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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.

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

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

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

## Introduction

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

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

## Materials & Methods

### Study site

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

declined 95% in extent in Canada since 1860 and is now severely threatened in the Georgia Basin region (Gedalof, Pellat & Smith, 2006; Lea, 2006; Bennett & Arcese, 2013). Mandarte Island supports a mix of mature shrubs in deeper soils and herbaceous meadows in shallower soils, and was managed for aboriginal plant food harvest prior to European colonization (e.g., Lea 2006, Arcese et al. 2014). Mandarte Island also hosts the largest seabird colony in south-western BC, with, over time, an estimated 200-1650 breeding pairs of pelagic (*P. pelagicus*) and double-crested cormorants (*P. auritus*), 100-150 pairs of pigeon guillemots (*Cepphus columba*) and 5-125 pairs of rhinoceros auklets (*Cerorhinca monocerata*), all nesting on cliff ledges (cormorants) or in burrows (Chatwin et al. 2002, P. Arcese unpubl. data). Glaucous-winged gulls (*Larus glaucescens*) nest mainly in the island's open or shrubby meadows and have varied in number from c 350 to 2500 breeding pairs, with peak counts in the 1980s (Drent & Guiguet, 1961; Drent et al., 1964; Campbell et al., 1990; Blight, 2012; Blight, Drever & Arcese, 2015). These species also nest on other islands throughout the Georgia Basin (Vermeer & Butler, 1989).

Historical records from Mandarte Island

Partial accounts of Mandarte Island flora and fauna appear as museum records as early as 1896, including notes on seabird presence and abundance, plant species occurrence, and photographs, all depicting a vegetation community historically characteristic of a maritime Garry oak ecosystem (e.g., Tompa 1963, Drent et al. 1964). Various researchers subsequently conducted periodic surveys after 1955, mainly recording plants as species lists and seabirds as counts, but also documenting early changes in the plant community and linking those changes to contemporary increases in gull and cormorant numbers (Drent et al. 1964). We compiled historical records of plant species occurrence from the archived museum reports, herbarium specimens and lists provided by Tompa (1963) and Drent et al. (1964), and then compared these lists to contemporary surveys conducted by P.A., M.G. and T.K.L. Here, we list all plant species recorded on Mandarte Island to 2012 and classified each as extirpated or extant, and as native or exotic to the Pacific coast of North America (Table S1). Historical photos of the island also allow qualitative 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 1m<sup>2</sup> 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 ( $\leq 0.14$  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



For permission to access above mentioned study sites, we thank the Tswaout and Tseycum bands for permitting access to Mandarte, Arbutus and unnamed Island, Parks Canada and the Gulf Islands National Park Reserve for permitting access to North and South Dock, Middle and Little Channel, Rum, Reay and Isabella Islands, and BC Ministry of Forests, Lands and Natural Resource Operations for permitting access to Amelia, North and South Ada, Wallace Point, Yeo and South Winchelsea Islands, US Fish and Wildlife Service for permitting access to Alex Rocks, Boulder, Fortress and Sentinel islands and Long and Skull Islets and P Green for permitting access to Coon and McConnell Island.

# Statistical analyses

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

## Results

### Historical Comparisons

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

### Contemporary Surveys

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

### Influence of Gull Colonies

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

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

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

## Discussion

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

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

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

#### Plant Species Cover and Richness

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

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

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

## Plant Communities and Gull Colonies

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

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

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## References

- Anderson WB., Polis GA. 1999. Nutrient fluxes from water to land : seabirds affect plant nutrient status on Gulf of California islands. *Oecologia* 118:324–332.
- Arcese P. 1989. Intrasexual competition, mating system and natal dispersal in song sparrows. *Animal Behaviour* 38:958–979.
- Arcese P., Schuster R., Campbell L., Barber A., Martin TG. 2014. Deer density and plant palatability predict shrub cover, richness and aboriginal food value in a North American island archipelago. *Diversity and Distributions* 20:1368–1378.
- Baayen RH., Davidson DJ., Bates DM. 2008. Mixed-effects modeling with crossed random effects for subjects and items. *Journal of Memory and Language* 59:390–412.
- Bakker JP., Olff H., Willems JH., Zobel M. 1996. Why do we need permanent plots in the study of long-term vegetation dynamics ? *Journal of Vegetation Science* 7:147–155.
- Bates D., Maechler M., Bolker B. 2012. lme4: Linear mixed-effects models using S4 classes.
- Baumberger T., Affre L., Torre F., Vidal E., Dumas P-J., Tatoni T. 2012. Plant community changes as ecological indicator of seabird colonies' impacts on Mediterranean Islands. *Ecological Indicators* 15:76–84.
- Bennett JR., Young EJ., Giblin DE., Dunwiddie PW., Arcese P. 2011. Avian Dispersal of Exotic Shrubs in an Archipelago. *Ecoscience* 18:369–374.
- Bennett JR., Dunwiddie PW., Giblin DE., Arcese P. 2012. Native versus exotic community patterns across three scales : Roles of competition , environment and incomplete invasion. *Perspectives in*



- 328 *Plant Ecology, Evolution and Systematics* 14:381–392.
- 329 Bennett JR. 2014. Comparison of native and exotic distribution and richness models across scales reveals
- 330 essential conservation lessons. *Ecography* 37:120–129.
- 331 Bennett JR., Arcese P. 2013. Human Influence and Classical Biogeographic Predictors of Rare Species
- 332 Occurrence. *Conservation Biology* 27:417–421.
- 333 Best RJ., Arcese P. 2009. Exotic herbivores directly facilitate the exotic grasses they graze: mechanisms
- 334 for an unexpected positive feedback between invaders. *Oecologia* 159:139–50.
- 335 Blight LK. 2012. Glaucous-winged Gulls *Larus glaucescens* as sentinels for a century of ecosystem
- 336 change - long term trends in population, diet, and egg production in North America's Salish Sea.
- 337 PhD dissertation, University of British Columbia.
- 338 Blight LK., Hobson K a., Kyser TK., Arcese P. 2014. Changing gull diet in a changing world: A 150-year
- 339 stable isotope (  $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$ ) record from feathers collected in the Pacific Northwest of North
- 340 America. *Global Change Biology* 21:1497–1507.
- 341 Blight LK., Drever MC., Arcese P. 2015. A century of change in Glaucous-winged Gull ( *Larus*
- 342 *glaucescens* ) populations in a dynamic coastal environment. *The Condor* 117:108–120.
- 343 Boutin C., Dobbie T., Carpenter D., Hebert CE. 2011. Effects of Double-Crested Cormorants
- 344 (*Phalacrocorax auritus* Less.) on Island Vegetation, Seedbank, and Soil Chemistry: Evaluating
- 345 Island Restoration Potential. *Restoration Ecology* 19:720–727.
- 346 Campbell W., Dawe NK., McTaggart-Cowan I., Cooper JM., Kaiser GW., McNall MC. 1990. *Birds of*
- 347 *British Columbia, Volume 2: Nonpasserines-Diurnal Birds of Prey through Woodpeckers.*
- 348 Vancouver: UBC press.
- 349 Caut S., Angulo E., Pisanu B., Ruffino L., Faulquier L., Lorvelec O., Chapuis JL., Pascal M., Vidal E.,
- 350 Courchamp F. 2012. Seabird modulations of isotopic nitrogen on islands. *PLoS ONE* 7:1–7.
- 351 Chatwin TA., Mather MH., Giesbrecht TD. 2002. Changes in Pelagic and Double-Crested Cormorant
- 352 Nesting Populations in the Strait of Georgia, British Columbia. *Northwestern Naturalist* 83:109–
- 353 117.



- 354 Croll DA., Maron JL., Estes JA., Danner EM., Byrd G V. 2005. Introduced predators transform subarctic  
355 islands from grassland to tundra. *Science* 307:1959–1961.
- 356 Davis MA., Grime JP., Thompson K. 2000. in plant communities : Fluctuating resources a general of  
357 invasibility theory. 88:528–534.
- 358 Drent R., van Tets GF., Tompa FS., Vermeer K. 1964. The breeding birds of Mandarte Island, British  
359 Columbia. *The Canadian field-naturalist* 78:208–263.
- 360 Drent RH., Guiguet C. 1961. *A Catalogue of British Columbia Seabird Colonies*. Victoria, BC.
- 361 Ellis JC. 2005. Marine Birds on Land: A Review of Plant Biomass, Species Richness, and Community  
362 Composition in Seabird Colonies. *Plant Ecology* 181:227–241.
- 363 Estes JA., Terborgh J., Brashares JS., Power ME., Berger J., Bond WJ., Carpenter SR., Essington TE.,  
364 Holt RD., Jackson JBC., Marquis RJ., Oksanen L., Oksanen T., Paine RT., Pikitch EK., Ripple WJ.,  
365 Sandin SA., Scheffer M., Schoener TW., Shurin JB., Sinclair ARE., Soulé ME., Virtanen R., Wardle  
366 DA. 2011. Trophic downgrading of planet Earth. *Science* 333:301–6.
- 367 García LV., Marañón T., Ojeda F., Clemente L., Redondo R., Garcia L V., Marainon T., Redondo R.  
368 2002. Seagull influence on soil properties , chenopod shrub distribution , and leaf nutrient status in  
369 semi-arid Mediterranean islands. *Oikos* 98:75–86.
- 370 Gedalof Z., Pellat M., Smith DJ. 2006. From Prairie to Forest : Three Centuries of Environmental Change  
371 at Rocky Point , Vancouver Island , British Columbia. *Northwest Science* 80:34–46.
- 372 Gonzales EK., Arcese P. 2008. Herbivory more limiting than competition on early and established native  
373 plants in an invaded meadow. *Ecology* 89:3282–3289.
- 374 Hebert CE., Duffe J., Weseloh DVC., Senese TED., Haffner GD. 2005. Unique island habitats may be  
375 threatened by Double-crested Cormorants. *Journal of Wildlife Management* 69:68–76.
- 376 Hobson KA., Blight LK., Arcese P. 2015. Human-Induced Long-Term Shifts in Gull Diet from Marine to  
377 Terrestrial Sources in North America’s Coastal Pacific: More Evidence from More Isotopes ( $\delta^2\text{H}$ ,  
378  $\delta^{34}\text{S}$ ). *Environmental Science & Technology*:150826155926009.
- 379 Hogg EH., Morton JK. 1983. The effects of nesting gulls on the vegetation and soil of islands in the Great

- Lakes. *Canadian Journal of Botany* 61:3240–3254.
- Isaac-Renton M., Bennett JR., Best RJ., Arcese P. 2010. ) on Native Plant Communities of the Southern Gulf Islands, British Columbia. *Ecoscience* 17:394–399.
- Ishida A. 1996. Effects of the common cormorant, *Phalacrocorax carbo*, on evergreen forests in two nest sites at Lake Biwa, Japan. *Ecological Research* 11:193–200.
- Ishida A. 1997. Seed germination and seedling survival in a colony of the common cormorant, *Phalacrocorax carbo*. *Ecological Research* 12:249–256.
- Klinkenberg B. 2012. E-Flora BC: Electronic Atlas of the Flora of British Columbia [eflora.bc.ca].
- Lea T. 2006. Historical Garry Oak Ecosystems of Vancouver Island , British Columbia , pre-European Contact to the Present. *Davidsonia* 17:34–50.
- MacDougall AS., Boucher J., Turkington R., Bradfield GE. 2006. Patterns of plant invasion along an environmental stress gradient. *Journal of Vegetation Science* 17:47.
- Macdougall AS., Turkington R. 2005. Are invasive species the drivers or passengers of change in degraded ecosystems? *Ecology* 86:42–55.
- Mcatee AWL. 2009. Distribution of Seeds by Birds. *American Midland Naturalist* 38:214–223.
- McKechnie I., Lepofsky D., Moss ML., Butler VL., Orchard TJ., Coupland G., Foster F., Caldwell M., Lertzman K. 2014. Archaeological Data Provide Alternative Hypotheses on Pacific Herring (*Clupea pallasii*) Distribution, Abundance, and Variability. *Proceedings of the National Academy of Sciences of the United States of America* 111:E807–E816.
- Mulder CPH., Anderson WB., Towns DR., Bellingham PJ. 2011. *Seabird islands: ecology, invasion, and restoration*. Oxford: Oxford University Press.
- Murdock TQ., Sobie SR., Eckstrand HD., Jackson E. 2012. Georgia Basin: Projected Climate Change, Extremes, and Historical Analysis. *Pacific Climate Impacts Consortium*.
- Pickett STA., Collins SL., Armesto JJ. 1987. A hierarchical consideration of causes and mechanisms of succession. *Vegetatio* 69:109–114.
- R Development Core Team. 2014. R: A language and environment for statistical computing.

- 406 Seabloom EW., Williams JW., Slayback D., Stoms DM., Viers JH., Dobson AP. 2006. Human impacts,  
407 plant invasion, and imperiled plant species in California. *Ecological applications : a publication of*  
408 *the Ecological Society of America* 16:1338–50.
- 409 Sobey ADG., Kenworthy JB. 1979. The relationship between Herring Gulls and the vegetation of their  
410 breeding colonies. *Journal of Ecology* 67:469–496.
- 411 Smith JNM., Keller LF., Marr AB., Arcese P. 2006. *Conservation and Biology of Small Populations: The*  
412 *Song Sparrows of Mandarte Island*. Oxford: Oxford University Press
- 413 Strayer DL., Eviner VT., Jeschke JM., Pace ML. 2006. Understanding the long-term effects of species  
414 invasions. *Trends in ecology & evolution* 21:645–51.
- 415 Tompa FS. 1963. Factors determining the numbers of Song Sparrows on Mandarte Island, B.C.  
416 University of British Columbia.
- 417 Vermeer K., Butler RW. 1989. *The ecology and status of marine and shoreline birds in the Strait of*  
418 *Georgia, British Columbia*. Ottawa: Spec. Publ. Can. Wild. Serv.
- 419 Wait D a., Aubrey DP., Anderson WB. 2005. Seabird guano influences on desert islands: soil chemistry  
420 and herbaceous species richness and productivity. *Journal of Arid Environments* 60:681–695.

# 1

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

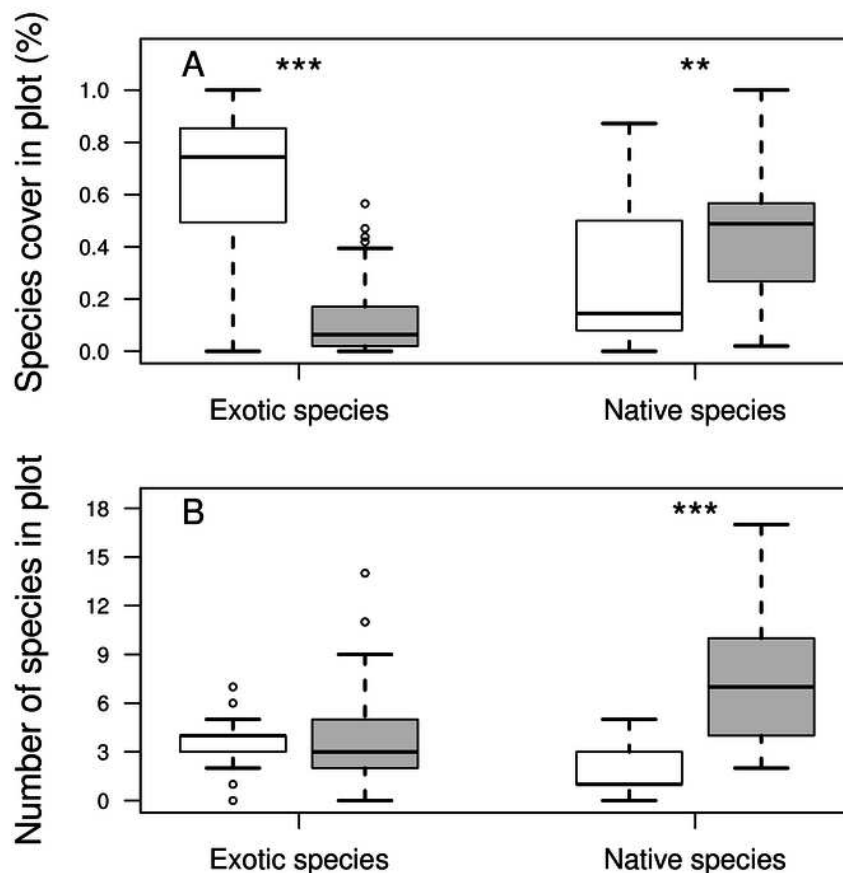
(A) Historical photograph from 1964 (by Peter Grant; Smith et al. 2006) and (B) a recent reproduction made in 2002 (by Peter Arcese). Note mature *Arbutus menziesii* and *Pseudotsuga menziesii* in the historical photograph. The latter include 3 individuals 0.8 – 1.4m in basal diameter, and estimated 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 <sup>1</sup>	N, C, S, B	B	0.4430	0.1879	2.357	0.0211
Exotic cover <sup>1</sup>	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 <sup>1</sup>	N, C, S, B	C	-0.01478	0.00730	-2.024	0.0535
Exotic richness <sup>2</sup>	N, C, S, B	None significant				
Native cover <sup>1</sup>	N, C, S, B	None significant				
Native richness <sup>2</sup>	N, C, S, B	B	-0.4646	0.0831	-5.591	0.0000

1

2 Response variables: <sup>1</sup> transformed using arcsine square root. <sup>2</sup> 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