Island biogeography of plants and humans

By

Fabio Mologni

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This thesis was conducted under the supervision of

Professor Kevin C. Burns (Primary Supervisor)

Victoria University of Wellington,

Wellington, New Zealand

Doctor Peter Bellingham (Secondary Supervisor)

Landcare Research – Manaaki Whenua,

Lincoln, New Zealand

Abstract

Islands have always attracted considerable research effort due to their unique geography and biota. However, the biogeography of islands still presents substantial challenges. For instance, islands often sustain high rates of plant invasions. The distributional patterning of exotic species on islands though is still poorly understood. Additionally, while species vary strongly in their life histories, rarely plant traits have been integrated with the investigation of the island biogeography of plant species. Islands are also commonly struck by storms and strong winds of oceanic origin, yet how ocean-borne disturbances affect island plant communities is unclear. Finally, in the last 50 years, researchers investigated the insular distribution of virtually every known taxon, but very little is known about variation in human population sizes on islands. The goal of this thesis is to investigate these understudied aspects within the theory of island biogeography framework in vascular plant species and humans.

To better understand plant invasions on islands, I compared the relationships between native and exotic species richness and island characteristics on 264 islands offshore Northern New Zealand. Native and exotic species displayed broadly similar biogeographical patterns; however, exotic species exhibited subtle, yet distinctive, invasion patterns. Trends in species richness were also scale-dependent, and increasingly for exotic species.

Second, I integrated plant life-history traits within the theory of island biogeography framework to investigate how exotic species with different traits relate to island characteristics on 264 islands offshore Northern New Zealand. Exotic species with traits associated with high invasion rates (i.e. high island occupancy rates) were more similar to native species both in occupancy and in relationships with island characteristics. Moreover, they were less commonly associated with human-related variables.

Third, I assessed how distributional patterns of native and exotic plant species varied depending on different levels of ocean-borne disturbances on 97 small New Zealand islands. Overall results show that both native richness and composition varied with different levels of disturbance. In striking contrast, distributional patterns of exotic species remained unchanged. Differences between natives and exotics might reflect a lack of coastal specialists in the exotic species pool.

Lastly, I explored relationships between human population sizes and island characteristics on 10 archipelagos worldwide, for a total of 486 islands. Overall results showed that, just like other animals, humans are strongly structured geographically. However, relationships between human population sizes and island characteristics vary markedly among archipelagos, often reflecting specific social, political and historical circumstances.

This thesis combines with a growing body of research on plant invasions on islands. It provides a fresh perspective on the subject by assessing previously overlooked aspects of the invasion process, such as the scale-dependency of the relationships between exotic species richness and island characteristics. Additionally, it integrated a trait-based approach within the theory of island biogeography framework. It also provided a test of how species of different biogeographic origins respond to varying levels of ocean-borne disturbances. Lastly, this work includes what is, to my knowledge, the first global test of the island biogeography of humans.

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Contents

List of Figures

List of Tables

Publications

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Thesis Declaration

I declare that this written submission is my own work. All material derived from literature has been cited and referenced. No part of this thesis has been previously submitted for another degree at this or any other institution.

Chapters 2, 3, 4, and 5 were written as individual papers. Therefore, some repetitions are inevitable between different sections of this work. Chapters 2, 3 and 5 contain relevant contributions from my supervisors, Kevin C. Burns and Peter J. Bellingham. Chapter 2 and 3 also contain contributions from Ewen K. Cameron, Khoi Dinh, Even Tjørve and Anthony E. Wright.

I thank my supervisors for the insightful comments on chapter 4 and for encouraging me to publish it as a sole author.

Chapter 1.   Introduction

1.1– The biogeography of islands

Islands have long fascinated biologists (Carlquist 1974). Observing the insular biota inspired much of Darwin's and Wallace's landmark work (Darwin 1859, Wallace 1880). Since then, islands have been the focus of considerable research effort (Lomolino 2016, Patiño et al. 2017). The interest in islands derives from their unique features: they are discrete, replicable entities, which allows researchers to isolate single processes and factors (Whittaker and Fernández-Palacios 2007). Moreover, while variable in their characteristics, they are simplified systems if compared to continents. Islands also host a unique biota, including a disproportionately high number of endemic species (Whittaker et al. 2017). Despite attracting much interest, understanding the biology of islands still presents substantial challenges (Warren et al. 2015, Patiño et al. 2017).

One of the most prominent works developed around islands is the theory of island biogeography (MacArthur and Wilson 1967). MacArthur and Wilson elaborated a mathematical model which describes the number of species on an island as a product of two main processes: immigration and extinction. The number of immigrants is regulated by the geographic isolation of an island. Remote islands are more difficult to reach, thus housing fewer species. Conversely, the size of an island controls extinction rates. Larger islands can host a greater number of species, thus lowering extinction rates. Similar mathematical models, focused on meta-population dynamics, identified the same two key variables in influencing population sizes (Hanski 1994). Several studies have revealed the picture to be more complex (Brown and Kodric-Brown 1977, Lomolino 1990, 2016, Whittaker et al. 2017) and several other factors can account for the number of species on an island (Denslow et al. 2009, Essl et al. 2019, Fois et al. 2020). However, after 50 years, the Theory of Island Biogeography still represents a general framework for understanding patterns of species richness on islands.

1.2 – Insular plant invasions

Biological invasions describe the expansion of a species to a new geographical region, typically with human mediated dispersal (Sinclair et al. 2020). After introduction, many species can successfully spread in a new range, often displacing native species in the process (Dostál et al. 2013). Furthermore, exotic species are often shared among countries. An unintended outcome is biotic homogenization, or the increase in genetic, taxonomic and functional similarity between spatially separated communities (McKinney and Lockwood 1999). The intensification of travel, commerce and relationships across the globe is promoting this process to an alarming degree (Lockwood et al. 2005). Therefore, biological invasions represent one of the greatest challenges to the conservation of local biodiversity worldwide (Simberloff et al. 2013).

Islands are often regarded as global biodiversity hotspots. Despite accounting for only 3.5% of the total Earth's land area, they contain 15 to 20% of all terrestrial species, of which a large number are endemic (Whittaker et al. 2017). Therefore, islands are particularly vulnerable to the introduction of new species. For instance, Pacific islands often contain as many exotic species as native species (Sax and Gaines 2008). With 43.9% of all vascular plant species exotic in origin (n = 1798, Brandt et al., 2021), and 85% of 2229 native plant species endemic (McGlone 2006), New Zealand is a striking example of this trend (Hulme 2020). One way to better understand plant invasions on islands is to investigate discrepancies in distributional patterns of both native and exotic species richness.

The number of exotic species inhabiting oceanic islands often increases with the number of native species (Lonsdale 1999, Seabloom et al. 2007, Sax and Gaines 2008, Denslow et al. 2009, Dyer et al. 2016, Carpio et al. 2017). One explanation is that both groups respond similarly to broad-scale variation in environmental conditions (Fridley et al. 2007, Stohlgren et al. 2007, Tomasetto et al. 2019). For instance, the relationship between species richness and island area is consistently

reported as positive for both native and exotic species (Baiser and Li 2018). Conversely, species-isolation relationships are sometimes contradictory. While natives generally decline in number with isolation (Kreft et al. 2008, Weigelt and Kreft 2013, Negoita et al. 2016), this is not always the case for exotics (Moody 2000, Kueffer et al. 2010, Blackburn et al. 2016, Moser et al. 2018). Several other factors had been investigated in the past, such as topographic complexity (Hu et al. 2011, Yu et al. 2012), climate (Kreft et al. 2008, Arianoutsou et al. 2010), substrate (Pretto et al. 2012) and age (Chown et al. 1998, Fattorini 2010). However, whether native and exotic respond similarly to island characteristics is still unclear (Rojas-Sandoval et al. 2020). Understanding which factors drive the richness of native and exotic species is essential to predict invasion success on islands and, ultimately, develop effective management plans to protect insular communities.

1.3 – Integrating island biogeography, functional and invasion ecology

MacArthur and Wilson's model (1967) provides a simple and effective tool to describe patterns in species richness on isolates. However, it assumes species to be functionally equivalent. Instead, they often exhibit different life-history traits. Species with similar suites of traits employ analogous strategies, which influence their fitness (Pérez-Harguindeguy et al. 2013, Reich 2014). Functional traits, or specific morphological, physiological and phenological features shared among species, have been extensively used to address many ecological and evolutionary questions (Bellingham and Sparrow 2000, Olden et al. 2004, Caccianiga et al. 2006, Grime and Pierce 2012, Warren et al. 2015, Burns 2016a, 2019, May et al. 2017), including the field of invasion ecology (Van Kleunen et al. 2010a, Guo et al. 2018, Hulme and Bernard-Verdier 2018a, b). However, their use in island biogeography is limited and their role in explaining the spatial distribution of island plant species understudied (Patiño et al. 2017, Ottaviani et al. 2020).

Functional traits may illustrate the ability of exotic species to colonize and persist on an island, influencing their invasion success (Ottaviani et al. 2020). For instance, species producing a larger number of seeds and with a short lifespan have higher propagule pressure (i.e. the number of seeds arriving at a site at a given time), and thus higher invasion rates (Lockwood et al. 2005, Mason et al. 2008). Likewise, species with high dispersal capabilities have more chances to reach both near and remote islands (Carlquist 1974, Heleno and Vargas 2015, Arjona et al. 2018). By contrast, species with low seed production, long lifespans and low dispersal capabilities will likely colonize fewer, less isolated islands (Higgins, Nathan, & Cain, 2003; Pérez-Harguindeguy et al., 2013;). Finally, more generalist species might more effectively colonize a larger number of habitats (Denelle et al. 2020), and thus islands. Perhaps they also utilize more opportunistic colonization pathways associated with humans (Sinclair et al. 2020). Identifying which traits are associated with high invasion rates and investigating their relationships with island characteristics might allow conservation bodies to more efficiently focus their efforts in managing insular plant invasions.

1.4– Disturbances: do they favour invasions?

Disturbances encompass all discrete events that remove plant biomass (Grime 1977, Whittaker 1995), regardless of their nature and origin. Islands are particularly susceptible to perturbations, especially ocean-related. For instance, the catastrophic effect of hurricanes and cyclones on islands in the Caribbean and the Pacific has been well documented, both on landscape (Terry 2007), ecosystems (Zimmerman et al. 1996) and plants (Hjerpe et al. 2001, Morrison and Spiller 2008, Morrison 2010). However, also less strong events (i.e. waves, salt spray and wind shear) can impact the insular biota (Abbott 1977, Whittaker 1995). Earlier studies found that this type of events can reduce the habitable area for plant species (Neufeld et al. 2017), increase their extinction rates (Burns and Neufeld 2009) and reduce plant species diversity (Abbott 1977). However, the

biogeographical role of ocean-borne disturbances is still poorly understood, especially regarding less

catastrophic events (Whittaker 1995, Burns 2016b).

Whether disturbances facilitate invasions is contentious (Denslow et al. 2009, Moles et al.

2012). Disturbances vary greatly in intensity, regime and, most importantly, type (Keeley and

Brennan 2012, Moles et al. 2012, Jauni et al. 2015). For instance, anthropogenic disturbances are

typically associated with plant invasions (Blackburn et al. 2008, Pretto et al. 2012, Chiarucci et al.

2017, Paudel et al. 2017). Instead, disturbances of natural origin have contrasting effects on exotic

species (Hobbs and Huenneke 1992, Safford and Harrison 2001, Moles et al. 2012). Natural

disturbances can promote (Bellingham et al. 2005, Alba et al. 2015), prevent (Smith and Knapp

1999), or have no effect on plant invasions (Stohlgren et al. 1999, Suding and Gross 2006). While on

islands ocean-borne disturbances generally have a negative effect on plant species (Abbott 1977,

Burns and Neufeld 2009, Neufeld et al. 2017), their effect on exotics is still understudied (Burns

2016b).

1.5 – The human occupancy of islands

Species colonize islands in predictable ways (MacArthur and Wilson 1967). Since the inception of

island biogeography over 50 years ago, the insular distribution of species has been extensively

explored (Patiño et al. 2017). Theoretical models were developed to investigate species distributions

at different taxonomic levels (i.e. metapopulation dynamics, theory of island biogeography,

MacArthur & Wilson, 1967; Hanski, 1999). These models enabled biologists to empirically quantify

the island distribution of plants (Abbott 1977, Weigelt and Kreft 2013, Barajas-Barbosa et al. 2020),

mammals (Lomolino 1990, Russell et al. 2004), birds (Sampson 1980, Blackburn et al. 2008), reptiles

(Ficetola and Padoa-schioppa 2009, Novosolov et al. 2013, Helmus et al. 2014), fish (Sandin et al.

2008, Pinheiro et al. 2017), invertebrates (Toft et al. 2016, Schmack et al. 2020), fungi (Peay et al.

2007, Glassman et al. 2017, Donghao et al. 2020) and even bacteria (Bell et al. 2005, Lear et al. 2013). However, the human biogeography of humans is still largely unexplored.

The first record of island colonization by a hominid species dates to almost a million years ago (Bednarik 1999). Since then, humans have colonized virtually every island in the world (Keegan and Diamond 1987). Understanding when and how humans colonized islands has long been the focus of researchers (Kirch and Joanna 1994, James Dixon 2001, Anderson et al. 2014, Walter et al. 2017, Napolitano et al. 2019, Ihara et al. 2020). However, these questions were approached mostly from an anthropological perspective. By contrast, ecologists have focused on the impact of human populations and activities on island ecosystems and biota (Ellis 2019, Santos et al. 2021), also within the island biogeography framework (Sax et al. 2002, Kueffer et al. 2010, Helmus et al. 2014, Guo 2015). Despite a call for an integration of biogeographical principles in understanding distributional patterns of humans on islands (Keegan and Diamond 1987), an overarching explanation for the variation in insular human populations has yet to be established.

1.6– Study system

In this thesis, I investigate patterns of species distributions across different island systems. In chapters 2–4, I selected two different study systems both encompassing islands offshore New Zealand's North Island. New Zealand is an island country located in the South Pacific, approximately 2000 km from the nearest continental landmass, Australia. It is formed by three main islands, North, South and Stewart; hereafter referred to as the mainland. The main islands are surrounded by a large number of smaller islands: 890 of over 1 ha in size (Carter et al. 2020).

The first study system comprises 264 offshore islands off the northern coast of the North Island. This set of islands stretches over 600 km from the northwesternmost and the southeasternmost island, encompassing 4° of latitude and 7° of longitude (34–38°S, 172–179°E).

They range from very small islets to large islands (0.0021 ha to 27,721 ha), some are intertidal islands (i.e. reachable on foot during low tide), while others are 50 km from the coast. Their geological composition is diverse (volcanic=51.51%, sedimentary=46.21%, mixed=2.27%) and were all connected to the mainland during the last glacial maximum. Exceptions are the Poor Knights Islands, not connected to the mainland for at least 1 mya (Fleming 1979), and the two youngest volcanic islands, Rangitoto and Whakaari/White Island, which are still active (Clarkson et al. 1986, Campbell and Landis 2009). Warm, temperate rainforest characterize these islands as other wet areas at low latitudes of New Zealand (Dawson 1988, Grubb et al. 2013). The original vegetation was though cleared and burnt after human settlement and, in many cases, the forests were replaced by an agricultural landscape (Bellingham et al. 2010). More recently, some islands were abandoned while others are still farmed. New Zealand endured two waves of human colonization. The first one by Maori, the indigenous people of New Zealand, and the second by European. Currently, people of both ethnicities still inhabit 41 (15.5%) islands.

The second study system comprises 97 intertidal islands located along the Wellington coastline. They represent a set of small, rocky outcrops (0.825-166 m²) and they are situated in close proximity to the coastline. Most islands are of homogeneous geological composition (i.e. greywacke) (Burns 2015) and recent origin. The coastline was uplifted by approximately 6 meters in 1855 during one of the most intense earthquakes hitting New Zealand (Burns 2016b). These islands often house seabird colonies, which enrich the soil with guano (Grant-Hoffman et al. 2010, Ellis et al. 2011). Numerous storms strike the region, mostly originating in southern latitudes (Pickrill and Mitchell 1979). Vegetation on rocky outcrops along the Wellington coast is dominated by a few low growing, stress-tolerant species, with leathery or succulent leaves (Dawson 1988). These islands are all close to main roads and inhabited areas.

Lastly, in chapter 5, I selected 10 different island systems across the globe. A total of 486 islands were investigated. Archipelagos were chosen to reflect the various climatic, geographic and environmental settings present on the planet.

1.7– Thesis overview

In this project, I explore biogeographical patterns of vascular plant species and humans on islands. I used an island-based approach to investigate their relationship with island characteristics. My goals are to (1) explore differences in patterns of native and exotic species richness on islands, (2) examine relationships between plant functional traits and invasions within the island biogeography theoretical framework, (3) assess how richness and composition of native and exotic species vary depending on different levels of ocean-borne disturbance, (4) investigate the insular distribution of humans and its spatial variation on a global scale.

In chapter 2, I explored differences in patterns of native and exotic species richness by assessing their relationship with island characteristics (i.e. area, isolation, exposure to ocean-borne disturbances, latitude, distance from the nearest urban area). First, I evaluated the relationship between native and exotic species richness. Next, I explored how the richness of native and exotic species relate to island characteristics. I then identified over- and under-invaded islands by investigating how the residual variation in the native-exotic richness relationship relates to island characteristics. Finally, I tested for scale-dependency in the relationships between island characteristics and the two groups of species.

In chapter 3, I quantified a few, simple life-history traits (i.e. growth forms, dispersal modes) and assessed which are distinctive of the species that invade most islands. Afterwards, I tested whether the richness and seed mass of exotic species with distinct growth forms and dispersal modes vary differently with island characteristics (i.e. area, isolation, exposure to ocean-borne disturbances, distance from the nearest urban area, conservation areas). Lastly, I asked whether results differ for native species.

In chapter 4, I selected a set of small intertidal islands subject to varying levels of disturbance originated by the ocean (i.e. inside and outside Wellington Harbour). Then, I tested whether the richness of native and exotic species differ in their relationship with island characteristics (i.e. area, isolation, height, elevation, slope, nearest dwelling) depending on island location. I then calculated Jaccard similarity indexes to assess whether composition and spatial turnover differ on inner and outer islands for the two sets of species.

In chapter 5, I investigated the island biogeography of humans. First, I selected 10 island systems across the globe. Next, I empirically tested the relationship between human population size and several island characteristics (e.g. area, elevation, isolation, latitude and longitude). I then explored how relationships between population size and island characteristics vary among different archipelagos.

In chapter 6, I discuss the results of previous chapters. The first three chapters of my thesis combine with a growing body of literature investigating differences in the distributional patterns of native and exotic species. By using a range of techniques (e.g. residuals) and approaches (e.g. trait-based) I was able to identify fine differences in how native and exotic species relate to island

characteristics. Chapter 2 also included the first test for the scale-dependency in the relationship between native and exotic species richness and island characteristics. Chapter 5 provides what is, to my knowledge, the first global test of the human biogeography of islands, representing a potential starting point for future studies investigating insular distributional patterns of humans.

Chapter 2.   Similar yet distinct distributional patterns characterize native and exotic plant species richness across islands in New Zealand

2.1 – Abstract

Aim A better understanding of plant invasions on islands can be gained from comparing patterns of exotic and native species richness. I asked four questions: (1) Is exotic species richness on islands related to native species richness? (2) If they are related, does this result from similar responses of native and exotic species to specific island characteristics? (3) Is residual variation in native-exotic richness relationships associated with distinctive island characteristics? (4) Are relationships between species richness and island characteristics scale-dependent, and do they differ between native and exotic species?

Location Northern New Zealand

Taxon Vascular plants

Methods I conducted field surveys and augmented my field data with previously published surveys to quantify the number of native and exotic plant species on 264 islands. I then explored the relationship of species richness and several island characteristics (e.g. area, isolation) using multiple and iterative regression techniques.

Results Seventy-two percent of among-island variation in exotic species richness was positively related to native species richness. Both native and exotic richness increased with island area, and declined with isolation and exposure to ocean-borne disturbances (a proxy for salt spray, wave action, etc.). However, exotic species responded more strongly to these three variables. Exotic richness also decreased with latitude and the distance from the nearest urban area, but native species did not. Island area was a better predictor of species richness on larger islands, while isolation and exposure were better predictors on smaller islands. Scale-dependent relationships between species richness and island characteristics were stronger for exotic species.

Main conclusions Insular distribution patterns of native and exotic plant species richness are governed by similar biogeographic principles. However, in New Zealand, exotic species exhibited subtle, yet distinctive, invasion patterns preferring larger, less isolated, less exposed islands that were located at higher latitudes, and closer to urban areas.

2.2 – Introduction

Biological invasions are a major threat to biodiversity worldwide (Whittaker and Fernández-Palacios 2007, Simberloff et al. 2013, Liao et al. 2020). Invasions by exotic plant species can gradually displace native species, resulting in global floristic homogenization (Pyšek and Richardson 2006, Qian and Ricklefs 2006, Castro and Jaksic 2008). Although floristic homogenization is widespread (Arianoutsou et al. 2010, Stotz et al. 2019), it is especially pronounced on islands for reasons that have yet to be fully resolved (Lonsdale 1999, Pyšek and Richardson 2006, Castro and Jaksic 2008, Kueffer et al. 2010).

The number of exotic species inhabiting oceanic islands often increases with the number of native species (Lonsdale 1999, Seabloom et al. 2007, Sax and Gaines 2008, Denslow et al. 2009, Dyer et al. 2016, Carpio et al. 2017). A variety of mechanisms may promote positive native–exotic richness relationships (Fridley et al. 2007, Burns 2016b, Smith and Côté 2019). Perhaps the simplest explanation is that both groups respond similarly to broad-scale variation in environmental conditions (Fridley et al. 2007, Stohlgren et al. 2007, Tomasetto et al. 2019).

The theory of island biogeography predicts that larger islands contain more species because they can support larger populations, which are less prone to extinction (MacArthur and Wilson 1967). It also predicts that less remote islands have more species, because they are more likely to intercept randomly dispersing propagules. In addition to area and isolation, islands can vary strongly in topography (Hu et al. 2011, Yu et al. 2012), climate (Kreft et al. 2008, Arianoutsou et al. 2010), disturbances of oceanic origin (e.g. salt spray, wave action, storms) (Burns and Neufeld 2009, Neufeld et al. 2017), and human occupation (Blackburn et al. 2016, Paudel et al. 2017), all of which can potentially regulate the number of native and exotic species (Moody 2000, Stohlgren et al. 2006, Kueffer et al. 2010, Moles et al. 2012).

Although exotic species richness on islands is often linked to the native species richness (Lonsdale 1999, Qian & Ricklefs 2006, Sax & Gaines 2008), covariance between native and exotic

44

richness can be weak. For example, although native and exotic species richness were positively related among islands in the South Pacific, the relationship explained less than half the among-island variation (Denslow *et al.*, 2009, *c.f.* Long *et al.*, 2009). This suggests that distinctive processes, operating differently on exotic and native species, are the reason for residual variation in native–exotic richness relationships.

Relationships between species richness and island characteristics can also be scale-dependent. Scale-dependency, which refers to when ecological patterns and processes vary with spatial scale, is pervasive in ecology (Wiens 1989, Swenson et al. 2006, Powell et al. 2013, Fung et al. 2019) and has been extensively explored in island biogeography. Studies typically focus on the effect of spatial scale on species–area relationships (Lomolino and Weiser 2001, Tjørve and Tjørve 2017, Guo et al. 2020), with a few also accounting for other island characteristics (Giladi et al. 2014, Menegotto et al. 2020, Schrader et al. 2020). The processes responsible for scale-dependent variation in species–area relationships are also poorly understood (Turner and Tjørve 2005). No previous study has tested whether scale-dependent relationships in insular species richness differ between native and exotic species.

To better understand patterns of invasion of exotic plant species on islands, I quantified the richness of 1677 vascular plant species on 264 islands off the northern coast of New Zealand. Naturalised exotic plant species comprise 43.9% (1798 species) of New Zealand's total vascular plant flora (Brandt et al. 2021), and 85% of the 2229 native plant species are endemic (McGlone 2006). I used multiple and iterative regression techniques to determine whether: (1) native and exotic species richness are related, (2) native and exotic species richness are related to the same island characteristics (e.g. island area, isolation, etc.), (3) residual variation in native–exotic richness relationships are associated with distinctive island characteristics, (4) invasion patterns are scale-dependent.

2.3 – Methods

Study site

New Zealand consists of two main islands (hereafter referred to as the "mainland") and hundreds of smaller, surrounding islands (Carter et al. 2020). In this study, I focused on 264 islands located off the northern coast of the North Island. The study system spans 4° of latitude and 7° of longitude (34–38°S, 172–179°E). Six hundred kilometres separate the northwesternmost and southeasternmost islands (Figure 2.1).

The studied islands range from 0.00002 to 277.21 km^2 in size. Some islands are barely isolated and can be reached by foot at low tide, while others are located over 50 km from the mainland. Just over half the islands are volcanic in origin (51.51%), while others are sedimentary in origin (46.21%). A small number of islands are of mixed composition geologically (2.27%). Most islands were connected to the mainland during the last glacial maximum, except for the Poor Knight Islands (separated c. 1 Mya; Fleming, 1979).

Before human arrival, most islands supported warm temperate rain forest (Wilmshurst et al. 2014). This forest type dominates low latitudes of New Zealand (34°20′ – 41°40′ S, Grubb *et al.*, 2013), particularly in wetter, more productive areas (Dawson 1988). Since first settlement 740 years ago, humans have had a marked effect on many islands. On some islands, the natural vegetation was cleared, burnt and replaced by an agricultural landscape (Bellingham et al. 2010). Some of these islands have since been abandoned and are now undergoing succession naturally, others are still being farmed. Currently, 41 islands (15.5%) are inhabited. Other islands were only visited occasionally by people and their floras were less heavily impacted.
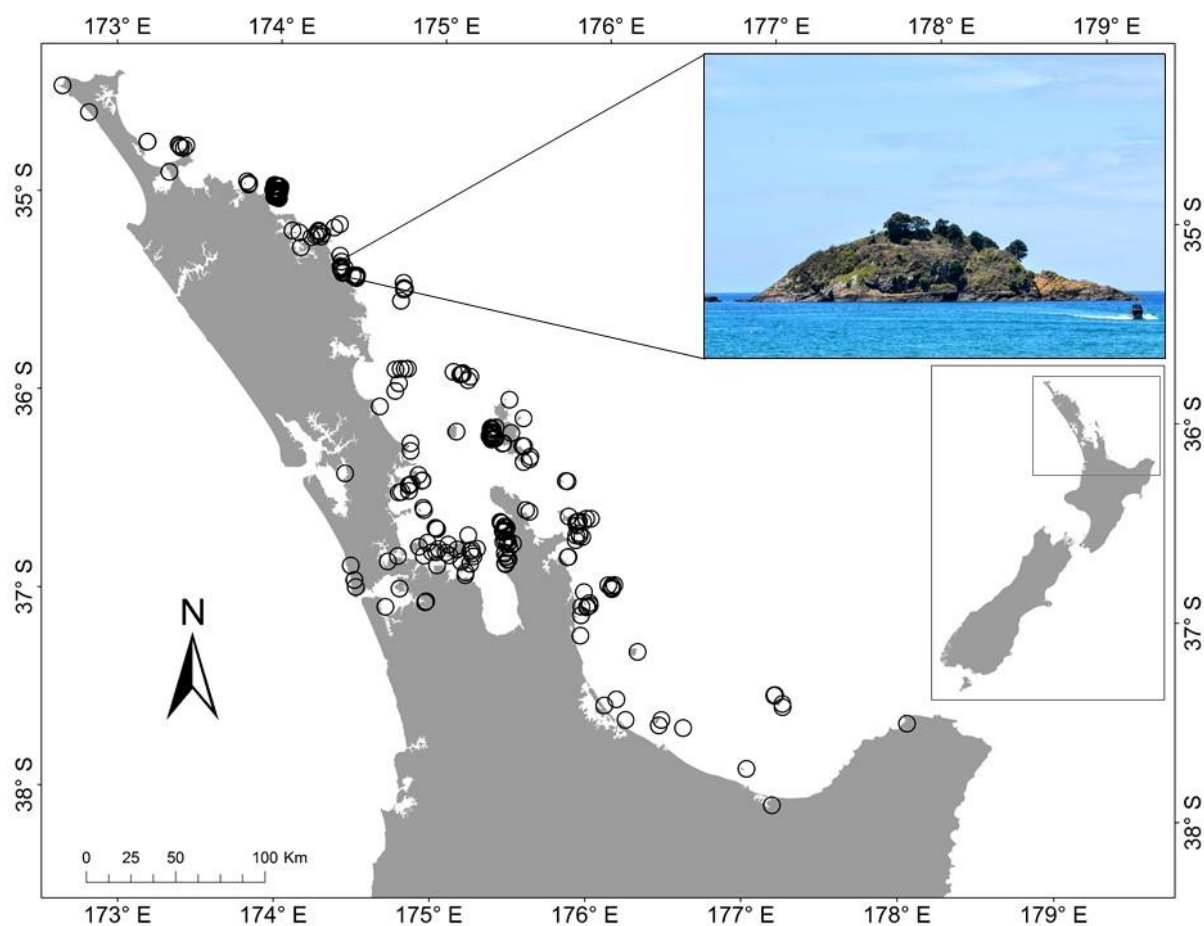
Figure 2.1 - Map of the study area off the Northern coast of the North Island of New Zealand and a photograph of a typical island.

Island species richness

A comprehensive botanical reconnaissance of vascular plants has been conducted on each of the 264 islands. Most were conducted after 1970, and my study includes published species lists (Appendix 1) and previously unpublished lists (by EKC and AEW for 12.9% of the islands). Several islands were surveyed multiple times and often studies collated previous records, dating back to the end of the 19th century (e.g. Wright 1980; Cameron & Davies 2013). I collated complete records for each island, from comprehensive lists and subsequent update lists for some (e.g. de Lange & McFadden 1995; Cameron & Young 2019). I applied consistent, updated nomenclature

(https://nzflora.landcareresearch.co.nz, accessed in July 2018) for all lists for each island. Permits were obtained for all unpublished surveys, issued by either the New Zealand's Department of Conservation or Māori and private island owners.

A total of 1677 vascular species were recorded during island censuses. All species were classified as either native to New Zealand, or having evolved elsewhere (i.e. 'exotic'). Just over half of all species on islands were exotic (50.96%), most of which were of European origin, but others come from temperate regions worldwide, notably Australia and South Africa. Due to taxonomic uncertainties, 18 species could not be unambiguously determined as either native or exotic and were excluded from analyses.

Island characteristics

The physical geography of islands was characterised using geographic software (ArcGIS 10.5.1, ESRI, 2011), as follows:

- Island area was quantified as total surface area when viewed vertically (km^2).

- Isolation is typically quantified as the shortest distance between an isolate and the mainland (MacArthur and Wilson 1967). However, in more crowded archipelagos, adjacent islands may act as source pools of dispersing propagules, in addition to the mainland (Diver 2008). Therefore, I chose a landscape measure of isolation, which characterises isolation as the total amount of land located in concentric belts surrounding each island (Diver 2008, Negoita et al. 2016, Carter et al. 2020). I derived a series of 'buffers' with radii of 250, 500, 1000, 1500, 2000, 2500, 3000 m and calculated the proportion of land within each one (%). By removing this value from the total area surrounding an island, I ensure that larger values match greater island isolation.

- Disturbances of oceanic origin were defined as the effect of waves, storm surges, wind shears and salt spray. Exposure to ocean-borne disturbances was quantified following Burns & Neufeld (2009) as the angle between two straight lines diverging from the centre of each island to the

edge of the nearest landmasses (mainland and islands larger than 5,000 ha) in QGIS 2.18.20

(QGIS Development Team 2018). The magnitude of the angle indicates the extent of open ocean

fronted by an island.

- Latitude and longitude were included as a proxy for geographic gradients in species diversity and

  climate (2nd decimal place) (Arianoutsou et al. 2010, Kueffer et al. 2010).

- To account for topographic complexity, I quantified, as proxies, elevation and perimeter (Kreft et

  al. 2008, Yu et al. 2012).

- One of the main sources of naturalising exotic species in New Zealand are gardens around

  dwellings, so the number of exotic species declines with distance from private gardens (Sullivan

  et al. 2005), huts (Lloyd et al. 2006) and towns (Timmins and Williams 1991). Therefore, I

  measured the shortest distance (m) from the nearest urban area, which I defined as having a

  population of 1,000 people or more (Statistics NZ Tatauranga Aotearoa 2018).

Variables pre-selection

The isolation radius was chosen by regressing each buffer against the residuals of the species–area

relationship (Negoita et al. 2016). I computed the Akaike information criterion aiming to retain the

metric with higher probability of predicting native and exotic species richness (Appendix 2, Table

A.2.1) and, on this basis, I selected a 1500 m radius.

Before inclusion in the model, I used a Pearson correlation coefficient to test for

independence among geographic variables, setting 0.8 as a cut-off (Appendix 2, Figure A.2.2) (Berry

and Feldman 1985). Three variables were then excluded due to multicollinearity: elevation and island

perimeter, both highly positively correlated with area (Pearson r = 0.82 and 0.99, respectively), and

longitude, positively correlated with latitude (Pearson r = 0.88) (Appendix 2, Figure A.2.3). I retained

island area as a more complex proxy of topographic complexity than either elevation or perimeter

alone. Latitude was preferred over longitude because it betters reflects global changes in environmental conditions.

I tested for spatial autocorrelation of dependent and independent variables, using Moran's I coefficients. There was no evidence of spatial autocorrelation in island area (Appendix 2, Table A.2.2). Islands were positively spatially autocorrelated, or clustered, with respect to native and exotic species richness, isolation, and distance from urban area, but with low but significant Moran's I values. Islands were also clustered with respect to ocean-borne disturbances but showed high and significant Moran's I values (Appendix 2, Table A.2.2).

Statistical analyses

Covariation in native and exotic species richness on islands was investigated by using simple linear regression. Native species richness was employed as an independent variable and exotic species richness as the dependent variable. Both variables were logarithm transformed prior to analyses to conform to normality assumptions. I added a value of 1 prior transformation to avoid undefined values.

To identify whether native and exotic species richness covary with similar island characteristics, I conducted two analogous linear models. Species richness was used as the dependent variable in both. Island area (km^2), isolation (%,), exposure to ocean-borne disturbances (º), latitude (linearized degree), and distance from the nearest urban area (m) were entered as independent variables. All variables were transformed where necessary to conform to assumptions (Table 2.1 and Appendix 2, Figure A.2.1).

To investigate uncorrelated variation in the native–exotic richness relationship, I explored residual variation in the native–exotic richness relationship. While covariation between native and exotic species richness suggests a similar relationship with island characteristics, unexplained

variation (residuals) indicates otherwise. Islands with increasingly positive (or negative) residuals are more (or less) heavily invaded than expected, suggesting exotics respond differently to island characteristics. By exploring only uncorrelated variation in the native–exotic relationship, I remove the component of island characteristics that has a similar effect on both sets of species. If exotics respond distinctively from natives to geographic variables, relationships should emerge between the residuals of the native–exotic relationship and island characteristics. To do so, I conducted a linear model using the residuals of the native–exotic richness relationship as the dependent variable and island characteristics as independent variables.

I used two analytical procedures to investigate the scale-dependency of relationships between species richness and island characteristics. Both techniques assessed how relationships between species richness, island area, isolation and exposure to ocean-borne disturbances vary among different island sizes. The first, 'sequential deletion' technique began by regressing species richness against each of the three island characteristics separately using the whole dataset (n = 264 islands). Islands were then ranked according to their area (largest to smallest) and the test was repeated with the largest island removed from the dataset. Afterwards, the test was repeated after the largest two islands were removed from the remaining dataset. This procedure was then repeated sequentially until there were only 70 islands left in the dataset. A similar analysis was conducted after ranking islands from smallest to largest. The second, 'moving window' procedure was calculated similarly, except that each test was restricted to only 70 islands, such that the sample size was identical in all analyses (Menegotto et al. 2020). The first test included only the 70 largest islands in the database, and each subsequent test was conducted after removing the largest island and including the next smallest island in the dataset. The test was repeated until only the 70 smallest islands remained in the database. In each iteration of both procedures, the coefficient of determination (r^2) was obtained for each independent variable to identify the best predictor of species richness among islands of different size. Native and exotic species were analysed separately to determine whether they had similar scale-dependent responses to island characteristics. All

analyses were performed in the R environment (R Core Team 2020). The moving window procedure was conducted using the *Zoo* package (Zeileis and Grothendieck 2005).

2.4 – Results

Exotic species richness on islands was strongly related to native species richness (log–log r^2 = 0.720, p < 0.001; Figure 2.2 and Appendix 2, Figure A.2.4). Total richness in both groups increased with island area, and declined with island isolation (radius = 1500 m) and exposure to ocean-borne disturbances (Table 2.1 and Appendix 2, Figure A.2.5). However, while exotic species richness also declined with latitude and distance from the nearest urban area, native species richness was unrelated to both (Table 2.1 and Appendix 2, Figure A.2.5).

Table 2-1 - Results from linear regression models exploring the relationship between native and exotic species richness and island characteristics on 264 islands off the coast of New Zealand. Entries are estimate, standard error, t and p values. In bold are significant relationships. The last row shows the adjusted r-squared for each model. Statistical significance: *P < 0.05, **P < 0.01, ***P < 0.001.

Variables	log(1+Natives)				log(1+Exotics)			
	Estimate	Standard error	t-value	p-value	Estimate	Standard error	t-value	p-value
log(Area)	0.315	0.018	17.294	**<=0.001**	0.373	0.021	18.099	**<=0.001**
arc sine(Isolation$_{1500}$)	-0.466	0.185	-2.516	**0.0125**	-0.981	0.209	-4.682	**<=0.001**
Exposure	-0.002	0.001	-2.297	**0.0224**	-0.006	0.001	-5.995	**<=0.001**
Latitude	-0.044	0.063	-0.705	0.4816	-0.171	0.071	-2.41	**0.0166**
square root(Urban)	0.000	0.001	-0.367	0.7137	-0.003	0.001	-3.158	**0.0018**
Adjusted r-squared	0.55				0.61			

Unexplained variation in the native–exotic richness relationship increased with area and declined with island isolation, exposure to ocean-borne disturbances, latitude and distance from the nearest urban area (

3). Therefore, exotic species richness was greater than native species richness on large, sheltered, high-latitude islands that were close to other landmasses and urban areas.

Relationships between plant species richness, island area, isolation and exposure to ocean-borne disturbances were scale-dependent; more strongly for exotic species (Figure 2.4). Area was a better predictor of plant species richness than isolation and exposure in larger island size classes, while isolation and exposure became increasingly important predictors of plant species richness as island area declined. The 'sequential deletion' method showed that in native species, the predicting power of area declined the smaller the islands were, while that of isolation and exposure increased. However, area remained the best predictor throughout. For exotics, isolation outweighed area after removing the 95 largest islands (mean area of samples removed for this iteration = 0.0145 km^2, range 0.00002–0.0622 km^2), whereas exposure surpassed area after removing the 66 largest islands ($\bar{x}$ = 0.0295 km^2, range 0.00002–0.1784 km^2). Results were consistent by ranking the islands from smallest to largest instead (Appendix 2, Figure A.2.6). The 'moving window' analytical approach yielded similar results. For native species, area was outweighed by isolation at the 108th iteration (mean area = 0.021 km^2, range 0.0072–0.0516 km^2) and by exposure at the 107th ($\bar{x}$ = 0.0216 km^2, range 0.0072–0.0520 km^2). Both trends inverted after 171 iterations ($\bar{x}$ = 0.004 km^2, range 0.0012–0.0086 km^2). In exotics, area and isolation overlapped at 75th iteration ($\bar{x}$ = 0.0544 km^2, range 0.0180–0.1301 km^2), the former was outweighed at the 93rd iteration ($\bar{x}$ = 0.0318 km^2, range 0.0105–0.0698 km^2). Exposure surpassed area after 32 iterations ($\bar{x}$ = 0.2745 km^2, range 0.0573–0.9485 km^2), the two overlapped after 50 iterations and exposure overridden area again at the 68th iteration

($\bar{x}$ = 0.0679 km^2, range 0.0214–0.1719 km^2). In both cases, the scale-dependency of island isolation

and exposure to ocean-borne disturbances were better predictors of exotic species richness.
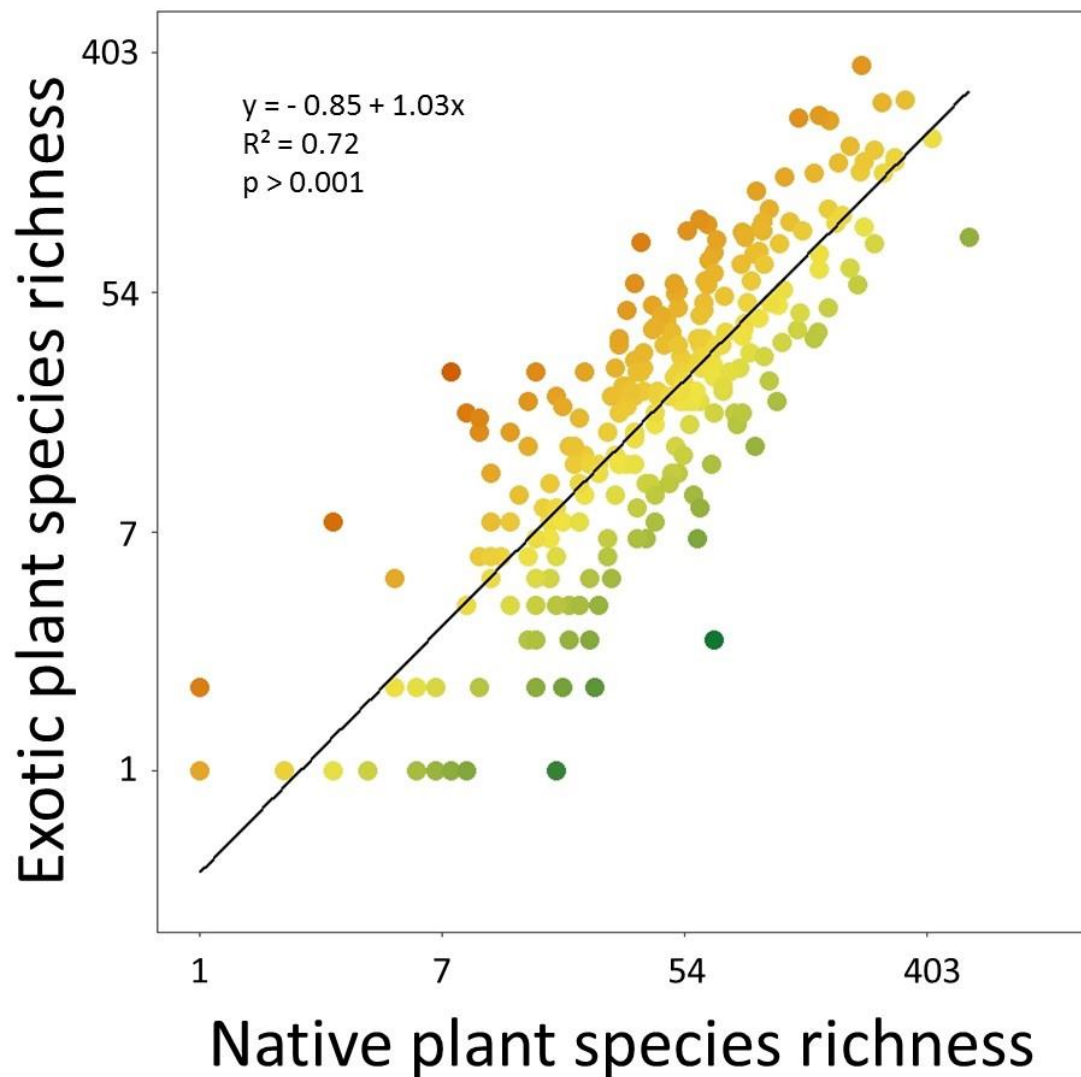
Figure 2.2 - Positive relationship between exotic plant species richness and native plant species richness on 264 islands off the north coast of New Zealand. Symbol colours represent unexplained (residual) variation in exotic plant species richness. Heavily invaded islands are coloured red, while relatively under-invaded islands are coloured green. Both axes are logarithm (+1) transformed to conform to assumptions.

2.5 – Discussion

Over 70% of the variation in exotic plant species richness across northern New Zealand islands was related to native plant species richness. Positive native–exotic richness relationships are commonly observed across large spatial scales, particularly on islands (Fridley et al. 2007, Sax and Gaines 2008). My results are also consistent with previous work indicating that positive native–exotic richness relationships result from both groups of species responding similarly to particular island characteristics (Fridley et al. 2007, Long et al. 2009, Carpio et al. 2017).

In this study, both native and exotic plant species richness increased with island area and declined with island isolation and exposure to ocean-borne disturbances (e.g. salt spray, wave action, storms). Positive relationships between species richness and island area are among the most commonly observed patterns in nature and can be generated by a variety of processes (Arrhenius 1921, Rosenzweig 1995, Turner and Tjørve 2005, Baiser and Li 2018, Guo et al. 2020). Larger islands are more likely to intercept randomly dispersing propagules (Gilpin and Diamond 1976, McGuinness 1984, Lomolino 1990). They can also support larger populations, which are more buffered from extinction (Lomolino and Weiser 2001, Turner and Tjørve 2005). Larger islands can also contain more habitats, hence more habitat specialists (Triantis and Sfenthourakis 2012, Chen et al. 2020). Species–isolation relationships are also commonplace and likely arise from the negative effect that geographic isolation often has on rates of island colonisation (MacArthur and Wilson 1967). Although the effects of disturbances on the number of species inhabiting islands are more poorly understood, previous work indicates that more exposed islands often exhibit higher extinction rates and impoverished floras (Morrison and Spiller 2008, Burns et al. 2009, Burns 2016b).
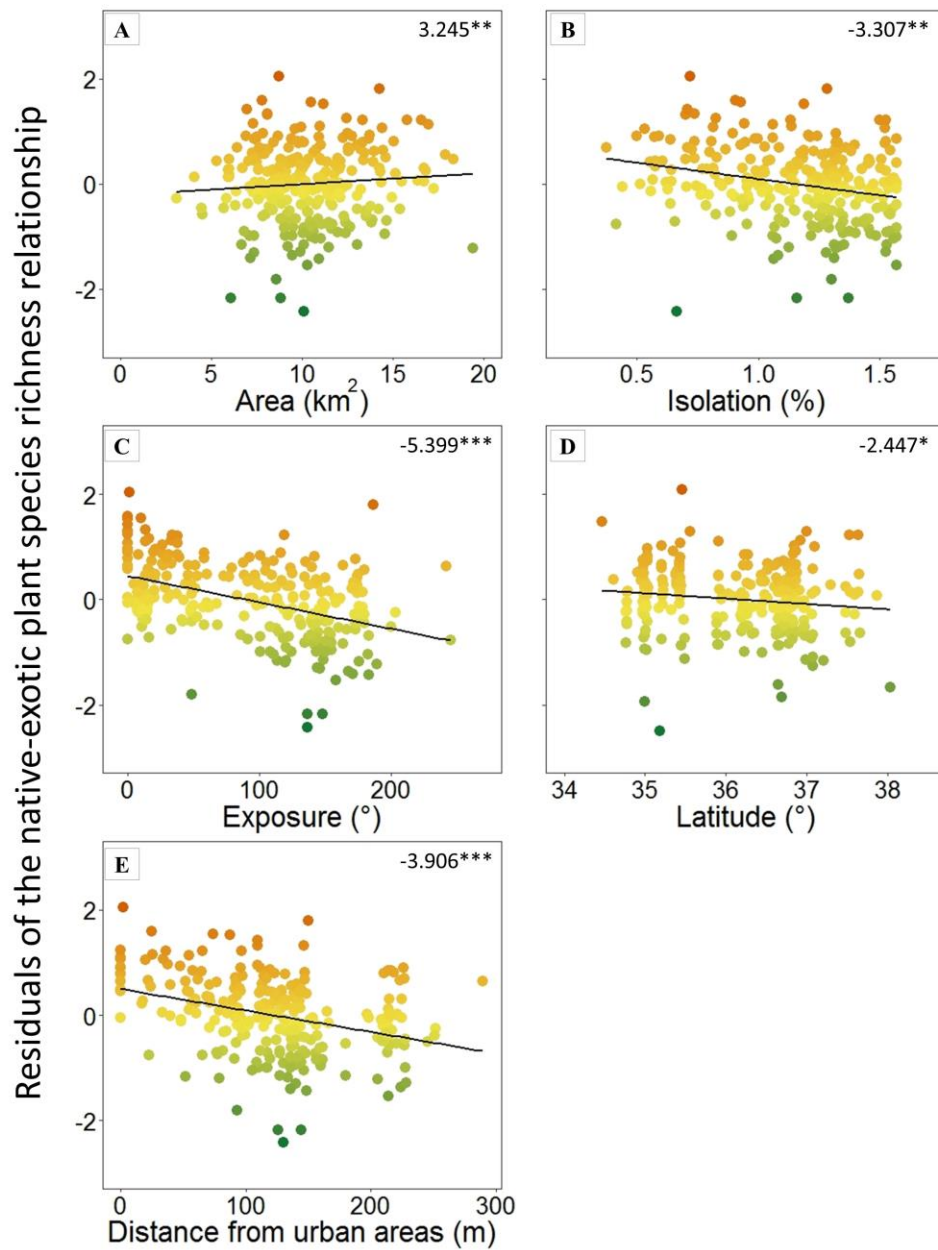
Figure 2.3 - Relationships between uncorrelated (residual) variation in the native-exotic richness relationship and island (A) area, (B) isolation, (C) exposure to ocean born disturbances, (D) latitude and (E) distance from the nearest urban area on 264 islands off the north coast of New Zealand. Symbol colours represent unexplained (residual) variation in exotic plant species richness. Heavily invaded islands are coloured red, while relatively uninvaded islands are coloured green. For each graph, the coefficient and the significance of its t-test are given (level of statistical significance: *P < 0.05, **P < 0.01, ***P < 0.001). To conform to assumptions, area was log-transformed, isolation arcsine-transformed and distance from the nearest urban area root squared-transformed.

Although exotic species plant richness was positively related to native species richness, 28% of the variation in exotic species was unrelated to that of natives. This result aligns with several previous studies both on islands (Lonsdale, 1999; Denslow *et al.*, 2009; Long *et al.*, 2009; Burns, 2016; but see Sax & Gaines, 2008) and on continents (Kumar et al. 2006, Qian and Ricklefs 2006, Seabloom et al. 2007, Bartomeus et al. 2012), suggesting that native–exotic richness relationships might mask subtle biogeographic dynamics between native and exotic species. Residuals of native–exotic richness relationships in my study showed that exotic species respond slightly differently to island area, isolation, exposure, latitude and distance from urban areas.

Exotic species were disproportionately abundant on large, less isolated islands. New Zealand was one of the last landmasses to be discovered by humans and most exotic plant species were introduced into New Zealand in the last 150 years (Williams and Cameron 2006). Many exotic species may still be in the process of dispersing to islands within my study system. Therefore, the more pronounced effect of area and isolation in exotic species might stem from a time-lag in the invasion process (i.e. ongoing invasion). Large islands offer a greater surface, increasing chances of being intercepted by colonizing propagules (Lomolino 1990). Conversely, less isolated islands present a weaker barrier to colonisation (MacArthur and Wilson 1967). During the initial stages of island colonisation, large and less isolated islands are more likely to be colonized first, as was shown in a study of plant invasions on New Zealand's two main islands, where the number of provinces colonized by exotic species increased with their time since introduction (Williams & Cameron 2006). Because species richness data for some islands in my study are up to 50 years old, some recent range expansions (or contractions) for some species might have gone undetected. In addition, islands located in close proximity are likely to share similar species (see Appendix 2, Table A.2.2). More detailed analyses are required to examine this possibility.

Sheltered islands also had disproportionately more exotic plant species. Most exotic species in this study evolved on continents and were adapted to human agricultural and horticultural practices (Lloret et al. 2005), and may be poorly adapted to rocky, windblown habitats with saline soils, which generally characterise island environments (Burns 2019). Therefore, disturbances of oceanic origins may be too frequent or too severe for exotic species to successfully establish and persist on exposed islands (Burns 2016b). On the other hand, plant species that are native to my study system are well-adapted to coastal habitats in New Zealand (Cockayne 1958). Islands were also clustered with respect to exposure to ocean-borne disturbances, a potential source of error that requires further investigation.

Exotic plant species were also disproportionately abundant on islands located closer to urban areas. Human settlements are often foci for plant invasions and denser populations of people may be serving as source pools for island emigrants (Castro & Jaksic 2008; Kueffer et al. 2010; Pretto et al. 2012; Paudel et al. 2017; Schmack et al. 2019 c.f. Löfgren & Jerling, 2002; Stohlgren *et al.*, 2006). Exotic species were also disproportionately abundant on islands located at higher latitudes. Climatic conditions become warmer and wetter in more northerly regions of my study system. Therefore, exotic species may be disproportionately diverse on lower latitude islands, due to elevated levels of primary productivity (Lawrence and Fraser 2020). Why native species fail to exhibit a similar trend is unclear. While direct measurements of climate conditions (e.g. temperature, precipitations) would probably improve my predictions, these data are unavailable for most islands in my study; the few data available are biased towards larger, inhabited islands.

Exotic plant richness is often related to human disturbance, as measured by numbers of buildings, lengths of roads, or the extent of agricultural fields (Seabloom et al. 2007, Pretto et al. 2012, Paudel et al. 2017). While I could have applied such an analysis across my islands, only 15.5% of the islands in my study are currently inhabited with variables like these that could be quantified. This would almost certainly underestimate effects of past human disturbance. Many of the islands in

my study were either permanently or temporarily settled by Māori (Holdaway et al. 2019) and many others burned (Bellingham et al. 2010). Others were farmed briefly after European settlement, then abandoned (Bellingham et al. 2010). More data are needed to quantify past disturbance across the islands in my study to permit an appraisal of human disturbance on native and exotic species richness.

Relationships between species richness and island characteristics were also scale-dependent. Results showed that the relative influence of island area on species richness declined with island area, while that the influence of island isolation and exposure strengthened. This is consistent with a 'small island effect', a situation where species richness varies more or less independently of sample area on small island size classes (MacArthur and Wilson 1967, Lomolino and Weiser 2001, Dengler 2010). A similar, multi-variable approach to that used here (i.e. sequential deletion, moving window) might be useful in future studies, as they alleviate some of the problems of previously used analytical techniques (Burns et al. 2009, Dengler 2010, Menegotto et al. 2020, Schrader et al. 2020).

The scale-dependent effect of island isolation may be explained by the target-area effect, which predicts that island immigration rates increase with island area, because bigger islands are bigger 'targets' for dispersing propagules (Gilpin and Diamond 1976, McGuinness 1984, Lomolino 1990). If bigger islands have higher immigration rates than smaller islands in my study system, the potential effects of island isolation on immigration rates might increase as the size of islands declines. Given that many exotic plant species are still in the process of invading islands within my study system, this process should be particularly strong in exotic species. However, other potential drivers of the area–isolation interaction might exist (e.g. stepping stones, island clustering, see MacArthur & Wilson, 1967). Future studies should explore this aspect with more appropriate tools (Weigelt and Kreft 2013).
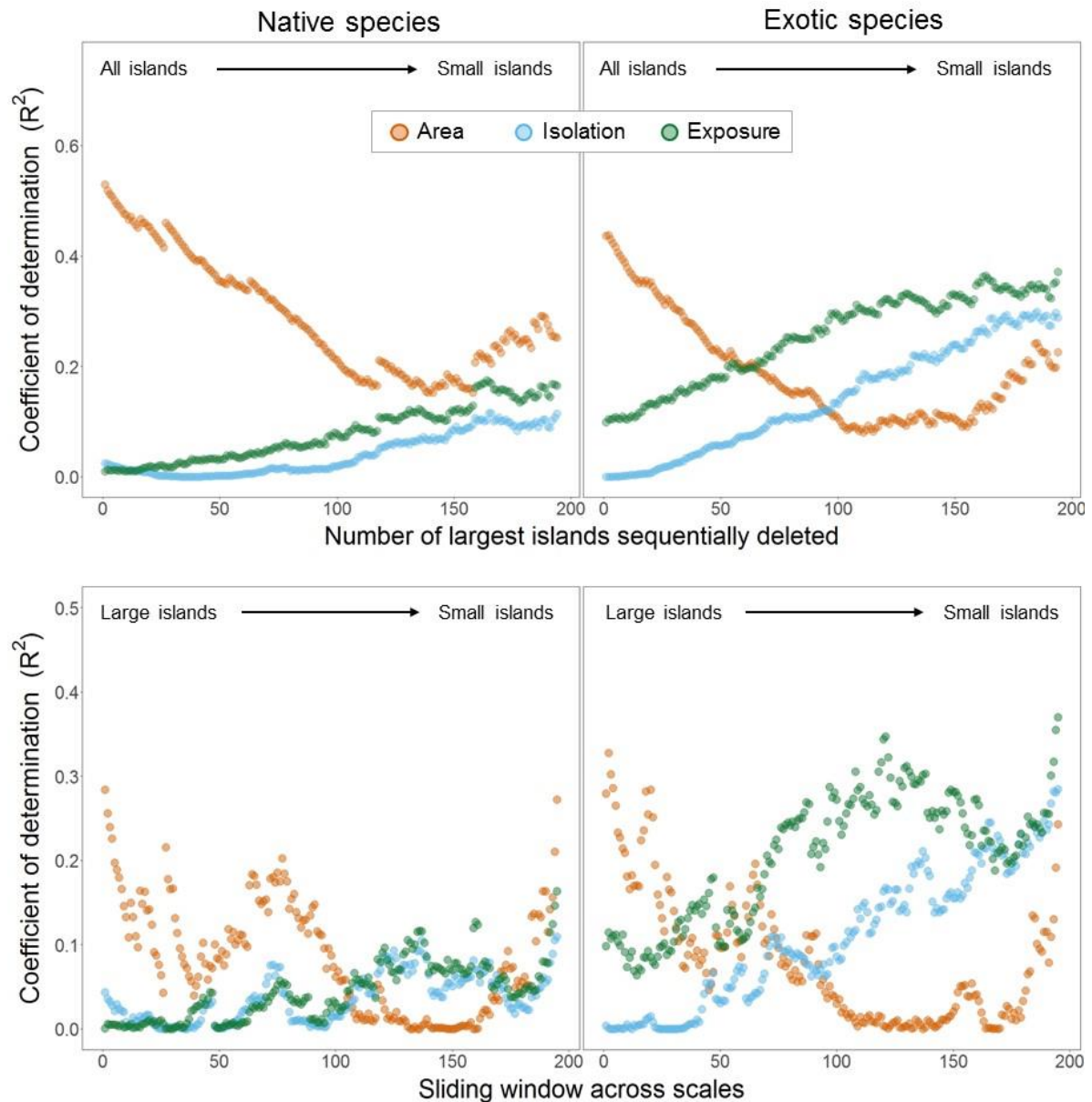
Figure 2.4 - Scale-dependent variation in relationships between plant species richness, island area (vermilion points), isolation (blue points) and exposure to ocean-borne disturbances (green points) on 264 islands off the north coast of New Zealand. Analyses of native species richness are shown at left and analyses of exotic species are shown at right. The top set of graphs illustrates the 'sequential deletion' method. Each point represents a separate linear model with the largest islands in the study system sequentially deleted. The bottom set of graphs illustrates the 'moving window' method. Each point represents a separate linear model on just 70 islands. Each point, moving left to right along the x-axis, represents a new set of 70 islands, wherein the largest island in the set was replaced with the next smallest in the following island in the series. The coefficient of determination (r2) is shown on the y-axes of all four graphs. On the top row, the x-axis shows the number of islands removed at each regression, while the bottom row represents the number of separate analysis conducted.

As island area declines, the effects of ocean-borne disturbances are likely to increase as well, because shorter distances separate the ocean from the interior of an island. Therefore, the effects of ocean-borne disturbances extend deeper into the centre of small islands, due to larger perimeter to area ratios (McGuinness 1984, Morrison and Spiller 2008, Neufeld et al. 2017). Ocean-borne disturbances structure plant communities on small islands in my study system (e.g. Gillham, 1960) and may act as a filter on invasions by exotic plants. The strong effects of disturbance on exotic species richness on very small islands may be because the total pool of exotic species, selected by people for agriculture and as ornamentals, has fewer species adapted to these conditions than native species. Small, isolated islands prone to ocean-borne disturbances in my study system also disproportionately contain large populations of breeding seabirds (Bellingham et al. 2010). These birds cause high levels of disturbance and their guano enriches soil nutrients, imposing a further strong filter on plant communities (Grant-Hoffman et al. 2010, Ellis et al. 2011) to which I expect proportionately fewer exotic plant species of the total pool are adapted.

In conclusion, my results indicate that while positive native–exotic plant species richness relationships reflect broadly similar distributional patterns between native and exotic species, they mask subtler trends in invasion patterns. This might stem from a time-lag in the invasion process and a strong link with human occupancy, climate and environmental filtering. My results underscore the importance of investigating the residual variation in native–exotic richness relationships and including the effect of scale to uncover differences in species distribution that are otherwise undetectable (Sax et al. 2002). Invasive species management should not rely solely on native species richness to predict the number of invasive species, as exotic species exhibit distributional patterns on islands similar, yet distinct, from native species.

Chapter 3.   Functional traits explain species richness and island occupancy of exotic plants on northern New Zealand islands

3.1 – Abstract

Functional traits vary strongly among exotic plant species. Interrelationships between traits and invasion success have been explored in several studies, but only a few have integrated relationships within the island biogeography theoretical framework. I explored relations between functional traits and plant distributions to assess which traits are distinctive of the species that invade most islands, test whether exotic richness and seed mass of growth forms and dispersal modes vary differently with island characteristics (e.g. area, isolation, exposure to ocean-borne disturbances, distance from the nearest urban area and conservation areas) and if results differ from native species. I assembled a database of 264 northern New Zealand offshore islands, amalgamating species lists from field surveys and previously published data, and comprising 822 native and 855 exotic species. I appraised several island characteristics and obtained values for functional traits from available databases. Exotic graminoids occurred on islands more frequently than forbs and woody species, and wind-, animal-dispersed species and those with unspecialized dispersal more than species with short-distance dispersal modes. Most differences among trait categories of exotic species were associated with human-related variables (i.e. distance from the nearest urban area and conservation areas); however, species displaying high occupancy were often unrelated to them. Overall, successful invaders (i.e. exotics with high occupancy) displayed both rates of occupancy and patterns in richness and seed mass similar to natives. My results illustrate that integrating trait-based approaches in the island biogeography framework can be a useful tool in understanding and predicting plant invasions.

3.2 – Introduction

Islands worldwide are often heavily invaded by species from other biogeographical regions (i.e. exotic species) (Pyšek and Richardson 2006, Denslow et al. 2009, Kueffer et al. 2010, Paudel et al. 2017). On some islands, exotic species richness equals that of native species (e.g. Hawaiʻi, New Zealand, and several other islands, see Sax and Gaines 2008). Therefore, identifying the traits of successful invasive exotic species before they invade is crucial for island conservation (Towns et al. 1990, Seabloom et al. 2007, Harris and Timmins 2009, Guo 2014).

Species in similar environments often exhibit similar morphological, physiological and phenological features, known as functional traits (Pérez-Harguindeguy et al. 2013, Ottaviani et al. 2020). Species with similar suites of traits employ analogous strategies, which influence their fitness (Pérez-Harguindeguy et al. 2013, Reich 2014). Functional traits and strategies have been extensively used to address many ecological and evolutionary questions (Bellingham and Sparrow 2000, Caccianiga et al. 2006, Grime and Pierce 2012, Burns 2016a, May et al. 2017), especially in the field of invasion ecology (Van Kleunen et al. 2010b, a, Guo et al. 2018, Hulme and Bernard-Verdier 2018a, b). This large body of research has prompted some authors to advocate for using functional traits in the context of island biogeographic theory (Patiño et al. 2017, Ottaviani et al. 2020). To date, only a few studies have employed this approach (Lloret et al. 2004, 2005, Whittaker et al. 2014, Negoita et al. 2016, Schrader et al. 2020, Taylor et al. 2021).

Some plant traits can be rapidly and easily assessed. Classifying plants into 'growth forms' (graminoids, forbs and woody plant species) provides a useful proxy for suites of functional traits and phylogenetic backgrounds (Pérez-Harguindeguy et al. 2013, Schrader et al. 2020). For example, many herbaceous species have relatively short lifespans, small stature, high seed production per unit biomass, and better dispersal capabilities (Ellenberg and Müller-Dombois 1967, Qiaoling et al. 2005, Pérez-Harguindeguy et al. 2013, Schrader et al. 2020). Conversely, woody species have longer lifespans, higher stature and lower dispersal potential (Pérez-Harguindeguy et al. 2013). By

amalgamating suites of functional traits, plant growth forms may be an effective determinant of invasion success.

The successful colonization of an island often requires overwater dispersal (Carlquist 1974, Heleno and Vargas 2015, Arjona et al. 2018). However, plants can vary greatly in their dispersal ability (van der Pijl 1982). Species with long range-dispersal might colonize more islands, because they have greater chances of reaching remote ones (Carlquist 1974, Heleno and Vargas 2015, Arjona et al. 2018). In contrast, species with poor dispersal capabilities likely colonize fewer, less isolated islands (Higgins et al. 2003). Dispersal distance can be estimated categorizing species by their dispersal mode (i.e. wind-dispersed, animal-dispersed, etc.) (Tamme et al. 2014, Liu et al. 2018).

If species are selected for traits associated with better dispersal ability, islands might contain a biota that is unbalanced in its functional composition (Lomolino 1984, Negoita et al. 2016, Ottaviani et al. 2020). Colonization of new habitats is promoted by allocating more resources to reproduction (Lloret et al. 2005, Hayes and Barry 2008) while investing in vegetative growth favours population persistence after colonisation (Bellingham and Sparrow 2000, Lloret et al. 2005). For instance, a good disperser might invest in a large number of seeds, to maximize chances of colonization, while reducing its size (Cody and Overton 1996, Burns 2019). However, smaller seeds result in fewer resources available to support a new individual's growth (Moles and Westoby 2004, Butler et al. 2007, Hodgson et al. 2020). By selecting for better dispersal, islands might contain a disproportionate number of species lacking in traits associated with persistence.

Islands vary greatly in their characteristics, which may favour certain functional traits. For instance, large, topographically complex islands contain more species (MacArthur and Wilson 1967, Triantis and Sfenthourakis 2012, Tjørve and Tjørve 2017), resulting in these islands have a greater variety of functional traits. However, islands can also be variably disturbed. For instance, islands disturbed frequently by salt spray, storms and waves (Abbott 1977), might favour species better

adapted to rugged coastal environments. Conversely, frequent and intense disturbance of human origin typically favours generalist species (Moles et al. 2012, Blackburn et al. 2016).

In this study, I explored how traits influence invasion success in exotic plant species inhabiting islands off the northern coast of New Zealand. Naturalized exotic species comprise 43.9% of New Zealand's total vascular plant flora of 4097 species (Brandt et al. 2021). I compiled a database of 264 islands distributed across more than 4° of latitude and 7° of longitude. For each island, I inventoried plant species richness using field and literature surveys and quantified their geographic characteristics using geospatial software, so that I could answer the following questions about the functional traits of successful invasive exotic plant species in the context of island biogeographic theory: (1) Which functional traits are distinctive of the species that invade most islands? (2) Does exotic richness of growth forms and dispersal modes vary differently with island characteristics (area, isolation, exposure to ocean-borne disturbances, and distance from nearest urban area)? If so, how? (3) Do exotics' seed masses, by different growth forms and dispersal modes, vary differently with island characteristics? If so, how? (4) Finally, do native species differ from exotic species in their functional traits, occupancy and in their relationships with island characteristics?

3.3 – Methods

Study site

The two main islands of New Zealand (hereafter referred to as the "mainland") are surrounded by 890 smaller islands (Carter et al. 2020). This study focused on 264 of these islands, located between 34–38°S and 172–179°E, off the northern North Island. Six hundred kilometres separate the northwesternmost and southeasternmost islands.

The islands span 7 orders of magnitude in size (0.000021–277.21 km^2). Some are intertidal islands; others are situated over 50 km from the mainland. Of the 264 islands, 136 (51.5%) are of

volcanic origin, ranging in age from 10 million years to currently active (Campbell and Landis 2009),

122 (46.2%) are of sedimentary origin, and 6 (2.3%) are of mixed composition. Most were connected

to the mainland during the last glacial maximum (Fleming 1979). The sole exceptions are the Poor

Knights Islands, which have been unconnected to the mainland for at least 1 my (Fleming 1979), and

the two youngest volcanic islands, Rangitoto and Whakaari/White Island that formed during the

Holocene (Clarkson et al. 1986, Campbell and Landis 2009).

New Zealand's climate is oceanic and temperate, which provides suitable conditions for the

development of warm temperate rain forest on the study islands (Peel et al. 2007, Wilmshurst et al.

2014). This forest type is dominated by evergreen dicot tree species and some conifers, forming the

canopy, and a lower tier of broadleaved small trees and shrubs. The understorey is composed

primarily of ferns, monocots (mostly sedges) and non-vascular species, and few grasses (Wardle

1991). Higher elevation forests on a few, very large islands support a mixed montane cloud forest

that is distinct but floristically poorer (Cameron and Young 2019).

After human settlement 740 years ago, these islands became the focus of many anthropic

activities (Atkinson 2004, Bellingham et al. 2010, Wilmshurst et al. 2014). Māori burned the original

vegetation cover of many islands to facilitate access for harvesting seabirds and to plant crops

(Daugherty et al. 1990, Bellingham et al. 2010). After Europeans colonized, from c. 1840 onwards,

some islands were extensively farmed and grazed (Bellingham et al. 2010, Wilmshurst et al. 2014).

Of these islands, some were subsequently abandoned and secondary succession to woody

vegetation is common (Bellingham 1984, Atkinson 2004), whereas others are still being farmed. On

recent volcanic islands, Whakaari/White Island and Rangitoto, vegetation is in a process of primary

succession (Clarkson and Clarkson 1994, Shane et al. 2013). Presently, 41 islands (15.5% of all

islands) are inhabited.

Species richness

The total number of vascular plant species occupying each island was established via field surveys and by carefully searching the literature. Two of us (EKC and AEW) have been studying island floras in the study system for decades. During this time, inventories of plant communities were conducted on as many islands as possible. Plant species lists were also obtained from the literature (Appendix 1 in supplementary material). Plant species lists for most islands were often obtained using both methods (i.e. field surveys and from published sources) in which cases, the cumulative number of species encountered in all censuses was obtained. In total, 264 islands were deemed to have adequate censuses and included in analyses.

All species encountered were classified as either 'native' to New Zealand or 'exotic', following Brandt et al. 2021. To account for differences in plant traits, each species was also classified according to its growth form and dispersal mode. Three structural categories were selected for growth forms: graminoids, forbs, and woody (Table 3.1). Dispersal modes were defined based on morphological adaptations of diaspores to long-distance dispersal (Negoita et al. 2016, Arjona et al. 2018, Burns 2019) as wind-dispersed, unspecialized, animal-dispersed, and diaspores with morphological adaptations for short-distance dispersal only (Table 3.1). Among growth forms, I excluded climbers (exotics=45, natives=36) and epiphytes (e=2, n=7) due to the small sample size. For the same reason, water-dispersed species (producing diaspores with corky tissues or air chambers) were excluded from dispersal syndromes (e=17, n=63).

Table 3-1 - Species richness of exotic and native species with different growth forms and dispersal modes on 264 islands offshore New Zealand. A description for each category is provided.

		Species richness	Description
Growth forms			
Graminoids	Exotics	128	grasses, sedges and rushes
	Natives	130	
Forbs	Exotics	515	herbaceous, non-graminoid
	Natives	402	
Woody species	Exotics	156	trees and shrubs
	Natives	234	
Total		**1565**	
Dispersal mode			
Wind-dispersed	Exotics	157	plumes, wings, dust diaspores
	Natives	408	(anemochory)
Unspecialized	Exotics	290	no evident or prevalent morphological adaptations
	Natives	119	(unspecialized)
Animal-dispersed	Exotics	167	fleshy fruits or adhesive barbs (endo and epizoochory)
	Natives	190	
Short-distance	Exotics	185	morphological adaptations for short-distance dispersal only (ballochory, myrmecory).
	Natives	34	
Total		**1550**	

Species seed mass

For each species, I also established the corresponding seed dry mass (mg). If data were unavailable, seed mass was estimated by seed length (mm) using the following equation:

$$m = 0.1329l^{2.2243},$$

where "*m*" indicates seed mass (mg), "*l*" is seed length (mm) and the two numeric values are constants (Sarah Richardson, personal communication, May 20, 2020). I gathered data from several sources, including literature (Thorsen et al. 2009, Grubb et al. 2013) and online databases (Kattge et al. 2020, Manaaki Whenua - Landcare Research 2020, New Zealand Plant Conservation Network 2020, Royal Botanic Gardens Kew 2020). Nomenclature followed recognised taxonomic authorities (https://nzflora.landcareresearch.co.nz, accessed in May 2020).

Island characteristics

I measured island area as the total surface of an island (km^2). Data were retrieved from available sources (Land Information New Zealand 2012) or manually digitized from aerial imagery (Google 2020). Isolation was defined by using a landscape measure of isolation, which incorporates both the mainland and adjacent islands as sources of dispersing propagules (Diver 2008). Isolation is measured by producing a series of concentric belts of different size surrounding each island (radii = 250, 500, 1000, 1500, 2000, 2500, 3000 m) and computing the proportion of land within each of them (Diver 2008, Weigelt and Kreft 2013, Negoita et al. 2016, Carter et al. 2020). To ensure larger values indicate greater isolation, I subtracted the amount of land from the total area of each buffer.

Table 3-2 - Seed mass of exotic and native species subdivided by growth forms and dispersal modes on 264 islands offshore New Zealand. Columns represent trait categories, species richness (after removing those lacking seed mass data), mean seed dry mass (geometric mean) and its geometric standard deviation. The last column includes t-values extracted from a generalized linear model (GLM) with quasipoisson distribution comparing exotic and native seed dry mass for each set trait (in bold when significant).

		Species richness	Mean seed dry mass (mg)	Standard deviation (±)	t-value
Growth forms					
Graminoids	Exotics	114	0.55	6.66	-0.643
	Natives	111	0.55	5.65	
Forbs	Exotics	396	0.92	7.60	**-2.804**
	Natives	151	0.27	5.87	
Woody	Exotics	132	12.08	17.45	**-2.526**
	Natives	161	3.62	13.26	
Total		**1065**			
Dispersal mode					
Wind-dispersed	Exotics	128	1.21	10.16	-1.209
	Natives	154	0.40	7.42	
Unspecialized	Exotics	244	0.72	9.58	-0.845
	Natives	85	0.69	6.26	
Animal-dispersed	Exotics	141	6.67	11.74	-1.220
	Natives	132	5.46	8.91	
Short-distance	Exotics	135	2.13	8.91	-1.940
	Natives	30	0.68	5.91	
Total		**1049**			

Storms, waves and salt spray characterise disturbances of oceanic origin. To quantify

exposure to ocean-borne disturbances I identified the centre of each island and draw two lines

connecting it to the edge of landmasses (either the mainland or islands larger than 5,000 ha). The

angle comprised between these two lines represents the degree of exposure of an island to ocean-

borne disturbances (Burns and Neufeld 2009). Human impacts were quantified first as the shortest

distance to the nearest urban area, as exotic species richness often increases with proximity to

settlements (Timmins and Williams 1991, Sullivan et al. 2005, Lloyd et al. 2006). Urban areas were

defined as having a population of 1,000 people or more (Statistics NZ Tatauranga Aotearoa 2018).

Next, I assessed whether an island is a public land managed for conservation (conservation area) or

not (Department of Conservation 2017). All spatial analyses were carried using ArcGIS 10 and QGIS 2

(ESRI 2011, QGIS Development Team 2018).

Statistical analyses

To test whether the number of islands occupied by exotic species can be predicted by plant traits, I

subsetted exotic species richness by growth forms and dispersal modes. For each species, I

calculated the number of islands occupied and amalgamated this information by trait. Differences in

occurrences across islands of growth forms and dispersal mode were analysed using a set of

generalized linear model (GLM) with quasipoisson distribution comparing each set of species

separately (e.g. exotic graminoids vs exotic forbs, exotic wind-dispersed vs exotic short-distance-

dispersed, etc.). A Bonferroni correction was applied to significance levels to account for multi-

comparison.

To test whether exotic richness of growth forms and dispersal modes vary differently with

island characteristics, I used a set of multiple linear regressions. Firstly, the richness of each subset of

exotic species (e.g. graminoids, forbs, animal-dispersed, unspecialized, etc.) was set as the

dependent variable, whereas area, isolation, exposure to ocean-borne disturbances and distance

from the nearest urban area were the independent variables. Conservation areas (i.e. whether an island is public land managed as a conservation area or not) was excluded from this model as not significantly related to species richness, regardless of trait category and status (i.e. exotic or native). Next, I ran a similar model, but using the richness of all species and including growth forms and dispersal syndromes as an interaction term. To conform to assumptions, species richness and area were log-transformed, isolation arcsine-transformed and distance from the nearest urban area square root-transformed. Variable pre-selection was previously conducted for these island characteristics and an isolation radius of 1,500 m was chosen accordingly (Mologni et al., in press).

To test whether the seed mass of growth forms and dispersal modes vary differently with island characteristics for exotic species, I devised a second set of multiple linear regressions. Prior to analyses, I averaged seed dry mass per island separately for each growth form and dispersal mode. Mean seed mass of each subset of exotic species was then set as the dependent variable, while as predictors I used area, isolation, exposure, distance from the nearest urban area and conservation areas. Next, I ran a similar model, but using the mean seed mass of all species and including growth forms and dispersal syndromes as an interaction term. To conform to assumptions, species richness and area were log-transformed, isolation arcsine-transformed and distance from the nearest urban area square root-transformed.

The same set of analyses was run for native species. Afterwards, the number of islands occupied by exotic species was compared with that of native species within each trait (e.g. exotic graminoids vs native graminoid) using a GLM with quasipoisson distribution. Patterns in species richness and seed mass of exotic and native species were compared using a linear model setting species richness (of each trait separately, e.g. graminoid species richness) as the dependent variable and as predictors the same variables used in the previous analyses. The status of each species was included in the model as an interaction term. All analyses were run in the R environment (R Core Team 2020).

3.4 – Results

Of the total 1677 species across the islands, 855 (50.96%) were exotic. There were more exotic forb species than either graminoid or woody species, which in turn were similar in richness (Table 3.1 and Appendix 2, Table A.2.3). Natives included fewer forbs and more woody species than exotics, but a similar number of graminoids (Table 3.1 and Appendix 2, Table A.2.3). Among dispersal modes, most exotic species were unspecialized, fewer species were either short-distance-dispersed, animal-dispersed or wind-dispersed (Table 3.1 and Appendix 2, Table A.2.3). Natives included more wind-dispersed species than exotics, but fewer were unspecialized or short-distance-dispersed (Table 3.1 and Appendix 2, Table A.2.3). A similar number of exotic and native species was dispersed by animals (Table 3.1 and Appendix 2, Table A.2.3).

Of the 1127 species included in seed mass analysis, 59.98% were exotic. Exotic forbs were the most represented growth form, followed by a similar number of graminoids and woody species (Table 3.2 and Appendix 2, Table A.2.4). The number of native and exotic graminoids were similar; but there were more native woody species and fewer native forbs than exotics (Table 3.2 and Appendix 2, Table A.2.4). Among dispersal modes, most exotic species were unspecialized, and the number of exotic species that were animal-dispersed, wind-dispersed or short-distance-dispersed was similar (Table 3.2 and Appendix 2, Table A.2.4). The number of native species that were animal-dispersed was similar to that of exotics. Slightly more native species were wind-dispersed but fewer were either unspecialized or short-distance-dispersed (Table 3.2 and Appendix 2, Table A.2.4). Among growth forms, exotic forbs and woody species had heavier seeds than their native counterparts, but the seed masses of exotic and native graminoids were not significantly different (Table 3.2 and Appendix 2, Table A.2.4). The seed mass of exotic and native species did not differ among dispersal modes (Table 3.2). For both species richness and seed mass analyses, some species were omitted due to lack of data (Appendix 2, Table A.2.6).

Figure 3.1 - Number of islands occupied by exotic species with different (a) growth forms and (b) dispersal modes. On the y-axis is the number of islands occupied by each species, log-transformed, while on the x-axis are trait categories. In the box on the top right is a comparison with native species.

Island occupancy

Exotic graminoid species occupied more islands than exotic forbs, which, in turn, occupied more islands than exotic woody species (Figure 3.1a and Appendix 2, Table A.2.7). Exotic graminoids also occupied a similar number of islands as native graminoids. Conversely, exotic forbs and woody species occurred on fewer islands than native forbs and graminoids. Among dispersal modes, exotic wind-dispersed and unspecialized species occupied a similar number of islands, more than short-distance-dispersed species but comparable to animal-dispersed (Figure 3.1b and Appendix 2, Table A.2.7). However, exotic animal-dispersed species also occupied a similar number of islands as exotic short-distance-dispersed species. Exotic wind-dispersed species occupied a similar number of islands to native wind-dispersed species, whereas the other dispersal modes of exotic species occurred on fewer islands than their native counterparts.

Patterns in species richness

Exotic species richness increased with island area across all growth forms, but with different slopes (Figures 3.2a) (for more details see also Appendix 2, Table A.2.8 and Table A.2.12). Moreover, the richness of all exotic growth forms similarly declined with isolation (woody species excepted) and with exposure to ocean-borne disturbance (Figure 3.2b and 2c). Exotic forbs and woody plant richness declined with distance from the nearest urban area, but exotic graminoid richness showed no significant relationship (Figure 3.2d). Exotic graminoid richness only differed from natives in relationship to exposure (natives were unrelated to it; Figure 3.2c) (for more details see Appendix 2, Table A.2.8, Table A.2.12 and Figure A.2.8). In contrast, the richness of exotic forbs responded differently from natives to all island characteristics, increasing with area and declining with exposure more steeply than natives, and natives were unrelated to isolation and distance from nearest urban area (Figures 3.2). The slope of the positive relationship between exotic woody species richness and

island area was less steep than for native woody species, and natives were also unrelated to distance from the nearest urban area (Figures 3.2a, 3.2d).

Regardless of their dispersal mode, the richness of all exotic species increased with area and declined with isolation similarly, even though animal-dispersed species were unrelated to island isolation (Figures 3.3a and 3.3b) (for more details see also Appendix 2, Table A.2.9 and Table A.2.12). Exotic species richness always declined with exposure but with different slopes (Figure 3.3c). The richness of short-distance-dispersed and animal-dispersed exotic species declined significantly with distance from the nearest urban area, but the richness of wind-dispersed and unspecialized exotic species showed no significant relationships (Figure 3.3d). Exotic wind-dispersed species differed from natives as they increased faster with island area (Figures 3.3a) (for more details see Appendix 2, Table A.2.9, Table A.2.12 and Figure A.2.9). Similarly, exotic unspecialized species differed from natives only in their relationship with exposure (natives were unrelated to it; Figures 3.3c). Compared to natives, exotic animal-dispersed declined more steeply with exposure and distance from the nearest urban area, while short-distance-dispersed exotics declined more steeply with isolation and distance from the nearest urban area (Figures 3.3b, 3.3c, 3.3d).

Patterns in seed mass

The mean seed mass of all exotic species across all growth forms increased with area and declined with exposure and distance from the nearest urban area, albeit with different slopes, but none was significantly related to island isolation (Figures 3.4a, 3.4b, 3.4c and 3.4d) (for more details see also Appendix 2, Table A.2.10 and Table A.2.12). In conservation areas, the mean seed mass of graminoids was lower than on other islands, that of woody species higher, while the mean seed mass of forbs was not significantly different (Figure 3.4e). Exotic graminoids' mean seed mass declined more steeply with island exposure than that of natives (Figures 3.4c) (for more details see Appendix 2, Table A.2.10, Table A.2.12 and Figure A.2.10). The mean seed mass of exotic forbs

increased with area and declined with exposure and distance from the nearest urban area more

steeply than that of natives (Figures 3.4a, 3.4c, 3.4d), and the mean seed mass of exotic woody

increased with area and declined with distance from the nearest urban area more steeply than that

of natives (Figures 3.4a, 3.4d).

The mean seed mass of all exotic species across all dispersal modes increased with island

area, although with different slopes (Figures 3.5a) (for more details see also Appendix 2, Table

A.2.11 and Table A.2.12). Only the mean seed mass of exotic wind-dispersed and short-distance-

dispersed species declined with island isolation, however differences among groups were not

significant (Figure 3.5b). Animal-dispersed and unspecialized alone declined with exposure, while the

mean exotic seed mass also declined significantly with distance from the nearest urban area for all

but wind-dispersed species (Figure 3.5c, 3.5d). Wind-dispersed and short-distance-dispersed had

smaller seed on conserved areas, those of animal-dispersed were larger, while there was no

significant difference was detected in the mean mass of unspecialized species on insular

conservation areas (Figure 3.5e). Differently from exotics, native wind-dispersed species increased

with area and declined with distance from the nearest urban area more steeply, exotics were

unrelated to the latter (Figures 3.5a, 3.5d) (for more details see also Appendix 2, Table A.2.11, Table

A.2.12 and Figure A.2.11). Exotic and native wind dispersed displayed a different relationship with

exposure, although neither trend was significant (Figures 3.5c). Similarly, exotic unspecialized

species differed from native only in their relationship with area and exposure, as natives were

unrelated to them (Figures 3.5a, 3.5c). Exotic animal-dispersed declined more steeply with exposure

and distance from the nearest urban area and had greater seed mass on conservation areas, while

natives did not (Figures 3.5c, 3.5d, 3.5e). In contrast to exotics, short-distance-dispersed natives did

not decline to isolation and distance from the nearest urban area, and they increased more steeply

with island area (Figures 3.5a, 3.5b, 3.5d).
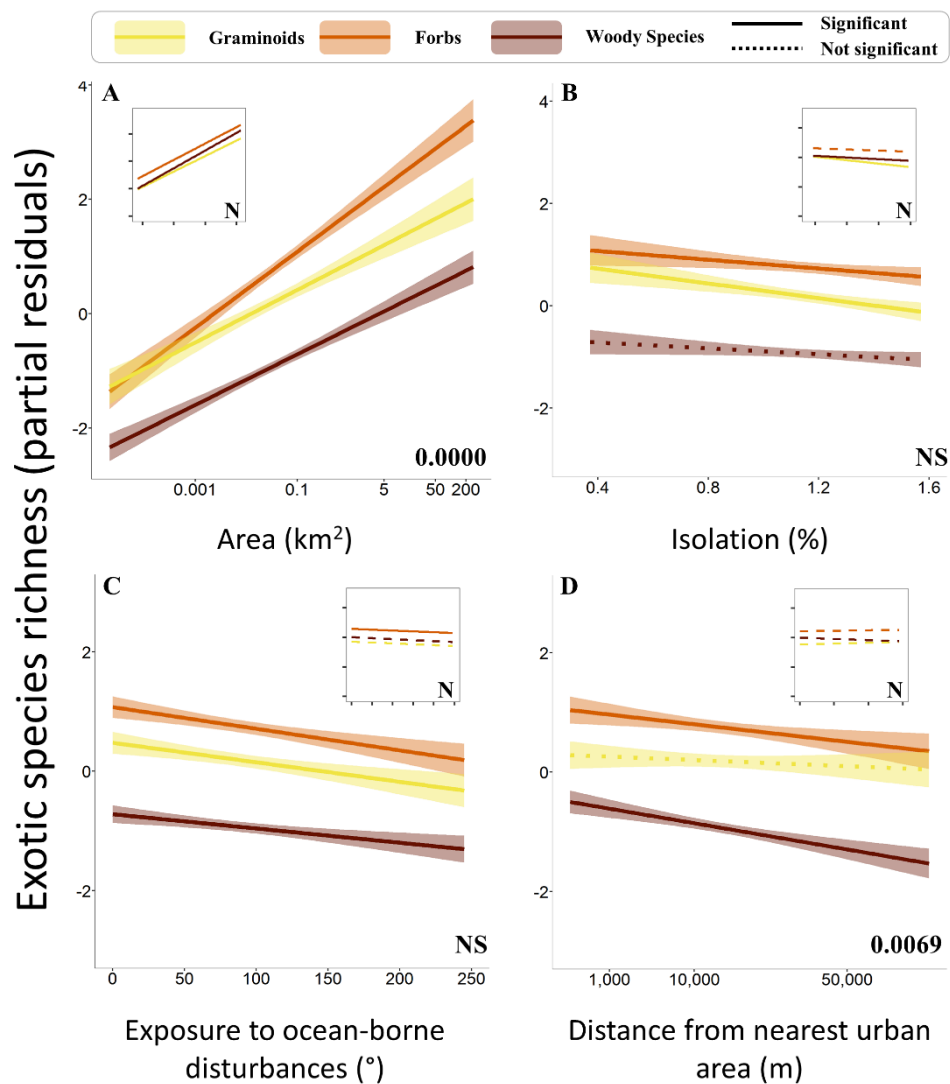
Figure 3.2 - Linear models illustrating relationships between exotic species richness with different growth forms and island characteristics on 264 New Zealand offshore islands. On the y-axis is species richness (partial residuals), while on the x-axis are island (A) area (log scale), (B) isolation, (C) exposure to ocean born disturbances, and (D) distance from the nearest urban area. Trendline (model predicted slope) and relative confidence interval (95%) colours represent graminoid (yellow), forb (vermilion) and woody species (brown). Trendline types indicate significant (solid, P<0.05) or non-significant (dotted) relationships. P-values for significant (P<0.05) or not significant (NS) differences among trends are at the bottom right. To conform to assumptions, species richness was log (+1) transformed, area log-transformed, isolation arcsine-transformed and distance from the nearest urban area squared-transformed. In the box on the top right is a comparison with native species (N).

3.5 – Discussion

Island occupancy

Functional traits predicted occurrence patterns in exotic plant species across northern New Zealand islands. Exotic herbs (i.e. graminoid and forb) occupied a larger number of these islands than exotic woody species. Exotic herbs generally have a relatively short lifespan, high seed production and better dispersal capabilities (Ellenberg and Müller-Dombois 1967, Qiaoling et al. 2005, Pérez-Harguindeguy et al. 2013, Díaz et al. 2016, Negoita et al. 2016, Schrader et al. 2020). However, many islands in my study system were farmed and perhaps a higher proportion of grasses and perhaps some forbs were directly introduced by humans. Among the exotic herbaceous species, graminoids invaded more islands than forbs, even though there are more species of the latter (Table 3.1). Perhaps many forbs were introduced for gardens (see Sullivan et al. 2005), suggesting a different invasion strategy (e.g. vegetative expansion) (Hodkinson and Thompson 1997). My results contrast with Mediterranean islands where growth forms of exotic species were unrelated to their occupancy (Lloret et al. 2005), which suggests that observed patterns may differ according to the island system investigated. For example, components of some isolated island floras can be under-represented or even lacking compared with continental floras (Carlquist 1974). For instance, annuals are poorly represented in the New Zealand native flora, but well represented among exotics (Brandt et al. 2021). Thus, islands offshore New Zealand might be especially prone to invasion by exotic annuals.

Wind and animal dispersal modes are generally associated with high dispersal potential (Carlquist 1974, Lloret et al. 2005, Tamme et al. 2014). Correspondingly, native and exotic species with wind or animal dispersal had high occupancy rates across islands in my study. Instead, species with unspecialized or short-distance-dispersed diaspores often have low island occupancy rates (Negoita et al. 2016, Arjona et al. 2018). However, species with multiple dispersal modes occurred on a large number of islands in my study system. Estimating dispersal potential from dispersal

modes is challenging. First, dispersal distances can vary strongly within dispersal modes (Thomson et al. 2011, Tamme et al. 2014). Second, vectors are typically context-dependent. For instance, many birds that disperse seeds within fleshy fruits and berries typically avoid islands that lack perching trees (Ferguson and Drake 1999, Negoita et al. 2016). Finally, dispersal modes do not account for non-standard means of dispersal, namely vectors that are different from what a diaspore's morphology suggests (Higgins et al. 2003, Nogales et al. 2012, Negoita et al. 2016, Arjona et al. 2018). Many non-hydrochorous species might successfully benefit from water-mediated pathways (Kowarik and Säumel 2008), especially in island systems.

Patterns in species richness

Positive species–area relationships are among the most common patterns in nature (Arrhenius 1921, Lomolino 2000a, Tjørve and Tjørve 2017), and have been identified previously both for exotic species (Baiser and Li 2018, Guo et al. 2021) and among growth forms (Schrader et al. 2020). I found consistent positive species–area relationships for exotic species with different dispersal modes and growth forms across northern New Zealand islands. Dispersal probabilities to islands typically decrease with island isolation, resulting in a decline in species richness (MacArthur and Wilson 1967, Weigelt and Kreft 2013). Since the maximum dispersal distance of a species is related to both growth forms and dispersal syndromes (Tamme et al. 2014), this could be expected to lead to differences in representation within growth forms and dispersal syndromes in relation to island isolation. However, in my study, negative richness–isolation relationships in exotic species did not differ significantly among growth forms or among dispersal syndromes.
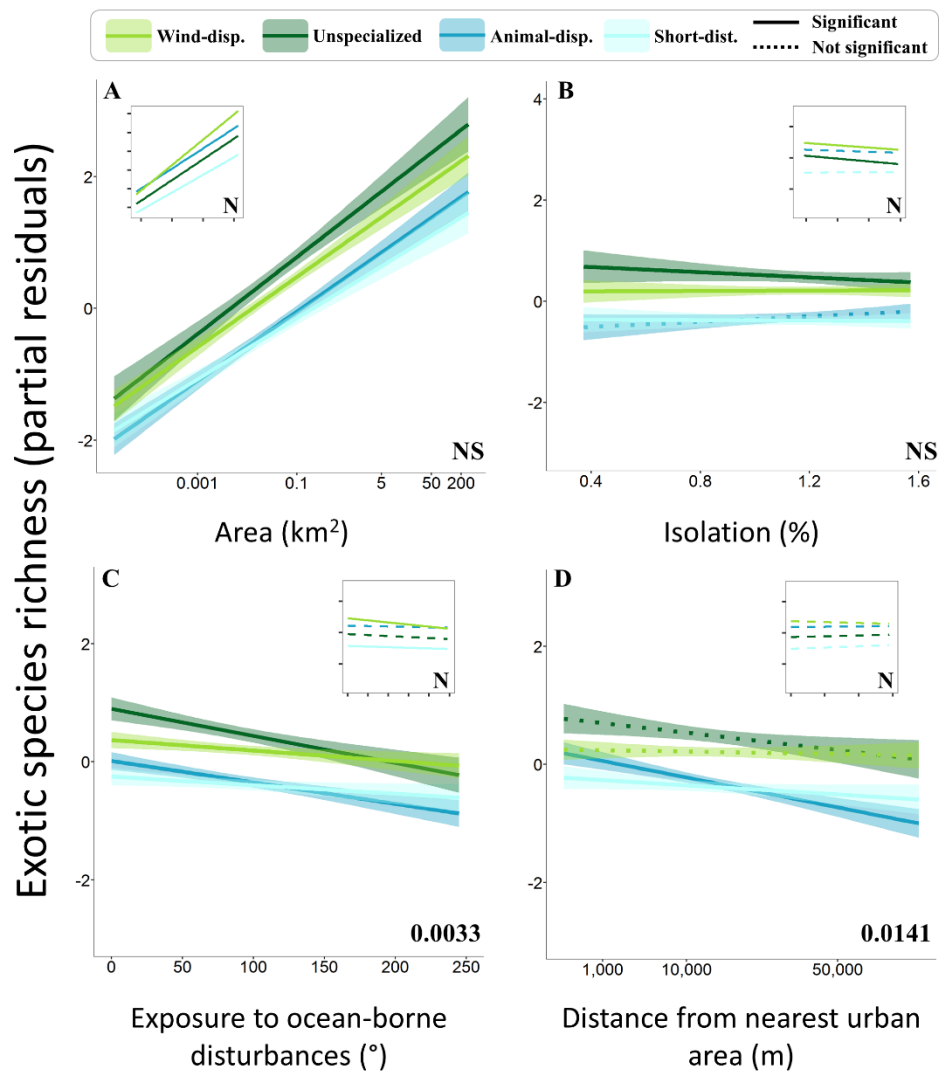
Figure 3.3 - Linear models illustrating relationships between exotic species richness with different dispersal modes and island characteristics on 264 New Zealand offshore islands. On the y-axis is species richness (partial residuals), while on the x-axis are island (A) area (log scale), (B) isolation, (C) exposure to ocean born disturbances, and (D) distance from the nearest urban area. Trendline (model predicted slope) and relative confidence interval (95%) colours represent animal-dispersed (dark blue), unspecialized (dark green), short-distance (light blue), and wind-dispersed species (light green). Trendline types indicate significant (solid, $P<0.05$) or non-significant (dotted) relationships. P-values for significant ($P<0.05$) or not significant (NS) differences among trends are at the bottom right. To conform to assumptions, species richness was log (+1) transformed, area log-transformed, isolation arcsine-transformed and distance from the nearest urban area squared-transformed. In the box on the top right is a comparison with native species (N).

Similarly, exotic species declined with exposure independently of trait categories. Exposed coastal habitats are particularly susceptible to storms and waves originated in the ocean, generating depauperate floras that are more subject to extinctions (Abbott 1977, Morrison and Spiller 2008, Burns and Neufeld 2009). Moreover, contrasting atmospheric conditions can limit wind currents and the movement patterns of dispersal vectors (Whitehead and Jones 1969, Tackenberg 2003).

The dispersal of exotic species is often determined by human activities. Surprisingly though, the richness of graminoid, wind-dispersed and unspecialized exotic species was unrelated to distance from the nearest urban area. After introduction, plants can utilize different anthropogenic pathways for dispersal, which often depend upon traits (Hodkinson and Thompson 1997). My metric might only encapsulate dispersal pathways associated with human habitation, such as escaping from gardens (Sullivan et al. 2005). Instead, graminoid, wind-dispersed and unspecialized species might exploit pathways associated with agricultural practice (e.g. disturbance of topsoil and vehicle movement). These trait categories though also exhibited high rates of island occupancy and thus might be at a later stage of invasion. As the invasion process progresses, exotics may be increasingly independent of humans for their dispersal (González-Moreno et al. 2017, Coutts et al. 2018). In addition, current estimates of human disturbance, such as current inhabitation, are likely to be confounded with island area, since larger islands are preferentially inhabited (mean area inhabited islands = 15 km2, x̄ uninhabited = 0.12 km^2, χ^2 = 14.64, p = 0.0001). Past disturbances, such as fires, may be underestimated and require better resolution in my study system, hence I believe better proxies for estimating human disturbance are needed to predict plant invasions more accurately (Mologni et al. 2021).

Patterns in seed mass

Regardless of growth form and dispersal mode, mean seed mass was higher on larger islands. Heavy, large seeds tend to result in larger plants (Butler et al. 2007), which also occupy a

larger amount of space. Thus, some islands may be too small to match the minimum area

requirements of large plant species (Turner and Tjørve 2005). In addition, large seeds require more

maternal resources, often leading to a reduction of total seed number (Moles and Westoby 2004,

2006, Hodgson et al. 2020). Fewer propagules reduce the chances of intercepting islands during

dispersal (Lonsdale 1999), especially when islands are small in area (Lomolino 1990).

Lighter seeds are often associated with long dispersal distances (Muller-Landau et al. 2008,

Auffret et al. 2017). However, most exotic species did not display a negative relationship between

seed mass and isolation. Having heavier seeds though does not necessarily diminish dispersal

potential (Thomson et al. 2011, Tamme et al. 2014), suggesting other factors, such as vectors'

behaviour and human pathways, might be important (Hodkinson and Thompson 1997, Negoita et al.

2016, Sinclair et al. 2020). Most exotic species showed negative relationships between seed mass

and exposure. Seed mass often correlates with leaf area (Butler et al. 2007), and large leaves are

more susceptible to mechanical damage and physiological stress caused by wind and waves (Burns

and Neufeld 2009, Anten et al. 2010). Only the mean seed mass of wind-dispersed and short-

distance-dispersed species though did not decline with exposure. Strong, contrasting wind currents

on exposed islands might favour some dispersal syndromes, regardless of their seed mass (Whittaker

1995).

The mean seed mass of exotic species increased with levels of human occupation, except for

wind-dispersed species. One explanation for this relationship is that species that produce heavier

seeds, also produce larger fruits (Benavides et al. 2021), which are sought preferentially in

agriculture and horticulture. Garden escapes also increase with human habitation (Sullivan et al.

2005), and popular garden species typically have larger seeds than other exotics (Hodkinson and

Thompson 1997). In contrast, wind-dispersed species might contain a high proportion of pasture

species, chosen for their biomass productivity rather than for their seed production. However, wind-
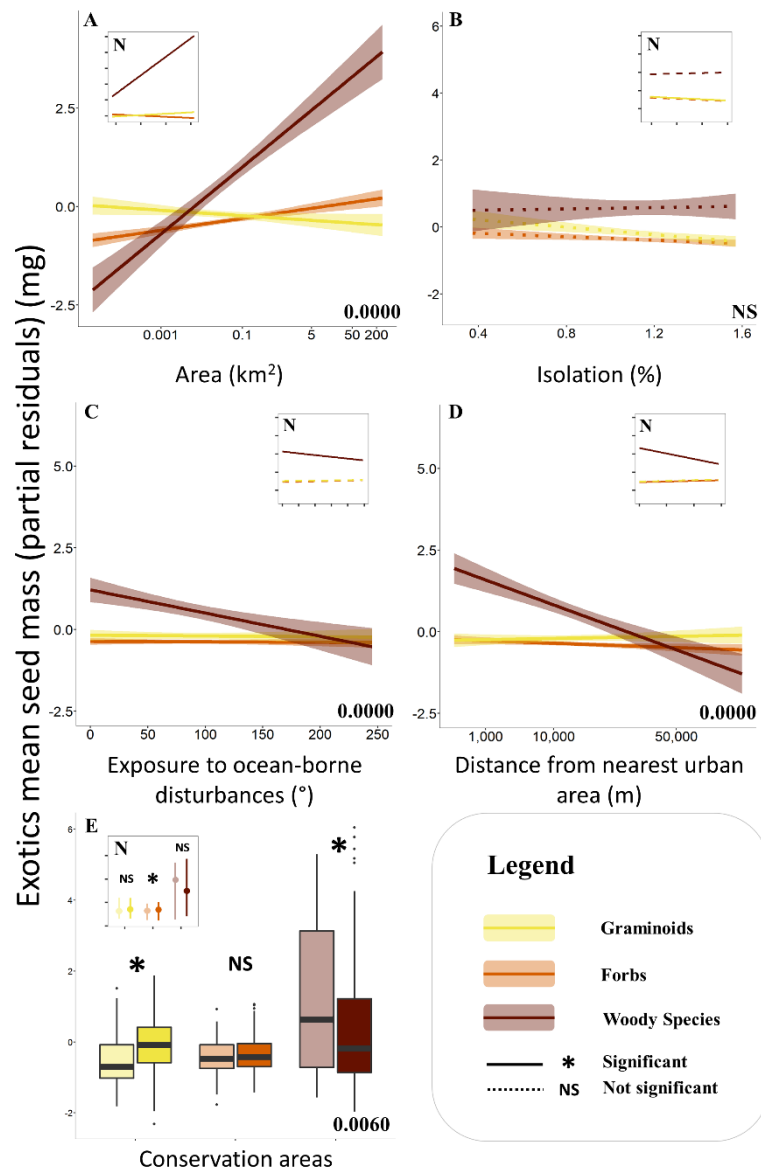
Figure 3.4 - Linear models illustrating relationships between the average seed mass of exotic and native species with different growth forms and island characteristics on 264 New Zealand offshore islands. On the y-axis is average seed mass (partial residuals), whereas on the x-axis are island (A) area (log scale), (B) isolation, (C) exposure to ocean born disturbances, (D) distance from the nearest urban area and (E) conservation areas. Colours represent graminoid (yellow), forb (vermilion) and woody species (brown). In plots A to D, trendline (model predicted slope) and relative confidence interval (95%) are represented. In plot E, light hues indicated publicly managed conservation areas, dark hues other islands. Significant relationships (P<0.05) are illustrated by solid trendline (A-D) and asterisks (E). P-values for significant (P<0.05) or not significant (NS) differences among trends are at the bottom right. To conform to assumptions, species richness was log (+1) transformed, area log-transformed, isolation arcsine-transformed and distance from the nearest urban area squared-transformed. In the box on the top right is a comparison with native species (N).

dispersed pasture species might also contain many Asteraceae species, which are generally small-seeded: future work should account for phylogeny.

Mean seed mass displayed contrasting trends with conservation areas depending on trait categories. On islands that are conservation areas, the lower seed mass of graminoids, wind- and short-distance-dispersed species, and greater seed mass of woody and animal-dispersed species may be a by-product of biosecurity measures and control measures against exotic species. For instance, small-seeded, lower-mass species might be less effectively detected by preventive measures. It is unclear though why the seed mass of other trait categories displayed an opposite trend or none at all. Altering biotic components of islands might have complex, multi-level indirect effects, to date poorly understood (Fukami et al. 2006, Bergstrom et al. 2009). Finally, I inferred seed mass from seed length for many species, and despite a strong allometric link between the two, this might be a potential source of error.

Differences with native species

Exotic and native species often show different distributional patterns on islands (Moser et al. 2018, Rojas-Sandoval et al. 2020, Guo et al. 2021, Mologni et al. 2021). Here, discrepancies between the species richness of exotic and native species hinged on functional traits. Exotic species with traits associated with high invasion rates (e.g. wind-dispersal and the graminoid growth form) were also more similar to native species both in occupancy and in their relationships with island characteristics. This suggests that the distribution of successful invaders (i.e. those with high occupancy rates) is shaped by similar processes to natives. Native patterns in seed mass differed from exotics with regards to area; however, with contrasting trends. Exotics generally declined more strongly with exposure, perhaps because native species are better adapted to rugged, coastal environments (Cockayne 1958, Burns 2016b). Surprisingly, some native species also declined in seed

mass with human habitation, although often less strongly than exotics, suggesting that natives might utilize similar dispersal pathways to exotics (Valery et al. 2009).

Future directions

My study was conducted at the regional scale, in a study system that spans 4° of latitude and 7° of longitude, and may not reflect local-scale and global-scale biogeographic dynamics. Future work may benefit from comparing invasion success at different scales (Lloret et al. 2005). Moreover, my results pinpoint plant traits associated with high invasion rates, which might not necessarily match those favouring the initial establishment in a new biogeographical region (Sinclair et al. 2020). In addition, disentangling whether growth form or dispersal mode was a greater influence was especially problematic in the case of exotic animal-dispersed species, as 50% of them are woody, and 60% of exotic woody species are animal-dispersed (Table S3.3). The importance of interactions among functional plant traits in determining the distribution of exotic species remains poorly understood and would be a fruitful avenue of future research (Negoita et al. 2016).

Exotic plant species are often favoured by soil enrichment (Huenneke et al. 1990, King and Buckney 2002, Blumenthal et al. 2017), especially when short-lived (Prober and Wiehl 2012). In my study system, both geological and biological factors can contribute to soil fertility. For instance, volcanic islands have generally richer soils, which favour island invasions (Pretto et al. 2012). Similarly, seabird guano augments soil nutrients across many islands in my study system, both of volcanic and sedimentary origin, and seabirds also create high disturbance levels through burrowing (Grant-Hoffman et al. 2010), which likely favours invasion by some exotic species (Hobbs and Huenneke 1992). Integrating geological and other biotic elements might give further insights into how traits influence plant invasions on islands.
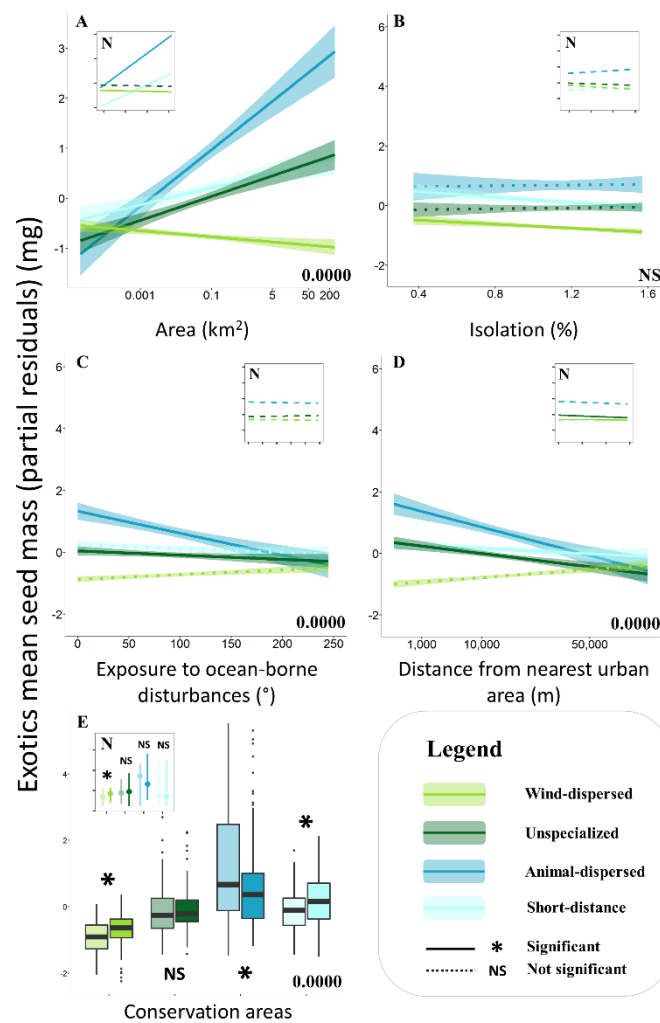
Figure 3.5 - Linear models illustrating relationships between the average seed mass of exotic and native species with different dispersal modes and island characteristics on 264 New Zealand offshore islands. On the y-axis is average seed mass (partial residuals), whereas on the x-axis are island (A) area (log scale), (B) isolation, (C) exposure to ocean born disturbances, (D) distance from the nearest urban area and (E) conservation areas. Colours represent animal-dispersed (dark blue), unspecialized (dark green), short-distance (light blue), and wind-dispersed species (light green). In plots A to D, trendline (model predicted slope) and relative confidence interval (95%) are represented. In plot E, light hues indicated publicly managed conservation areas, dark hues other islands. Significant relationships (P<0.05) are illustrated by solid trendlines (A-D) and asterisks (E). P-values for significant (P<0.05) or not significant (NS) differences among trends are at the bottom right. To conform to assumptions, species richness was log (+1) transformed, area log-transformed, isolation arcsine-transformed and distance from the nearest urban area squared-transformed. In the box on the top right is a comparison with native species (N).

Conclusions

Plant functional traits (growth forms, dispersal modes, and seed mass) were predictors of exotic species that were successful invaders (i.e. displaying high island occupancy rates) of northern New Zealand islands (graminoid, wind-dispersed and unspecialized species) and these, in turn, were related to island characteristics. Differences in species richness and seed mass among traits were mostly associated with human-related variables (i.e. distance from the nearest urban area and conservation areas), with successful invaders often unrelated to them. Moreover, exotics with high rates of island occupancy showed distributional patterns similar to natives, suggesting comparable processes regulate both sets of species. Management of exotics on islands should focus on graminoid, wind-dispersed and species with unspecialized diaspores. Future work should concentrate on unravelling the complexity of indirect effects of island management on plant seed mass. Overall, my results illustrate that integrating trait-based approaches in the island biogeography framework (e.g. Aikio et al. 2020; König et al. 2020; Ottaviani et al. 2020) can be a useful tool in understanding and predicting plant invasions.

Chapter 4.   Different levels of disturbance influence the distributional patterns of native but not exotic species on New Zealand small islands

Adapted from: Mologni F (In prep.) Different levels of disturbance influence the distributional patterns of native but not exotic species on New Zealand small islands.

4.1 – Abstract

Disturbances of oceanic origin can severely affect plant communities on islands, but it is unclear whether they promote or deter biological invasions. Here, I explored 97 small islands subject to different levels of ocean-borne disturbances (i.e. inside and outside Wellington Harbour, New Zealand). First, I tested how relationships between the richness of native and exotic species and island characteristics (e.g. area, isolation, height, elevation, slope, nearest dwelling) changed depending on island location. Next, I assessed compositional differences on inner and outer islands for both native and exotic species, and how they vary with geographic distance (i.e. distance-decay). Results show that native species richness was differently related to slope (i.e. the steepness of an island) depending on island location, but not to other island characteristics. Natives declined in number with slope only on outer, more disturbed islands. Moreover, natives on outer islands were floristically more homogenous, and compositional differences changed less strongly with distance than on inner islands. In stark contrast, exotics exhibited no differences in their distributional patterns depending on island location. Different levels of ocean-borne disturbances might explain distinct distributional patterns in native species. Conversely, results for exotic species might reflect a lack of coastal specialists in the species pool. Perhaps time-lags in the invasion process and non-equilibrium dynamics play a role as well. Conservation bodies should similarly manage islands sustaining different levels of ocean-borne disturbances.

4.2 – Introduction

Disturbances can have devastating effects on insular floras (Whittaker 1995, 2000, Morrison and Spiller 2008, Burns and Neufeld 2009). Perturbations can remove plant biomass (Grime and Pierce 2012), increase extinction rates (Whittaker 1995), and change the compositional structure of insular communities (Morrison 2014). However, whether disturbance promotes island invasion is still poorly understood.

The notion that disturbances facilitate biological invasions is debated (Hobbs and Huenneke 1992, Moles et al. 2012, Jauni et al. 2015). Earlier work shows that context, type of disturbance and its frequency and severity are all crucial factors (Moles et al. 2012). On islands, one of the most pervasive types of disturbance are those of oceanic origin, such as waves, storms and wind shear (Whittaker 1995). Ocean-borne disturbances can severely influence insular floras (Whittaker 2000, Morrison and Spiller 2008). In protected locations, disturbance events are generally less intense and frequent, and conditions more lenient for vascular plants (Abbott 1977, Morrison 2014). Results to date though are contrasting whether exotic species are facilitated (Bellingham et al. 2005, Burns 2016b) or deterred (Mologni et al. 2021, see chapter 2) by ocean-borne disturbances.

Species richness on islands often decline with ocean-borne disturbances (Abbott 1977, Mologni et al. 2021). Waves and winds can reduce the habitable surface area of an island (Neufeld et al. 2017). Thus, given two islands of similar size and height, those in more disturbed locations will have fewer species (Abbott 1977, Neufeld et al. 2017, Mologni et al. 2021). Additionally, species on smaller islands are more prone to extinction, a process enhanced by perturbation (Whittaker 1995). After each extinction event, species need to recolonize (MacArthur and Wilson 1967). Then, populations in disturbed locations might more strongly depend on immigration from nearby communities. In addition, other factors might interplay with perturbations. Topography can influence water flow velocity, run-off and accumulation (Yu et al. 2015), regulating the amount and

permanence of seawater on islands. Human activities might compound natural disturbances, further reducing species richness on islands.

Disturbances of oceanic origin can alter the compositional structure of the insular biota (Whitehead and Jones 1969, Morrison 2014). On the one hand, they open up space for colonization by new species (Grime and Pierce 2012). In parallel, they are likely to select specialists well adapted to disturbed islands (Whitehead and Jones 1969). By favouring species colonization, islands in more disturbed locations will have a more heterogeneous flora. However, if disturbances select for specialist species, disturbances will generate a more homogeneous flora. Either way, compositional differences increase with distance (i.e. distance-decay, Soininen *et al.* 2007). Therefore, a heterogeneous flora will show a stronger spatial turnover than a homogeneous flora.

In this study, I explored the insular distribution of native and exotic vascular plant species subject to different levels of ocean-borne disturbances. I selected 97 intertidal, small islands inside (less disturbed) and outside (more disturbed) Wellington Harbour, New Zealand. First, I used multiple linear regression to test whether the richness of native and exotic species have a different relationship with island characteristics depending on island location. Second, I calculated Jaccard similarity indexes to test whether floristic composition differs on inner and outer islands for the two sets of species. Third, I used generalized linear models to investigate distance-decay relationships inside and outside the harbour and how they differed for native and exotic species.

4.3 – Methods

Study system

The Wellington coastline (41°16'47" S, 174°49'56" E) is surrounded by numerous small islands, situated in close proximity to the coast. Most of them emerged recently, during an intense earthquake that uplifted the coastline by approximately 6 meters in 1855 (Burns 2016b). The study

system is homogeneous in its geological composition (i.e. greywacke) (Burns 2015) and contains

several seabird colonies. The region is struck by numerous storms, mostly originating in southern

latitudes (Pickrill and Mitchell 1979).
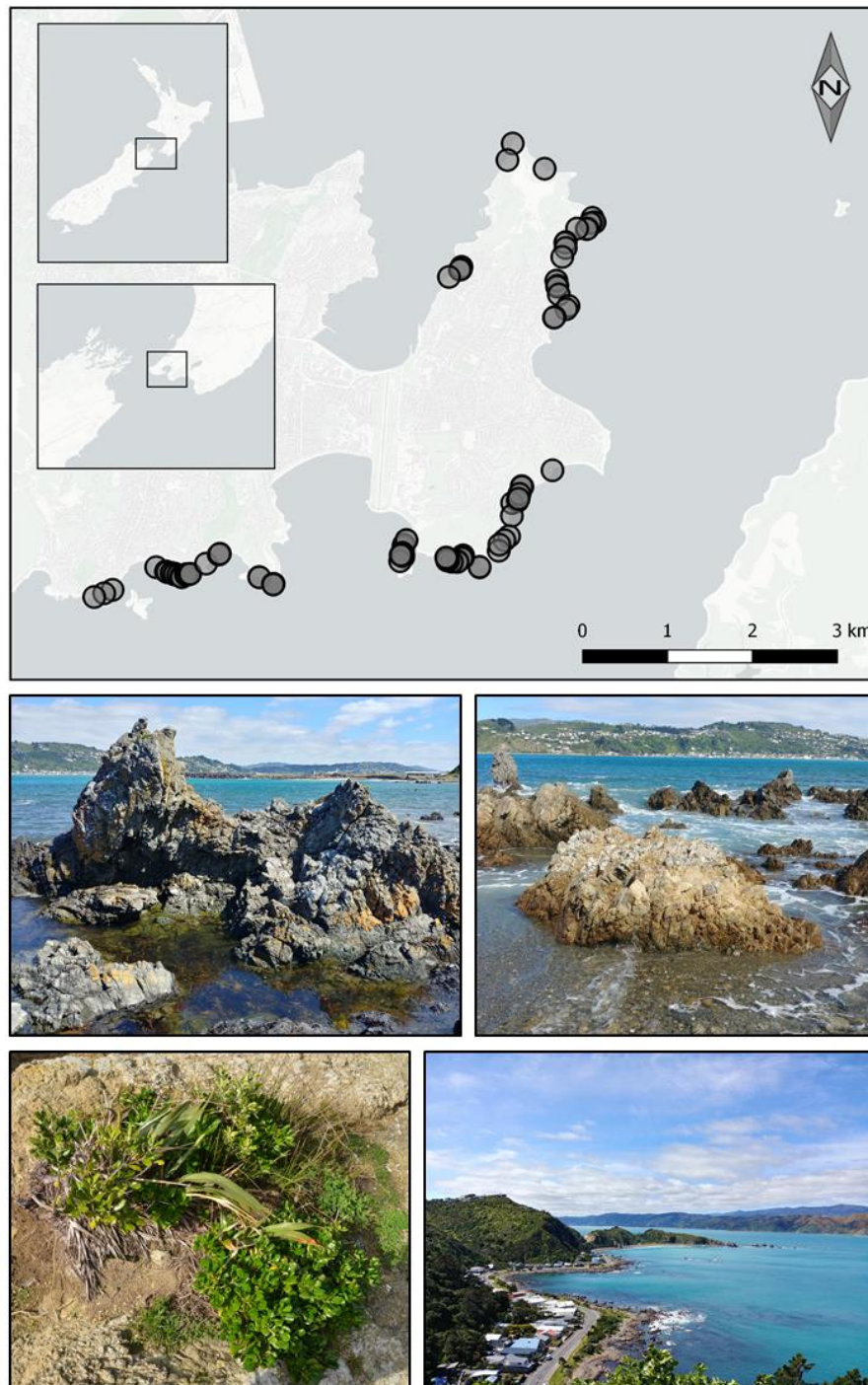
Figure 4.1 - Map of the study area (top), two of the surveyed islands (centre), a typical plant community (bottom left) and the landscape (bottom right) of the study system.

In this study system, I surveyed 97 small, easily accessible intertidal islands (Appendix 2, Table A.2.14). They are mainly rocky outcrops, with small amounts of soil occasionally accumulating in rock cracks. Vegetation on rocky outcrops along the Wellington coast is dominated by a few low growing, stress-tolerant species, with leathery or succulent leaves (Dawson 1988). These islands are generally close to human settlement.

Data collection

I thoroughly surveyed each island and quantified the number of vascular plant species for a total of 38 (Appendix 2, Table A.2.13 & S4.3). For each species, I assessed its origin (i.e. native or exotic). Species origin and nomenclature were compiled following the New Zealand Plant Conservation Network (New Zealand Plant Conservation Network 2021, accessed in January 2021).

Island characteristics were manually quantified in the field and by using geospatial software (ESRI 2011, QGIS Development Team 2018). I estimated island area (m²) by multiplying islands' widths and lengths measured at the widest and longest point. Isolation was quantified as the shorter distance separating an island from the nearest plant community (m). I calculated height as the vertical distance between the top of an island and the lower limit of the intertidal zone, delimited by the lowest lichen boundary. I also retrieved a digital elevation model (Geographx 2016) and extracted elevation from the mean sea level (m) and, to account for topographic complexity, slope (i.e. the steepness of an island, °) and the rugosity index. Rugosity is a measure of landscape ruggedness and it is calculated as the ratio between surface and planar area (Jenness 2013), as in the following equation:

$$RU = \frac{Area_s}{Area_p} = \frac{\sum_{i=cell}^{N}(c^2 \cos(S\left(\frac{\pi}{180}\right)))}{c^2 * n}$$

where $Area_s$ and $Area_p$ are, respectively, surface and planar area, c is the cell size of a digital

elevation model (DEM), S is the slope of each cell and n is the number of cells in the DEM. Lastly, I

calculated the distance from the nearest dwelling (hereafter nearest dwelling) to account for human

activities.

Compositional differences between pairs of islands were calculated using a Jaccard similarity

index. I computed the index in R, using the Vegan package (Oksanen et al. 2020). Then, I measured

the distance between each pair of islands using the proximity tool in ArcGIS 10 (ESRI 2011).

Statistical analyses

To test whether species richness responds differently to island characteristics inside and outside the

harbour, I used a linear model with species richness as the independent variable and island

characteristics (area, isolation, height, elevation, slope and nearest dwelling) as predictors. Location

(inside/outside the harbour) was included as an interaction term. Species richness (+1), area,

isolation and height were log-transformed, slope and nearest dwelling were square root-

transformed, while elevation was not transformed. This analysis was run for native and exotic

species richness separately.

Before inclusion in a model, I examined each independent variable using a Pearson

correlation coefficient and a variance inflation factor (VIFs). I set as a cut-off 0.8 and 3, respectively

(Berry and Feldman 1985, Zuur et al. 2010). Rugosity and slope exceeded both thresholds (Appendix

2, Table A.2.16 and Figure A.2.12). As they both describe topographic complexity, I retained slope as

the simplest measurement.

To test if islands inside and outside the harbour show compositional differences, I used a

Jaccard similarity index. I then contrasted Jaccard indexes between islands inside and outside the

harbour. Since Jaccard indexes were slightly right-skewed, I used both a linear and a quasipoisson model. Analyses were run separately for native and exotic species. Islands lacking in either native or exotic species were excluded (natives=1, exotics=52).

To test whether distance-decay relationships differ between inner and outer islands, I regressed the Jaccard similarity index between two islands with the distance separating them. I used both a linear and quasipoisson model and variables were not transformed. The same approach was employed for native and exotic species separately.

4.4 – Results

Native plant species richness across the islands displayed similar relationships with area, isolation, height, elevation, and nearest dwelling regardless of island location (Table 4.1). However, the number of native species declined with increased slope on outer islands, but not on inner islands (Table 4.1 & Appendix 2, Table A.2.17 & Figure A.2.13). The richness of exotic species exhibited similar relationships with all island characteristics irrespective of island location (Table 4.1 & Appendix 2, Table A.2.17 & Figure A.2.13).

Jaccard similarity indexes were significantly lower on outer islands for native species, indicating they vary less strongly in composition than inner islands (Figure 4.2a). On the other hand, compositional differences in exotic species did not differ between the inside or outside of the harbour (Figure 4.2b). Results were consistent using a linear or quasipoisson model (Appendix 2, Table A.2.19).

Negative distance-decay curves were observed on both inner and outer islands for native species (Figure 4.3a & Appendix 2, Table A.2.18). However, Jaccard similarity indexes declined faster with the distance separating two islands on inner than outer islands. Conversely, distance-decay curves were not significant for exotic species and did not differ between inner and outer islands

(Figure 4.3b & Appendix 2, Table A.2.18). Results were consistent using a linear or a quasipoisson model (Appendix 2, Table A.2.19).

Table 4-1 - Differences in how the richness of native and exotic species respond to island characteristics on 97 islands inside and outside Wellington Harbour, New Zealand. T and p-values testing for discrepancies between inner and outer islands are reported (in bold if p < 0.05). The last column specifies the typology of the relationship between species richness and island characteristics on inner and outer islands (for more details see Appendix, Table A.2.17 & Figure A.2.13).

	Native species		Exotic species		
	t-value	p-value	t-value	p-value	Relationship
Area	0.873	0.3848	-1.090	0.2788	Positive
Isolation	1.455	0.1491	0.389	0.6980	Non-significant for native species, negative for exotic species
Height	0.548	0.5849	-0.151	0.8803	Positive
Elevation	-1.410	0.1620	-0.279	0.7807	Non-significant
Slope	**-3.014**	**0.0034**	-0.765	0.4462	Negative, non-significant for native species on inner islands
Nearest dwelling	-0.549	0.5842	-0.707	0.4814	Positive

4.5 – Discussion

Native plant species richness responded differently to slope depending on island location, but not to other island characteristics. Natives declined in number with slope only on outer, more disturbed islands. Furthermore, natives were floristically more homogenous on outer than inner islands. Lastly,

native species spatially turned over more rapidly inside than outside the harbour. In stark contrast, exotic species did not differ in either richness or composition depending on island location.

Relationships between species richness and both area and height were positive and similar between inner and outer islands, and for both native and exotic species. Large, tall islands typically have a greater surface; thus, they can accommodate more species (MacArthur and Wilson 1967). Additionally, I observed that islands greater in size and height have a larger proportion of soil accumulating in rock cracks. Even small amounts of sediments can allow several species to survive by providing anchorage, retaining water, and supplying nutrients. Future studies should consider including a measure of soil availability (Schrader et al. 2019). Tall, large islands are also less likely to be overtopped by waves (Abbott 1977, Whittaker 1995, Burns and Neufeld 2009). Species richness was related to height, manually quantified, but not to elevation, computed by geospatial software, suggesting the former is a better predictor of species richness in this study system.
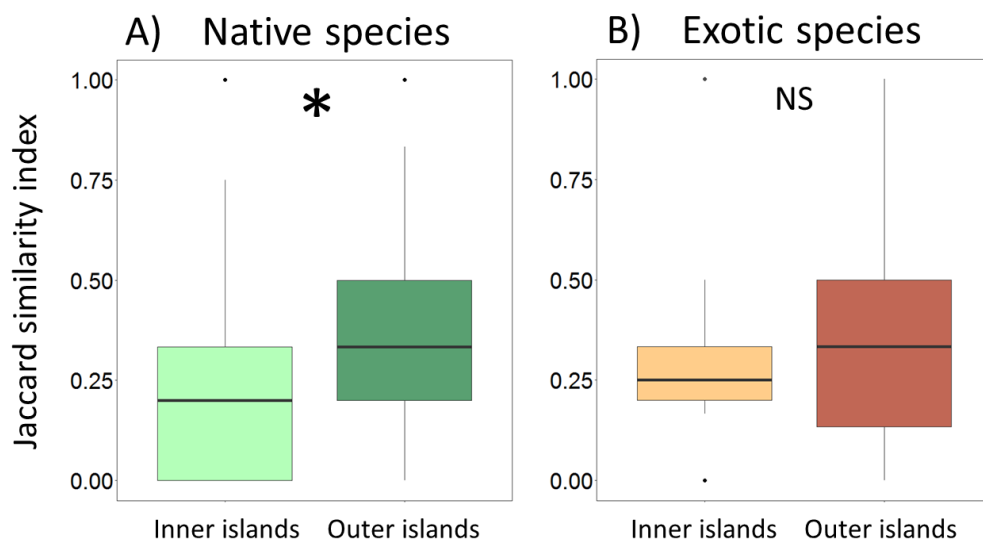
Figure 4.2 - Compositional differences among 97 islands off the coast of Wellington, New Zealand. On the y-axis are Jaccard similarity indexes, while on the x-axis are inner and outer islands. On top are all species (a), below native (b) and exotic (c) species. Symbol colours indicate all (greys), native (greens) and exotic (reds) species, whereas hues show inner (lights) and outer (darker) islands. Asterisks indicate significant differences between inner and outer islands.

Relationships between richness and isolation were similar on inner and outer islands for both groups of species; however, exotics declined in number with it whereas natives did not. Species richness typically decreases with distance from the source pool due to reduced immigration rates (MacArthur and Wilson 1967). Islands within our study system though are very close to mainland plant communities, a possible explanation why natives were consistently unrelated to isolation. By contrast, negative exotic species-isolation relationships might reflect time-lags in the invasion process (González-Moreno et al. 2017, Coutts et al. 2018).

Both native and exotic species richness declined with proximity to the nearest dwelling, on inner and outer islands alike, which is surprising since proximity to humans usually favours biological invasions (Blackburn et al. 2008, Pretto et al. 2012, Chiarucci et al. 2017, Paudel et al. 2017). Here, only a very narrow stretch of land exists between the forested hills and the sea, which is the only available area for grasslands and specialized coastal communities. Most of this area is now in urban housing, which has reduced the propagule pressure from the mainland, thus lowering immigration rates (Shmida and Wilson 1985). Alternatively, I observed that islands distant from houses often host larger seabird communities (e.g. at Moa Point). Seabirds guano increase soil nutrients (Grant-Hoffman et al. 2010, Ellis et al. 2011), allowing more species to successfully colonize them. Additionally, seabirds might also act as seed dispersers (Abbott 1977, Ellis 2005, Magnússon et al. 2009, Calvino-Cancela 2011).

Native species richness declined with slope only on outer, more disturbed islands. Water run-up (i.e. maximum elevation reached by waves relative to shoreline position) on the foreshore is higher on steeper surfaces (Nielsen and Hanslow 1991, Ruggiero et al. 2004, Stockdon et al. 2006). Therefore, steep islands are more likely to be overtopped by waves. In addition, slope is also a proxy for topographic complexity (Yu et al. 2015), and irregular surfaces in this study system can accumulate seawater in rock pockets for prolonged periods, reducing the island's habitable area. On outer, more disturbed islands, these processes might have a much stronger impact.

Natives on outer islands were compositionally more homogenous than on inner islands. If

these islands are subject to more frequent or intense storms, waves and winds, only a few,

specialized species might survive on them (i.e. environmental filtering, Gillham 1960b, Liu et al.

2019) Conversely, in more lenient conditions a larger number of species can establish a viable

population (Abbott 1977), generating a greater compositional variability. Additionally, contrasting

winds might favour the immigration of species with specific dispersal syndromes, such as water- or

wind-dispersed (Abbott and Black 1980, Whittaker 1995). Where winds and storms are more

frequent, species with such dispersal syndromes might be more common, homogenizing insular

floristic composition.
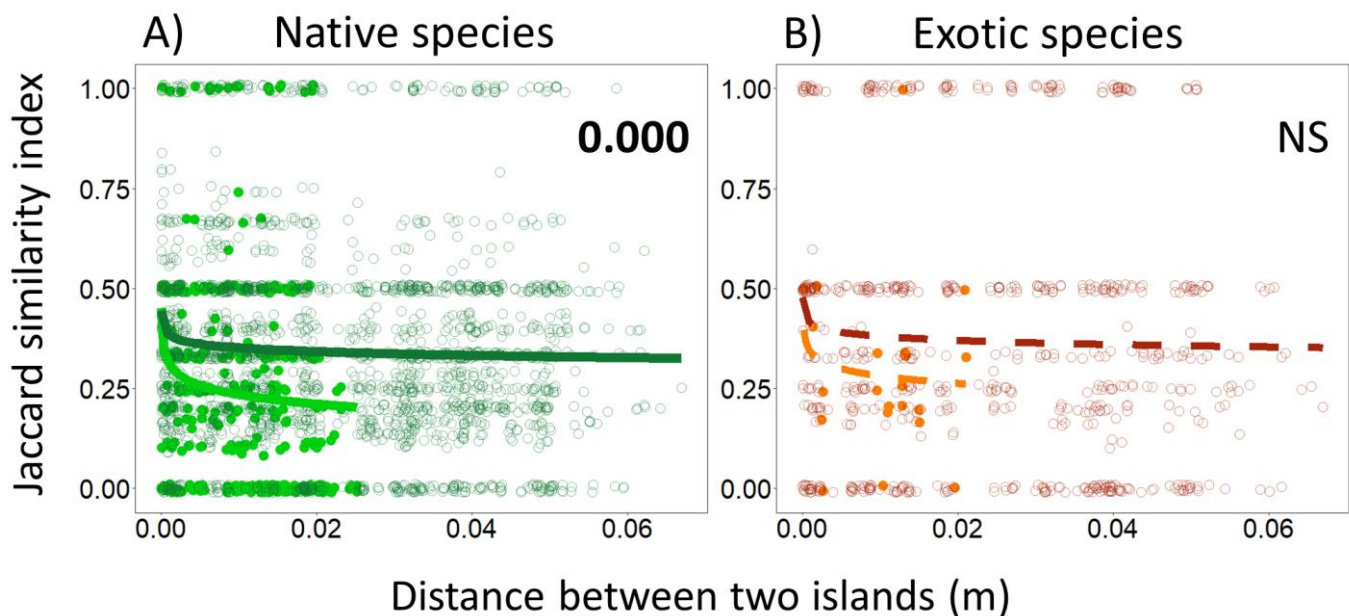
Figure 4.3 - Distance-decay relationships on 97 islands off the coast of Wellington, New Zealand. On the y-axis are Jaccard similarity indexes, while on the x-axis is the distance between each pair of islands. From the top are all (a), native (b) and exotic (c) species. Symbol colours illustrate all (greys), native (greens) and exotic (reds) species, whereas hues indicate inner (lights) and outer (darker) islands. On the top right are significant (p-value in bold) or not significant (NS) differences between inner and outer islands.

Compositional differences in native species increased with distance among islands, and

more so inside the harbour. This archipelago is composed of very small islands, which can only house

a few species (Lomolino and Weiser 2001). Therefore, early colonization could be crucial for

establishing a viable population. If so, species close to an island have more chances to be early, successful colonizers. Assuming floristic differences among mainland communities increase with distance as well, this process might generate insular distance-decay relationships in native species. Additionally, differences between inner and outer islands might be a product of a more homogenous flora on the former.

While the distributional patterns of native species differed on inner and outer islands, those of exotics did not. First, exotic richness declined with slope both on inner and outer islands, indicating that perhaps disturbances originated by the ocean are too severe or frequent for exotic species regardless of island location. Second, their composition was relatively homogeneous on both inner and outer islands and no significant distance-decay relationships were observed, a further indication that maybe only a few, well-adapted exotics can survive on these islands (Burns 2016b).

Results seem to indicate that differences in native and exotic species are the product of a lack of coastal specialists in the exotic species pool. Additionally, many exotic species might be still in the process of invading this archipelago (González-Moreno et al. 2017, Coutts et al. 2018). A previous study in the same location found the number of exotic species to increase through time (Burns 2015). However, almost a decade separates the two studies and the total number of exotics has not changed since. Perhaps then, exotics cyclically recolonize these islands after extinction following each major disturbance event (i.e. non-equilibrium dynamics, Whittaker 1995, 2000; Morrison 2010).

In this study, I identified differences in native and exotic plant species richness and composition on inner and outer islands. However, of 97 islands, only 27 were found inside the harbour. Thus, the analytical power of the model might be limited. Moreover, my database contains only islands occupied by vascular plant species. Previous studies though have highlighted the importance of empty islands as part of the among-island variation (Dengler 2010, Morrison 2014, Wang et al. 2016). Future studies should consider islands devoid of species.

Overall results show that both native richness and composition changed depending on island location in Wellington Harbour. This pattern might derive from differences in the frequency and intensity of disturbances originated by the ocean on inner and outer islands. In striking contrast, distributional patterns of exotic species did not differ depending on island location. One possibility is a lack of coastal specialists in the exotic species pool (Hulme 2020). Alternatively, this result might stem from time-lags in the invasion process (Coutts et al. 2018) or non-equilibrium dynamics (Whittaker 1995, 2000). Exotic species management should not treat islands differently depending on their level of ocean-borne disturbances.

Chapter 5.   The Island Biogeography of Humans

5.1 – Abstract

For decades, biogeographers have sought a better understanding of how organisms are distributed among islands, yet the island biogeography of humans is still largely unknown. Here, I investigate how human population size varies with island area, elevation, isolation, latitude and longitude in 10 archipelagos across the globe. Results illustrate that, similar to plants and animals, populations of humans on islands are strongly structured geographically. Humans consistently preferred larger islands. However, relationships with elevation, isolation, latitude and longitude varied idiosyncratically among archipelagos, and were often associated with specific social, political and historical circumstances. Despite underlying similarities in their distribution, overall results from this study suggest the island biogeography of humans may be different from that of other organisms.

5.2 – Introduction

Humans occupy virtually every island on the planet. However, some archipelagos are densely populated (e.g. New York Harbour, Singapore), while others are nearly uninhabited (e.g. Svalbard Islands, Tristan da Cunha). Although the geographic correlates of human population sizes are well known on continents (Cohen and Small 1998, Small et al. 2000, Small and Naumann 2001, Small and Cohen 2004, Yue et al. 2005, Gaughan et al. 2013), an overarching explanation for global variation in insular population sizes has yet to be established (Keegan and Diamond 1987, Cherry and Leppard 2018, c.f. Gavin and Sibanda 2012).

Other species occupy islands in predictable ways (MacArthur and Wilson 1967, Hanski 1999). Larger islands typically support bigger populations. On the other hand, remote islands are more difficult to disperse to, and have correspondingly smaller populations (MacArthur and Wilson 1967, Hanski 1999). Differences in insular population size may also be related to other island characteristics, including altitudinal and climatic variation (Small and Cohen 2004, Arianoutsou et al. 2010, Kerkhoff et al. 2014, Lawrence and Fraser 2020, Hollenbeck and Sax 2021). While these drivers of island distributional patterns have been thoroughly explored for other species (Lomolino 1990, Bell et al. 2005, Kalmar and Currie 2006, Helmus et al. 2014, Pinheiro et al. 2017, Donghao et al. 2020, Schmack et al. 2020, Mologni et al. 2021), they remain largely unknown for humans (Keegan and Diamond 1987, Gavin and Sibanda 2012).

Humans though differ from most other species. We are characterised not just by our biological traits, but also by cultural traits (Darwin 1871, Cavalli-Sforza and Feldman 1981, Boyd and Richerson 1988). Cultural traits are social attributes that both originate and transmit through non-genetic pathways (Cavalli-Sforza and Feldman 1981, Mesoudi et al. 2006). When sets of cultural traits are shared among individuals, distinct societies are generated (Whiten 2019). Societies turnover through both space and time (Mesoudi et al. 2006, Mesoudi 2016), often resulting in

complex economic, historical and political circumstances (Gray et al. 2009, Gavin and Sibanda 2012).

Thus, cultural differences may affect spatial variation in human population size on islands.

Here, I investigate the island biogeography of humans on 10 archipelagos across the globe. I

characterized the geography of 486 islands and used generalized linear models to assess how: (1)

humans occupy islands differing in area, isolation, elevation, latitude and longitude, and (2) how

these relationships vary among archipelagos.

5.3 – Methods

Study system and island characteristics

I selected 10 archipelagos across the globe, to encompass a wide range of climatic, environmental

and geographic conditions (total n = 486 islands, Table 1). Population size was extracted from the

latest available census (Appendix 1, Table S1). Census information was unavailable for small islands

in Northern New Zealand, so in this instance I assayed human population size by the total number of

dwellings visible from aerial imagery.

To examine relationships between human population size and island geography, I measured

five island characteristics (see Appendix 1, Table S2). Estimates of island area (km^2) and elevation (m)

were obtained from freely available sources (Kueffer et al. 2010). When estimates of island area

were not available, islands were manually digitized and their total planar area calculated using

geospatial software (ESRI 2011). Isolation was measured as the shortest distance from the mainland

(km), which I defined as the closest landmass to the archipelago that was at least three orders of

magnitude larger. The latitude and longitude of each island was extracted from digitized mapping.

Table 5-1 - List of archipelagos investigated and associated number of islands, hemisphere, continent and climate.

Archipelago	Number of islands	Hemisphere	Continent	Climate
Northern New Zealand	70	Southern	Oceania	Temperate to subtropical
Seychelles	79	Southern	Africa	Tropical
Samoa	22	Southern	Oceania	Tropical
Channel Islands	40	Northern	Europe	Temperate
Hawaii	45	Northern	Oceania	Tropical
Zhoushan	66	Northern	Asia	Temperate to subtropical
Kuril Islands	33	Northern	Asia	Continental to subantarctic
Virgin Islands	48	Northern	America	Tropical
Ionian Islands	48	Northern	Europe	Temperate/Mediterranean
Shetland	35	Northern	Europe	Temperate to subpolar
Total	**486**			

To determine the geographic correlates of human population size within each archipelago, I conducted separate generalized linear models. I used population size as the dependent variable and island characteristics (i.e. area, isolation, elevation, latitude and longitude) as independent variables. I employed generalized linear models because the dependent variables consisted of counts and therefore followed a Poisson distribution. In cases of overdispersion, I used quasipoisson models (Appendix 1, Table A.2.22). Predictors were variously transformed to conform to assumptions. Island area and elevation were log-transformed, except for elevation in the Kuril Islands. Isolation, latitude and longitude conformed to assumptions without transformation. Isolation was square root-transformed for Northern New Zealand and Hawaii, and log-transformed for the Ionian Islands) (Appendix 1, Figure A.2.14). All analyses were conducted in the R environment (R Core Team 2020).

Figure 5.1 - Map of the globe displaying the investigated archipelagos.

Prior to analyses, I tested for multi-collinearity among predictors using Pearson's product motion correlation, with cut-offs at r = 0.80 (Berry and Feldman 1985). Elevation was often

correlated with area, and both latitude and longitude were commonly correlated with isolation (Appendix 1, Figure A.2.14). In these circumstances, I chose area and isolation because they are the most commonly used variables in island biogeography (MacArthur and Wilson 1967, Hanski 1999). Analyses of multi-collinearity using Variance Inflation Factors yield consistent results.

5.4 – Results

Population sizes increased with island area in all 10 archipelagos (Table 5.2, Figure 5.2). Elevation was strongly correlated with island area in most cases and was therefore only included in two models. Population size declined with it in the Kuril Islands but not in the Seychelles. In 5 archipelagos, the number of people declined with isolation (i.e. Northern New Zealand, Samoa, Kuril Islands, Ionian Island and Shetland). However, in the other 5 archipelagos human-isolation relationships were either positive (i.e. Channel Islands, Zhoushan) or non-significant (i.e. Seychelles, Hawaii, Virgin Islands). Latitude was included in six models and was not significant in 3 of them (i.e. Northern New Zealand, Virgin Islands, Ionian Islands). Population size increased with latitude in Samoa and the Channel Islands, while declined with it in the Kuril Islands. Longitude was included only in one model, Shetland, and population size declined with it.

Table 5-2 - Generalized linear models exploring the relationship between human occupancy and island characteristics on 10 study systems worldwide. Entries are estimates (± standard errors) and t-values.

	Area		Elevation		Isolation		Latitude		Longitude	
	Estimate ± S.E.	t-value	Estimate ± S.E.	t-value	Estimate ± S.E.	t-value	Estimate ± S.E.	t-value	Estimate ± S.E.	t-value
Northern New Zealand	1.15 ± 0.20	**5.80**			-0.02 ± 0.01	**-2.08**	-0.10 ± 0.50	-0.21		
Seychelles	1.51 ± 0.37	**4.14**	0.31 ± 0.43	0.70	0.01 ± 0.00	1.65				
Samoa	0.97 ± 0.07	**14.92**			-0.04 ± 0.01	**-6.47**	5.98 ± 0.30	**19.68**		
Channel Islands	1.92 ± 0.02	**116.10**			0.00 ± 0.00	**2.60**	2.57 ± 0.1	**28.69**		
Hawaii	0.61 ± 0.16	**3.78**			0.88 ± 1.04	0.84				
Zhoushan	1.37 ± 0.05	**30.43**			0.02 ± 0.00	**5.50**				
Kuril Islands	2.46 ± 0.33	**7.37**	-0.00 ± 0.00	**-4.11**	-0.01 ± 0.00	**-5.86**	-0.98 ± 0.13	**-7.37**		
Virgin Islands	1.55 ± 0.33	**4.74**			0.01 ± 0.00	1.45	1.15 ± 0.76	1.53		

5.5 – Discussion

The number of people inhabiting islands was strongly structured geographically. Similar to most species of plants and animals, humans were consistently more abundant on large islands. Positive relationships between population size and island area are among the most common patterns in ecology (Arrhenius 1921, Gleason 1922, Lomolino 2000b), and they can arise from a variety of processes (Turner and Tjørve 2005, Tjørve and Tjørve 2017). Perhaps the simplest explanation is that larger islands offer more inhabitable space (MacArthur and Wilson 1967, Hanski 1999, Tjørve and Tjørve 2017). So, if humans were distributed randomly across the globe, larger islands would house larger populations than smaller islands all else being equal (Tjørve and Tjørve 2017). Human population sizes in the Seychelles, Hawaii and Virgin Islands were associated only with island area.

Differently to island area, relationships between human population size and elevation, isolation, latitude and longitude varied markedly among archipelagos. Population sizes in Northern New Zealand and the Ionian Islands decreased with island isolation. Negative abundance-isolation relationships are also commonly observed in plants and animals (MacArthur and Wilson 1967, Hanski 1999, Burns 2019), and are typically attributed to the negative effect isolation has on immigration rates (MacArthur and Wilson 1967).

In the Samoan archipelago, population size declined with isolation, but also increased with latitude. The effect of latitude on population size is consistent with modern political boundaries. The Samoan archipelago is partitioned into two different political units, Samoa and American Samoa (The Editors of Encyclopaedia Britannica 2020), the latter located further south. Differences in foreign economic subsidy and immigration may therefore account for this result.

In the Channel Islands, population size increased with both isolation and latitude. This archipelago was disputed between the French and the English for centuries and was acquired by the latter in 1259 (Rothwell 1975). It has been a British crown dependency ever since (Beswick 2020).
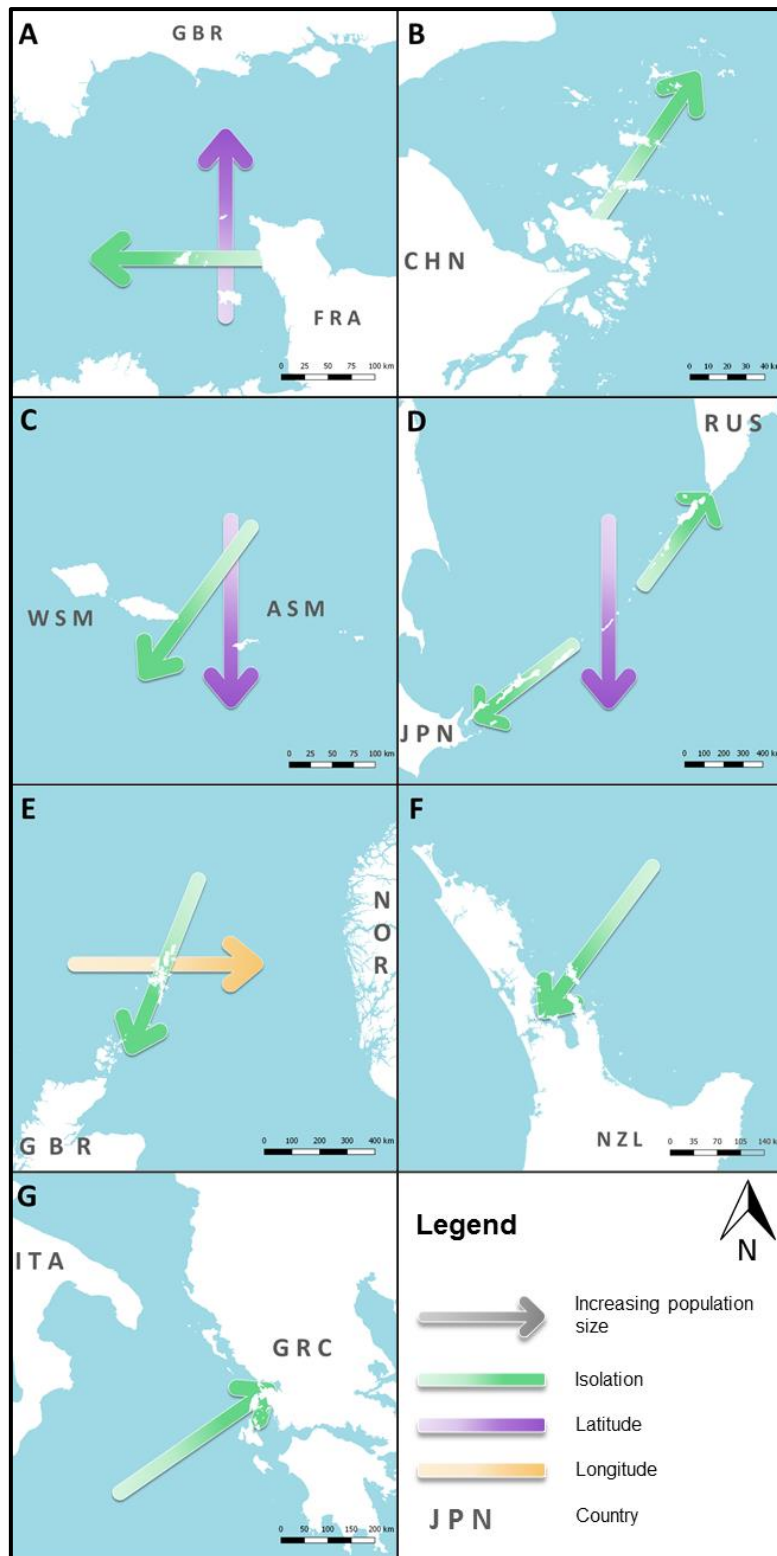
Figure 5.2 - Map representing the effect of isolation, latitude and longitude on human population size on archipelagos across the planet. From top left: Channel Islands (A), Zhoushan (B), Samoa (C), Kuril Islands (D), Shetland (E), Northern New Zealand (F), Ionian Islands (G). Arrow direction and shade (light to dark) show increasing population size. Arrow colour show isolation (green), latitude (purple) and longitude (yellow). Country codes follow the International Organization for Standardization alphabetic codes (ISO 3).

Population sizes were higher on islands closer to England perhaps because they were less exposed to potential invasions from continental Europe (Beswick 2020).

Positive population size - isolation relationships were detected also in the Zhoushan archipelago. Historically, these islands had a predominantly maritime economy, characterized by fishing and piracy (Gernet 1996). After suppressing piracy, Zhoushan became an important commercial port (The Editors of Encyclopaedia Britannica 2011). In this context, islands distant from mainland authorities and with easy access to the sea might had been preferred for settlement.

In the Kuril Islands, humans declined in number with isolation, elevation and latitude. Geographically, the Kuril Islands lie in a chain between Russia in the north and Japan in the south, and population sizes were higher on islands closer to both mainland source pools. Whereas elevation and latitudinal gradients may be explained by climatic conditions, which might be increasingly prohibitive for humans on taller islands located at higher latitudes.

Population sizes in the Shetland Islands declined with isolation and longitude. Islands in the northern part of this archipelago are located closer to the pole and perhaps more inhospitable. One explanation for higher population sizes in islands located in the eastern extremities of the archipelago is that they are less exposed to oceanic currents (Whittaker and Fernández-Palacios 2007). Alternatively, larger populations on southwestern islands might reflect two different immigration waves, one from the Scandinavian peninsula in the 9th century, and a second from Scotland, which begun in the 13th century (Fenton 1997).

Archipelagos were chosen for this study because they encompass a wide range of climatic, environmental and geographic conditions. Although this resulted in a total sample size of 486 islands, many more remain uninvestigated across the globe. Additionally, the use of islands by humans is likely to have changed radically through time, so investigating historical differences in island occupancy would be an interesting avenue of future research. Lastly, along with population size several other estimates of human land use can be measured, such as dwellings, docks and farms

(Paudel et al. 2017, Sanchez-Ortiz et al. 2019, Schmack et al. 2020), which can potentially yield interesting information on how humans utilize islands.

Overall results illustrate that, similar to other species, insular distributional patterns of human populations are strongly structured geographically (MacArthur and Wilson 1967, Hanski 1999). However, trends varied idiosyncratically among most archipelagos and appear to be driven by site-specific cultural differences, resulting from social, political and historical factors (Gray et al. 2009, Gavin and Sibanda 2012). Therefore, the island biogeography of humans might differ fundamentally from that of other species.

Chapter 6. Discussion

6.1 – Thesis summary

This thesis combines with a growing body of work in the invasion ecology of islands, focusing particularly on how the distributional patterns of exotic vascular plants differ from those of natives. It also includes the first investigation of the human biogeography of islands. Results from chapter 2 show that the insular distributional patterns of native and exotic species richness are regulated by similar biogeographic principles. However, exotic species exhibited subtle, yet distinctive, invasion patterns. In chapter 3, I integrated interrelationships between traits and invasion success (i.e. high island occupancy rates) with the island biogeography theoretical framework. Results show that successful invaders were associated with specific life-history traits and displayed both rates of occupancy and patterns in richness and seed mass similar to natives. Moreover, most differences among trait categories in exotic species regarded relationships with human-related variables. In chapter 4, I explored how different levels of ocean-borne disturbances influence the richness and composition of native and exotic species on islands. Patterns in richness and composition varied depending on island location (i.e. inside the harbour and less disturbed or outside and more disturbed) for native species, but not for exotic species. In chapter 5, I tested the island biogeography of humans on 10 archipelagos across the globe. Human population sizes on islands were strongly structured geographically, similar to other species. However, relationships often varied idiosyncratically among archipelagos.

Biological invasions are one of the main threats to the insular biota (Whittaker and Fernández-Palacios 2007, Simberloff et al. 2013, Liao et al. 2020, Rojas-Sandoval et al. 2020). Exotic species often displace native species by monopolizing space and resources, a process that often leads to the local extinctions of natives and biotic homogenization (Pyšek and Richardson 2006, Qian and Ricklefs 2006, Castro and Jaksic 2008). However, plant invasions on islands are still poorly understood. Additionally, the invasion process is often facilitated by humans (Stohlgren et al. 2006,

Seabloom et al. 2007). Despite a key role in biological invasions, the insular distributional patterns of humans are still largely unknown (Keegan and Diamond 1987).

Overall, this thesis significantly contributes to the fields of island biogeography and invasion ecology by highlighting previously overlooked aspects of the invasion process on islands. Results support that exotics have distinct distributional patterns from natives, providing indications on how to manage insular plant invasions. It also presents what is, to my knowledge, the first attempt to empirically evaluate global variation in human population sizes on islands, providing a start point for future studies in the field of island biogeography of humans.

6.2 – Synthesis

6.2.1 Comparing native and exotic species

Here, I compared the distributional patterns of native and exotic species to better understand plant invasions on islands. Trends in species richness were broadly similar in native and exotic species, in contrast with other studies (Long et al. 2009, Blackburn et al. 2016, Moser et al. 2018, Rojas-Sandoval et al. 2020, Guo et al. 2021). However, several differences emerged at a more detailed analysis. For instance, in chapter 2 I found exotic species to prefer larger, less isolated islands more than natives. New Zealand was one of the last landmasses to be discovered by humans and most exotic plant species were introduced in the last 150 years (Williams and Cameron 2006). Many exotics might be still in the process of colonizing islands within this study system (i.e. ongoing invasion (González-Moreno et al. 2017, Coutts et al. 2018); thus, they would reach first larger, less isolated islands (MacArthur and Wilson 1967, Lomolino 1990).

Differences in the distribution of native and exotic species emerged also by investigating exotics with different life-history traits. Results show that successful invaders (e.g. high island

occupancy rates) displayed both rates of occupancy and patterns in richness and seed mass similar

to natives. Traits were largely used to explore invasion patterns (Van Kleunen et al. 2010b, a, Guo et

al. 2018, Hulme and Bernard-Verdier 2018b, a), but less so in the context of the island biogeography

theory (Patiño et al. 2017, Ottaviani et al. 2020). Here, using a trait-based approach helped

understanding how the biogeography of islands differentially influence plant invaders with distinct

traits. On the one hand, this result supports an ongoing invasion process. Species with specific traits

(e.g. short life span, long-distance dispersal) might colonize islands within a new range faster than

species lacking those traits. In contrast, these trends might simply reflect idiosyncratic differences in

island occupancy among species with different life histories. Nonetheless, overall results strongly

argue for integrating trait-based approaches in the theory of island biogeography framework

(Ottaviani et al. 2020).

Relationships between species richness and island characteristics were also scale-dependent.

Results showed that the relative influence of island area on species richness declined with island

area, whereas the influence of other island characteristics, such as isolation and exposure to ocean-

borne disturbances, strengthened. Scale is a component of many ecological processes (Whittaker

2000, Fridley et al. 2007, Ladau and Eloe-Fadrosh 2019, King et al. 2020). However, studies in island

biography typically focus on species-area relationships alone (Whitehead and Jones 1969, Lomolino

and Weiser 2001, Turner and Tjørve 2005, Burns et al. 2009, Dengler 2010, Morrison 2014, Li 2020).

These results combined with recent work assessing the scale-dependency of other biogeographic

drivers of species richness on islands (Menegotto et al. 2020, Schrader et al. 2020). Additionally,

scale-dependent relationships were stronger for exotic species, supporting the hypothesis of time-

lags in the invasion process.

6.2.2 Human proximity and species richness

Human activities generally promote invasions (Stohlgren et al. 2006, Seabloom et al. 2007).
Accordingly, in Chapter 2 exotic species increased in number with human proximity. However,
relationships between exotic species richness and human-related variables depended on life-history
traits (see chapter 3). Exotic species with traits associated with high invasion success (i.e. high island
occupancy rates) were less commonly related to human-related variables. One possible explanation
is that species with specific traits (e.g. short life cycle, high seed production, long-distance dispersal)
spread more rapidly (Pérez-Harguindeguy et al. 2013, Díaz et al. 2016, Arjona et al. 2018). As the
invasion process progresses, these species might be increasingly independent of humans for their
dispersal. Alternatively, successful invaders might rely upon humans only for their initial
introduction.

In chapter 4, exotic species richness declined with proximity to human settlements instead.
While human settlements are often foci for plant invasions (Castro & Jaksic, 2008; Pretto *et al.*,
2012; Paudel *et al.*, 2017; Schmack *et al.*, 2020 c.f. Löfgren & Jerling, 2002; Stohlgren *et al.*, 2006),
here they reduce natural areas available to coastal communities, thus lowering source population
sizes and immigration rates (i.e. reduced propagule pressure, Lockwood *et al.*, 2005). Additionally,
human disturbances are too frequent or severe for exotic species to take advantage of them.
Conversely, human activities generally disfavour native species (Paudel et al. 2017, Sanchez-Ortiz et
al. 2019). Interestingly though, results from chapter 3 show that on some occasions native species
increased in number with proximity to human settlements. It is possible that, just like exotics, also
natives can opportunistically exploit human-mediated dispersal pathways (Valery et al. 2009).
Perhaps plant-human relationships are more complex than previously thought, as for other aspects
of invasion biology (Jeschke 2014).

Human disturbances are often measured by numbers of buildings, lengths of roads or extent
of agricultural fields (Seabloom et al. 2007, Pretto et al. 2012, Paudel et al. 2017). In chapters 2, 3

and 4 though, I explored human impacts mainly by measuring proximity to the nearest settlement,

because most of the islands investigated are currently uninhabited and records of human impacts

are unavailable. This likely underestimates the effect of current and past human disturbance.

Uninhabited islands in New Zealand though are generally smaller in size than occupied islands, a

trend consistent across the globe (see chapter 5). Thus, other archipelagos might present a similar

issue. Additionally, uninhabited islands are likely to sustain lower human disturbances than occupied

islands, suggesting that human impacts might vary with scale similar to other biogeographic drivers.

6.2.3 The role of ocean-borne disturbances

It is still contentious whether disturbances promote biological invasions (Denslow et al. 2009, Moles

et al. 2012). Earlier work suggests different types of natural disturbance can either promote

(Bellingham et al. 2005, Alba et al. 2015), prevent (Smith and Knapp 1999) or have no effect on plant

invasions (Stohlgren et al. 1999, Suding and Gross 2006). In particular, ocean-borne disturbances

were previously found to affect the distributional patterns of exotic species (Burns 2016b), but it is

unclear how. In chapter 2, the richness of exotic species declined with exposure to ocean-borne

disturbances, and more strongly than natives. Overall, this result was consistent among species with

different life-history traits (chapter 3). In chapter 4, different levels of disturbance affected both the

richness and composition of natives, but not that of exotic species. One explanation for these

discrepancies is that the exotic species pool lacks coastal specialists. Exotic species are often

selected by humans for agricultural and ornamental purposes (Lloret et al. 2005). Then, they might

represent a subset of species poorly adapted to coastal habitats.

 Other processes though, might be in play. For instance, a previous study in Wellington

Harbour found the number of exotic species to increase through time (Burns 2015), suggesting a

progressive invasion of the study system. However, after almost a decade since that census, the

total number of exotics remained unchanged. Exotics were also previously found to turnover more

rapidly on exposed islands (Burns 2016b). Perhaps then exotic species cyclically recolonize these

islands after extinction following each major disturbance event (i.e. non-equilibrium dynamics,

Whittaker 1995, 2000, Morrison and Spiller 2008). A similar process might be at work in Northern

New Zealand as well. All in all, these results seem to indicate that disturbances of oceanic origin

prevent biological invasions.

6.2.4 The island biogeography of humans

Human distributions on islands were strongly structured geographically. Similar to other species,

population sizes increased with island area consistently across the globe. Positive relationships with

area are one of the most common patterns in ecology (Arrhenius 1921, MacArthur and Wilson 1967,

Lomolino 2000b, Tjørve and Tjørve 2017), and might be explained by several processes (Turner and

Tjørve 2005). For instance, larger islands can offer more species and a greater amount and variety of

resources (Turner and Tjørve 2005, Tjørve and Tjørve 2017).

Human population sizes often declined with isolation. Negative abundance-isolation

relationships are also commonly observed in plants and animals (MacArthur and Wilson 1967,

Hanski 1999, Burns 2019), and are typically attributed to the negative effect isolation has on

immigration rates (MacArthur and Wilson 1967). However, in many cases, abundance-isolation

relationships were either positive or non-significant. Similarly, relationships with elevation, latitude

and longitude often varied idiosyncratically among archipelagos. While in some cases trends can be

interpreted as a product of climatic, geographic and ecological gradients, in others a distinct suite of

factors may be at work.

For instance, some relationships between human population size and island characteristics

may be interpreted in light of current political circumstances. Archipelagos subdivided into different

political units might undergo distinct economic and social processes. Other relationships appeared to reflect historical factors. Archipelagos that were long disputed might display human distributional patterns that reflect main invasion pathways (Fenton 1997, Beswick 2020). Lastly, some results seemed to be linked to economic factors. Archipelagos with distinctive economic circumstances might exhibit distributional patterns that vary accordingly (Gernet 1996, The Editors of Encyclopaedia Britannica 2011). In all these cases, processes that are political, economic or historical may account for human insular distributions. Overall results suggest that, despite underlying similarities in their distribution, the island biogeography of humans may be fundamentally different from that of other organisms.

6.3 – Conclusions & future directions

This thesis combines a growing body of research on plant invasions on islands (Burns 2016b, Celesti-Grapow et al. 2016, Paudel et al. 2017, Moser et al. 2018, Butt et al. 2020, Fois et al. 2020, Rojas-Sandoval et al. 2020). It provided a fresh perspective on the subject by assessing previously overlooked aspects of the invasion process, such as the scale-dependency of the relationships between native and exotic species richness and island characteristics. Moreover, it integrated a trait-based approach in the theory of island biogeography framework. Lastly, this work includes what is, to my knowledge, the first attempt to empirically evaluate global variation in human population sizes on islands.

In chapters 2, 3 and 4, I found that native and exotic species displayed broadly similar biogeographical patterns; however, with some differences. Discrepancies hinged on scale-dependent processes, life-history traits and varying levels of ocean-borne disturbances. Comparing the distribution of native and exotic species might help conservation bodies in better focusing their efforts in controlling plant invasions on islands (Rojas-Sandoval et al. 2020). Future studies though should consider integrating other factors, both biotic and abiotic. One example is seabirds, whose

burrowing activities and guano can modify the physical and chemical characteristics of the substrate (Bellingham et al. 2010, Ellis et al. 2011). Similarly, the amount and type of soil might act as environmental filters (Schrader et al. 2019).

In chapter 3, I used a trait-based approach to explore patterns of island invasions by exotic plant species. In particular, I used easily accessible traits, such as growth forms and dispersal syndromes. However, several other aspects of the life history of a plant can be explored, such as their introduction history. For example, exotic species can exploit several human-related pathways (Hodkinson and Thompson 1997). Forecasting preferential invasion pathways may enable us to prevent new introductions altogether (Sinclair et al. 2020). Moreover, traits such as time since first introduction are important determinants of invasion success (Williams & Cameron, 2006; Ni *et al.*, 2021). Lastly, the biogeographic origin of a species is often a good predictor of impact severity (Ni et al. 2021). For instance, species evolved in areas matching the climatic conditions of the new range generally have better chances to become successful invaders (Hayes and Barry 2008, Brandt et al. 2021).

In chapter 5, I found that similar to other species, insular distributional patterns of human populations are strongly structured geographically (MacArthur and Wilson 1967, Hanski 1999). In many cases though, results were perhaps better explained by political, economic and historical factors. To better understand how interrelationships among humans might influence our patterns of island occupancy, I am now integrating specific measures of human aggregation. Additionally, human population sizes varied idiosyncratically among archipelagos. Currently, I am investigating whether similar changes in the relationships between human population size and island characteristics occur on a temporal scale.

Overall, this thesis significantly contributes to the fields of island biogeography and invasion ecology by highlighting previously overlooked aspects of the invasion process on islands. Results help further my understanding of complex and often unresolved relationships between plant species

and island characteristics. It also presents what is, to my knowledge, the first attempt to empirically

evaluate global variation in human population sizes on islands, providing a starting point for future

studies in the field of the island biogeography of humans.

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Appendix 2

Table A.2.1 - Explained variance (R^2), delta AIC (ΔAIC) and model probabilities (AICw) of isolation buffers for predicting the residuals of the species-area relationship. The isolation buffer with the highest model probability was retained.

Native species			
Isolation buffers	**R^2**	**ΔAIC**	**AICw**
Arcsine (1500 m)	0.0393	0.0000	0.3605
Arcsine (1000 m)	0.0365	0.7500	0.2478
Arcsine (500 m)	0.0347	1.2529	0.1927
Arcsine (2000 m)	0.0288	2.8561	0.0864
Arcsine (250 m)	0.0247	3.9593	0.0498
Arcsine (2500 m)	0.0216	4.8106	0.0325
Arcsine (3000 m)	0.0211	4.9567	0.0302

Exotic species			
Isolation buffers	**R^2**	**ΔAIC**	**AICw**
Arcsine (1500 m)	0.1244	0.0000	0.4787
Arcsine (3000 m)	0.1215	0.8686	0.3101
Arcsine (2000 m)	0.1166	2.3483	0.1480
Arcsine (2500 m)	0.1102	4.2332	0.0577
Arcsine (1000 m)	0.0944	8.8995	0.0056
Arcsine (500 m)	0.0401	24.2703	0.0000
Arcsine (250 m)	0.0094	32.5657	0.0000

Table A. 2.2 - Moran's Index for spatial autocorrelation of the variables employed in this study. Entries are independent and dependent variables, Moran's Indexes, z-scores and p-values. Latitude was excluded as not suitable for testing.

Variables	Moran's Index	z-score	p-value
Area	0.010	0.291	0.7705
Isolation$_{1500}$	0.251	3.114	**0.0018**
Exposure	0.951	11.614	**0.0000**
Urban	0.506	6.219	**0.0000**
Native richness	0.246	3.113	**0.0018**
Exotic richness	0.226	2.859	**0.0042**

Table A. 2.3 - Chi-square test of independence for the richness of growth forms and dispersal syndromes employed investigating patterns of species richness across 264 New Zealand offshore islands.

Growth forms		Chi-squared	p-value
Exotic graminoids	Exotic forbs	232.92	**0.0000**
Exotic graminoids	Exotic woody	2.76	0.0966
Exotic forbs	Exotic woody	192.07	**0.0000**
Exotic graminoids	Native graminoids	0.016	0.9009
Exotic forbs	Native forbs	13.93	**0.0002**
Exotic woody	Native woody	15.60	**0.0000**
Dispersal mode			
Exotic wind-dispersed	Exotic unspecialized	39.57	**0.0000**
Exotic wind-dispersed	Exotic short-distance	2.29	0.1300
Exotic wind-dispersed	Exotic animal-dispersed	0.31	0.5785
Exotic unspecialized	Exotic short-distance	23.21	**0.0000**
Exotic unspecialized	Exotic animal-dispersed	33.11	**0.0000**
Exotic short-distance	Exotic animal-dispersed	0.92	0.3374
Exotic wind-dispersed	Native wind-dispersed	111.51	**0.0000**
Exotic unspecialized	Native unspecialized	71.49	**0.0000**
Exotic short-distance	Native short-distance	104.11	**0.0000**
Exotic animal-dispersed	Native animal-dispersed	1.48	0.2235

Table A. 2.4 - Chi-square test of independence for the richness of growth forms and dispersal syndromes employed investigating patterns of species seed mass across 264 New Zealand offshore islands.

Growth forms		Chi-squared	p-value
Exotic graminoids	Exotic forbs	155.93	**0.0000**
Exotic graminoids	Exotic woody	1.32	0.2511
Exotic forbs	Exotic woody	132.00	**0.0000**
Exotic graminoids	Native graminoids	0.04	0.8415
Exotic forbs	Native forbs	2.87	0.0902
Exotic woody	Native woody	109.73	**0.0000**
Dispersal mode			
Exotic wind-dispersed	Exotic unspecialized	36.17	**0.0000**
Exotic wind-dispersed	Exotic short-distance	0.19	0.6660
Exotic wind-dispersed	Exotic animal-dispersed	0.63	0.4280
Exotic unspecialized	Exotic short-distance	31.35	**0.0000**
Exotic unspecialized	Exotic animal-dispersed	27.56	**0.0000**
Exotic short-distance	Exotic animal-dispersed	0.13	0.7180
Exotic wind-dispersed	Native wind-dispersed	2.40	0.1216
Exotic unspecialized	Native unspecialized	76.84	**0.0000**
Exotic short-distance	Native short-distance	66.82	**0.0000**
Exotic animal-dispersed	Native animal-dispersed	0.30	0.5860

Table A. 2.5 - Contingency table of growth forms and dispersal syndromes for exotic and native species.

Exotics

	graminoids	forbs	woody	total
wind	19	99	34	152
unspecialized	61	192	29	282
animals	24	51	71	146
short-distance	21	134	19	174
total	125	476	153	

Natives

	graminoids	forbs	woody	total
wind	38	276	66	380
unspecialized	54	38	24	116
animals	15	31	133	179
short-distance	2	22	10	34
total	109	367	233	

Table A. 2.6 - Species omitted from analyses. Entries are the number of species omitted, the corresponding proportion of exotic and native species, the reason for exclusion and the analyses they were excluded from.

Number of species omitted	Exotic (%)	Native (%)	Reason	Excluded from
13	NA	NA	Status cannot be determined (i.e. exotics or native)	All analyses
99	49.0	51.0	Growth form cannot be classified as graminoid, forb or woody.	Growth form analyses only
114	43.	57.0	Dispersal syndrome cannot be classified as wind-, animal-dispersed, unspecialized or short-distance.	Dispersal analyses only
167	4.8	95.2	Seedless vascular plants	Seed mass analyses only
370	44.3	55.7	Lack of data in seed mass	Seed mass analyses only

Table A. 2.7 - List of generalized linear models (GLM) with quasipoisson distribution comparing the occurrence of species with different functional traits and origin (i.e. exotic and native). Columns are the compared set of species, t-value, p-value and the level of significance (alpha). Alpha levels are adjusted with a Bonferroni correction, or divided by the number of tests run in each case. Significant p-values are in bold.

Growth forms		t-value	p-value	alpha
Exotic graminoids	Exotic forbs	3.72	**0.0002**	0.0167
Exotic graminoids	Exotic woody	-6.47	**0.0000**	0.0167
Exotic forbs	Exotic woody	-3.32	**0.0010**	0.0167
Native graminoids	Native forbs	1.17	0.2430	0.0167
Native graminoids	Native woody	-0.59	0.5560	0.0167
Native forbs	Native woody	0.51	0.6110	0.0167
Exotic graminoids	Native graminoids	0.80	0.4240	0.0500
Exotic forbs	Native forbs	4.40	**0.0000**	0.0500
Exotic woody	Native woody	5.96	**0.0000**	0.0500
Dispersal mode				
Exotic wind-dispersed	Exotic unspecialized	0.33	0.7400	0.0083
Exotic wind-dispersed	Exotic short-distance	3.28	**0.0012**	0.0083
Exotic wind-dispersed	Exotic animal-dispersed	2.25	0.0253	0.0083
Exotic unspecialized	Exotic short-distance	3.78	**0.0002**	0.0083
Exotic unspecialized	Exotic animal-dispersed	2.51	0.0123	0.0083
Exotic short-distance	Exotic animal-dispersed	-1.36	0.1750	0.0083
Native wind-dispersed	Native unspecialized	-0.83	0.4060	0.0083
Native wind-dispersed	Native short-distance	-1.61	0.1080	0.0083
Native wind-dispersed	Native animal-dispersed	-1.84	0.0657	0.0083
Native unspecialized	Native short-distance	-1.04	0.3030	0.0083
Native unspecialized	Native animal-dispersed	-0.64	0.5240	0.0083
Native short-distance	Native animal-dispersed	0.51	0.6140	0.0083
Exotic wind-dispersed	Native wind-dispersed	0.85	0.3970	0.0500
Exotic unspecialized	Native unspecialized	2.17	**0.0305**	0.0500
Exotic short-distance	Native short-distance	5.23	**0.0000**	0.0500
Exotic animal-dispersed	Native animal-dispersed	4.44	**0.0000**	0.0500

Table A. 2.8 - Results from multiple linear regressions exploring the relationship between exotic and native species richness of different growth forms and island characteristics on 264 New Zealand offshore islands. To conform to assumptions, species richness was log (+1) transformed, area log-transformed, isolation arcsine-transformed and distance from the nearest urban area squared-transformed. T and p values are reported for each island characteristic. Statistical significance: *P < 0.05, **P < 0.01, ***P < 0.001.

		Area		Isolation		Exposure		Urban	
		t-value	p-value	t-value	p-value	t-value	p-value	t-value	p-value
Graminoids	**Exotic**	12.519	**0.0000**	-3.763	**0.0002**	-4.895	**0.0000**	-1.236	0.2175
	Native	16.895	**0.0000**	-4.112	**0.0000**	- 1.825	0.0691	0.663	0.5082
	Interaction	0.2681		0.7774		**0.0093**		0.1697	
Forbs	**Exotic**	17.296	**0.0000**	-4.062	**0.0000**	-5.145	**0.0000**	-2.524	**0.0122**
	Native	17.211	**0.0000**	-1.546	0.1232	-2.659	**0.0083**	0.582	0.5609
	Interaction	**0.0122**		**0.0216**		**0.0205**		**0.0305**	
Woody species	**Exotic**	13.412	**0.0000**	-1.887	0.0603	-3.914	**0.0001**	-6.358	**0.0000**
	Native	18.161	**0.0000**	-2.732	**0.0067**	-1.869	0.0627	-1.121	0.2635
	Interaction	**0.0003**		0.5247		0.1629		**0.0003**	

Table A. 2.9 - Results from multiple linear regressions exploring the relationship between exotic and native species richness of different dispersal syndromes and island characteristics on 264 New Zealand offshore islands. To conform to assumptions, species richness was log (+1) transformed, area log-transformed, isolation arcsine-transformed and distance from the nearest urban area squared-transformed. T and p values are reported for each island characteristic. Statistical significance: *P < 0.05, **P < 0.01, ***P < 0.001.

		Area		Isolation		Exposure		Urban	
		t-value	p-value	t-value	p-value	t-value	p-value	t-value	p-value
Wind-dispersed	**Exotic**	18.517	**0.0000**	-4.104	**0.0000**	-4.602	**0.0000**	-1.400	0.1630
	Native	17.689	**0.0000**	-3.185	**0.0016**	-3.234	**0.0014**	0.237	0.8128
	Interaction	**0.0474**		0.8971		0.6847		0.2854	
Unspecialized	**Exotic**	14.303	**0.0000**	-3.939	**0.0001**	-5.229	**0.0000**	-1.947	0.0527
	Native	18.210	**0.0000**	-3.797	**0.0001**	-1.880	0.0612	0.607	0.5445
	Interaction	0.1517		0.2777		**0.0013**		0.0521	
Animal-dispersed	**Exotic**	15.562	**0.0000**	-1.218	0.2240	-5.636	**0.0000**	-5.868	**0.0000**
	Native	15.994	**0.0000**	-1.543	0.1240	-1.143	0.2540	-0.250	0.8030
	Interaction	0.9401		0.8445		**0.0012**		**0.0000**	
Short-distance	**Exotic**	14.584	**0.0000**	-3.471	**0.0006**	-2.969	**0.0033**	-3.156	**0.0018**
	Native	15.609	**0.0000**	1.180	0.2391	-3.035	**0.0027**	1.150	0.2513
	Interaction	0.1541		**0.0006**		0.7036		**0.0016**	

Table A. 2.10 - Results from multiple linear regressions exploring the relationship between exotic and native average seed mass of different growth forms and island characteristics on 264 New Zealand offshore islands. To conform to assumptions, average seed mass and area were log-transformed, isolation arcsine-transformed and distance from the nearest urban area squared-transformed. T and p values are reported for each island characteristic. Statistical significance: *P < 0.05, **P < 0.01, ***P < 0.001.

		Area		Isolation		Exposure		Urban		Conservation areas	
		t-value	p-value	t-value	p-value	t-value	p-value	t-value	p-value	t-value	p-value
Graminoids	**Exotic**	2.346	**0.0196**	-0.421	0.6744	-2.909	**0.0040**	-2.431	**0.0158**	-2.114	**0.0355**
	Native	4.901	**0.0000**	-2.345	**0.0198**	-0.498	0.6189	-0.319	0.7499	-0.380	0.7040
	Interaction	0.2902		0.2858		**0.0428**		0.0799		0.1436	
Forbs	**Exotic**	11.273	**0.0000**	-1.658	0.0986	-3.572	**0.0004**	-6.427	**0.0000**	-0.146	0.8843
	Native	3.322	**0.0010**	-1.250	0.2124	0.829	0.4079	-2.186	**0.0297**	-3.538	**0.0005**
	Interaction	**0.0000**		0.3786		**0.0004**		**0.0000**		0.1279	
Woody species	**Exotic**	9.770	**0.0000**	-1.845	0.0663	-3.748	**0.0002**	-5.475	**0.0000**	2.011	**0.0454**
	Native	6.898	**0.0000**	-0.973	0.3316	-2.185	**0.0298**	-3.036	**0.0026**	0.749	0.4543
	Interaction	**0.0072**		0.4663		0.1798		**0.0394**		0.3168	

Table A. 2.11 - Results from multiple linear regressions exploring the relationship between exotic and native average seed mass of different dispersal syndromes and island characteristics on 264 New Zealand offshore islands. To conform to assumptions, average seed mass and area were log-transformed, isolation arcsine-transformed and distance from the nearest urban area squared-transformed. T and p values are reported for each island characteristic. Statistical significance: *P < 0.05, **P < 0.01, ***P < 0.001.

		Area		Isolation		Exposure		Urban		Conservation areas	
		t-value	p-value	t-value	p-value	t-value	p-value	t-value	p-value	t-value	p-value
Wind-dispersed	**Exotic**	5.299	**0.0000**	-2.729	**0.0068**	-1.930	0.0547	-0.349	0.7270	-2.477	**0.0139**
	Native	5.594	**0.0000**	-0.122	0.9031	0.1403	0.4028	-2.880	**0.0043**	-2.548	**0.0114**
	Interaction	**0.0013**		0.3679		**0.0370**		**0.0113**		0.1492	
Unspecialized	**Exotic**	7.103	**0.0000**	-0.070	0.9440	-2.416	**0.0164**	-5.704	**0.0000**	0.523	0.6013
	Native	0.851	0.3954	0.718	0.4732	1.470	0.1429	-2.522	**0.0123**	0.502	0.6159
	Interaction	**0.0000**		0.5533		**0.0054**		0.0777		0.9645	
Animal-dispersed	**Exotic**	8.329	**0.0000**	-0.885	0.3770	-5.970	**0.0000**	-4.121	**0.0000**	2.960	**0.0034**
	Native	9.080	**0.0000**	-0.471	0.6380	-0.484	0.6290	-0.255	0.7990	0.000	1.0000
	Interaction	0.2758		0.8038		**0.0002**		**0.0099**		**0.0465**	
Short-distance	**Exotic**	7.934	**0.0000**	-2.971	**0.0033**	-1.363	0.1741	-3.049	**0.0025**	-2.753	**0.0063**
	Native	9.431	**0.0000**	0.362	0.7180	-0.964	0.3360	1.013	0.3120	0.075	0.9400
	Interaction	**0.0465**		**0.0276**		0.8769		**0.0061**		0.0651	

Table A. 2.12 - ANCOVA tests investigating how among exotic growth forms and dispersal syndromes relationships with island characteristics differ. Above is species richness, below is species seed mass. F and p values are reported for each island characteristic. Significant p-values in bold. To conform to assumptions, average seed mass and area were log-transformed, isolation arcsine-transformed and distance from the nearest urban area squared-transformed. Statistical significance: *P < 0.05, **P < 0.01, ***P < 0.001.

	Growth forms		Dispersal syndrome	
	F-value	**p-value**	**F-value**	**p-value**
	Richness			
Area	9.644	**0.0000**	1.737	NS
Isolation	2.146	NS	2.403	NS
Exposure	1.005	NS	4.610	**0.0033**
Urban	5.015	**0.0069**	3.548	**0.0141**
	Seed mass			
Area	87.460	**0.0000**	42.122	**0.0000**
Isolation	1.987	NS	1.488	NS
Exposure	21.835	**0.0000**	26.451	**0.0000**
Urban	15.229	**0.0000**	7.935	**0.0000**
Conservation areas	5.145	**0.0060**	8.657	**0.0000**

Table A. 2.13 - Plant species found on 97 islands during field surveys. Entries are species' family, binomial name and status (i.e. exotic or native).

Family	Species	Status
Primulaceae	*Anagallis arvensis*	Exotic
Apiaceae	*Apium prostratum*	Native
Asteracerae	*Arctotheca calendula*	Exotic
Aspleniaceae	*Asplenium appendiculatum*	Native
Amaranthaceae	*Atriplex prostrata*	Exotic
Chenopodiaceae	*Chenopodium triandrum*	Native
Caryophyllaceae	*Colobanthus* sp.	Native
Rubiaceae	*Coprosma repens*	Native
Crassulaceae	*Cotyledon orbiculata*	Exotic
Crassulaceae	*Crassula sieberiana*	Native
Crassulaceae	*Crassula* sp.	Exotic
Mesembryanthemaceae	*Disphyma australe*	Native
Poaceae	*Ehrharta erecta*	Exotic
Cyperaceae	*Ficinia nodosa*	Native
Asteraceae	*Gazania rigens*	Exotic
Poaceae	*Lagurus ovatus*	Exotic
Fabaceae	*Lupinus arboreus*	Exotic
Malvaceae	*Malva arborea*	Exotic
Fabaceae	*Melilotus indicus*	Exotic
Myrtaceae	*Metrosideros excelsa*	Native
Polygonaceae	*Muehlenbeckia complexa*	Native
Scrophulariaceae	*Myoporum laetum*	Native
Poaceae	*Parapholis incurva*	Exotic
Urticaceae	*Parietaria judaica*	Exotic
Asphodelaceae	*Phormium* sp.	Native
Pittosporaceae	*Pittosporum crassifolium*	Native
Plantaginaceae	*Plantago coronopus*	Exotic
Poaceae	*Poa cita*	Native
Primulaceae	*Samolus repens*	Native
Amaranthaceae	*Sarcocornia quinqueflora*	Native
Goodeniaceae	*Selliera radicans*	Native
Asteraceae	*Senecio elegans*	Exotic
Asteracerae	*Senecio lautus*	Native
Caryophyllacee	*Silene uniflora*	Exotic
Asteracerae	*Sonchus oleraceus*	Exotic
Caryophyllacee	*Spergularia* sp.	Exotic
Aizoaceae	*Tetragonia implexicoma*	Native
Poaceae	*Trisetum antarcticum*	Native

Table A. 2.14 - List of parameters used to investigate patterns in species richness on 97 small islands off the coast of Wellington, New Zealand. For each parameter, unit of measurement, range, mean, standard deviation and description are provided. Values for range, mean and standard deviation are provided for all islands (all), islands inside (inner) and outside (outer) the harbour.

Variable	Unit of measurement	Range			Mean			SD			Description
		All	Inner	Outer	All	Inner	Outer	All	Inner	Outer	
Area	Squared metre	0.825 − 166	0.825 − 166	0.980 − 89.8	18.9	18.5	19.1	22.5	34.1	16.4	Island area in squared meters
Isolation	meters	0.00 − 41.3	0 − 30.9	1 − 41.3	8.81	5.86	9.95	8.28	7.15	8.45	Distance from the nearest plant community
Height	meters	0.200 − 5.00	0.200 − 2.6	0.250 − 5.00	1.44	1.25	1.51	0.917	0.701	0.984	Height above the lowest lichens boundary
Nearest dwelling	meters	20 − 840	20 − 840	25 − 610	228.76	190.00	243.71	210.84	209.60	210.91	Distance form nearest dwelling
Elevation	meters	-0.38 − 4.31	-0.13 − 3.85	-0.38 − 4.31	1.14	1.30	1.08	0.84	0.96	0.79	Max elevation above mean sea level
Rugosity	-	1.00 − 2.14	1.00 − 1.73	1.00 − 2.14	1.17	1.19	1.17	0.19	0.18	0.20	Ratio surface to planar area
Slope	°	0.45 − 64.04	3.32 − 53.34	0.45 − 64.04	25.41	27.52	24.60	14.59	14.99	14.47	Slope

Table A. 2.15 - Native and exotic species richness on 97 small islands off the coast of Wellington. For each group, range, mean and standard deviation are provided. Values are provided for all islands (all), islands inside (inner) and outside (outer) the harbour.

| | Number | Range | | | Mean | | | SD | | |
		All	Inner	Outer	All	Inner	Outer	All	Inner	Outer
Natives	20	0 - 9	1 - 9	0 - 9	2.9	2.7	3	2.1	2.2	2
Exotics	18	0 - 5	0 - 5	0 - 5	0.9	0.7	1	1.3	1.4	1.3

Table A. 2.16 - Variance inflation factor for the variables included in the two models. Values above 3 indicates high collinearity between two variables.

	VIF
Area	1.571
Isolation	1.514
Height	1.745
Elevation	1.408
Rugosity	**3.460**
Slope	**3.097**
Nearest dwelling	1.340

Table A. 2.17 - Results from multiple linear regression models exploring the relationship between the plant richness of native and exotic species and island characteristics on 97 islands off the coast of Wellington, New Zealand. Entries are t and p values on inner and outer islands for each group of species. Statistical significance: *P < 0.05, **P < 0.01, ***P < 0.001.

		Area	Isolation	Height	Elevation	Slope	Nearest dwelling
Native	Inner	3.37**	-1.78	2.47*	1.75	1.45	3.15**
	Outer	4.50***	-0.26	3.08**	1.63	-2.54*	2.73**
Exotic	Inner	5.33***	-3.33**	1.51	1.85	-0.92	3.63**
	Outer	2.59*	-2.15*	2.15*	2.45*	-2.45*	2.33*

Table A. 2.18 - Distance-decay relationships of native and exotic species on inner and outer islands. Entries are t and p values. Significant differences are reported in bold. Significant relationships are in bold.

		linear		quasipoisson	
		t-value	p-value	t-value	p-value
Native	Inner	-4.009	**0.0000**	-3.909	**0.0001**
	Outer	-3.84	**0.0001**	-3.838	**0.0001**
Exotic	Inner	-0.117	0.9080	-0.117	0.9081
	Outer	-1.825	0.0684	-1.824	0.0686

Table A. 2.19 - Results of linear and quasipoisson models contrasting Jaccard similarity indexes and distance-decay relationships of inner and outer islands for all, native and exotic species. Entries are t and p values. Significant differences are reported in bold.

| | Jaccard similarity indexes | | | | Distance-decay relationships | | | |
| | linear | | quasipoisson | | linear | | quasipoisson | |
	t-value	p-value	t-value	p-value	t-value	p-value	t-value	p-value
Natives	7.482	**0.0000**	7.373	**0.0000**	3.503	**0.0005**	4.244	**0.0000**
Exotics	1.185	0.237	1.183	0.237	-0.033	0.9736	-0.009	0.9928

Table A. 2.20 - Full list of online sources consulted for population sizes, island area and elevation. For island area and elevation, the Island Directory (http://islands.unep.ch/isldir.htm, Dahl 1991) and a topographic map (https://en-nz.topographic-map.com/, Yamazaki et al. 2017) were also consulted.

Archipelago	Population	Area, elevation
Northern New Zealand	Number of dwellings counted manually inspecting aerial imagery on Google Earth, https://www.stats.govt.nz/	https://data.linz.govt.nz/layer/50768-nz-contours-topo-150k/
Seychelles	https://www.nbs.gov.sc/	
Samoa	https://www.sbs.gov.ws/, https://www.usa.gov/statistics, https://www.census.gov/en.html	
Channel Islands	https://www.gov.gg/, https://www.gov.je/Pages/default.aspx	
Hawaii	http://dbedt.hawaii.gov/economic/, https://www.usa.gov/statistics, https://www.census.gov/en.html	
Zhoushan	Yu et al. 2019 (https://doi.org/10.1016/j.baae.2019.05.002), Yu et al. 2020 (https://doi.org/10.1111/jbi.13790)	
Kuril Islands	https://eng.rosstat.gov.ru/	https://www.burkemuseum.org/static/okhotskia/ikip/index.htm
Virgin Islands	https://bvi.gov.vg/statistics, https://www.usa.gov/statistics, https://www.census.gov/en.html	
Ionian Islands	https://www.statistics.gr/en/home/	
Shetland	https://www.shetland.gov.uk/	

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Table A. 2.21 - Island characteristics of 10 archipelagos across the globe. Entries are mean and standard deviation for area, elevation, isolation, latitude and longitude.

Archipelago	Population		Area (km²)		Elevation (m)		Isolation (km)		Latitude		Longitude	
	mean	sd	mean	sd	mean	sd	mean	sd	mean	sd	mean	sd
Northern New Zealand	77.59	440.56	8.92	35.42	115.14	124.00	9.00	11.79	36.22	0.82	174.94	0.78
Seychelles	1369.49	10707.63	5.84	22.10	68.56	143.40	1132.30	260.68	6.39	2.33	52.73	3.63
Samoa	11138.00	32967.94	137.63	422.06	316.47	469.19	2778.18	75.50	13.88	0.67	171.23	0.970
Channel Is.	4086.85	18166.54	5.01	21.06	24.08	54.72	28.87	12.37	49.51	0.18	2.28	0.19
Hawaii	30242.20	145157.30	369.88	1590.41	3645.08	827.14	327.41	183.64	22.10	2.33	160.35	6.62
Zhoushan	16399.59	79399.27	17.79	63.19	151.48	122.02	45.94	25.43	30.44	0.38	122.45	0.25
Kuril Is.	581.46	1811.04	314.63	709.11	770.00	665.21	368.33	182.28	47.03	2.54	151.23	3.61
Virgin Is.	3036.94	10776.35	13.54	38.22	112.60	132.00	355.79	30.82	18.30	0.18	64.94	31.87
Ionian Is.	5055.15	17001.23	104.90	361.32	248.18	330.97	13.30	15.47	38.37	0.94	20.87	0.80
Shetland	661.91	3162.47	42.21	165.10	106.97	105.6633	210.91	30.50	60.33	0.25	1.23	0.28

Table A. 2.22 - Overdispersion parameter and model chosen for statistical analyses for 10 archipelagos across the globe.

Archipelago	Overdispersion parameter	Model
Northern New Zealand	209.49	Quasipoisson
Seychelles	3765.52	Quasipoisson
Samoa	177.23	Quasipoisson
Channel Islands	0.23	Poisson
Hawaii	89062.43	Quasipoisson
Zhoushan	2124.9	Quasipoisson
Kuril Islands	96.92	Quasipoisson
Virgin Islands	2523.36	Quasipoisson
Ionian Islands	4095.68	Quasipoisson
Shetland	191.20	Quasipoisson
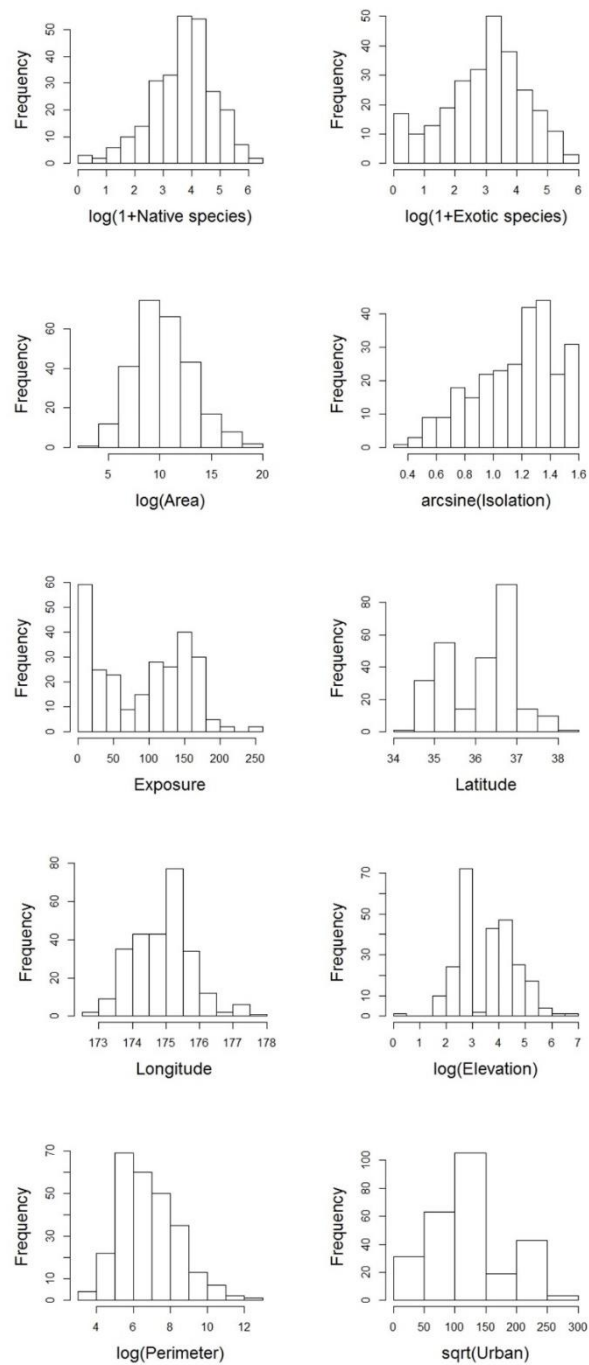
Figure A.2.1 - Frequency plots for plant species richness (native and exotic) and island characteristics of 264 islands off the north coast of New Zealand.
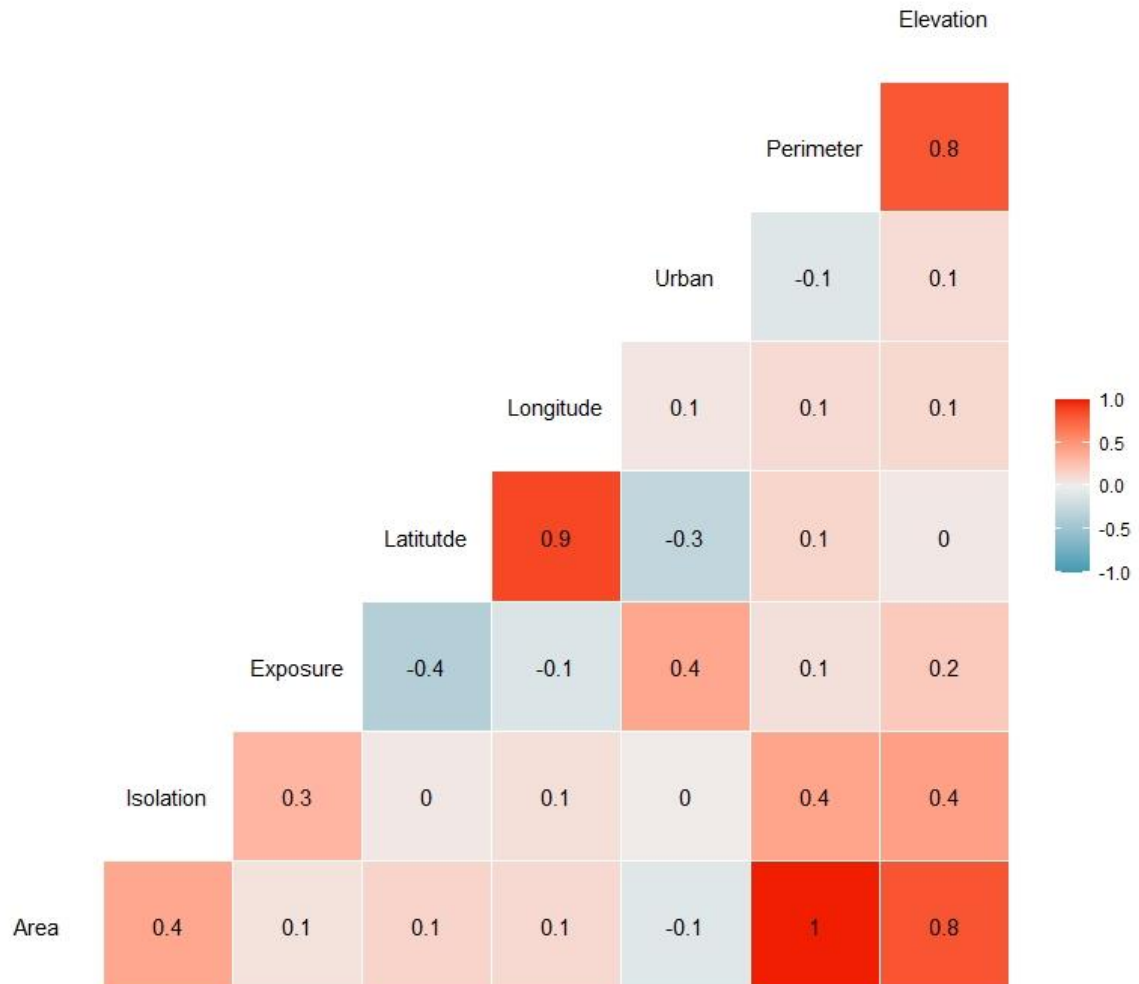
Figure A.2.2 - Correlation matrix displaying the Pearson's correlation coefficient between island characteristics of 264 islands off the north coast of New Zealand. Only one variable was retained if the coefficient was above 0.80. Correlation was tested on transformed variables. Area, perimeter and elevation are log-transformed, isolation arcsine-transformed and urban is squared-transformed. Isolation is the total amount of landmasses surrounding each island within a radius of 1.500 m, minus the value of 1. Urban is distance from the nearest urban area.
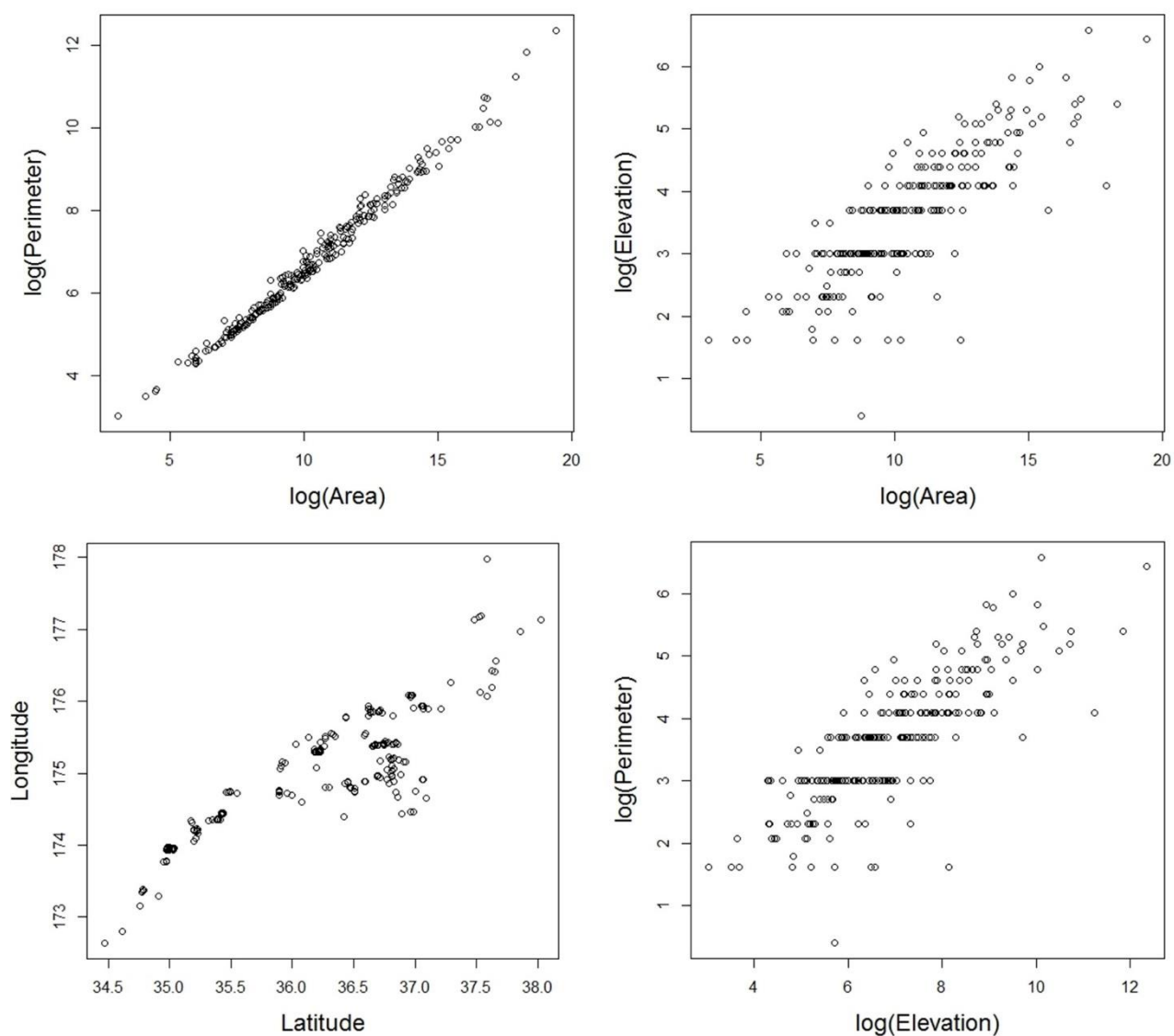
Figure A.2.3 - Correlation plots for island characteristics displaying a Pearson's correlation coefficient above 0.80.
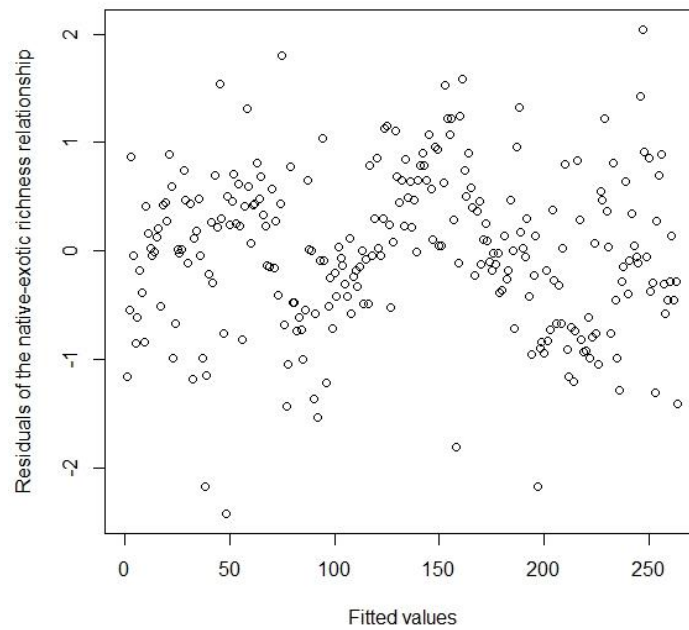
Figure A.2.4 - Residuals plot of the native-exotic richness relationship for 264 islands off the north coast of New Zealand.
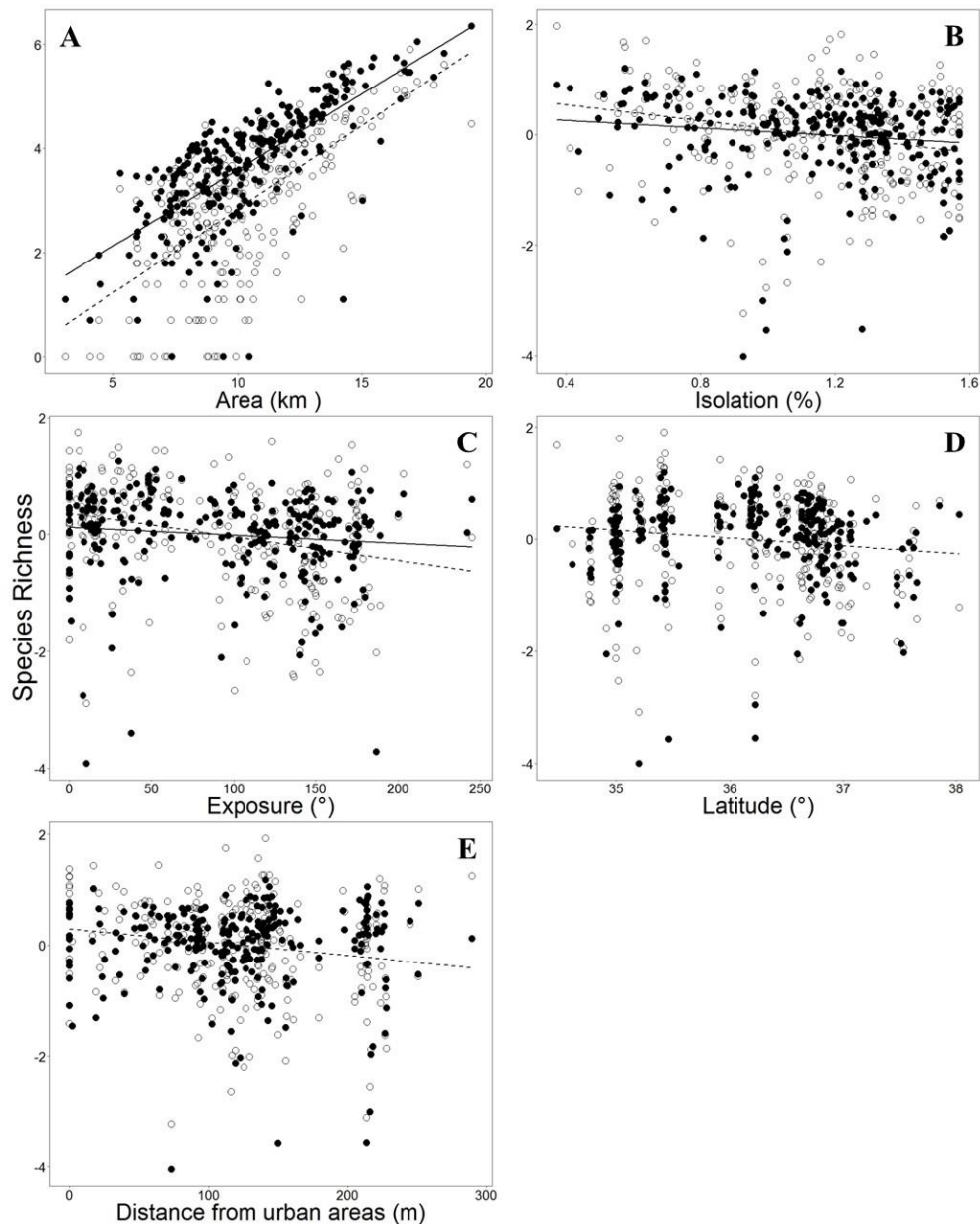
Figure A.2.5 - Relationships between native and exotic plant species richness and island characteristics on 264 New Zealand offshore islands. On the y-axis is species richness and on the x-axis are island (A) area, (B) isolation, (C) exposure to ocean born disturbances, (D) latitude and (E) distance from the nearest urban area. Trendline types indicate native (solid) and exotic (dashed) species. Trendline are represented only for significant relationships. To conform to assumptions, species richness was log (+1) transformed, area log-transformed, isolation arcsine-transformed and distance from the nearest urban area squared-transformed.
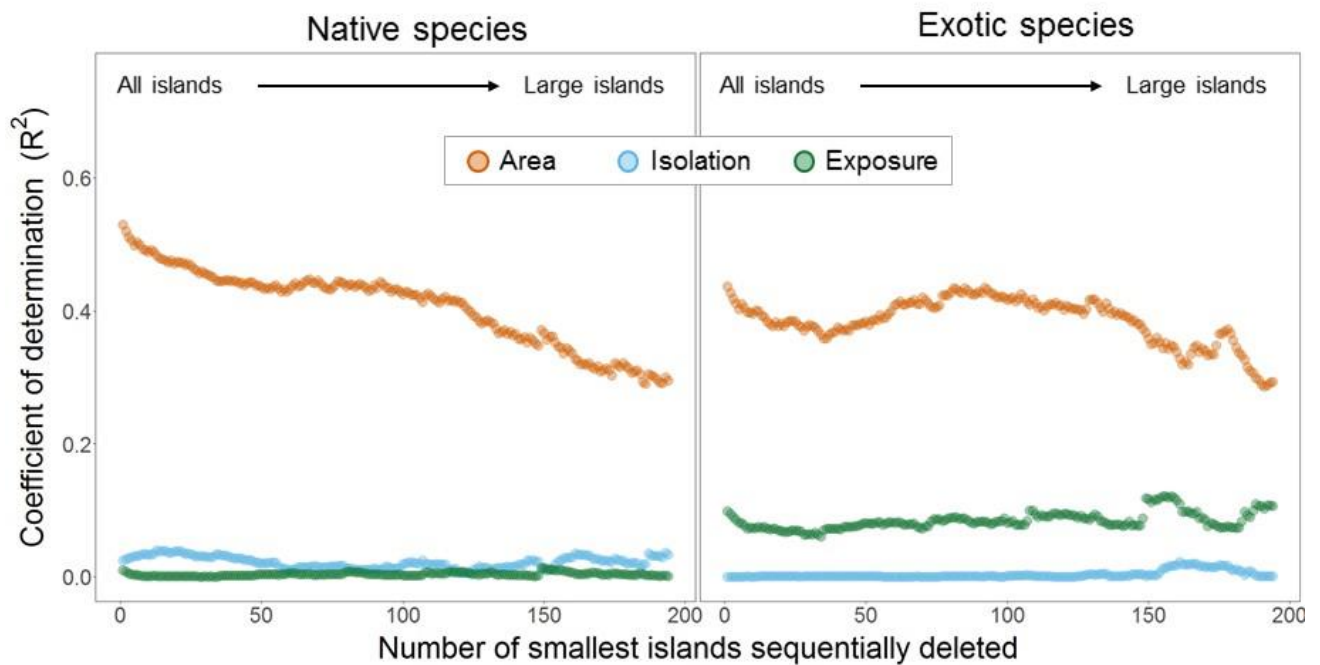
Figure A.2.6 - Scale-dependent variation in relationships between plant species richness, island area (vermilion points), isolation (blue points) and exposure to ocean-borne disturbances (green points) on 264 islands off the north coast of New Zealand. Analyses of native species richness are shown at left and analyses of exotic species are shown at right. The graphs illustrate an analysis similar to the 'sequential deletion' method. In this case though, islands are ranked from smallest to largest. Each point represents a separate linear model with the smallest islands in the study system sequentially deleted. The coefficient of determination (r2) is shown on the y-axis while the x-axis shows the number of islands removed at each regression.
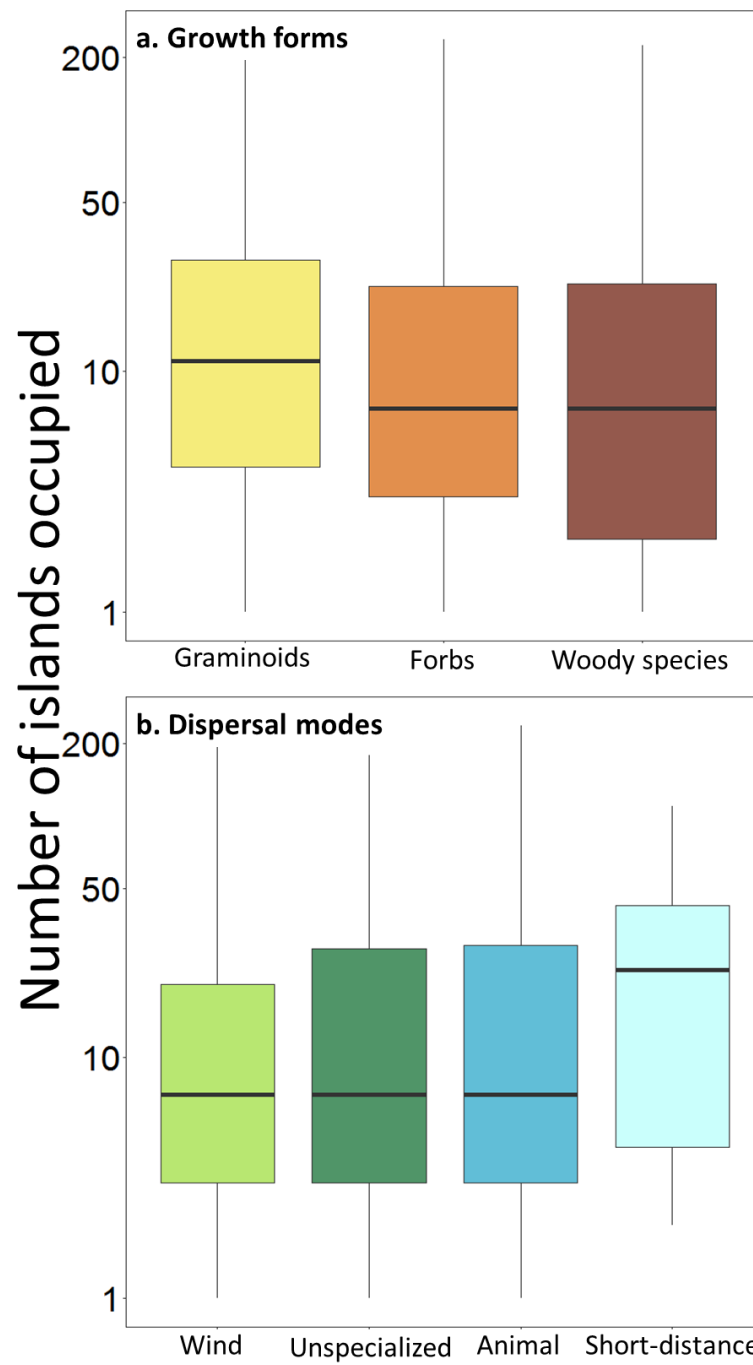
Figure A.2.7 - Number of islands occupied by native species with different (a) growth forms and (b) dispersal modes. On the y-axis is the number of islands occupied by each species, log-transformed, while on the x-axis are trait categories.
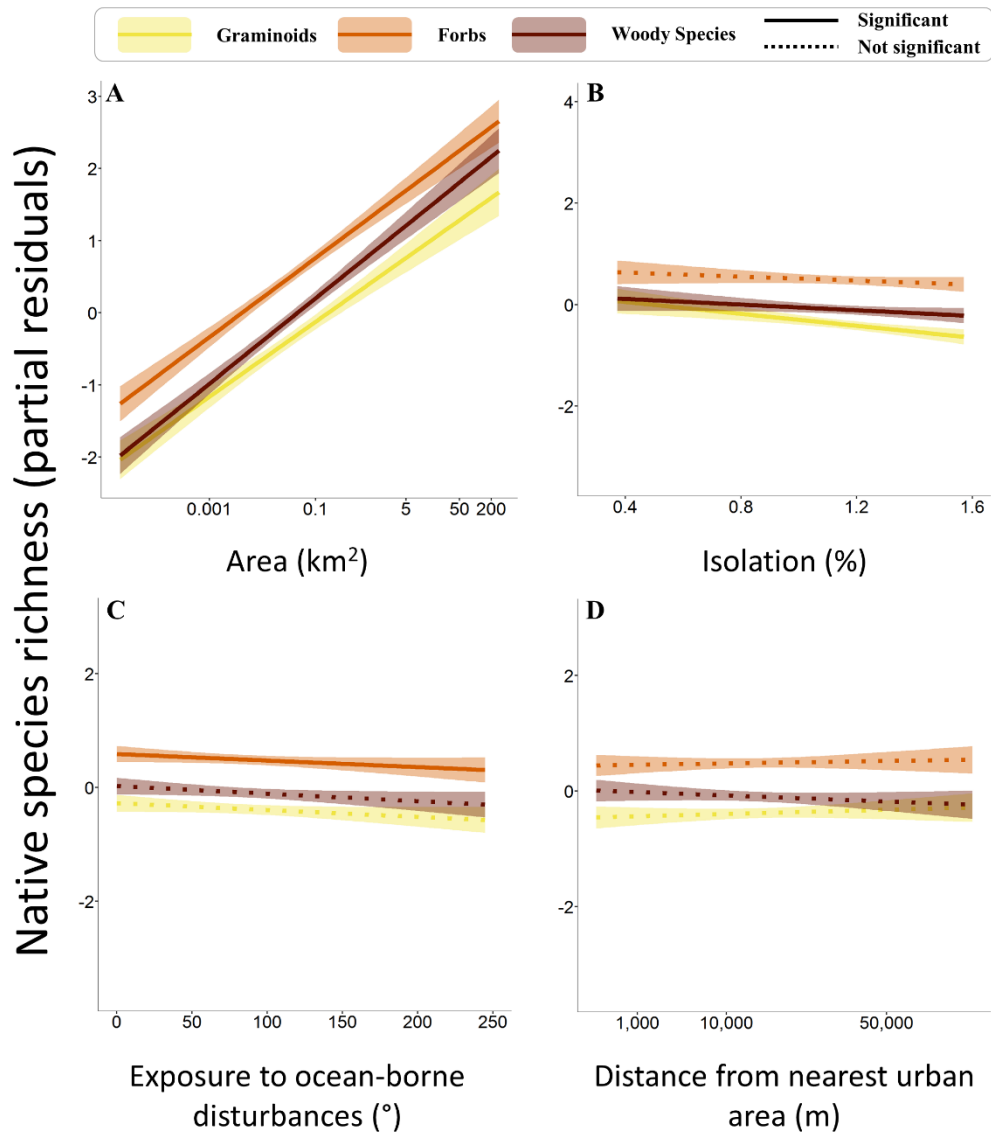
Figure A.2.8 - Linear models illustrating relationships between native species richness with different growth forms and island characteristics on 264 New Zealand offshore islands. On the y-axis is species richness (partial residuals), while on the x-axis are island (A) area (log scale), (B) isolation, (C) exposure to ocean born disturbances, and (D) distance from the nearest urban area. Trendline (model predicted slope) and relative confidence interval (95%) colours represent graminoid (yellow), forb (vermilion) and woody species (brown). Trendline types indicate significant (solid, P<0.05) or non-significant (dotted) relationships. To conform to assumptions, species richness was log (+1) transformed, area log-transformed, isolation arcsine-transformed and distance from the nearest urban area squared-transformed.

Figure A.2.9 - Linear models illustrating relationships between native species richness with different dispersal modes and island characteristics on 264 New Zealand offshore islands. On the y-axis is species richness (partial residuals), while on the x-axis are island (A) area (log scale), (B) isolation, (C) exposure to ocean born disturbances, and (D) distance from the nearest urban area. Trendline (model predicted slope) and relative confidence interval (95%) colours represent animal-dispersed (dark blue), unspecialized (dark green), short-distance (light blue), and wind-dispersed species (light green). Trendline types indicate significant (solid, P<0.05) or non-significant (dotted) relationships. To conform to assumptions, species richness was log (+1) transformed, area log-transformed, isolation arcsine-transformed and distance from the nearest urban area squared-transformed.

Figure A.2.10 - Linear models illustrating relationships between the average seed mass of native species with different growth forms and island characteristics on 264 New Zealand offshore islands. On the y-axis is average seed mass (partial residuals), whereas on the x-axis are island (A) area (log scale), (B) isolation, (C) exposure to ocean born disturbances, (D) distance from the nearest urban area and (E) conservation areas. Colours represent graminoid (yellow), forb (vermilion) and woody species (brown). In plots A to D, trendline (model predicted slope) and relative confidence interval (95%) are represented. In plot E, light hues indicated publicly managed conservation areas, dark hues other islands. Significant relationships (P<0.05) are illustrated by solid trendline (A-D) and asterisks (E). To conform to assumptions, species richness was log (+1) transformed, area log-transformed, isolation arcsine-transformed and distance from the nearest urban area squared-transformed.

Figure A.2.11 - Linear models illustrating relationships between the average seed mass of native species with different dispersal modes and island characteristics on 264 New Zealand offshore islands. On the y-axis is average seed mass (partial residuals), whereas on the x-axis are island (A) area (log scale), (B) isolation, (C) exposure to ocean born disturbances, (D) distance from the nearest urban area and (E) conservation areas. Colours represent animal-dispersed (dark blue), unspecialized (dark green), short-distance (light blue), and wind-dispersed species (light green). In plots A to D, trendline (model predicted slope) and relative confidence interval (95%) are represented. In plot E, light hues indicated publicly managed conservation areas, dark hues other islands. Significant relationships (P<0.05) are illustrated by solid trendlines (A-D) and asterisks (E). To conform to assumptions, species richness was log (+1) transformed, area log-transformed, isolation arcsine-transformed and distance from the nearest urban area squared-transformed.

Figure A.2.12 - Correlation matrix displaying the Pearson's correlation coefficient (upper right) and relative correlation plots (lower left) between island characteristics of 97 islands off the coast of Wellington, New Zealand. Variables were retained only with coefficients lower 0.80. In the centre are frequency plots for each island characteristics. Area, dist (distance), height and RU (rugosity) were log-transformed, slope and dist_dwe (nearest dwelling) square root-transformed while elev (elevation) was not transformed.
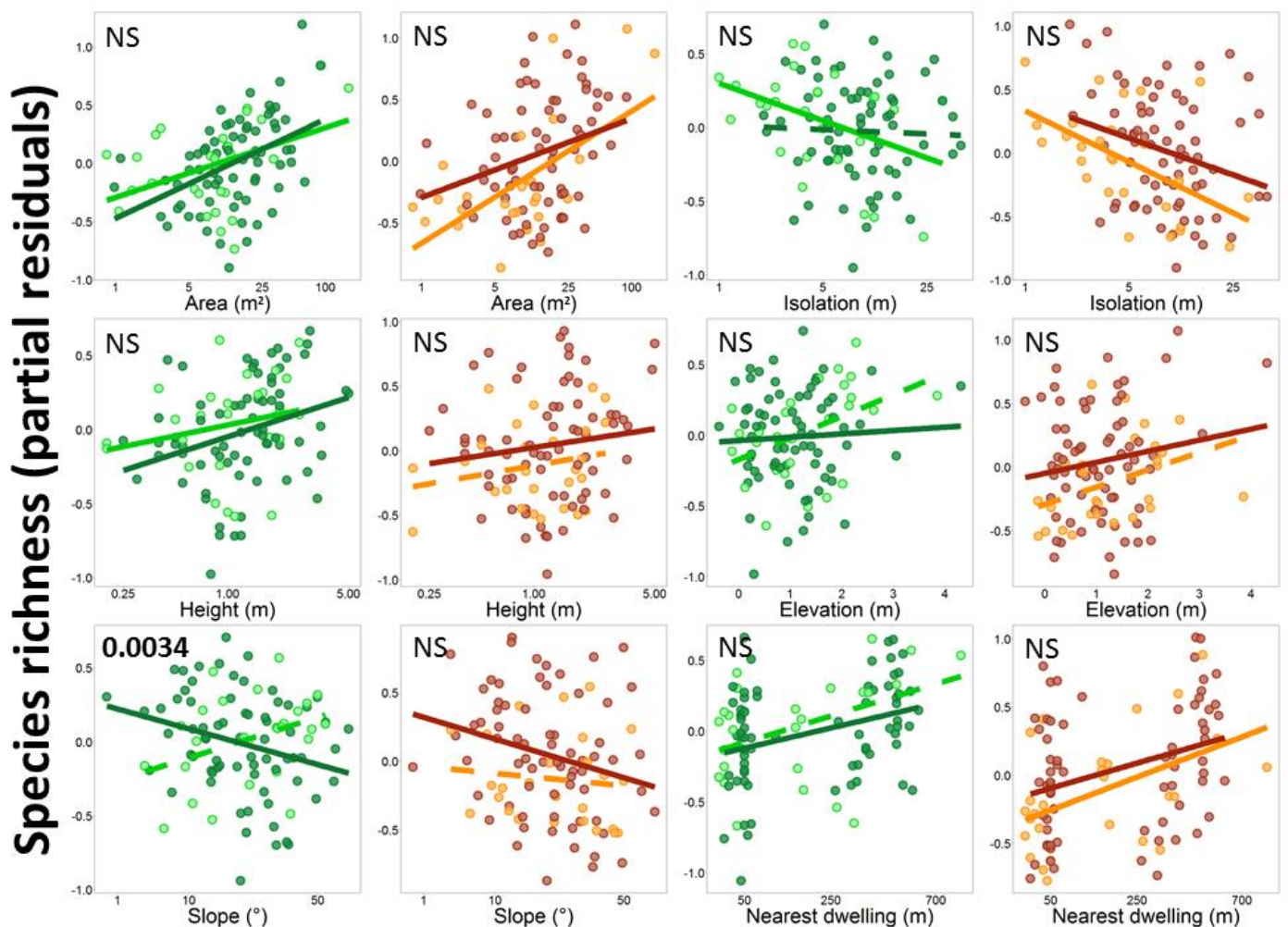
Figure A.2.13 - Relationships between native and exotic species richness (partial residuals) and island area, isolation, height, exposure, elevation, slope and nearest dwelling on 97 islands off the coast of Wellington, New Zealand. Green and red colour illustrate native and exotic species, respectively, while light and dark colours indicate inner and outer islands, respectively. Solid lines indicate significant relationships, while dashed lines display non-significant relationships. In each graph is displayed the coefficient of significance of an ANCOVA test between inner and outer islands (significant t-test are in bold). To conform to assumptions, species richness (+1), area, isolation and height were log-transformed, slope and nearest dwelling were square root-transformed and exposure and elevation were not-transformed.
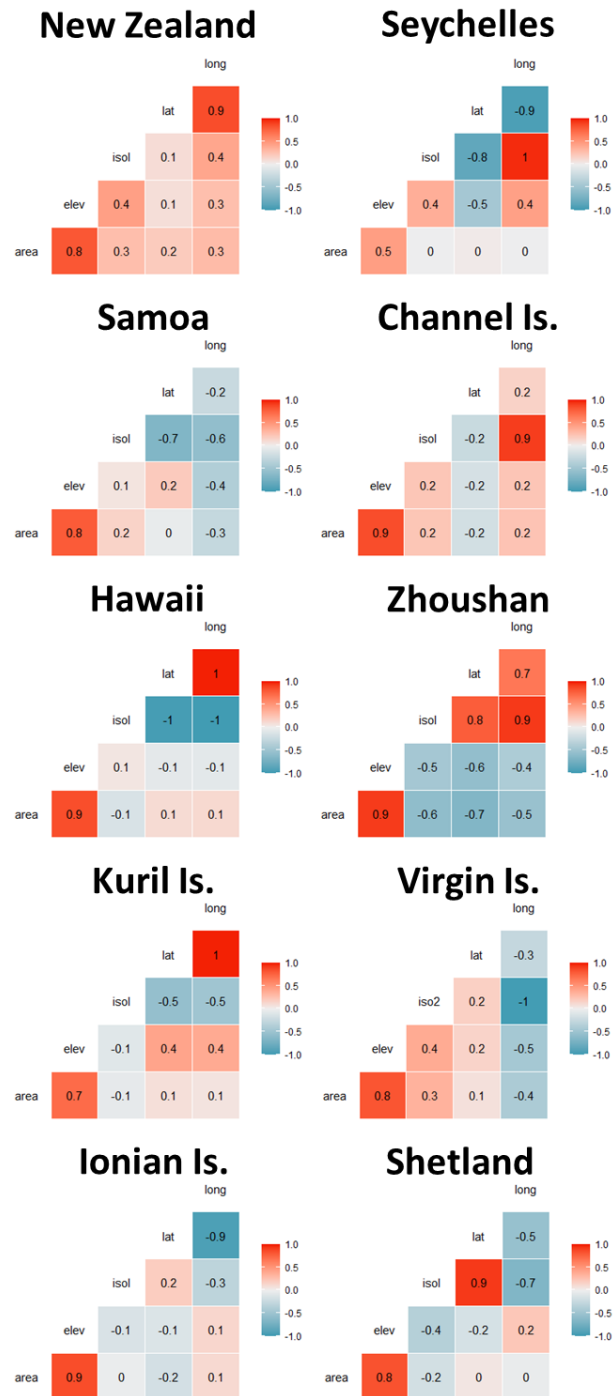
Figure A.2.14 - Correlation matrices for 10 archipelagos across the globe. Variables were removed from model with correlation coefficients above 0.8. Area was always preferred over elevation and isolation over latitude or longitude. Latitude was preferred over longitude. Elevation though was maintained in the model if the effect was opposite from that of island area (i.e. positive effect of area, negative of elevation). Island area and elevation were log-transformed (but elevation was not transformed for the Kuril Islands), isolation, latitude and longitude were not transformed (except for isolation, square root-transformed for Northern New Zealand and Hawaii, log-transform.

Appendix 3

Table A.3.1 - Characteristics of 264 islands offshore northern New Zealand. Island locations (longitude and latitude) are not publicly available due to private ownership and issues of data sovereignty of concern to Māori. The data is publicly available from the Manaaki Whenua data repository at https://doi.org/10.7931/ndkt-zw49.

Island name	Native species	Exotic species	Area (m²)	Isolation (%)	Exposure to ocean-borne disturbances (°)	Elevation (m)	Perimeter (m)	Distance from nearest urban area (m)	Conservation status (Y=1/N=0)
Terakau-tuhaka	26	3	24470.9	97.62	113.4	20	847.88	32238.9	1
Motu Puruhi	39	10	30705.3	97.25	113	40	819.83	32229.4	1
Walker Island	10	11	209120	87.21	26.2	20	2331.5	14248	1
Tuputuputungahau/Whale	62	28	127632	97.6	112.9	40	2274.65	23491.9	0
Moturoa	24	4	109451	99.34	142.2	40	2073.18	26084.2	0
Trig	15	3	2505.82	97.56	115.2		214.67	25927.5	0
Sugarloaf	17	6	23886.9	97.9	124.7	20	669.85	24411.8	0
Green	18	5	48488.7	98.52	130.2	40	1296.76	24762.8	0
Rocky	14	2	23809.6	96.1	163.4	40	862.09	24524.1	0
Stephenson Island (Ririwha or Mahinepua Island)	130	97	1124760	99.39	150.1	120	8403.05	12253	0
Ririwh?iti (Come I)	61	34	69751.9	93.88	152.6	80	1561.23	14283.2	0
Easternmost Woolshed Bay Islet	26	12	1634.53	84.33	15.1		163.93	12782.2	0
West Woolshed Islet	17	7	1479.53	84.25	16.6		147.66	12814.2	0
Milktree Islet	35	16	2157.65	85.19	15.1		201.51	12475.3	0
P? Point Islet	16	8	380.34	84.06	12.7	20	75.22	12726.6	0
Motukawanui	179	109	3820850	97.16	169.9	160	15763	13082.1	1
Algal Rocks	17	4	11148.6	91.39	107.9		621.77	13567.7	0
Hamaruru	63	46	85429.8	91.55	174.2	40	1970.38	16202.8	0
Haraweka	38	28	62212.8	86.63	174.2	60	965.08	16535.2	0
Horonui	17	10	7069.94	97.65	174.2	20	361.47	16156	0
Kahangaro	41	48	55663.6	93.69	115.9	40	1262.83	12419.1	0
Kahangaroiti	35	30	1429.21	92.26	123.4		148.6	12663.8	0
Kaitirehe	5	0	1188.9	77.65	108.2		157.73	13646.2	0
Motuharakeke (Flax Island)	28	6	54160.4	99.33	154.3	40	1242.35	16156.5	0
Motuhuia	18	8	8237.12	93.75	125.7	20	378.59	13864.8	0
Motukahakaha	8	3	5218.63	96.85	103.8		285.9	12140.5	0
Motukaroro	18	8	7696.27	74.48	95.1	20	356.18	14148.2	0
Motukawaiti	87	89	459122	98.46	110.7	100	4315.89	13089.2	0
Motumahanga	45	34	6821.41	64.44	88.8	20	358.34	13717.7	0
Motumuka	68	29	25023.4	86.28	98.2	40	639.88	13709.5	0
Moturahurahu	37	27	10521.6	56.9	73	20	505.62	14574.4	0
Motutakupu	20	2	10135.2	97.21	175.9	20	547.51	17775.6	0
Motutapere	49	26	52042.5	96.93	174.5	80	985.78	16369.7	0

Nukutaunga	63	36	130065	95.84	175.9	100	1769.5	17449.7	0
Panaki	63	49	153132	92.61	174.9	60	2630.96	16612.3	0
Piraunui	30	13	26648.9	97.67	103.1	40	686.42	11896.3	0
Tarawera	5	0	8705.93	87.22	100.5		387.3	13529.8	0
Te Anaputa	18	0	6857.03	91.63	136.3	20	312.44	15818.2	0
Te Anaputaiti	6	0	769.19	96.65	148.8		110.22	16157.7	0
Te Karo	33	12	2459.4	71.34	7.8		189.96	13121.7	0
Te Toi	33	20	1961.86	59.94	123.7		169.85	15154.9	0
Tuturowae	22	7	6838.09	93.35	175.8	40	328.69	17499	0
Whatapuke	41	39	10744.6	88.41	105.1		483.61	13618	0
Whatapukeiti	23	13	19479.6	89.64	106	20	556.49	13205.7	0
Motupapa Island	0	1	35702.7	80.1	10.5	20	1049.14	5418.72	1
Moturoa Island	262	178	1592680	96.51	43.8	80	7739.09	3505.81	0
Motukokako (Piercy Island)	83	18	65187.5	95.31	245	140	1076.71	20380.6	0
Unnamed near Cape Brett	69	2	24466.6	61.73	136.8	40	582.55	16840.4	0
Urupukapuka Island	194	160	2228080	92.31	125.2	100	13432.6	8271.91	1
Moturua Island	144	90	1621920	95.98	112.8	80	8140.22	5036.88	1
Motuarohia (Roberton Island)	96	74	653516	97.45	96.5	60	6783.51	2842.34	0
Waewaetorea	109	109	512048	85.63	134.9	60	4240.7	8369.69	1
Motukiekie	94	59	335742	83.55	120.8	80	3539.83	6763.62	0
Okahu	101	92	277120	94.13	139.7	60	2598.22	8471.78	1
Poroporo Island	60	36	81984.9	91.01	111.7	20	2010.36	7633.6	1
Motungarara Island	28	5	13287.6	87.51	134.3	20	474.23	8232.1	0
Motutara (Henry Island)	61	44	12389.8	91.54	96.7	20	635.98	22068.2	0
Motuti	9	16	3173.9	64.57	0	20	226.6	21327.8	0
Motukehua (Nops Island)	65	57	41748.3	71.69	79.2	40	1419.4	19832	0
Motukowhai	57	29	13689.4	53.5	83	40	481.35	19178.3	0
Moturahurahu	20	14	1777.06	52.71	77.1	10	171.78	19125.3	0
Omahu Islets (Twin Rocks)	33	24	196.68	54.54	52.6	10	76.96	20815.6	0
Okiore Point/ Rugged Point	69	75	21424.9	67.09	39.4	20	1143.88	21677	0
"Rapata" Islet	29	22	1737.94	67.1	60.3	12	169.92	20733.8	0
Whitikau Rock	30	28	616.02	64.99	26.7		101.25	21705.4	0
Rimariki Island	119	81	181021	90.53	171.5	40	4001.28	19341.3	1
Cocker's Rock	52	31	3225.77	93.87	171.7	20	212.33	19997.4	0
Motuwharariki	42	17	5666.55	97.12	175.7	20	336.62	19697.9	0
Otawhanga	52	21	15501.2	94.79	178.2	40	599.84	18318.5	0
Little Otawhanga	22	18	2763.18	95.63	179.5	10	199.31	18535.6	0
Ngataurua I	19	7	1469.59	84.92	134.1	20	157.42	20281.4	0
Ngataurua II	9	5	380.57	85.38	138	20	73.08	20349.7	0
Ngataurua III	12	3	554.17	85.72	139.4	20	100.4	20374.8	0
Ngataurua IV	13	9	1137.82	86.05	134.5	20	208.1	20385.7	0
Tawhiti Rahi	2	7	1559270	95.84	186.6	180	10718.1	22563	1
Aorangi	228	57	1038380	96.06	183.2	200	5991.63	21279.2	1
Aorangaia	60	6	55176.1	87.36	183.3	100	1355.42	22082	1
Archway	58	9	60317.1	87.91	182.1	80	1674.52	21388.4	1

188

North Pinnacle (High Peak rocks)	14	14	17966	99.87	172.7	80	632.32	17316.1	1
Taranga (Hen Island)	262	81	4885880	99.98	131.9	400	13373.6	15374.6	1
Lady Alice	214	66	1505640	95.92	140.3	140	7502.52	23151.1	1
Whatupuke	163	38	989410	89.46	143.2	220	6152.53	24138.1	1
Coppermine	178	47	768196	93.46	144.5	180	6364.88	25326.4	1
Mauitaha	109	25	247484	99.06	137.4	120	2600.19	21761.7	1
Sail Rock	39	6	35781	100	124.2	120	715.87	12165.4	0
Fanal Island (Motukino)	138	39	768015	99.94	160.2	120	5720.21	48704.8	1
Burgess Island (Pokohinu)	103	97	563682	96.76	163.7	100	5267.09	49720.1	1
Hokoromea Island	70	34	119656	91.39	161.3	60	2085.15	48989.2	1
Atihau Island	69	33	171936	94.74	160.6	60	2514.15	48600.8	1
Lizard Isle	24	2	12629.7	88.19	167.8	10	500	50131.2	1
Maori Rocks (largest islet)	3	0	9661.71	99.96	165.9	10	500.99	51482.6	1
Tatapihi (Groper Island)	19	1	29708.9	100	158.3	20	691.78	45754.6	1
Goat Island	123	55	133813	69.46	102.7	60	1527.64	2339.75	1
Mathesons Bay Islet	12	16	14838.1	50.7	26.5	20	454.78	380.5	0
Little Barrier Island (Hauturu)	422	196	30793100	99.94	114.7	720	24708.8	22859.1	1
Great Barrier Island (Aotea)	572	86	2.77E+08	96.88	189.1	620	234036	42171.4	1
Aiguilles Island	121	35	705290	96.49	200.1	120	4887.28	60050.8	0
Rakitu Island (Arid Island)	240	93	3123310	99.84	203.2	200	12331.5	63253.9	1
Rosalie Bay islet	50	11	8872.81	61.1	100.7	40	349.99	45570.6	0
Te Pani	55	21	90184.9	69.07	118.8	100	1112.73	43916.4	0
Motu Tohora	74	23	118590	70.53	42	80	1353.8	42190.3	0
Kaikoura Island	309	162	5288100	81.8	20.6	180	16488.8	46298.7	0
Moturako	35	15	8578.47	88.39	60.2	40	372.38	45407.7	0
Saddle Island (Grey Group Islands)	54	22	27290.9	98.21	61.2	20	974.45	44970.9	0
Northern Inner Grey Group Islet (west)	61	21	9702.3	81.96	49.6	40	360.88	45850.3	0
Northern Inner Grey Group Islet (east)	56	17	3537.37	80.72	48.5	20	241.82	45932.3	0
Westernmost Inner Grey	51	27	15263.8	81.61	48.4	40	469.52	45829.5	0
Easternmost Inner Grey	40	10	2917.58	73.4	33.3	20	206.95	46111.2	0
Islet northeast of Opakau (north)	57	21	4291.25	78.48	48.2	20	257.33	45466.2	0
Islet northeast of Opakau (south)	59	23	5669.22	77.81	48.3	20	285.63	45442.3	0
Opakau	93	32	30704.1	90.35	53	20	732.19	44877.5	0
Islet between Opakau and Motutaiko	31	12	6385.76	91.15	57.3	20	294.33	44363.9	0
Islet southeast of Akatarere Point	53	25	3655.08	49.2	7.6	15	242.09	45856.9	0
Mahuki	105	31	458366	88.51	58.4	80	3972.33	44204.8	0
Motutaiko	88	39	205963	93.86	67.6	100	2683.25	43480	0
Papakuri	50	14	4353.33	91.22	68.37	15	264.68	43640.3	0
Rangiahua	50	53	622989	81.01	58.2	60	6289.27	44144.8	0
North Junction	89	41	7786.56	67.78	8.7	20	324.56	46070.1	0
Middle Junction	35	22	22935.5	72.61	9.1	40	620.05	46025.1	0
West Junction	0	0	12249.7	84	37.9	20	465.01	45650.7	0
South Junction	189	96	77466.9	82.13	30.2	60	1361.62	45973.3	0

Whangara (Cliff)	89	41	66855.4	75.25	4.2	60	1279.45	50366.9	0
Small stack on south side of Whangara	35	22	820.83	80.49	5.1	10	111.1	50473.4	0
Rangitoto	234	364	23256900	87.14	33	240	25744	3003.25	1
Pudding Island	14	21	1443.9	80.83	16.5	10	138.31	658.07	0
Kawau	233	149	20565500	99.9	48.7	180	45311.7	3662.05	0
Challenger Island	69	19	28813.3	77.39	10.9	20	802.73	8487.52	0
Little Markham Island	11	5	4714.46	77.1	32.7	20	264.25	8873.03	0
Motukaraka (Flat Island)	65	95	57322.2	90.7	13.9	20	944.31	0	0
Motuketekete	89	86	276743	97.8	33	40	2596.59	3794.44	0
Moturekareka	100	76	180077	96.69	29.6	40	2354.97	2991.5	1
Motutara	64	59	47333	97.15	27.4	20	1022.36	2697.55	1
Kohatutara (Rocky Islets)	21	12	9266.39	96.21	28.5	10	579.08	3183.24	1
Motuora Island	124	143	857467	100	31.4	60	5209.55	3314.93	1
Te Haupa (Saddle)	86	68	59148.6	97.08	21.2	20	1510.88	0	1
Tiritiri Matangi Island	277	266	1922310	99.96	51.1	80	7721.63	0	1
Wooded Island	28	16	5967.55	85.57	51.4	20	288.46	288.18	0
Waiheke	337	272	92242704	99.79	45.9	220	139381	0	0
Horuhoru Rock (Gannet Rock)	10	4	12136.1	100	42.4	20	552.03	1593.57	0
Koi Island	51	47	3431.79	76.05	0	15	285.84	468.48	0
Papakohatu (Crusoe Island)	66	70	24002	97.03	29.8	15	995.79	0	0
Motukaha	70	84	5924.78	55.71	0	15	292.27	0	0
Passage Rock "Three Sisters"	51	54	4586.02	96.86	0			0	0
Nani Island	46	42	2969.27	66.51	46.2	15	224.25	0	0
Te Whau (unnames islet)	33	46	21333.7	72.71	0	20	874.91	0	0
Kahakaha (Frenchmans Cap)	38	32	2571.98	92.58	0	20	188.44	1570.69	0
Tarahiki (Shag Island)	91	49	60852.6	99.99	37	60	1229.38	2969.8	0
Pakatoa	98	126	273888	96.89	0	60	2950.97	1401.93	0
Rotoroa Island	180	228	892411	93.36	0	60	6815.48	2217.69	0
Ruthe/Motukahakaha islet	76	38	13545	81.6	11.5	20	630.3	3643.8	0
Ponui Island	280	147	17966900	98.8	0	160	35794.1	1117.1	0
Pakihi Island (Sandspit Island)	159	147	1148760	98.21	0	120	6363.32	5910.35	0
Karamuramu	37	82	71890.6	92.78	0	20	1027.62	7640.66	0
Motutapu	140	234	15586000	90.59	38	120	22800.8	4255.43	1
Motuihe Island	165	239	1805210	99.87	38	60	9074.09	1137.7	1
Motukorea (Browns Island)	55	90	603734	99.74	34	60	3481.84	1321.47	1
Otata Island	105	68	168036	98.93	48.7	60	2191.39	7991.36	0
Scott Island	25	1	5370.55	96.4	48.8	5	305.71	8615.31	0
Motuhoropapa	100	43	86080.1	97.95	49.9	40	1820.71	8921.39	0
Pollen Island (Motumanawa)	35	58	258454	73.45	0	5	3458.79	0	1
Watchman Island	8	19	2351.09	78.63	0	5	184.61	614.57	0
Wekarua	44	44	60268.3	80.05	18.6	40	1324.15	9449.73	0
Tataweka (esler#2)	48	38	17418.5	73.72	17.6	40	566.81	9064.46	0
Rangipukea	49	58	335250	94.69	19.4	60	3980.79	9132.68	0
Waimate	103	90	695006	96.39	15.8	120	4553.12	5059.94	0

Cow Island	33	23	9874.59	100	20.1		598.66	8749.65	0
Motutapere	166	65	456531	81.64	14.8	160	3105.26	5051.33	1
Motukopake	75	52	132102	91.84	12.1	60	1893.05	4706.94	0
Calf Island	10	7	391.94	99.34	20.3		77.91	9211.21	0
Motukakarikitahi	87	37	39125.8	89.43	7	60	855.13	2287	0
Motuokino	24	12	6252.85	95.26	17.9	40	392.72	7369.16	0
Motumorirau	38	23	4389.07	93.18	12	20	306.09	5165.6	0
Motukaramea	43	22	9176.82	90.76	15	20	407.42	6181.59	0
Motuoruhi (Goat Island)	166	74	558311	99.33	15	160	4553.97	5613.8	0
Unnamed Ngamotukaraka grp (Esler #14)	59	23	22899.3	96.47	15.3	40	655.66	8689.5	0
Unnamed Ngamotukaraka grp (Esler #15)	42	19	7193.42	96.06	15.6	20	354.28	9221.8	0
Unnamed Ngamotukaraka grp (Esler #16)	23	9	5510.54	96.01	15	20	318.58	8882.35	0
Moturua (Rabbit Island)	73	34	269168	98.87	13.7	80	3459.29	8254.44	0
Unnamed (Esler #18)	30	9	1122.41	94.35	14	33	141.03	9520.1	0
Motukaramarama (Bush Island)	85	28	104642	97.28	11.8	60	1904.6	9864.73	0
Motuwinukenuke (Square Island)	43	23	20821.1	96.6	7.6	40	635.64	8748.36	0
Motuwi (Double Island)	71	26	185286	98.83	8.7	60	3381.52	9267.34	0
Unnamed (Esler #22)	17	6	1957.26	96.05	10.6	33	222.77	10400.5	0
Motuwhakakewa	32	24	13177.2	97.23	13.3	40	507.22	12560.3	0
Motukahaua (Happy Jack Island)	47	22	178295	99.52	15.6	60	3274.27	12839.6	0
Motumakareta	42	9	33677.4	97.59	16.5	40	780.72	13708.9	0
Unnamed Matariki (Esler #26)	18	22	2481.42	78.04	20.9	20	212.07	11999.4	0
Unnamed Matariki (Esler #27)	15	27	3235.93	67.3	13.3	20	225.1	11991.4	0
Unnamed Matariki (Esler #28)	10	5	392.62	73.27	20.7	20	78.29	12194.1	0
Cuvier Island	189	96	1693310	99.85	157.3	200	9795.67	38703.8	1
Scotts Monument	26	11	4581.19	81.59	158.1	40	277.05	39197.1	1
Great Mercury Island	241	162	18407800	99.78	143.7	220	46144.6	17438.4	0
Stanley Island/Kawhitu	141	45	948518	99.84	150	120	5174.39	21693.4	1
Red Mercury Island	116	21	2133300	99.4	155	140	7864.88	25549.9	1
Middle Island/Atiu	69	26	109948	99.54	147.9	80	1987.33	20671.9	1
Arch Rock	1	0	392.22	98.03	147.4	8	84.45	20536.2	1
Hole Rock	18	0	432.87	98.03	147.7	8	79.19	20787.9	1
Haunted House	20	3	893.22	98.05	147.6	16	118.47	20808.1	1
Double Island	14	2	288864	94.74	152.7	100	3514.24	24335.7	1
Green Island	42	7	22964.4	97.52	146	40	705.59	19648.3	1
Korapuki	118	48	171697	99.68	145.2	80	2798.5	18010.8	1
Old Man Rock	9	1	8280.77	100	141.3	60	367.36	14146.5	0
Ohinauiti	51	11	52780.9	95.54	143.9	40	1389.66	16213.5	0
Flat Island	21	14	27125.3	99.28	143	5	716.9	15522.8	0
Black Rocks	35	12	4140.25	99.38	143.6	20	305.07	16189.4	0
Needle Rock	36	8	15303.2	99.22	139.5	60	570.33	12392.8	0
Motueka Island	78	27	55871.1	95.23	88.6	60	1175.19	6826.04	0
Poikeke Island	48	11	6803.88	88.5	86	20	360.99	6602.43	0

Kawetoto Reef	22	10	2261.54	58.11	92.7	10	178.52	15651	0
Rocky islet (Waikawau Bay)	4	4	17300.6	72.31	92.4	5	663.42	15096.8	0
Plate Island (Motunau)	15	2	42130.5	99.95	120.3	40	1743.86	11781	0
Shoe Island (Motuhoa)	97	14	457156	99.91	120.3	120	3369.63	2642.35	0
Slipper Island (Whakahau)	82	19	2345850	99.06	122.3	140	11640.4	5827.04	0
Penguin Island	61	8	94738.1	90.28	119.4	60	1370.35	6249.31	0
Rabbit Island	47	10	96107.9	98.63	118.2	40	1596.63	6024.32	0
Motuhaua Rock (Opoutere Beach)	31	34	1683.35	59.68	100.8	10	193.22	4120.2	0
Hikunui (Opoutere Beach)	12	7	1985.66	69.66	98.8	10	180.97	7996.15	0
Ruamahuanui	83	17	303555	97.3	154.6	160	3092.03	20078.7	1
Ruamahuaiti	67	12	237880	98.52	150.2	180	2616.19	18500.7	1
Hongiora	36	6	155492	99.91	149.9	60	2430.22	16940.1	1
Middle Chain	53	13	217600	94.93	152.6	100	4382.28	18630.2	1
Half Island	22	3	12898.5	93.79	150.3	40	506.28	18374.9	1
Nga Horo ('Hernia' Island)	18	3	35858.3	93.91	150.6	60	1136.83	18454.9	1
Mayor Island (Tuhua)	309	167	13203600	99.96	134.7	340	22745.9	27116.8	0
Hauturu Island (Clarks Island)	87	19	97212.5	81.48	91.3	80	1324.67	493.78	0
Karewa Island	29	4	44790	99.99	111.1	60	1222.91	11027.9	1
Matakana Island	213	184	60140900	95.23	104.8	60	75794.7	578.33	0
Motuotau Island	36	27	31232.6	82.46	109.3	40	685.67	0	1
Motiti	61	100	7013670	99.9	119	40	16524.3	9371.75	0
Taumaihi Island	34	23	19557.2	95.64	117.1	20	626.63	8648.29	0
Motohora/Whale Island	201	103	1738100	100	113.6	340	7638.35	7293.28	1
Pataua Island	159	36	117124	40.17	0	40	1516.63	4219.32	1
White Island (Whakaari)	19	20	3393300	99.9	141.7	320	8817.23	47568.6	0
West Volkner	6	1	4082.26	99.66	143.3	40	260.53	51625.8	0
Volkner Central Stack	5	0	1560.89	99.62	143.5	20	160.67	51869.9	0
East Volkner	7	0	20312.5	99.89	143.6	100	564.53	52018.9	0
Club Rock (off White Island)	2	0	6428.65	86.75	140.3	20	556.51	46985.4	0
Stack near Cape Runaway	14	5	582.57	52.86	62	10	119.92	27686.2	0
Motuopao Island	69	63	301037	92.69	242	100	2566.23	83913	1
Matapia Island	15	4	21281.1	100	153	40	746.99	63130.9	0
Moturemu Island	110	49	51634.1	100	6	40	945.44	17058.4	0
Kauwahaia Island	51	34	6285.92	54.51	91.4	20	308.63	4983.92	0
Taitomo (Camel) Island	62	31	26973	59.86	126	60	810.07	8272.29	0
Nun Rock	15	6	1230.26	64.83	148	20	139.77	8501.11	0
Paratahi Island	4	1	3101.78	58.76	150	10	264.45	10551.8	0
Kauritutahi Island	9	18	1038.36	64.94	0	5	122.26	11975.5	0
Ihumatao Islet	7	27	6256.84	65.93	1.2	1.5	304.56	4.35	0
Orona Island	23	27	1014.93	47.81	0	6	127.32	0	0
Kopuahingahinga Island	52	23	107548	42.53	0	10	1509.52	0	0
Leatherjacket Islet	0	0	1571.43	83.47	8.5	20	149.82	46719.9	0
Islet between Castle Peak and Rangiahua	74	24	7245.03	59.46	41	20	323.11	45411.9	0
Islet off slipper	22	7	1956.41	80.2	121.7	20	169.81	7128.69	0
Green Stack	15	1	1510.84	95.8	146	10	171.68	19618.6	0

Sentinel rock	31	19	383.97	70.93	99.9	20	100.79	309.07	0
Oruawharo (Memory I)	42	40	2049.4	36.43	88	15	196.08	51405.8	0
Stone Jetty	31	36	1803.12	54.14	58	8	161.27	51211.4	0
Tern Islet	5	1	4564.33	96.02	173.3	8	272.66	19261	0
Mid Stack	3	0	89.71	95.12	172.8	5	39.9	19246.3	0
Tall Stack	6	1	285.71	95.32	172.8	10	74.37	19247.4	0
East Pillar	2	0	21.12	94.8	172.5	5	20.83	19293.2	0
West Pillar	1	0	58.33	94.66	178.5	5	33.35	19285.3	0
East Stack	6	1	84.45	95.72	179.7	8	37.89	18596.2	0
Second Stack	2	0	335.99	95.89	179.9	8	88.76	18595.1	0
Holey Stack	8	0	1297.14	96.66	170.6	8	170.61	18342.9	0

Table A. 3.2 - Characteristics of 97 islands offshore Wellington harbour, New Zealand.

Islands	Location	All species	Native species	Exotic species	South	East	Area (m²)	Height (m)	Distance (m)	Exposure to ocean-borne disturbances (°)	Rugosity	Slope (°)	Nearest dwelling (m)
IS001	out	9	5	4	41.33077	174.83074	37.2	5	8	115.05	1.0608	22.2681	105
IS002	out	5	3	2	41.33300	174.82640	47.36	1.3	6.4	96.138	1.07643	10.3995	50
IS003	out	1	1	0	41.33307	174.82649	63.8	0.9	18.4	96.518	1.15833	32.9631	60
IS004	out	1	1	0	41.33308	174.82640	7.8725	1	9.78	96.231	1.13344	26.5789	55
IS005	out	3	2	1	41.33410	174.82608	17.514	2	4.5	112.539	1.02363	3.88317	50
IS006	out	1	1	0	41.33511	174.82580	31.28	1.1	8.85	115.7	1.18439	24.075	55
IS007	out	2	2	0	41.33538	174.82506	12.42	0.7	13.5	107.337	1.30868	45.453	45
IS008	out	3	3	0	41.34061	174.82397	9.18	2	9	147.905	1.19979	34.4519	45
IS009	out	2	2	0	41.34444	174.82048	14.76	1.48	7.2	140.714	1.68635	49.2768	325
IS010	out	2	2	0	41.34437	174.82047	36.05	1.2	9.41	139.717	1.08671	22.4822	320
IS011	out	5	3	2	41.33410	174.82610	8.806	1.43	2.57	112.304	1.03535	19.6216	50
IS012	out	2	2	0	41.33479	174.82593	6.3	1.2	8	114.343	1.20499	30.5231	45
IS013	out	1	1	0	41.33479	174.82596	3.9375	1.2	10.2	115.255	1.37177	40.1095	50
IS014	out	5	2	3	41.34124	174.82326	11.475	0.55	1	133.086	1.04498	13.563	40
IS015	out	3	2	1	41.34276	174.81815	5	1.7	5.35	102.366	1.01907	14.782	375
IS016	out	3	2	1	41.34277	174.81811	13.225	0.75	2.4	101.881	1.09371	29.6565	375
IS017	out	2	2	0	41.34310	174.81811	21.6	1.17	12.9	120.822	1.17635	14.7043	390
IS018	out	5	4	1	41.34306	174.81804	17.655	1.1	7.5	117.447	1.00637	5.34457	385
IS019	out	7	5	2	41.34315	174.81801	7.875	1.4	5	124.432	1.0948	10.7339	400
IS020	out	6	5	1	41.34316	174.81797	16.2	1.5	9.6	125.159	1.02446	0.447133	405
IS021	out	9	5	4	41.34357	174.81736	33.75	2	13.9	146.862	1.00345	3.30675	470
IS022	out	4	2	2	41.34368	174.81735	9.6	1.5	22.9	148.137	1.36473	37.9744	475
IS023	out	8	6	2	41.34366	174.81657	7.25	2.8	1.8	149.956	1.2018	38.1267	535
IS024	out	10	6	4	41.34348	174.81606	47.47	3.5	5.1	145.434	1.79215	57.1474	565
IS025	out	4	2	2	41.34316	174.81580	17.92	3.3	5.9	120.084	1.29004	33.8185	580
IS026	out	13	8	5	41.34305	174.81578	16.34	4.85	9.4	116.513	1.53239	53.3884	570
IS027	in	13	9	4	41.29523	174.83637	17.98	2.6	2.15	185.804	1.25282	15.23	400
IS028	in	3	3	0	41.29589	174.83642	11.9	1.6	9.85	183.863	1.37446	47.4378	365
IS029	in	3	3	0	41.29585	174.83667	8.06	1.9	30.9	190.066	1.04831	17.6342	385
IS030	in	1	1	0	41.29596	174.83608	13.6	1.8	22.8	189.567	1.00435	5.81851	330
IS031	in	1	1	0	41.29675	174.83567	10.08	1.1	10.1	140.369	1.15739	15.0516	270
IS032	in	14	9	5	41.29680	174.83556	165.675	2.6	3.6	137.635	1.14928	33.9445	250
IS033	in	3	2	1	41.29673	174.83420	9	2	5.3	78.66	1.00095	3.3174	155
IS034	in	1	1	0	41.29863	174.83260	13.09	1	8.5	106.048	1.01314	10.7493	40
IS035	in	2	2	0	41.29874	174.83255	12.42	1	1.4	106.536	1.18364	24.5833	35
IS036	in	3	3	0	41.29947	174.83260	5.67	2	4	115.901	1.22906	34.2174	45
IS037	in	4	4	0	41.30073	174.83212	24.72	1.5	10.2	121.695	1.44149	45.4849	50
IS038	in	2	2	0	41.30407	174.83129	10.58	0.7	0.3	120.418	1.29074	46.1318	30
IS039	in	1	1	0	41.30409	174.83129	11.1	0.9	2.9	120.07	1.11902	25.1119	25
IS040	in	1	1	0	41.30479	174.83143	6.24	0.6	1.6	119.337	1.00987	9.32547	20

194

IS041	in	2	2	0	41.30492	174.83139	2.24	1.3	1.4	117.476	1.26531	41.9562	20
IS042	in	2	2	0	41.30601	174.83163	10.14	1.9	7.9	109.909	1.01934	11.4872	25
IS043	in	9	6	3	41.30763	174.83299	90.75	1	5	144.236	1.08519	27.5128	40
IS044	in	3	3	0	41.30808	174.83270	2.42	0.9	2.8	132.648	1.30114	34.8165	40
IS045	in	4	3	1	41.30919	174.83104	32	1.75	0.2	99.209	1.23533	33.926	25
IS046	in	6	4	2	41.30928	174.83095	8.84	2.2	0	96.04	1.73383	53.3423	25
IS047	out	2	1	1	41.34760	174.76879	4.2	0.85	3.2	131.201	1.08028	26.3935	30
IS048	out	1	0	1	41.34808	174.76761	12.15	0.8	7	133.163	1.04634	22.3542	45
IS049	out	7	5	2	41.34861	174.76620	33.63	1.8	10.6	133.625	1.20367	32.4915	70
IS050	out	1	1	0	41.34442	174.77493	5.06	0.5	9.9	115.507	1.01418	10.7933	50
IS051	out	9	4	5	41.34501	174.77630	24.32	1.6	1.6	123.515	1.10482	13.4106	60
IS052	out	3	2	1	41.34512	174.77650	21.6	0.7	1.1	125.005	1.13956	21.4086	60
IS053	out	1	1	0	41.34522	174.77709	6.12	0.4	4.4	126.375	1.14247	29.8818	50
IS054	out	1	1	0	41.34525	174.77714	1.12	0.45	5.6	126.899	1.0675	20.4973	50
IS055	out	2	2	0	41.34534	174.77755	13.34	0.5	3.1	128.377	1.05346	12.911	45
IS056	out	3	2	1	41.34533	174.77756	10.14	0.25	3	127.601	1.05415	7.95648	45
IS057	out	2	2	0	41.34538	174.77755	21.25	0.9	4.5	127.222	1.10236	30.4216	50
IS058	out	5	4	1	41.34545	174.77753	41.6	1.4	12.5	129.451	1.08589	23.8534	50
IS059	out	8	7	1	41.34554	174.77802	59.78	0.55	4.1	128.754	1.03666	18.4181	50
IS060	out	11	9	2	41.34573	174.77843	89.79	3	10	129.416	1.09807	24.5693	60
IS061	out	6	5	1	41.34582	174.77853	30.4	2.2	13	128.445	1.05525	23.347	70
IS062	out	6	4	2	41.34540	174.77913	17.98	1.5	3.65	127.841	1.0375	9.27748	35
IS063	out	3	3	0	41.34549	174.77913	21.6	1.3	6.8	128.669	1.09585	24.614	45
IS064	out	5	4	1	41.34544	174.77951	32.76	1.8	8	128.967	1.10407	10.4066	50
IS065	out	2	2	0	41.34540	174.77963	21.35	1.68	5.6	129.319	1.0293	16.3452	50
IS066	out	1	1	0	41.34536	174.77973	10	2.2	10	128.145	1.1767	24.6215	50
IS067	out	9	7	2	41.34391	174.78195	28.8	2.9	3.5	107.435	1.06138	7.44661	35
IS068	out	1	1	0	41.34264	174.78375	22.4	1.2	2.2	58.035	1.18487	38.2291	25
IS069	out	2	2	0	41.34259	174.78383	13.5	2.6	4.4	64.502	1.38027	41.7169	30
IS070	out	1	1	0	41.34252	174.78389	7.5	0.55	6.5	74.48	1.19457	33.6806	40
IS071	out	1	1	0	41.34581	174.78942	6.435	0.75	10.8	128.046	1.07904	7.02959	340
IS072	out	1	1	0	41.34584	174.78947	3.12	1.1	14.5	127.403	1.04399	15.0198	345
IS073	out	10	6	4	41.34676	174.79148	29.16	1.6	30.9	128.789	1.35684	49.7991	495
IS074	out	3	3	0	41.34683	174.79141	11.88	1.8	36.5	128.884	2.13673	64.0401	505
IS075	out	3	2	1	41.34679	174.79138	8.96	1.6	36.5	129.976	1.57272	43.2828	500
IS076	out	6	5	1	41.34687	174.79142	42.68	3.45	41.3	128.459	1.54908	57.8003	510
IS077	in	5	3	2	41.28830	174.82963	17.92	0.55	14.1	135.055	1.14454	36.4431	505
IS078	in	2	2	0	41.28476	174.82513	2.72	0.2	3.6	187.534	1.03785	12.877	840
IS079	in	2	2	0	41.28708	174.82440	0.825	0.4	2.2	157.551	1.51847	49.9696	575
IS080	in	1	1	0	41.30213	174.81793	1.44	0.5	1.1	98.921	1.05408	23.3625	165
IS081	in	1	1	0	41.30249	174.81783	1.61	0.2	0.9	97.422	1.13122	35.6565	150
IS082	in	1	1	0	41.30253	174.81769	1.08	0.8	2.8	106.934	1.10682	8.54284	150
IS083	in	1	1	0	41.30355	174.81616	7.44	0.85	2.65	117.906	1.18287	38.9936	170
IS084	out	2	2	0	41.34146	174.80975	7	0.7	13.2	112.216	1.05154	17.6436	375
IS085	out	1	1	0	41.34125	174.80982	3.91	0.55	10.9	111.468	1.12925	25.5052	350
IS086	out	3	3	0	41.34064	174.81018	8.64	2	13.8	62.66	1.26941	38.9645	275

IS087	out	2	2	0	41.34058	174.81018	16.12	2.9	14.7	65.32	1.21565	31.0212	265
IS088	out	9	7	2	41.34240	174.80959	36.9	1.8	27	115.291	1.05729	16.6944	470
IS089	out	8	6	2	41.34257	174.80961	19.25	1.3	12.6	114.372	1.01256	12.0572	490
IS090	out	5	5	0	41.34247	174.80969	11.4	1.95	23.4	117.25	1.02431	8.94758	480
IS091	out	1	1	0	41.34272	174.80975	2.72	0.95	17.5	116.994	1.04016	16.8218	505
IS092	out	1	1	0	41.34297	174.80974	7.5	0.9	3	116.925	1.25303	37.6046	535
IS093	out	5	4	1	41.34270	174.80935	15.34	0.9	6	116.454	1.09099	30.0709	515
IS094	out	5	4	1	41.34357	174.80929	22.78	1.9	5.4	119.311	1.04878	16.0631	610
IS095	out	3	2	1	41.34271	174.80954	5.1	0.4	4.4	116.595	1.01003	6.45984	505
IS096	out	2	1	1	41.34269	174.80950	3	0.3	6.3	115.992	1.02053	10.8067	510
IS097	out	1	1	0	41.34272	174.80936	0.98	0.4	4.7	116.29	1.07205	16.4391	515

Permits

- Chapters 2 and 3: Permits were obtained for all unpublished surveys, issued by either the New Zealand's Department of Conservation or Māori and private island owners.

- Chapters 4: A regular permit was obtained from the Wellington City Council. Thanks also to local Iwi for permission to collect data in the Wellington area.

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