

1 Time of naturalization is key to explaining non-native plant invasions on  
2 islands

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4 Running title: Naturalization time drives island invasions  
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34 **Abstract**

35 Aim

36 Relatively long periods of time can elapse between the naturalization and spread of non-  
37 native plant species. However, time lags on islands are poorly understood, especially if  
38 integrating plant life histories. We asked whether (1) there is a time lag in the invasion  
39 process, (2) there were distinct periods of naturalization in the non-native plants that invaded  
40 islands and (3) non-native plants that naturalized more recently occur more frequently on  
41 islands that are large, less isolated and close to urban areas. Then, we contrasted trends across  
42 growth forms, dispersal modes and biogeographic origins.

43

44 Location

45 264 offshore islands in northern Aotearoa New Zealand

46

47 Taxa

48 Vascular plant species

49

50 Methods

51 We combined field surveys and published data for 848 non-native plant species. We  
52 categorized each species according to its growth form, dispersal mode and biogeographic  
53 origin and identified its year of naturalization in Aotearoa New Zealand. We contrasted  
54 period of naturalization, time lags and relationships with island area, isolation and distance  
55 from the nearest urban area by growth form, dispersal mode and biogeographic origin using  
56 ANCOVA and generalized linear models (GLMs).

57

58 Results

59 We identified time lags, similar across all trait and biogeographic origin categories. Species  
60 with different trait and biogeographic origin categories first naturalized at different periods in  
61 time. Herbaceous species, those with unspecialized dispersal modes, and those originating  
62 from Eurasia and the Mediterranean basin were disproportionately introduced earlier than  
63 other categories. Non-native plants that naturalized more recently occur more frequently on  
64 large islands close to urban areas, but not less isolated ones. Relationships with island  
65 characteristics did not differ among trait and biogeographic origin categories.

66

## 67 Main Conclusions

68 Overall, we found that the time of naturalization is more important than trait and  
69 biogeographic origin categories in explaining non-native plant invasion patterns on islands.  
70 Since similar time lags were identified for all categories, management bodies should focus on  
71 species of trait and biogeographic origin categories that naturalized more consistently in  
72 recent times (e.g. woody species from other regions within Oceania), and on large islands  
73 close to urban areas. Plant life histories do not always play a role in explaining plant  
74 distributions on islands.

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77 **Key Words:** *Aotearoa New Zealand, Biogeographic origin, Dispersal modes, Growth forms,*  
78 *Island biogeography, Naturalization time, Plant species, Time lags*

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## 84 **Introduction**

85 The introduction of non-native species poses considerable threats to islands' biodiversity  
86 (Kueffer et al., 2010; Lonsdale, 1999; Pyšek & Richardson, 2006). Large numbers of species  
87 have been introduced to islands (Sax & Gaines, 2008, Wilkinson 2004) but, for some of  
88 these, a long time can elapse before they spread (i.e. there is a time lag, or invasion debt;  
89 González-Moreno et al., 2017; Kowarik, 1995; Seabloom et al., 2006). Time lags in invasion  
90 might be regulated by species' life history traits (Duncan, 2021, Fristoe et al., 2023; Moyano,  
91 2023). However, our understanding of time lags within insular environments remains limited,  
92 and how the introduction and life histories of non-native species intersect is still largely  
93 unexplored (Kinlock et al., 2022; Schrader et al. 2021a).

94 Rates of non-native species introduction have varied over time. The number of new  
95 species introduced worldwide remained relatively low until the 19th century (Seebens et al.,  
96 2017). After that, numbers increased consistently until now, with the exception of the period  
97 1914–1945, marked by two major wars and rather constant introduction numbers (Pyšek et  
98 al., 2020; Seebens et al., 2017). After 1945, rates of non-native species introduction increased  
99 and are not slowing, correlated with increasing volumes of commerce worldwide (Pyšek et  
100 al., 2020; Seebens et al., 2017). Clearly quantifying time lags between first introduction and  
101 naturalization and later spread will help forecast future range expansions and guide  
102 management focused on early containment or eradication.

103 Species introduced earlier are likely to occupy a larger number of islands than recent  
104 introductions. However, island colonization is also regulated by island characteristics  
105 (MacArthur & Wilson, 1967). Large islands offer a bigger target for dispersing propagules  
106 and therefore are more likely to be occupied first (i.e. target island effect, Lomolino, 1990).  
107 Similarly, less isolated islands are more easily reached by dispersing propagules and thus will  
108 be occupied before more isolated islands (MacArthur & Wilson, 1967). Since the

109 introduction and naturalization of non-native species often rely on humans, islands that are  
110 inhabited or close to human communities are likely to be more readily invaded (Sullivan et  
111 al., 2005; Timmins & Williams, 1991). Interactions between these determinants of island  
112 invasions and time lags have not been adequately investigated.

113         Time of introduction, time lags, and island characteristics that favour initial  
114 colonization of islands are likely to be related to plant life-histories. For instance, a  
115 disproportionate number of herbaceous European species were initially introduced in many  
116 parts of the world for agricultural purposes and in an attempt to “recreate” a landscape  
117 familiar to settlers (Crosby, 2004; Lenzner et al., 2022). Time lags might be shorter for  
118 species that disperse more efficiently, either because of shorter life cycles (e.g. herbs) or  
119 because of morphological adaptations allowing for long-distance dispersal (Arjona et al.,  
120 2018; Mologni et al., 2022; Negoita et al., 2016 but see Duncan, 2021). Similarly, species  
121 that originate from biogeographic areas with similar climates (i.e. climate matching) are  
122 likely to have an advantage when establishing new populations (Richardson & Pyšek, 2012).  
123 These traits might also affect how they relate to island characteristics. For instance, long-  
124 distance dispersal species might show weaker relationships with isolation (Arjona et al.,  
125 2018; Negoita et al., 2016), while high propagule pressure in species with short life cycles  
126 might mask a target island effect.

127         Here, we aim to better understand the role of introduction histories and plant traits in  
128 explaining non-native plant invasions on islands. We calculated non-native species richness  
129 on 264 islands off the northern coast of Aotearoa New Zealand, for a total of 848 non-native  
130 vascular plant species. We asked: (1) Is there a time lag in the invasion process on the  
131 islands? If so, is it consistent across growth forms, dispersal modes, and biogeographic  
132 origins? (2) Do the non-native plants on the islands show distinct periods of naturalization in  
133 Aotearoa New Zealand? If so, were periods of naturalization similar across growth forms,

134 dispersal modes and biogeographic origins? (3) If non-native plant species colonize larger,  
135 less isolated islands that are close to urban areas first, does the average (a) area, (b) isolation  
136 and (c) distance from urban areas of the islands where a species occurs respectively decline,  
137 increase and increase with time since first naturalization? If so, is it consistent across growth  
138 forms, dispersal modes and biogeographic origins?

139

## 140 **Methods**

### 141 *Study system*

142 The study system comprises 264 islands off the northern coast of Aotearoa New Zealand's  
143 North Island (hereafter the 'mainland'). The study system spans six hundred kilometres (34–  
144 38 °S, 172–179 °E, Figure 1). The islands vary in area from 0.00002 to 277.21 km<sup>2</sup>, and  
145 range from islands connected to the mainland at low tides to those >50 km from the coast.  
146 Most are land-bridge islands that were connected to the mainland during the last glacial  
147 maximum (Poor Knight Islands excepted, Fleming, 1979). They supported warm temperate  
148 rain forests before human settlement (circa 740 years ago, Wilmshurst et al., 2014). Humans  
149 cleared, burned and farmed many islands (Bellingham et al., 2010), some of which were  
150 abandoned in only the last few decades. Northern Aotearoa New Zealand is the most  
151 populous region of the country (Statistics NZ Tatauranga Aotearoa, 2018), and 41 islands are  
152 still inhabited within the study system. A more detailed description of the study system is  
153 provided by Mologni et al., 2022.

154

### 155 *Data collection*

156 The total number of non-native vascular plant species occupying each island was quantified  
157 by collating previously published material and field surveys (see Mologni et al., 2021 for  
158 more details). For each species, we obtained the year of their naturalization from the New

159 Zealand Plant Conservation Network and Gatehouse (2008). Then, we used as a proxy for  
160 their time since first naturalization (i.e. the number of years they resided in Aotearoa New  
161 Zealand) the current year (2023) minus the year of the first record. Of the 848 non-native  
162 species, only 784 were included in our analyses. Thirty-three were removed due to taxonomic  
163 uncertainty, while 31 were not included due to a lack of first-naturalization data.

164 We classified non-native species according to their growth form, dispersal mode and  
165 biogeographic region (Table 1). Five categories of growth forms were identified: graminoids,  
166 forbs, woody species, lycophytes and lianas and climbers. Five categories of dispersal modes  
167 were defined based on morphological adaptations to long-distance dispersal: wind-, water-,  
168 animal-dispersed, unspecialized and short-distance (Arjona et al., 2018; Burns, 2019;  
169 Mologni et al., 2022; Negoita et al., 2016). Nine categories of biogeographic origin were  
170 delineated: Cosmopolitan, Eurasia (excl. Mediterranean basin), Mediterranean (i.e.  
171 Mediterranean basin), Tropical, Southern Africa, Oceania (excl. Aotearoa New Zealand),  
172 North America (i.e. species restricted to North America), Other American (i.e. species  
173 ranging across all America or temperate South America) and Macaronesia (see Table 1 for  
174 more details). All species could be categorized based on their growth forms; however, 18 and  
175 40 species were respectively excluded from dispersal mode and biogeographic origin  
176 analyses due to a lack of data. Of these categories, seven were removed due to the small  
177 sample size: lycophytes (number of species = 1), lianas and climbers (n = 41), water-  
178 dispersed (n = 16), cosmopolitan (n = 36), North America (n = 31), Other American (n = 16),  
179 Macaronesia (n = 6). In total, we used 3 categories for growth forms, 4 for dispersal modes  
180 and 6 for biogeographic origins (Table 1).

181 Island characteristics were quantified using ArcGIS 10.5.1 (ESRI, 2011). The size of  
182 an island was calculated as the total surface area in km<sup>2</sup>. Isolation was measured as the total  
183 amount of water surrounding each island (Carter et al., 2020; Diver, 2008; Negoita et al.,

184 2016). The greater the amount of water, the more isolated an island is. For each island, we  
185 created several concentric buffers with radii of 250, 500, 1000, 1500, 2000, 2500 and 3000  
186 m. Then, we calculated the amount of water within each radius (%). To quantify the effect of  
187 isolation from human communities, we calculated the shortest distance from the nearest  
188 urban area (m). We defined as urban built-up areas having a population of 1000 people or  
189 more (Statistics NZ Tatauranga Aotearoa, 2018).

190

### 191 *Statistical analyses*

192 To test for time lags in the invasion process, we used a generalized linear model (GLM). We  
193 set the number of islands occupied by each species as the dependent variable and years since  
194 first naturalization time as the independent variable. Since the dependent variable was right-  
195 skewed even after transformation, we modelled data using linear, quasipoisson and negative  
196 binomial models for all species. Results were consistent and, for simplicity, we opted for a  
197 linear model. We assessed differences in slopes among different trait and biogeographic  
198 origin categories with ANCOVA tests. The number of occurrences was log-transformed in all  
199 linear models to conform to assumptions of normality.

200 To test whether non-native species show distinct periods of their naturalization to  
201 Aotearoa New Zealand, modes were extracted for each trait and biogeographic origin  
202 category after binning the year of naturalization by 20-year periods. Additionally, we  
203 contrasted the distribution of each category of growth forms, dispersal modes and  
204 biogeographic origin using ANOVAs.

205 To test whether non-native plants that naturalized more recently occur more  
206 frequently on islands that are large, less isolated and close to urban areas, we set the average  
207 area, isolation and distance from urban areas of occupied islands by each species as the  
208 dependent variables in three separate linear models. Years since first naturalization was used

209 as the independent variable. To conform to assumptions of normality, the average area,  
210 isolation and distance from urban areas of occupied islands were respectively log-, arcsine-  
211 and square root-transformed. Tests were run for all species first, then ANCOVA tests were  
212 used to contrast slopes among different trait and biogeographic origin categories. All analyses  
213 were conducted in R (R Core Team, 2023). A post hoc Tukey test and Bonferroni correction  
214 were applied for multiple testing at all stages (Hothorn et al. 2008).

215

## 216 **Results**

217         There was a time lag in the invasion process: the earlier a non-native plant species had  
218 naturalized in Aotearoa New Zealand, the more islands it occupied (Figure 1 & Table S1).  
219 The slopes of relationships between time since first naturalization and number of islands  
220 occupied did not differ significantly among different non-native plant growth forms, dispersal  
221 modes or biogeographic origins (Table S2).

222         The non-native plant species on the islands had mainly two 20-year bin periods of  
223 peak naturalization – 1850 to 1870 and 1970 to 1990 (Figure 2, Table 2 & Table S3). Non-  
224 native graminoids and forbs on the islands had disproportionately first naturalized in  
225 Aotearoa New Zealand between 1850–1870, whereas woody species had disproportionately  
226 first naturalized between 1970–1990 (Figure 2, Table 2 & Table S3). Differences between  
227 non-native woody species and other growth forms were significant (ANOVA and Tukey  
228 tests: Table S4). Among dispersal modes, unspecialized and animal-dispersed species on the  
229 islands had disproportionately first naturalized in Aotearoa New Zealand between 1850–  
230 1870, whereas short-distance species had disproportionately first naturalized between 1970–  
231 1990 (Figure 2, Tables 2 & Table S3). Wind-dispersed species first naturalized  
232 disproportionately 1930–1950 (Figure 2, Tables 2 & Table S3). Differences between  
233 unspecialized species and other dispersal modes were significant (ANOVA and Tukey tests:

234 Table S4). Non-native Eurasian and Mediterranean plant species on the islands had  
235 disproportionately first naturalized during 1850–1870, those from Southern Africa in both  
236 1930–1950 and 1970–1990, and those from Oceania and tropical regions during 1970–1990  
237 (Figure 2, Table 2 & Table S3); a significant difference was identified between Eurasian and  
238 Mediterranean species and those from other biogeographic regions (ANOVA, Tukey tests:  
239 Table S4).

240 The average area and distance from urban areas of islands where a species occurred  
241 respectively declined and increased with time since first naturalization (Table 3). No  
242 significant relationship was detected between the average isolation of islands where a species  
243 occurred and time since first naturalization (Table 3). There were no significant differences in  
244 non-native plants' growth forms, dispersal modes and biogeographic origins for the average  
245 area, isolation and distance from urban areas of islands where a species occurred (Table 3 &  
246 Table S5).

247

## 248 **Discussion**

249 Time lags in the invasion process are commonly reported (Duncan, 2021; Kowarik, 1995;  
250 Pyšek et al., 2020; Seabloom et al., 2006). Here, we found evidence of time lags in the  
251 invasion of non-native plants on islands in northern Aotearoa New Zealand. Moreover, there  
252 were differences in periods of first naturalization among growth forms, dispersal modes and  
253 biogeographic origins. Consistent with studies in the same system (Mologni et al., 2021),  
254 large islands close to humans were more frequently colonized first by invading species.  
255 However, once time of first naturalization was accounted for, and in contrast to an earlier  
256 study (Mologni et al., 2022), there were no differences across categories of growth forms,  
257 dispersal modes and biogeographic origin.

258           Once time of naturalization was accounted for, it was a better predictor than life  
259 history traits in explaining non-native plant invasions on the islands. For example, non-native  
260 woody plant species have proportionately colonized fewer islands but most of them have  
261 naturalized more recently than other growth forms. Herbaceous species used for agriculture  
262 were introduced and naturalized disproportionately early, whereas woody, ornamental species  
263 naturalized disproportionately recently (Gatehouse, 2008). Among dispersal modes, more  
264 unspecialized plant species naturalized early, perhaps reflecting a higher efficiency in  
265 exploiting human-related pathways. Among biogeographic origins, more plant species from  
266 Eurasia and the Mediterranean naturalized early, a reflection of European settlement  
267 (Gatehouse, 2008; Lenzner et al., 2022). In particular, species originating from other regions  
268 within Oceania (mostly Australian species) are disproportionately woody (60.3%, see Table  
269 S6), indicating this trait combination is of utmost importance for future management  
270 endeavours.

271           If there are similar invasion time lags irrespective of trait and biogeographic origin  
272 categories, we might expect that, in time, more non-native woody species will invade more  
273 islands, as the earlier-naturalized herbaceous species have already done (Howell, 2019). Even  
274 so, the time lag for woody species may still be longer since woody species will generally be  
275 slower to reach reproductive maturity than herbaceous species (Grime 2002). In support of  
276 this view, the naturalization of non-native conifers in Aotearoa New Zealand continued at a  
277 linear rate to this day (Howell, 2019), even though there had been no or few introductions of  
278 new non-native conifer species to the country since its 1993 Biosecurity Act significantly  
279 reduced introduction rates of non-native species (Seebens et al., 2017). Similar trends might  
280 be expected for other categories that were more consistently introduced in recent times.

281           Previous work in the study system found that graminoids and long-distance dispersal  
282 species have higher occupancy rates than other trait categories and distributional patterns

283 more similar to native species (Mologni et al., 2022). Here, we found that their invasion  
284 success is not associated with shorter time lags. Other processes might be at play. For  
285 instance, these species might have been purposely introduced more consistently than other  
286 categories. Alternatively, species introduced and naturalized early might negatively impact  
287 the establishment of other non-native species (i.e. priority effect, Fraser et al., 2015, Catford  
288 et al. 2022). For instance, herbaceous European and Mediterranean non-native species that  
289 naturalized early and invaded the islands might reduce the probability of successful  
290 establishment by herbaceous non-native species from other biogeographic regions through  
291 niche pre-emption (Fukami 2015).

292         Non-native plants that naturalized more recently occurred more frequently on large  
293 islands, consistently with the target island effect (Lomolino, 1990). However, large islands in  
294 the region are also inhabited (Mologni et al., 2021). Whether the more consistent colonization  
295 of large islands reflects autonomous or human-mediated dispersal is unclear, both processes  
296 though are likely at play. Since they both increase the likelihood of large over small island  
297 colonization, island area might then simultaneously encapsulate a “geographic” target island  
298 effect (i.e. species colonize larger islands first because they offer a bigger target) and a  
299 “human-mediated” target islands effect (i.e. human inhabit larger islands, disproportionately  
300 introducing non-native species).

301         Non-native plants that naturalized more recently did not occur more frequently on less  
302 isolated islands. However, a negative effect of isolation on non-native species richness was  
303 previously identified (Mologni et al., 2021). Perhaps this pattern is simply more difficult to  
304 capture, and, over time, less isolated islands still accumulate more species than more isolated  
305 islands through multiple colonization events. In contrast, non-native plants that naturalized  
306 more recently occurred more frequently on islands that are close to urban areas. Since non-  
307 native species often use human-related pathways (Pyšek et al., 2020; Sinclair et al., 2020),

308 islands close to urban areas are more likely to be colonized just by proximity (Sullivan et al.,  
309 2005; Timmins & Williams, 1991). For non-native species in this study system, isolation  
310 might be more strongly associated with humans than with geography.

311         The relationships between island characteristics and time since first naturalization  
312 were similar across trait and biogeographic origin categories. This suggests that the same  
313 processes regulate the initial colonization of these islands, irrespective of plant life histories.  
314 This is surprising since a growing body of literature has identified differences in island  
315 species distributions based on traits (Conti et al., 2022; Mologni et al., 2022; Schrader et al.,  
316 2021b; Schrader et al., 2023; Walentowitz et al., 2022). Alternatively, other traits might be  
317 more important. For instance, wind-pollinated species are independent of biological carriers  
318 for dispersing their pollen, an advantage in newly occupied islands (Cox et al., 1997).  
319 Propagule pressure is another trait that likely influences the ability to rapidly colonize more  
320 islands (Lockwood et al., 2005). Future studies should assess a broad suite of traits when  
321 assessing the importance of time lags in the invasion process on islands.

322         The year of naturalization was used to identify periods of non-native plant species'  
323 naturalizations. However, in many cases, long periods of time can elapse between the  
324 introduction, naturalization and identification of newly naturalized species. This is  
325 particularly important for earlier introductions, more likely to go unnoticed due to a lack of  
326 awareness of biological invasions. Conversely, we can expect current monitoring activities to  
327 be more effective in identifying new non-native species (Pyšek et al., 2020). Unfortunately,  
328 accounting for this form of error will be challenging.

329         Since similar time lags were identified for all trait and biogeographic origin categories  
330 despite different periods of naturalization, management bodies should focus on species of  
331 categories that naturalized more consistently in recent times, such as woody species (Howell,  
332 2019) originating from other regions within Oceania and short-distance dispersal species, and

333 on large islands close to urban areas. Additionally, this work builds on and aligns with a  
334 growing body of literature implementing traits in island biogeography (Ottaviani et al., 2020;  
335 Schrader et al., 2023; Whittaker et al., 2014), suggesting, however, that plant life histories do  
336 not always play a role in explaining plant distributions on islands.

337

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491 **Data availability statement**

492 Data are available as supplementary material. Island locations (longitude and latitude) are not  
493 publicly available due to private ownership and issues of data sovereignty of concern to

494 Māori.

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505 **Tables**

506 **Table 1** Description and the number of species for growth form, dispersal mode and  
 507 biogeographic origin categories across 264 Aotearoa New Zealand offshore islands.

Category	Description	Number of species
<b>Growth forms</b>		<b>784</b>
Graminoids	Grasses, sedges and rushes	125
Forbs	Herbaceous, non-graminoid	472
Woody species	Trees and shrubs	145
Lycophytes	Lycophytes	1
Climbers and lianas	Herbaceous or woody climbers	41
<b>Dispersal modes</b>		<b>766</b>
Wind-dispersed	Plumes, wings, dust diaspores (anemochory)	141
Water-dispersed	Buoyant propagules, e.g. corky tissues, air pockets (hydrochory)	16
Animal-dispersed	Fleshy fruits or adhesive barbs (endo and epizoochory)	157
Unspecialized	No evident or prevalent morphological adaptations (unspecialized)	286
Short-distance	Morphological adaptations for short-distance dispersal only (ballochory, myrmecory)	166
<b>Biogeographic origin</b>		<b>749</b>
Eurasia	Europe (excl. Mediterranean basin), Asia, North Africa and the Arabian Peninsula	310
Cosmopolitan	Cosmopolitan, subcosmopolitan and temperate areas of the northern hemisphere	36
Other American	All America (North, Central, South) or Temperate South America	16
Mediterranean	Mediterranean basin	94
North America	Nearctic	31
Oceania	Australia, Pacific	63

Southern Africa	South Africa, Eswatini, Lesotho, and Namibia	66
Tropical	Tropical Africa, Asia, Central and South America, Madagascar and Pantropical	127
Macaronesia	Macaronesia	6

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530 **Table 2** Peak of naturalization (mode) and the number of species introduced per 20-  
 531 year bin period for growth form, dispersal mode and biogeographic origin categories across  
 532 264 Aotearoa New Zealand offshore islands.

Category	Peak of introduction (Mode)	Number of species introduced
<b>Growth forms</b>		
Graminoids	1850–1870	34
Forbs	1850–1870	129
Woody species	1970–1990	51
<b>Dispersal modes</b>		
Wind-dispersed	1930–1950	27
Animal-dispersed	1850–1870	37
Unspecialized	1850–1870	89
Short-distance	1970–1990	37
<b>biogeographic origin</b>		
Eurasia	1850–1870	100
Mediterranean	1850–1870	27
Oceania	1970–1990	20
South Africa	1930–1950, 1970–1990	15, 15
Tropical	1970–1990	27

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541 **Table 3** Top section: separate linear relationships between the average area, isolation  
 542 and distance from urban areas (average urban) of occupied islands and time since first  
 543 naturalization across all species. Entries are model, estimate, t- and p-value. Bottom section:  
 544 Interaction terms extracted from ANCOVA models between the average area, isolation and  
 545 distance from urban areas (average urban) of occupied islands and time since first  
 546 naturalization by growth forms, dispersal modes and biogeographic origin. Entries are model,  
 547 sum of squares, t- and p-value. P-values are in bold when significant (<0.05).

<b>Overall models</b>			
<b>Model</b>	<b>Estimate</b>	<b>t-value</b>	<b>p-value</b>
log (average area) ~ time since first naturalization	-0.00 ± 0.00	-3.68	<b>&lt;0.001</b>
arcsine (average isolation) ~ time since first naturalization	0.00 ± 0.000	0.44	0.662
square root (average urban) ~ time since first naturalization	0.25 ± 0.03	7.60	<b>&lt;0.001</b>
<b>Interaction terms</b>			
<b>Model</b>	<b>Sum of squares</b>	<b>t-value</b>	<b>p-value</b>
log (average area) ~ time since first naturalization *growth forms	3.60	1.71	0.181
log (average area) ~ time since first naturalization *dispersal modes	8.30	2.55	0.054
log (average area) ~ time since first naturalization *biogeographic origin	3.40	0.78	0.536
arcsine (average isolation) ~ time since first naturalization *growth forms	0.04	0.67	0.513
arcsine (average isolation) ~ time since first naturalization *dispersal modes	0.15	1.60	0.188
arcsine (average isolation) ~ time since first naturalization *biogeographic origin	0.15	1.23	0.295
square root (average urban) ~ time since first naturalization *growth	3345.00	0.90	0.405
square root (average urban) ~ time since first naturalization *dispersal	9098.00	1.54	0.203
square root (average urban) ~ time since first naturalization *biogeographic origin	14467.00	1.93	0.105

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552 **Figure Captions**

553 **Figure 1** Relationships between the number of islands occupied by a species and years  
554 since first naturalization for growth form (top), dispersal mode (centre) and biogeographic  
555 origin (bottom) categories across 264 Aotearoa New Zealand offshore islands. No statistical  
556 differences were identified in contrasting categories.

557 **Figure 2** Frequency plots displaying the number of species naturalized per 20-year bin  
558 period for growth form (top), dispersal mode (centre) and biogeographic origin (bottom)  
559 categories across 264 Aotearoa New Zealand offshore islands. Numbers illustrate the number  
560 of species introduced at the mode (introduction peak) by category. Two modes were  
561 identified for Southern African species. Asterisks indicate significant differences in the  
562 number of species naturalized by 20-year intervals (p-value <0.05).

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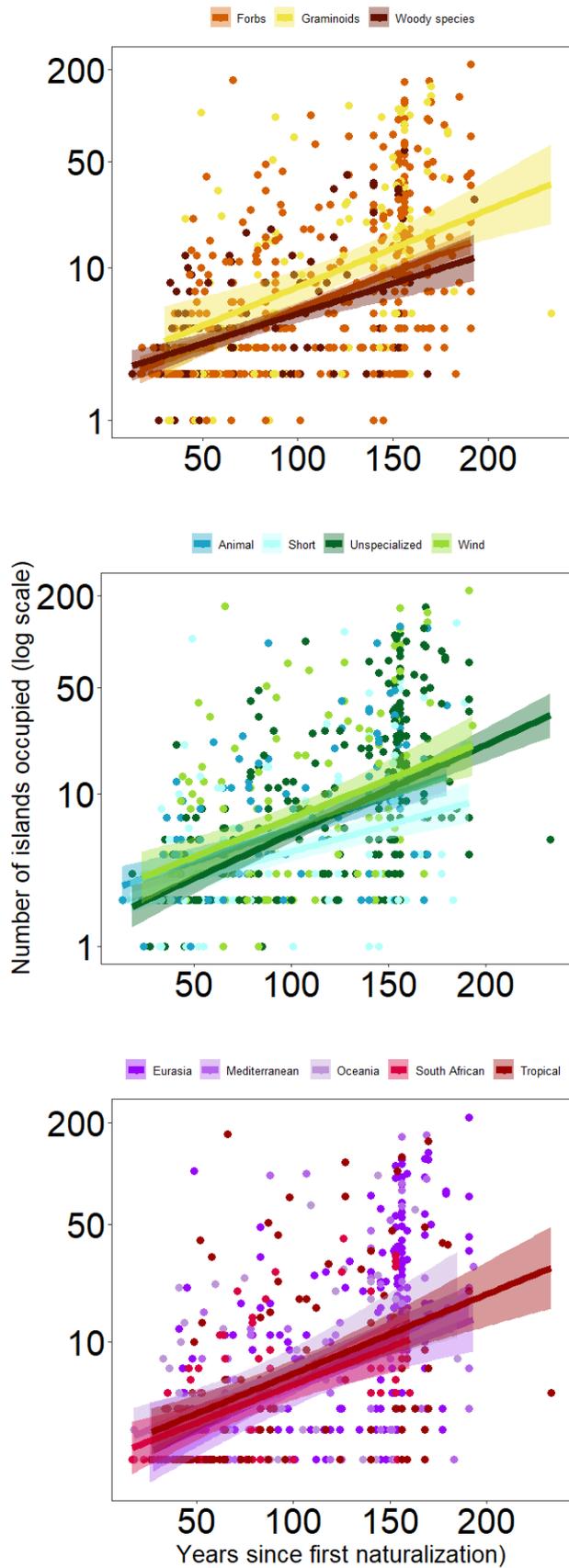
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572 **Figure 1**



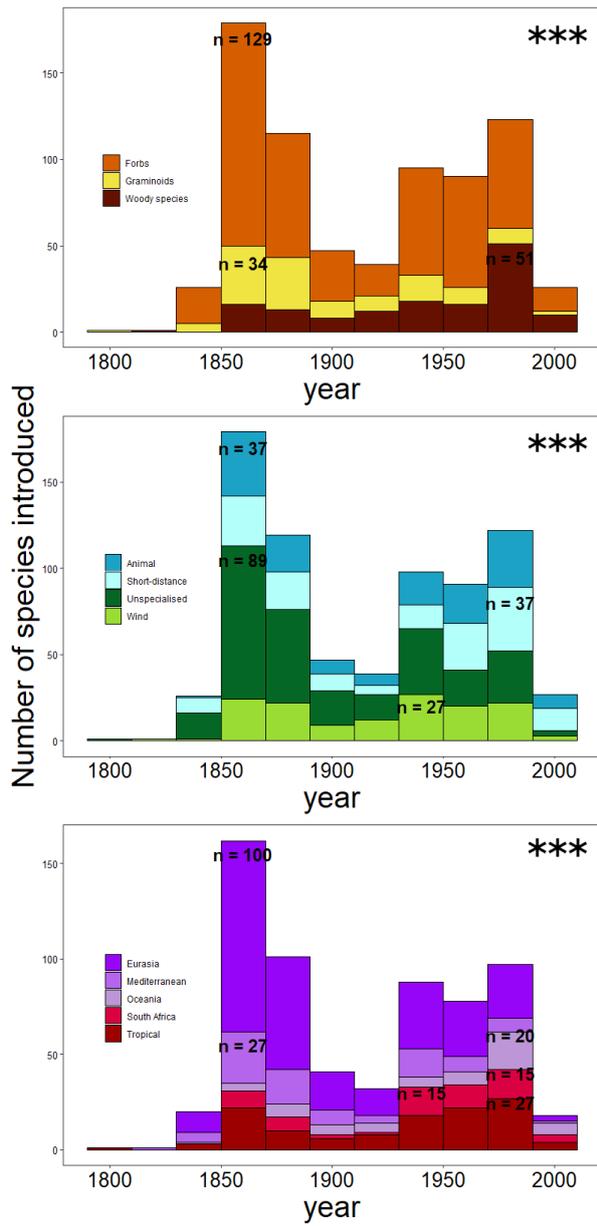
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577 **Figure 2**



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580 **Supplementary Material**

581 **Table S1** Relationships between the number of islands occupied and time since first  
582 naturalization of all species across 264 Aotearoa New Zealand offshore islands. Entries are  
583 model utilized, estimate, t- and p-value. P-values are in bold when significant (<0.05).

Model	Estimate	t-value	p-value
Linear (log-transformed)	0.01 ± 0.00	14.85	<b>&lt;0.001</b>
Quasipoisson	0.02 ± 0.00	10.49	<b>&lt;0.001</b>
Negative binomial	0.02 ± 0.00	17.82	<b>&lt;0.001</b>

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599 **Table S2** ANOVA and Tukey tests for multiple comparisons of relationships between  
600 the number of islands occupied by a species and its time since first naturalization across  
601 categories of growth forms, dispersal modes and biogeographic origin. In brackets is the level  
602 of significance of ANOVA tests (NS > 0.05, \* < 0.05, \*\* < 0.01, \*\*\* < 0.001). Columns are  
603 categories and estimates, t- and p-values of Tukey tests.  $\alpha$  was set at 0.003 after applying a  
604 Bonferroni correction for multiple comparisons.

Category	Estimate	t-value	p-value
<b>Growth forms (NS)</b>			
Graminoids - Forbs	0.28 ± 0.31	0.90	0.633
Woody - Forbs	0.13 ± 0.22	0.62	0.805
Woody - Graminoids	-0.14 ± 0.33	-0.43	0.902
<b>Dispersal modes (NS)</b>			
Unspecialized - Short-distance	-0.27 ± 0.24	-1.09	0.698
Unspecialized - Animal	-0.43 ± 0.26	-1.68	0.332
Unspecialized - Wind	0.41 ± 0.28	1.47	0.458
Wind - Animal	-0.02 ± 0.29	-0.06	1.000
Wind - Short-distance	0.15 ± 0.28	0.53	0.951
Short-distance - Animal	-0.17 ± 0.25	-0.66	0.911
<b>Biogeographic origin (NS)</b>			
Eurasia - Mediterranean	0.19 ± 0.37	0.53	0.984
Eurasia - Oceania	0.33 ± 0.33	1.01	0.850
Eurasia - Southern Africa	0.20 ± 0.34	0.60	0.975
Eurasia - Tropical	0.30 ± 0.27	1.10	0.805
Mediterranean - Oceania	0.14 ± 0.42	0.32	0.998
Mediterranean - Southern Africa	0.01 ± 0.43	0.02	1.000
Mediterranean - Tropical	0.11 ± 0.38	0.28	0.999
Oceania - Southern Africa	-0.13 ± 0.40	-0.32	0.998
Oceania - Tropical	-0.03 ± 0.34	-0.08	1.000
Tropical - Southern Africa	0.10 ± 0.36	0.28	0.999

605 **Table S3** Peak of naturalization (Mode) and the number of species introduced by 20-  
606 year bin period for growth form, dispersal mode and biogeographic origin categories across  
607 264 Aotearoa New Zealand offshore islands.

Category	1790–1810	1810–30	1830–50	1850–70	1870–90	1890–1910	1910–30	1930–50	1950–70	1970–90	1990–2010
<b>Growth forms</b>											
Graminoids	1	0	5	34	30	10	9	15	10	9	2
Forbs	0	0	21	129	72	29	18	62	64	63	14
Woody species	0	1	0	16	13	8	12	18	16	51	10
<b>Dispersal modes</b>											
Wind	0	1	1	24	22	9	12	27	20	22	3
Animal	0	0	1	37	21	8	7	19	23	33	8
Unspecialized	1	0	15	89	54	20	15	38	21	30	3
Short-distance	0	0	9	29	22	10	5	14	27	37	13
<b>Biogeographic origin</b>											
Eurasia	0	0	11	100	59	20	14	35	29	28	3
Mediterranean	0	1	5	27	18	8	4	15	8	7	1
Oceania	0	0	1	4	7	5	5	5	7	20	6
South Africa	0	0	0	9	7	2	1	15	12	15	4
Tropical	1	0	3	22	10	6	8	18	22	27	4

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615 **Table S4** ANOVA and Tukey tests for multiple comparisons of naturalization time  
616 frequency distributions across categories of growth forms, dispersal modes and  
617 biogeographic origins. In brackets is the level of significance of ANOVA tests (NS > 0.05, \*  
618 < 0.05, \*\* < 0.01, \*\*\* < 0.001). Columns are categories and estimates, t- and p-values of  
619 Tukey tests. P-values are in bold when significant,  $\alpha$  was set at 0.003 after applying a  
620 Bonferroni correction for multiple comparisons.

Category	Estimate	t-value	p-value
<b>Growth forms (***)</b>			
Graminoids - Forbs	-12.95 ± 4.71	-2.75	0.016
Woody - Forbs	30.62 ± 4.44	6.89	<b>&lt;0.001</b>
Woody - Graminoids	43.57 ± 5.71	7.63	<b>&lt;0.001</b>
<b>Dispersal modes (***)</b>			
Unspecialized - Short-distance	-26.15 ± 4.63	-5.65	<b>&lt;0.001</b>
Unspecialized - Animal	-24.11 ± 4.71	-5.12	<b>&lt;0.001</b>
Unspecialized - Wind	20.92 ± 4.88	4.29	<b>&lt;0.001</b>
Wind - Animal	-3.198 ± 5.50	-0.58	0.9373
Wind - Short-distance	-5.24 ± 5.43	-0.96	0.7682
Short-distance - Animal	2.04 ± 5.28	0.39	0.9802
<b>Biogeographic origin (***)</b>			
Eurasia - Mediterranean	-0.21 ± 5.32	-0.04	1.000
Eurasia - Oceania	42.10 ± 6.37	6.60	<b>&lt;0.001</b>
Eurasia - Southern Africa	37.12 ± 6.17	6.02	<b>&lt;0.001</b>
Eurasia - Tropical	26.76 ± 4.85	5.51	<b>&lt;0.001</b>
Mediterranean - Oceania	42.31 ± 7.44	5.68	<b>&lt;0.001</b>
Mediterranean - Southern Africa	37.33 ± 7.27	5.13	<b>&lt;0.001</b>
Mediterranean - Tropical	26.97 ± 6.19	4.35	<b>&lt;0.001</b>
Oceania - Southern Africa	-4.99 ± 8.07	-0.62	0.971
Oceania - Tropical	-15.35 ± 7.11	-2.16	0.190
Tropical - Southern Africa	-10.36 ± 6.93	-1.49	0.555

622 **Table S5** Tukey tests for multiple comparisons of relationships between the average  
623 area, isolation and distance from urban areas (urban) of occupied islands and time since first  
624 naturalization across categories of growth forms, dispersal modes and biogeographic origins.  
625 Columns are island characteristics and t-values of Tukey tests.  $\alpha$  was set at 0.003 after  
626 applying a Bonferroni correction for multiple comparisons.

Category	Area	Isolation	Urban
<b>Growth forms</b>			
Graminoids - Forbs	-0.50	0.26	1.90
Woody - Forbs	-0.80	2.16	-0.208
Woody - Graminoids	-0.01	1.08	-1.880
<b>Dispersal modes</b>			
Unspecialized - Short-distance	-0.93	1.08	1.182
Unspecialized - Animal	1.77	-2.00	2.348
Unspecialized - Wind	0.08	0.98	-0.867
Wind - Animal	1.68	-0.74	1.262
Wind - Short-distance	-0.75	2.00	0.175
Short-distance - Animal	2.72	-3.00	1.237
<b>Biogeographic origins</b>			
Eurasia - Mediterranean	-0.23	-1.72	1.86
Eurasia - Oceania	1.42	1.75	-0.07
Eurasia - Southern Africa	-0.10	-1.80	1.19
Eurasia - Tropical	0.74	0.91	0.78
Mediterranean - Oceania	1.31	2.86	-1.68
Mediterranean - Southern Africa	0.12	0.04	-0.64
Mediterranean - Tropical	0.76	2.31	-1.23
Oceania - Southern Africa	-1.25	-2.98	1.08
Oceania - Tropical	-0.76	-0.94	0.69
Tropical - Southern Africa	0.66	2.42	-0.54

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628 **Table S6** Contingency table of biogeographical origin and growth forms (top) and  
 629 dispersal modes (bottom).

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	Graminoids	Forbs	Woody species	Total
Eurasia	53	200	45	298
Mediterranean	8	63	19	90
Oceania	13	12	38	63
South Africa	6	49	9	64
Tropical	20	72	19	111
Total	100	396	130	626

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	Wind-dispersed	Animal-dispersed	Unspecialized	Short-distance	Total
Eurasia	47	66	132	58	303
Mediterranean	11	15	35	33	94
Oceania	15	23	12	11	61
South Africa	20	3	27	14	64
Tropical	23	35	38	23	119
Total	116	142	244	139	641

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