–285. https://doi.org/10.1016/S0169-5347(00)01874-7

Nathan, R., Perry, G., Cronin, J. T., Strand, A. E., & Cain, M. L. (2003). Methods for Estimating Long-Distance Dispersal. *Oikos*, *103*(2), 261–273. https://doi.org/10.1034/j.1600-0706.2003.12146.x

Nathan, R., Schurr, F. M., Spiegel, O., Steinitz, O., Trakhtenbrot, A., & Tsoar, A. (2008). Mechanisms of Long-Distance Seed Dispersal. *Trends in Ecology and Evolution*, *23*(11), 638–647. https://doi.org/10.1016/j.tree.2008.08.003

Nielsen, A., & Bascompte, J. (2007). Ecological Networks, Nestedness and Sampling Effort. *Journal of Ecology*, *95*(5), 1134–1141. https://doi.org/10.1111/j.1365-2745.2007.01271.x

Norton, D. A. (1991). *Restoration of Indigenous Vegetation on Sites Disturbed by Alluvial Gold Mining in Westland. Resource Allocation Report 3*. Wellington, New Zealand.

O'Donnell, C. F. J., & Dilks, P. J. (1994). Foods and Foraging of Forest Birds in Temperate Rainforest, South Westland, New Zealand. *New Zealand Journal of Ecology*, *18*(2), 87–107. https://doi.org/10.1093/iis/etq042

O'Neill, R. V., Milne, B. T., Turner, M. G., & Gardner, R. H. (1988). Resource Utilization Scales and Landscape Pattern. *Landscape Ecology*, *2*(1), 63–69. https://doi.org/10.1007/BF00138908

Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., Mcglinn, D., … Szoecs, E. (2017). *vegan: Community Ecology Package. R package version 2.4-5*.

Okuyama, T., & Holland, J. N. (2008). Network Structural Properties Mediate the Stability of Mutualistic Communities. *Ecology Letters*, *11*(3), 208–216. https://doi.org/10.1111/j.1461-0248.2007.01137.x

Olesen, J. M., Bascompte, J., Dupont, Y. L., Elberling, H., Rasmussen, C., & Jordano, P. (2011). Missing and Forbidden Links in Mutualistic Networks. *Proceedings of the Royal Society B: Biological Sciences*, *278*(1706), 725–732. https://doi.org/10.1098/rspb.2010.1371

Olesen, J. M., Bascompte, J., Dupont, Y. L., & Jordano, P. (2007). The Modularity of Pollination Networks. *Proceedings of the National Academy of Sciences*, *104*(50), 19891–19896. https://doi.org/10.1073/pnas.0706375104

Pagen, R. W., Thompson, F. R., & Burhans, D. E. (2002). A Comparison of Point-Count and Mist-Net Detections of Songbirds by Habitat and Time-of-Season. *Journal of F*, *73*(1), 53–59.

Palomino, D., & Carrascal, L. M. (2007). Threshold Distances to Nearby Cities and Roads Influence the Bird Cmmunity of a Mosaic Landscape. *Biological Conservation*, *140*(1–2), 100–109. https://doi.org/10.1016/j.biocon.2007.07.029

Pardieck, K., & Waide, R. B. (1992). Mesh Size as a Factor in Avian Community Studies Using Mist Nets. *Journal of Field Ornithology*, *63*(3), 250–255.

Pejchar, L., Pringle, R. M., Ranganathan, J., Zook, J. R., Duran, G., Oviedo, F., & Daily, G. C. (2008). Birds as Agents of Seed Dispersal in a Human-Dominated Landscape in Southern Costa Rica. *Biological Conservation*, *141*(2), 536–544. https://doi.org/10.1016/j.biocon.2007.11.008

Peralta, G., Frost, C. M., Rand, T. A., Didham, R. K., & Tylianakis, J. M. (2014). Complementarity and Redundancy of Interactions Enhance Attack Rates and Spatial Stability in Host-Parasitoid Food Webs. *Ecology*, *95*(7), 1888–1896. https://doi.org/10.1890/13-1569.1

Pereira, H. M., Leadley, P. W., Proença, V., Alkemade, R., Scharlemann, J. P. W., Araújo, M. B., … Robert, J. (2010). Scenarios for Global Biodiversity in the 21st Century. *Science*.

Pizo, M. A., & dos Santos, B. T. P. (2011). Frugivory, Post-Feeding Flights of Frugivorous Birds and the Movement of Seeds in a Brazilian Fragmented Landscape. *Biotropica*, *43*(3), 335–342. https://doi.org/10.1111/j.1744-7429.2010.00695.x

Poisot, T., Mouquet, N., & Gravel, D. (2013). Trophic Complementarity Drives the Biodiversity-Ecosystem Functioning Relationship in Food Webs. *Ecology Letters*, *16*(7), 853–861. https://doi.org/10.1111/ele.12118

Pulliam, H. R. (1988). Sources, Sinks, and Population Regulation. *The American Naturalist*, *132*(5), 652–661.

Purcell, S., Neale, B., Todd-Brown, K., Thomas, L., Ferreira, M. A. R., Bender, D., … Sham, P. C. (2007). PLINK: A Tool Set for Whole-Genome Association and Population-Based Linkage Analyses. *The American Journal of Human Genetics*, *81*(3), 559–575. https://doi.org/10.1086/519795

R Development Core Team. (2017). R. A Language and Environment for Statistical Computing.

Rattenbury, J. A. (2011). Unequal Sex-Ratios in Geniostoma - a Genetical Interpretation. *Auckland Bot. Soc.*, *66*, 144–151.

Reay, S. D., & Norton, D. A. (1999). Assessing the Success of Restoration Plantings in a Temperate New Zealand Forest. *Restoration Ecology*, *7*(3), 298–308. https://doi.org/10.1046/j.1526-100X.1999.72023.x

Reiss, J., Bridle, J. R., Montoya, J. M., & Woodward, G. (2009). Emerging Horizons in Biodiversity and Ecosystem Functioning Research. *Trends in Ecology & Evolution*, *24*, 505–514. https://doi.org/10.1016/j.tree.2009.03.018

Ribeiro da Silva, F., Montoya, D., Furtado, R., Memmott, J., Pizo, M. A., & Rodrigues, R. R. (2015). The Restoration of Tropical Seed Dispersal Networks. *Restoration Ecology*, *23*(6), 852–860. https://doi.org/10.1111/rec.12244

Rico, Y., & Wagner, H. H. (2016). Reduced Fine-Scale Spatial Genetic Structure in Grazed Populations of Dianthus carthusianorum. *Heredity*, *117*(5), 367–374. https://doi.org/10.1038/hdy.2016.45

Robertson, O. J., & Radford, J. Q. (2009). Gap-Crossing Decisions of Forest Birds in a Fragmented Landscape. *Austral Ecology*, *34*(4), 435–446. https://doi.org/10.1111/j.1442-9993.2009.01945.x

Rodewald, A. D., Rohr, R. P., Fortuna, M. A., & Bascompte, J. (2014). Community-Level Demographic Consequences of Urbanization: An Ecological Network Approach. *Journal of Animal Ecology*, *83*(6), 1409–1417. https://doi.org/10.1111/1365-2656.12224

Rodríguez-Rodríguez, M. C., Jordano, P., & Valido, A. (2017). Functional Consequences of Plant-Animal Interactions Along the Mutualism-Antagonism Gradient. *Ecology*, *98*(5), 1266–1276. https://doi.org/10.1002/ecy.1756

Rother, D. C., Pizo, M. A., & Jordano, P. (2016). Variation in Seed Dispersal Effectiveness: The Redundancy of Consequences in Diversified Tropical Frugivore Assemblages. *Oikos*, *125*(3), 336–342. https://doi.org/10.1111/oik.02629

Rudd, H., Vala, J., & Schaefer, V. (2002). Importance of Backyard Habitat in a Comprehensive Biodiversity Conservation Strategy: a Connectivity Analysis of Urban Green Spaces. *Restoration Ecology*, *10*(2), 368–375. https://doi.org/10.1046/j.1526-100X.2002.02041.x

Ruffell, J., & Didham, R. K. (2017). Conserving Biodiversity in New Zealand's Lowland Landscapes: Does Forest Cover or Pest Control Have a Greater Effect on Native Birds? *New Zealand Journal of Ecology*, *41*(1), 23–33. https://doi.org/10.20417/nzjecol.41.12

Russell, J. C., & Stanley, M. C. (2018). An Overview of Introduced Predator Management in Inhabited Landscapes. *Pacific Conservation Biology*. https://doi.org/10.1071/PC18013

Russo, S. E., & Augspurger, C. K. (2004). Aggregated Seed Dispersal by Spider Monkeys Limits Recruitment to Clumped Patterns in Virola calophylla. *Ecology Letters*, *7*(11), 1058–1067. https://doi.org/10.1111/j.1461-0248.2004.00668.x

Sandström, U. G., Angelstam, P., & Mikusiński, G. (2006). Ecological Diversity of Birds in Relation to the Structure of Urban Green Space. *Landscape and Urban Planning*, *77*(1–2), 39–53. https://doi.org/10.1016/j.landurbplan.2005.01.004

Santamaría, L., Rodríguez-Pérez, J., Larrinaga, A. R., & Pias, B. (2007). Predicting Spatial Patterns of Plant Recruitment Using Animal-Displacement Kernels. *PLoS ONE*, *2*(10). https://doi.org/10.1371/journal.pone.0001008

Sasal, Y., & Morales, J. M. (2013). Linking Frugivore Behavior to Plant Population Dynamics. *Oikos*, *122*(1), 95–103. https://doi.org/10.1111/j.1600-0706.2012.20669.x

Schleuning, M., Böhning-Gaese, K., Dehling, D. M., & Burns, K. C. (2014a). At a Loss for Birds: Insularity Increases Asymmetry in Seed-Dispersal Networks. *Global Ecology and Biogeography*, *23*, 385–394. https://doi.org/10.1111/geb.12134

Schleuning, M., Fruend, J., Klein, A.-M., Abrahamczyk, S., Alarcón, R., Albrecht, M., … Blüthgen, N. (2012). Specialization of Mutualistic Interaction Networks Decreases toward Tropical Latitudes. *Current Biology*, *22*, 1925–1931. https://doi.org/10.1016/j.cub.2012.08.015

Schleuning, M., Fründ, J., & García, D. (2015). Predicting Ecosystem Functions from Biodiversity and Mutualistic Networks: An Extension of Trait-Based Concepts to Plant-Animal Interactions. *Ecography*, *38*(4), 380–392. https://doi.org/10.1111/ecog.00983

Schleuning, M., Ingmann, L., Strauss, R., Fritz, S. A., Dalsgaard, B., Dehling, D. M., … Dormann, C. F. (2014b). Ecological, Historical and Evolutionary Determinants of Modularity in Weighted Seed-Dispersal Metworks. *Ecology Letters*, *17*, 454–463. https://doi.org/10.1111/ele.12245

Schupp, E. W. (1993). Quantity, Quality and the Effectiveness of Seed Dispersal by Animals. *Vegetatio*, *107/108*, 15–29.

Schupp, E. W., Jordano, P., & Gómez, J. M. (2010). Seed dispersal Effectiveness Revisited: a Conceptual Review. *The New Phytologist*, *188*(2), 333–353. https://doi.org/10.1111/j.1469-8137.2010.03402.x

Schupp, E. W., Jordano, P., & Gómez, J. M. (2017). A General Framework for Effectiveness Concepts in Mutualisms. *Ecology Letters*, *20*(5), 577–590. https://doi.org/10.1111/ele.12764

Sekercioglu, C. H., Loarie, S. R., Oviedo Brenes, F., Ehrlich, P. R., & Daily, G. C. (2007). Persistence of Forest Birds in the Costa Rican Agricultural Countryside. *Conservation Biology*, *21*(2), 482–494. https://doi.org/10.1111/j.1523-1739.2007.00655.x

Sfair, J. C., Arroyo-Rodríguez, V., Santos, B. A., & Tabarelli, M. (2016). Taxonomic and Functional Divergence of Tree Assemblages in a Fragmented Tropical Forest. *Ecological Applications*, *26*(6), 1816–1826. https://doi.org/10.1890/15-1673.1

Shurin, J. B., Amarasekare, P., Chase, J. M., Holt, R. D., Hoopes, M. F., & Leibold, M. A. (2004). Alternative Stable States and Regional Community Structure. *Journal of Theoretical Biology*, *227*(3), 359–368. https://doi.org/10.1016/j.jtbi.2003.11.013

Simmons, B. I., Sutherland, W. J., Dicks, L. V., Albrecht, J., Farwig, N., García, D., … González-Varo, J. P. (2018). Moving From Frugivory to Seed Dispersal: Incorporating the Functional Outcomes of Interactions in Plant–Frugivore Networks. *Journal of Animal Ecology*, *87*(4), 995–1007. https://doi.org/10.1111/1365-2656.12831

Simpson, P. (2017). *Tōtara, a Natural and Cultural History*. Auckland: Auckland University Press.

Snow, B., & Snow, D. W. (1988). *Birds and Berries*. T & AD Poyser.

Sol, D., Bartomeus, I., González-Lagos, C., & Pavoine, S. (2017). Urbanisation and the Loss of Phylogenetic Diversity in Birds. *Ecology Letters*, *20*(6), 721–729. https://doi.org/10.1111/ele.12769

Spiegel, O., & Nathan, R. (2007). Incorporating Dispersal Distance Into the Disperser Effectiveness Framework: Frugivorous Birds Provide Complementary Dispersal to Plants in a Patchy Environment. *Ecology Letters*, *10*, 718–728. https://doi.org/10.1111/j.1461-0248.2007.01062.x

Stachowicz, J. J. (2001). Mutualism, Facilitation, and the Structure of Ecological Communities. *BioScience*, *51*(3).

Städele, V., & Vigilant, L. (2016). Strategies for Determining Kinship in Wild Populations Using Genetic Data. *Ecology and Evolution*, *6*(17), 6107–6120. https://doi.org/10.1002/ece3.2346

Stanley, M. C., & Bassett, I. E. (2014). Environmental Weeds in New Zealand: Impacts and Management. In *Austral Ark: The State of Wildlife in Australia and New Zealand* (p. 134). Cambridge University Press.

Stanley, M. C., & Lill, A. (2002). Avian Fruit Consumption and Seed Dispersal in a Temperate Australian Woodland. *Austral Ecology*, *27*, 137–148.

Stansbury, C. D. (2001). Dispersal of the Environmental Weed Bridal Creeper, Asparagus asparagoides, by Silvereyes, Zosterops lateralis, in South-Western Australia. *Emu*, *101*(1), 39–45. https://doi.org/10.1071/MU00069

Strauss, S. Y., & Irwin, R. E. (2004). Ecological and Evolutionary Consequences of Multispecies Plant-Animal Interactions. *Annual Review of Ecology, Evolution, and Systematics*, *35*(1), 435–466. https://doi.org/10.1146/annurev.ecolsys.35.112202.130215

Taylor, H. R., Kardos, M. D., Ramstad, K. M., & Allendorf, F. W. (2015). Valid Estimates of Individual Inbreeding Coefficients From Marker-Based Pedigrees are not Feasible in Wild Populations with Low Allelic Diversity. *Conservation Genetics*, *16*(4), 901–913. https://doi.org/10.1007/s10592-015-0709-1

Thompson, R. M., Brose, U., Dunne, J. A., Hall, R. O., Hladyz, S., Kitching, R. L., … Tylianakis, J. M. (2012). Food Webs: Reconciling the Structure and Function of Biodiversity. *Trends in Ecology and Evolution*, *27*(12), 689–697. https://doi.org/10.1016/j.tree.2012.08.005

Tilman, D. (1994). Competition and Biodiversity in Spatially Structured Habitats. *Ecology*, *75*(1), 2–16.

Tilman, D., Knops, J., Wedin, D., Reich, P., Ritchie, M., & Siemann, E. (1997). The Influence of Functional Diversity and Composition on Ecosystem Processes. *Science*, *277*(5330), 1300–1302. https://doi.org/10.1126/science.277.5330.1300

Trakhtenbrot, A., Nathan, R., Perry, G., & Richardson, D. M. (2005). The Importance of Long-Distance Dispersal in Biodiversity Conservation. *Diversity and Distributions*, *11*(2), 173–181. https://doi.org/10.1111/j.1366-9516.2005.00156.x

Traveset, A., Heleno, R. H., & Nogales, M. (2014). The Ecology of Seed Dispersal. In R. S. Gallagher (Ed.), *Seeds: The ecology of Regeneration in Plant Communities* (3rd Edition, Vol. 2, pp. 85–110). CAB International.

Traveset, A., & Richardson, D. M. (2006). Biological Invasions as Disruptors of Plant Reproductive Mutualisms. *Trends in Ecology and Evolution*, *21*(4), 208–216. https://doi.org/10.1016/j.tree.2006.01.006

Traveset, A., & Richardson, D. M. (2014). Mutualistic Interactions and Biological Invasions. *Annual Review of Ecology, Evolution, and Systematics*, *45*(1), 89–113. https://doi.org/10.1146/annurev-ecolsys-120213-091857

Tylianakis, J. M. (2008). Understanding the Web of Life: the Birds, the Bees, and Sex with Aliens. *PLoS Biology*, *6*(2). https://doi.org/10.1371/journal.pbio.0060047

Tylianakis, J. M., Didham, R. K., Bascompte, J., & Wardle, D. A. (2008). Global Change and Species Interactions in Terrestrial Ecosystems. *Ecology Letters*, *11*(12), 1351–1363. https://doi.org/10.1111/j.1461-0248.2008.01250.x

Tylianakis, J. M., Laliberté, E., Nielsen, A., & Bascompte, J. (2010). Conservation of Species Interaction Networks. *Biological Conservation*, *143*(10), 2270–2279. https://doi.org/10.1016/j.biocon.2009.12.004

Tylianakis, J. M., & Morris, R. J. (2017). Ecological Networks Across Environmental Gradients. *Annual Review of Ecology, Evolution, and Systematics*, *48*, 25–48. https://doi.org/10.1146/annurev-ecolsys-110316-022821

Tylianakis, J. M., Tscharntke, T., & Lewis, O. T. (2007). Habitat Modification Alters the Structure of Tropical Host – Parasitoid Food Webs. *Nature*, *445*(January). https://doi.org/10.1038/nature05429

Uriarte, M., Anciães, M., Silva, M. T. B., Rubim, P., Johnson, E., Bruna, E. M., … Anciães, M. (2011). Disentangling the Drivers of Reduced Long-Distance Seed Dispersal by Birds in an Experimentally Fragmented Landscape. *Ecology*, *92*(4), 924–937. https://doi.org/10.1890/10-0709.1

Valiente-Banuet, A., Aizen, M. a., Alcántara, J. M., Arroyo, J., Cocucci, A., Galetti, M., … Zamora, R. (2015). Beyond Species Loss: the Extinction of Ecological Interactions in a Changing World. *Functional Ecology*, *29*(3), 299–307. https://doi.org/10.1111/1365-2435.12356

van Heezik, Y., Smyth, A., Adams, A., & Gordon, J. (2010). Do Domestic Cats Impose an Unsustainable Harvest on Urban Bird Populations? *Biological Conservation*, *143*(1), 121–130. https://doi.org/10.1016/j.biocon.2009.09.013

van Heezik, Y., Smyth, A., & Mathieu, R. (2008). Landscape and Urban Planning Diversity of Native and Exotic Birds Across an Urban Gradient in a New Zealand City. *Landscape and Urban Planning*, *87*, 223–232. https://doi.org/10.1016/j.landurbplan.2008.06.004

Vázquez, D. P., & Aizen, M. A. (2003). Null Model Analyses of Specialization in Plant-Pollinator Interactions. *Ecology*, *84*(9), 2493–2501.

Vázquez, D. P., & Aizen, M. A. (2004). Asymmetric Specilization: a Pervasive Feature of Plant-Pollinator Interactions. *Ecology*, *85*(5), 1251–1257. https://doi.org/10.1890/03-3112

Vázquez, D. P., Blüthgen, N., Cagnolo, L., & Chacoff, N. P. (2009). Uniting Pattern and Process in Plant-Animal Mutualistic Networks: A Review. *Annals of Botany*, *103*(9), 1445–1457. https://doi.org/10.1093/aob/mcp057

Vázquez, D. P., Chacoff, N. P., & Cagnolo, L. (2009). Evaluating Multiple Determinants of the Structure of Plant-Animal Mutualistic Networks. *Ecology*, *90*(8), 2039–2046.

Vázquez, D. P., Morris, W. F., & Jordano, P. (2005). Interaction Frequency as a Surrogate for the Total Effect of Animal Mutualists on Plants. *Ecology Letters*, *8*(10), 1088–1094. https://doi.org/10.1111/j.1461-0248.2005.00810.x

Wang, B. C., & Smith, T. B. (2002). Closing the Seed Dispersal to Loop. *Trends in Ecology and Evolution*, *17*, 379–386.

Wang, J. (2007). Triadic IBD Coefficients and Applications to Estimating Pairwise Relatedness. *Genetical Research*, *89*(3), 135–153. https://doi.org/10.1017/S0016672307008798

Wang, J. (2011). COANCESTRY: A Program for Simulating, Estimating and Analysing Relatedness and Inbreeding Coefficients. *Molecular Ecology Resources*, *11*(1), 141–145. https://doi.org/10.1111/j.1755-0998.2010.02885.x

Wang, J. (2013). An Improvement on the Maximum Likelihood Reconstruction of Pedigrees from Marker Data. *Heredity*, *111*(2), 165–174. https://doi.org/10.1038/hdy.2013.34

Wang, J., & Santure, A. W. (2009). Parentage and Sibship Inference from Multilocus Genotype Data Under Polygamy. *Genetics*, *181*(4), 1579–1594. https://doi.org/10.1534/genetics.108.100214

Wenny, D. G. (2001). Advantages of Seed Dispersal: A Re-Evaluation of Directed Dispersal. *Evolutionary Ecology Research*, *3*(1), 51–74. https://doi.org/10.1002/(SICI)1098-2345(200004)50:4<275::AID-AJP4>3.0.CO;2-K

Wenny, D. G., & Levey, D. J. (1998). Directed Seed Dispersal by Bellbirds in a Tropical Cloud Forest, *95*(May), 6204–6207.

Wheelwright, N. T., & Orians, G. H. (1982). Seed Dispersal by Animals : Contrasts with Pollen Dispersal , Problems of Terminology , and Constraints on Coevolution. *American Society of Naturalists*, *119*(3), 402–413.

Whitaker, A. H. (1987). The Roles of Lizards in New Zealand Plant Reproductive Strategies. *New Zealand Journal of Botany*, *25*(2), 315–328. https://doi.org/10.1080/0028825X.1987.10410078

Wilcox, M. D. (2012). *Auckland´s Remarkable Urban Forest*. Auckland Botanical Society.

Williams, P. A. (2006). The Role of Blackbirds (Turdus merula) in Weed Invasion in New Zealand. *New Zealand Journal of Ecology*, *30*(2), 285–291. https://doi.org/10.2307/24056350

Williams, P. A., & Karl, B. J. (1996). Fleshy fruits of Indigenous and Adventuve Plants in the Diet of Birds in Forest Remnants, Nelson, New Zealand. *New Zealand Journal of Botany*, *20*(1990), 127–145.

Willson, M. F., Irvine, A. K., & Walsh, N. G. (1989). Vertebrate Dispersal Syndromes in Some Australian and New Zealand Plant Communities. *Biotropica, 21*(2), 133–147.

Willson, M. F., Rice, B. L., & Westoby, M. (1990). Seed Dispersal Spectra: A Comparison of Temperate Plant Communities. *Journal of Vegetation Science*, *1*(4), 547–562. https://doi.org/10.2307/3235789

Wood, V., Seddon, P. J., Beaven, B., & van Heezik, Y. (2016). Movement and Diet of Domestic Cats on Stewart Island/Rakiura, New Zealand. *New Zealand Journal of Ecology*, *40*(December 2004), 186–190.

Woodward, G., Speirs, D. C., & Hildrew, A. G. (2005). Quantification and Resolution of a Complex, Size Structured Food Web. *Advances in Ecological Research*, *36*(August 2015), 85–135. https://doi.org/10.1016/S0065-2504(05)36002-8

Wotton, D. M., & Kelly, D. (2012). Do Larger Frugivores Move Seeds Further? Body Size, Seed Dispersal Distance, and a Case Study of a Large, Sedentary Pigeon. *Journal of Biogeography*, *39*(11), 1973–1983. https://doi.org/10.1111/jbi.12000

Wotton, D. M., & McAlpine, K. G. (2015). Seed Dispersal of Fleshy-Fruited Environmental Weeds in New Zealand. *New Zealand Journal of Ecology*, *39*(2), 155–169.

Wright, J. S. (2002). Plant Diversity in Tropical Forests: a Review of Mechanisms of Species Coexistence. *Oecologia*, *130*(1), 1–14. https://doi.org/10.1007/s004420100809

Zamora, R. (2000). Functional Equivalence in Plant-Animal Interactions: Ecological and Evolutionary Consequences. *Oikos*, *88*(2), 442–447. https://doi.org/10.1034/j.1600-0706.2000.880222.x

Zuur, A. F., Leno, E. N., Smith, G. M., Saveliev, A. A., & Walker, N. (2009). *Mixed Effects Models and Extensions in Ecology with R*.

Appendix A – Supplementary information for Chapter 2

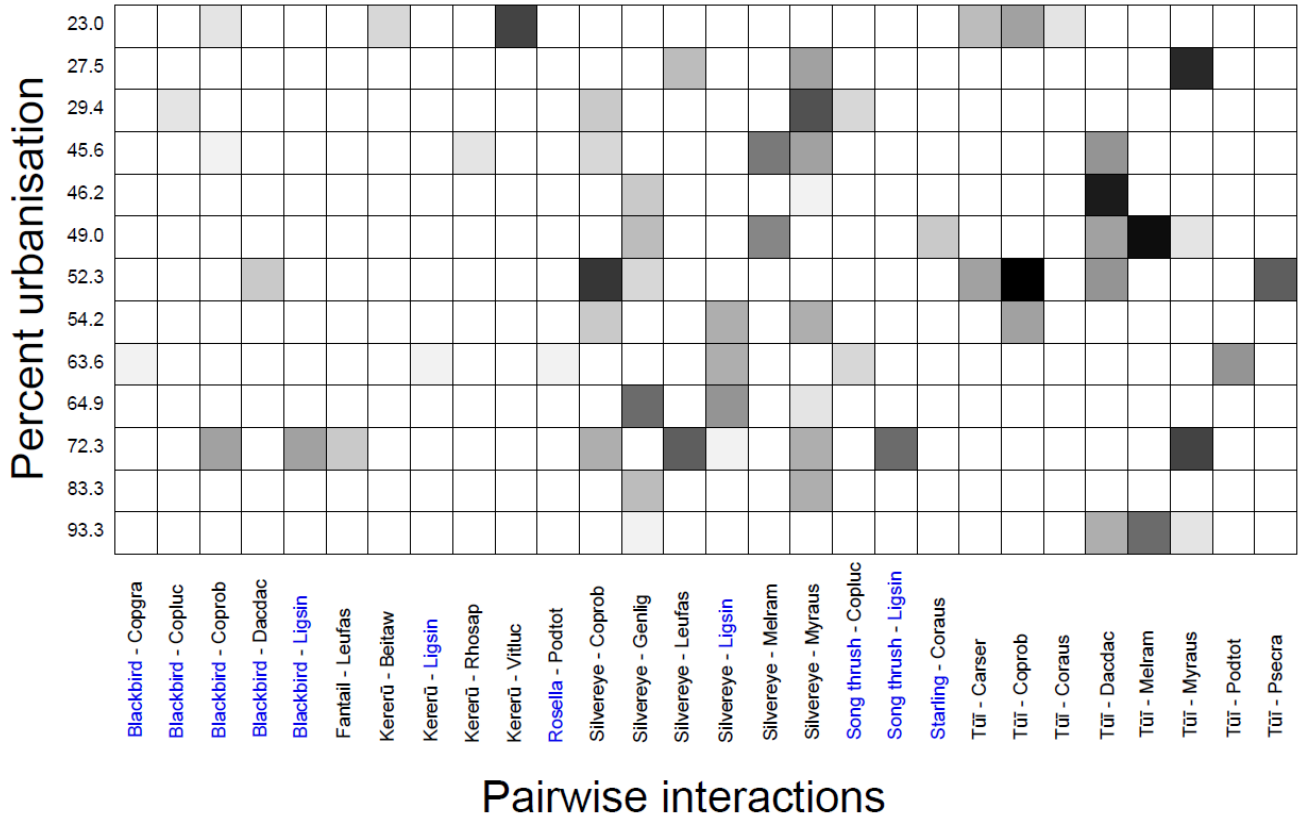


Figure A1. Site-species interaction matrix showing the presence and frequency of interactions across the urbanisation gradient. Rows are sites and are labelled by the percent of urbanisation cover within a 2,000 m radius of the habitat fragment. Columns are pairwise plant-frugivore interactions. Matrix square shading indicates the number of interactions recorded for each plant-frugivore pair at habitat fragment. Exotic species are denoted in blue. Plant species scientific names are: Copgra, *Coprosma grandifolia*; Copluc, *Coprosma lucida*; Coprob, *Coprosma robusta*; Dacdac; *Dacrycarpus dacrydioides*; Ligsin, *Ligustrum sinense*; Leufas, Leucopogon fasciculatus; Beitaw, *Beilschmiedia tawa*; Rhosap, *Rhopalostylis sapida*; Vitluc, *Vitex lucens*; Podtot, *Podocarpus totara*; Genlig, *Geniostoma ligustrifolium*; Melram, *Melicytus ramiflorus*; Myraus, *Myrsine australis*; Coraus, *Cordyline australis*; Carser, *Carpodetus serratus*; Psecra, *Pseudopanax crassifolius*.

Table A1. Location and size details of the sites used for focal and mist-netting sampling of plant-frugivore interactions.

Site name	Code	Geographical location	Size (ha)	Size category
Awaruku Bush Reserve	AWA	36˚ 41’ 45’’ / 174˚ 44’ 11’’	3.36	Medium
Coventry Way Reserve	COV	36˚ 41’ 32’’ / 174˚ 44’ 25’’	0.64	Small
Cyclarama Reserve	CYC	36˚ 50’ 02’’ / 174˚ 36’ 29’’	1.28	Small
Fernhill Escarpment	FER	36˚ 44’ 18’’ / 174˚ 42’ 59’’	13.5	Large
Fitzwilliam Drive Reserve	FIT	36˚ 41’ 37’’ / 174˚ 43’ 70’’	1.38	Small
Emlyn Place Reserve	FIT2	36˚ 41’ 52’’ / 174˚ 43’ 39’’	0.9	Small
Gills Reserve	GIL	36˚ 43’ 15’’ / 174˚ 41’ 16’’	8.38	Large
Kemp Park	KEM	36˚ 50’ 11’’ / 174˚ 36’ 76’’	1.11	Small
Saddleback Reserve	SAD	36˚ 44’ 02’’ / 174˚ 44’ 22’’	8.52	Large
Shakespear Regional Park	SHA	36˚ 36’ 11’’ / 174˚ 49’ 08’’	17.54	Large
Silverdale Reserve	SIL	36˚ 36’ 57’’ / 174˚ 40’ 34’’	4.62	Medium
Unsworth Reserve	UNS	36˚ 45’ 27’’ / 174˚ 42’ 60’’	4.00	Medium
Zita Maria Park	ZIT	36˚ 50’ 59’’ / 174˚ 36’ 47’’	4.83	Medium

Table A2. Variance inflation factor values.

Model response	Fixed effect	Variance inflation factor
Fruit consumption	Frugivore richness	1.165663
	Frugivore complementarity	1.279963
	Bird abundance	1.188615
	Percent urbanisation	1.766004
	Percent forest	2.099471
	Fragment size	1.525619
Frugivore richness	Percent urbanisation	1.492791
	Percent forest	1.786563
	Fragment size	1.242850
Frugivore complementarity	Frugivore richness	1.058379
	Percent urbanisation	1.561973
	Percent forest	1.829427
	Fragment size	1.280389
Bird abundance	Percent urbanisation	1.495965
	Percent forest	1.819561
	Fragment size	1.267470

Table A3. Plant and bird species recorded across all sites in the study.

Plants			
Common name	**Scientific name**	**Plant family**	**Fruit type**
Nikau	*Rhopalostylis sapida*	Arecaceae	fleshy fruit
Horoeka	*Pseudopanax crassifolius*	Araliaceae	fleshy fruit
Cabbage tree	*Cordyline australis*	Asparagaceae	fleshy fruit
Tall Mingimingi	*Leucopogon fasciculatus*	Ericaceae	fleshy fruit
Puriri	*Vitex lucens*	Lamiaceae	fleshy fruit
Hangehange	*Geniostoma ligustrifolium*	Langoniaceae	capsule (sticky seeds)
Tawa	*Beilschmiedia tawa*	Lauraceae	fleshy fruit
Mapau	*Myrsine australis*	Myrsinaceae	fleshy fruit
Chinese privet *	*Ligustrum sinense*	Oleaceae	fleshy fruit
Kahikatea	*Dacrydium dacydioides*	Podocarpaceae	fleshy cone
Tōtara	*Podocarpus totara*	Podocarpaceae	fleshy cone
Putaputaweta	*Carpodetus serratus*	Rousseaceae	capsule
Kanoko	*Coprosma grandifolia*	Rubiaceae	fleshy fruit
Shiny Karamu	*Coprosma lucida*	Rubiaceae	fleshy fruit
Karamu	*Coprosma robusta*	Rubiaceae	fleshy fruit
Mahoe	Melicytus ramiflorus	Violaceae	fleshy fruit

*Exotic species

Birds		
Common name	**Scientific name**	**Bird family**
Kererū	*Hemiphaga novaeseelandiae*	Columbidae
Eastern Rosella *	*Platycercus eximius*	Psittacidae
Tūī	*Prosthemadera novaeseelandiae*	Meliphagidae
Starling *	*Sturnus vulgaris*	Sturnidae
Fantail	*Rhipidura fuliginosa*	Rhipiduridae
Blackbird *	*Turdus merula*	Turdidae
Song Thrush *	*Turdus philomelos*	Turdidae
Silvereye **	*Zosterops lateralis*	Zosteropidae

*Exotic species, introduced by European colonists in the 19th century (Kelly et al., 2010).

**Species that naturally colonized New Zealand from Australia in the past 200 years, therefore considered as native (Burns, 2012).

Appendix B – Supplementary information for Chapter 3

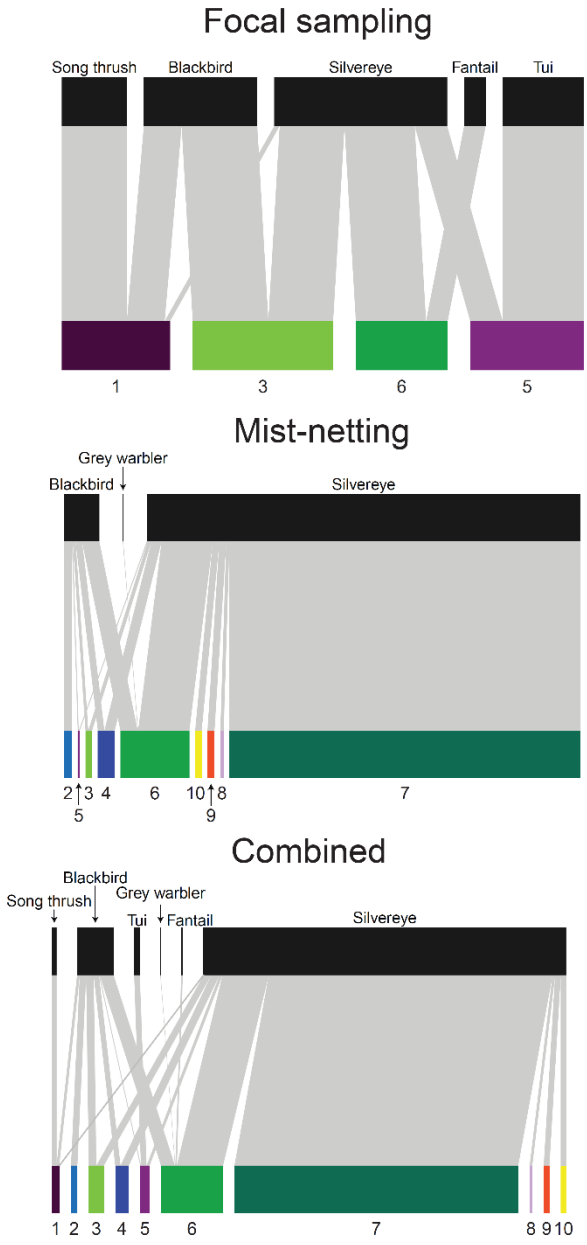


Figure B1. Bipartite network diagrams for different sampling methods for one site (Zita Maria Park) pooled by seasons, showing high level species (birds) on the top and low level species (plants) on the bottom. The width of links between birds and plants represents the proportional number of interactions for each species pair in the network. Plant species are represented as number 1= *Ligustrum sinense*, 2= *Lonicera japonica*, 3= *Coprosma robusta*, 4= *Cordyline australis*, 5= *Myrsine australis*, 6= *Leucopogon fasciculatus*, 7= *Geniostoma ligustrifolium*, 8= *Pseudopanax arboreus*, 9= *Melicytus ramiflorus*, 10= *Ficus carica*.

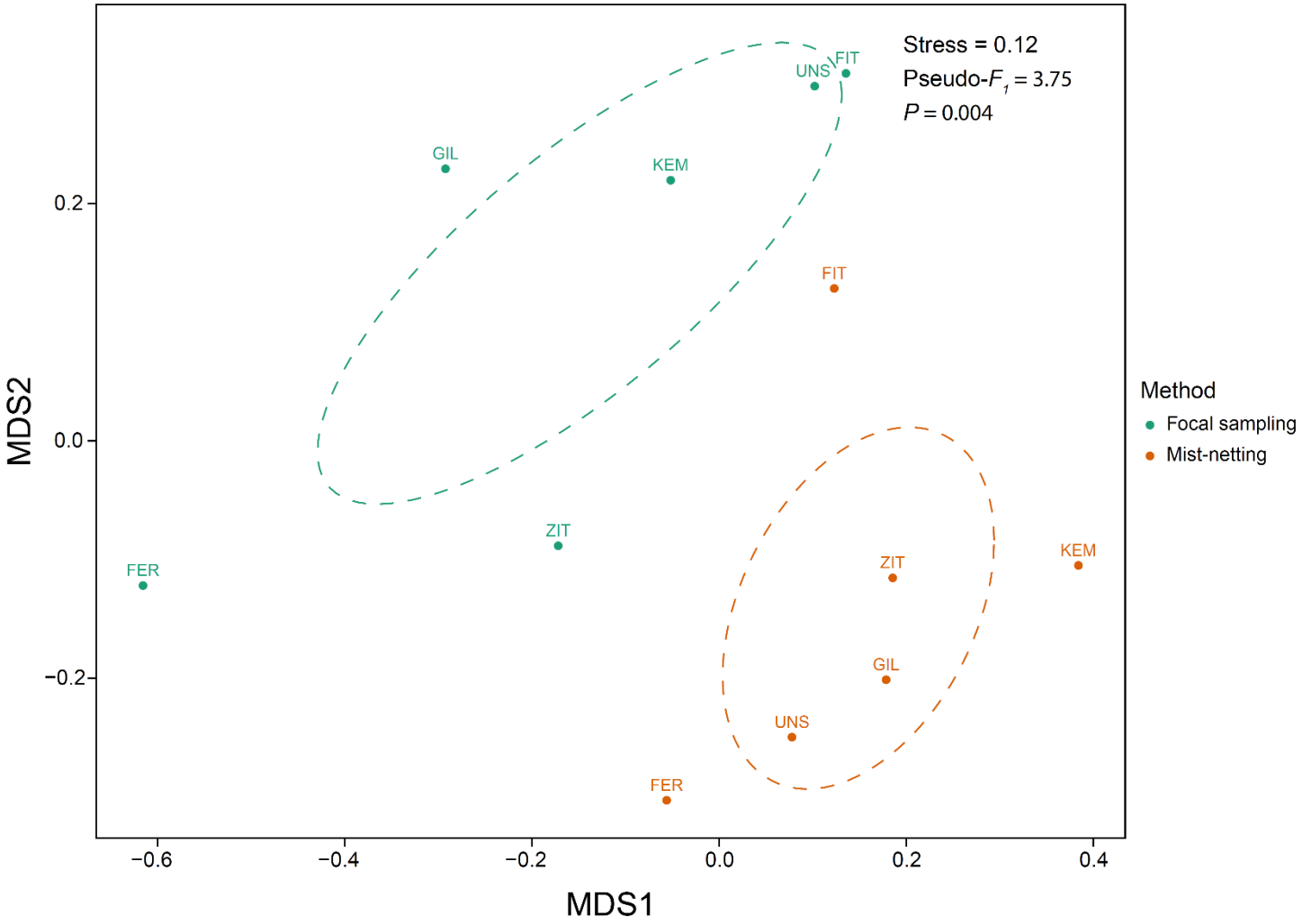


Figure B2. NMDS ordination of the composition of plant-frugivore interactions (binary) for focal sampling and mist-netting methods. The dotted ellipses denote the 95% confidence interval for each sampling method. Abbreviated study site names are given for each network (see Table B1 for full description of sites).

Table B1. Location and size details of the sites used for focal and mist-netting sampling of plant-frugivore interactions.

Site name	Code	Geographical location	Size (ha)
Fernhill Escarpment	FER	36˚ 44’ 18’’ / 174˚ 42’ 59’’	13.50
Fitzwilliam Drive Reserve	FIT	36˚ 41’ 37’’ / 174˚ 43’ 70’’	1.38
Gills Reserve	GIL	36˚ 43’ 15’’ / 174˚ 41’ 16’’	8.38
Kemp Park	KEM	36˚ 50’ 11’’ / 174˚ 36’ 76’’	1.11
Unsworth Reserve	UNS	36˚ 45’ 27’’ / 174˚ 42’ 60’’	4.00
Zita Maria Park	ZIT	36˚ 50’ 59’’ / 174˚ 36’ 47’’	4.83

Table B2. Plant and bird species recorded across all sites for both methods in the study.

Plants

Common name	Scientific name	Plant family	Fruit type
Five-finger	*Pseudopanax arboreus*	Araliaceae	fleshy fruit
Climbing asparagus *	*Asparagus scandens*	Asparagaceae	fleshy fruit
Cabbage tree	*Cordyline australis*	Asparagaceae	fleshy fruit
Japanese honeysuckle *	*Lonicera japonica*	Caprifoliaceae	fleshy fruit
Tall Mingimingi	*Leucopogon fasciculatus*	Ericaceae	fleshy fruit
Hangehange	*Geniostoma ligustrifolium*	Langoniaceae	capsule (sticky seeds)
Fig *	*Ficus carica*	Moraceae	fleshy fruit
Mapau	*Myrsine australis*	Myrsinaceae	fleshy fruit
Chinese privet *	*Ligustrum sinense*	Oleaceae	fleshy fruit
Tanekaha	*Phyllocladus trichomanoides*	Phyllocladaceae	fleshy cone
Inkweed *	*Phytolacca octandra*	Phytolaccaceae	fleshy fruit
Kahikatea	*Dacrydium dacydioides*	Podocarpaceae	fleshy cone
Totara	*Podocarpus totara*	Podocarpaceae	fleshy cone
Blackberry *	*Rubus fruticosus*	Rosaceae	fleshy fruit
Kanoko	*Coprosma grandifolia*	Rubiaceae	fleshy fruit
Shiny Karamu	*Coprosma lucida*	Rubiaceae	fleshy fruit
Twiggy Coprosma	*Coprosma rhamnoides*	Rubiaceae	fleshy fruit
Karamu	*Coprosma robusta*	Rubiaceae	fleshy fruit
Woolly Nightshade *	*Solanum mauritianum*	Solanaceae	fleshy fruit
Black Nightshade *	*Solanum nigrum*	Solanaceae	fleshy fruit
Large-leaved mahoe	Melicytus macrophyllus	Violaceae	fleshy fruit
Mahoe	Melicytus ramiflorus	Violaceae	fleshy fruit

*Exotic species

Birds

Common name	Scientific name	Bird family
Grey warbler	*Gerygone igata*	Acanthizidae
Kererū	*Hemiphaga novaeseelandiae*	Columbidae
Chaffinch *	*Fringilla coelebs*	Fringillidae
Eastern Rosella	*Platycercus eximius*	Psittacidae
Tūī	*Prosthemadera novaeseelandiae*	Meliphagidae

Fantail	*Rhipidura fuliginosa*	Rhipiduridae
Blackbird *	*Turdus merula*	Turdidae
Song Thrush *	*Turdus philomelos*	Turdidae
Silvereye **	*Zosterops lateralis*	Zosteropidae

*Exotic species, introduced by European colonists in the 19th century (Kelly et al., 2010).
**Species that naturally colonized New Zealand from Australia in the past 200 years, therefore considered as native (Burns, 2012).

Table B3. Literature sources from which number of seeds per fruits were obtained.

Common name	**Scientific name**	**Number of seeds per fruit**	**Literature source**
Tall Mingimingi	*Leucopogon fasciculatus*	1	Cowan, 1992
Hangehange	*Geniostoma ligustrifolium*	30	Rattenbury, 2011
Mapau	*Myrsine australis*	1	Cowan, 1992
Chinese privet *	*Ligustrum sinense*	1	Williams & Karl, 1996
Kahikatea	*Dacrydium dacydioides*	1	Williams & Karl, 1996
Totara	*Podocarpus totara*	1	Cowan, 1992
Kanoko	*Coprosma grandifolia*	2	Cowan, 1992
Shiny Karamu	*Coprosma lucida*	2	Cowan, 1992
Karamu	*Coprosma robusta*	2	Cowan, 1992

*Exotic species

Table B4. Nestedness values of plant-frugivore interactions as detected by focal sampling within interactions detected by mist-netting and vice versa. Values of 0 indicate non-nestedness and values of 100 perfect nesting.

Site	**Focal sampling within mist-netting**	**Mist-netting within focal sampling**
FER	33.33	0
FIT	66.66	0
GIL	25	0
KEM	33.33	0
UNS	100	0
ZIT	44.44	0

Table B5. Spearman's and Pearson's rank correlation statistics for network-level and group-level metrics.

	Spearman's			Pearson's		
Network metric	**S**	***P*-value**	**rho (ρ)**	**t-value**	***P*-value**	**r**
Connectance	11.66	0.15	0.67	2.38	0.07	0.77
Number of bird species	15.30	0.25	0.56	1.47	0.21	0.59
Number of plant species	40.40	0.77	-0.15	-0.41	0.70	-0.20
Interaction strength asymmetry (ISA)	28.91	0.74	0.17	0.51	0.63	0.25
Interaction evenness	38	0.92	-0.09	-0.78	0.48	-0.36
Generality	28	0.71	0.2	0.18	0.87	0.08
Vulnerability	14.52	0.22	0.58	1.13	0.32	0.49

Table B6. Percentage of plant-frugivore interactions detected at each site with focal sampling and mist-netting methods pooled by seasons. Estimated values of richness were computed using the Chao 2 estimator. S_o, observed interaction richness; S_E, estimated asymptotic species richness; *%*, sampling completeness.

Site	**Method**	**No. of census**	**Time investment (hrs)**	S_o	S_E	**%**
FER	Focal	36	7.2	6	18	33
FER	Mist-netting	4	40	15	23	66
FIT	Focal	12	7.2	3	4	77
FIT	Mist-netting	4	40	7	23	31
GIL	Focal	36	7.2	4	7	58
GIL	Mist-netting	4	40	11	16	71
KEM	Focal	12	7.2	3	3	87
KEM	Mist-netting	4	40	5	13	40
UNS	Focal	36	7.2	2	3	67
UNS	Mist-netting	4	40	18	50	36
ZIT	Focal	36	7.2	9	27	34
ZIT	Mist-netting	4	40	13	19	68

Table B7. Summary statistics for GLMMs used to determine differences in metric values between focal sampling vs. mist-netting methods.

Metric	**Estimate**	**Standard error**	**df**	**t-value**	***p*-value**	**Distribution used**	**Response (value/log)**
Connectance	-0.01	0.08	5	-0.11	0.9158	Gamma with log link	Log
Number of bird species	-0.16	0.41	5	-0.41	0.6855	Truncated Poisson	Value
Number of plant species	1.11	0.28	5	3.92	0.0000876	Truncated Poisson	Value
Interaction strength asymmetry (ISA)	-0.43	0.14	5	-3.01	0.0297	Gaussian	Value
Interaction evenness	-0.24	0.27	5	-0.88	0.379	Gamma with log link	Log
Generality	0.25	0.07	5	3.41	0.0006	Gamma with log link	Log
Vulnerability	-0.07	0.05	5	-1.56	0.118	Gamma with log link	Log

Appendix C – Supplementary information for Chapter 4

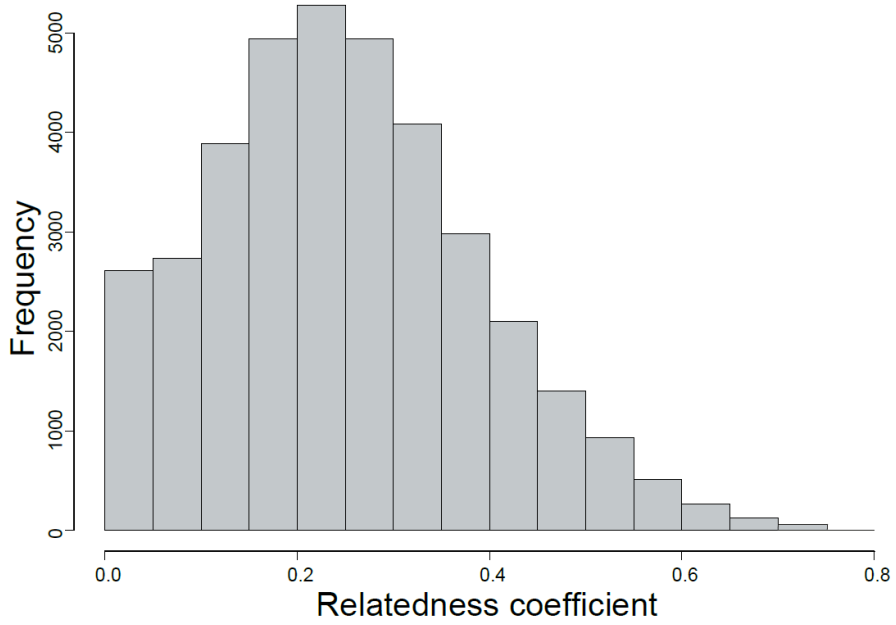


Figure C1. Distribution of relatedness coefficients among the 273 tōtara individuals.

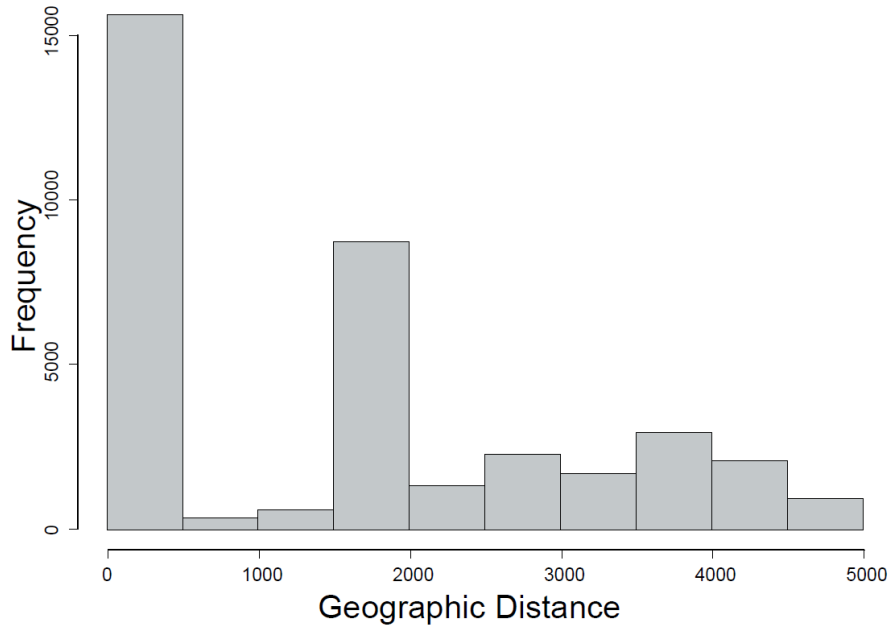


Figure C2. Distribution of geographic distances among the 273 tōtara individuals.

Table C1. Location and size details of the sites used for sampling of tōtara individuals. Details of the sampling method used at each fragment are also included.

Site name	Code	Geographical location	Size (ha)	Sampling protocol
Ark in the Park	ARK	36˚ 53’ 02’’ / 174˚ 31’ 22’’	2,000	Random
Eskdale Reserve	ESK	36˚ 74’ 42’’ / 174˚ 43’ 07’’	15	Random
Fernhill Escarpment	FER	36˚ 44’ 18’’ / 174˚ 42’ 59’’	13.5	Exhaustive, but only for a sub area of the fragment
Gills Reserve	GIL	36˚ 43’ 15’’ / 174˚ 41’ 16’’	8.38	Exhaustive
Saddleback Reserve	SAD	36˚ 44’ 02’’ / 174˚ 44’ 22’’	8.52	Exhaustive
Unsworth Reserve	UNS	36˚ 45’ 27’’ / 174˚ 42’ 60’’	4.00	Exhaustive

Table C2. Full-sibling tōtara relationships and probabilities found in this study by COLONY.

Offspring 1 ID	Offspring 2 ID	Probability	Offspring 1 ID	Offspring 2 ID	Probability
TCF-1	TGC-31	1	TCF-8	TR-F10	0.944
TCF-10	TCF-18	1	TGC-42	TUC-17	0.943
TCF-11	TFM-49	1	TFM-27	TGM-14	0.942
TCF-11	TMF-1	1	TR-F10	TUC-7	0.941
TCF-11	TMF-14	1	TCF-3	TCF-8	0.939
TCF-11	TR-F11	1	TR-F26	TUM-50	0.939
TCF-12	TR-F20	1	TPC-3	TR-F7	0.937
TCF-13	TFM-49	1	TPM-9	TR-F20	0.937
TCF-13	TR-F11	1	TPC-7	TPC-8	0.934
TCF-13	TR-F3	1	TFM-27	TGC-10	0.932
TCF-18	TCF-27	1	TGC-5	TR-F56	0.931
TCF-18	TMF-11	1	TCF-10	TR-F46	0.93
TCF-18	TR-F32	1	TCF-27	TR-F17	0.929
TCF-18	TR-F46	1	TGM-20	TPM-11	0.929
TCF-19	TGM-48	1	TCF-7	TFM-4	0.928
TCF-19	TPC-5	1	TCF-3	TCF-7	0.927
TCF-20	TFM-49	1	TCF-7	TMF-3	0.927
TCF-20	TMF-1	1	TCF-7	TR-F37	0.927
TCF-20	TR-F11	1	TGM-168	TUM-13	0.927
TCF-20	TR-F3	1	TCF-12	TUC-15	0.926
TCF-24	TPC-3	1	TCF-7	TPM-6	0.926
TCF-24	TPM-8	1	TFM-1	TGM-20	0.926
TCF-24	TR-F7	1	TCF-3	TUM-48	0.925
TCF-27	TFC-15	1	TFM-22	TUC-2	0.925
TCF-27	TMF-11	1	TGM-166	TGM-93	0.923
TCF-27	TMF-12	1	TMF-3	TPM-6	0.921
TCF-27	TMF-7	1	TCF-7	TCF-8	0.919
TCF-3	TFM-4	1	TCF-27	TFC-17	0.917

TCF-3	TMF-3	1	TGC-18	TUM-48	0.915
TFM-1	TUM-10	1	TGC-1	TGM-14	0.914
TFM-49	TMF-1	1	TGC-45	TGC-50	0.914
TFM-49	TR-F11	1	TFM-3	TR-F46	0.913
TGC-13	TGC-23	1	TFM-4	TPM-6	0.909
TGC-13	TGC-49	1	TGM-169	TGM-175	0.909
TGC-13	TGM-162	1	TFC-17	TMF-7	0.908
TGC-13	TGM-82	1	TMF-3	TUC-7	0.907
TGC-13	TUM-2	1	TFC-17	TUC-2	0.903
TGC-15	TGM-26	1	TGC-17	TR-F5	0.903
TGC-23	TGC-49	1	TCF-28	TGC-10	0.901
TGC-23	TGM-162	1	TMF-10	TR-F10	0.898
TGC-23	TUM-2	1	TCF-23	TFM-13	0.895
TGC-25	TGC-44	1	TCF-27	TFM-3	0.895
TGC-25	TGM-118	1	TR-F56	TUM-10	0.894
TGC-25	TGM-75	1	TCF-8	TGC-2	0.893
TGC-25	TGM-83	1	TCF-7	TR-F10	0.892
TGC-25	TGM-86	1	TFM-27	TGC-26	0.892
TGC-26	TGM-14	1	TMF-12	TR-F60	0.891
TGC-33	TGC-4	1	TPM-8	TR-F48	0.888
TGC-34	TGC-45	1	TR-F20	TUC-15	0.887
TGC-34	TGC-52	1	TCF-7	TGC-18	0.886
TGC-34	TGM-167	1	TCF-2	TCF-24	0.885
TGC-39	TGM-174	1	TMF-7	TR-F60	0.883
TGC-4	TGC-50	1	TGC-42	TPM-4	0.878
TGC-44	TGM-118	1	TMF-10	TR-F37	0.874
TGC-44	TGM-75	1	TCF-7	TUC-7	0.873
TGC-44	TGM-83	1	TGC-33	TGC-45	0.864
TGC-44	TGM-86	1	TFM-3	TR-F60	0.862
TGC-49	TGM-162	1	TGM-7	TPM-11	0.862
TGC-5	TGM-20	1	TGC-33	TGC-52	0.861
TGC-50	TGC-52	1	TMF-13	TR-F11	0.861
TGC-51	TGM-10	1	TMF-2	TUM-10	0.86
TGC-52	TGM-167	1	TFM-22	TR-F60	0.859
TGC-6	TGM-1	1	TPM-9	TUC-15	0.857
TGC-6	TGM-173	1	TGM-169	TGM-174	0.85
TGC-6	TGM-18	1	TFM-22	TR-F17	0.849
TGM-1	TGM-173	1	TFC-21	TFM-4	0.841
TGM-100	TGM-161	1	TGC-5	TPM-11	0.84
TGM-118	TGM-75	1	TGM-172	TUM-13	0.837
TGM-118	TGM-83	1	TR-F10	TUM-48	0.837
TGM-118	TGM-86	1	TFM-1	TGM-7	0.831
TGM-162	TUM-2	1	TR-F54	TR-F7	0.82
TGM-169	TPM-2	1	TFM-27	TGM-4	0.818
TGM-173	TGM-18	1	TGC-4	TGC-52	0.815
TGM-174	TPC-2	1	TCF-8	TFM-4	0.81
TGM-20	TGM-7	1	TR-F10	TR-F37	0.809
TGM-20	TUC-1	1	TFC-17	TFM-22	0.805
TGM-43	TR-F5	1	TGC-2	TR-F10	0.805
TGM-48	TPC-13	1	TR-F33	TR-F46	0.8
TGM-48	TPC-5	1	TCF-7	TMF-10	0.793

TGM-48	TUM-50	1	TR-F48	TR-F7	0.792
TGM-7	TUM-10	1	TR-F17	TR-F33	0.79
TGM-75	TGM-83	1	TGM-26	TMF-21	0.787
TGM-75	TGM-86	1	TCF-5	TUM-50	0.785
TGM-82	TUM-2	1	TFM-22	TMF-7	0.779
TGM-83	TGM-86	1	TFC-21	TGC-2	0.777
TGM-93	TPM-5	1	TPM-6	TUC-7	0.76
TMF-1	TMF-14	1	TR-F56	TUC-1	0.76
TMF-1	TR-F11	1	TGC-2	TMF-10	0.759
TMF-1	TR-F3	1	TFC-21	TMF-10	0.747
TMF-11	TMF-12	1	TGC-18	TMF-10	0.741
TMF-11	TMF-8	1	TR-F17	TR-F60	0.738
TMF-11	TR-F46	1	TCF-7	TFC-21	0.734
TMF-12	TMF-8	1	TFM-4	TGC-2	0.733
TMF-14	TR-F11	1	TFM-3	TR-F17	0.725
TMF-19	TR-F5	1	TFM-46	TPC-14	0.71
TPC-13	TPC-5	1	TGC-5	TUC-1	0.705
TPC-2	TPM-2	1	TGM-20	TR-F56	0.705
TPC-3	TPM-8	1	TFM-22	TFM-3	0.69
TPC-3	TR-F48	1	TFC-21	TMF-3	0.682
TR-F11	TR-F3	1	TMF-2	TUC-1	0.679
TR-F44	TUC-3	1	TFC-17	TR-F60	0.675
TUC-4	TUM-19	1	TGM-168	TUC-17	0.655
TUM-14	TUM-47	1	TGC-41	TPC-6	0.645
TUM-42	TUM-47	1	TMF-7	TR-F33	0.634
TCF-10	TMF-11	0.999	TGC-3	TGM-1	0.616
TCF-11	TR-F3	0.999	TR-F37	TUM-48	0.61
TCF-12	TUC-16	0.999	TGC-28	TGM-169	0.606
TCF-13	TCF-20	0.999	TCF-10	TFM-3	0.605
TCF-13	TMF-1	0.999	TCF-18	TFM-3	0.598
TCF-27	TR-F46	0.999	TFC-17	TR-F33	0.592
TCF-28	TGC-26	0.999	TGM-100	TR-F1	0.578
TFC-15	TR-F17	0.999	TGC-15	TMF-21	0.572
TFC-17	TR-F32	0.999	TCF-7	TUM-48	0.568
TFM-22	TMF-8	0.999	TFC-21	TPM-6	0.568
TFM-3	TMF-8	0.999	TFM-3	TUC-2	0.567
TFM-4	TUM-48	0.999	TGC-33	TGC-46	0.567
TFM-49	TMF-14	0.999	TGC-34	TGC-46	0.567
TGC-10	TGM-4	0.999	TGC-4	TGC-46	0.567
TGC-23	TGM-82	0.999	TGC-46	TGC-7	0.564
TGC-34	TGC-50	0.999	TGC-46	TGM-167	0.561
TGC-45	TGM-167	0.999	TGC-46	TGC-52	0.558
TGC-49	TGM-82	0.999	TMF-10	TUC-7	0.551
TGC-49	TUM-2	0.999	TGC-4	TGC-45	0.547
TGC-51	TUC-14	0.999	TGC-46	TGC-50	0.542
TGM-162	TGM-82	0.999	TPC-4	TPC-7	0.542
TGM-172	TUC-17	0.999	TMF-10	TPM-6	0.538
TMF-11	TR-F60	0.999	TFC-21	TUM-48	0.536
TMF-12	TR-F46	0.999	TFM-21	TUC-5	0.532
TMF-14	TR-F3	0.999	TMF-3	TUM-48	0.528
TMF-2	TPM-11	0.999	TGC-12	TGM-168	0.521

TMF-7	TR-F17	0.999	TUC-1	TUM-10	0.518
TMF-8	TR-F46	0.999	TCF-28	TGM-4	0.516
TMF-8	TUC-2	0.999	TGM-169	TPC-2	0.513
TPC-10	TR-F4_1	0.999	TFM-4	TUC-7	0.512
TPC-2	TUC-12	0.999	TMF-3	TR-F10	0.497
TPM-11	TR-F56	0.999	TFM-22	TR-F87	0.489
TPM-8	TR-F7	0.999	TCF-27	TR-F87	0.488
TCF-10	TCF-27	0.998	TMF-11	TR-F87	0.484
TCF-10	TMF-12	0.998	TCF-10	TMF-8	0.481
TCF-18	TFC-15	0.998	TPM-6	TUM-48	0.479
TCF-18	TFC-17	0.998	TCF-10	TR-F87	0.473
TCF-18	TFM-22	0.998	TFC-15	TR-F87	0.47
TCF-18	TMF-12	0.998	TGC-1	TGC-10	0.47
TCF-19	TUM-50	0.998	TR-F87	TUM-47	0.468
TCF-27	TFM-22	0.998	TMF-8	TR-F87	0.46
TCF-27	TMF-8	0.998	TMF-12	TR-F87	0.459
TFC-15	TR-F46	0.998	TR-F33	TR-F87	0.459
TFC-17	TMF-12	0.998	TGC-18	TR-F10	0.444
TFM-49	TR-F3	0.998	TMF-13	TR-F3	0.44
TGC-14	TUC-14	0.998	TR-F32	TR-F87	0.44
TGC-2	TMF-3	0.998	TR-F87	TUM-42	0.436
TGC-4	TGM-167	0.998	TGC-46	TGC-51	0.433
TGM-172	TPM-4	0.998	TGC-28	TUC-12	0.418
TGM-175	TUC-12	0.998	TR-F38	TR-F87	0.418
TMF-11	TUC-2	0.998	TMF-7	TR-F87	0.394
TMF-12	TUC-2	0.998	TGC-39	TPM-2	0.39
TPC-13	TUM-50	0.998	TCF-7	TGC-2	0.382
TPC-4	TPM-10	0.998	TR-F17	TR-F87	0.382
TCF-10	TFC-15	0.997	TFM-3	TMF-7	0.379
TCF-10	TMF-7	0.997	TGC-46	TUC-14	0.362
TCF-18	TMF-7	0.997	TMF-8	TR-F60	0.342
TCF-27	TUC-2	0.997	TR-F87	TUC-2	0.323
TFC-15	TMF-12	0.997	TR-F60	TR-F87	0.303
TFC-21	TR-F37	0.997	TCF-18	TR-F87	0.288
TGC-18	TMF-3	0.997	TGC-17	TMF-19	0.288
TGC-33	TGC-7	0.997	TR-F46	TR-F87	0.268
TGC-4	TGC-7	0.997	TPC-4	TPC-8	0.253
TGC-50	TGM-167	0.997	TCF-2	TR-F54	0.246
TMF-8	TR-F17	0.997	TPM-2	TUC-12	0.244
TPC-7	TPM-10	0.997	TGC-28	TPM-2	0.221
TR-F38	TUM-42	0.997	TMF-7	TMF-8	0.214
TUM-14	TUM-42	0.997	TR-F87	TUM-14	0.211
TCF-18	TUC-2	0.996	TMF-8	TR-F33	0.202
TCF-24	TR-F48	0.996	TGC-7	TGM-167	0.2
TFC-17	TMF-8	0.996	TCF-20	TMF-13	0.199
TFM-3	TMF-11	0.996	TGC-45	TGC-46	0.182
TFM-4	TR-F10	0.996	TGC-46	TGM-10	0.177
TGC-10	TGM-14	0.996	TGC-14	TGM-10	0.169
TGC-2	TUC-7	0.996	TGC-39	TUC-12	0.163
TGC-34	TGC-7	0.996	TFC-17	TFM-3	0.15
TGM-20	TMF-2	0.996	TFC-17	TR-F87	0.148

TR-F20	TUC-16	0.996	TCF-11	TCF-14	0.143
TCF-10	TR-F33	0.995	TCF-13	TCF-14	0.143
TCF-13	TMF-14	0.995	TCF-14	TCF-20	0.143
TCF-20	TMF-14	0.995	TCF-14	TFM-49	0.143
TCF-5	TR-F26	0.995	TCF-14	TMF-1	0.143
TCF-8	TMF-3	0.995	TCF-14	TMF-14	0.143
TFC-15	TFM-22	0.995	TCF-14	TR-F11	0.143
TFC-15	TMF-11	0.995	TCF-14	TR-F3	0.143
TGC-1	TGC-26	0.995	TCF-14	TMF-13	0.14
TGM-10	TUC-14	0.995	TGC-45	TGC-7	0.135
TMF-7	TR-F32	0.995	TFM-3	TR-F87	0.129
TPM-4	TUC-17	0.995	TGC-28	TGM-175	0.118
TR-F17	TR-F32	0.995	TGM-175	TPM-2	0.11
TR-F32	TR-F46	0.995	TPM-9	TUC-16	0.11
TR-F38	TUM-47	0.995	TFM-52	TR-F9	0.097
TCF-18	TR-F17	0.994	TFM-3	TR-F32	0.094
TCF-3	TR-F10	0.994	TCF-8	TGC-18	0.083
TCF-3	TUC-7	0.994	TGC-2	TPM-6	0.077
TFC-15	TMF-7	0.994	TFM-3	TR-F33	0.074
TFC-15	TR-F32	0.994	TCF-10	TCF-7	0.072
TFC-17	TR-F17	0.994	TCF-18	TCF-7	0.072
TFM-22	TR-F33	0.994	TCF-27	TCF-7	0.072
TGC-28	TGC-39	0.994	TCF-7	TMF-11	0.072
TGC-50	TGC-7	0.994	TCF-7	TR-F46	0.072
TGM-1	TGM-18	0.994	TCF-7	TFC-17	0.071
TPC-5	TUM-50	0.994	TCF-7	TFM-22	0.071
TPM-6	TR-F37	0.994	TCF-7	TMF-12	0.071
TCF-18	TMF-8	0.993	TCF-7	TMF-8	0.071
TFC-15	TUC-2	0.993	TCF-7	TR-F32	0.071
TGC-12	TUM-13	0.993	TCF-7	TR-F60	0.069
TGC-14	TGC-51	0.993	TCF-7	TUC-2	0.069
TGC-17	TGM-43	0.993	TCF-7	TFM-3	0.068
TGM-174	TUC-12	0.993	TCF-7	TFC-15	0.067
TMF-11	TR-F33	0.993	TGM-20	TUM-10	0.067
TPM-6	TR-F10	0.993	TCF-7	TMF-7	0.065
TUC-7	TUM-48	0.993	TCF-7	TR-F33	0.058
TCF-10	TUC-2	0.992	TCF-19	TUM-20	0.053
TCF-3	TGC-18	0.992	TGM-48	TUM-20	0.053
TCF-8	TMF-10	0.992	TPC-13	TUM-20	0.053
TFC-15	TMF-8	0.992	TPC-5	TUM-20	0.053
TFC-21	TUC-7	0.992	TUM-20	TUM-50	0.053
TGC-33	TGC-50	0.992	TCF-11	TR-F61	0.052
TGC-34	TGC-4	0.992	TMF-1	TR-F61	0.052
TR-F33	TUC-2	0.992	TFM-49	TR-F61	0.051
TCF-8	TR-F37	0.991	TMF-13	TR-F61	0.051
TGC-17	TGC-21	0.991	TR-F11	TR-F61	0.051
TGC-18	TGC-2	0.991	TR-F3	TR-F61	0.051
TGC-2	TR-F37	0.991	TR-F26	TUM-20	0.05
TGC-21	TR-F5	0.991	TCF-5	TUM-20	0.049
TCF-5	TPC-5	0.99	TMF-14	TR-F61	0.049
TFC-21	TR-F10	0.99	TCF-13	TR-F61	0.048

TGC-2	TUM-48	0.99	TCF-20	TR-F61	0.046
TGC-21	TGM-43	0.99	TGM-7	TUC-1	0.036
TGC-26	TGM-4	0.99	TCF-18	TFM-13	0.035
TGM-7	TR-F56	0.99	TCF-27	TFM-13	0.035
TMF-11	TR-F17	0.99	TFC-17	TFM-13	0.035
TR-F32	TR-F60	0.99	TFM-1	TR-F56	0.035
TFM-4	TMF-10	0.989	TFM-13	TMF-11	0.035
TGC-21	TMF-19	0.989	TFM-13	TMF-8	0.035
TGM-169	TUC-12	0.989	TFM-13	TR-F32	0.035
TGM-174	TPM-2	0.989	TFM-13	TR-F46	0.035
TMF-7	TR-F46	0.989	TFM-13	TFM-22	0.034
TR-F37	TUC-7	0.989	TFM-13	TR-F87	0.034
TGC-28	TGM-174	0.988	TGC-3	TGC-33	0.034
TMF-3	TR-F37	0.988	TGC-3	TGC-34	0.034
TPC-3	TR-F54	0.988	TGC-3	TGC-4	0.032
TR-F32	TUC-2	0.988	TCF-10	TFM-13	0.031
TCF-19	TCF-5	0.987	TCF-28	TGC-42	0.031
TCF-3	TFC-21	0.987	TFC-15	TFM-13	0.03
TCF-8	TPM-6	0.987	TFM-13	TMF-12	0.03
TFC-17	TR-F46	0.987	TGC-10	TGC-42	0.03
TFM-22	TR-F32	0.987	TGC-10	TGM-168	0.03
TGC-18	TR-F37	0.987	TGC-26	TGM-168	0.03
TGC-52	TGC-7	0.987	TGC-3	TGC-7	0.03
TCF-11	TCF-20	0.986	TGC-42	TGM-4	0.03
TCF-2	TPC-3	0.986	TGM-168	TGM-4	0.03
TGC-33	TGM-167	0.986	TFM-13	TUC-2	0.029
TFM-22	TMF-11	0.985	TGC-3	TGM-167	0.029
TMF-11	TR-F32	0.985	TCF-28	TGM-168	0.028
TMF-12	TR-F17	0.985	TFM-13	TFM-3	0.028
TPC-8	TPM-10	0.985	TGM-14	TGM-168	0.028
TPM-4	TUM-13	0.985	TGC-26	TGC-42	0.027
TCF-10	TFC-17	0.984	TGM-100	TGM-166	0.027
TCF-10	TFM-22	0.984	TGC-14	TGC-46	0.026
TCF-11	TCF-13	0.984	TCF-12	TMF-21	0.024
TCF-19	TR-F26	0.984	TFM-13	TR-F17	0.024
TFM-1	TMF-2	0.984	TGC-3	TGC-50	0.024
TFM-22	TR-F46	0.984	TCF-7	TR-F17	0.023
TGC-12	TGM-172	0.984	TFM-13	TMF-7	0.023
TGM-48	TR-F26	0.984	TFM-46	TUM-47	0.023
TPC-5	TR-F26	0.984	TFM-27	TGM-168	0.022
TPM-8	TR-F54	0.984	TGC-42	TGM-14	0.022
TCF-3	TMF-10	0.983	TFM-27	TGC-42	0.021
TFC-15	TR-F60	0.983	TGM-43	TMF-19	0.021
TFM-4	TMF-3	0.983	TR-F9	TUC-15	0.021
TPC-13	TR-F26	0.983	TFM-13	TR-F60	0.02
TCF-19	TPC-13	0.982	TMF-21	TUC-16	0.02
TFM-3	TMF-12	0.982	TFM-46	TUM-42	0.018
TMF-12	TR-F32	0.982	TGC-28	TPC-2	0.018
TCF-10	TR-F60	0.981	TGC-3	TGC-45	0.016
TCF-5	TGM-48	0.981	TGM-166	TR-F1	0.015
TFM-22	TMF-12	0.981	TGM-93	TPC-8	0.015

TGC-42	TUM-13	0.981	TCF-12	TPM-9	0.014
TMF-8	TR-F32	0.981	TCF-28	TUM-13	0.014
TGC-12	TUC-17	0.98	TFM-13	TR-F33	0.014
TR-F46	TR-F60	0.98	TFM-27	TUC-14	0.014
TCF-8	TFC-21	0.979	TGC-10	TGC-12	0.014
TR-F17	TR-F46	0.979	TGC-10	TUM-13	0.014
TR-F48	TR-F54	0.979	TGC-12	TGC-26	0.014
TFM-1	TUC-1	0.978	TGC-12	TGM-14	0.014
TR-F17	TUC-2	0.978	TGC-26	TUM-13	0.014
TFC-15	TFC-17	0.977	TGM-166	TPC-8	0.014
TMF-10	TMF-3	0.977	TGC-1	TGM-168	0.012
TMF-12	TR-F33	0.977	TGC-12	TGM-4	0.012
TR-F60	TUC-2	0.977	TPC-8	TPM-5	0.012
TCF-18	TR-F33	0.976	TCF-28	TGC-12	0.011
TCF-2	TR-F7	0.976	TFM-27	TGC-14	0.011
TCF-3	TPM-6	0.976	TFM-46	TUM-14	0.011
TFC-17	TMF-11	0.976	TGC-1	TGC-12	0.011
TGM-175	TPC-2	0.976	TCF-7	TR-F87	0.01
TR-F32	TR-F33	0.976	TGC-5	TMF-2	0.01
TCF-28	TFM-27	0.975	TFM-46	TR-F87	0.009
TCF-24	TR-F54	0.974	TGC-18	TPM-6	0.009
TGC-1	TGM-4	0.974	TFM-27	TGC-12	0.008
TMF-1	TMF-13	0.974	TMF-21	TR-F20	0.008
TCF-27	TR-F33	0.972	TFM-46	TR-F38	0.007
TGC-5	TGM-7	0.972	TGC-12	TPM-4	0.007
TGM-174	TGM-175	0.971	TGC-17	TGC-33	0.007
TMF-10	TUM-48	0.971	TGC-17	TGC-34	0.007
TGM-168	TGM-172	0.97	TGC-17	TGC-4	0.007
TGM-168	TPM-4	0.97	TGC-17	TGC-45	0.007
TCF-27	TR-F32	0.969	TGC-17	TGC-50	0.007
TCF-8	TUC-7	0.969	TGC-17	TGC-52	0.007
TGC-39	TGM-169	0.969	TGC-17	TGM-167	0.007
TCF-5	TPC-13	0.968	TFM-27	TUM-13	0.006
TGC-12	TGC-42	0.968	TGC-17	TGC-46	0.006
TGM-7	TMF-2	0.968	TGM-161	TGM-166	0.006
TMF-13	TMF-14	0.968	TMF-21	TPM-9	0.006
TCF-28	TGC-1	0.967	TCF-8	TGC-28	0.005
TFM-4	TGC-18	0.967	TCF-8	TGC-39	0.005
TCF-10	TR-F32	0.966	TCF-8	TGM-169	0.005
TGC-3	TGM-173	0.966	TCF-8	TGM-174	0.005
TCF-27	TR-F60	0.965	TCF-8	TGM-175	0.005
TFC-15	TFM-3	0.965	TCF-8	TPC-2	0.005
TGM-166	TPM-5	0.964	TCF-8	TPM-2	0.005
TMF-7	TUC-2	0.964	TCF-8	TUC-12	0.005
TMF-2	TR-F56	0.963	TFM-27	TGM-10	0.005
TFC-21	TGC-18	0.962	TGC-17	TGC-7	0.005
TCF-11	TMF-13	0.961	TFM-1	TPM-11	0.004
TGC-3	TGC-6	0.961	TFM-27	TGC-46	0.004
TGC-42	TGM-168	0.96	TGC-39	TGM-175	0.004
TCF-8	TUM-48	0.959	TGC-39	TPC-2	0.004
TFM-49	TMF-13	0.958	TCF-10	TFM-46	0.003

TGC-3	TGM-18	0.957	TCF-18	TFM-46	0.003
TMF-12	TMF-7	0.957	TCF-27	TFM-46	0.003
TR-F33	TR-F60	0.957	TCF-7	TFM-13	0.003
TCF-18	TR-F60	0.956	TFC-15	TFM-46	0.003
TCF-2	TR-F48	0.956	TFC-17	TFM-46	0.003
TMF-11	TMF-7	0.956	TFM-22	TFM-46	0.003
TCF-3	TGC-2	0.955	TFM-3	TFM-46	0.003
TUC-15	TUC-16	0.955	TFM-46	TMF-11	0.003
TCF-10	TR-F17	0.954	TFM-46	TMF-12	0.003
TGC-10	TGC-26	0.954	TFM-46	TMF-7	0.003
TGC-33	TGC-34	0.954	TFM-46	TMF-8	0.003
TCF-3	TR-F37	0.953	TFM-46	TR-F17	0.003
TFC-15	TR-F33	0.952	TFM-46	TR-F32	0.003
TFM-4	TR-F37	0.951	TFM-46	TR-F33	0.003
TGC-45	TGC-52	0.951	TFM-46	TR-F46	0.003
TR-F38	TUM-14	0.951	TFM-46	TR-F60	0.003
TCF-13	TMF-13	0.95	TFM-46	TUC-2	0.003
TGC-42	TGM-172	0.95	TGC-7	TPC-8	0.003
TGC-18	TUC-7	0.949	TGC-7	TPM-5	0.003
TUC-17	TUM-13	0.949	TCF-22	TCF-29	0.001
TFM-27	TGC-1	0.948	TCF-3	TFM-46	0.001
TGC-13	TUM-20	0.947	TCF-7	TFM-46	0.001
TGC-23	TUM-20	0.947	TFM-4	TFM-46	0.001
TGC-49	TUM-20	0.947	TFM-46	TGC-2	0.001
TGM-162	TUM-20	0.947	TFM-46	TPM-6	0.001
TGM-82	TUM-20	0.947	TFM-46	TR-F37	0.001
TUM-2	TUM-20	0.947	TGC-3	TGC-52	0.001
TGM-161	TR-F1	0.946	TGC-7	TGM-93	0.001
TCF-28	TGM-14	0.945	TGM-14	TGM-4	0.001
TR-F46	TUC-2	0.945			

Table C3. Tōtara family clusters as determined by COLONY.

Offfspring ID	**Mother ID**	**Cluster**	**Probability**	**Mean gographic distance (m) among individuals from same cluster**
TGC-41	-	1	0.5759	4,380.23
TPC-6	-	1	0.5759	
TR-F61	TR-F36	2	0.5770	8.55
TCF-14	TR-F52	3	0.7589	49.55
TCF-11	-	3	0.7589	
TCF-13	-	3	0.7589	
TCF-20	-	3	0.7589	
TFM-49	-	3	0.7589	
TMF-1	-	3	0.7589	
TMF-13	-	3	0.7589	
TMF-14	-	3	0.7589	
TR-F11	-	3	0.7589	

TR-F3	-	3	0.7589	
TGC-28	-	4	0.8598	2,606.20
TGC-39	-	4	0.8598	
TGM-169	-	4	0.8598	
TGM-174	-	4	0.8598	
TGM-175	-	4	0.8598	
TPC-2	-	4	0.8598	
TPM-2	-	4	0.8598	
TUC-12	-	4	0.8598	
TCF-19	-	5	0.9343	2,484.43
TCF-5	-	5	0.9343	
TGC-13	-	5	0.9343	
TGC-23	-	5	0.9343	
TGC-49	-	5	0.9343	
TGM-162	-	5	0.9343	
TGM-48	-	5	0.9343	
TGM-82	-	5	0.9343	
TPC-13	-	5	0.9343	
TPC-5	-	5	0.9343	
TR-F26	-	5	0.9343	
TUM-2	-	5	0.9343	
TUM-20	-	5	0.9343	
TUM-50	-	5	0.9343	
TCF-22	TFC-46	6	0.9768	37.37
TCF-29	TR-F39	7	0.9784	143.51
TFM-1	-	8	0.9847	2,612.33
TGC-5	-	8	0.9847	
TGM-20	-	8	0.9847	
TGM-7	-	8	0.9847	
TMF-2	-	8	0.9847	
TPM-11	-	8	0.9847	
TR-F56	-	8	0.9847	
TUC-1	-	8	0.9847	
TUM-10	-	8	0.9847	
TUM-19	TR-F34	9	0.9934	2,026.09
TUC-4	TR-F34	9	0.9934	
TUC-3	TR-F34	9	0.9934	
TGC-16	TR-F34	9	0.9934	
TR-F44	TR-F34	9	0.9934	
TGC-17	-	9	0.9934	
TGC-21	-	9	0.9934	
TGC-25	-	9	0.9934	
TGC-44	-	9	0.9934	
TGM-118	-	9	0.9934	
TGM-43	-	9	0.9934	
TGM-75	-	9	0.9934	
TGM-83	-	9	0.9934	
TGM-86	-	9	0.9934	
TMF-19	-	9	0.9934	
TPC-10	-	9	0.9934	
TR-F4_1	-	9	0.9934	

TR-F5	-	9	0.9934	
TCF-1	-	10	0.9992	1,956.12
TGC-31	-	10	0.9992	

Slash (-) in mother IDs denotes those cases in which a mother from the pool of sampled individuals could not be matched.

Table C4. Pairwise distances among individuals from family clusters included in the analysis.

Individual 1 ID	Individual 2 ID	Cluster	Distance (m)
TGC-41	TPC-6	1	4,380.23
TR-F3	TCF-20	3	1.42
TCF-20	TMF-14	3	3.48
TR-F3	TMF-14	3	4.88
TCF-11	TCF-13	3	9.57
TMF-13	TCF-14	3	11.18
TCF-13	TCF-14	3	14.01
TCF-14	TCF-11	3	23.14
TCF-13	TMF-13	3	25.19
TMF-13	TMF-14	3	32.17
TCF-11	TMF-13	3	34.19
TCF-20	TMF-13	3	34.85
TR-F3	TMF-13	3	35.80
TR-F11	TFM-49	3	38.05
TCF-14	TR-F11	3	39.03
TMF-13	TR-F11	3	39.81
TFM-49	TMF-13	3	41.06
TMF-14	TCF-14	3	41.16
TR-F11	TCF-13	3	42.74
TCF-14	TCF-20	3	43.39
TR-F3	TCF-14	3	44.12
TCF-11	TMF-1	3	47.53
TFM-49	TCF-14	3	49.49
TCF-11	TR-F11	3	50.19
TFM-49	TMF-14	3	51.28
TMF-14	TCF-13	3	53.46
TFM-49	TCF-20	3	54.70
TCF-20	TCF-13	3	55.26
TR-F3	TCF-13	3	55.80
TMF-1	TCF-13	3	57.09
TCF-11	TMF-14	3	60.35
TCF-13	TFM-49	3	61.47
TCF-20	TCF-11	3	61.79
TCF-11	TR-F3	3	62.16
TR-F11	TMF-14	3	68.53
TMF-1	TCF-14	3	70.39
TFM-49	TCF-11	3	71.01

TCF-20	TR-F11	3	71.77
TR-F11	TR-F3	3	72.98
TMF-13	TMF-1	3	81.09
TMF-1	TR-F11	3	92.46
TMF-14	TMF-1	3	102.02
TR-F3	TMF-1	3	102.38
TMF-1	TFM-49	3	118.33
TPC-2	TPM-2	4	2.39
TGM-175	TGM-174	4	4.39
TGM-169	TGM-174	4	21.67
TGM-169	TGM-175	4	22.09
TGC-28	TGM-175	4	30.37
TGM-174	TGC-28	4	32.99
TGC-28	TGM-169	4	51.51
TGC-39	TGM-169	4	103.11
TGM-174	TGC-39	4	124.34
TGM-175	TGC-39	4	125.19
TGC-39	TGC-28	4	153.91
TUC-12	TPC-2	4	3,360.96
TPM-2	TUC-12	4	3,362.40
TGC-39	TPM-2	4	4,051.88
TGC-39	TPC-2	4	4,053.54
TPM-2	TGM-169	4	4,128.06
TPC-2	TGM-169	4	4,129.68
TPM-2	TGM-174	4	4,140.66
TPC-2	TGM-174	4	4,142.28
TPM-2	TGM-175	4	4,144.21
TGM-175	TPC-2	4	4,145.83
TGC-28	TPM-2	4	4,172.63
TPC-2	TGC-28	4	4,174.24
TUC-12	TGC-39	4	4,849.83
TUC-12	TGM-174	4	4,855.13
TGM-169	TUC-12	4	4,857.93
TGM-175	TUC-12	4	4,859.48
TUC-12	TGC-28	4	4,873.02
TGC-23	TGM-82	5	8.41
TGC-13	TGM-48	5	14.34
TGM-162	TGC-49	5	22.79
TGC-13	TGC-23	5	36.31
TGM-82	TGC-13	5	39.10
TGM-48	TGC-23	5	43.96
TGM-82	TGM-48	5	44.14
TCF-19	TCF-5	5	47.28
TUM-20	TUM-2	5	61.78
TR-F26	TCF-5	5	88.42
TPC-5	TPC-13	5	106.40
TGC-13	TGC-49	5	129.73
TR-F26	TCF-19	5	133.53
TGM-162	TGC-13	5	135.28
TGM-48	TGC-49	5	138.92
TGM-48	TGM-162	5	142.55

TGC-23	TGC-49	5	150.93
TGC-49	TGM-82	5	158.38
TGM-162	TGC-23	5	160.63
TGM-162	TGM-82	5	167.52
TCF-19	TGM-82	5	1,712.34
TGC-23	TCF-19	5	1,717.23
TCF-5	TGM-82	5	1,731.19
TCF-5	TGC-23	5	1,736.25
TGC-13	TCF-19	5	1,750.83
TGM-48	TCF-19	5	1,751.16
TGM-48	TCF-5	5	1,769.48
TGC-13	TCF-5	5	1,769.50
TR-F26	TGM-82	5	1,795.61
TR-F26	TGC-23	5	1,800.89
TGM-48	TR-F26	5	1,833.12
TGC-13	TR-F26	5	1,833.64
TGC-49	TCF-19	5	1,854.06
TGM-162	TCF-19	5	1,870.33
TCF-5	TGC-49	5	1,874.57
TGM-162	TCF-5	5	1,890.47
TR-F26	TGC-49	5	1,941.09
TGM-162	TR-F26	5	1,956.49
TR-F26	TUM-2	5	2,732.41
TUM-20	TR-F26	5	2,788.19
TUM-2	TCF-5	5	2,819.67
TUM-2	TCF-19	5	2,860.44
TCF-5	TUM-20	5	2,875.58
TCF-19	TUM-20	5	2,916.57
TPC-5	TUM-20	5	3,167.70
TPC-5	TUM-2	5	3,184.25
TPC-13	TUM-20	5	3,250.17
TPC-13	TUM-2	5	3,267.94
TPC-5	TR-F26	5	3,832.18
TPC-5	TCF-5	5	3,894.56
TPC-13	TR-F26	5	3,938.02
TCF-19	TPC-5	5	3,938.09
TCF-5	TPC-13	5	4,000.21
TCF-19	TPC-13	5	4,043.69
TGM-48	TPC-5	5	4,288.63
TPC-5	TGM-82	5	4,292.48
TGC-23	TPC-5	5	4,300.71
TPC-5	TGC-13	5	4,301.64
TUM-2	TGM-82	5	4,351.25
TUM-2	TGC-23	5	4,358.45
TUM-2	TGM-48	5	4,378.52
TGM-48	TPC-13	5	4,379.95
TGC-13	TUM-2	5	4,383.92
TPC-13	TGM-82	5	4,384.35
TPC-13	TGC-23	5	4,392.56
TGC-13	TPC-13	5	4,393.03
TGM-82	TUM-20	5	4,399.66

TGC-23	TUM-20	5	4,406.89
TPC-5	TGM-162	5	4,410.02
TPC-5	TGC-49	5	4,416.89
TGM-48	TUM-20	5	4,426.62
TUM-20	TGC-13	5	4,432.13
TGM-162	TPC-13	5	4,500.38
TGC-49	TPC-13	5	4,507.53
TGC-49	TUM-2	5	4,509.19
TUM-2	TGM-162	5	4,518.55
TGC-49	TUM-20	5	4,557.69
TUM-20	TGM-162	5	4,566.87
TGM-20	TGM-7	8	10.99
TUM-10	TUC-1	8	32.49
TGM-20	TGC-5	8	36.78
TMF-2	TR-F56	8	47.33
TGC-5	TGM-7	8	47.71
TFM-1	TMF-2	8	571.49
TFM-1	TR-F56	8	607.64
TGM-7	TFM-1	8	1,432.51
TGM-20	TFM-1	8	1,432.55
TFM-1	TGC-5	8	1,437.71
TGM-7	TMF-2	8	1,998.95
TGM-20	TMF-2	8	1,999.47
TGC-5	TMF-2	8	2,006.05
TGM-7	TR-F56	8	2,030.82
TR-F56	TGM-20	8	2,031.53
TGC-5	TR-F56	8	2,038.73
TR-F56	TUC-1	8	2,704.50
TUM-10	TR-F56	8	2,732.11
TUC-1	TMF-2	8	2,750.71
TUM-10	TMF-2	8	2,778.25
TUC-1	TPM-11	8	3,238.11
TPM-11	TUM-10	8	3,259.56
TUC-1	TFM-1	8	3,260.79
TUM-10	TFM-1	8	3,289.70
TR-F56	TPM-11	8	3,877.01
TPM-11	TMF-2	8	3,911.75
TPM-11	TFM-1	8	4,009.55
TGM-7	TPM-11	8	4,371.27
TGM-20	TPM-11	8	4,381.32
TGC-5	TPM-11	8	4,416.51
TGM-7	TUC-1	8	4,525.37
TGM-20	TUC-1	8	4,529.75
TUC-1	TGC-5	8	4,548.49
TGM-7	TUM-10	8	4,556.42
TUM-10	TGM-20	8	4,560.77
TGC-5	TUM-10	8	4,579.44
TGC-16	TGC-17	9	0.00
TGM-75	TGC-21	9	3.63
TUC-4	TUC-3	9	5.83
TGC-16	TGM-75	9	7.24

TGM-75	TGC-16	9	7.24
TMF-19	TR-F5	9	8.88
TGC-16	TGC-21	9	10.78
TGC-21	TGC-16	9	10.78
TGC-25	TGM-83	9	12.50
TGC-16	TGM-43	9	15.19
TGM-43	TGC-16	9	15.19
TGM-75	TGM-43	9	22.42
TGC-21	TGM-43	9	25.93
TUM-19	TUC-4	9	29.42
TGM-86	TGC-25	9	32.33
TGM-83	TGM-86	9	33.32
TUC-3	TUM-19	9	33.92
TR-F4_1	TMF-19	9	35.35
TGM-43	TGC-25	9	41.76
TR-F4_1	TR-F5	9	43.13
TGM-43	TGM-83	9	51.97
TGC-16	TGC-25	9	54.58
TGC-25	TGM-75	9	61.11
TGM-83	TGC-16	9	63.38
TGC-16	TGM-83	9	63.38
TGC-21	TGC-25	9	64.70
TGM-86	TGM-43	9	68.89
TGM-75	TGM-83	9	69.38
TGM-83	TGC-21	9	72.86
TGC-16	TGM-86	9	83.41
TGM-86	TGC-16	9	83.41
TGM-86	TGM-75	9	90.43
TGC-44	TGM-118	9	93.74
TGM-86	TGC-21	9	94.06
TGM-43	TGC-44	9	131.08
TGM-86	TGC-44	9	135.39
TGC-16	TGC-44	9	139.36
TGC-44	TGC-16	9	139.36
TGC-25	TGC-44	9	142.60
TGC-21	TGM-118	9	143.20
TGC-44	TGM-75	9	143.62
TGM-118	TGM-75	9	144.16
TGM-118	TGC-16	9	144.44
TGC-44	TGC-21	9	145.02
TGM-118	TGM-43	9	145.98
TGC-44	TGM-83	9	153.95
TGM-118	TGC-25	9	178.59
TGM-86	TGM-118	9	188.08
TGM-83	TGM-118	9	191.03
TR-F4_1	TR-F44	9	224.19
TMF-19	TR-F44	9	257.47
TR-F5	TR-F44	9	263.22
TGM-83	TR-F5	9	1,654.17
TGM-83	TMF-19	9	1,663.03
TR-F5	TGC-25	9	1,666.24

TGM-86	TR-F5	9	1,671.30
TMF-19	TGC-25	9	1,675.11
TGM-86	TMF-19	9	1,680.16
TGC-16	TR-F5	9	1,690.31
TR-F5	TGC-16	9	1,690.31
TGM-75	TR-F5	9	1,690.32
TGM-43	TR-F5	9	1,690.61
TR-F5	TGC-21	9	1,691.29
TGM-83	TR-F4_1	9	1,693.92
TGC-16	TMF-19	9	1,699.19
TGM-43	TMF-19	9	1,699.49
TMF-19	TGC-21	9	1,700.17
TR-F4_1	TGC-25	9	1,705.96
TGM-86	TR-F4_1	9	1,711.33
TGM-75	TR-F4_1	9	1,729.47
TGC-16	TR-F4_1	9	1,729.53
TR-F4_1	TGC-16	9	1,729.53
TR-F4_1	TGM-43	9	1,729.99
TGC-21	TR-F4_1	9	1,730.40
TGC-44	TR-F5	9	1,806.49
TGC-44	TMF-19	9	1,815.35
TR-F5	TGM-118	9	1,834.47
TMF-19	TGM-118	9	1,843.35
TGM-83	TR-F44	9	1,846.11
TGC-44	TR-F4_1	9	1,846.45
TGC-25	TR-F44	9	1,857.79
TGM-86	TR-F44	9	1,866.06
TGM-118	TR-F4_1	9	1,873.59
TGM-75	TR-F44	9	1,875.93
TR-F44	TGC-21	9	1,876.52
TGC-16	TR-F44	9	1,876.67
TR-F44	TGC-16	9	1,876.67
TGM-43	TR-F44	9	1,878.55
TGC-44	TR-F44	9	1,999.89
TR-F44	TGM-118	9	2,019.19
TUC-3	TR-F44	9	2,653.22
TUC-4	TR-F44	9	2,658.62
TUM-19	TR-F44	9	2,671.19
TUC-3	TR-F4_1	9	2,871.86
TUC-4	TR-F4_1	9	2,877.22
TUM-19	TR-F4_1	9	2,889.29
TUC-3	TMF-19	9	2,906.79
TMF-19	TUC-4	9	2,912.15
TUC-3	TR-F5	9	2,913.51
TR-F5	TUC-4	9	2,918.88
TMF-19	TUM-19	9	2,924.27
TR-F5	TUM-19	9	2,931.06
TUC-3	TPC-10	9	3,215.42
TUC-4	TPC-10	9	3,218.40
TPC-10	TUM-19	9	3,246.66
TPC-10	TR-F44	9	3,849.18

TPC-10	TR-F4_1	9	4,017.64
TPC-10	TR-F5	9	4,034.24
TMF-19	TPC-10	9	4,034.70
TGC-21	TPC-10	9	4,310.22
TGM-75	TPC-10	9	4,313.15
TGC-16	TPC-10	9	4,319.90
TPC-10	TGC-16	9	4,319.90
TGM-43	TPC-10	9	4,334.16
TUC-3	TGM-83	9	4,337.69
TUC-4	TGM-83	9	4,343.45
TUC-3	TGC-21	9	4,344.78
TUC-3	TGM-75	9	4,345.42
TUC-3	TGC-25	9	4,347.35
TGC-16	TUC-3	9	4,348.52
TGC-21	TUC-4	9	4,350.54
TUC-4	TGM-75	9	4,351.18
TGC-25	TUC-4	9	4,353.10
TGC-16	TUC-4	9	4,354.28
TGM-83	TPC-10	9	4,355.02
TGM-43	TUC-3	9	4,355.27
TGC-25	TPC-10	9	4,356.58
TGM-43	TUC-4	9	4,361.03
TGM-83	TUM-19	9	4,361.52
TUC-3	TGM-86	9	4,365.00
TGM-118	TPC-10	9	4,365.10
TUM-19	TGC-21	9	4,369.00
TUM-19	TGM-75	9	4,369.62
TGM-86	TUC-4	9	4,370.75
TGC-25	TUM-19	9	4,371.21
TGC-16	TUM-19	9	4,372.69
TUM-19	TGC-16	9	4,372.69
TUM-19	TGM-43	9	4,379.36
TGM-86	TPC-10	9	4,387.99
TUM-19	TGM-86	9	4,388.72
TPC-10	TGC-44	9	4,435.92
TUC-3	TGM-118	9	4,475.25
TUC-4	TGM-118	9	4,481.02
TUC-3	TGC-44	9	4,486.07
TUC-4	TGC-44	9	4,491.83
TUM-19	TGM-118	9	4,499.78
TUM-19	TGC-44	9	4,510.11
TCF-1	TGC-31	10	1,956.12