Integrating Phylogeny and Functional Traits into Evaluations of Nestedness in Island Floras

Running title: Nestedness in Island Floras

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Abstract

Questions

Understanding the composition and structure of island floras is crucial for making informed conservation decisions. Island floras are often nested, i.e. lower species richness assemblages are frequently subsets of those higher in richness. However, the circumstances under which this occurs on islands are often unclear. Moreover, research in island biogeography rarely integrates phylogeny and functional traits in nestedness studies. Here, we integrated phylogenetic and functional traits in the investigation of relationships between taxonomic nestedness and island characteristics to gain insight into the processes that shape the composition and structure of island floras. We asked whether (i) native plant species assemblages are nested according to their phylogeny and functional traits and (ii) whether nested patterns are related to island characteristics.

Location

264 islands offshore from northern Aotearoa New Zealand.

Methods

We combined field surveys and published data for 775 native plant species across the islands. We compiled information about their phylogeny at the fine (species) and coarse level (i.e. ferns and allies, conifers, monocots, and dicots). Then, for each species, we determined three plant functional traits (growth forms, dispersal modes, and species maximum height). We quantified nestedness by organizing species incidence matrices using the NODF (i.e. nestedness metric based on overlap and decreasing fill) and fixed-fixed null models. Finally, we correlated island nestedness ranks with three island characteristics (area, isolation, and exposure to ocean-borne disturbances).

Results

All plant categories were nested, except for ferns and water-dispersed species. Nestedness ranks were consistently related to island area, strongly supporting the selective extinction hypothesis. Relationships with isolation and exposure to ocean-borne disturbances were less strong and varied by phylogeny and functional traits, suggesting weaker support for selective immigration and habitat nestedness.

Conclusions

These findings highlight the importance of nestedness studies and the integration of phylogeny and functional traits for identifying conservation priority areas. The overarching effect of island area in shaping insular plant composition underscores the key role of large islands for conserving plant diversity.

Keywords: Aotearoa New Zealand, Island biogeography, Island Conservation, Island flora, Native species, Nestedness, NODF, Plants, Species composition, Taxonomic Nestedness

Introduction

Islands harbour a disproportionately high number of endemic plant species, many of which are under significant threat (Caujapé-Castells et al. 2010; Fernández-Palacios et al. 2021; Schrader et al. 2024). Thus, understanding the structure and composition of island plant communities is essential for making informed conservation decisions. Island floras frequently exhibit a nested structure, where species-poor assemblages are subsets of richer ones (Hu, Feeley, Wu, Xu, and Yu 2011; Morrison 2013; Patterson and Atmar 1986; Traveset, Kueffer, and Daehler 2014). However, the circumstances under which this occurs and the implications for island conservation remain poorly understood.

Nested patterns can be generated by three main ecological processes. First, extinction rates on small islands are often higher than on larger islands (MacArthur and Wilson 1967), especially for species with larger minimum area requirements (Higgins, Willig, and Strauss 2006; Tjørve and Turner 2009) or with smaller population sizes (Matthews, Cottee-Jones, and Whittaker 2015). If extinctions are non-random, then communities on small, species-poor islands become subsets of larger, species-rich islands, a process known as selective extinction (Atmar and Patterson 1993; Chen, Zhan, and Wang 2022; Higgins et al. 2006; Lomolino 1996; Millien, Zhan, Li, Wang, and Wang 2024). Second, colonization rates are often lower on more isolated islands, especially for species with limited capacity for dispersal (Higgins et al., 2006). If colonization events are non-random, then communities on isolated, species-poor islands become subsets of less isolated, species-rich islands, a process known as selective colonization (Chen et al. 2022; Higgins et al. 2006; Hu et al. 2011; Lomolino 1996; Millien et al. 2024). Third is habitat nestedness (Chen et al. 2022; Higgins et al. 2006; Millien et al. 2024). In circumstances where habitats are nested, specialists disappear as their habitat does, while generalists do not (Higgins et al. 2006). Islands are typically exposed to disturbances originating from the ocean (e.g. strong wind, salt spray, storms, etc.), which will favour specialists of coastal habitats (Mologni 2022; Mologni et al. 2021; Morrison and Spiller 2008; Neufeld, Starko, and Burns 2017). As exposure to these disturbances declines, so will the number of specialists, promoting nested patterns.

Traditionally, research has focused on taxonomic nestedness. Similar to the theory of island biogeography, this approach treats species as equivalent and independent of one another (MacArthur and Wilson 1967). More recent research that recognizes species are neither equivalent nor independent has led to evaluations of phylogenetic (Johnson, Adler, and Cherry 2000; Sanmartín, Van Der Mark, and Ronquist 2008; Valente, Phillimore, and Etienne 2018; Weigelt and Kreft 2013) and functional island biogeography (Barajas Barbosa et al. 2023; Mologni et al. 2022; Schrader, Wright, Kreft, and Westoby 2021; Walentowitz, Troiano, Christiansen, Steinbauer, and Barfod 2022; Whittaker et al. 2014). Phylogenetic and functionally informed approaches have gradually extended to studies of nestedness (Chen et al. 2022; Millien et al. 2024; Zhan, Li, Chen, and Wang 2024). Implementing this approach has revealed distinct patterns in the nestedness of amphibians (Chen et al., 2022) and mammals (Millien et al., 2024; Zhan et al., 2024), both dependent on their phylogenetic relationships and functional traits. However, little is known about how phylogeny and traits influence nested patterns of native plant communities on islands.

One way to integrate plant phylogeny in taxonomic nestedness studies on islands is by using broad phylogenetic categories, such as monocots, dicots, ferns, and conifers. While some of these groups are highly diverse and occupy a wide range of habitats, others are not. For instance, many fern species are confined to shaded, humid habitats (Mehltreter 2010), hence, islands without forest cover or highly exposed to the ocean might be too open or too lacking in humidity for many of them. Similarly, several traits can be integrated in taxonomic nestedness studies. For example, identifying traits associated with plant body size might help characterize the role of island area and selective extinction in shaping island plant communities. Most woody species are bigger than herbs (Pérez-Harguindeguy et al. 2013) and have higher minimum area requirements. Instead, other traits could be associated with selective colonization. Vectors vary among species, and while some, such as the wind, allow species to disperse over extended distances, others, such as ants, will limit the distance a species can disperse to (Arjona, Nogales, Heleno, and Vargas 2018; Mologni et al. 2022; Negoita et al. 2016). Similarly, taller plants can disperse over longer distances (Thomson, Moles, Auld, and Kingsford 2011) but they might also have higher minimum area requirements due to their larger body size.

There are several nestedness metrics (Almeida-Neto, Guimarães, Guimarães, Loyola, and Ulrich 2008; Atmar and Patterson 1993; Ulrich, Almeida-Neto, and Gotelli 2009; Wright, Patterson, Mikkelson, Cutler, and Atmar 1998). The nestedness metric based on overlap and decreasing fill (‘NODF’ hereafter) is generally considered the most appropriate (Almeida-Neto et al. 2008; Chen et al. 2022; Matthews et al. 2015; Ulrich, Almeida-Neto, et al. 2009). That is because it quantifies nestedness not exclusively for a whole presence/absence matrix (NODF), but also for columns (i.e. NODFc, or species composition across sites) and rows (i.e. NODFr, or species incidence) separately, allowing to determine the independent contribution of each component (Almeida-Neto et al. 2008; Chen et al. 2022). Quantifying column nestedness allows for assessing whether communities are nested among islands, while row nestedness for evaluating if specialists and rare species are present on islands that have generalists and widespread species (Traveset et al. 2014). Moreover, the NODF focuses on the overlap of species occurrences between sites rather than on unexpected presences or absences in the matrix. This reduces the risk of over- and underestimating nested patterns, respectively (Ulrich, Almeida-Neto, et al. 2009; Wright et al. 1998). The NODF is also more robust to variations in matrix fill (i.e. the proportion of non-zero elements), size (i.e. the total number of elements), and shape (i.e. the number of columns and rows), enabling the comparison of markedly different matrices (Almeida-Neto et al. 2008).

Here, we investigated patterns of taxonomic nestedness of island floras in relation to island characteristics (i.e. area, isolation, and exposure to ocean-borne disturbances). We integrated phylogenetic and functional traits to gain insight into the processes that shape the composition and structure of island native floras. We focused on 264 islands offshore from northern Aotearoa New Zealand. We combined field surveys and published data for 775 native plant species. We compiled information about their phylogeny and functional traits and explored nestedness patterns using species incidence matrices and correlation techniques. We asked whether (i) plant species assemblages are nested according to their phylogeny and functional traits and (ii) whether nested patterns are related to island characteristics.

Methods

Study system

The islands in the study system are located between 34–38° S and 172–179° E, spanning over 600 km, and vary markedly in their characteristics (Figure 1). The smallest island is only 21 m^2 and the least isolated are tidal islands (i.e. separated from the mainland only at high tide). Conversely, the largest island is over *27*7 km^2 and the most isolated is over 50 km from the mainland. Geologically, the islands are nearly evenly split between volcanic (n=136, 51.5%) and sedimentary (n=122, 46.2%), with a small number having a mixed composition (n=6, 2.3%). Except for the Poor Knights Islands/Tawhitirāhi and Rangitoto, all were connected during the last glacial maximum (Fleming, 1979, Shane et al., 2013).

The climate of the islands is temperate and oceanic (McGlone, Buitenwerf, and Richardson 2016) and all but the smallest islands and those with <5 m maximum elevation originally supported warm temperate rain forests (Grubb, Bellingham, Kohyama, Piper, and Valido 2013; Peel, Finlayson, and McMahon 2007; Wilmshurst et al. 2014). Most islands have elevations <400 m, where the forests were comprised of evergreen angiosperms and conifers, the latter often emergent over angiosperms (Dawson 1988; Grubb et al. 2013). Today, old-growth forests are rare in the study system, and confined to the largest islands (e.g. Cameron & Young, 2019).

Most of the islands were deforested since human settlement of Aotearoa New Zealand in c. 1250 CE (Atkinson 2004; Bellingham et al. 2010; Daugherty, Gibbs, Towns, and Atkinson 1990; Wilmshurst et al. 2014). Both burning and agriculture were abandoned on most islands, which are now in a process of secondary succession such that most islands are now dominated by second-growth warm temperate rain forests (Atkinson 2004; P J Bellingham 1984). Common, widespread trees in these second-growth forests include *Brachyglottis repanda* (Asteraceae), *Coprosma macrocarpa* and *C. repens* (Rubiaceae), *Corynocarpus laevigatus* (Corynocarpaceae), *Kunzea ericoides* s.l. (Myrtaceae), *Melicope ternata* (Rutaceae), *Melicytus novae-zelandiae* and *M. ramiflorus* (Violaceae), *Metrosideros excelsa* (Myrtaceae), *Piper excelsum* (Piperaceae), *Pittosporum crassifolium* (Pittosporaceae), *Planchonella costata* (Sapotaceae), and *Pseudopanax lessonii* (Araliaceae) (Atkinson 2004; Wardle, Bellingham, Bonner, and Mulder 2009). Two of the largest islands (Hauturu-a-Toi/Little Barrier Island, 30.79 km^2, and Aotea/Great Barrier Island, 277.21 km^2), with elevations up to 722 m, support floristically distinct old-growth original forests above 500 m (Cameron and Young 2019; Ogden and Perry 2023). Active and recent volcanic islands (i.e. Whakaari/White Island and Rangitoto) are undergoing primary succession, in which *M. excelsa* is the dominant colonising tree (Clarkson and Clarkson 1994; Shane et al. 2013). Non-native plant species, most introduced since the 19th century, comprise approximately half of the total flora of the study system (Mologni et al. 2021). Presently, 41 islands (15.5% of all islands) are inhabited.

Species lists and plant functional traits

We collated lists of plant species native to Aotearoa New Zealand (>80% endemic; McGlone et al., 2001) for each of the 264 islands using both published material and field surveys (see Mologni et al., 2021, 2022 for more details). After removing duplicates and aggregating records at the species level, a total of 810 native plant species were recorded. We removed 35 species due to taxonomic uncertainty (e.g. genus only noted in species lists), thus only 775 were used in the analyses. A further 25 and 3 species were removed from dispersal modes and plant height analyses due to a lack of data (Table 1). Lists were combined into a presence/absence matrix. Plant species lists follow consistent vascular plant taxonomy (Allan Herbarium 2023b, 2023a).

To account for phylogeny, we organized species matrices using both fine (species level) and coarse phylogenetic levels (i.e. dicots, monocots, conifers, and ferns and allies, Table 1). To account for plant functional traits, we organized species according to their growth forms and dispersal modes and determined species maximum height. We used five categories for growth forms: graminoids, forbs, woody species, climbers and lianas, and epiphytes (Table 1). We used five categories for dispersal modes: unspecialized, short-distance, wind-, animal-, and water-dispersed (Table 1). Data for each species' maximum height were obtained in July 2024 mostly from the New Zealand Plant Conservation Network (2024) and the Manaaki Whenua - Landcare Research (2005, see Appendix 2 for the full list), with additions from expert knowledge (PJB). For species that lacked data for maximum height, we used average height data instead. For hybrids, we used the average of the parent species' maximum or average height. We then organized species in three categories: short (maximum height < 1 m), medium (1–10 m), and tall (> 10 m, Table 1). We excluded categories with a sample size below 50 species, namely conifers (n = 12), climbers and lianas (n = 35), epiphytes (n = 8), and short-distance (n = 34, Table 1).

Island characteristics

We quantified three island characteristics: area, isolation, and exposure to ocean-borne disturbances (e.g. storms, waves, and salt spray). We measured island area as the surface of an island viewed from above (km^2) using available sources or manually digitizing it (Mologni et al. 2021). Isolation was measured as a series of concentric belts of different radii surrounding each island (radii = 250, 500, 1000, 1500, 2000, 2500, 3000 m, see Carter, Perry, and Russell 2020; Diver 2008; Mologni et al. 2021; Negoita et al. 2016; Weigelt and Kreft 2013). We quantified the proportion of land within each radius and subtracted this value from the total area, to ensure that greater values indicate greater isolation. We utilized the radius that performed best (Mologni et al. 2021). We estimated exposure to ocean-borne disturbances by drawing two lines starting from the centre of an island and connecting to the edge of the nearest landmasses (the mainland or islands larger than 50 km^2). The angle between these two lines represents the degree of exposure of an island to ocean-borne disturbances (Burns and Neufeld 2009). All spatial analyses were carried out using ArcGIS 10 and QGIS 2 (ESRI 2011; QGIS Development Team 2018).

Statistical analyses

For all phylogenetic and trait categories, we calculated Nestedness based on overlap and decreasing fill (NODF, Almeida-Neto et al., 2008). Nestedness was assessed on the entire matrix (NODF), on columns (i.e. species composition, NODFc) and rows (i.e. species incidence, NODFr). We employed a fixed-fixed null model with a ‘quasi-swap’ algorithm and 999 simulations to test for significant nestedness (Millien et al. 2024; Ulrich, Almeida-Neto, et al. 2009). Fixed-fixed null models maintain row and column totals fixed, which reduces the number of possible arrangements in the randomized matrices and thus the likelihood of identifying statistically significant nested patterns (Matthews et al. 2015). This is a more conservative approach which reduces the risk of type I errors (Ulrich, Almeida-Neto, and Gotelli 2009).

Relationships between island nestedness ranks and the three island characteristics were quantified using partial Spearman correlation coefficients (Millien et al. 2024). This method enables the comparison of more than 3 predictors and the assessment of the independent effect of each one (Frick, Hayes, and Heady III 2009; Millien et al. 2024; Shipley 2016). We extracted island nestedness ranks from the nested incidence matrix and correlated them with island characteristics (i.e. area, isolation, exposure to ocean-borne disturbances). Nestedness ranks assign higher values to species-poor sites and species that occur less frequently. If, for instance, species disappear as area declines so that communities on small islands are subsets of communities on large islands, this will result in a negative relationship between nestedness ranks and island area. Plant categories whose distribution is not significantly nested, or nested only according to rows (i.e. species incidence, NODFr) will be excluded from this analysis. A Bonferroni correction was applied to account for multiple tests and reduce type I error rates.

This approach was applied to all native species (fine phylogenetic level) and all subsets separately (coarse phylogenetic level, growth forms, dispersal modes, and plant height categories). Spearman correlation coefficients were calculated for all comparisons with more than one predictor, but no correlation exceeded the threshold of 0.7 (Appendix 3, Figure S1). All analyses were conducted in R. Nestedness was quantified using the package *vegan* (Oksanen et al. 2024), nestedness ranks using the package *bipartite* (Dormann, Gruber, and Fründ 2008), and Spearman partial correlation coefficients using the package *ppcor* (Seongho Kim 2012).

Results

Most native species groups were significantly nested based on at least one of the 3 nestedness metrics ($P<0.039$, full matrix, rows, and columns, Table 2). All species (fine phylogenetic level), dicots, forbs, wind-dispersed, short and medium-height species were nested based on both the full matrix and columns (Table 2). Graminoids, unspecialized, and medium-height species were nested only according to columns (i.e. species composition, Table 2). Tall species were nested based on both the full matrix and rows, while woody species and animal-dispersed species were nested only according to rows (i.e. species incidence, Table 2). Monocots were nested according to both columns and rows, but not across the entire matrix (i.e., both species composition and incidence, Table 2). Ferns and allies and water-dispersed species were not significantly nested ($P>0.05$, Table 2).

Island area was negatively related to island nestedness ranks of all plant categories that were significantly nested according to the full matrix (NODF) or columns (i.e. species composition, see Figure 2 & Appendix 3, Table S1). Isolation was positively related to the island nestedness ranks of all species (fine phylogenetic level), monocots among the coarse phylogenetic categories, graminoids among growth forms, wind-dispersed and unspecialized species among dispersal modes, and short and medium-height species among plant height categories. The island nestedness ranks of dicots, forbs, and tall species were not significantly related to isolation ($P>0.05$). Exposure to ocean-borne disturbances was positively related to the island nestedness ranks of all phylogenetic groups (all species, monocots, dicots), forbs among growth forms, wind-dispersed species among dispersal modes, and all plant height categories (short, medium, and tall). The island nestedness ranks of graminoids and unspecialized species were not significantly related to exposure to ocean-borne disturbances.

Discussion

Assemblages of the highly endemic native plant species across 264 offshore islands in Aotearoa New Zealand are largely nested, regardless of phylogenetic and functional trait categories, except for ferns and water-dispersed species assemblages. With light propagules (e.g. spores) and the ability to take advantage of water currents, these plant categories can disperse over long distances (Thomson et al. 2011), potentially reaching most islands and overriding nested patterns. Woody and animal-dispersed species were nested only according to rows (i.e., species incidence), indicating that widespread species occur across most sites, while rarer species are restricted to sites with higher diversity. This pattern is likely influenced by differences in plant traits, such as variations in the dispersal capacity of carriers for animal-dispersed species. The nestedness ranks of plant categories nested according to the full matrix or columns (i.e. species composition) were generally correlated with island area, isolation, and exposure to disturbance, with variations depending on phylogenetic and functional trait categories.

Nestedness ranks of native plant species were consistently related to island area, irrespective of the phylogenetic or functional group considered. Island area is a well-established predictor of plant diversity (Arrhenius 1921; MacArthur and Wilson 1967). Larger islands provide more space, more diverse habitats, and more resources, supporting higher species richness (Tjørve and Turner 2009). Previous work in the same study system found that larger islands contain more species, regardless of plant functional traits (Mologni et al. 2021, 2022). In the current study, we observed that native plant assemblages on smaller islands were consistently subsets of those of larger islands. This pattern aligns with the selective extinction hypothesis, which posits that as islands get smaller, species with larger area requirements or smaller population sizes are more likely to become extinct, generating nested patterns (Higgins et al. 2006; Matthews et al. 2015; Tjørve and Turner 2009). In addition, the effect of island area was at least twice as great as that of other predictors, suggesting selective extinction might be the dominant process in the study system (see Figure 2). However, the effect size of island area was comparable across all groups. If both large- and small-bodied species (e.g. woody species and graminoids, short and medium-height species) exhibit similar responses to island area, then minimum area requirements might be less important in plants than in animals (Millien et al. 2024).

The pronounced effect of area on island floras has strong conservation implications. In the longstanding debate on whether it is best to protect a single large area versus several small ones (Wright and Reeves 1992), our overall results support protecting larger islands (Diamond 1975; Donaldson, Wilson, and Maclean 2017; Fahrig et al. 2022; Tjørve and Tjørve 2008). However, options to protect larger islands in Aotearoa New Zealand are limited simply because there are few of them and most of the islands >100 ha in our study region are either wholly or largely managed for nature conservation (e.g., Armitage, 2011; Veitch & Wade, 2019). Their long-term protection gives the best prospect of safeguarding the greatest number of native plant species. Nationally and in our study region over 70% of protected islands are <100 ha (Towns and Ballantine 1993). The smaller islands in our study region need long-term protection to preserve the diversity of plant categories that are not nested, such as ferns, water-dispersed, and tall species, as well as endemic plant species that are confined to or are most abundant on small islands with high densities of nesting seabirds and with strong maritime climatic influences (Cameron 1990; Gillham 1960; Norton, Delange, Garnock-Jones, and Given 1997).

A second process linked to nested patterns is selective immigration, when, due to varying dispersal capabilities, communities on isolated islands become subsets of those on less isolated islands. However, the effect of isolation was less consistent than that of area, and three categories did not respond to it: dicots, forbs, and tall species. One explanation is that these categories might simply be more homogenous in their dispersal capabilities. For instance, tall species are likely to be consistently better dispersers than short and medium-height species (Thomson et al. 2011).

Similarly, the effect of islands' exposure to ocean-borne disturbances varied across groups. This suggests that habitat nestedness, or the systematic disappearance of specialists following their habitat, does not apply to all cases. Among growth forms, graminoids were the only category unrelated to exposure. Some grasses deposit high amounts of silica in their leaves (Lanning and Eleuterius 1983), increasing resistance to sand, salt, and other particulate matter carried by the wind, making graminoids more resistant to ocean-borne disturbances. Among dispersal modes, only wind-dispersed species were related to exposure. Strong oceanic winds will likely blow propagules away, preventing colonization (Carlquist 1974; Cody and Overton 1996). If so, this pattern might be better explained by selective immigration than habitat nestedness. Alternatively, ocean-borne disturbances might simply increase the chance of extinction events, resulting in the depauperate floras of exposed islands being a subset of the floras found on sheltered islands. Other studies have also shown that pressure from disturbances results in nestedness (e.g. in breeding bird communities, Wang, Ding, Chen, and

Zheng 2013). Ocean-borne disturbances are likely to play a role in explaining the effect of island area as well, given that species on smaller islands are more prone to extinction (MacArthur and Wilson 1967).

Most of the islands in northern Aotearoa New Zealand were connected to the mainland during the last glacial maximum (Fleming, 1979, Shane et al., 2013). As such, relictual plant populations might homogenize the flora and mitigate nested patterns. More recently, human activities have heavily modified these islands. The land was often burned or cleared for agriculture. Historic deforestation and subsequent secondary successions, which are likely to have been influenced at least in part by dispersal of species among islands and from the mainland, are also likely to have homogenized the flora (Christensen and Peet 1984) and mitigated nested patterns. Finally, a large number of non-native species were introduced and they now amount to half of the total flora (Mologni et al. 2021), some of which are invasive and highly competitive. Habitat loss and invasive species most likely drove more than one native species to extinction, influencing nestedness patterns. Unfortunately, we could not account for these factors. Data are lacking for relictual populations and habitat loss, while non-native and native species have similar distributions within this study system (Mologni et al. 2021), rendering any interpretation potentially circular.

In this study, we focused only on ecological processes such as selective extinction and immigration. However, nested patterns can also be generated by stochastic processes, prominently passive sampling (i.e. rare species are underrepresented in the community compared to abundant species) and collecting artifacts (i.e. the disproportional sampling of rare species or small assemblages, Higgins, Willig, and Strauss 2006; Hu, Feeley, Wu, Xu, and Yu 2011). Unfortunately, we lack data to investigate the role of these processes. Additionally, we used a fixed-fixed null model and the Bonferroni correction, both very conservative approaches. While this reduces the risk of type I errors, they inevitably increase the risk of type II errors. Similar trade-offs also apply to other methods, and we thus advise caution in interpreting the results.

Overall, native plant communities were nested across northern Aotearoa New Zealand islands but varied according to plant phylogeny and functional traits. This aligns with previous work on animals (Chen et al., 2022; Millien et al., 2024; Zhan et al., 2024), and highlights the importance of incorporating phylogeny and functional traits into studies of island nestedness of plants (Schrader et al. 2021). Furthermore, island floras were largely nested according to area, which emphasises the need to protect large islands, since, at least in our study system, some of the larger islands are also inhabited, highly modified, and more invaded (Mologni et al. 2021; Mologni, Bellingham, Cameron, and Wright 2024). Nestedness studies can suggest probable processes that determine insular community composition and aid in identifying conservation priority islands.

Data availability statement

The data in this research were collected from islands owned by Māori or from islands over which they have customary authority. The authors recognise their sovereignty and authority to control data about their lands under the CARE Principles for Indigenous Data Governance. Data for island characteristics are available from the Manaaki Whenua data repository at https://doi.org/10.7931/ndkt-zw49. Island locations (longitude and latitude) are not publicly available due to private ownership and issues of data sovereignty of concern to Māori.

Code availability statement

The code used for this research is available at as supplementary material.

Tables

Table 1 - Description of phylogenetic and functional trait categories utilized to investigate taxonomic nestedness across 264 Aotearoa New Zealand offshore islands. Numbers with an asterisk indicate categories excluded due to the small sample size (n<50).

Category	**Description**	**Number**
Phylogenetic categories		
Fine level	All species	*775*
Coarse level		*775*
Ferns and allies	Ferns and lycophytes	157
Conifers	Conifers	12*
Monocots	Monocotyledons	220
Dicots	Dicotyledons	386
Functional trait categories		
Growth forms		*775*
Graminoids	Grasses, sedges, and rushes	123
Forbs	Herbaceous, non-graminoid	393
Woody species	Trees and shrubs	216
Climbers and lianas	Herbaceous or woody climbers	35*
Epiphytes	Plants that grow upon other plants	8*
Dispersal modes		*750*
Water-dispersed	Buoyant propagules, e.g., corky tissues, air pockets (hydrochory)	61
Unspecialized	No evident or prevalent morphological adaptations (unspecialized)	110
Short-distance	Morphological adaptations for short-distance dispersal only (ballochory, myrmecochory)	34*
Animal-dispersed	Fleshy fruits or adhesive barbs (endo and epizoochory)	176
Wind-dispersed	Plumes, wings, dust diaspores (anemochory)	369

Plant height		*772*
Short	Maximum height below 1 m	361
Medium	Maximum height between 1 and 10 m	335
Tall	Maximum height above 10 m	76

Table 2 - Nestedness parameters for matrices including all species (phylogenetic fine level) and phylogenetic (coarse level) and functional (growth forms, dispersal modes, plant height) categories. In bold are significant nested patterns. In grey are categories that are not significantly nested for any parameter.

Category	**NODF**	**p-value**	**NODFr**	**p-value**	**NODFc**	**p-value**
Phylogenetic categories						
Fine level	**55.27**	**0.003**	64.29	0.303	**54.231**	**0.003**
Coarse level						
Ferns and allies	56.24	0.509	53.52	0.439	63.94	0.959
Monocots	54.84	0.659	**53.96**	**0.005**	**56.12**	**0.005**
Dicots	**55.07**	**0.007**	64.31	0.529	**50.76**	**0.003**
Functional trait categories						
Growth forms						
Graminoids	53.83	0.533	53.00	0.089	**57.70**	**0.007**
Forbs	**57.71**	**0.001**	65.14	0.473	**54.37**	**0.001**
Woody species	59.79	0.201	**62.86**	**0.039**	55.19	0.899
Dispersal modes						
Wind-dispersed	**59.52**	**0.015**	64.58	0.253	**56.91**	**0.025**
Water-dispersed	61.95	0.249	62.33	0.391	54.69	0.163
Unspecialized	48.84	0.053	48.23	0.209	**52.36**	**0.033**
Animal-dispersed	66.44	0.137	**70.73**	**0.005**	56.77	0.393

Plant height						
Short	**56.65**	**0.001**	61.60	0.053	**54.00**	**0.003**
Medium	**56.83**	**0.019**	63.84	0.413	**52.48**	**0.011**
Tall	**51.74**	**0.033**	**50.19**	**0.047**	70.63	0.495

Figures

Figure 1 Map and example photos of the 264 islands offshore northern Aotearoa New Zealand investigated.

Figure 2 Relationships between the nestedness rankings of phylogenetic and functional trait categories and island characteristics across 264 islands offshore northern Aotearoa New Zealand. On the x-axis are species categories. Categorizations were phylogenetic (fine - all species; coarse - monocots and dicots), growth forms (graminoids and forbs), dispersal modes (wind-dispersed and unspecialized) and plant height categories (short, medium, and tall). On the y-axis are rho values, which quantify the strength and direction of the relationship between two variables. A Bonferroni correction was applied to reduce type 1 error rates. The alpha level was set at 0.005, dividing 0.05 by the number of categories (n = 10).

Figure 1

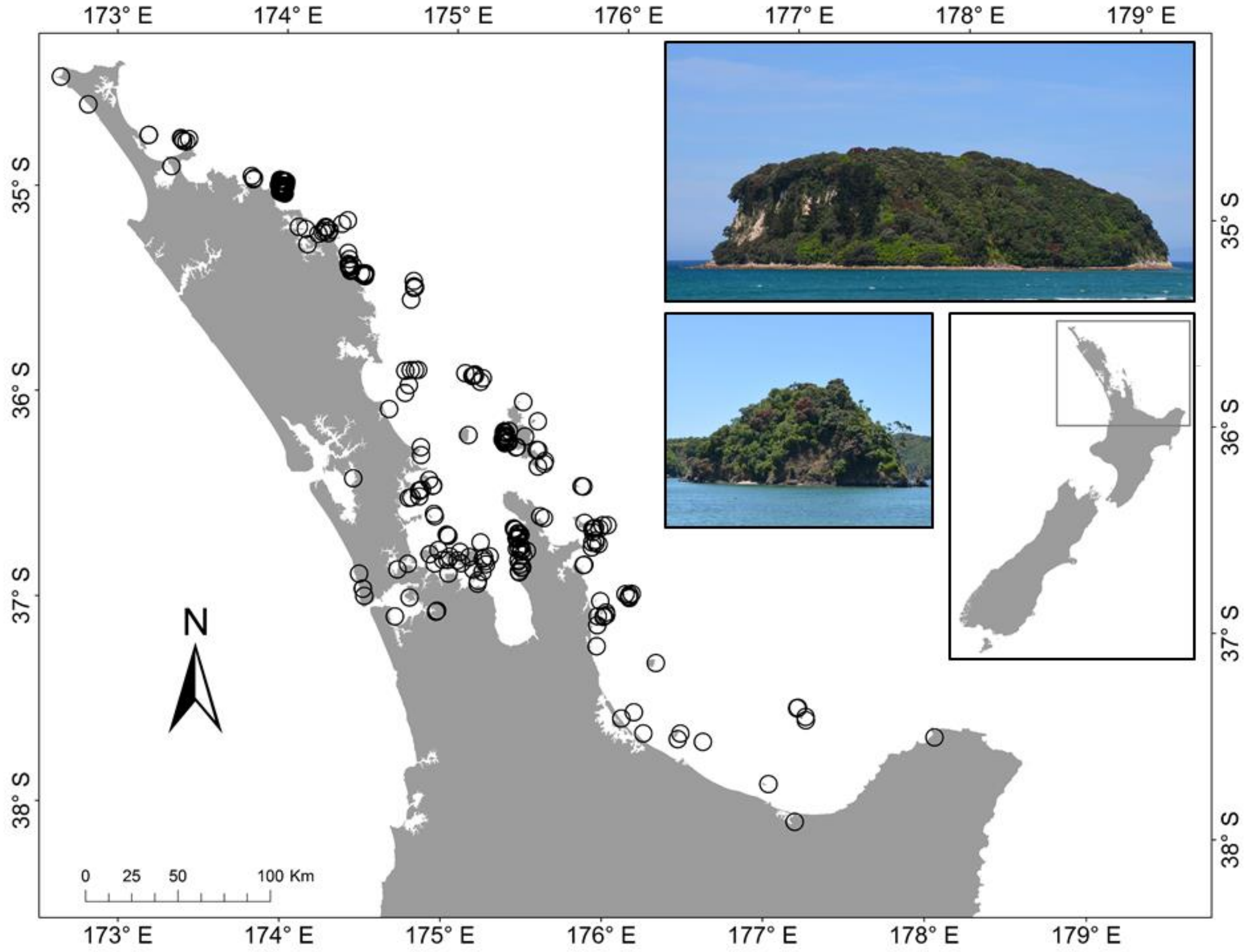
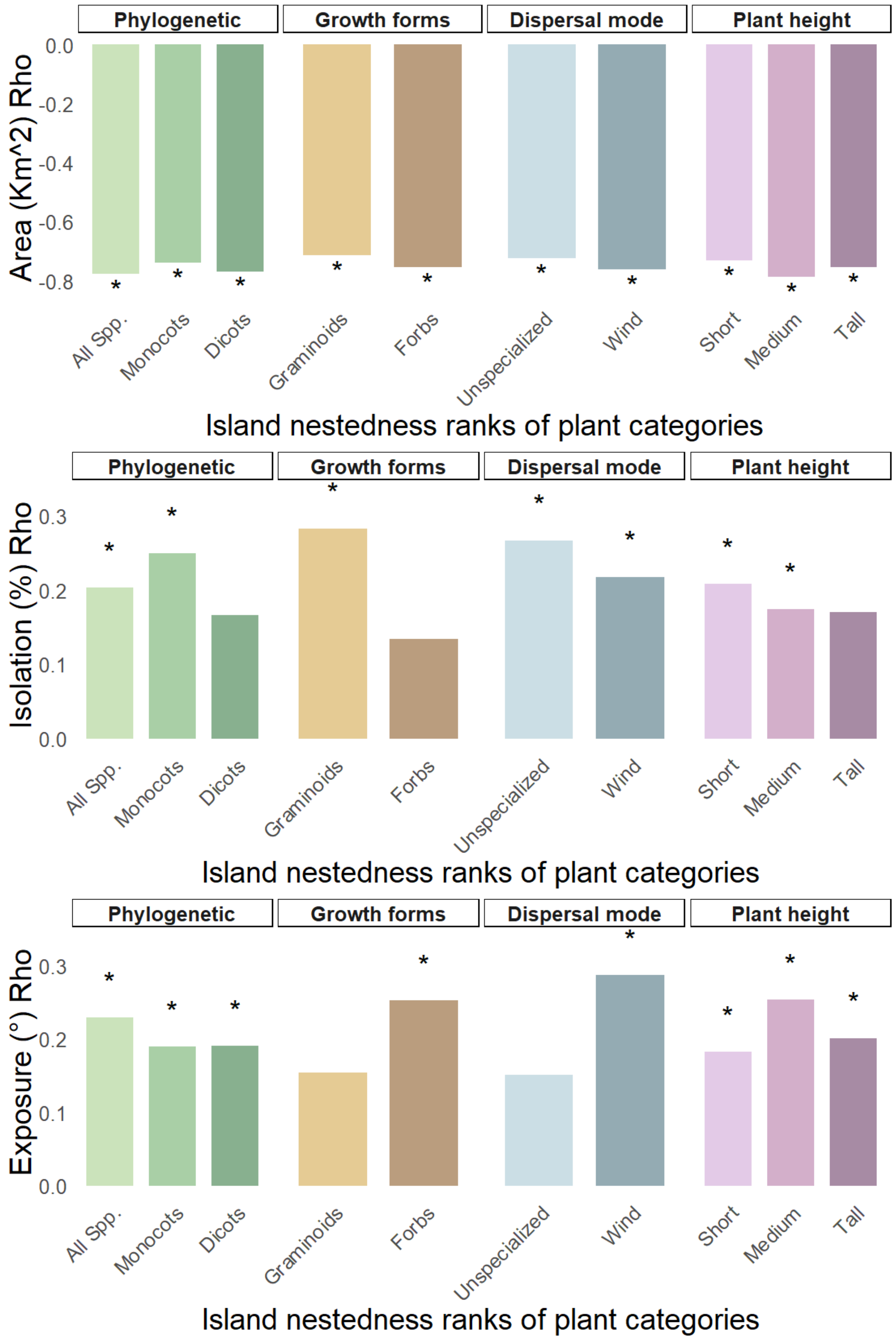

173° E
174° E
175° E
176° E
177° E
178° E
179° E
35° S
36° S
37° S
38° S
N
0 25 50 100 Km

Figure 2


Phylogenetic
Growth forms
Dispersal mode
Plant height
Area (Km^2) Rho
0.0
-0.2
-0.4
-0.6
-0.8
All Spp.
Monocots
Dicots
Graminoids
Forbs
Unspecialized
Wind
Short
Medium
Tall
Island nestedness ranks of plant categories
Phylogenetic
Growth forms
Dispersal mode
Plant height
Isolation (%) Rho
0.3
0.2
0.1
0.0
All Spp.
Monocots
Dicots
Graminoids
Forbs
Unspecialized
Wind
Short
Medium
Tall
Island nestedness ranks of plant categories
Phylogenetic
Growth forms
Dispersal mode
Plant height
Exposure (°) Rho
0.3
0.2
0.1
0.0
All Spp.
Monocots
Dicots
Graminoids
Forbs
Unspecialized
Wind
Short
Medium
Tall
Island nestedness ranks of plant categories

References

Allan Herbarium. (2023a). Checklist of the New Zealand Flora – Ferns and Lycophytes. Manaaki Whenua Landcare Research.

Allan Herbarium. (2023b). Checklist of the New Zealand Flora – Seed plants. Manaaki Whenua Landcare Research.

Almeida-Neto, M., Guimarães, P., Guimarães, P. R., Loyola, R. D., & Ulrich, W. (2008). A consistent metric for nestedness analysis in ecological systems: reconciling concept and measurement. Oikos, 117(8), 1227–1239. https://doi.org/10.1111/j.0030-1299.2008.16644.x

Arjona, Y., Nogales, M., Heleno, R., & Vargas, P. (2018). Long-distance dispersal syndromes matter: diaspore–trait effect on shaping plant distribution across the Canary Islands. Ecography, 41(5), 805–814. https://doi.org/10.1111/ecog.02624

Armitage, D. (ed.). (2011). Great Barrier Island. Revised edition. Canterbury University Press. Christchurch, New Zealand.

Arrhenius, O. (1921). Species and Area. Journal of Ecology, 9(1), 95–99. https://doi.org/10.2307/2255763

Atkinson, I. A. E. (2004). Successional processes induced by fires on the northern offshore islands of New Zealand. New Zealand Journal of Ecology, 28(2), 181–193.

Atmar, W., & Patterson, B. D. (1993). The measure of order and disorder in the distribution of species in fragmented habitat. Oecologia, 96(3), 373–382. https://doi.org/10.1007/BF00317508

Barajas Barbosa, M. P., Craven, D., Weigelt, P., Denelle, P., Otto, R., Díaz, S., … Kreft, H. (2023). Assembly of functional diversity in an oceanic island flora. Nature, 619(7970), 545–550. https://doi.org/10.1038/s41586-023-06305-z

Bellingham, P J. (1984). Forest regeneration on Lady Alice Island, Hen and Chickens group. Tane, 30, 31–42.

Bellingham, P. J., Towns, D. R., Cameron, E. K., Davis, J. J., Wardle, D. A., Wilmshurst, J. M., & Mulder, C. P. H. (2010). New Zealand island restoration: seabirds, predators, and the importance of history. New Zealand Journal of Ecology, 34(1), 115–136.

Burns, K. C., & Neufeld, C. J. (2009). Plant extinction dynamics in an insular metacommunity. Oikos, 118(2), 191–198. https://doi.org/10.1111/j.1600-0706.2008.16816.x

Cameron, E. K. (1990). Flora and vegetation of Middle Island, Mercury Islands Group, eastern Coromandel, northern New Zealand. Journal of the Royal Society of New Zealand, 20(3), 273–285. https://doi.org/10.1080/03036758.1990.10416822

Cameron, E. K., & Young, M. E. (2019). In Vegetation and vascular fora. In: Wade L, Veitch D (eds) Hauturu—the history, flora and fauna of Te Hauturu-o-Toi Little Barrier. (pp. 166–213). Auckland: Massey University Press.

Carlquist, S. J. (1974). Island biology. New York: Columbia University Press. https://doi.org/10.5962/bhl.title.63768

Carter, Z. T., Perry, G. L. W., & Russell, J. C. (2020). Determining the underlying structure of insular isolation measures. Journal of Biogeography, 47(4), 955–967. https://doi.org/10.1111/jbi.13778

Caujapé-Castells, J., Tye, A., Crawford, D. J., Santos-Guerra, A., Sakai, A., Beaver, K., … Kueffer, C. (2010). Conservation of oceanic island floras: Present and future global challenges. Perspectives in Plant Ecology, Evolution and Systematics, 12(2), 107–129. https://doi.org/10.1016/j.ppees.2009.10.001

Chen, C., Zhan, C., & Wang, Y. (2022). Do functional and phylogenetic nestedness follow the same mechanisms as taxonomic nestedness? Evidence from amphibians in the largest archipelago of China. Journal of Animal Ecology, 91(12), 2424–2436. https://doi.org/10.1111/1365-2656.13824

Christensen, N. L., and R. K. Peet. (1984). Convergence During Secondary Forest Succession. Journal of Ecology, 72(1), 25–36. https://doi.org/10.2307/2260004

Clarkson, B. D., & Clarkson, B. R. (1994). Vegetation decline following recent eruptions on White Island (Whakaari), Bay of Plenty, New Zealand. New Zealand Journal of Botany, 32(1), 21–36. https://doi.org/10.1080/0028825X.1994.10410404

Cody, M. L., & Overton, J. McC. (1996). Short-term evolution of reduced dispersal in island plant populations. Journal of Ecology, 84(1), 53–61. https://doi.org/10.2307/2261699

Daugherty, C. H., Gibbs, G. W., Towns, D. R., & Atkinson, I. A. E. (1990). The significance of the biological resources of New Zealand islands for ecological restoration. Conservation Sciences Publication (New Zealand), (2). Retrieved from https://agris.fao.org/search/en/providers/122578/records/6471d3902a40512c710e72f6

Dawson, J. (1988). Forest vines to snow tussocks: the story of New Zealand plants. Wellington: Victoria Univ. Press.

Diamond, J. M. (1975). The island dilemma: Lessons of modern biogeographic studies for the design of natural reserves. Biological Conservation, 7(2), 129–146. https://doi.org/10.1016/0006-3207(75)90052-X

Diver, K. C. (2008). Not as the crow flies: assessing effective isolation for island biogeographical analysis. Journal of Biogeography, 35(6), 1040–1048. https://doi.org/10.1111/j.1365-2699.2007.01835.x

Donaldson, L., Wilson, R. J., & Maclean, I. M. D. (2017). Old concepts, new challenges: adapting landscape-scale conservation to the twenty-first century. Biodiversity and Conservation, 26(3), 527–552. https://doi.org/10.1007/s10531-016-1257-9

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

ESRI. (2011). ArcGIS desktop: release 10.

Fahrig, L., Watling, J. I., Arnillas, C. A., Arroyo-Rodríguez, V., Jörger-Hickfang, T., Müller, J., … May, F. (2022). Resolving the SLOSS dilemma for biodiversity conservation: a research agenda. Biological Reviews, 97(1), 99–114. https://doi.org/10.1111/brv.12792

Fernández-Palacios, J. M., Kreft, H., Irl, S. D. H., Norder, S., Ah-Peng, C., Borges, P. A. V., … Drake, D. R. (2021). Scientists' warning – The outstanding biodiversity of islands is in peril. Global Ecology and Conservation, 31, e01847. https://doi.org/10.1016/j.gecco.2021.e01847

Fleming, C. A. (1979). The geological history of New Zealand and its life. Auckland: Auckland University Press.

Frick, W. F., Hayes, J. P., & Heady III, P. A. (2009). Nestedness of desert bat assemblages: species composition patterns in insular and terrestrial landscapes. Oecologia, 158(4), 687–697. https://doi.org/10.1007/s00442-008-1168-x

Gillham, M. E. (1960). Plant communities of the Mokohinau Islands, northern N.Z. Transactions of the Royal Society of New Zealand, 88(1), 79–98.

Grubb, P. J., Bellingham, P. J., Kohyama, T. S., Piper, F. I., & Valido, A. (2013). Disturbance regimes, gap-demanding trees and seed mass related to tree height in warm temperate rain forests worldwide: Gap-demanders in warm temperate rain forests. Biological Reviews, 88(3), 701–744. https://doi.org/10.1111/brv.12029

Higgins, C. L., Willig, M. R., & Strauss, R. E. (2006). The role of stochastic processes in producing nested patterns of species distributions. Oikos, 114(1), 159–167. https://doi.org/10.1111/j.2006.0030-1299.14720.x

Hu, G., Feeley, K. J., Wu, J., Xu, G., & Yu, M. (2011). Determinants of plant species richness and patterns of nestedness in fragmented landscapes: evidence from land-bridge islands. Landscape Ecology, 26(10), 1405–1417. https://doi.org/10.1007/s10980-011-9662-7

Johnson, K. P., Adler, F. R., & Cherry, J. L. (2000). Geneitc and phylogenetic consequences of island biogeography. Evolution, 54(2), 387–396. https://doi.org/10.1111/j.0014-3820.2000.tb00041.x

Lanning, F. C., & Eleuterius, L. N. (1983). Silica and ash in tissues of some coastal plants. Annals of Botany, 51(6), 835–850. https://doi.org/10.1093/oxfordjournals.aob.a086534

Lomolino, M. V. (1996). Investigating causality of nestedness of insular communities: selective immigrations or extinctions? Journal of Biogeography, 23(5), 699–703. https://doi.org/10.1111/j.1365-2699.1996.tb00030.x

MacArthur, R., & Wilson, E. (1967). The theory of island biogeography. location Princeton, U.S.A.: Princeton University Press.

Manaaki Whenua - Landcare Research. (2005). Ecological traits of New Zealand Flora. Retrieved July 15, 2024, from https://ecotraits.landcareresearch.co.nz/SearchForm.aspx

Matthews, T. J., Cottee-Jones, H. E. W., & Whittaker, R. J. (2015). Quantifying and interpreting nestedness in habitat islands: a synthetic analysis of multiple datasets. Diversity and Distributions, 21(4), 392–404. https://doi.org/10.1111/ddi.12298

McGlone, M. S., Buitenwerf, R., & Richardson, S. J. (2016). The formation of the oceanic temperate forests of New Zealand. New Zealand Journal of Botany, 54(2), 128–155. https://doi.org/10.1080/0028825X.2016.1158196

McGlone, M. S., Duncan, R. P., & Heenan, P. B. (2001). Endemism, species selection and the origin and distribution of the vascular plant flora of New Zealand. Journal of Biogeography, 28(2), 199–216. https://doi.org/10.1046/j.1365-2699.2001.00525.x

Mehltreter, K. (2010). Fern Conservation. In Mehltreter K, Walker LR, Sharpe JM (eds). Fern Ecology (pp. 323–359). Cambridge: Cambridge University Press.

Millien, V., Zhan, C., Li, Y., Wang, J., & Wang, Y. (2024). A global assessment of nested patterns in insular mammal assemblages. Global Ecology and Biogeography, 33(9), e13885. https://doi.org/10.1111/geb.13885

Mologni, F. (2022). Different levels of disturbance influence the distributional patterns of native but not exotic plant species on New Zealand small islands. Frontiers of Biogeography, 14(2), e54598. https://doi.org/10.21425/F5FBG54598

Mologni, F., Bellingham, P. J., Cameron, E. K., Dinh, K., Wright, A. E., & Burns, K. C. (2022). Functional traits explain non-native plant species richness and occupancy on northern New Zealand islands. Biological Invasions, 24(7), 2135–2154. https://doi.org/10.1007/s10530-022-02762-1

Mologni, F., Bellingham, P. J., Cameron, E. K., & Wright, A. E. (2024). Time since first naturalization is key to explaining non-native plant invasions on islands. Journal of Biogeography, 51(8), 1340–1350. https://doi.org/10.1111/jbi.14825

Mologni, F., Bellingham, P. J., Tjørve, E., Cameron, E. K., Wright, A. E., & Burns, K. C. (2021). Similar yet distinct distributional patterns characterize native and exotic plant species richness across northern New Zealand islands. Journal of Biogeography, 48(7), 1731–1745. https://doi.org/10.1111/jbi.14110

Morrison, L. W. (2013). Nestedness in insular floras: spatiotemporal variation and underlying mechanisms. Journal of Plant Ecology, 6(6), 480–488. https://doi.org/10.1093/jpe/rtt002

Morrison, L. W., & Spiller, D. A. (2008). Patterns and processes in insular floras affected by hurricanes. Journal of Biogeography, 35(9), 1701–1710. https://doi.org/10.1111/j.1365-2699.2008.01910.x

Negoita, L., Fridley, J. D., Lomolino, M. V., Mittelhauser, G., Craine, J. M., & Weiher, E. (2016). Isolation-driven functional assembly of plant communities on islands. Ecography, 39(11), 1066–1077. https://doi.org/10.1111/ecog.01551

Neufeld, C. J., Starko, S., & Burns, K. C. (2017). Disturbance and diversity in a continental archipelago: a mechanistic framework linking area, height, and exposure. Ecosphere, 8(10), e01957. https://doi.org/10.1002/ecs2.1957

New Zealand Plant Conservation Network. (2024). New Zealand Plant Conservation Network. Retrieved from https://www.nzpcn.org.nz/

Norton, D. A., Delange, P. J., Garnock-Jones, P. J., & Given, D. R. (1997). The role of seabirds and seals in the survival of coastal plants: lessons from New Zealand Lepidium

(Brassicaceae). Biodiversity & Conservation, 6(6), 765–785. https://doi.org/10.1023/B:BIOC.0000010401.93153.29

Ogden, J., & Perry, G. L. W. (2023). Ranges of woody plant species and ferns on forested elevational gradients on Aotea-Great Barrier Island, New Zealand: the role of zones of permanent and temporary establishment. New Zealand Journal of Ecology, 47(1), 3512. https://doi.org/10.20417/nzjecol.47.3512

Oksanen, J., Simpson, G. L., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., … Weedon, J. (2024). vegan: Community Ecology Package. https://doi.org/10.32614/CRAN.package.vegan

Patterson, B. D., & Atmar, W. (1986). Nested subsets and the structure of insular mammalian faunas and archipelagos. Biological Journal of the Linnean Society, 28(1–2), 65–82. https://doi.org/10.1111/j.1095-8312.1986.tb01749.x

Peel, M. C., Finlayson, B. L., & McMahon, T. A. (2007). Updated world map of the Köppen-Geiger climate classification. Hydrology and Earth System Sciences, 11(5), 1633–1644. https://doi.org/10.5194/hess-11-1633-2007

Pérez-Harguindeguy, N., Díaz, S., Garnier, E., Lavorel, S., Poorter, H., Jaureguiberry, P., … Cornelissen, J. H. C. (2013). New handbook for standardised measurement of plant functional traits worldwide. Australian Journal of Botany, 61(3), 167–234. https://doi.org/10.1071/BT12225

QGIS Development Team. (2018). QGIS Geographic Information System. Retrieved from http://qgis.osgeo.org/

Sanmartín, I., Van Der Mark, P., & Ronquist, F. (2008). Inferring dispersal: a Bayesian approach to phylogeny-based island biogeography, with special reference to the Canary Islands. Journal of Biogeography, 35(3), 428–449. https://doi.org/10.1111/j.1365-2699.2008.01885.x

Schrader, J., Weigelt, P., Cai, L., Westoby, M., Fernández-Palacios, J. M., Cabezas, F. J., …

Kreft, H. (2024). Islands are key for protecting the world's plant endemism. Nature, 634(8035), 868–874. https://doi.org/10.1038/s41586-024-08036-1

Schrader, J., Wright, I. J., Kreft, H., & Westoby, M. (2021). A roadmap to plant functional island biogeography. Biological Reviews, 96(6), 2851–2870. https://doi.org/10.1111/brv.12782

Seongho Kim. (2012, October 29). ppcor: Partial and Semi-Partial (Part) Correlation. https://doi.org/10.32614/CRAN.package.ppcor

Shane, P., Gehrels, M., Zawalna-Geer, A., Augustinus, P., Lindsay, J., & Chaillou, I. (2013). Longevity of a small shield volcano revealed by crypto-tephra studies (Rangitoto volcano, New Zealand): Change in eruptive behavior of a basaltic field. Journal of Volcanology and Geothermal Research, 257, 174–183. https://doi.org/10.1016/j.jvolgeores.2013.03.026

Shipley, B. (2016). Cause and Correlation in Biology: A User's Guide to Path Analysis, Structural Equations and Causal Inference with R (2nd ed.). Cambridge University Press. https://doi.org/10.1017/CBO9781139979573

Thomson, F. J., Moles, A. T., Auld, T. D., & Kingsford, R. T. (2011). Seed dispersal distance is more strongly correlated with plant height than with seed mass: Dispersal distance and seed mass. Journal of Ecology, 99(6), 1299–1307. https://doi.org/10.1111/j.1365-2745.2011.01867.x

Tjørve, E., & Tjørve, K. M. C. (2008). The species-area relationship, self-similarity, and the true meaning of the z-value. Ecology, 89(12), 3528–3533. https://doi.org/10.1890/07-1685.1

Tjørve, E., & Turner, W. R. (2009). The importance of samples and isolates for species-area relationships. Ecography, 32(3), 391–400. https://doi.org/10.1111/j.1600-0587.2008.05515.x

Towns, D. R., & Ballantine, W. J. (1993). Conservation and restoration of New Zealand Island ecosystems. Trends in Ecology & Evolution, 8(12), 452–457. https://doi.org/10.1016/0169-5347(93)90009-E

Traveset, A., Kueffer, C., & Daehler, C. C. (2014). Global and regional nested patterns of non-native invasive floras on tropical islands. Journal of Biogeography, 41(4), 823–832. https://doi.org/10.1111/jbi.12243

Ulrich, W., Almeida-Neto, M., & Gotelli, N. J. (2009). A consumer’s guide to nestedness analysis. Oikos, 118(1), 3–17. https://doi.org/10.1111/j.1600-0706.2008.17053.x

Ulrich, W., Almeida-Neto, M., & Gotelli, N. J. (2009). A consumer’s guide to nestedness analysis. Oikos, 118(1), 3–17. https://doi.org/10.1111/j.1600-0706.2008.17053.x

Valente, L., Phillimore, A. B., & Etienne, R. S. (2018). Using molecular phylogenies in island biogeography: it’s about time. Ecography, 41(10), 1684–1686. https://doi.org/10.1111/ecog.03503

Veitch, C. R., & Wade, L. (2019). Hauturu: the history, flora and fauna of Te Hauturu-o-Toi Little Barrier Island. Massey University Press.

Walentowitz, A., Troiano, C., Christiansen, J. B., Steinbauer, M. J., & Barfod, A. S. (2022). Plant dispersal characteristics shape the relationship of diversity with area and isolation. Journal of Biogeography, 49(9), 1599–1608. https://doi.org/10.1111/jbi.14454

Wang, Y., Ding, P., Chen, S., & Zheng, G. (2013). Nestedness of bird assemblages on urban woodlots: Implications for conservation. Landscape and Urban Planning, 111, 59–67. https://doi.org/10.1016/j.landurbplan.2012.11.008

Wardle, D. A., Bellingham, P. J., Bonner, K. I., & Mulder, C. P. H. (2009). Indirect effects of invasive predators on litter decomposition and nutrient resorption on seabird-dominated islands. Ecology, 90(2), 452–464. https://doi.org/10.1890/08-0097.1

Weigelt, P., & Kreft, H. (2013). Quantifying island isolation - insights from global patterns of insular plant species richness. Ecography, 36(4), 417–429. https://doi.org/10.1111/j.1600-0587.2012.07669.x

Whittaker, R. J., Rigal, F., Borges, P. A. V., Cardoso, P., Terzopoulou, S., Casanoves, F., … Triantis, K. A. (2014). Functional biogeography of oceanic islands and the scaling of functional diversity in the Azores. Proceedings of the National Academy of Sciences, 111(38), 13709–13714. https://doi.org/10.1073/pnas.1218036111

Wilmshurst, J. M., Moar, N. T., Wood, J. R., Bellingham, P. J., Findlater, A. M., Robinson, J. J., & Stone, C. (2014). Use of pollen and ancient DNA as conservation baselines for offshore islands in New Zealand. Conservation Biology, 28(1), 202–212. https://doi.org/10.1111/cobi.12150

Wright, D. H., Patterson, B. D., Mikkelson, G. M., Cutler, A., & Atmar, W. (1998). A comparative analysis of nested subset patterns of species composition. Oecologia, 113(1), 1–20. https://doi.org/10.1007/s004420050348

Wright, D. H., & Reeves, J. H. (1992). On the meaning and measurement of nestedness of species assemblages. Oecologia, 92(3), 416–428. https://doi.org/10.1007/BF00317469

Zhan, C., Li, B., Chen, C., & Wang, Y. (2024). Taxonomic, phylogenetic, and functional nestedness of mammal assemblages in the Zhoushan Archipelago, China. Current Zoology, 70, 728–738. https://doi.org/10.1093/cz/zoae006

Appendix 1 - Full list of sources consulted to collect data for plant height

Edgar E, Connor HE 2010 Flora of New Zealand Volume V Grasses. 2nd edition. Manaaki Whenua Press, Lincoln.

Heenan PB 2017 A taxonomic revision of Cardamine L. (Brassicaceae) in New Zealand. Phytotaxa 330, 1–154.

Heenan PB, Mitchell AD, De Lange PJ 2004 Arthropodium bifurcatum (Asparagaceae), a new species from northern New Zealand. New Zealand Journal of Botany 42, 233–246.

McGlone MS, Richardson SJ 2023. Sexual systems in the New Zealand angiosperm flora. New Zealand Journal of Botany 61, 201–231.

Merrett MF, Clarkson BD 2000 Reinstatement of Alseuosmia quercifolia (Alseuosmiaceae) from New Zealand. New Zealand Journal of Botany 38, 153–164.

Raven PH, Raven TE 1976 The Genus Epilobium (Onagraceae) in Australasia: A Systematic and Evolutionary Study. New Zealand Department of Scientific and Industrial Research Bulletin 216: 1–321.

Allan HH 1961 Flora of New Zealand Volume 1 (Vol. 1). Manaaki Whenua Press.

Brownsey PJ 1977a A taxonomic revision of the New Zealand species of Asplenium. New Zealand Journal of Botany 15: 39–86.

Brownsey PJ 1977b Asplenium hybrids in the New Zealand flora. New Zealand Journal of Botany 15: 601–637.

Brownsey P, Perrie L 2014 Lygodiaceae. In: Breitwieser, I.; Heenan, P.B.; Wilton, A.D. Flora of New Zealand—Ferns and Lycophytes. Fascicle 2. Manaaki Whenua Press, Lincoln. https://doi.org/10.7931/J26Q1V5T

Brownsey P, Perrie L (2015a). Loxsomataceae. In: Breitwieser, I.; Heenan, P.B.; Wilton, A.D. Flora of New Zealand—Ferns and Lycophytes. Fascicle 6. Manaaki Whenua Press, Lincoln. https://doi.org/10.7931/B1WC7J

Brownsey P, Perrie L 2015b. Psilotaceae. In: Breitwieser, I.; Heenan, P.B.; Wilton, A.D. Flora of New Zealand—Ferns and Lycophytes. Fascicle 6. Manaaki Whenua Press, Lincoln. https://doi.org/10.7931/B1MW2B

Brownsey P, Perrie L 2017 Lindsaeaceae. In: Breitwieser, I.; Wilton, A.D. Flora of New Zealand—Ferns and Lycophytes. Fascicle 17. Manaaki Whenua Press, Lincoln. https://doi.org/10.7931/B1D59W

Brownsey P, Perrie L 2021a Dryopteridaceae. In: Breitwieser, I.; Heenan, P.B.; Wilton, A.D. Flora of New Zealand—Ferns and Lycophytes. Fascicle 31. Manaaki Whenua Press, Lincoln. https://doi.org/10.7931/5SNH-WV42

Brownsey P, Perrie L 2021b Pteridaceae. In: Breitwieser, I.; Heenan, P.B.; Wilton, A.D. Flora of New Zealand—Ferns and Lycophytes. Fascicle 30. Manaaki Whenua Press, Lincoln. https://doi.org/10.7931/DTKJ-X078

Brownsey PJ, Smith-Dodsworth JC 2000 New Zealand ferns and allied plants. Revised edition. David Bateman, Auckland.

Carter SN, Miller S, Meyer SJ, Gemmill CEC 2018 A New Species of Pittosporum Described from the Poor Knights Islands, Northland, Aotearoa/New Zealand. Systematic Botany, 43: 633–643. https://doi.org/10.1600/036364418X697355

Garnock-Jones PJ 2023 Veronica. Flora of New Zealand–Seed Plants. Fascicle 9.

Manaaki Whenua - Landcare Research 2005 Ecological traits of New Zealand Flora. https://ecotraits.landcareresearch.co.nz/SearchForm.aspx

Moore LB, Edgar E 1970 Flora of New Zealand Volume II. Manaaki Whenua Press.

New Zealand Plant Conservation Network 2024 New Zealand Plant Conservation Network. https://www.nzpcn.org.nz/

Royal Botanic Gardens and Domain Trust, Sydney 2024 PlantNET (The NSW Plant Information Network System). https://plantnet.rbgsyd.nsw.gov.au

Royal Botanic Gardens Victoria 2024 VicFlora—Flora of Victoria. https://vicflora.rbg.vic.gov.au/

Webb CJ, Sykes WR, Garnock-Jones PJ 1988 Flora of New Zealand Volume IV. Manaaki Whenua Press.

Appendix 2 - Supplementary analyses

Table S1 - Spearman partial correlation coefficients for each plant category and island characteristics. Columns represent rho and p-values for each variable. In bold are significant relationships. A Bonferroni correction was applied to reduce type 1 error rates. The alpha level was set at 0.005, dividing 0.05 by the number of categories (n = 10).

Category		**Area (km2)**		**Isolation (%)**		**Exposure (°)**	
		Rho	**p**	**Rho**	**p**	**Rho**	**p**
Phylogenetic - Fine	All species	**-0.777**	**<0.0001**	**0.203**	**0.0010**	**0.229**	**<0.0001**
Phylogenetic - Coarse	Monocots	**-0.740**	**<0.0001**	**0.249**	**<0.0001**	**0.190**	**0.0020**
	Dicots	**-0.768**	**<0.0001**	0.166	0.0069	**0.191**	**0.0020**
Functional - Growth forms	Graminoids	**-0.713**	**<0.0001**	**0.282**	**<0.0001**	0.154	0.0124
	Forbs	**-0.755**	**<0.0001**	0.134	0.0302	**0.252**	**<0.0001**
Functional - Dispersal modes	Unspecialised	**-0.723**	**<0.0001**	**0.267**	**<0.0001**	0.151	0.0141
	Wind	**-0.762**	**<0.0001**	**0.218**	**0.0004**	**0.287**	**<0.0001**
Plant height	Short	**-0.731**	**<0.0001**	**0.208**	**0.0007**	**0.182**	**0.0031**
	Medium	**-0.786**	**<0.0001**	**0.174**	**0.0047**	**0.254**	**<0.0001**
	Tall	**-0.755**	**<0.0001**	0.170	0.0058	**0.201**	**0.0011**

Figure S1 Correlation matrix for the island characteristics used in the models.