Plant invasions reduce the degree of nestedness on warm temperate islands

Running title: Nestedness in Island Floras

*Fabio Mologni[1]

Peter J. Bellingham[2]

Ewen Kenneth Cameron[3]

Anthony Ernest Wright[4]

Yanping Wang[5]

1. University of Vienna, Vienna, Austria

2. Manaaki Whenua—Landcare Research, Lincoln, Aotearoa New Zealand

3. Auckland War Memorial Museum, Auckland, Aotearoa New Zealand

4. Canterbury Museum, Christchurch, Aotearoa New Zealand

5. Nanjing Normal University, Nanjing, China

* Corresponding author

Postal address: Department of Botany and Biodiversity Research, University of Vienna, Rennweg 14, 1030, Vienna, Austria

Phone: +43 670 1812022

Email: fabio.mologni@univie.ac.at, fabio.mologni@gmail.com

ORCiD: https://orcid.org/0000-0003-4750-9974

Abstract

Questions

Understanding the composition and structure of island floras is crucial for making informed conservation decisions, especially in the context of biological invasions. Island floras are often nested, i.e. species-poor assemblages are frequently subsets of species-rich ones. However, the circumstances under which this occurs on islands are often unclear. To gain insight into the processes that shape the composition and structure of island floras, we incorporated taxonomic and trait categories to investigate the relationships between the degree of nestedness of native and non-native species and island characteristics. We hypothesise that the degree of nestedness (1) declines with island area (non-random local extinctions), increases with isolation (non-random colonisation), declines with exposure to ocean-borne disturbances (non-random local extinction of specialists with their habitat), and is higher on volcanic compared to sedimentary islands (assembly rules). We also hypothesise that (2) plant invasions will reduce overall nestedness and (3) plant assemblages will be more nested if smaller in size (e.g. grasses, forbs) and not adapted to long-dispersal (e.g. wind-dispersed, ferns).

Location

264 islands offshore from northern Aotearoa New Zealand.

Methods

We combined field surveys and published data for 1,543 native and non-native plant species across 264 islands. We compiled information about their taxonomy at the fine (species) and coarse level (i.e. ferns and allies, conifers, monocots, and dicots), and categorised each species

by their growth form (i.e. graminoids, forbs, woody species, climbers and lianas, and epiphytes) and dispersal mode (i.e. water-dispersed, unspecialised, short-distance, animal-dispersed, and wind-dispersed). We quantified nestedness by organising species incidence matrices using the NODF (i.e. nestedness metric based on overlap and decreasing fill) and fixed-fixed null models. Finally, we related island nestedness ranks with four island characteristics (area, isolation, exposure to ocean-borne disturbances, and geological origin).

Results

All plant categories were nested, with a few exceptions. However, non-native species reduced the overall degree of nestedness. Nestedness ranks were consistently related to island area and largely to exposure to ocean-borne disturbances, but rarely to isolation and geological origin. This results strongly support the selective extinction (i.e., small, species-poor islands are subsets of larger, species-rich islands due to non-random local extinctions) and habitat nestedness (i.e., nested patterns generated by the non-random local extinction of specialists with their habitat) hypotheses.

Conclusions

Non-native species reduce the overall degree of nestedness, modifying the species composition of island floras. The overarching effect of island area in shaping insular plant composition underscores the key role of large islands for conserving plant diversity. Nestedness studies can suggest probable processes that determine insular community composition and aid in identifying conservation priority islands.

Keywords: Aotearoa New Zealand, Biological invasions, Island biogeography, Native species, Non-native species, Nestedness, NODF, Plants, Plant traits, Species composition

Introduction

Islands harbour disproportionately high numbers of both endemic and non-native plant species, with the former often under significant threat from the latter (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 within the same region frequently exhibit nested patterns (hereafter, nestedness), where species-poor assemblages are subsets of richer ones (Patterson and Atmar 1986; Wilson 1988; Hu et al. 2011; Morrison 2013; Traveset, Kueffer, and Daehler 2014). However, the circumstances under which this occurs, the impact of non-native species on nestedness (e.g. Wilson 1988), and the implications for island conservation remain poorly understood.

Nested patterns within a region can be generated by four main ecological processes. First, local 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 local 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; Lomolino 1996; Higgins, Willig, and Strauss 2006; Chen, Zhan, and Wang 2022; Millien et al. 2024). Second, colonisation rates are often lower on more isolated islands, especially for species with limited capacity for dispersal (Carlquist 1974; Higgins, Willig, and Strauss 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 (Lomolino 1996; Higgins, Willig, and Strauss 2006; Hu et al. 2011; Chen, Zhan, and Wang 2022; Millien et al. 2024). Third is habitat nestedness (Higgins, Willig, and Strauss 2006; Chen, Zhan, and Wang 2022; Millien et al.

2024). In circumstances where habitats are nested, specialists disappear as their habitat does, while generalists do not (Higgins, Willig, and Strauss 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 (Morrison and Spiller 2008; Neufeld, Starko, and Burns 2017; Mologni et al. 2021; Mologni 2022). As exposure to these disturbances declines, so will the number of specialists, promoting nested patterns. Finally, ordered patterns of community structure might derive from assembly rules (Diamond 1975a). For instance, fertility is generally higher in volcanic than in sedimentary soils (Pretto et al. 2012). Often, this results in dominance by highly competitive species (Tilman 1982), and therefore species-poor communities on fertile, volcanic islands.

Nestedness can be strongly modified by plant invasions, much like other species distribution patterns. For instance, non-native species modify both species-area and species-isolation relationships (Long, Trussell, and Elliman 2009; Moser et al. 2018; Guo et al. 2021). Previous work suggests biological invasions may also reduce nestedness (Ladle and Whittaker 2011; Matthews, Cottee-Jones, and Whittaker 2015). Such a decrease in nestedness after invasions might arise from several processes, including the island-specific nature of species introductions, biotic interactions, non-equilibrium dynamics, and ongoing invasions (Wilson 1988; Matthews, Cottee-Jones, and Whittaker 2015; Mologni et al. 2021; Mologni 2022). All of these processes carry significant implications for island conservation.

Most research on plant communities to date 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 recognises species are neither equivalent nor independent has led to evaluations of phylogenetic (Johnson, Adler, and Cherry 2000; Sanmartín, Van Der Mark, and Ronquist 2008; Weigelt et al. 2015; Valente, Phillimore, and Etienne 2018) and functional island biogeography (Whittaker et al. 2014; Schrader et al. 2021; Mologni et al. 2022; Walentowitz et al. 2022;

Barajas Barbosa et al. 2023; Li et al. 2025). 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, Zhan, and Wang 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 incorporate plant phylogeny in taxonomic nestedness studies on islands is by using taxonomic categories, such as monocots, dicots, ferns, and conifers (König et al. 2016). 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; Wu et al. 2025), 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 incorporated in taxonomic nestedness studies. For example, identifying traits associated with plant body size might help characterise 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 colonisation. 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 (Negoita et al. 2016; Arjona et al. 2018; Mologni et al. 2022). Similarly, taller plants can disperse over longer distances (Thomson et al. 2011) but they might also have higher minimum area requirements due to their larger body size.

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 incorporated taxonomy and plant 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 771 native plant species. We compiled information about their taxonomy and traits and explored nestedness patterns using species incidence matrices and modelling techniques. We hypothesise that the degree of nestedness (1) declines with island area (non-random local extinctions), increases with isolation (non-random colonisation), declines with exposure to ocean-borne disturbances (non-random local extinction of specialists with their habitat), and is higher on volcanic compared to sedimentary islands (assembly rules). We also hypothesise that (2) plant invasions will reduce overall nestedness and (3) plant assemblages will be more nested if smaller in size (e.g. grasses, forbs) and not adapted to long-dispersal (e.g. wind-dispersed, ferns).

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 islands range in area from 0.000021 to 277 km^2 and in isolation from some only separated from the mainland of Aotearoa New Zealand's North Island/Te Ika-a-Māui at high tide to others over 50 km from it. 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%). All but the Poor Knights Islands/Tawhitirāhi and Rangitoto were connected to the mainland 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 (Peel, Finlayson, and McMahon 2007; Grubb et al. 2013; 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 and 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 et al. 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 (Bellingham 1984; Atkinson 2004). 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 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 traits

We collated lists of plant species native and non-native to Aotearoa New Zealand 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 1604 plant species were recorded. We removed 48 species due to taxonomic (e.g. genus only noted in species lists) and 13 due to status uncertainty, thus only 1543 were used in the analyses. A further 112 species were removed from dispersal analyses (native = 23, non-native = 89, see Table 1). Lists were combined into a presence/absence matrix. Species names were standardised following a consistent nomenclatural reference for New Zealand flora (Allan Herbarium 2023b, 2023a).

To account for different taxonomic categories, we organised species matrices using both fine (species level) and coarse taxonomic levels (i.e. dicots, monocots, conifers, and ferns and allies, Table 1). To account for plant traits, we organised species according to their growth forms and dispersal modes. 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: unspecialised, short-distance, wind-, animal-, and water-dispersed (Table 1). We excluded categories with a sample size below 50 species. Conifers (all species = 22, native = 12, non-native = 10) were excluded from all taxonomic analyses but were assessed in evaluations of nestedness of woody species. Obligate epiphytes (all species = 10, native = 8, non-native = 2) were excluded from all analyses. Climbers and lianas were included only in overall analyses (native = 35, non-native = 41), ferns and water-dispersed species were excluded for non-native analyses (non-native = 8 and 17, respectively), and short-distance species were excluded only for native analyses (native = 34, Table 1).

Island characteristics

We quantified four island characteristics: area, isolation, exposure to ocean-borne disturbances (e.g. storms, waves, and salt spray), and geological origin. We measured island area as the surface of an island viewed from above (km^2) using available sources or manually digitising it (Mologni et al. 2021). Isolation was measured as a series of concentric belts of different radii initiating from the coastline of each island (radii = 250, 500, 1000, 1500, 2000, 2500, 3000 m, see Diver 2008; Weigelt and Kreft 2013; Negoita et al. 2016; Carter, Perry, and Russell 2020; Mologni et al. 2021). Within each radius, we quantified the proportion of land and subtracted it from the total area of that radius. This ensures that greater values indicate greater isolation. We utilised 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 towards the open ocean. The orientation of each line was changed in opposite directions until they were tangential to the coastline of landmasses larger than 50 km^2 (the mainland or other islands). The angle between these two lines facing the open ocean 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). The geological origin of each island was extracted from the GNS's Geological Map of New Zealand (1:250.000). Islands were categorised as sedimentary, volcanic, or mixed based on the geological composition of their substrates.

Statistical analyses

For all taxonomic and trait categories, we calculated nestedness using the NODF (i.e., nestedness based on overlap and decreasing fill, Almeida-Neto et al., 2008). Although there are several nestedness metrics (Wilson 1988; Atmar and Patterson 1993; Wright et al. 1998; Almeida-Neto et al. 2008; Ulrich, Almeida-Neto and Gotelli 2009), the nestedness metric based on overlap and decreasing fill ('NODF' hereafter) is generally considered the most appropriate

(Almeida-Neto et al. 2008; Ulrich, Almeida-Neto and Gotelli 2009; Matthews, Cottee-Jones, and Whittaker 2015; Chen, Zhan, and Wang 2022). 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, Zhan, and Wang 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, Kueffer, and Daehler 2014). The NODF evaluates nestedness by reordering the matrix's column and row totals in a decreasing order (i.e., decreasing fill). Columns (sites) are ordered from left to right by decreasing species richness, while rows (species) are ordered from top to bottom by decreasing incidence. Then, the NODF tests for overlaps in species composition between pairs of sites (columns) and in species incidence between pairs of species (rows). By focusing on overlaps instead then on unexpected presences or absences in the matrix, this approach reduces the risk of over- and underestimating nested patterns, respectively (Wright et al. 1998; Ulrich, Almeida-Neto and Gotelli 2009). 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).

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 (Ulrich, Almeida-Neto and Gotelli 2009; Millien et al. 2024). Fixed-fixed null models maintain row and column totals fixed, which reduces the number of possible arrangements in the randomised matrices and thus the likelihood of identifying statistically significant nested patterns (Matthews,

Cottee-Jones, and Whittaker 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 (i.e., the ranking of islands based on their position within a nested matrix) and island characteristics were quantified using Generalised Additive Models (GAM). Island nestedness ranks were standardised and set as a response variable, while island characteristics were set as predictors. Standardised nestedness ranks range between 0 and 1 and assign higher values to species-poor sites and species that occur less frequently. If, for instance, species decline in number as area does, 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. Spearman correlation coefficients were calculated for continuous variables, but no correlation exceeded the threshold of 0.7 (Appendix S4).

We selected the best model across 5 candidates. As baseline, we used two general additive models (GAMs), one of which with a smooth term to account for non-linearity in continuous variables. Nestedness ranks though produce normalised values (0-1). Data bounded between 0 and 1 are best modelled using beta and quasi-binomial regressions. We run two additional GAM models but by setting beta as family, one of which with a smooth term to account for non-linearity in continuous variables. The beta distribution requires data to be within the open interval (0, 1), so we adjusted the boundary values by replacing 0 with 0.001 and 1 with 0.999. We run the quasi-binomial model using generalised linear models (GLMs). To select the best model, we regressed the nestedness ranking of the whole flora against the four islands characteristics and then computed both the Akaike Information Criterion (AIC) and the Root Mean Squared Error (RMSE) for each model. The best model was the Beta regression with smooth terms (Appendix S6). In addition, only 5 of the islands are of mixed geological origin and we opted to exclude them. To ensure these 5 data points did not influence results, we modelled

only continuous variables with and without mixed geology islands using a beta regression. Results were consistent, and thus we excluded them from further analyses (Appendices S7, S8). Area was log transformed in all instances to reduce data separation. Finally, we also calculated partial Spearman correlation coefficients among continuous predictors (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; Shipley 2016; Millien et al. 2024).

Plant categories whose distribution is not significantly nested, or nested only according to rows (i.e. species incidence, NODFr) will be excluded from modelling. A Bonferroni correction was applied to account for multiple tests and reduce type I error rates. This approach was applied to all, native, and non-native species and to all subsets.

All analyses were conducted in R. Nestedness was quantified using the package *vegan* (Oksanen et al. 2024) and nestedness ranks using the package *bipartite* (Dormann, Gruber, and Fründ 2008). For modelling, we used *mgcv* (GAMs), *betareg* (beta regression), and *ppcorr* (Spearman partial correlation coefficients*,* Cribari-Neto and Zeileis 2010, Kim 2012, Wood 2017).

Results

Most Common Native and Non-Native Plant Species

The ten most common native species across the 264 islands are *Disphyma australe* (Aizoaceae, dicot herb; number of islands = 236), *Coprosma repens* (Rubiaceae, dicot tree; n = 222), *Senecio lautus* (Asteraceae, dicot herb; n = 220), *Ficinia nodosa* (Cyperaceae, monocot herb; n = 219), *Dichondra repens* (Convolvulaceae, dicot herb; n = 201), *Metrosideros excelsa* (Myrtaceae, dicot tree; n = 200), *Muehlenbeckia complexa* (Polygonaceae, dicot liana; n = 199), *Sarcocornia quinqueflora* (Amaranthaceae, dicot herb; n = 191), *Phormium tenax*

(Asphodelaceae, monocot herb; n = 184), and *Asplenium oblongifolium* (Aspleniaceae, fern; n = 178). Of 769 species, 442 (57.5%) were present on 10 or fewer islands.

The ten most common non-native species across the 264 islands are *Sonchus oleraceus* (Asteraceae, dicot herb; number of islands = 215), *Erigeron sumatrensis* (Asteraceae, dicot herb; n = 171), *Lysimachia arvensis* (Primulaceae, dicot herb; n = 171), *Polycarpon tetraphyllum* (Caryophyllaceae, dicot herb; n = 168), *Hypochaeris radicata* (Asteraceae, dicot herb; n = 165), *Sporobolus africanus* (Poaceae, monocot herb; n = 155), *Vulpia bromoides* (Poaceae, monocot herb; n = 133), *Phytolacca octandra* (Phytolaccaceae, dicot herb; n = 125), *Centaurium erythraea* (Gentianaceae, dicot herb; n = 125), and *Anthoxanthum odoratum* (Poaceae, monocot herb; n = 122). Of 774 species, 563 (72.7%) were present on 10 or fewer islands.

Nestedness and Relationships with Island Characteristics

Most species groups were significantly nested based on at least one of the 3 nestedness metrics (full matrix, rows, and columns), except for ferns and allies, water-dispersed species and non-native graminoids and animal-dispersed (Table 2, Appendices S1, S2, S3). Nestedness rankings of plant categories that were significantly nested according to the full matrix (NODF) or columns (i.e. species composition) were:

- Negatively related to island area across all models, indicating plant assemblages on small islands were subsets of those on larger islands (Figures 2 and 3 & Appendices S7-S13)
- Not associated with isolation across all models, indicating plant assemblages on isolated islands are not subsets of those on less isolated islands (Figures 2 and 3 & Appendices S7-S13, but see results for the partial Spearman correlation coefficients in Appendix S5)

- Positively associated with exposure to ocean-borne disturbances across all models for most categories (18 of 21 models, 86%), indicating that plant assemblages on exposed islands were subsets of those on sheltered islands (Figures 2 and 3 & Appendices S7-S13)
- Not associated with geology in all models for most categories (18 of 21 models, 86%), indicating that plant assemblages on volcanic islands are not more nested than those on sedimentary islands (Figures 2 and 3 & Appendices S7-S13)

Including non-native species in the nestedness models yielded statistically significant results more frequently, but smaller NODF values, indicating floras are less nested. Overall, the total flora was more commonly nested (64% of tests, 25 significant on 39 in total), than the native flora alone (42% of tests, 14 significant on 33 in total) or the non-native flora alone (40% of tests, 12 significant on 30 in total, Table 2). By contrast, the degree of nestedness for the whole flora (mean = 47.34, range = 30.98–64.70) was lower than the native flora (58.04, 48.23–70.83) but higher than the non-native flora (36.96, 6.91–57.65). The direction of the relationships between nestedness rankings and island characteristics were similar for all, native, and non-native species. However, only non-native species displayed a significant difference between geological origins. Non-native plant communities were more nested on volcanic islands compared to sedimentary.

Discussion

Assemblages of the highly native and non-native plant species across 264 offshore islands in Aotearoa New Zealand are largely nested. However, non-native species decreased the overall degree of nestedness, in line with a previous study on the flora of 23 forested islands in a lake in cool temperate Aotearoa New Zealand (Wilson 1988). Ongoing invasions have been proposed to explain differences in the distribution of native and non-native species in this system (Mologni

et al. 2021, Mologni et al. 2024). Other contributing processes might include the island-specific nature of species introductions and non-equilibrium dynamics (Wilson 1988; Matthews, Cottee-Jones, and Whittaker 2015). Despite a lower degree of nestedness, non-native species amount to half of the total flora of the islands (Mologni et al. 2021), and some are invasive and highly competitive. This may lead to local extinctions of native species, altering nested patterns in ways not fully captured by our analyses.

Species assemblages were nested regardless of taxonomic and 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. Consistent with previous results on Aotearoa New Zealand lacustrine islands, native trees and shrubs were more highly nested than herbs (Wilson 1988), whereas non-native species showed the opposite pattern. Non-native woody species were less nested than herbs, likely due to the longer time required for these species to reach maturity and spread. Six categories (18%) 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. The nestedness ranks of plant categories nested according to the full matrix or columns (i.e. species composition) were generally related to island area and exposure to ocean-borne disturbances, but not isolation and geological origin, with a few exceptions.

Nestedness ranks of native plant species were consistently related to island area, irrespective of the taxonomic or trait category 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

(Quinn, Wilson, and Mark 1987, Tjørve and Turner 2009). Furthermore, larger islands are a larger target for dispersing propagules, enhancing the chance of island colonisation by new species (Lomolino 1990, Mologni et al. 2021). 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 the smaller the island, the more likely it is that species with larger area requirements or smaller population sizes will become extinct, generating nested patterns (Higgins, Willig, and Strauss 2006; Tjørve and Turner 2009; Matthews, Cottee-Jones, and Whittaker 2015). 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 and 3). 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 seem to support protecting larger islands (Diamond 1975b; Tjørve and Tjørve 2008; Donaldson, Wilson, and Maclean 2017; Fahrig et al. 2022). 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 and Wade, 2019). Although the flora of smaller islands is often nested within that of larger islands, small islands can be critical for the protection of some rare and threatened plant species (Richardson et al. 2015). Given that nationally and in our study region over 70% of protected islands are

421 <100 ha (Towns and Ballantine 1993), smaller islands should not be neglected in conservation
422 planning. In our study region, the smaller islands need long-term protection to preserve the
423 diversity of plant categories that are not nested, such as ferns, water-dispersed, and tall
424 species, as well as endemic plant species that are confined to or are most abundant on small
425 islands with high densities of nesting seabirds and with strong maritime climatic influences
426 (Gillham 1960; Cameron 1990; Norton et al. 1997).

427 Similarly, the effect of islands' exposure to ocean-borne disturbances was relatively
428 consistent across groups. This suggests that habitat nestedness, or the systematic
429 disappearance of specialists as their habitat does, applies in most cases. Alternatively, ocean-
430 borne disturbances might simply increase the chance of local extinction events, resulting in the
431 depauperate floras of exposed islands being a subset of the floras found on sheltered islands.
432 Other studies have also shown that pressure from disturbances results in nestedness (e.g. in
433 breeding bird communities, Wang et al. 2013). Ocean-borne disturbances are likely to play a
434 role in explaining the effect of island area as well, given that species on smaller islands are
435 more prone to local extinction (MacArthur and Wilson 1967).

436 Another process linked to nested patterns is selective immigration, when, due to varying
437 dispersal capabilities, communities on isolated islands become subsets of those on less isolated
438 islands. However, isolation was consistently a non-significant predictor, suggesting selective
439 immigration is not a primary process in this system. Weak or inconsistent isolation effects were
440 also reported in previous work on these islands (Mologni et al. 2022, Mologni et al. 2024). The
441 spatial arrangement of the islands, which are often clustered and relatively close to the coast,
442 may reduce the effect of geographic isolation. Similarly, the geological origin of the islands had
443 little impact on nested patterns, except for non-native species (3 out of 4 tests). Non-native
444 communities were often more nested on volcanic than on sedimentary islands. This supports
445 the assembly rule hypothesis for non-native communities on volcanic islands, where fertile soils

drive competitive exclusion, resulting in species-poor communities. This contrast with previous findings in the Mediterranean, where volcanic islands were generally invaded by more non-native species (Pretto et al. 2012).

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 homogenised the flora (Christensen and Peet 1984) and mitigated nested patterns. Habitat loss most likely drove more than one native species to extinction, influencing nestedness patterns and likely homogenised the native flora. Unfortunately, we could not account for these factors since data are lacking for relictual populations and habitat loss.

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 et al. 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.

Overall, native plant communities were nested across northern Aotearoa New Zealand islands but non-native species reduced the overall degree of nestedness. This aligns with previous work on lacustrine islands in Aotearoa New Zealand (Wilson 1988). The degree of

nestedness varied according to plant taxonomy and traits, in line with prior research on animals (Chen, Zhan, and Wang 2022; Millien et al. 2024; Zhan et al. 2024), and highlights the importance of incorporating taxonomic categories and 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 et al. 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. The matrix and code used for this research are available as supplementary material (Appendices S14 and S15, respectively). Island locations (longitude and latitude) and species identity are not publicly available due to private ownership and issues of data sovereignty of concern to Māori. We thank Jill Rapson and other two anonymous reviewers whose comments improved the manuscript.

Tables

Table 1 - Description of taxonomic and trait categories utilised 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	All Species	Native	Non-native
Taxonomic categories				
Fine level	All species	*1543*	*769*	*774*
Coarse level		*1543*	*769*	*774*
Ferns and allies	Ferns and lycophytes	165	157	*8**
Conifers	Conifers	*22**	*12**	10*
Monocots	Monocotyledons	428	217	211
Dicots	Dicotyledons	928	383	545
Trait categories				
Growth forms		*1543*	*769*	*774*
Graminoids	Grasses, sedges, and rushes	236	122	114
Forbs	Herbaceous, non-graminoid	868	391	477
Woody species	Trees and shrubs	353	213	140
Climbers and lianas	Herbaceous or woody climbers	76	*35**	*41**

Epiphytes	Plants that grow upon other plants	*10**	*8**	*2**
Dispersal modes		*1431*	*746*	*685*
Water-dispersed	Buoyant propagules, e.g., corky tissues, air pockets (hydrochory)	78	61	*17**
Unspecialised	No evident or prevalent morphological adaptations (unspecialised)	378	110	268
Short-distance	Morphological adaptations for short-distance dispersal only (ballochory, myrmecochory)	155	*34**	121
Animal-dispersed	Fleshy fruits or adhesive barbs (endo and epizoochory)	325	175	150
Wind-dispersed	Plumes, wings, dust diaspores (anemochory)	495	366	129

498

499

500

501

502

503

504

505

Table 2 - Nestedness parameters for matrices including taxonomic (fine and coarse) and trait (growth forms and dispersal modes) categories for all, native, and non-native species. The column NODF (nestedness based on overlap and decreasing fill) is the overall nestedness parameter, while NODFr and NODFc are nestedness of rows and columns, respectively. Values range from 0 to 100, where 0 indicates a non-nested pattern and 100 a perfectly nested matrix. In bold are significant nested patterns (P>0.05). In grey are categories that are not significantly nested for any parameter.

	All species			**Natives**			**Non natives**		
Category	**NODF**	**NODFr**	**NODFc**	**NODF**	**NODFr**	**NODFc**	**NODF**	**NODFr**	**NODFc**
Taxonomic categories									
Fine level (all species)	**39.62**	**39.00**	**60.76**	**55.93**	**54.94**	64.33	**36.50**	**35.07**	48.83
Coarse level									
Ferns and allies	55.65	61.19	53.49	56.24	63.94	53.52	*not applicable*		
Monocots	**44.16**	**41.72**	50.58	55.46	**57.68**	**53.96**	38.50	**38.63**	38.41
Dicots	**37.78**	**35.88**	**61.36**	**55.51**	**51.30**	64.39	**37.09**	**33.87**	50.82
Trait categories									
Growth forms									
Graminoids	**48.96**	**47.49**	50.13	53.99	**58.65**	53.00	40.21	44.91	39.34
Forbs	**40.59**	**38.60**	62.19	**58.19**	**55.02**	65.13	**40.07**	**36.43**	51.95

	All species			Natives			Non natives		
Woody species	**45.86**	**38.03**	59.87	60.27	56.04	**63.02**	11.26	**26.75**	6.91
Climbers & Lianas	**41.56**	31.90	**42.36**	*not applicable*					
Dispersal modes									
Wind-dispersed	**51.89**	**48.27**	64.65	**59.84**	**57.37**	64.58	54.62	**41.88**	57.65
Water-dispersed	60.68	46.53	61.91	61.95	54.69	62.33	*not applicable*		
Unspecialised	**42.29**	**40.00**	**47.00**	48.84	**52.36**	48.23	**38.99**	**41.39**	36.53
Animal-dispersed	**48.88**	**38.45**	**64.70**	66.68	57.24	**70.83**	28.39	30.54	27.70
Short-distance	34.94	**30.98**	36.30	*not applicable*			33.19	**28.26**	34.22

513

514

Figures

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

Figure 2 Partial effect plots showing the relationship between nestedness rankings of the full matrix (all species, mixed geology islands excluded) and island characteristics across 264 islands offshore northern Aotearoa New Zealand. For continuous predictors, solid lines represent significant relationships, and dashed non-significant ones. For categorical predictors, opaque colours represent significant effects, and transparent non-significant ones. Significance is also marked with asterisks (*) and non-significance with "NS". Full plots for all other categories can be found in the supplementary material (Appendices 10, 11, 12, 13). A Bonferroni correction was applied to reduce type 1 error rates. The alpha level was set at 0.002, dividing 0.05 by the number of categories (n = 21).

Figure 3 Relationships between the nestedness rankings of all taxonomic and trait categories and island characteristics across 264 islands offshore northern Aotearoa New Zealand. On the y-axis are species categories. Categorisations were taxonomic (fine - all species; coarse - monocots and dicots), growth forms (graminoids, forbs, woody species, and climbers and lianas), and dispersal modes (wind-dispersed, unspecialised, and wind-dispersed). On the x-axis are partial effects. The geological origins of the islands are sedimentary (S) and volcanic (V). Full plots can be found in the supplementary material (Appendices 10, 11, 12, 13). A Bonferroni correction was applied to reduce type 1 error rates. The alpha level was set at 0.002, dividing 0.05 by the number of categories (n = 21). Abbreviation are woody species (woody sp.), animal-dispersed species (animal-disp.), unspecialised (espec.), and wind-dispersed species (wind-disp.)

Figure 1

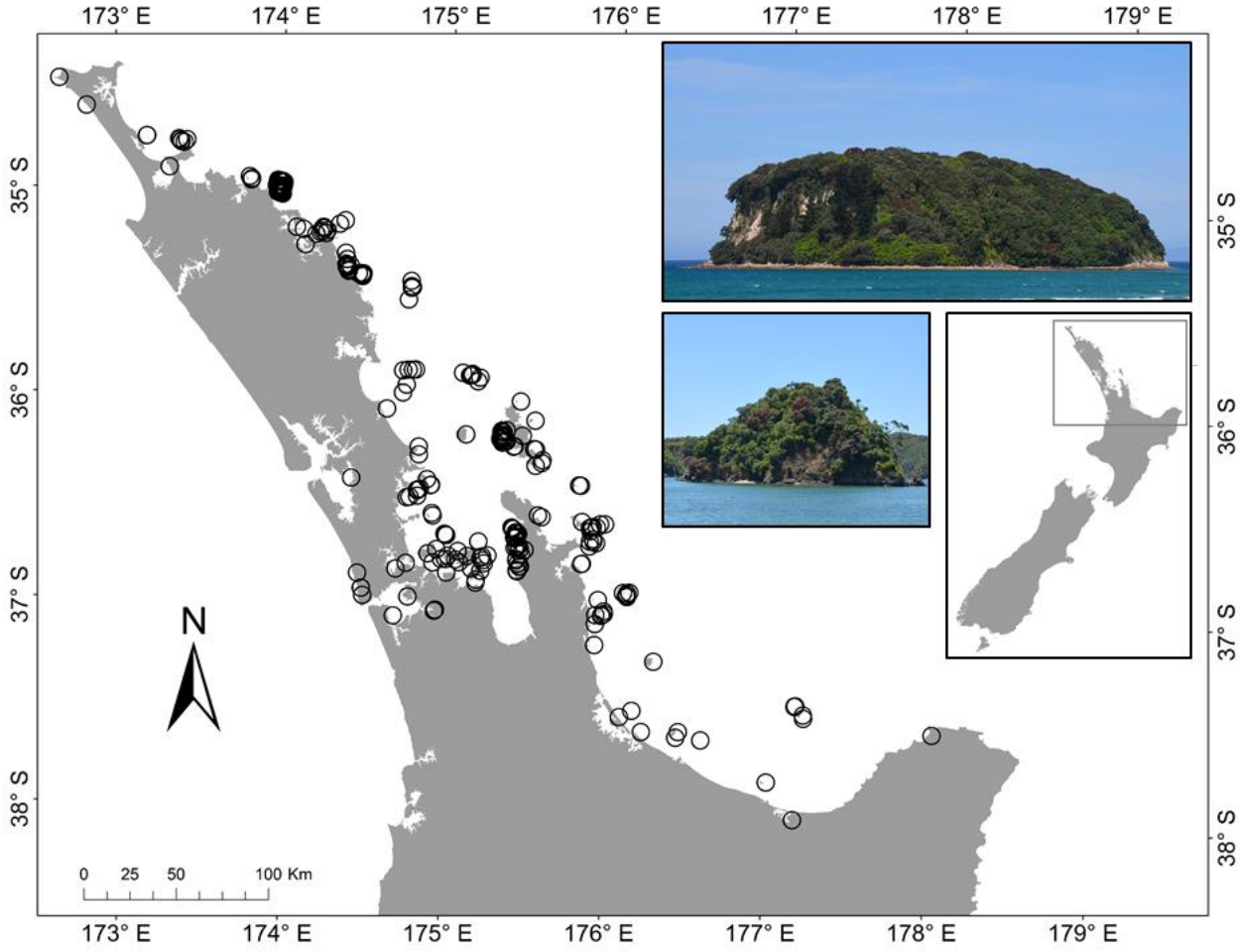

173° E
174° E
175° E
176° E
177° E
178° E
179° E
35° S
36° S
37° S
38° S
N
0 25 50 100 Km

Figure 2

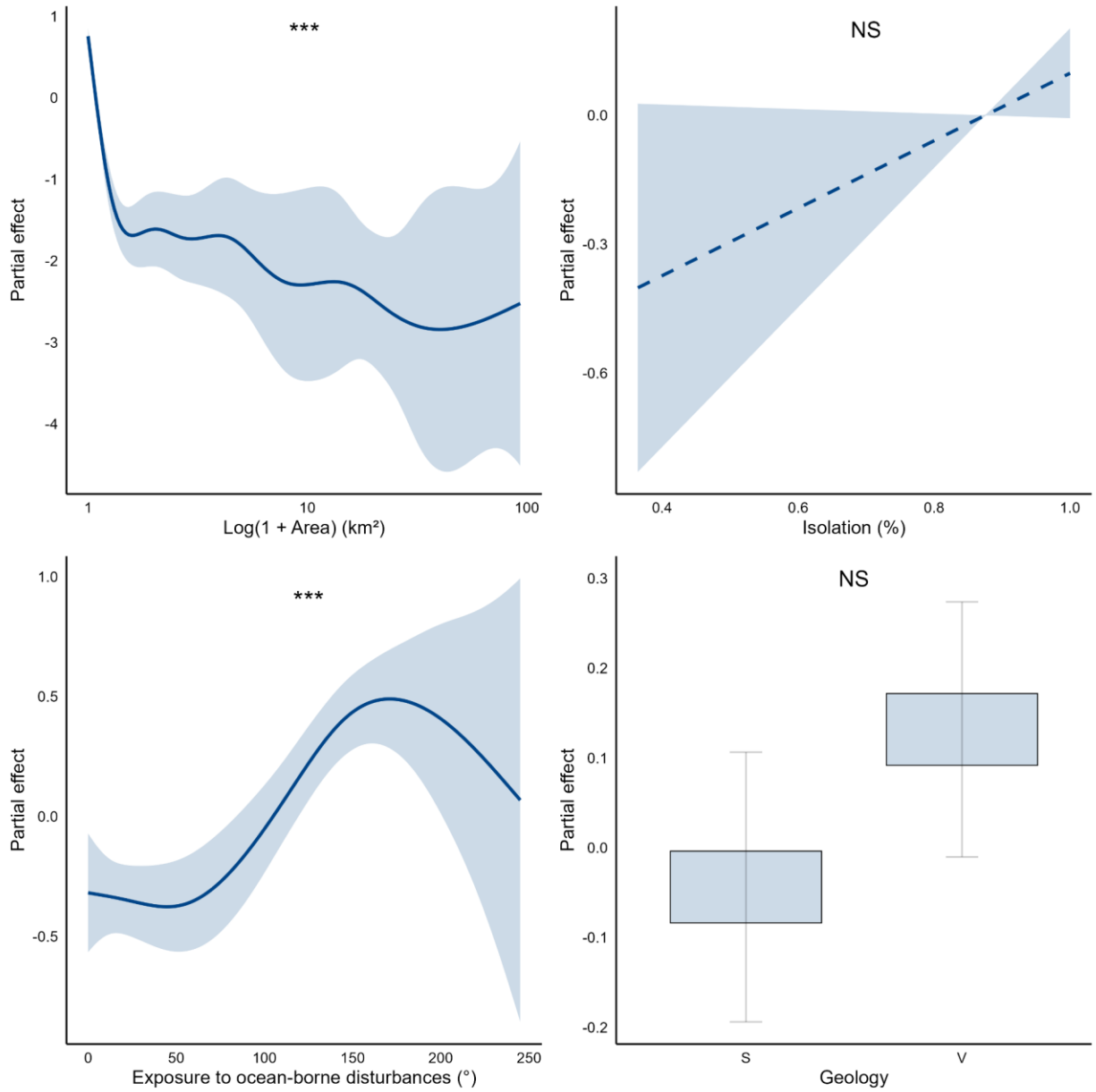
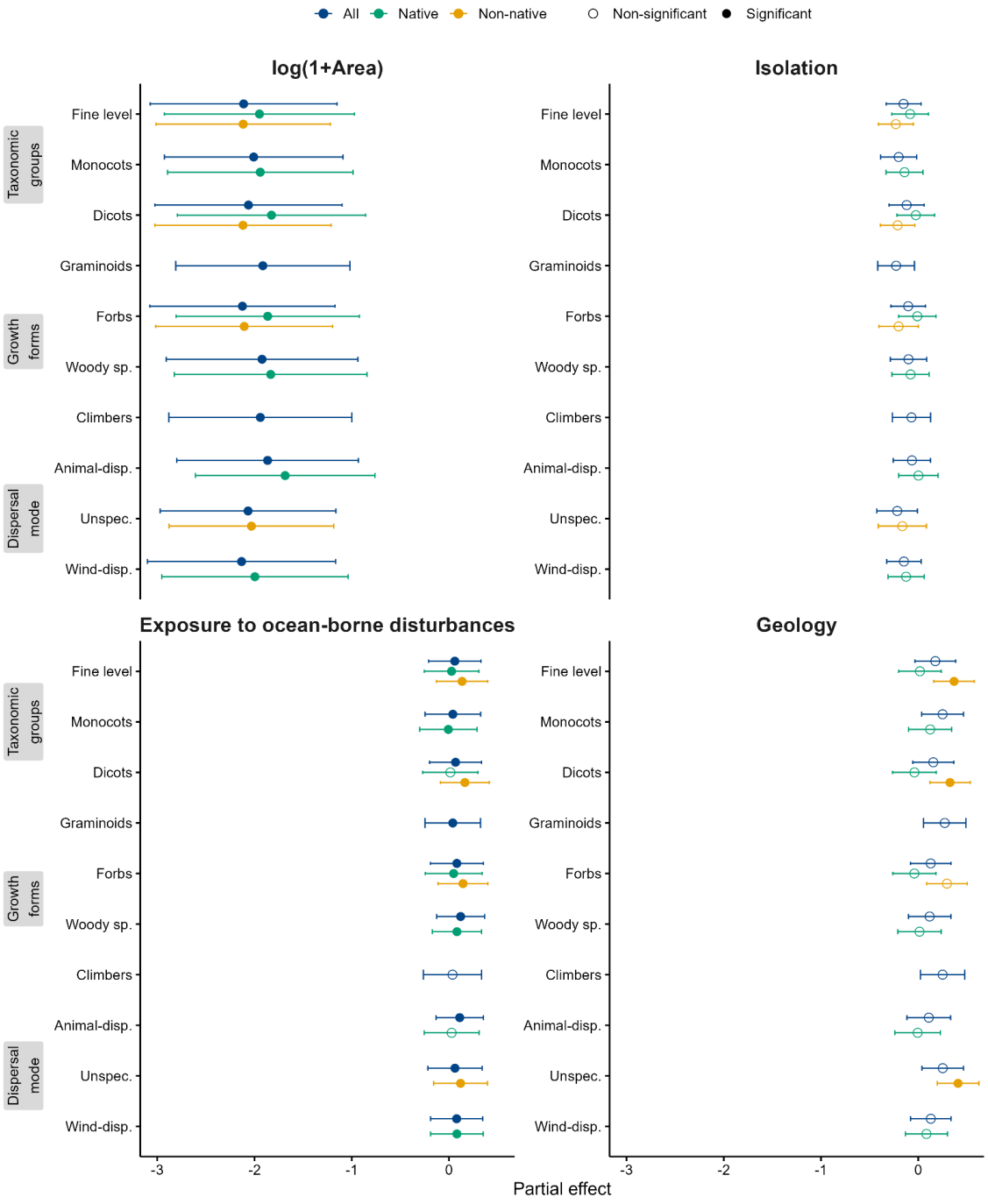

***
Partial effect
Log(1 + Area) (km²)
NS
Isolation (%)
***
Exposure to ocean-borne disturbances (°)
NS
S
V
Geology

Figure 3


All
Native
Non-native
Non-significant
Significant
log(1+Area)
Isolation
Exposure to ocean-borne disturbances
Geology
Taxonomic groups
Growth forms
Dispersal mode
Fine level
Monocots
Dicots
Graminoids
Forbs
Woody sp.
Climbers
Animal-disp.
Unspec.
Wind-disp.
-3
-2
-1
0
Partial effect

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. et al. (2023). Assembly of functional diversity in an oceanic island flora. Nature, 619(7970), 545–550. https://doi.org/10.1038/s41586-023-06305-z

586 Bellingham, P J. (1984). Forest regeneration on Lady Alice Island, Hen and Chickens group.
587 Tane, 30, 31–42.
588 Bellingham, P. J., Towns, D. R., Cameron, E. K. et al. (2010). New Zealand island restoration:
589 seabirds, predators, and the importance of history. New Zealand Journal of Ecology,
590 34(1), 115–136.
591 Burns, K. C., & Neufeld, C. J. (2009). Plant extinction dynamics in an insular metacommunity.
592 Oikos, 118(2), 191–198. https://doi.org/10.1111/j.1600-0706.2008.16816.x
593 Cameron, E. K. (1990). Flora and vegetation of Middle Island, Mercury Islands Group, eastern
594 Coromandel, northern New Zealand. Journal of the Royal Society of New Zealand,
595 20(3), 273–285. https://doi.org/10.1080/03036758.1990.10416822
596 Cameron, E. K., & Young, M. E. (2019). In Vegetation and vascular fora. In: Wade L, Veitch D
597 (eds) Hauturu—the history, flora and fauna of Te Hauturu-o-Toi Little Barrier. (pp. 166–
598 213). Auckland: Massey University Press.
599 Carlquist, S. J. (1974). Island biology. New York: Columbia University Press.
600 https://doi.org/10.5962/bhl.title.63768
601 Carter, Z. T., Perry, G. L. W., & Russell, J. C. (2020). Determining the underlying structure of
602 insular isolation measures. Journal of Biogeography, 47(4), 955–967.
603 https://doi.org/10.1111/jbi.13778
604 Caujapé-Castells, J., Tye, A., Crawford, D. J. et al. (2010). Conservation of oceanic island
605 floras: Present and future global challenges. Perspectives in Plant Ecology, Evolution
606 and Systematics, 12(2), 107–129. https://doi.org/10.1016/j.ppees.2009.10.001
607 Chen, C., Zhan, C., & Wang, Y. (2022). Do functional and phylogenetic nestedness follow the
608 same mechanisms as taxonomic nestedness? Evidence from amphibians in the largest
609 archipelago of China. Journal of Animal Ecology, 91(12), 2424–2436.
610 https://doi.org/10.1111/1365-2656.13824
611 Christensen, N. L., and R. K. Peet. (1984). Convergence During Secondary Forest Succession.

612 Journal of Ecology, 72(1), 25–36. https://doi.org/10.2307/2260004
613 Clarkson, B. D., & Clarkson, B. R. (1994). Vegetation decline following recent eruptions on
614 White Island (Whakaari), Bay of Plenty, New Zealand. New Zealand Journal of Botany,
615 32(1), 21–36. https://doi.org/10.1080/0028825X.1994.10410404
616 Cribari-Neto, F., and Zeileis, A. (2010). Beta Regression in R. Journal of Statistical Software,
617 34(2). https://doi.org/10.18637/jss.v034.i02
618 Daugherty, C. H., Gibbs, G. W., Towns, D. R., & Atkinson, I. A. E. (1990). The significance of
619 the biological resources of New Zealand islands for ecological restoration. Conservation
620 Sciences Publication (New Zealand), (2). Retrieved from
621 https://agris.fao.org/search/en/providers/122578/records/6471d3902a40512c710e72f6
622 Dawson, J. (1988). Forest vines to snow tussocks: the story of New Zealand plants. Wellington:
623 Victoria Univ. Press.
624 Diamond, J. M. (1975a). Assembly of species communities. In *Ecology and Evolution of*
625 *Communities (ed. By M.L. Cody and J.M. Diamond)* (pp. 342–444). Harvard University
626 Press.
627 Diamond, J. M. (1975b). The island dilemma: Lessons of modern biogeographic studies for the
628 design of natural reserves. Biological Conservation, 7(2), 129–146.
629 https://doi.org/10.1016/0006-3207(75)90052-X
630 Diver, K. C. (2008). Not as the crow flies: assessing effective isolation for island biogeographical
631 analysis. Journal of Biogeography, 35(6), 1040–1048. https://doi.org/10.1111/j.1365-
632 2699.2007.01835.x
633 Donaldson, L., Wilson, R. J., & Maclean, I. M. D. (2017). Old concepts, new challenges:
634 adapting landscape-scale conservation to the twenty-first century. Biodiversity and
635 Conservation, 26(3), 527–552. https://doi.org/10.1007/s10531-016-1257-9
636 Dormann, C. F., Gruber, B., & Fründ, J. (2008). Introducing the bipartite Package: Analysing
637 Ecological Networks, 8.

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

Fahrig, L., Watling, J. I., Arnillas, C. A. et al. (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. et al. (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

Guo, Q., Cen, X., Song, R., McKinney, M. L., & Wang, D. (2021). Worldwide effects of non-native species on species–area relationships. *Conservation Biology*, *35*(2), 711–721. https://doi.org/10.1111/cobi.13573

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

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

Ladle, R., & Whittaker, R. J. (2011). *Conservation Biogeography*. Wiley-Blackwell.

König, C., Weigelt, P., & Kreft, H. (2017). Dissecting global turnover in vascular plants. *Global Ecology and Biogeography*, *26*(2), 228–242. https://doi.org/10.1111/geb.12536

Li, S., Pan, Q., Yang, X., Gao, Y., & Xu, M. (2025). Differential influences of island biogeographic effects on the diversity among three plant life-forms. Global Ecology and Conservation, 58, e03499. https://doi.org/10.1016/j.gecco.2025.e03499

Lomolino, M. V. (1990). The target area hypothesis: the influence of island area on immigration rates of non-volant mammals. Oikos, 57(3), 297–300.

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

Long, J. D., Trussell, G. C., & Elliman, T. (2009). Linking invasions and biogeography: Isolation differentially affects exotic and native plant diversity. *Ecology*, *90*(4), 863–868. https://doi.org/10.1890/08-1337.1

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

690 nestedness in habitat islands: a synthetic analysis of multiple datasets. Diversity and
691 Distributions, 21(4), 392–404. https://doi.org/10.1111/ddi.12298
692 McGlone, M. S., Buitenwerf, R., & Richardson, S. J. (2016). The formation of the oceanic
693 temperate forests of New Zealand. New Zealand Journal of Botany, 54(2), 128–155.
694 https://doi.org/10.1080/0028825X.2016.1158196
695 Mehltreter, K. (2010). Fern Conservation. In Mehltreter K, Walker LR, Sharpe JM (eds). Fern
696 Ecology (pp. 323–359). Cambridge: Cambridge University Press.
697 Millien, V., Zhan, C., Li, Y., Wang, J., & Wang, Y. (2024). A global assessment of nested
698 patterns in insular mammal assemblages. Global Ecology and Biogeography, 33(9),
699 e13885. https://doi.org/10.1111/geb.13885
700 Mologni, F. (2022). Different levels of disturbance influence the distributional patterns of native
701 but not exotic plant species on New Zealand small islands. Frontiers of Biogeography,
702 14(2), e54598. https://doi.org/10.21425/F5FBG54598
703 Mologni, F., Bellingham, P. J., Cameron, E. K., Dinh, K., Wright, A. E., & Burns, K. C. (2022).
704 Functional traits explain non-native plant species richness and occupancy on northern
705 New Zealand islands. Biological Invasions, 24(7), 2135–2154.
706 https://doi.org/10.1007/s10530-022-02762-1
707 Mologni, F., Bellingham, P. J., Cameron, E. K., & Wright, A. E. (2024). Time since first
708 naturalization is key to explaining non-native plant invasions on islands. Journal of
709 Biogeography, 51(8), 1340–1350. https://doi.org/10.1111/jbi.14825
710 Mologni, F., Bellingham, P. J., Tjørve, E., Cameron, E. K., Wright, A. E., & Burns, K. C. (2021).
711 Similar yet distinct distributional patterns characterize native and exotic plant species
712 richness across northern New Zealand islands. Journal of Biogeography, 48(7), 1731–
713 1745. https://doi.org/10.1111/jbi.14110
714 Morrison, L. W. (2013). Nestedness in insular floras: spatiotemporal variation and underlying
715 mechanisms. Journal of Plant Ecology, 6(6), 480–488. https://doi.org/10.1093/jpe/rtt002

716 Morrison, L. W., & Spiller, D. A. (2008). Patterns and processes in insular floras affected by
717 hurricanes. Journal of Biogeography, 35(9), 1701–1710. https://doi.org/10.1111/j.1365-
718 2699.2008.01910.x
719 Moser, D., Lenzner, B., Weigelt, P. et al. (2018). Remoteness promotes biological
720 invasions on islands worldwide. *Proceedings of the National Academy of Sciences*,
721 *115*(37), 9270–9275. https://doi.org/10.1073/pnas.1804179115
722 Negoita, L., Fridley, J. D., Lomolino, M. V., Mittelhauser, G., Craine, J. M., & Weiher, E. (2016).
723 Isolation-driven functional assembly of plant communities on islands. Ecography, 39(11),
724 1066–1077. https://doi.org/10.1111/ecog.01551
725 Neufeld, C. J., Starko, S., & Burns, K. C. (2017). Disturbance and diversity in a continental
726 archipelago: a mechanistic framework linking area, height, and exposure. Ecosphere,
727 8(10), e01957. https://doi.org/10.1002/ecs2.1957
728 New Zealand Plant Conservation Network. (2024). New Zealand Plant Conservation Network.
729 Retrieved from https://www.nzpcn.org.nz/
730 Norton, D. A., Delange, P. J., Garnock-Jones, P. J., & Given, D. R. (1997). The role of seabirds
731 and seals in the survival of coastal plants: lessons from New Zealand Lepidium
732 (Brassicaceae). Biodiversity & Conservation, 6(6), 765–785.
733 https://doi.org/10.1023/B:BIOC.0000010401.93153.29
734 Ogden, J., & Perry, G. L. W. (2023). Ranges of woody plant species and ferns on forested
735 elevational gradients on Aotea-Great Barrier Island, New Zealand: the role of zones of
736 permanent and temporary establishment. New Zealand Journal of Ecology, 47(1), 3512.
737 https://doi.org/10.20417/nzjecol.47.3512
738 Oksanen, J., Simpson, G. L., Blanchet, F. G. et al. (2024). vegan: Community Ecology Package.
739 https://doi.org/10.32614/CRAN.package.vegan
740 Patterson, B. D., & Atmar, W. (1986). Nested subsets and the structure of insular mammalian
741 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. et al. (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

Pretto, F., Celesti-Grapow, L., Carli, E., Brundu, G., & Blasi, C. (2012). Determinants of non-native plant species richness and composition across small Mediterranean islands. *Biological Invasions*, *14*(12), 2559–2572. https://doi.org/10.1007/s10530-012-0252-7

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

Quinn

, S. L., Wilson, J. B., & Mark, A. F. (1987). The island biogeography of Lake Manapouri, New Zealand. Journal of Biogeography, 14(6), 569–-581. https://doi.org/10.2307/2844881

Richardson, S. J., Clayton, R., Rance, B. D., Broadbent, H., McGlone, M. S., & Wilmshurst, J. M. (2015). Small wetlands are critical for safeguarding rare and threatened plant species. Applied Vegetation Science, 18(2), 230–241. https://doi.org/10.1111/avsc.12144

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. et al. (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

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

Tilman, D. (1982). *Resource Competition and Community Structure*. Princeton University Press.

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

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., Kissling, D. W., Kisel, Y. et al. (2015). Global patterns and drivers of phylogenetic structure in island floras. Sci Rep 5:12213. https://doi.org/ 10.1038/srep12213

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

Whittaker, R. J., Rigal, F., Borges, P. A. V. et al. (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. et al. (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

Wilson, J. B. (1988). Community structure in the flora of islands in Lake Manapouri, New Zealand. Journal of Ecology, 76(4), 1030–1042. https://doi.org/10.2307/2260631

Wood, S. N. (2017). *Generalized Additive Models: An Introduction with R, Second Edition* (2nd ed.). Chapman and Hall/CRC. https://doi.org/10.1201/9781315370279

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

Wu, G., Ye, Q., Liu, H. et al. (2025). Shaded habitats drive higher rates of fern diversification. *Journal of Ecology*, *113*(5), 1200–1208. https://doi.org/10.1111/1365-2745.70026

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

Supplementary material

Appendix S1 - NODF results for all species

Appendix S2 - NODF results for native species

Appendix S3 - NODF results for non-native species

Appendix S4 - Correlation matrix for the continuous predictors used in the models

Appendix S5 - Spearman partial correlation coefficients for all, native, and non-native species

Appendix S6 - Model selection

Appendix S7 - Beta models with smooth term including all islands and excluding geology

Appendix S8 - Beta models with smooth term excluding mixed geology islands and geology

Appendix S9 - Beta models with smooth term including mixed geology islands and geology

Appendix S10 - Partial effect plots showing the relationship between nestedness rankings and area

Appendix S11 - Partial effect plots showing the relationship between nestedness rankings and isolation

Appendix S12 - Partial effect plots showing the relationship between nestedness rankings and exposure to ocean-borne disturbances

Appendix S13 - Partial effect plots showing the relationship between nestedness rankings and geology

Appendix S14 - R script

Appendix S15 - Full matrix