

UC Merced

Frontiers of Biogeography

Title

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

Permalink

<https://escholarship.org/uc/item/4qx086dz>

Journal

Frontiers of Biogeography, 14(2)

Author

Mogni, Fabio

Publication Date

2022

DOI

10.21425/F5FBG54598

Supplemental Material

<https://escholarship.org/uc/item/4qx086dz#supplemental>

Copyright Information

Copyright 2022 by the author(s). This work is made available under the terms of a Creative Commons Attribution License, available at <https://creativecommons.org/licenses/by/4.0/>

Peer reviewed



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

Fabio Mologni^{1*} 

¹School of Biological Sciences, Victoria University of Wellington, P.O. Box 600, Wellington, New Zealand.

*Correspondence: fabio.mologni@vuw.ac.nz

Abstract

Disturbances of oceanic origin can severely affect plant communities on islands, but it is unclear whether they promote or deter biological invasions. Here, I collected floristic data from 97 small islands subject to different levels of ocean-borne disturbances (i.e. inside and outside Wellington Harbour, New Zealand). First, I tested how relationships between the richness of native and exotic species and island characteristics (e.g. area, isolation, height, distance from nearest dwelling) changed depending on island location. Next, I assessed compositional differences on inner and outer islands for both native and exotic species, and how they vary with geographic distance between islands (i.e. distance-decay). Results show that the richness of both native and exotic plant species was similarly related to island characteristics regardless of island location. Both native and exotic species richness consistently increased with area and nearest dwelling. However, only exotics richness always declined with isolation, while natives richness alone consistently increased with height (elevation). Natives on outer, more exposed islands were floristically more homogenous, and compositional differences changed less strongly with the distance between islands than inside Wellington harbour. In contrast, exotics exhibited similar distributional patterns regardless of island location. Different levels of ocean-borne disturbances might explain distinct distributional patterns in native species. Conversely, results for exotic species might reflect a lack of coastal specialists in the species pool. Perhaps time-lags in the invasion process and non-equilibrium dynamics play a role as well. Conservation bodies should similarly manage islands sustaining different levels of ocean-borne disturbances.

Highlights

- How disturbances of oceanic origin influence plant invasions on islands is still poorly understood.
- I addressed this problem by investigating how native and exotic species are distributed on 97 small islands sustaining varying levels of ocean-borne disturbances.
- Native and exotic species richness were similarly related to island characteristics (area, isolation, height, nearest dwelling) regardless of island location.
- Native species composition was more homogenous and changed less strongly with distance between islands on outer, more exposed islands; however, exotic species composition did not change depending on island location.
- While results for natives might reflect differences in disturbance levels, those for exotics may be related to lack of coastal specialists in the species pool, invasion time-lags and non-equilibrium dynamics.

Keywords: composition, distance-decay, disturbances, island biogeography, Jaccard, New Zealand, small islands, species richness

Introduction

Disturbances can have devastating effects on insular floras (Whittaker 1995, Whittaker 2000, Morrison and Spiller 2008, Burns and Neufeld 2009). Perturbations can remove plant biomass (Grime and Pierce 2012), increase extinction rates (Whittaker 1995), and change

the compositional structure of insular communities (Morrison 2014). However, whether disturbance promotes island invasion is still poorly understood.

The notion that disturbances facilitate biological invasions is debated (Hobbs and Huenneke 1992, Moles et al. 2012, Jauni et al. 2015). Earlier work

shows that context, type of disturbance and frequency and severity of the disturbance are all crucial factors (Moles et al. 2012). On islands, one of the most pervasive types of disturbance are those of oceanic origin, such as waves, storms and wind shear (Whittaker 1995). Ocean-borne disturbances can severely influence insular floras (Whittaker 2000, Morrison and Spiller 2008). In protected locations, disturbance events are generally less intense and frequent, and conditions more lenient for vascular plants (Abbott 1977, Morrison 2014). Results to date vary as to whether exotic species are facilitated (Bellingham et al. 2005, Burns 2016) or disadvantaged (Mologni et al. 2021) by ocean-borne disturbances.

Species richness on islands often declines with ocean-borne disturbances (Abbott 1977, Morrison 2002, Mologni et al. 2021). Waves and winds can reduce the habitable surface area of an island (Neufeld et al. 2017). Thus, given two small islands of similar size and height, the one in a more disturbed location will have fewer species (Abbott 1977, Neufeld et al. 2017, Mologni et al. 2021). Additionally, species on smaller islands are more prone to extinction, a process enhanced by perturbation (Whittaker 1995). After each extinction event, species need to recolonize (MacArthur and Wilson 1967). Thus, populations in disturbed locations might depend more strongly on immigration from nearby communities.

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

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

Materials and Methods

Study system

The Wellington coastline (41°16'47" S, 174°49'56" E) is surrounded by numerous small islands, situated in close proximity to the coast. Most of them emerged recently, during an intense earthquake that uplifted the coastline by approximately 6 meters in 1855 (Burns 2016). The study system is homogeneous in its geological composition (i.e. greywacke) (Burns 2015) and contains several seabird colonies. The region is struck by numerous storms, mostly originating in southern latitudes (Pickrill and Mitchell 1979).

I surveyed 97 small, easily accessible intertidal islands, 70 outside Wellington harbour and 27 inside (Fig. 1, Appendix S1 and Table S1). They are mainly rocky outcrops, with small amounts of soil occasionally accumulating in rock cracks. Vegetation on rocky outcrops along the Wellington coast is dominated by a few low growing, stress-tolerant species, with leathery or succulent leaves (Dawson 1988). These islands are generally close to human settlement (Appendix S1, Table S1).

Environmental conditions vary inside and outside the harbour. Inner islands are more protected and predominantly hit by north-westerlies, whereas outer islands are fully exposed to south-easterlies. Inner islands are also undergoing intense mammal eradication activities (Predator Free Wellington 2021). Eradication efforts on outer islands are comparably lower (except for the easternmost islands); however, they contain the larger seabird community in the study system, and they are part of, or in close proximity to, a Marine Reserve.

Data collection

I thoroughly surveyed each island during the 2020-2021 austral summer and quantified the number of vascular plants for a total of 37 species (Table S2 & S3). Islands were searched until no more species could be found for at least 5 minutes. This process was repeated twice. For each species, I assessed its origin (i.e. native or exotic). Species origin and nomenclature were compiled following the New Zealand Plant Conservation Network (New Zealand Plant Conservation Network 2021, accessed in January 2021).

Island characteristics were manually quantified in the field and by using ArcGIS 10 (ESRI 2011). I estimated island area (m²) by multiplying islands' widths and lengths measured at the widest and longest point. Isolation was quantified as the shorter distance separating an island from the nearest mainland plant community (m). I calculated height as the vertical distance between the top of an island and the lower limit of the intertidal zone, delimited by the lowest lichen boundary. Lastly, I calculated the distance from the nearest dwelling (hereafter nearest dwelling) to account for human activities.

Compositional differences between pairs of islands were calculated using a Jaccard similarity index. I computed the index in R, using the Vegan package,

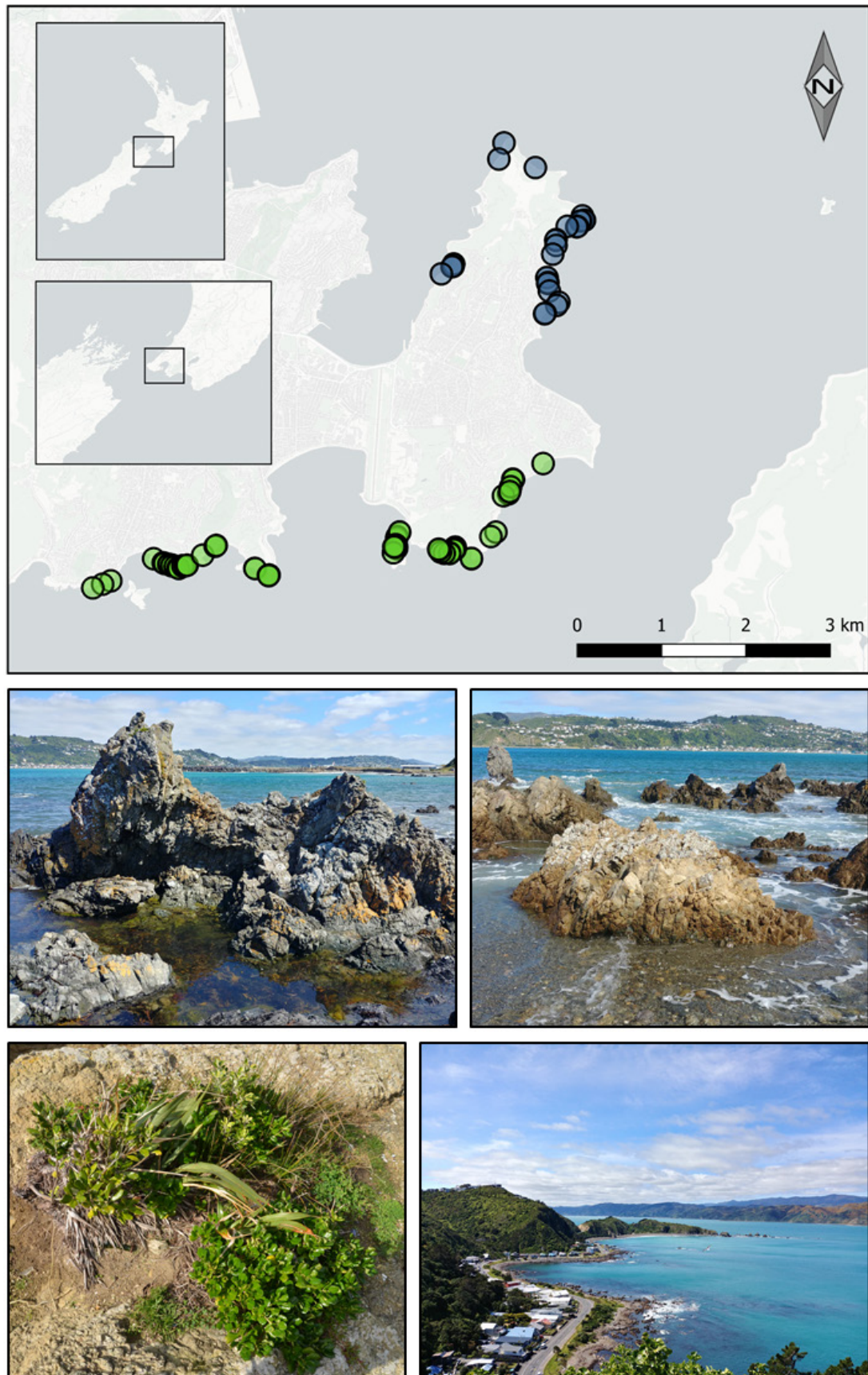


Figure 1. Map of the study area (top). Inner islands ($n = 27$) are in blue and outer islands ($n=70$) are in green. In the centre are two of the surveyed islands, while at the bottom are a typical plant community (left) and the landscape (right) of the study system.

version 2.5-7 (Oksanen et al. 2020). Then, I measured the distance between each pair of islands using the proximity tool in ArcGIS 10 (ESRI 2011).

Statistical analyses

Before inclusion in a model, I examined each independent variable using a Pearson correlation coefficient and a variance inflation factor (VIFs). I set as a cut-off 0.8 and 3, respectively (Berry and Feldman 1985, Zuur et al. 2010). No variable exceeded these thresholds (Table S4 and Figure S1).

To test whether species richness responds differently to island characteristics inside and outside the harbour, I used a linear model with species richness as the response variable and island characteristics (area, isolation, height, and nearest dwelling) as predictors. Location (inside/outside the harbour) was included as an interaction term. Species richness (+1), area, isolation and height were log-transformed, and nearest dwelling was square root-transformed. This analysis was run for native and exotic species richness separately.

To test if islands inside and outside the harbour show compositional differences, I used a Jaccard similarity index. I then contrasted Jaccard indexes between islands inside and outside the harbour. Since Jaccard indexes were slightly right-skewed, I used both a linear and a quasipoisson model. Analyses were run separately for native and exotic species. Islands lacking in either native or exotic species were excluded (number of islands lacking natives=1, number of islands lacking exotics=52).

To test whether distance-decay relationships differ between inner and outer islands, I regressed the Jaccard similarity index between two islands with the distance separating them. I used both a linear and quasipoisson model and variables were not transformed. The same approach was employed for native and exotic species separately. All analyses were run in R 4.0.4 (R Core Team 2020).

Results

Of the total 37 species across the islands, 20 (54.05%) were native and 17 (45.95%) were exotic. On average, islands contained 2.9 native species and 0.9 exotic species (Table S3). Islands ranged in size from less than a square meter to 166 m² and were all found within 41.3 metres from the nearest mainland plant community (Table S1). The tallest island reached 5 meters, while the lowest was only 0.2 metres high (Table S1). They were located from 20 m to 840 m from the nearest dwelling (Table S1).

The plant richness of both native and exotic species displayed similar relationships with area, isolation, height, and nearest dwelling regardless of island location (Table S5). Native and exotic species richness consistently increased with area and nearest dwelling (Fig. 2 and & Table S5 & Table S6). Exotic species richness always displayed negative relationships with isolation, while native species richness declined with isolation on inner islands but was unrelated to it on

outer islands (Fig. 2 and & Table S5 & Table S6). Native species richness always showed positive relationships with height, while exotic species richness increased with height on outer islands but was unrelated to it on inner islands (Fig. 2 and & Table S5 & Table S6).

Jaccard similarity indexes were significantly higher on outer islands for native species, indicating they vary less strongly in composition than inner islands (Fig. 3a). On the other hand, compositional differences in exotic species did not differ between the inside or outside of the harbour (Fig. 3b). Results were consistent using a linear or quasipoisson model (Table S7).

Negative distance-decay curves were observed on both inner and outer islands for native species (Fig. 4a & Table S8). However, Jaccard similarity indexes declined faster with the distance separating two islands on inner than outer islands. Conversely, distance-decay curves were not significant for exotic species and did not differ between inner and outer islands (Fig. 4b & Table S8). Results were consistent using a linear or a quasipoisson model (Table S7).

Discussion

In this study, I compiled a database of plant species richness and composition for 97 very small islands inside and outside Wellington Harbour, New Zealand. Overall results show that native and exotic plant species richness responded similarly to all island characteristics. However, native species were floristically more homogenous on outer than inner islands. Additionally, native species spatially turned over more rapidly on islands inside than outside the harbour. In contrast, exotic species did not differ in composition depending on island location.

Relationships between species richness and both area and height were generally positive and similar between inner and outer islands, and for both native and exotic species. Large, tall islands typically have a greater surface; thus, they can accommodate more species (MacArthur and Wilson 1967). Additionally, I observed that islands greater in size and height have a larger proportion of soil accumulating in rock cracks. Even small amounts of sediments can allow several species to survive by providing anchorage, retaining water, and supplying nutrients. Future studies should consider including a measure of soil availability (Schrader et al. 2019). Tall, large islands are also less likely to be overtopped by waves (Abbott 1977, Burns and Neufeld 2009).

Relationships between richness and isolation were similar on inner and outer islands for both groups of species. However, exotics declined in number with isolation whereas natives on inner islands were only weakly related to isolation, and natives on outer islands were not significantly related. Species richness typically decreases with distance from the source pool due to reduced immigration rates (MacArthur and Wilson 1967). However, islands within this study system are very close to mainland plant communities, providing a possible explanation why native richness was consistently unrelated to isolation. By contrast, negative exotic species-isolation relationships might

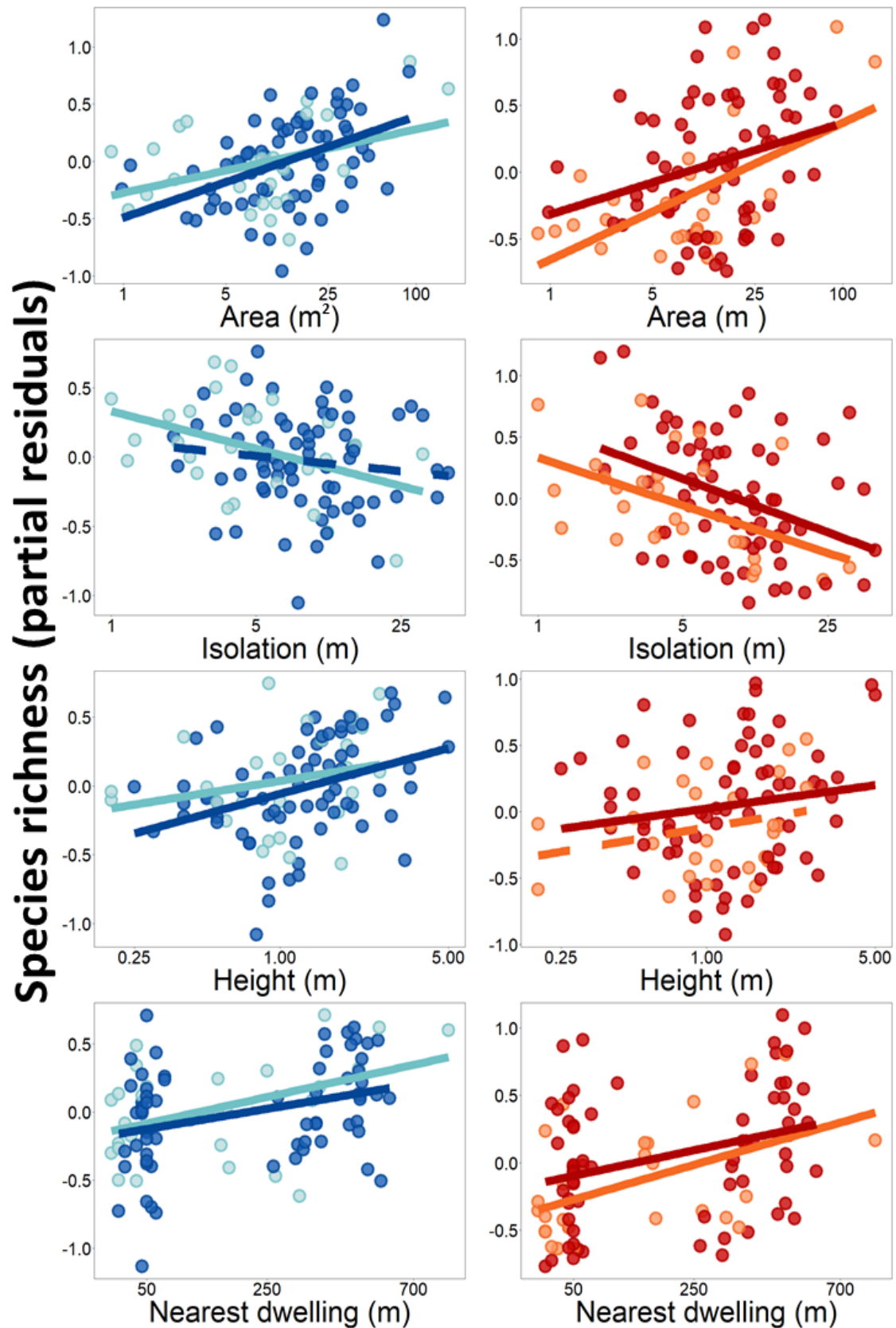


Figure 2. Relationships between native and exotic plant species richness (partial residuals) and island area, isolation, height and nearest dwelling on 97 islands off the coast of Wellington, New Zealand. Blue and red colours illustrate native and exotic species, respectively, while light and dark colours indicate inner and outer islands, respectively. Solid lines indicate significant relationships, while dashed lines display non-significant relationships. To conform to assumptions, species richness (+1), area, isolation and height were log-transformed, and nearest dwelling was square root-transformed.

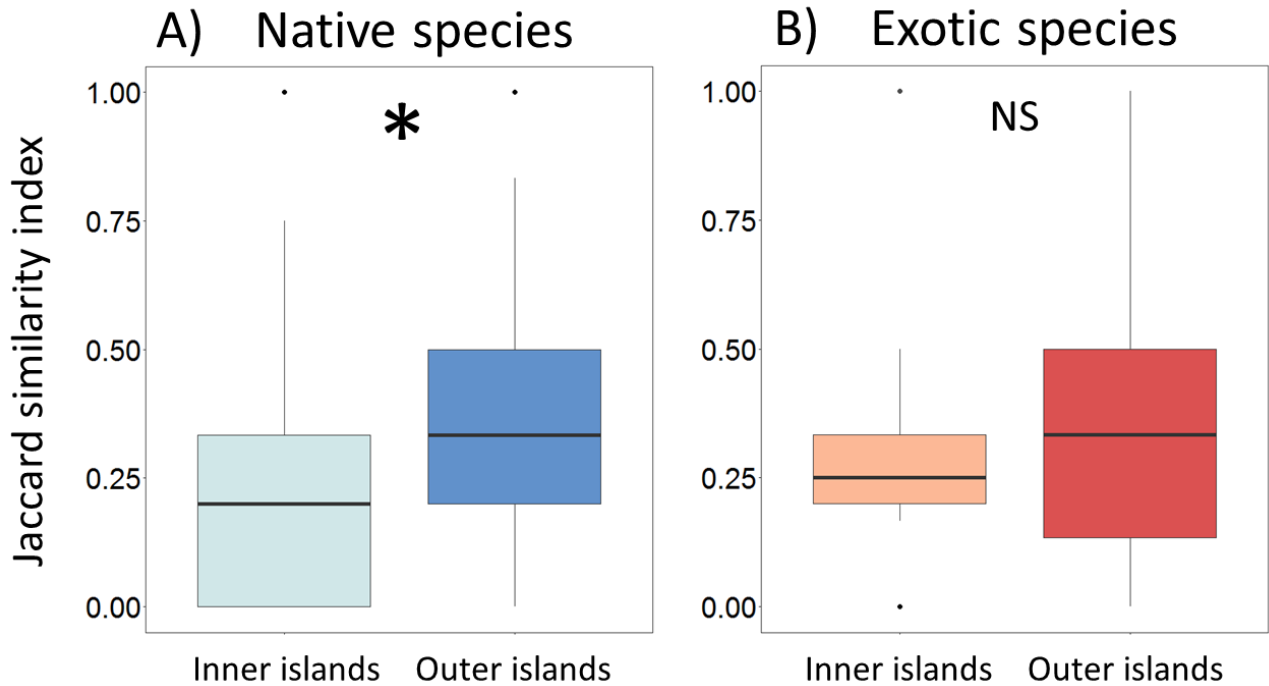


Figure 3. Compositional differences of plant species among 97 islands off the coast of Wellington, New Zealand. On the y-axis are Jaccard similarity indexes, while on the x-axis are inner and outer islands. On the left are native species (A), while on the right are exotic species (B). Symbol colours indicate native (blues) and exotic (reds) species, whereas hues show inner (light) and outer (dark) islands. Asterisks indicate significant differences between inner and outer islands.

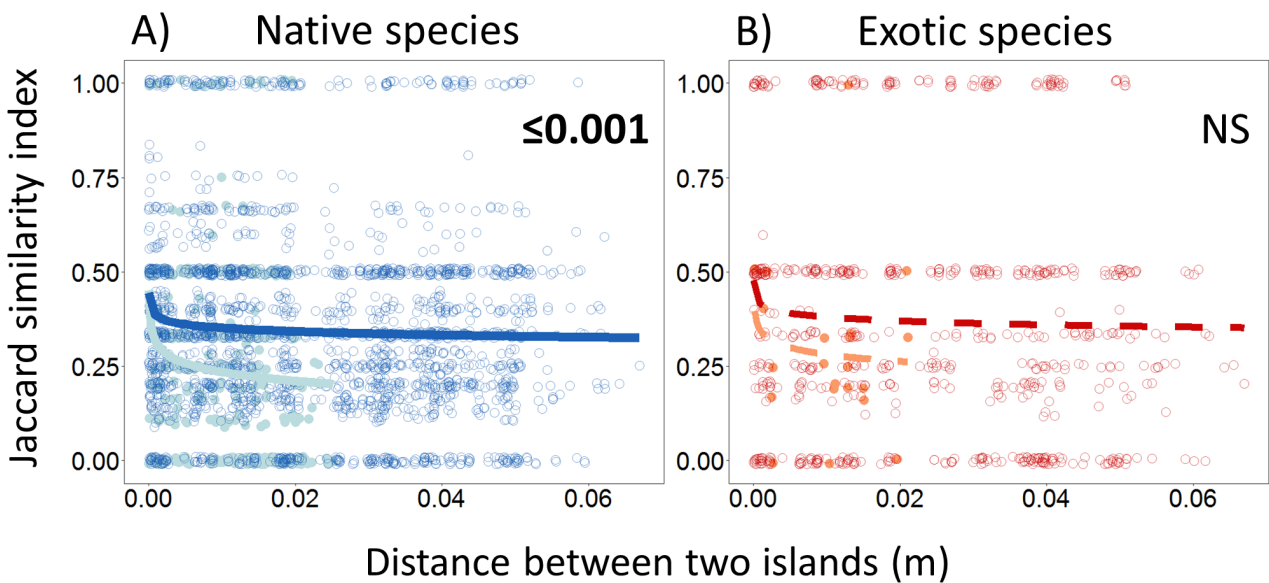


Figure 4. Distance-decay relationships of plant species on 97 islands off the coast of Wellington, New Zealand. On the y-axis are Jaccard similarity indexes, while on the x-axis is the distance between each pair of islands. On the left are native species (A), while on the right are exotic species (B). Symbol colours illustrate native (blues) and exotic (reds) species, whereas hues indicate inner (light) and outer (dark) islands. On the top right are significant (p-value in bold) or not significant (NS) differences between inner and outer islands.

reflect time-lags in the invasion process (González-Moreno et al. 2017, Coutts et al. 2018).

Both native and exotic species richness declined with proximity to the nearest dwelling, on inner

and outer islands alike, which is surprising since proximity to humans usually favours biological invasions (Blackburn et al. 2008, Pretto et al. 2012, Chiarucci et al. 2017, Paudel et al. 2017). Here, only a

very narrow stretch of land exists between the forested hills and the sea, which is the only available area for grasslands and specialized coastal communities. Most of this area is now in urban housing, which has reduced the propagule pressure from the mainland, thus lowering immigration rates (Shmida and Wilson 1985). Alternatively, I observed that islands distant from houses often host larger seabird communities (e.g. at Moa Point). Seabirds' guano increase soil nutrients (Grant-Hoffman et al. 2010, Ellis et al. 2011), allowing more species to successfully colonize them. Additionally, seabirds might also act as seed dispersers (Abbott 1977, Ellis 2005, Magnússon et al. 2009, Calvino-Cancela 2011).

Natives on outer islands were compositionally more homogenous than on inner islands. If these islands are subject to more frequent or intense storms, waves and winds, only a few, specialized species might survive on them (i.e. environmental filtering, Gillham 1960b, Liu et al. 2019). Conversely, in more lenient conditions a larger number of species can establish a viable population (Abbott 1977), generating a greater compositional variability. Additionally, contrasting winds might favour the immigration of species with specific dispersal syndromes, such as water- or wind-dispersed (Abbott and Black 1980, Whittaker 1995). Where winds and storms are more frequent, species with such dispersal syndromes might be more common, homogenizing insular floristic composition.

Compositional differences in native species increased with distance between islands, and more so inside the harbour. This archipelago is composed of very small islands, which can only house a few species (Lomolino and Weiser 2001). Therefore, early colonization could be crucial for establishing a viable population. If so, species close to an island have more chances to be early, successful colonizers. Assuming floristic differences among mainland communities increase with distance as well, this process might generate insular distance-decay relationships in native species. Additionally, differences between inner and outer islands might be a product of a more homogenous flora on the former.

While the distributional patterns of native species differed on inner and outer islands, those of exotics did not. First, exotic species composition was relatively homogeneous on both inner and outer islands. Second, no significant distance-decay relationships were observed. Both results might be an indication that maybe only a few, well-adapted exotics can survive on these islands (Burns 2016).

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

extinction following each major disturbance event (i.e. non-equilibrium dynamics, Whittaker 1995, 2000; Morrison 2010).

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

In this study, native species composition, but not richness, changed depending on island location, perhaps due to varying disturbance levels. In contrast, distributional patterns of exotic species were similar on all islands. Only a few, well-adapted exotic species appear to be able to withstand harsh coastal environments, indicating that biological invasions are not always favoured by disturbances (Moles et al. 2012). Previous work indicates that exotic species are particularly susceptible to ocean-borne disturbances, especially on small islands (Mologni et al. 2021). I suggest exotic species management not to treat these islands differently depending on levels of disturbance. Overall, this study illustrates that investigating species distributional patterns on very small islands can substantially contribute to our understanding of insular plant invasions (Burns 2015, Burns 2016).

Acknowledgements

I thank K.C. Burns and P.J. Bellingham for their invaluable insights. Funding was awarded to FM by the Victoria University of Wellington through a Doctoral Research Scholarship. A regular permit was obtained from the Wellington City Council and Health and Safety procedures were carefully followed during fieldwork.

Data Accessibility Statement

The data are available as supplementary material.

Supplementary Material

The following materials are available as part of the online article at <https://escholarship.org/uc/fb>

Table S1. List of parameters used to investigate patterns in plant species richness on 97 small islands off the coast of Wellington, New Zealand.

Table S2. Plant species found during field surveys.

Table S3. Native and exotic plant species richness on 97 small islands off the coast of Wellington.

Table S4. Variance inflation factor for the parameters included in the models.

Table S5. Differences in how the richness of native and exotic plant species respond to island characteristics.

Table S6. Results from multiple linear regression models exploring the relationship between the plant

richness of native and exotic species and island characteristics.

Table S7. Results of linear and quasipoisson models contrasting Jaccard similarity indexes and distance-decay relationships of inner and outer islands for native and exotic plant species.

Table S8. Distance-decay relationships of native and exotic plant species on inner and outer islands.

Figure S1. Correlation matrix displaying the Pearson's correlation coefficients and relative plots.

Appendix S1. Characteristics of 97 islands offshore Wellington harbour, New Zealand.

References

- Abbott, I. (1977) Species richness, turnover and equilibrium in insular floras near Perth, Western Australia. *Australian Journal of Botany*, 25, 193–208. <https://doi.org/10.1071/BT9770193>.
- Abbott, I. & Black, R. (1980) Changes in species composition of floras on islets near Perth, Western Australia. *Journal of Biogeography*, 7, 399. <https://doi.org/10.2307/2844658>.
- Bellingham, P.J., Tanner, E.V.J. & Healey, J.R. (2005) Hurricane disturbance accelerates invasion by the alien tree *Pittosporum undulatum* in Jamaican montane rain forests. *Journal of Vegetation Science*, 16, 675–684. <https://doi.org/10.1111/j.1654-1103.2005.tb02410.x>.
- Berry, W.D. & Feldman, S. (1985) Multiple regression in practice (Quantitative applications in the social sciences), SAGE Publications, Thousand Oaks, CA.
- Blackburn, T.M., Cassey, P. & Lockwood, J.L. (2008) The island biogeography of exotic bird species. *Global Ecology and Biogeography*, 17, 246–251. <https://doi.org/10.1111/j.1466-8238.2007.00361.x>.
- Burns, K.C. (2015) A theory of island biogeography for exotic species. *The American Naturalist*, 186, 441–451. <https://doi.org/10.1086/682934>.
- Burns, K.C. (2016) Native-exotic richness relationships: a biogeographic approach using turnover in island plant populations. *Ecology*, 97, 2932–2938. <https://doi.org/10.1002/ecy.1579>.
- Burns, K.C. & Neufeld, C.J. (2009) Plant extinction dynamics in an insular metacommunity. *Oikos*, 118, 191–198. <https://doi.org/10.1111/j.1600-0706.2008.16816.x>.
- Calvino-Cancela, M. (2011) Gulls (Laridae) as frugivores and seed dispersers. *Plant Ecology*, 212, 1149–1157. <https://doi.org/10.1007/s11258-011-9894-2>.
- Chiarucci, A., Fattorini, S., Foggi, B., Landi, S., Lazzaro, L., Podani, J. & Simberloff, D. (2017) Plant recording across two centuries reveals dramatic changes in species diversity of a Mediterranean archipelago. *Scientific Reports*, 7, 1–11. <https://doi.org/10.1038/s41598-017-05114-5>.
- Coutts, S.R., Helmstedt, K.J. & Bennett, J.R. (2018) Invasion lags: the stories we tell ourselves and our inability to infer process from pattern. *Diversity and Distributions*, 24, 244–251. <https://doi.org/10.1111/ddi.12669>.
- Dawson, J.W. (1988) Forest vines to snow tussocks: the story of New Zealand plants. Victoria University Press, Wellington, NZ.
- Dengler, J. (2010) Robust methods for detecting a small island effect. *Diversity and Distributions*, 16, 256–266. <https://doi.org/10.1111/j.1472-4642.2010.00646.x>.
- Ellis, J.C. (2005) Marine birds on land: a review of plant biomass, species richness, and community composition in seabird colonies. *Plant Ecology*, 181, 227–241. <https://doi.org/10.1007/s11258-005-7147-y>.
- Ellis, J.C., Bellingham, P.J., Cameron, E.K., Croll, D.A., Kolb, G.S., Kueffer, C., Mittelhauser, G.H., Schmidt, S., Vidal, E. & Wait, D.A. (2011) Effects of seabirds on plant communities. In: *Seabird islands: ecology invasions, and restoration* (ed. by P.J. Mulder, C.P.H., Anderson, W.B., Towns and D.R., Bellingham), pp. 177–211. Oxford University Press, New York.
- ESRI (2011) ArcGIS Desktop: release 10.
- Gillham, M.E. (1960) Vegetation of Little Brother Island, Cook Strait, in relation to spray-bearing winds, soil salinity, and pH. *Transactions and Proceedings of the Royal Society of New Zealand*, 88, 405–424.
- González-Moreno, P., Pino, J., Cózar, A., García-de-Lomas, J. & Vilà, M. (2017) The effects of landscape history and time-lags on plant invasion in Mediterranean coastal habitats. *Biological Invasions*, 19, 549–561. <https://doi.org/10.1007/s10530-016-1314-z>.
- Grant-Hoffman, M.N., Mulder, C.P.H. & Bellingham, P.J. (2010) Effects of invasive rats and burrowing seabirds on seeds and seedlings on New Zealand islands. *Oecologia*, 162, 1005–1016. <https://doi.org/10.1007/s00442-009-1500-0>.

- Grime, J.P. & Pierce, S. (2012) The evolutionary strategies that shape ecosystems. Wiley-Blackwell.
- Hobbs, R.J. & Huenneke, L.F. (1992) Disturbance, diversity, and invasion: implications for conservation. *Conservation Biology*, 6, 324–337. <https://doi.org/10.1046/j.1523-1739.1992.06030324.x>.
- Jauni, M., Gripenberg, S. & Ramula, S. (2015) Non-native plant species benefit from disturbance: a meta-analysis. *Oikos*, 124, 122–129. <https://doi.org/10.1111/oik.01416>.
- Liu, J.J., Matthews, T.J., Zhong, L., Liu, J.J., Wu, D. & Yu, M. (2019) Environmental filtering underpins the island species—area relationship in a subtropical anthropogenic archipelago. *Journal of Ecology*, 108, 424–432. <https://doi.org/10.1111/1365-2745.13272>.
- Lomolino, M. V. & Weiser, M.D. (2001) Towards a more general species-area relationship: diversity on all islands, great and small. *Journal of Biogeography*, 28, 431–445. <https://www.jstor.org/stable/827392>.
- MacArthur, R.H. & Wilson, E.O. (1967) The theory of island biogeography. Princeton University Press, Princeton, New Jersey.
- Magnússon, B., Magnússon, S. & Fridriksson, S. (2009) Developments in plant colonization and succession on Surtsey during 1999–2008. *Surtsey Research*, 12, 57–76.
- Moles, A.T., Flores-Moreno, H., Bonser, S.P., et al. (2012) Invasions: the trail behind, the path ahead, and a test of a disturbing idea. *Journal of Ecology*, 100, 116–127. <https://doi.org/10.1111/j.1365-2745.2011.01915.x>.
- 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 islands in New Zealand. *Journal of Biogeography*, 48, 1731–1745. <https://doi.org/10.1111/jbi.14110>.
- Morrison, L.W. (2002) Determinants of plant species richness on small Bahamian islands. *Journal of Biogeography*, 29, 931–941. <https://doi.org/10.1046/j.1365-2699.2002.00730.x>.
- Morrison, L.W. (2010) Long-term non-equilibrium dynamics of insular floras: a 17-year record. *Global Ecology and Biogeography*, 19, 663–672. <https://doi.org/10.1111/j.1466-8238.2010.00543.x>.
- Morrison, L.W. (2014) The small-island effect: empty islands, temporal variability and the importance of species composition. *Journal of Biogeography*, 41, 1007–1017. <https://doi.org/10.1111/jbi.12264>.
- Morrison, L.W. & Spiller, D.A. (2008) Patterns and processes in insular floras affected by hurricanes. *Journal of Biogeography*, 35, 1701–1710. <https://doi.org/10.1111/j.1365-2699.2008.01910.x>.
- 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, 1–15. <https://doi.org/10.1002/ecs2.1957>.
- New Zealand Plant Conservation Network (2020) New Zealand Plant Conservation Network. Accessed on: 15/04/2021. Available at: <https://www.nzpcn.org.nz/>.
- Oksanen, J., Blanchet, F.G., Friendly, M., et al. (2020) vegan: community Ecology Package. R package version 2.5-7.
- Paudel, S., Benavides, J.C., Macdonald, B., Longcore, T., Wilson, G.W.T. & Loss, S.R. (2017) Determinants of native and non-native plant community structure on an oceanic island. *Ecosphere*, 8, 1–18. <https://doi.org/10.1002/ecs2.1927>.
- Pickrill, R.A. & Mitchell, J.S. (1979) Ocean wave characteristics around New Zealand. *New Zealand Journal of Marine and Freshwater Research*, 13, 501–520. <https://doi.org/10.1080/00288330.1979.9515827>.
- 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, 2559–2572. <https://doi.org/10.1007/s10530-012-0252-7>.
- R Core Team (2020) R: A language and environment for statistical computing. Available at: <http://www.r-project.org/index.html>
- Schrader, J., Moeliono, S., Keppel, G. & Kreft, H. (2019) Plants on small islands revisited: the effects of spatial scale and habitat quality on the species–area relationship. *Ecography*, 42, 1–10. <https://doi.org/10.1111/ecog.04512>.
- Shmida, A. & Wilson, M. V. (1985) Biological determinants of species diversity. *Journal of Biogeography*, 12, 1–20. <https://www.jstor.org/stable/2845026>.

- Soininen, J., McDonald, R. & Hillebrand, H. (2007) The distance decay of similarity in ecological communities. *Ecography*, 30, 3–12. <https://doi.org/10.1111/j.0906-7590.2007.04817.x>.
- Wang, Y., Millien, V. & Ding, P. (2016) On empty islands and the small-island effect. *Global Ecology and Biogeography*, 25, 1333–1345. <https://doi.org/10.1111/geb.12494>.
- Whitehead, D.R. & Jones, C.E. (1969) Small islands and the equilibrium theory of insular biogeography. *Evolution*, 23, 171–179. <https://doi.org/10.2307/2406492>.
- Whittaker, R.J. (1995) Disturbed island ecology. *Trends in Ecology and Evolution*, 10, 421–425. [https://doi.org/10.1016/S0169-5347\(00\)89164-8](https://doi.org/10.1016/S0169-5347(00)89164-8).
- Whittaker, R.J. (2000) Scale, succession and complexity in island biogeography. *Global Ecology and Biogeography*, 9, 75–86. <https://doi.org/10.1046/j.1365-2699.2000.00200.x>.
- Zuur, A.F., Ieno, E.N. & Elphick, C.S. (2010) A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution*, 1, 3–14. <https://doi.org/10.1111/j.2041-210X.2009.00001.x>.

Submitted: 5 September 2021

First decision: 28 October 2021

Accepted: 30 January 2022

Edited by Spyros Sfenthourakis and Robert J. Whittaker