



Functional traits explain non-native plant species richness and occupancy on northern New Zealand islands

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Abstract Plant functional traits can greatly influence invasion success on islands. However, inter-relationships between traits and invasion success are rarely integrated with the island biogeography theory. Here, we explored relations between functional traits and plant distributions to assess which traits are associated with invasion success (i.e. high island occupancy), test whether non-native richness and seed mass of species with distinct growth forms and dispersal modes vary differently with

island characteristics (e.g. area, isolation, exposure to ocean-borne disturbances, distance from the nearest urban area, and whether islands were managed for conservation), and whether results differ from native species. We assembled a database of 264 northern New Zealand offshore islands, amalgamating species lists from field surveys and previously published data, and comprising 822 native and 855 non-native species. Non-native graminoids occurred on islands more frequently than forbs and woody species, and long-distance dispersal modes (wind, animal, unspecialized) more than species with short-distance dispersal modes. Most differences among trait categories of non-native species were associated with human-related variables (i.e. distance from the nearest urban area, and whether islands were conservation areas). Non-native plant species with high island occupancy were less commonly associated with human-related variables than non-native species with low island occupancy. Instead, they were more similar in their distributional patterns to native species within the same trait category, suggesting comparable processes regulate both sets of species. Our results illustrate that integrating trait-based approaches in the island biogeography framework can be a useful tool in understanding and predicting plant invasions.

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Introduction

Islands worldwide are often heavily invaded by species from other biogeographical regions (i.e. non-native species; Pyšek and Richardson 2006; Denslow et al. 2009; Kueffer et al. 2010; Paudel et al. 2017). On some islands, non-native species richness is similar to that of native species (e.g. Hawai'i, New Zealand, see Sax and Gaines 2008). Because invasions of these magnitudes can occur on islands, identifying successful non-native species before they invade is crucial for island conservation (Townsend et al. 1990; Seabloom et al. 2007; Harris and Timmins 2009; Guo 2014).

An approach to this problem is to assess the functional traits of non-native species (i.e. their morphological, physiological and phenological features; Pérez-Harguindeguy et al. 2013; Ottaviani et al. 2020). Species with similar suites of traits employ analogous strategies, which influence their fitness (Pérez-Harguindeguy et al. 2013; Reich 2014). Functional traits and strategies have been extensively used to address many ecological and evolutionary questions (Bellingham and Sparrow 2000; Caccianiga et al. 2006; Grime and Pierce 2012; Burns 2016a, 2019; May et al. 2017), especially in the field of invasion ecology (Van Kleunen et al. 2010a, b; Guo et al. 2018; Hulme and Bernard-Verdier 2018a, b). Using trait-based approaches may advance our understanding of the ecology of species on islands (Patiño et al. 2017; Ottaviani et al. 2020; Schrader et al. 2021b). Island biogeography theory is based on a mathematical model that describes species' distributions on islands based on their colonization, establishment, and survivorship (MacArthur and Wilson 1967) but which has generally considered species to be functionally equivalent. Using functional traits in the context of island biogeographic theory has further advanced our understanding of species distributions on islands (Whittaker et al. 2014; Negoita et al. 2016; Schrader et al. 2020; Taylor et al. 2021), including that of non-native species (Lloret et al. 2004, 2005; Guo et al. 2021; Chiarucci et al. 2021).

Some plant functional traits can be rapidly and easily assessed. Classifying plants into 'growth forms' (graminoids, forbs and woody plant species) provides a useful proxy for suites of functional traits and phylogenetic backgrounds (Pérez-Harguindeguy et al. 2013; Schrader et al. 2020). For example, many

herbaceous species have relatively short lifespans, small stature, and high seed production per unit biomass (Ellenberg and Mueller Dombois 1967; Qiaoling et al. 2005; Pérez-Harguindeguy et al. 2013; Díaz et al. 2016; Schrader et al. 2020). Conversely, woody species have longer lifespans and taller stature (Pérez-Harguindeguy et al. 2013). Suites of functional traits that are strongly linked with particular plant growth forms may also be strongly linked with invasion success.

Biological invasions on islands often require over-water dispersal (Carlquist 1974; Heleno and Vargas 2015; Arjona et al. 2018). However, plants vary greatly in their dispersal ability (van der Pijl 1982). Species with long range-dispersal might colonize more islands, because they have greater chances of reaching remote ones (Carlquist 1974; Heleno and Vargas 2015; Arjona et al. 2018; Schrader et al. 2021b). In contrast, species with poor dispersal capabilities likely colonize fewer, less isolated islands (Higgins et al. 2003). Maximum dispersal distance can be estimated based on a plant's dispersal mode (e.g. wind-dispersed, animal-dispersed) and growth form (Tammé et al. 2014).

If invaders are selected to have traits associated with better dispersal ability, islands might contain a non-native biota that is unbalanced in its functional composition (Lomolino 1984; Negoita et al. 2016; Ottaviani et al. 2020). Colonization of new habitats is promoted by allocating more resources to reproduction (Lloret et al. 2005; Hayes and Barry 2008) while investing in vegetative growth favours population persistence after colonisation (Bellingham and Sparrow 2000; Lloret et al. 2005). For instance, a good disperser might invest in a large number of seeds, to maximize chances of colonization, while reducing seed size and mass (Cody and Overton 1996; Burns 2019; Schrader et al. 2021b). However, smaller, lighter seeds result in fewer resources available to support a new individual's growth (Moles and Westoby 2004, 2006; Butler et al. 2007; Hodgson et al. 2020). If the non-native plants that colonise islands invest disproportionately in dispersal, they may lack traits associated with competitive ability and vegetative persistence.

Islands vary greatly in their characteristics, which may favour non-native species with certain functional traits. For instance, large, topographically complex islands contain more species (MacArthur and Wilson

1967; Lomolino 2000; Triantis and Sfenthourakis 2012; Tjørve and Tjørve 2017), resulting in these islands having a greater variety of functional traits. However, islands can also be variably disturbed. For instance, islands disturbed frequently by salt spray, storms and waves (Abbott 1977), might favour species better adapted to rugged coastal environments. Conversely, frequent and intense anthropogenic disturbances typically favour generalist species (i.e. species that can occupy a range of habitats) (Moles et al. 2012; Blackburn et al. 2016; Irl et al. 2021), including generalist non-native species (Marvier et al. 2004).

Non-native species often differ from native species in their relationships with island characteristics. For instance, the intentional human introduction of non-native species can generate non-negative species–isolation relationships (Moody 2000; Blackburn et al. 2008; Guo 2014). Additionally, non-natives are often a subset of species directly selected by humans or associated with anthropogenic habitats (Lloret et al. 2005). Consequently, non-native species with traits associated with natural environments (e.g. coastal habitats, Mologni et al. 2021) may be poorly represented, whereas those with traits associated with anthropogenic habitats might be disproportionately abundant.

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

dispersal modes, vary differently with island characteristics? If so, how? (4) Finally, do native plant species differ from non-native species in their functional traits, occupancy and in their relationships with island characteristics?

Methods

Study site

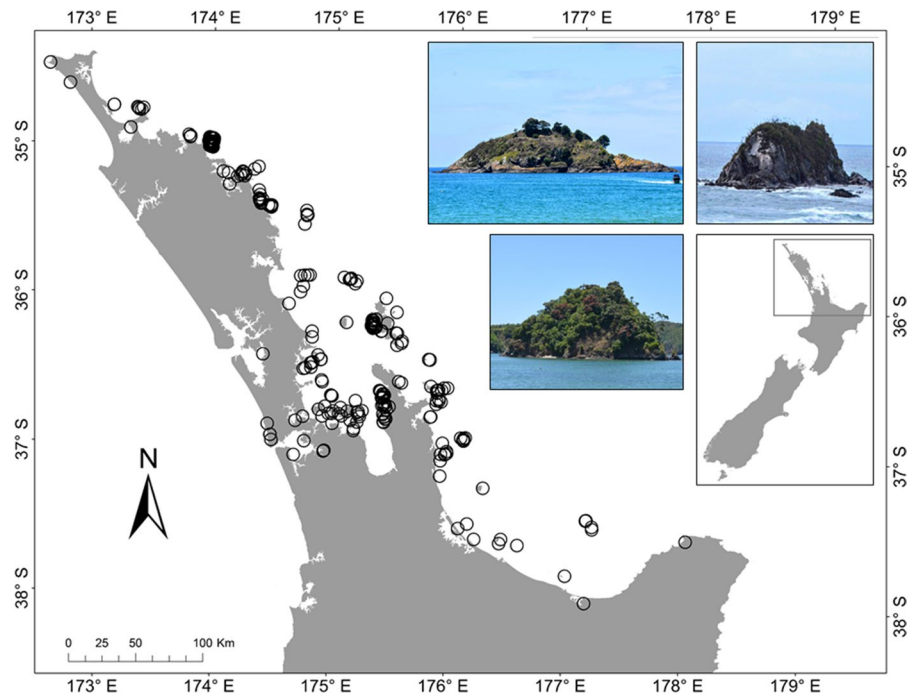
The two main islands of New Zealand (hereafter referred to as the “mainland”) are surrounded by 890 smaller islands (Carter et al. 2020). This study focused on 264 of these islands, located between 34–38° S and 172–179° E, off the northern North Island (Fig. 1). 600 km separate the northwesternmost and southeasternmost islands.

The islands span 7 orders of magnitude in size (0.000021–277.21 km²). Some are separated from the mainland only at high tide while others are situated over 50 km from the mainland. Of the 264 islands, 136 (51.5%) are of volcanic origin, ranging in age from 10 million years to currently active (Campbell and Landis 2009), 122 (46.2%) are of sedimentary origin, and 6 (2.3%) are of mixed composition. Most were connected to the mainland during the last glacial maximum (approximately 0.02 Mya, Fleming 1979). The sole exceptions are the Poor Knights Islands, which have been unconnected to the mainland for at least 1 my (Fleming 1979), and the volcanic island Rangitoto, which formed c. 1500 to 500 years ago (Shane et al. 2013).

New Zealand's climate is oceanic and temperate, which provides suitable conditions for the development of warm temperate rain forest on the study islands (Peel et al. 2007; Wilmshurst et al. 2014). This forest is dominated by evergreen dicot tree species and some conifers, forming the canopy, and a lower tier of broadleaved small trees and shrubs. The understorey is composed primarily of pteridophytes, monocots (mostly sedges) and non-vascular species, and few grasses (Wardle 1991). Higher elevation forests on a few, very large islands support a mixed montane cloud forest that is distinct but floristically poorer (Cameron and Young 2019).

After human settlement 740 years ago, these islands became the focus of many anthropic activities (Atkinson 2004; Bellingham et al. 2010; Wilmshurst

Fig. 1 Map of the study system and photographs of a range of islands off the northern coast of New Zealand



et al. 2014). Māori burned the original vegetation cover of many islands to facilitate access for harvesting seabirds and to plant crops (Daugherty et al. 1990; Bellingham et al. 2010; Wilmshurst et al. 2014). After Europeans colonized, from c. 1840 onwards, some islands were extensively farmed and grazed (Bellingham et al. 2010). Of these islands, some were subsequently abandoned and secondary succession to woody vegetation is common (Bellingham 1984; Atkinson 2004), whereas others are still being farmed. On active or recent volcanic islands, Whakaari/White Island and Rangitoto, vegetation is in a process of primary succession (Clarkson and Clarkson 1994; Shane et al. 2013). Presently, 41 islands (15.5% of all islands) are inhabited.

Species richness

The total number of vascular plant species occupying each island was established via field surveys and by searching the literature (Online Appendix 1 in supplementary material). Plant species lists for most islands were often obtained using both methods (i.e. field surveys and from published sources) in which cases, the cumulative number of species in all censuses was obtained.

All species encountered were classified as either 'native' to New Zealand or 'non-native', following Brandt et al. (2021). Each species was also classified according to its growth form and dispersal mode. Three structural categories were selected for growth forms: graminoids, forbs, and woody (Table 1). Dispersal modes were defined based on morphological adaptations of diaspores to long-distance dispersal (Negoita et al. 2016; Arjona et al. 2018; Burns 2019) as wind-dispersed, unspecialized, animal-dispersed, and diaspores with morphological adaptations for short-distance dispersal only (Table 1). Among growth forms, we excluded lianas and climbers (non-natives = 45, natives = 36) and epiphytes (n -n = 2, n = 7) due to their small sample size. For the same reason, water-dispersed species (producing diaspores with corky tissues or air chambers) were excluded from dispersal modes (n -n = 17, n = 63). We could not determine the status, growth form or dispersal mode of, respectively, 13, 99 and 114 species, and these were omitted from calculations (Online Appendix 2, Table S4).

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

	Species richness		Description
	Non-natives	Natives	
<i>Growth forms</i>			
Graminoids	128	130	Grasses, sedges and rushes
Forbs	515	402	Herbaceous, non-graminoid
Woody species	156	234	Trees and shrubs
Total	799	766	
<i>Dispersal mode</i>			
Wind-dispersed	157	408	Plumes, wings, dust diaspores (anemochory)
Unspecialized	290	119	No evident or prevalent morphological adaptations (unspecialized)
Animal-dispersed	167	190	Fleshy fruits or adhesive barbs (endo and epizoochory)
Short-distance	185	34	Morphological adaptations for short-distance dispersal only (ballochory, myrmecory)
Total	799	751	

Species seed mass

For each species, we also determined its seed dry mass (mg). If data were unavailable, seed mass was estimated by seed length (mm) using the equation:

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

where “*m*” is estimated seed mass (mg), “*l*” is seed length (mm) and the two numeric values are constants. The equation was parametrized based on a linear model with both variables log-transformed, a sample size of 695 species with directly measured seed mass (74% of which are native species) across 297 genera and 100 families, and a fit of $R^2 = 0.865$ (Sarah Richardson, personal communication, May 20, 2020). We gathered data for seed mass and length from several sources, including literature (Thorsen et al. 2009; Grubb et al. 2013) and online databases (Kattge et al. 2020; Manaaki Whenua - Landcare Research 2020; New Zealand Plant Conservation Network 2020; Royal Botanic Gardens Kew 2020). Nomenclature followed recognised taxonomic authorities (<https://nzflora.landcareresearch.co.nz>, accessed in May 2020). Pteridophytes ($n = 167$) were excluded from seed mass analyses, and a further 370 species were omitted due to lack of data in seed mass (Online Appendix 2, Table S4).

Island characteristics

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

Storms, waves and salt spray characterise disturbances of oceanic origin. To quantify exposure to ocean-borne disturbances we identified the centre of each island and drew two lines connecting it to the edge of the nearest landmasses (either the mainland or islands larger than 50 km^2). The angle comprised between these two lines represents the degree of exposure of an island to ocean-borne disturbances (Burns and Neufeld 2009). Human impacts were quantified first as the shortest distance to the nearest urban area,

as non-native species richness often increases with proximity to settlements (Timmins and Williams 1991; Sullivan et al. 2005; Lloyd et al. 2006). Urban areas were defined as settlements having a population of 1000 people or more (Statistics NZ Tauranga Aotearoa 2018). Next, we assessed whether an island is public land managed for conservation (conservation area) or not (Department of Conservation 2017). All spatial analyses were carried using ArcGIS 10 and QGIS 2 (ESRI 2011; QGIS Development Team 2018).

Statistical analyses

To address question (1), whether the number of islands occupied by non-native species can be predicted by plant traits, we tallied the number of islands on which each non-native species occurred. We then aggregated the non-native species by growth forms and dispersal modes. Differences in occurrences across islands of growth forms and dispersal mode were analysed using a generalized linear model (GLM) with quasipoisson distribution. A Tukey Multiple Comparison test was used to account for multiple testing (Hothorn et al. 2008). We used the same method to contrast occurrences across islands of non-natives with natives within each trait (e.g. non-native graminoids vs. native graminoids) to answer question (4).

To address question (2), whether non-native richness of growth forms and dispersal modes differ according to island characteristics, we used a set of multiple linear regressions. Firstly, the richness of subsets of non-native species (e.g. graminoids, forbs, animal-dispersed, unspecialized, etc.) was set as dependent variables, and area, isolation, exposure to ocean-borne disturbances and distance from the nearest urban area were independent variables. Conservation areas (i.e. whether an island is public land managed as a conservation area or not) was excluded from this model as it was not significantly related to species richness, regardless of trait category and status (i.e. non-native or native). Next, we ran a model with the same predictors, but using the richness of all non-native species and including growth forms and dispersal modes as interaction terms. To contrast trends with native species (question 4), a third model was devised, with the same predictors, the richness of each trait category as a dependent variable (e.g. all

graminoid species) and the status of each species as an interaction term.

To address question (3), whether the seed mass of growth forms and dispersal modes vary differently with island characteristics for non-native species, we devised a second set of multiple linear regressions. Before analyses, we averaged seed dry mass per island separately for each growth form and dispersal mode. The mean seed mass of each subset of non-native species was then set as the dependent variable, while as predictors we used area, isolation, exposure, distance from the nearest urban area and conservation areas. Next, we ran a model with the same predictors but using the mean seed mass of all non-native species and including growth forms and dispersal modes as interaction terms. To contrast trends with native species (question 4), a third model was devised, with the same predictors, the average seed mass of each trait category as a dependent variable and the status of each species as an interaction term.

In all multiple linear models, species richness and area were log-transformed, isolation arcsine-transformed and distance from the nearest urban area square root-transformed to conform to the assumptions of normality and linearity. Variables were previously tested for collinearity, and an isolation radius of 1500 m was chosen by retaining the metric with higher probability of predicting species richness after controlling for island area (Mologni et al. 2021). All analyses were run in the R environment (R Core Team 2020).

Results

Of the total 1677 species across the islands, 855 (50.96%) were non-native. Non-native species comprised 119 families, of which Poaceae was the most species-rich (number of species=101), followed by Asteraceae (n=84), Fabaceae (n=55), Rosaceae (n=34) and Brassicaceae (n=33), accounting for 36.2% of all non-native species. Native species comprised 137 families, with Cyperaceae the most species-rich (n=76), followed by Orchidaceae (n=60), Asteraceae (n=50), Poaceae (n=36) and Rubiaceae (n=35), accounting for 32.5% of all native species.

There were more non-native forb species than either graminoid or woody species (Table 1 and Online Appendix 2, Table S1). Natives included

fewer forbs and more woody species than non-natives, but a similar number of graminoids (Table 1 and Online Appendix 2, Table S1). Among dispersal modes, most non-native species were unspecialized (Table 1 and Online Appendix 2, Table S1). Natives included more wind-dispersed species than non-natives, but fewer were unspecialized or short-distance-dispersed (Table 1 and Online Appendix 2, Table S1).

Of the 1127 species included in seed mass analysis, 59.98% were non-native (Table 2 and Online Appendix 2, Table S2). Among growth forms, non-native forbs and woody species had heavier seeds than their native counterparts, but the seed masses of non-native and native graminoid species were not significantly different (Table 2 and Online Appendix 2, Table S2). The seed mass of non-native and native species did not differ among dispersal modes (Table 2). Less than a third of all species in each trait category were removed from analyses due to a lack of seed mass data. The only exceptions were native forbs and wind-dispersed species, where 62% of species were removed (Online Appendix 2, Table S5), including all pteridophytes, which comprise 40% of all native forbs and wind-dispersed species.

Island occupancy (question 1)

Non-native graminoid species occupied more islands than non-native forb species, which, in turn, occupied more islands than non-native woody species (Fig. 2a and Online Appendix 2, Table S6). Non-native graminoid species occupied a similar number of islands as native graminoid species, while the other growth forms of non-native species occurred on fewer islands than their native counterparts (Online Appendix 2, Table S6). Among dispersal modes, non-native wind-dispersed and unspecialized species occupied more islands than short-distance-dispersed species. Non-native wind-dispersed and unspecialized species occupied a similar number of islands to native wind-dispersed and unspecialized species, whereas the other dispersal modes of non-native species occurred on fewer islands than their native counterparts (Online Appendix 2, Table S6).

Patterns in species richness (question 2)

Species richness increased with island area for non-native species across all growth forms and dispersal modes (Figs. 3a, 4a, Online Appendix 2, Tables S7, S8 and S11). Conversely, non-native species richness always declined with exposure to ocean-borne disturbances, and generally declined with isolation (Figs. 3b, c and 4b, 4c). Among growth forms,

Table 2 Seed mass of non-native and native species subdivided by growth forms and dispersal modes on 264 islands offshore New Zealand.

	Species richness		Mean seed dry mass (mg)		Standard error of the mean (\pm)		t-value
	Non-natives	Natives	Non-natives	Natives	Non-natives	Natives	
<i>Growth forms</i>							
Graminoids	114	111	2.41	1.98	0.45	0.44	- 0.643
Forbs	396	151	7.35	1.34	1.03	0.23	- 2.804
Woody	132	161	416.63	89.07	151.83	29.74	- 2.526
Total	642	423					
<i>Dispersal mode</i>							
Wind-dispersed	128	154	23.36	3.06	80.38	1.05	- 1.614
Unspecialized	244	85	55.98	5.27	32.30	1.92	- 0.845
Animal-dispersed	141	132	208.98	79.85	116.86	25.22	- 1.220
Short-distance	135	30	90.00	2.35	2.22	0.69	- 0.350
Total	648	401					

Columns represent trait categories, species richness (after removing those lacking seed mass data), mean seed dry mass and its standard error. The last column includes t-values extracted from a generalized linear model (GLM) with quasipoisson distribution comparing non-native and native seed dry mass for each set trait (in bold when significant, $P < 0.05$)

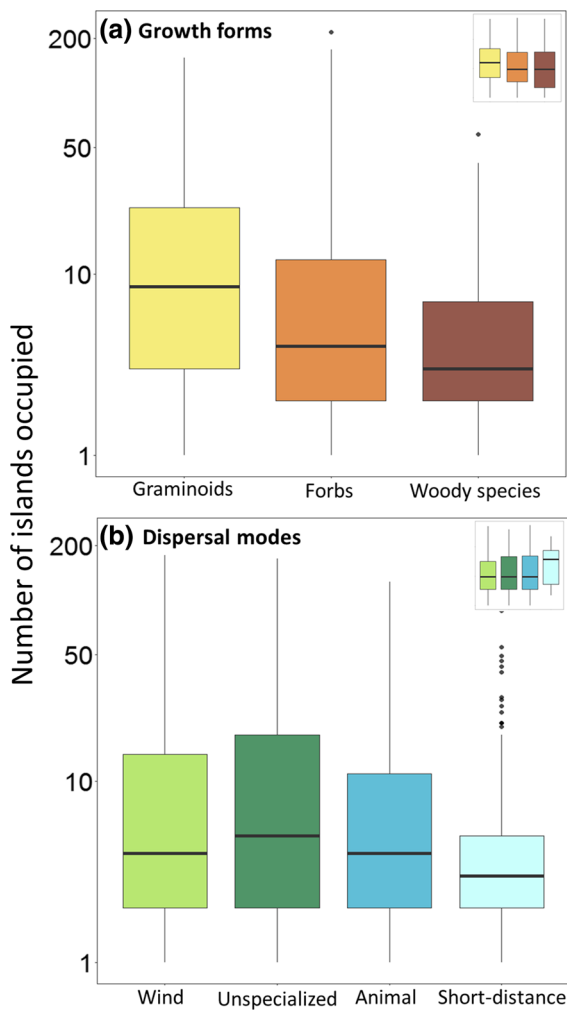


Fig. 2 Number of islands occupied by non-native species with different **a** growth forms and **b** dispersal modes. On the y-axis is the number of islands occupied by each species, on a log scale, while on the x-axis are trait categories. The inset boxes are values for native species

non-native forbs and woody species richness declined with distance from the nearest urban area, but non-native graminoid richness showed no significant relationship (Fig. 3d). Among dispersal modes, the richness of short-distance- and animal-dispersed non-native species declined significantly with distance from the nearest urban area, but the richness of wind-dispersed and unspecialized non-native species showed no significant relationships (Fig. 4d). Native species richness always increased with island area and was always unrelated to distance from the nearest urban area (Figs. 3a, d and 4a, d and Online

Appendix 2, Tables S9, S10, S11 and Figures S2, S3). Native species richness generally exhibited a weaker decline with island exposure and isolation than non-native species richness (Figs. 3b, c and 4b, c).

Patterns in seed mass (question 3)

The mean seed mass of non-native species increased with island area for all growth forms and dispersal modes (Figs. 5a, 6a and Online Appendix 2, Tables S7, S8, S11). Non-native species' mean seed mass generally declined with increasing exposure and distance from the nearest urban area (Figs. 5, 6); exceptions among species were usually short distance- and wind-dispersed species. Non-native species' mean seed mass was unrelated to island isolation (except short distance and wind-dispersed). The mean seed mass of non-native graminoids, wind- and short-distance-dispersed was lower on conservation area islands than on other islands (Figs. 5e, 6e). Woody and animal-dispersed non-native species exhibited the opposite trend, while non-native forbs and unspecialized species were unrelated to islands' conservation status. The mean seed mass of native species also generally increased with area and was unrelated to isolation (Figs. 5a, b and 6a, b and Online Appendix 2, Tables S9, S10, S11, Figures S4, S5). However, native species' mean seed mass was commonly unrelated to exposure and conservation areas (Figs. 5c, e and 6c, e). Relationships between native species' mean seed mass and distance from the nearest urban area were mixed, with some trait categories declining (forbs, woody species, wind-dispersed, unspecialized) and others unrelated.

Discussion

Non-native plant species occupancy across 264 northern New Zealand islands was related to their functional traits. Non-native graminoids occurred on islands more frequently than non-native forbs and woody species, and non-native species with long-distance dispersal modes (wind, animal, unspecialized) occurred on more islands than those with short-distance dispersal modes. Non-native plant species richness and seed mass varied among traits categories with respect to characteristics of the islands they invaded, and most differences were

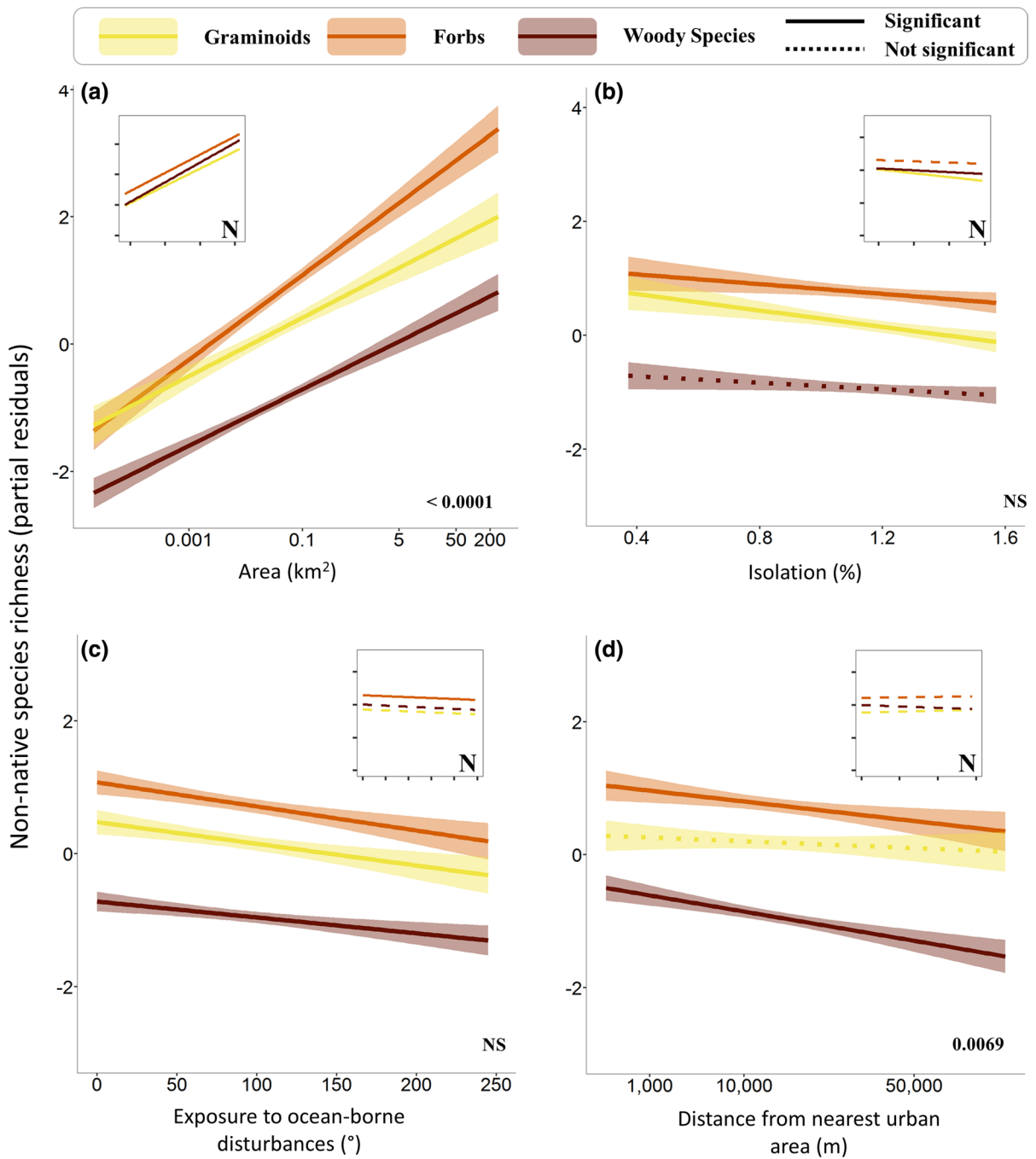
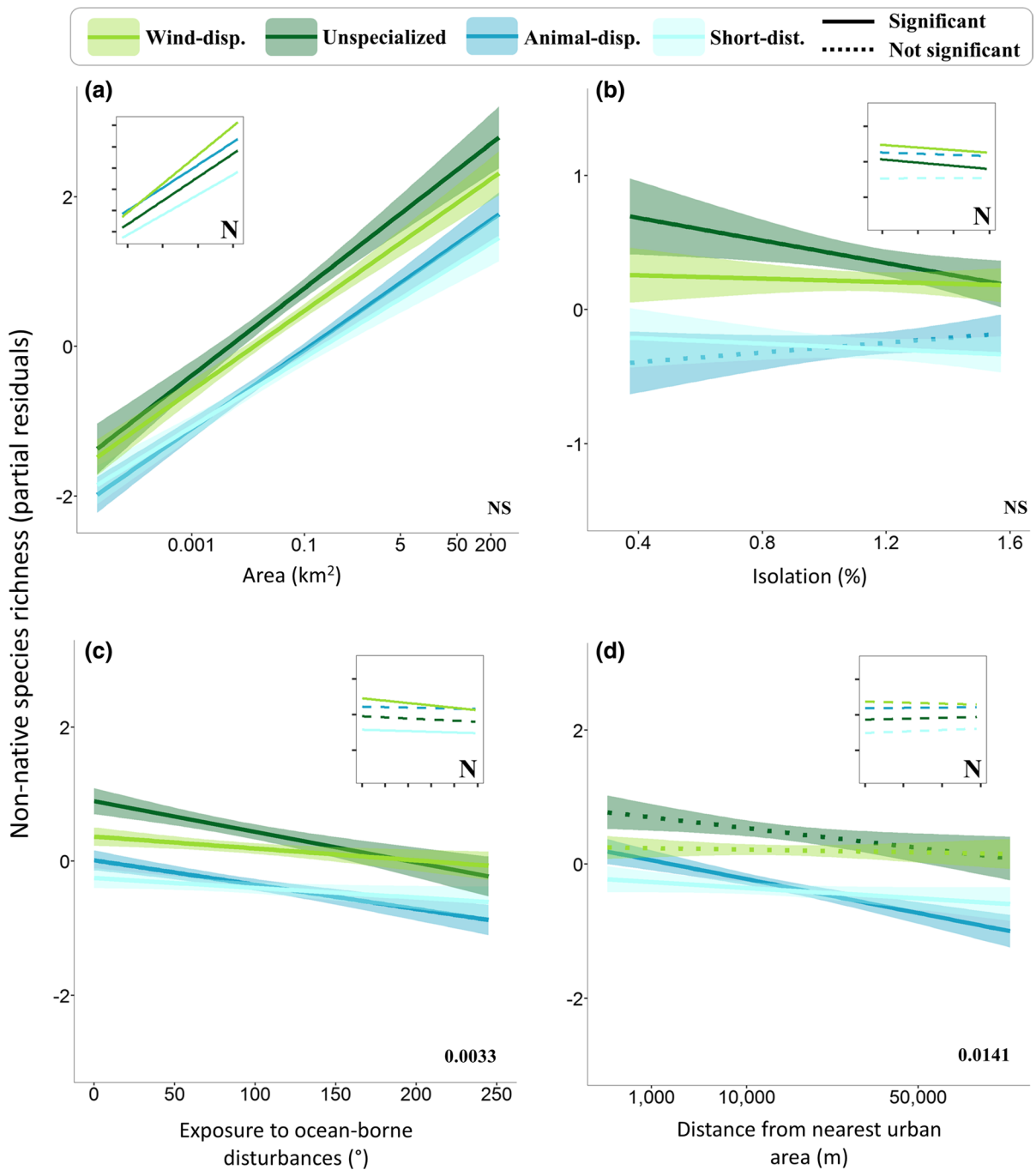


Fig. 3 Linear models illustrating relationships between non-native species richness with different growth forms and island characteristics on 264 New Zealand offshore islands (adj. $R^2=0.66$). On the y-axis is species richness (partial residuals), while on the x-axis are island **A** area (log scale), **B** isolation (arcsine-transformed values on linear scale), **C** exposure to ocean born disturbances, and **D** distance from the nearest urban area (square root scale). Trendline (model predicted slope) and relative confidence interval (95%) colours repre-

sent graminoid (yellow), forb (vermillion) and woody species (brown). Trendline types indicate significant (solid, $P < 0.05$) or non-significant (dotted) relationships. P -values for significant ($P < 0.05$) or not significant (NS) differences in the response between growth forms are at the bottom right. To conform to assumptions, species richness was log (+1) transformed, area log-transformed, isolation arcsine-transformed and distance from the nearest urban area squared-transformed. Each inset box is an equivalent figure for native species (N)



associated with human-related variables (i.e. distance from the nearest urban area and whether an island was a conservation area). However, non-native plant species with traits associated with high occupancy (i.e., non-native graminoids and wind-dispersed and unspecialized species) were less

commonly related to human-related variables than those with low island occupancy. Non-native plant species with high island occupancy had relationships in species richness and seed mass that were generally similar to those of native species within the same trait category.

Fig. 4 Linear models illustrating relationships between non-native species richness with different dispersal modes and island characteristics on 264 New Zealand offshore islands (adj. $R^2=0.59$). On the y-axis is species richness (partial residuals), while on the x-axis are island **A** area (log scale), **B** isolation (arcsine-transformed values on linear scale), **C** exposure to ocean born disturbances, and **D** distance from the nearest urban area (square root scale). Trendline (model predicted slope) and relative confidence interval (95%) colours represent animal-dispersed (dark blue), unspecialized (dark green), short-distance (light blue), and wind-dispersed species (light green). Trendline types indicate significant (solid, $P < 0.05$) or non-significant (dotted) relationships. P -values for significant ($P < 0.05$) or not significant (NS) differences in the response between dispersal modes are at the bottom right. To conform to assumptions, species richness was log (+1) transformed, area log-transformed, isolation arcsine-transformed and distance from the nearest urban area squared-transformed. Each inset box is an equivalent figure for native species (N)

Island occupancy

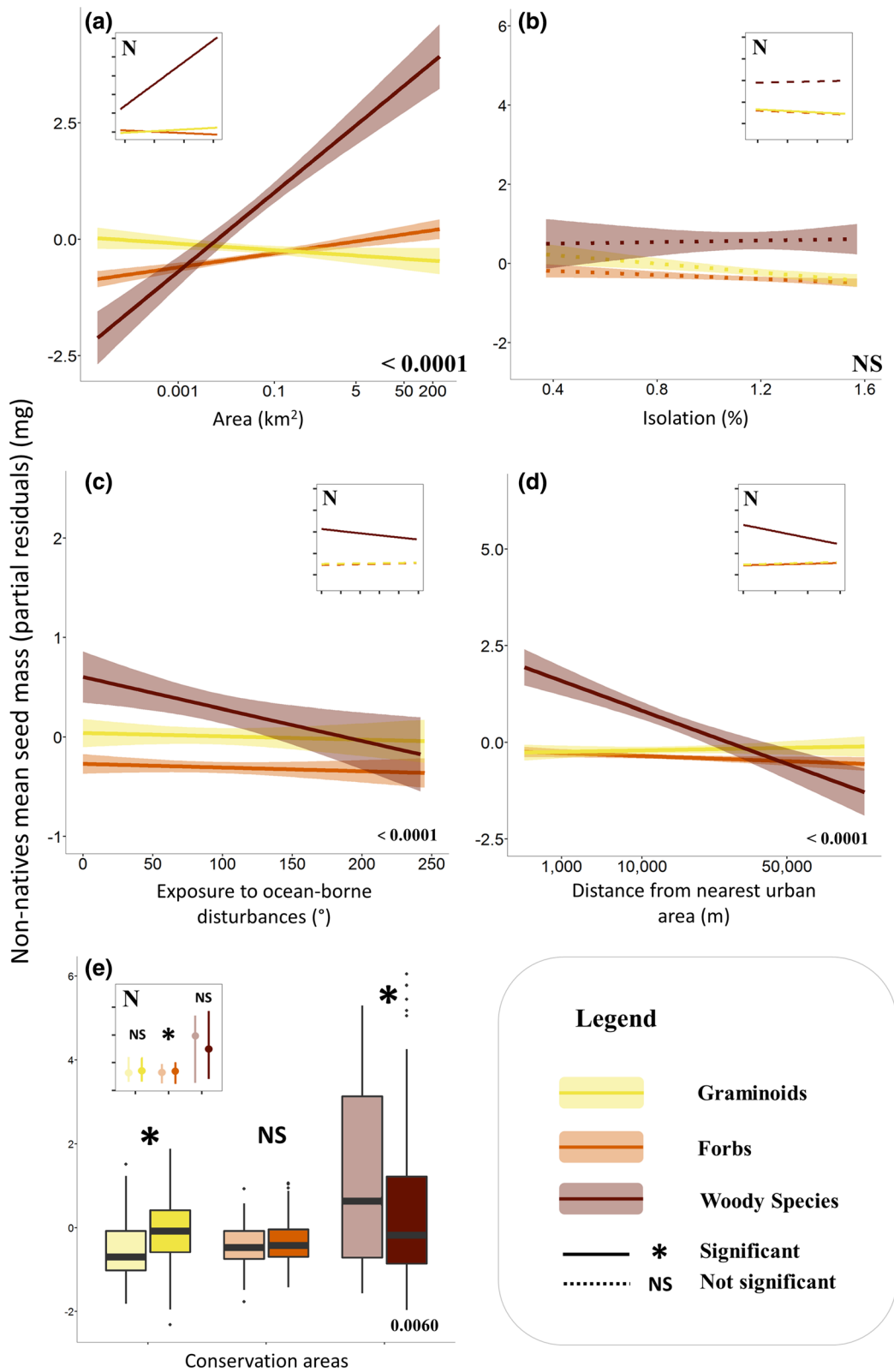
Growth forms and dispersal modes predicted occurrence patterns in non-native plant species across the islands. Non-native graminoids and forbs occupied a larger number of islands than non-native woody species, which is expected given woody species are a minority of the total pool of New Zealand's non-native species (Brandt et al. 2021). Non-native graminoid and forb species generally have a relatively short lifespan, high seed production and good dispersal capabilities (Ellenberg and Müller-Dombois 1967; Qiaoling et al. 2005; Pérez-Harguindeguy et al. 2013; Díaz et al. 2016; Negoita et al. 2016; Schrader et al. 2020). However, many islands in our study system were farmed and perhaps a higher proportion of grasses and forbs on these islands were directly introduced by humans. Among the non-native herbaceous species, graminoids invaded more islands than forb species (Table 1). Perhaps many forb species were introduced for gardens (see Sullivan et al. 2005), suggesting a different invasion strategy (Hodkinson and Thompson 1997). Our results contrast with Mediterranean islands, where growth forms of non-native species were unrelated to their occupancy (Lloret et al. 2005), which suggests that observed patterns may differ according to the island system investigated. New Zealand is more isolated from continents than Mediterranean islands, leading to a more disharmonic flora and thus more invasion opportunities. For example, New Zealand's offshore islands might be especially prone to invasion by annual species, which

are severely underrepresented in the native flora (Brandt et al. 2021).

Native and non-native species with wind or animal dispersal had high occupancy rates across islands in our study. Wind and animal dispersal modes are generally associated with high dispersal potential (Carlquist 1974; Lloret et al. 2005; Tamme et al. 2014). Species with unspecialized or short-distance-dispersed diaspores often have low island occupancy rates (Negoita et al. 2016; Arjona et al. 2018). However, species with unspecialized diaspores occurred on many islands in our study system. Estimating dispersal potential from dispersal modes is challenging. First, dispersal distances can vary strongly within dispersal modes (Thomson et al. 2011; Tamme et al. 2014). Second, vectors are typically context-dependent. For instance, many birds that disperse seeds within fleshy fruits and berries avoid islands that lack perching trees (Ferguson and Drake 1999; Negoita et al. 2016), and while most islands in our study have forest cover, some are either severely deforested or are too small to support many woody plants. Finally, dispersal modes do not account for vectors that are different from that suggested by a diaspore's morphology (i.e. human-related dispersal means; Higgins et al. 2003; Nogales et al. 2012; Negoita et al. 2016; Arjona et al. 2018). Many non-hydrochorous species might successfully benefit from water-mediated pathways (Kowarik and Sämel 2008), especially in island systems.

Patterns in species richness

The theory of island biogeography predicts that species richness increases with island area (MacArthur and Wilson 1967; Lomolino 2000; Tjørve and Tjørve 2017), and positive species–area relationships have been identified previously on islands both for non-native species (Baiser and Li 2018; Guo et al. 2021) and among growth forms (Schrader et al. 2020). We found consistent, positive species–area relationships for non-native species with different dispersal modes and growth forms across northern New Zealand islands. Dispersal probabilities to islands typically decrease with island isolation, resulting in a decline in species richness (MacArthur and Wilson 1967; Weigelt and Kreft 2013). Since the maximum dispersal distance of a species is related to both growth forms and dispersal modes (Tamme et al. 2014), this



◀**Fig. 5** Linear models illustrating relationships between the average seed mass of non-native and native species with different growth forms and island characteristics on 264 New Zealand offshore islands (adj. $R^2=0.48$). On the y-axis is average seed mass (partial residuals), whereas on the x-axis are island **A** area (log scale), **B** isolation (arcsine-transformed values on linear scale), **C** exposure to ocean born disturbances, **D** distance from the nearest urban area (square root scale) and **E** conservation areas. Colours represent graminoid (yellow), forb (vermilion) and woody species (brown). In plots **A–D**, trendline (model predicted slope) and relative confidence interval (95%) are represented. In plot **E**, light hues indicated publicly managed conservation areas, dark hues other islands. Significant relationships ($P<0.05$) are illustrated by solid trendline (**A–D**) and asterisks (**E**). P -values for significant ($P<0.05$) or not significant (NS) differences in the response between growth forms are at the bottom right. To conform to assumptions, seed mass was log (+1) transformed, area log-transformed, isolation arcsine-transformed and distance from the nearest urban area squared-transformed. Each inset box is an equivalent figure for native species (N)

could be expected to lead to differences in representation within growth forms and dispersal modes in relation to island isolation. However, in our study, negative richness–isolation relationships in non-native species did not differ significantly among growth forms or among dispersal modes.

Similarly, non-native species richness declined with island exposure independently of trait categories. Exposed coastal habitats are particularly susceptible to storms and waves, generating depauperate floras that are more subject to extinctions (Abbott 1977; Morrison and Spiller 2008; Burns and Neufeld 2009). Non-native species are often selected by humans for agricultural and horticultural purposes and might be poorly adapted to coastal environments regardless of the traits investigated in this study (Lloret et al. 2005; Mologni et al. 2021).

The dispersal of non-native species is often determined by human activities. Surprisingly though, the richness of graminoid, wind-dispersed and unspecialized non-native species on islands was unrelated to distance from the nearest urban area. After introduction, plants can utilize different anthropogenic pathways for dispersal, which often depend upon traits (Hodkinson and Thompson 1997). Distance from the nearest urban area might only encapsulate dispersal pathways associated with human habitation, such as escaping from gardens (Sullivan et al. 2005). Instead, graminoid, wind-dispersed and unspecialized species might exploit different pathways for their dispersal.

These trait categories though also exhibited high rates of island occupancy and thus might be at a later stage of invasion. As the invasion process progresses, non-natives may be increasingly independent of humans for their dispersal (González-Moreno et al. 2017; Coutts et al. 2018).

Human disturbances can favour the spread of non-native species (Seabloom et al. 2007; Dimitrakopoulos et al. 2021). However, current estimates of human disturbance, such as current inhabitation, are likely to be confounded with island area, since larger islands are preferentially inhabited (mean area inhabited islands = 15 km², \bar{x} uninhabited = 0.12 km², $\chi^2=14.64$, $p=0.0001$). Past disturbances, such as fires, may be underestimated and require better resolution in our study system, hence we believe better proxies for estimating human disturbance are needed to predict plant invasions more accurately (Mologni et al. 2021).

Patterns in seed mass

Regardless of growth form and dispersal mode, the mean seed mass of non-native species was higher on larger islands. Heavy, large seeds tend to result in larger plants (Butler et al. 2007), which also occupy more space. Thus, some islands may be too small to match the minimum area requirements of large plant species (Turner and Tjørve 2005). In addition, large seeds require more maternal resources, often leading to a reduction of total seed number (Moles and Westoby 2004, 2006; Hodgson et al. 2020). Fewer propagules reduce the chances of intercepting islands during dispersal (Lonsdale 1999), especially when islands are small in area (Lomolino 1990). Finally, larger islands often have more complex forest structures, favouring taller species and thus heavier seeds (Schrader et al. 2021a).

Lighter seeds are often associated with long dispersal distances (Muller-Landau et al. 2008; Aufret et al. 2017). However, most non-native species did not display a negative relationship between seed mass and island isolation. Having heavier seeds though does not necessarily diminish dispersal potential (Thomson et al. 2011; Tamme et al. 2014), suggesting other factors, such as vectors' behaviour and human pathways, might be important (Hodkinson and Thompson 1997; Negoita et al. 2016; Sinclair et al. 2020).

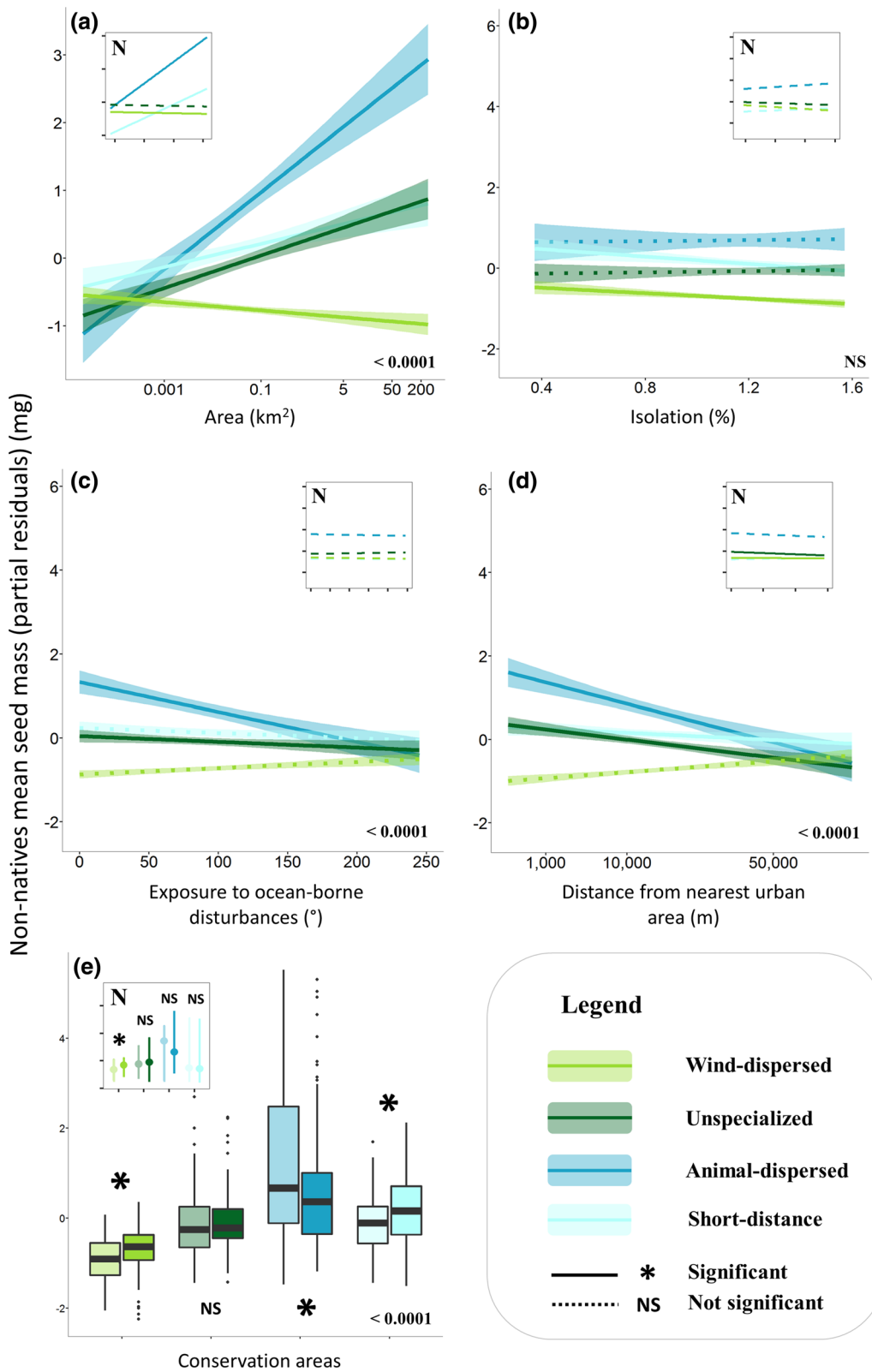


Fig. 6 Linear models illustrating relationships between the average seed mass of non-native and native species with different dispersal modes and island characteristics on 264 New Zealand offshore islands (adj. $R^2=0.51$). On the y-axis is average seed mass (partial residuals), whereas on the x-axis are island **A** area (log scale), **B** isolation (arcsine-transformed values on linear scale), **C** exposure to ocean born disturbances, **D** distance from the nearest urban area (square root scale) and **E** conservation areas. Colours represent animal-dispersed (dark blue), unspecialized (dark green), short-distance (light blue), and wind-dispersed species (light green). In plots **A–D**, trendline (model predicted slope) and relative confidence interval (95%) are represented. In plot **E**, light hues indicated publicly managed conservation areas, dark hues other islands. Significant relationships ($P<0.05$) are illustrated by solid trendlines (**A–D**) and asterisks (**E**). P -values for significant ($P<0.05$) or not significant (NS) differences in the response between dispersal modes are at the bottom right. To conform to assumptions, seed mass was log (+1) transformed, area log-transformed, isolation arcsine-transformed and distance from the nearest urban area squared-transformed. Each inset box is an equivalent figure for native species (N)

Most non-native species showed negative relationships between seed mass and island exposure. Seed mass often correlates with leaf area (Butler et al. 2007), and large leaves are more susceptible to mechanical damage and physiological stress caused by wind and waves (Burns and Neufeld 2009; Anten et al. 2010). The mean seed mass of wind-dispersed and short-distance-dispersed species did not decline with exposure. Strong, contrasting wind currents on exposed islands might favour some dispersal modes, regardless of their seed mass (Whittaker 1995).

The mean seed mass of non-native species on the islands increased with proximity to urban areas, except for wind-dispersed species. One explanation for this relationship is that species that produce heavier seeds, also produce larger fruits (Martínez et al. 2007), which are sought preferentially in agriculture and horticulture (Hodkinson and Thompson 1997). In contrast, wind-dispersed species might contain a high proportion of pasture species, chosen for their biomass productivity rather than for their seed production.

Mean seed mass displayed contrasting trends with respect to islands' conservation status, depending on trait categories. On islands that are conservation areas, the lower seed mass of graminoids, wind- and short-distance-dispersed species, and greater seed mass of woody and animal-dispersed species may be a by-product of biosecurity and control measures against non-native species. For

instance, small-seeded, lower-mass species might be less effectively detected by preventive measures. In addition, conservation management often favours reforestation (Townsend et al. 1990), and species with larger seeds are usually more competitive in forested ecosystems (Coomes and Grubb 2003). However, it remains unclear why these trends are inconsistent among trait categories. Other biological invasions of islands, such as mammalian invasions, have been demonstrated to cause complex, multi-level indirect effects (Fukami et al. 2006; Bergstrom et al. 2009; Schrader et al. 2021b) and the consequent alterations to disturbance regimes, nutrient levels, and habitat changes may favour non-native species of particular trait sets, and often conservation management of islands removes mammalian invaders. Finally, we inferred seed mass from seed length for many species, and despite the strong allometric link between the two, this might be a potential source of error.

Differences between native and non-native species

The island biogeography of non-native and native species often differs (Mologni et al. 2021; Moser et al. 2018; Rojas-Sandoval et al. 2020; Guo et al. 2021). In this study, we have shown that discrepancies between non-native and native species richness were related to their functional traits. Non-native species with traits associated with high invasion rates (e.g. wind-dispersal and the graminoid growth form) were more similar to native species both in occupancy and in their relationships with island characteristics. This suggests that the distribution of successful invaders (i.e. those with high occupancy rates) is shaped by similar processes to natives. Non-natives generally declined more strongly with exposure, perhaps because native species are better adapted to rugged, coastal environments (Cockayne 1958; Burns 2016b). Surprisingly, some native species also declined in seed mass with human habitation, although often less strongly than non-natives, suggesting that native species might utilize similar dispersal pathways to non-natives (Valery et al. 2009). Forty percent of native forbs and wind-dispersed species were pteridophytes and were thus removed from seed mass analyses, potentially limiting our ability to compare trends with other non-native forbs and wind-dispersed species.

Future directions

Our results pinpoint plant functional traits that are associated with high invasion rates, which might not necessarily match those favouring the initial establishment in a new biogeographical region (Sinclair et al. 2020). However, it is unclear which of these traits promote dispersal to islands and which promote persistence on them. Moreover, disentangling whether growth form or dispersal mode was a greater influence is especially problematic in the case of non-native animal-dispersed species, as 50% of them are woody, and 60% of non-native woody species are animal-dispersed (Table S3). The importance of interactions among functional plant traits in determining the distribution of non-native species remains poorly understood and would be a fruitful avenue of future research (Negoita et al. 2016).

Non-native plant species are often favoured by soil enrichment (Huenneke et al. 1990; King and Buckney 2002; Blumenthal et al. 2017), especially when short-lived (Prober and Wiehl 2012). In our study system, both geological and biological factors can contribute to soil fertility. For instance, volcanic islands have generally richer soils, which favour island invasions (Pretto et al. 2012). Similarly, seabird guano augments soil nutrients across many islands in our study system, both of volcanic and sedimentary origin, and seabirds also create high disturbance levels through burrowing (Grant-Hoffman et al. 2010), which likely favours invasion by some non-native species (Hobbs and Huenneke 1992). Such a variety of geological and biological factors are likely to differentially affect which traits promote non-native plant species establishment and persistence on an island.

Conclusions

Growth forms and dispersal modes were predictors of non-native plant species that were successful invaders (i.e. those with high occupancy rates) of northern New Zealand islands (graminoid, wind-dispersed and unspecialized species) and these, in turn, were related to island characteristics. Differences in species richness and seed mass among trait categories were mostly associated with human-related variables (i.e. distance from the nearest urban area and conservation areas), with successful invaders often unrelated

to these variables. Moreover, non-native species with high rates of island occupancy showed distributional patterns more similar to those of native species within the same trait category, suggesting comparable processes regulate both sets of species. Biosecurity efforts on islands should focus on non-native graminoid, wind-dispersed and species with unspecialized diaspores. Future work should concentrate on unravelling the complexity of indirect effects of island conservation management on plant seed mass. Overall, our results illustrate that integrating trait-based approaches in the island biogeography framework (e.g. Aikio et al. 2020; König et al. 2021; Ottaviani et al. 2020; Schrader et al. 2021b) can be a useful tool in understanding and predicting plant invasions.

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Data availability The data associated with the paper is available from the Manaaki Whenua data repository at <https://doi.org/10.7931/ndkt-zw49>. Island locations (longitude and latitude) are not publicly available due to private ownership and issues of data sovereignty of concern to Māori.

Code availability Not applicable.

Declarations

Conflict of interest The authors have not disclosed any conflict of interest.

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