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A century of ecosystem change: human and seabird impacts on plant species extirpation and invasion on islands

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We used 116-years of floral and faunal records from Mandarte Island, British Columbia, Canada, to estimate the indirect effects of humans on plant communities via their effects on the population size of a surface-nesting, colonial seabird, the Glaucous-winged gull (*Larus glaucescens*). Comparing current to historical records revealed 18 extirpations of native plant species (32% of species historically present), 31 exotic species introductions, and one case of exotic introduction followed by extirpation. Contemporary surveys indicated that native species cover declined dramatically from 1986 to 2006, coincident with the extirpation of 'old-growth' conifers. Because vegetation change co-occurred with an increasing gull population locally and regionally, we also tested predictions from the hypothesis that the presence and activities of seabirds help to explain those changes. Specifically, we predicted we would observe high nutrient loading and exotic plant species richness and cover on nearby islands with versus without gull colonies as a consequence of competitive dominance in species adapted to high soil nitrogen and trampling. As predicted, we found that native plant species cover and richness were lower, and exotic species cover and richness higher, on islands with versus without gull colonies. In addition, we found that soil carbon and nitrogen on islands with nesting gulls were positively related to soil depth and exotic species richness and cover across plots and islands. Our results suggest that gulls have the potential to drive rapid change in insular plant communities by increasing nutrients and disturbing vegetation. Because human activities have contributed to long-term change in gull populations, our results further suggest compelling, indirect links between human management decisions and plant community composition on islands of the Georgia Basin.

1 **A century of ecosystem change: human and seabird impacts on plant species extirpation and**
2 **invasion on islands**

3

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20

21 **Suggested running head:** Seabirds and island plant communities

22

23 The authors declare that they have no conflict of interest

24 **Abstract**

25 We used 116-years of floral and faunal records from Mandarte Island, British Columbia, Canada, to
26 estimate the indirect effects of humans on plant communities via their effects on the population size of a
27 surface-nesting, colonial seabird, the Glaucous-winged gull (*Larus glaucescens*). Comparing current to
28 historical records revealed 18 extirpations of native plant species (32% of species historically present), 31
29 exotic species introductions, and one case of exotic introduction followed by extirpation. Contemporary
30 surveys indicated that native species cover declined dramatically from 1986 to 2006, coincident with the
31 extirpation of ‘old-growth’ conifers. Because vegetation change co-occurred with an increasing gull
32 population locally and regionally, we also tested predictions from the hypothesis that the presence and
33 activities of seabirds help to explain those changes. Specifically, we predicted we would observe high
34 nutrient loading and exotic plant species richness and cover on nearby islands with versus without gull
35 colonies as a consequence of competitive dominance in species adapted to high soil nitrogen and
36 trampling. As predicted, we found that native plant species cover and richness were lower, and exotic
37 species cover and richness higher, on islands with versus without gull colonies. In addition, we found that
38 soil carbon and nitrogen on islands with nesting gulls were positively related to soil depth and exotic
39 species richness and cover across plots and islands. Our results suggest that gulls have the potential to
40 drive rapid change in insular plant communities by increasing nutrients and disturbing vegetation.
41 Because human activities have contributed to long-term change in gull populations, our results further
42 suggest compelling, indirect links between human management decisions and plant community
43 composition on islands of the Georgia Basin.

44 **Suggested key words:** *exotic species invasion, native species extirpation, seabirds, islands, Garry oak*
45 *ecosystem, maritime meadow, soil nutrients, plant communities*

46 Introduction

47 Drivers of species invasion and long-term change in communities are key themes in ecology (Pickett,
48 Collins & Armesto, 1987; Strayer et al., 2006) but rarely studied over multiple decades (Bakker et al.,
49 1996). Comparing contemporary and historical surveys can help rectify this deficit and enhance
50 understanding of long-term ecological change (Macdougall & Turkington, 2005; Arcese et al., 2014;
51 McKechnie et al., 2014). In particular, human disturbance and habitat conversion via exotic species
52 invasion are both identified as drivers of plant community change (Davis, Grime & Thompson, 2000;
53 Macdougall & Turkington, 2005; Seabloom et al., 2006), with recent evidence indicating that human
54 impacts can arise indirectly via predator removal or herbivore introductions that facilitate trophic
55 cascades, particularly in island systems (Estes et al., 2011; Arcese et al., 2014). Observational results
56 further suggest that humans can affect island plant communities via their impacts on island-nesting
57 seabirds, including via predator introduction, changes in harvest rate, the provision of anthropogenic
58 foods or depletion of native prey species (Croll et al., 2005; Mulder et al., 2011; Baumberger et al., 2012).
59 These activities can in turn affect rates of physical disturbance and chemical input to vegetation linked to
60 changes in nest density or guano deposition, as has been described for gulls (Laridae) and cormorants
61 (Phalacrocoracidae; Sobey and Kenworthy 1979, Ishida 1996, 1997, Ellis 2005). On islands with
62 historically low seabird abundances, increases of guano deposition in particular can cause long-lasting
63 changes in soil chemistry and nutrients (García et al., 2002; Wait, Aubrey & Anderson, 2005; Caut et al.,
64 2012) that facilitate increases to the cover and richness of species adapted to nutrient-rich soils
65 (Baumberger et al., 2012) or reduce the cover and richness of species adapted to poor, shallow soils
66 (García et al., 2002; Ellis, 2005). As a consequence, we expect that increases in seabird populations and
67 guano deposition on islands will favour some plant species over others and drive change in plant
68 communities (Baumberger et al., 2012).
69

70 In this paper, we provide a case study to illustrate these ideas using multiple data sources to examine the
71 effects of seabirds on plant communities on islands of the Georgia Basin, British Columbia (BC), Canada.
72 We focus on Mandarte Island, which has had sporadic vegetation surveys and hosted an increasing
73 nesting population of glaucous-winged gulls (*Larus glaucescens*) over much of the twentieth century,
74 linked to the cessation of human harvest of gulls and their eggs, and possibly also facilitated by the
75 decimation of bald eagles (*Haliaeetus leucocephalus*) in the early 1900s (Blight et al., 2014; Blight,
76 Drever & Arcese, 2015; Hobson, Blight & Arcese, 2015). Cormorants (*Phalacrocorax* spp.) also nest on
77 Mandarte Island and also increased in abundance to the mid-1980s (Chatwin, Mather & Giesbrecht,
78 2002), likely also due to cessation of human persecution. We wished to explore whether the direct and
79 indirect impacts of humans on regional seabird populations contributed to long-term vegetation change on
80 Mandarte Island. Specifically, we used non-continuous information collected over 116 years, including
81 historical photographs, expedition notes, published accounts, and historical and contemporary surveys of
82 plant species cover, richness and soil nutrients to ask: 1) how native and exotic plant species richness and
83 cover changed on Mandarte Island from 1896 to 2012; and 2) what contemporary relationships exist
84 between gull presence and plant community composition on islands in our study region with and without
85 gull breeding colonies. Our results add to literature showing how human impacts on seabird populations
86 can affect plant communities (cf. Croll et al. 2005), and they imply that as gull populations increased over
87 the last century, those increases facilitated rapid changes in plant communities on islands hosting colonial
88 seabirds.

89

90 **Materials & Methods**

91 Study site

92 Contemporary surveys of plant communities occurred on Mandarte (48.38 N, 123.17 W; 6.8 ha) and 24
93 nearby islands (0.3 – 11.5 ha, within a 100 km radius of Mandarte), which all experience a sub-
94 Mediterranean climate regime of mild, wet winters and warm, dry summers (MacDougall et al., 2006)
95 and support maritime meadow and Garry oak (*Quercus garryana*) ecosystem flora. This ecosystem has

96 declined 95% in extent in Canada since 1860 and is now severely threatened in the Georgia Basin region
97 (Gedalof, Pellat & Smith, 2006; Lea, 2006; Bennett & Arcese, 2013). Mandarte Island supports a mix of
98 mature shrubs in deeper soils and herbaceous meadows in shallower soils, and was managed for
99 aboriginal plant food harvest prior to European colonization (e.g., Lea 2006, Arcese et al. 2014).

100 Mandarte Island also hosts the largest seabird colony in south-western BC, with, over time, an estimated
101 200-1650 breeding pairs of pelagic (*P. pelagicus*) and double-crested cormorants (*P. auritus*), 100-150
102 pairs of pigeon guillemots (*Cepphus columba*) and 5-125 pairs of rhinoceros auklets (*Cerorhinca*
103 *monocerata*), all nesting on cliff ledges (cormorants) or in burrows (Chatwin et al. 2002, P. Arcese
104 unpubl. data). Glaucous-winged gulls (*Larus glaucescens*) nest mainly in the island's open or shrubby
105 meadows and have varied in number from c 350 to 2500 breeding pairs, with peak counts in the 1980s
106 (Drent & Guiguet, 1961; Drent et al., 1964; Campbell et al., 1990; Blight, 2012; Blight, Drever & Arcese,
107 2015). These species also nest on other islands throughout the Georgia Basin (Vermeer & Butler, 1989).

108

109 Historical records from Mandarte Island

110 Partial accounts of Mandarte Island flora and fauna appear as museum records as early as 1896, including
111 notes on seabird presence and abundance, plant species occurrence, and photographs, all depicting a
112 vegetation community historically characteristic of a maritime Garry oak ecosystem (e.g., Tompa 1963,
113 Drent et al. 1964). Various researchers subsequently conducted periodic surveys after 1955, mainly
114 recording plants as species lists and seabirds as counts, but also documenting early changes in the plant
115 community and linking those changes to contemporary increases in gull and cormorant numbers (Drent et
116 al. 1964). We compiled historical records of plant species occurrence from the archived museum reports,
117 herbarium specimens and lists provided by Tompa (1963) and Drent et al. (1964), and then compared
118 these lists to contemporary surveys conducted by P.A., M.G. and T.K.L. Here, we list all plant species
119 recorded on Mandarte Island to 2012 and classified each as extirpated or extant, and as native or exotic to
120 the Pacific coast of North America (Table S1). Historical photos of the island also allow qualitative
121 comparisons to a 1964 photo by P. Grant, which we replicated in 2002 (Fig. 1).

122

123 Vegetation surveys

124 To estimate temporal change in shrub species richness and cover on Mandarte Island, we surveyed
125 vegetation cover from June-July, 1986 and 2006, in 132, 20 x 20 m grid-squares mapped onto a 1974 air
126 photo. Surveys comprised c 90% of island area, but excluded some areas at the edge of sparsely- or non-
127 vegetated bluffs. In each square we estimated the percent cover of all perennial shrubs and common
128 herbaceous plants by species, exposed rock, and all graminoids as a group. Soil depth was estimated by
129 hammering a graduated rod into the soil at five equidistant locations at the square and 1m in from each
130 corner of the square.

131

132 In June 2012, we also conducted contemporary surveys on islands adjacent to Mandarte Island to compare
133 native species richness and cover, exotic species richness and cover, and total N and C in soil on islands
134 with and without nesting glaucous-winged gulls, including three islands with gull colonies ('gull
135 islands'), namely Mandarte, Arbutus (48.71 N, -123.44 W, 35-150 nesting pairs, 1976 – 2010) and the
136 unnamed islet south of Mandarte (48.63 N, -123.28 W, 0-106 nesting pairs, 1962 - 2010; Drent et al.
137 1964, Blight 2012). Cover of herbaceous and grass species and bare soil were estimated following
138 Bennett et al. (2012; N = 14 x 1m² quadrats on Mandarte Island; N = 4 on Arbutus Island; N = 3 on
139 unnamed islet). Quadrat locations were selected randomly within grid cells, for a random set of all
140 mapped grid-squares that including meadow habitat. Plot-level data on soil depth was collated as the
141 mean of four depths at quadrat corners. Total soil nitrogen, carbon and moisture were estimated by
142 collecting 100 g of soil from five sub-samples ca. 2 cm below the rooting zone, then sieved (2 mm) and
143 ground (≤ 0.14 mm) for analysis (Fisons NA-1500 combustion elemental analyser). Soil moisture was
144 estimated from oven-dried (105 °C) sub-samples. Data from 21 quadrats collected on the three gull
145 islands, above, were compared to 57 quadrats from 22 islands in the same region not known to have
146 supported persisting gull populations ('non-gull islands'; Table S2).

147

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149 permitting access to Mandarte, Arbutus and unnamed Island, Parks Canada and the Gulf Islands National
150 Park Reserve for permitting access to North and South Dock, Middle and Little Channel, Rum, Reay and
151 Isabella Islands, and BC Ministry of Forests, Lands and Natural Resource Operations for permitting
152 access to Amelia, North and South Ada, Wallace Point, Yeo and South Winchelsea Islands, US Fish and
153 Wildlife Service for permitting access to Alex Rocks, Boulder, Fortress and Sentinel islands and Long
154 and Skull Islets and P Green for permitting access to Coon and McConnell Island.

155

156 Statistical analyses

157 Vegetation survey data from Mandarte Island collected in paired plots in 1986 and 2006 were compared
158 using Wilcoxon matched-pairs tests. Comparisons of quadrat data on gull and non-gull islands used
159 Wilcoxon signed-rank tests to test for differences in native and exotic species richness and cover and total
160 soil N and C. To test for links between native and exotic species richness, cover, and soil conditions on
161 gull vs. non-gull islands we used generalized linear mixed models. Specifically, we constructed models to
162 explain cover and richness, native cover and richness, and the proportion of exotic vs. native cover and
163 richness using soil depth, total soil N and C, and presence of seabirds as fixed effects. We included island
164 identity as a random factor in these models to account for repeat sampling within islands. Percentage
165 cover was transformed using arcsine square root (for proportion) and richness was transformed using
166 $\log+1$ to normalize residual errors. We selected models based on AIC and estimated p -values for
167 predictors using Markov-chain Monte Carlo sampling (Baayen, Davidson & Bates, 2008). Total N and C
168 were highly correlated; however, because exploratory models indicated that each variable explained an
169 independent fraction of variation in plant survey data, both variables were retained in our analyses, but
170 interpreted cautiously. All mixed models used the Lme4 package (Bates, Maechler & Bolker, 2012) in R
171 v.2.15.1 (R Development Core Team, 2014).

172

173 Results

174 Historical Comparisons

175 Over 116 years we detected 18 extirpations of native species from Mandarte Island, representing a loss of
176 32% of all native plant species recorded there. In contrast, we detected 31 colonization events by exotic
177 species, two apparent colonisations of native species, and four extirpations of exotic species known to
178 have become established prior to 1960 (Supplementary material Appendix Table A1). Forty-five native
179 and one exotic species identified on Mandarte Island prior to 1960 remained extant on the island as of
180 2012, but 94% of exotic colonization events occurred after 1960. Visual comparison of historic and
181 contemporary photos (Fig. 1) and our own observations over 32 years (PA) also suggest long-term
182 declines in the cover of shrub and extent of bare rock. Photos also document the extirpation of three tree
183 species: grand fir (*Abies grandis*), arbutus (*Arbutus menziesii*) and Douglas-fir (*Pseudotsuga menziesii*).
184 Comparing the diameter of dead Douglas-fir on Mandarte (c 60-180 cm DBH) to felled trees of similar
185 size on adjacent islands imply that the largest individuals on Mandarte Island recruited approximately 300
186 yrs BP (unpubl. observations).

187

188 Contemporary Surveys

189 Comparisons of contemporary surveys in 1986 and 2006 indicate a 31% decline in shrub cover on
190 Mandarte Island (N = 132, p = 0.002). On average, snowberry (*Symphoricarpos albus*) declined from
191 33% to 19% cover (p < 0.001), Nootka rose (*Rosa nutkana*) from 24% to 20% (p = 0.04), and gooseberry
192 (*Ribes divericatum*), from 3% to 0.8% (p < 0.001), whereas the exotic Himalayan blackberry (*Rubus*
193 *armeniacus*) and native red elderberry (*Sambucus racemosa*) increased from 2 to 18% and 1 to 6%,
194 respectively (p < 0.001). The extent of bare rock also declined from 38 to 34% (p = 0.03) as grass cover
195 increased (31 to 40%; p < 0.001).

196

197 Influence of Gull Colonies

198 Our surveys of island meadow-plants indicated that exotic species cover was significantly higher on
199 islands with (63%, N = 21) versus without gull colonies (12%, N = 57; Fig. 2). In contrast, native species
200 cover and richness were lower on islands with versus without gull colonies (cover: $28.7 \pm 6.1\%$ with vs.
201 $45.9 \pm 3.2\%$ without; $p = 0.01$; richness: 1.67 ± 0.30 species with versus 7.30 ± 0.49 species without; $p <$
202 0.001 ; Fig. 2).

203

204 Quadrats on gull islands yielded higher concentrations of total nitrogen (N) and total carbon (C) than on
205 non-gull islands (nitrogen: $2.86 \pm 0.17\%$ with vs. $1.66 \pm 0.10\%$ without; $p < 0.001$; carbon: $30.31 \pm 2.03\%$
206 with vs. $23.19 \pm 1.44\%$ without; $p = 0.01$). Total C and N were also positively related to soil depth ($r =$
207 0.58 , $p = 0.006$ and $r = 0.51$, $p = 0.02$; respectively), but only on gull-islands. In contrast, mean soil depth
208 was similar on both gull and non-gull islands (11.14 ± 1.33 with vs 19.37 ± 2.51 cm).

209

210 The presence of gull colonies was the only fixed effect retained in generalized mixed models to predict
211 exotic cover (positive effect), the proportion of exotic versus native cover (positive effect), and native
212 richness (negative effect; Table 1). In contrast, total C was the only fixed effect retained in models
213 predicting exotic richness (negative effect) and native cover (positive effect). Both total C and total N
214 were retained in the top model to predict proportion exotic and native species richness, whereas soil depth
215 was not retained in any top model (Table 1).

216

217 Discussion

218 Our comparison of historical and modern vegetation survey data suggest that substantial changes in plant
219 species cover, richness and origin occurred on Mandarte Island from 1896 – 2012. These changes
220 coincided with population increases in gull and cormorant abundance into the 1980s (Chatwin, Mather &
221 Giesbrecht, 2002; Blight, Drever & Arcese, 2015). Gulls and other surface-nesting seabirds such as
222 cormorants have been identified as agents of change in soil and plant communities elsewhere (Ellis, 2005;
223 Mulder et al., 2011). Thus, despite a lack of experimental evidence and limits on the quality and

224 comprehensiveness of the data we assembled from this 116 year period, our results are consistent with the
225 hypothesis that long-term vegetation change on Mandarte Island may in part be due to human activities
226 via their effects on seabird abundance.

227

228 Direct impacts of seabirds on vegetation include the input and distribution of guano, which can be toxic or
229 inhibit photosynthesis in some plants (Ishida, 1997), and physical disturbance due to trampling, nest
230 construction and territorial defence (Sobey & Kenworthy, 1979; Ellis, 2005). We found that islands with
231 gull colonies exhibited higher concentrations of soil C and N in meadows than those without them, as also
232 shown elsewhere (Anderson & Polis, 1999; Wait, Aubrey & Anderson, 2005). Ellis (2005) further
233 suggested that surface-nesting seabirds enhanced soil depth in systems without mammalian herbivores by
234 facilitating litter accumulation, which is consistent with an observed decline in exposed rock on Mandarte
235 Island and positive correlations between soil depth and C and N concentrations on islands with gull
236 colonies.

237

238 Plant Species Cover and Richness

239 A key result of our work was the observation that 32% of 63 native plant species historically extant on
240 Mandarte Island were extirpated by 2012. Our casual observations from 1981 to the present also suggest
241 that dramatic declines in the abundance of edible native plant species, e.g., *Camassia leichtlinii*,
242 *Fritillaria affinis*, previously facilitated by aboriginal land management practices (primarily controlled
243 burning) prior to c 1860, have also occurred (see also Arcese et al. 2014). In contrast, we documented 31
244 colonizations of Mandarte Island by exotic plant species. Although we lack precise dates for any
245 introductions, many are likely to have been facilitated by exotic birds (e.g., European starling *Sturnus*
246 *vulgaris*, which began using Mandarte Island as a night roost from July to December in the 1970s) given
247 their widespread occurrence in the region and the documented role of frugivorous birds as seed dispersers
248 (Arcese, 1989; Mcatee, 2009; Bennett et al., 2011). Given that many of the exotic plant species we
249 detected are widely distributed in the Georgia Basin and exhibit good dispersal abilities (Bennett, 2014),

250 it is also possible that some invasions we detected were facilitated by human visitors to Mandarte Island.
251 For example, two exotic invasive grasses with high cover on Mandarte Island in 2012, *Bromus rigidus*
252 (19.6%) and *Dactylis glomerata* (14.5%) are known to thrive in invaded oak and maritime meadows (e.g.,
253 Gonzales and Arcese 2008, Bennett et al. 2012), especially in nutrient-rich soils (Klinkenberg, 2012).
254 This suggests that the invasion, establishment and dominance of at least some exotic species in the region
255 have been facilitated by interactions between birds, humans and associated changes in soil disturbance
256 and chemistry.

257

258 Three tree species established on Mandarte Island prior to 1896 remained extant into the 1960s (arbutus),
259 1980s (grand fir) and 1990s (Douglas-fir), but were extirpated by 2002, including individual Douglas-firs
260 likely to have been ≥ 300 years-old (Fig. 1). Although declines in the survival of conifers have been
261 linked to decreased precipitation in our study region (Murdock et al., 2012), guano and physical damage
262 from perching cormorants is known to kill trees in other systems (Hebert et al., 2005; Boutin et al., 2011)
263 and was reported on Mandarte Island in the early 1960s (Drent et al., 1964). Declines in shrub cover on
264 Mandarte Island may have also been partly due to guano deposition by seabirds, although the trampling
265 and shredding of shrubs and adventitious shoots by gulls was widely evident after 1981 (P.A., unpubl.
266 observations). The accumulation of soil N and C and promotion of grass cover at the expense of shrub
267 recruitment is also well-documented in certain seabird families (Ishida, 1996, 1997; Ellis, 2005). In
268 addition, it is possible that the colonization and spread of exotic blackberry and native red elderberry has
269 contributed to reduced native shrub cover, many of which are adapted to shallow soils and summer
270 drought, whereas the aforementioned species favor moist, nutrient-rich soils that have developed more
271 recently on Mandarte Island (e.g., Bennett et al. 2012). Overall, we conclude that observed declines in
272 native shrub cover on Mandarte Island have probably resulted via a combination of mechanisms above.
273 However, if physical disturbance by seabirds is a primary cause of decline, we predict that native shrub
274 cover will increase in future because gull and cormorant populations have been in decline since the 1980s.
275

276 Plant Communities and Gull Colonies

277 Our observation that exotic species cover was higher on gull islands versus non-gull islands is consistent
278 with our finding of enrichment in total C and N on islands with gulls, and also consistent with the
279 suggestions of previous researchers that increased exotic species cover on islands often co-occurs with
280 modern increases in gull and cormorant abundance (Hogg & Morton, 1983; Ellis, 2005; Baumberger et
281 al., 2012). However, Best and Arcese (2009) showed experimentally that trampling by exotic Canada
282 geese (*Branta canadensis*) also reduced native species richness and increased exotic species dominance in
283 maritime meadows in the Georgia Basin, indicating that other disturbances have also influenced plant
284 community change, particularly on small islets that represent the most intact remaining examples of
285 threatened Garry oak and maritime meadows in the region (Best & Arcese, 2009; Isaac-Renton et al.,
286 2010; Bennett & Arcese, 2013).

287

288 The future effects of nesting gulls and cormorants on island plant communities in our study region remain
289 uncertain, particularly given recent reductions in the local population sizes of these birds. In gulls,
290 temporal reductions in diet quality linked to human overfishing of prey and the substitution of
291 anthropogenic foods (e.g., from garbage dumps) for marine foods, likely aided by the recovery of bald
292 eagle populations, have combined to reduce their populations, including on Mandarte Island (Blight et al.,
293 2014; Blight, Drever & Arcese, 2015). Declines in cormorant populations have also occurred but remain
294 unexplained (Chatwin, Mather & Giesbrecht, 2002). It remains to be seen whether these changes will
295 lead to subsequent recovery of native vegetation in meadows via reduced disturbance, or whether any
296 seabird-derived soil and nutrient changes have contributed to permanent alterations to the vegetation on
297 Mandarte Island, implying that the vegetation has reached an alternative stable state. However, continuing
298 to monitor vegetation change on Mandarte and other islands in the region with and without seabirds
299 (and/or exotic vertebrate herbivores) could further elucidate the causes and mechanisms of landscape-
300 level vegetation change on islands.

301

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307

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1

Comparison of photographs of central woodland on Mandarte Island (1964 - 2002).

(A) Historical photograph from 1964 (by Peter Grant; Smith et al. 2006) and (B) a recent reproduction made in 2002 (by Peter Arcese). Note mature *Arbutus menziesii* and *Pseudotsuga menziesii* in the historical photograph. The latter include 3 individuals 0.8 – 1.4m in basal diameter, and estimated at 250-400 years-old by comparison to newly harvested trees on adjacent islands.



2

Native and exotic species cover and richness on islands with and without gull colonies.

Box-plots showing differences in (A) species cover and (B) species richness of exotic and native species, on islands with gull colonies (white columns) and without (grey columns).

Asterisks denote significant differences in Wilcoxon tests (double: $p < 0.01$; triple: $p < 0.001$).

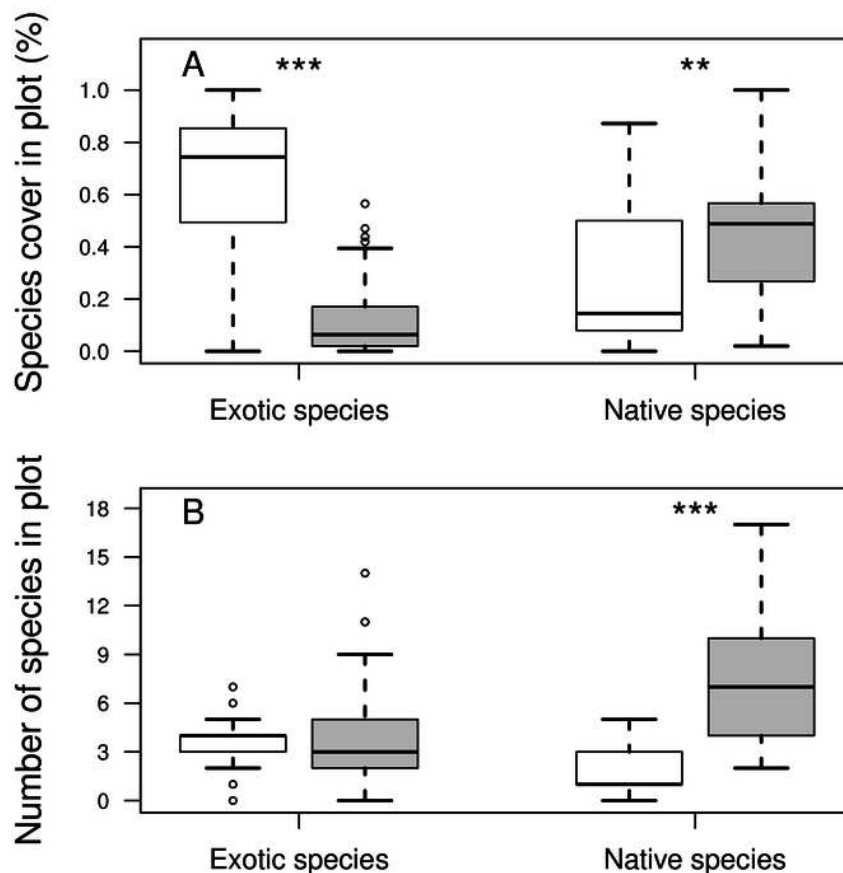


Table 1 (on next page)

Significant coefficients from several generalized mixed models relating vegetation composition and environmental variables.

Response variable	Predictor variables	Coefficients	Coefficient value	Standard error	t	P
Proportion exotic cover ¹	N, C, S, B	B	0.4430	0.1879	2.357	0.0211
Exotic cover ¹	N, C, S, B	B	0.4652	0.1280	3.607	0.0006
		C	-0.0146	0.0072	-2.033	0.0457
		N	0.1651	0.0974	1.695	0.0944
Proportion exotic richness ¹	N, C, S, B	C	-0.01478	0.00730	-2.024	0.0535
Exotic richness ²	N, C, S, B	None significant				
Native cover ¹	N, C, S, B	None significant				
Native richness ²	N, C, S, B	B	-0.4646	0.0831	-5.591	0.0000

1

2 Response variables: ¹ transformed using arcsine square root. ² transformed using log (+1)

3 Predictor variables: N = total nitrogen concentration, C = total carbon concentration, S = log mean soil

4 depth, B = presence of gull colonies on island (with or without gull colonies).

5