AN ANTHROPOCENE ISLAND FLORA: THE FATE OF NATIVE AND ALIEN PLANTS IN THE SAN JUAN ISLAND ARCHIPELAGO

by

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ABSTRACT

The core premise of the Anthropocene is that we have unintentionally altered the earth so much that we have entered a new geological period. One of the most concerning of these unintentional consequences is the widespread movement of species across continents. This movement is causing natural communities to become simpler and more self-similar, a process called biotic homogenization. This thesis explores how much biotic homogenization is occurring and could occur in the future within the flora of the San Juan Island archipelago of Washington State, which is a hotspot of floristic diversity. This thesis addresses five main questions 1) what proportion of the flora are alien species, 2) are rare species disproportionately impacted by alien species, 3) what factors influence the number and distribution of alien species, 4) how much biotic homogenization could occur in the future, and 5) is biotic homogenization occurring now?

Currently, alien species comprise between 38 and 47% of the San Juan Island flora, and most alien species present are invasive in other parts of the United States. Invasive species are most common in meadow habitats which also have the greatest number of rare and imperiled species. The most important factors determining the frequency of alien species are residence time, invasiveness, island size, and how impacted the island is by human development. In addition, because most of the alien flora has recently arrived, the future flora could become up to 20% more similar by 2079. Finally, current evidence suggests the most diverse small meadow islands are rapidly losing native species and being mostly colonized by alien species. The synergistic impacts of invasive annual grass, introduced Canada geese, and over-abundant black-tailed deer are hastening this

change. However, each island is changing uniquely, currently causing no directional change towards homogenization or differentiation.

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Acknowledgements

Any large writing project is a community endeavor, especially during what became a devastating three-year global pandemic, one that almost perfectly coincided with my entire graduate experience. I often thought of what C.S. Lewis said in “Learning in Wartime” (1939):

> “If men had postponed the search for knowledge and beauty until they were secure the search would never have begun. Plausible reasons have never been lacking for putting off all merely cultural activities until some imminent danger has been averted or some crying injustice put right. But humanity long ago chose to neglect those plausible reasons. They wanted knowledge and beauty now, and would not wait for the suitable moment that never come. This is not panache; it is our nature.”

Thankfully, during this time of imminent catastrophe, I was and continue to be blessed with several supportive and encouraging people who shepherded and mentored me through both graduate school and writing this thesis.

First, I would like to thank Peter Dunwiddie for more than a decade of mentorship, friendship, encouragement, and support. He first introduced me to island life in the San Juans more than a decade ago when we rowed a boat out to a tiny island off Lopez to plant golden paintbrush. This thesis would not have occurred had I not been on that trip and taken by the beauty and oddities of those tiny rocks in the sea. One of the great gifts of life is finding, apprenticing to, and having a mentor who helps bring out our curiosity and passion – may I always be the kind of scientist, mentor, and person Peter has been for me. Our adventures collecting plants in little-known or visited places in the islands will be with me for my life.

Second, I would like to thank Katy Beck, Steve Ulvi, Peter Zika, and the numerous folks who have for helping look for and document plants on many of the

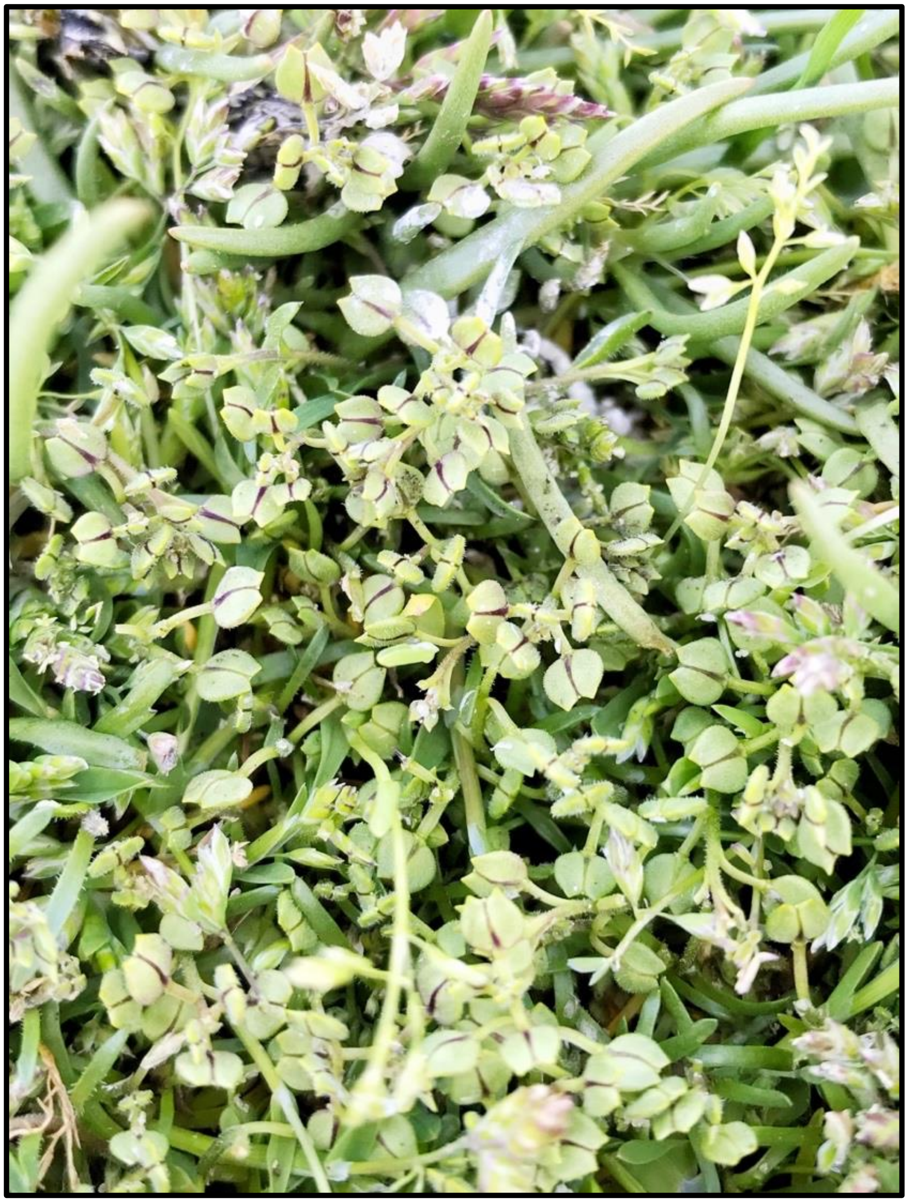
islands. Katy helped resurvey many islands in 2021. Steve was our intrepid and skilled mariner. Peter Zika was a constant companion and mentor in the field and was vital to understanding the sedge and other obscure plant taxa in the field and herbarium – to be so lucky as to have a real-life plant taxonomist with you in the field. I am deeply grateful for him and all the time he has spent on the islands looking for plants. His dog-eared and deeply annotated copy of Atkinson and Sharpe's flora was a treasure trove of information. Finally, this thesis work rests on the shoulders of the many botanists and curious naturalists that came before. In particular, the many folks part of the first botanical inventories of the islands in the early 2000s – including David Giblin, Phil Green, Eliza Habegger, and others. I also thank John Withey for so much positive encouragement and helpful feedback and for taking the time to read through and help craft this document. I also want to thank the Washington Native Plant Society for financial assistance for field work; their contribution helped pay for boat time, making fieldwork easier and possible. My work colleagues have also been a wonderful support, encouraging me and letting me take the time needed to complete such a big project.

Lastly, I'd like to thank my partner Rebecca, who has been steadfast support, and I surely could not have completed this without her. She forgave the many long days and nights of me cloistered at the writing desk and weeks away doing fieldwork. She always assured me and helped me remember the joy at the heart of learning through my many periods of graduate school-induced stress and anxiety.

DEDICATION

I dedicate this work to my grandparents, Ralph and Guida Martin, who passed on many years ago but are always close to my heart. They were with me on all my island adventures. My love of natural history stems from my Grandfather's patience in following a young boy among the cobble beaches of Maine, picking up hermit crabs and periwinkles, scrambling among the hills and rocks of Acadia National Park, and catching fire-flies in the backyard. My love for words, writing, and plants came from my grandmother, an English teacher, who spent many mornings patiently working with me through the newspaper word puzzles. She sent me on many missions out the door to pick blueberries for muffins. The time eating berries among the wild bushes was key to my delight in plants.

Secondly, I dedicate this work to the many unique and rare plants of the islands. *Lepidium oxycarpum* (sharp-fruited pepper grass), a quarter-sized plant, is a State Endangered species and a long-distance disjunct from its primary locality in California. The photo on the following page, taken during thesis fieldwork, represents a new population in Washington State. Before this, it was only known from one site. The entire species exists in an area about the size of a large conference table and is likely one of the rarest plants in Washington State. The wonder and curiosity of how this species arrived on a single small island a thousand miles from the next known population drove most of the inspiration for writing and working on this thesis. Such a species encapsulates all that I appreciate and gain from studying plants and symbolizes all I have learned during my time in Graduate school. May their stories inspire us to continue caring for the little green things that fill our world.



Lepidium oxycarpum (sharp-fruited pepper grass)

“I take infinite pains to know the phenomena of the spring, for instance, thinking that I have here the entire poem, and then, to my chagrin, I hear that it is but an imperfect copy that I possess and have read, that my ancestors have torn out many of the first leaves and grandest passages, and mutilated it in many places. I should not like to think that some demigod had come before me and picked out some of the best of the stars. I wish to know an entire heaven and an entire earth”

- Henry David Thoreau, *Walden*

“Nature first, then theory. Or, better, nature and theory closely intertwined while you throw all your intellectual capital at the subject. Love the organisms for themselves first, then strain for general explanations, and with good fortune, discoveries will follow. If they don’t, the love and pleasure will have been enough.”

- E. O. Wilson, *The Naturalist*

INTRODUCTION

Biodiversity loss is one of the most devastating aspects of the Anthropocene . Loss occurs through 1) the extinction of species (Wilson, 1985; Pimm & Raven, 2000; Barnosky et al., 2011; Valiente-Banuet et al., 2015; Briggs, 2017; Ceballos, Ehrlich & Raven, 2020), 2) the decline of species abundance (Davies, 2011; Vogel, 2017; Leather, 2018; Goulson, 2019), 3) and the unraveling of ecological interactions (Valiente-Banuet et al., 2015; Pérez-Méndez et al., 2016; Ulrich et al., 2020). These three kinds of biodiversity loss negatively impact humanity, ecosystems, and the organisms themselves (Tilman, 2000; Wilson, 2002; Cardinale et al., 2012; Cafaro & Primack, 2014). The causes of biodiversity loss are well known and well documented and include habitat destruction, invasive species, pollution, human overpopulation, and overharvesting (Clavero & Garciaberthou, 2005; Liu et al., 2019; Ney-Nifle & Mangel, 2000; E. O. Wilson, 2002; Young et al. 2016; Pyšek et al., 2020; Vitousek et al., 1997).

Islands are one of the most frequent places where scientists documented the causes and consequences of biodiversity loss (Cook, Dawson & MacDonald, 2006; Sax & Gaines, 2008; Quammen, 2012; Johnson et al., 2017), especially losses due to the introduction of alien taxa and from human exploitation. Famous examples of species loss on oceanic islands include the cascading influence of the brown tree snake on the extinction of the endemic fauna of Guam, the introduction of mosquitos with malaria into Hawaii, which facilitated the extinction of endemic birds, and the extinction of flightless birds in New Zealand after settlement of the islands by the first Polynesians and later colonization from Europeans (Engbring & Fritts, 1988; Quammen, 2012; Johnson et al., 2017).

Though plants on islands are more likely to go extinct than plants on mainlands (Gray, 2019), there are fewer well-known examples, though Easter Island's extinction of the Toromiro tree may be a notable exception (Maunder et al., 2000). However, since 1900, an average of 2.3 seed-bearing plants are going extinct each year, and islands have the highest extinction rate. For example, since 1900, 79 plants have gone extinct on the island of Hawaii (Humphreys et al., 2019).

The current and future impact of alien species on native plant species and communities is a pressing concern. Alien species are responsible for at least 27% of global documented plant extinctions (Bellard, Cassey & Blackburn, 2016). Currently, alien plant species make up more than 20% of continental floras, and this number will likely continue to increase. In the conterminous United States, alien species comprise nearly 11% of the flora, and some states have up to 47% of their flora comprised of alien taxa (Vitousek et al., 1997a). Washington State is no exception, as alien species comprise 30% of the state's flora[1], and the state is in the upper 10th percentile of global hotspots of established alien species (Pyšek et al., 2020).

This thesis explores how invasive and alien species and human development affect the biodiversity of vascular plants in the San Juan Islands of Washington State, a continental island archipelago in the Pacific Northwest of North America. The San Juan Islands are an ideal locality to study biodiversity loss for three reasons. First, there are disproportional numbers of species given the archipelago's land area. The plant species found in the San Juan Islands represent 25% of the state's plant richness despite the land

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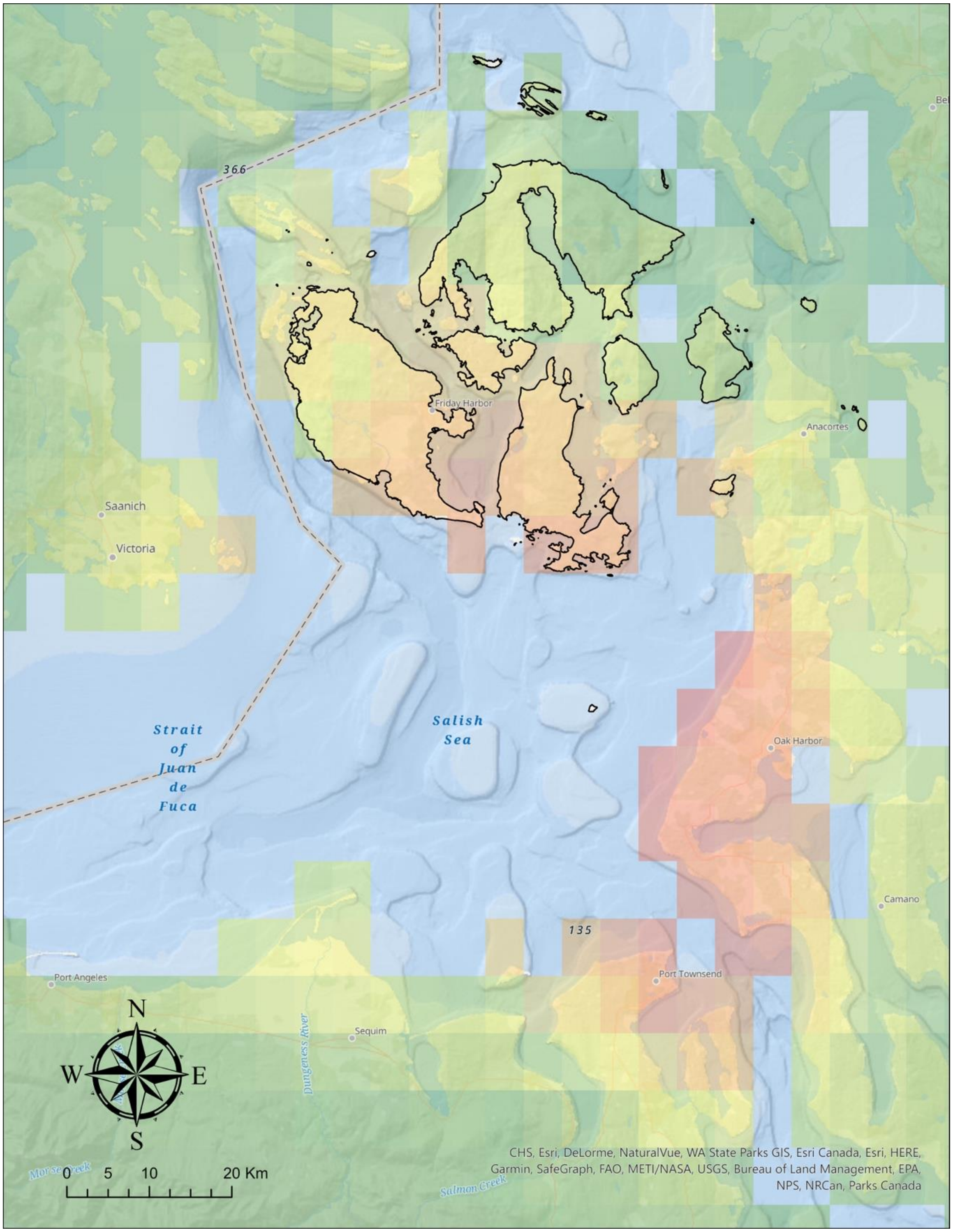
[1] https://biology.burke.washington.edu/herbarium/waflora/checklist.php

area of the archipelago comprising less than half a percent (0.26%) of the State (USDA PLANTS database, 2018, WNPS, 2018). The archipelago is also a hotspot of alien species, which comprise 34% of the flora (Atkinson & Sharpe, 2000).

Second, the high plant richness of the archipelago is likely related to the diversity of habitats found across the archipelago, despite its latitude. Several reasons may explain the high habitat diversity found in the archipelago, including being within the rain shadow of the Olympic Mountains and the high topographic diversity found among and within the islands. The Olympic Mountains and portions of Vancouver Island form significant orographic barriers that strongly influence the climate in downwind areas. Prevailing southwesterly winds are responsible for the major rainfall events in the region, creating a pronounced rain shadow across extensive portions of the archipelago and significantly buffers the region from dramatic precipitation events (Figure 1; Lorente-Plazas et al., 2018). The Olympic Mountains have likely significantly influenced the archipelago's climate since at least the Miocene (~14 MYA), when the mountains uplifted (Brandon, Roden-Tice & Garver, 1998). In conjunction with the stabilizing influence of the Pacific maritime climate, it has likely been a climate refugia for species present when the climate was cooler and drier during the Miocene (Pellatt, Hebda & Mathewes, 2001; Retallack, 2001; Leopold et al., 2016).



CHS, Esri, DeLorme, NaturalVue, WA State Parks GIS, Esri Canada, Esri, HERE, Garmin, SafeGraph, FAO, METI/NASA, USGS, Bureau of Land Management, EPA, NPS, NRCan, Parks Canada

Figure 1. Precipitation map of the Salish Sea, data produced by www.worldclim.org (Fick and Hijmans 2017), red squares are drier (50mm a year), dark green are wetter (2120mm a year).

While topographic heterogeneity is important at large scales by producing rain shadows, topography can have important influences at smaller scales too. Topographic heterogeneity is also positively correlated with microhabitat diversity and species diversity (Morelli et al., 2020). For example, in the San Juan Archipelago, Mount Constitution on Orcas Island is a hotspot for elevational disjuncts (Atkinson & Sharpe, 2000). The cool north-facing slopes and small bog habitats of the mountain are home to several taxa more common in mountain and boreal environments, such as the alpine disjuncts *Carex pauciflora, Saxifraga bronchialis,* and *Geum triflorum*. The topographic relief on Mount Constitution is likely one of the main reasons both xeric and mesic species have been present on the mountain over the last 7,000 years through rapid regional climatic changes (Sugimura et al., 2008; Leopold et al., 2016).

The third reason the San Juan Islands is an ideal study system is the configuration and distribution of islands and how it relates to human use and density. Several large islands served by State-sponsored ferries (San Juan, Lopez, Orcas, Shaw) comprise the center of the archipelago. Surrounding these large islands are several hundred smaller islands– many of which are uninhabited and either state parks or protected as refuges (Price, 2017; Dunwiddie, 2018). The large ferry-served islands are visited by millions of people each year (Whittaker, Shelby & Shelby, 2018) and serve as the pathway through which most recreation occurs on the smaller islands.

Seabloom et al. (2006) found that alien species proceed into natural areas well before the wave of human development. Given the well-known relationship between recreation and alien species establishment (Jordan, 2000; Dickens, Gerhardt & Collinge, 2005; Wells, Lauenroth & Bradford, 2012; Ballantyne, Gudes & Pickering, 2014; Marion et al., 2016), such a configuration of large and small islands are an ideal study system for understanding the influence of source-floras and rates of colonization after introduction.

THE IMPORTANCE OF BIOTIC HOMOGENIZATION

This thesis uses the concept of biotic homogenization as a lens through which to study biodiversity loss. Understanding how floras are becoming simpler and more similar through time is a core research topic in conservation biogeography (Olden, 2006). The simplification of the earth's floras ("biotic homogenization") is driven by the combined effects of the widespread introduction of alien plants into a region and the extinction and extirpation of regional native species (Olden & Poff, 2003, p. 443). However, species introductions and extinctions can have a lagged response, named invasion debt (Rouget et al., 2016) and extinction debt (Hanski & Ovaskainen, 2002). While most biotic homogenization research examines whether biotic homogenization is presently occurring or has occurred, I found no studies yet that aim to explicitly assess how much homogenization is likely to occur in an area in the future – a "homogenization debt."

Yet, there is sufficient theory to begin to postulate plausible scenarios for how ecological communities are likely to change in the future, given knowledge of the known flora, the factors that promote the colonization of alien species, and the factors that increase the risk of extinctions – tools that the field of both biogeography and conservation are well suited. The primary challenge to understanding what a homogenization debt of an area could be are the well-known 'Darwinian' and 'Wallacean' shortfalls – knowing what species are present in an area and how they are distributed (Richardson & Whittaker, 2010; Ladle & Whittaker, 2011; Diniz-Filho et al., 2013).

ADDRESSING THE DARWINIAN AND WALLACEAN SHORTFALLS

To address this first challenge, what species are present (Darwinian shortfall) and how are they distributed (Wallacean shortfall), the tools and methods of floristic botany were used (McLaughlin, 1994; Palmer, Wade & Neal, 1995). Floristic botany aims to accurately describe the total number of species found in a focal region – from an individual meadow to an entire biogeographic region such as the Pacific Northwest (Hitchcock & Cronquist, 2018). A list and description of the species present is a fundamental unit of biodiversity conservation (Wilson, 1999). Unfortunately, for vascular plants, many areas of the planet are woefully inventoried. Botanical collecting is in troubling decline (Prather et al., 2004a,b), despite the importance of herbarium collections and natural history work in general for conservation (Shaffer, Fisher & Davidson, 1998; Tewksbury et al., 2014; Greve et al., 2016; Nualart et al., 2017; Roberts & Moat, 2022).

In the San Juan Islands, the first effort at a systematic vascular flora of the region was made in 1985 by Atkinson and Sharpe. In addition, some work has been done for mosses (Harpel, 1997). Before this work, plant collecting had been done sporadically since the first collections made in 1892 by Louis F. Henderson on the Summit of Mount Constitution. From 2005 to 2009, botanists associated with the Burke Herbarium began a systematic effort to inventory the many small islands of the archipelago ("Floristic Atlas of the San Juan Islands - WTU Herbarium," 2010). This effort continued in 2018 to document the floras of the many small islands that became part of the new National Monument (Dunwiddie, 2018). Work as part of this thesis continued in 2018, led by Peter

Dunwiddie, Peter Zika, and myself, to continue inventorying yet-to-be-visited islands, better sample the larger islands in the archipelago, and revisit islands originally surveyed in the initial 2005 - 2009 effort. The combined efforts of botanists over the last century have led to at least 10,140 known collections across the islands. The majority (75%) have occurred since the systematic efforts beginning in 2005 (Figure 2).

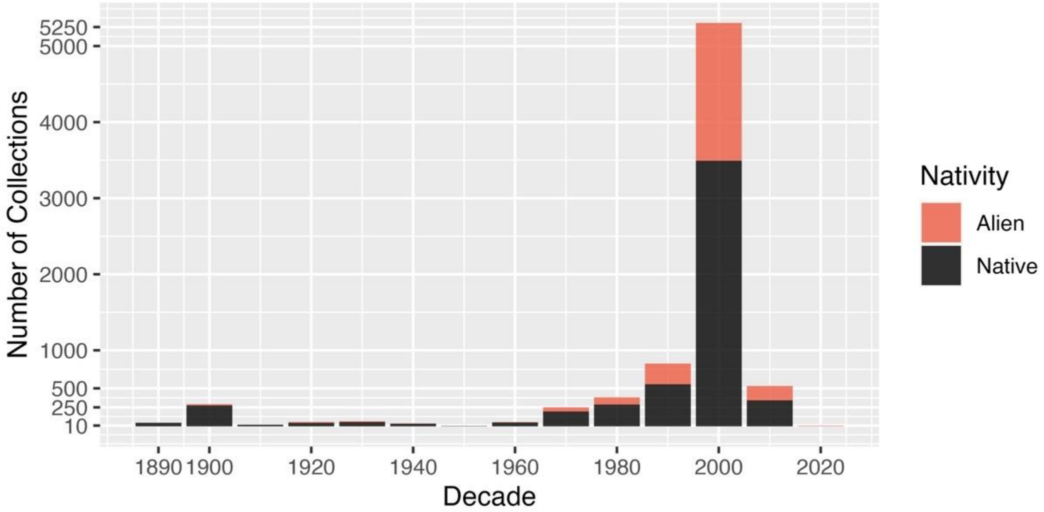


Figure 2. The number of herbarium collections of native and alien vascular plants within the San Juan Island archipelago by decade.

Field inventories were supplemented by iNaturalist observations, past collecting efforts databased in the Consortium of Pacific Northwest Herbaria, and species lists compiled by local land management agencies, botanists, and other naturalists. By 2022, there have now been 153 islands completely inventoried and five large islands (Orcas, San Juan, Lopez, Shaw, and Blakely) extensively surveyed, for 158 total islands used as a dataset for this thesis.

One of the troubling patterns in this broad-scale work is the steady increase in the proportion of alien plant species found in the flora. For example, in 1985, Atkinson and Sharpe recorded 829 taxa (34.1% alien species), and they updated their flora in 2000 and recorded 970 species (36.1% alien). By 2022, there are now 1,010 documented taxa, and 38.7% is comprised of alien taxa, a pattern generally seen in the proportion of decadal collections comprised of alien taxa (Figure 3).

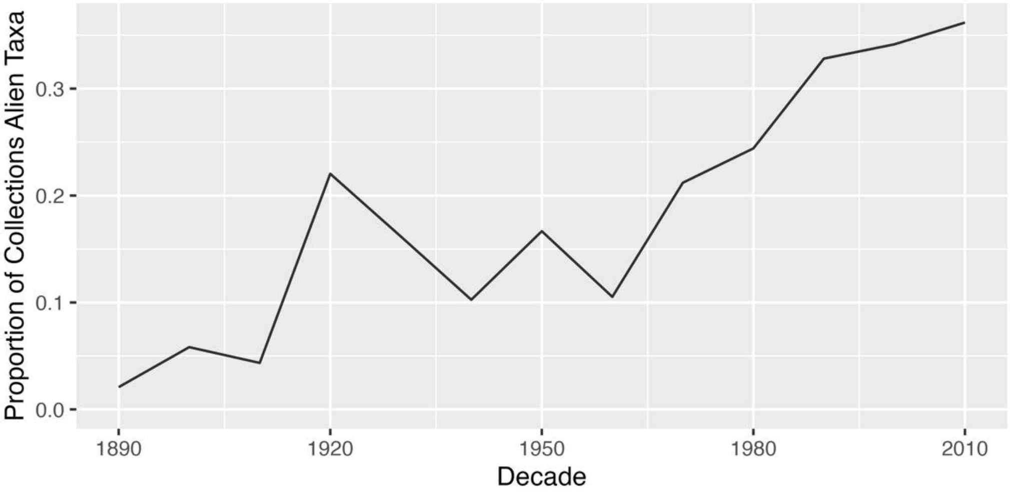


Figure 3. The proportion of herbarium collections within the San Juan Island archipelago comprised of alien taxa by decade.

Further, of the 156 islands, 145 (93%) had at least one alien species present, and the islands that did not have alien taxa were all very small rocks with a flora comprised solely of shoreline specialists well adapted to salt spray. Yet across all islands, alien taxa comprised an average of 32% of an individual island's flora (CI_{90} = 2%), even though island sizes ranged from 3 m^2 (a small rock off Boulder Island) to 14,840 hectares (Orcas Island). The stability and precision of this invasion estimate suggest alien species are remarkably adept at colonizing islands regardless of their size. This ability has implications for the long-term conservation and integrity of natural communities since most islands are small, largely inaccessible, and not inhabited or visited by people.

WHAT DRIVES THE COLONIZATION OF ALIEN SPECIES?

While understanding the factors that predict where an alien species will become invasive continues to be a focus of intense research (Rejmanek & Richardson, 1996; Milbau & Stout, 2008; van Kleunen, Weber & Fischer, 2010; Fei, Phillips & Shouse, 2014; van Kleunen, Dawson & Maurel, 2015; Klinerová, Tasevová & Dostál, 2018; Nunez-Mir et al., 2019), general patterns remain elusive (Thompson & Davis, 2011). Despite this, increasing evidence suggests the factors that influence the establishment of alien species in new localities (Pyšek & Richardson, 2006; Milbau & Stout, 2008; Richardson & Pyšek, 2012; Pyšek et al., 2015).

Key factors related to the establishment of alien species include their residence time in a region, how long they have been associated with human settlement, their evolutionary history, and specific plant traits. One of the most important aspects of determining if an alien species becomes established is how long they have been in a new focal region (Wilson et al., 2007; Sorte & Pyšek, 2009; Pyšek et al., 2015). Species that have been present in a region longer are more likely to be naturalized and are more frequent. Related to the concept of residence time is the idea that plants that have been associated with human disturbance for a long time 'archeophytes,' are more likely to establish that plants associated with more recent aspects of globalization 'neophytes' (Pyšek, Richardson & Williamson, 2004; Preston, Pearman & Hall, 2004; Williamson et al., 2008; Sorte & Pyšek, 2009). Other research has found that the specific plant families of alien species, especially natural areas, are over-represented by members of Poaceae, Fabaceae, and to a lesser extent Rosaceae (Daehler, 1998). Finally, several plant traits are associated with the naturalization of alien plants, including clonality, nitrogen-fixation ability, and whether an ornamental species (Milbau & Stout, 2008).

The above information on alien plants – their residence time in an area, whether they are long-term associated with humanity, their evolutionary history, and plant traits are readily, if tediously, available in the literature and herbarium records. When assessed in concert with the well-known factors related to the extinction risk of native plants (narrow geographic range, habitat specialization, and small population size; (Primack, 2014, pp. 157–173), modeling exercises can elucidate the potential plant community implications of those future distributions. Such modeling exercises can be particularly effective if a thorough effort has been made to catalog the number and distribution of native alien species in a region.

POSITIONALITY ON ALIEN SPECIES AND CONSERVATION

In the harsh light of the Anthropocene, conservationists and others are increasingly questioning the utility or importance of controlling alien species (Kareiva, 2011; Davis et al., 2011; Kareiva, Marvier & Lalasz, 2012; Thomas, 2013, 2017, 2019; Orion, 2015). These thinkers suggest that the impact of alien species on natural communities is overblown, management actions are cruel, discourse surrounding it is racist, xenophobic, and the value judgments inherent in invasive species research are unscientific (Colautti & MacIsaac, 2004; Sagoff, 2005; Warren, 2007; Larson, 2007; Keulartz & van der Weele, 2009; Inglis, 2020). Some authors even suggest invasive species will be the solution to the ecological crisis (Pearce, 2016). Despite these bold and sometimes polemical claims, several authors have strongly refuted most of the core claims of those denying the negative consequences of invasive species and highlighted the various logical fallacies of critics of invasion biology and invasive species management (Simberloff, 2003; Russell & Blackburn, 2017; Ricciardi & Ryan, 2018a,b; Hayward et al., 2019; Callen et al., 2020), and the implicit and unarticulated values of critics of traditional conservation (Doak et al., 2014; Hamilton, 2015; Baskin, 2015).

In particular, finding the ideal terminology for invasion biology has been problematic (Ladle & Whittaker, 2011, pp. 26–28). I believe using neutral terminology as proposed by Colautti and MacIssac (2004) obfuscates implicit values with their Stage I-V categories, and I am unsatisfied with the clunky terminology of 'non-native', 'non-indigenous', 'potentially harmful species' (Inglis, 2020), or 'human symbionts' (Larson, 2005). While I acknowledge terms such as "exotic", "alien", and "invader" can have painful and troubling social connotations, and not all alien species are invasive, such parallelisms are, in many instances, unfounded, unfair, and problematic themselves (Simberloff, 2003). I use the term alien to describe species not native to the San Juan Island archipelago for two pragmatic reasons. First, biogeographic origin matters (Buckley & Catford, 2016), and the primary definition of alien as an adjective is "belonging or relating to another person, place or thing." The second reason is to have a consistent terminology readily searchable in literature databases (Pyšek et al., 2004).

Finally, while some have tried to reconcile the invasive species debate, the value differences likely remain intractable (O'Brien, 2006; Keulartz & van der Weele, 2009; Frank et al., 2019; Coghlan & Cardilini, 2022). The differences may represent a case of "non-overlapping magestiera" (Gould, 1999) and a continuation of the long-standing "two cultures debate" (Snow & Snow, 1959) between rhetorical arguments based on the post-modern literary tradition's conceptions of power, privilege, and 'contested narratives' (Larson, 2005; Warren, 2007, 2021; Inglis, 2020), and those based on empirical data and scientific reasoning demonstrating measurable harm to the natural world, human health, and human economies (Clavero & Garciaberthou, 2005; Bellard, Cassey & Blackburn, 2016; Frank et al., 2019; Blackburn, Bellard & Ricciardi, 2019; Pyšek et al., 2020). Despite the siloed stalemate, there has also been some criticism of the narratives put forth by invasive species skeptics from within the humanities. For example, the work of Mastnak, Elyachar & Boellstorff (2014) on the idea of 'botanical decolonialism' represents a forceful and compelling critique of the typical critical framing of invasive species management as nativist, fascist and xenophobic.

I position myself towards thinkers that base their claims on empirical data and scientific reasoning, especially when attempting to make claims about the material world and what to do with it; broadly situating myself within the philosophical tradition of 'weak critical realism' (Carolan, 2005), especially when evaluating ideas in the context of management choices (Mingers, 2006). I disagree with the claim that science is value-free or that value-based reasoning is unscientific and fallacious (Colautti & MacIsaac, 2004; Inglis, 2020). I believe that articulated values form the basis of several branches of important inquiry, such as human health (Leung & Van Merode, 2019) and conservation (Soulé, 1985; Meine, Soulé & Noss, 2006). These values are well articulated in David Hume's moral philosophy (Cohon, 2018). Concerning alien species, I agree with the values articulated by Buckley and Catford (2016) that considering the biogeographic origin of species (*i.e.,* accounting for alien species) is a key aspect of managing and understanding natural communities. There is overwhelming evidence that alien species have negative consequences on the communities they colonize, but biogeographic origin alone should not be the sole basis for management decisions. Such values are generally articulated by invasion and conservation biologists (Frank et al., 2019), despite strawman arguments to the contrary.

Conservation biology is an explicitly value-laden field of inquiry that is often in the middle of political and policy issues. Conservation science can be rhetorically easy to dismiss if such values are not named and accounted for as objectively as possible. In one of the seminal papers on conservation ethics, Callicott et al. (2000) created a conceptual model of normative concepts in conservation. They divided these normative concepts into two normative paradigms along a continuum from compositionalist to functionalist values. Compositionalist norms emphasize the importance of species and species assemblages. Compositionalist norms emphasize native versus alien species, view most human actions through the lens of ecological degradation, and strongly prioritize the protection and promotion of the native biodiversity of a region. Functionalist norms place much less importance on the identity of species or species assemblages and more so on ecological processes and ecosystem services.

This thesis strongly emphasizes compositionalist conservation norms (Callicott, Crowder & Mumford, 2000; Ladle & Whittaker, 2011, pp. 31–32) and places the greatest weight on preserving and protecting biota native to a given region. I have been strongly shaped by the work of E. O. Wilson (Wilson, 1985, 1999, 2002), especially the sense of biophilia he articulates (Wilson, 1984; Simaika & Samways, 2010). Further, I have been strongly influenced by the ethics of the deep ecology movement, especially and belief in the intrinsic value of the natural world (Soulé, 1985; Devall, 1988; Soulé & Lease, 1995;

Oelschlaeger, 2014; Smith, 2019; Callicott, 1984), and the belief that extinction is a moral wrong (Cafaro & Primack, 2014). Thus, the primary goal of my conservation practice is halting the extirpation and extinction of native species and regionally unique communities.

ANALYTICAL FRAMEWORK

Weak critical realism prioritizes empirical ways of knowing and accepts the difference between the claims to knowledge about an object or subject and the object or subject themselves (Bhaskar, 1997). Such an approach is readily amenable to multi-model reasoning (Hilborn & Mangel, 1997; Anderson & Burnham, 2004) and Bayesian inference (Mingers, 2006; McElreath, 2020). Multi-model reasoning posits there can be several plausible explanations (*i.e.*, models) that can effectively describe observed phenomena (Hilborn & Mangel, 1997), which operationalizes the belief that knowledge claims about things are separate from the things themselves. Bayesian reasoning can evaluate the relative plausibility of knowledge claims (Wintle et al., 2003; Link & Barker, 2006; Jarosz & Wiley, 2014; Navarro, 2020; Vehtari et al., 2021). Such an analytical framework accepts that there is a 'real' world beyond the observer and that there is always uncertainty in how much and what an observer can know about the 'real'.

In the context of species presence on islands, the historical contingency of geology, climate, and non-replicability of the data make the epistemology of frequentist statistics ("what is the likelihood of the hypothesis being true given a frequency distribution of imagined replications of the data?") untenable since there are no replicates of the San Juan Islands or replications of the contingent distribution of species present among them. In contrast, the Bayesian conception of probability, 'what is the likelihood of my hypothesis being true given the data?' is readily and intuitively interpretable (Ellison, 2004; Kruschke, 2010; Wagenmakers et al., 2018).

CHAPTER SUMMARIES

The first chapter of this thesis explores the relationship between the invasion debt of alien species, the extinction risk of native species, and how both could influence biotic homogenization. Specifically, I examine what factors predict the current distribution of alien species and, given time, how those distributions might change in the future. Using the results of the modeling exercise, I postulate how biotic homogenization would change in two human generations (by the year 2100) given the 90% percentile worst-case scenario of alien species spread and the loss of all rare species (those found on fewer than five islands). I posit such a question is conceptually significant because species diversity is considered the bedrock of resiliency to massive ecosystem change (Wilson, 1999; Cadotte & Davies, 2010; Richardson et al., 2012; Primack, 2014; Leitão et al., 2016), and understanding the risk of invasive and alien plants to the native flora is fundamental to their current and future conservation. This question is practically significant because given spatially explicit information on where alien and native species are in the islands, this work can help target which islands and species should be the focus of conservation, restoration, and invasive species management and which native species should be the focus of conservation actions.

The second chapter addresses the issue of biotic homogenization among some of the most botanically unique small maritime meadow islands in the archipelago along the southern edge of Lopez Island. These islands were originally surveyed in 2005-2009 and have been well known by local botanists as one of the highest-density areas of rare plants anywhere in the State. I was curious about the rate of change among islands completely protected from human recreation and human use and if protected areas are protecting natural communities.

Specifically, I was interested in how the rates of alien plant colonization and native species extirpation were related to three growing conservation concerns in meadow habitats across the region that can readily impact natural areas with no direct human disturbance; invasive annual grasses, Canada geese, and deer. First, invasive annual grasses can rapidly convert perennial grasslands into annual grasslands and increase fire risk (Abatzoglou & Kolden, 2011; Davies, 2011; Balch et al., 2013; Garbowski et al., 2021). Second, a population of non-native resident Canada geese introduced in the 1980s has rapidly expanded across the San Juan and Gulf Islands, with strong evidence that they are degrading meadow habitats at alarming rates (Best & Arcese, 2009; Isaac-Renton et al., 2010; Bennett et al., 2011). Third, due to the changing social perceptions of hunting, as well as the loss of primary predators in the islands, deer are rapidly exploding in numbers across the islands, which are dramatically altering the structure and richness of island plant communities (Martin, Arcese & Scheerder, 2011; Arcese et al., 2014). Chapter two evaluates if the interaction of all three of these factors constitutes a potential extinction vortex for native species (Gilpin, 1986). Conceptually, such work continues the research agenda put forth by Seabloom et al. (2016). The analysis performed in chapter two can inform future management across these biologically and ecologically important islands.

CHAPTER 1 – INVASION DEBT AND EXTINCTION RISK OF VASCULAR PLANTS IN THE SAN JUAN ARCHIPELAGO

INTRODUCTION

Understanding how floras are becoming simpler and more similar through time is a core research topic in conservation biogeography (Olden, 2006). The simplification of the earth's floras ("biotic homogenization") is driven by the combined effects of the widespread introduction of non-native plants into a region and the extinction and extirpation of regional native species (Olden & Poff, 2003, p. 443). However, species introductions and extinctions can have a lagged response, named invasion debt (Rouget et al., 2016) and extinction debt (Hanski & Ovaskainen, 2002). While most biotic homogenization research examines whether biotic homogenization is presently occurring, I know no studies that explicitly assess how much future homogenization is likely to occur; a "homogenization debt" (Purvis, 2003).

The idea of an "invasion debt" was coined by Seabloom et al. (2006) in a study of the impact of alien species on the imperiled flora of California. The authors found that many alien species had much smaller ranges than similar native species and argued that, given time, alien plants would likely establish more widely across the state. The idea was further developed by Essl et al. (2011). They found that many of the current problematic invasive alien species were not recently introduced into a region but were legacies of prior socio-economic activities. Yet a framework for measuring invasion debt did not occur until the publication of Rouget et al. (2016).

Rouget et al. (2016) separated invasion debt into four components; introduction debt, establishment debt, spread debt and impact debt. Introduction debt is the number of species not in a focal region that are likely to become introduced. Establishment debt is the number of species present in a focal region but not yet expanded beyond a limited locality. Spread debt is the amount of area in a focal region that has yet to become occupied by a given alien species. Finally, impact debt is the likely ecological and economic cost of 'paying' the invasion debt.

Extinction debt is an older idea first introduced by Tilman et al. (1994), who suggests that there can be a lag between the degradation or loss of habitat and the loss of species. Rare species can be a particularly important component of extinction debt because they are often already at the greatest risk of extinction (Hartley & Kunin, 2003). Furthermore, the loss of rare species can be insidious because rare species can comprise a disproportionate amount of a region's diversity (Mi et al., 2012; Richardson et al., 2012; Leitão et al., 2016; Thorn et al., 2020). While rare species may not comprise large amounts of total cover, their importance may only become apparent during ecosystem stress (Jain et al., 2014).   For example, in oak meadows on Vancouver island, areas with more rare species are more resistant to invasion and more resilient to environmental stressors (MacDougall et al., 2013). The importance of rare species in times of ecosystem stress may be due to the disproportionate amount of functional diversity found in rare species (Mouillot et al., 2013; Leitão et al., 2016). Thus, rare species can act as 'insurance' during times of stress (Tilman & Downing, 1994; Chapin III, Torn & Tateno, 1996), and their loss can hasten degradation (MacDougall et al., 2013).

One important outcome of the interaction of both species invasions and extinction is biotic homogenization, the non-random process of community change where common, widespread species replace diverse assemblages of native taxa (Quammen, D, 1998;

McKinney & Lockwood, 1999). In their classic 1999 paper, McKinney and Lockwood describe the 'winners' of biotic homogenization are rapidly dispersing habitat generalists with large geographic ranges. Conversely, the 'losers' of biotic homogenization tend to have the opposite species traits; they are small-ranged habitat specialists with slow dispersal rates – typically the species endemic or unique to a region.

More recent research finds biotic homogenization causes highly skewed taxonomic distributions (McKinney, 2002; Olden & Poff, 2003) For example, plant species in *Fabaceae* and *Poaceae* disproportionately comprise the invasive and introduced plant species of natural areas (Daehler, 1998). Thus, while alien plant species tend to increase the local species richness of an area (Sax & Gaines, 2003), if they are all closely related evolutionarily and have similar functional traits, such combinations of species can decrease the resiliency of these novel plant assemblages to disturbances (Olden et al., 2004). For example, since 1500 AD, the species richness of vascular plants in Europe has increased by 1,621 species. Yet, phylogenetic alpha and beta diversity have decreased because more closely related species comprise the resultant flora (Winter et al., 2009).

Even the addition of a single alien species can rapidly homogenize a region’s flora. In the Rhön UNESCO Biosphere reserve in Germany, the N-fixing sub-shrub *Lupinus polyphyllus*, which was originally introduced to improve soil conditions, ended up rapidly spreading and homogenizing the flora of the regionally unique alpine hay meadows (Hansen et al., 2020). Many native species comprising the flora of the *Rhön* cannot coexist in meadows dominated by *L. polyphyllus*, especially grasses, which did not persist in invaded meadows. These invaded meadows were more homogenous in species composition and functional traits, and present species leaned towards more competitive species and species that could survive under cover of *L. polyphyllus*. In Spain, the invasion of plants in the genus *Carpobrotus* reduced species and functional richness, functional dispersion, and redundancy (Pino et al., 2009).

However, while the literature on current biotic homogenization has bloomed, I have yet to find any literature assessing the idea of a homogenization debt. While the idea of a "homogecene debt" was mentioned in passing in a book review (Purvis, 2003), the idea has not been developed further in the literature. To develop the idea of a homogenization debt and determine some potential mechanisms that could underly it, we use a comprehensive floristic database of 156 islands from the San Juan Islands in the Pacific Northwest of North America. Islands are particularly useful model systems in community ecology because they have clearly defined boundaries and are replicated and isolated, thus making delineating species pools more tractable (Warren et al., 2015).

The San Juan Islands in the Pacific Northwest of North America are an ideal system to study these questions because it has many small islands that can be reasonably censused. There have been extensive and systematic collecting efforts across the archipelago since 2000. Further, the physical and socio-economic history of the San Juan islands sets up an ideal experiment since the archipelago is reasonably isolated from the mainland and most of the small islands cluster near the large islands. Most smaller islands are uninhabited or used for recreation, with limited or no consistent human use. In contrast, the large islands are inhabited by several thousand people and served by a state ferry system that brings millions of people to the islands during the spring and summer months. Thus, the large islands are ideal source locations for new alien plants, and being a hub from which many then recreate the smaller islands, a reasonable source location from which new invasions could occur.

In this chapter, I use a mixture of herbarium data and detailed and exhaustive botanical inventory work to generate comprehensive species lists for 156 islands in the San Juan archipelago and a flora for the whole archipelago. With this data, I examine how the pool of likely introduced alien species, the pool of imperiled native species, and where they are located influence the amount of current biotic homogenization and the amount of homogenization possible in the future.

Since species diversity is considered the bedrock of resiliency to massive ecosystem change (Tilman & Downing, 1994; Chapin III, Torn & Tateno, 1996; MacDougall et al., 2013), understanding the risk of invasive and alien plants to the native flora is fundamental to their current and future conservation. Because herbarium and atlas data provide spatially explicit information on where alien and native species are, our dataset provides a framework for regional conservation planning. Specifically, in the islands, this work can help target which islands and species should be the focus of conservation, restoration, and invasive species management and which native species should be the focus of conservation actions.

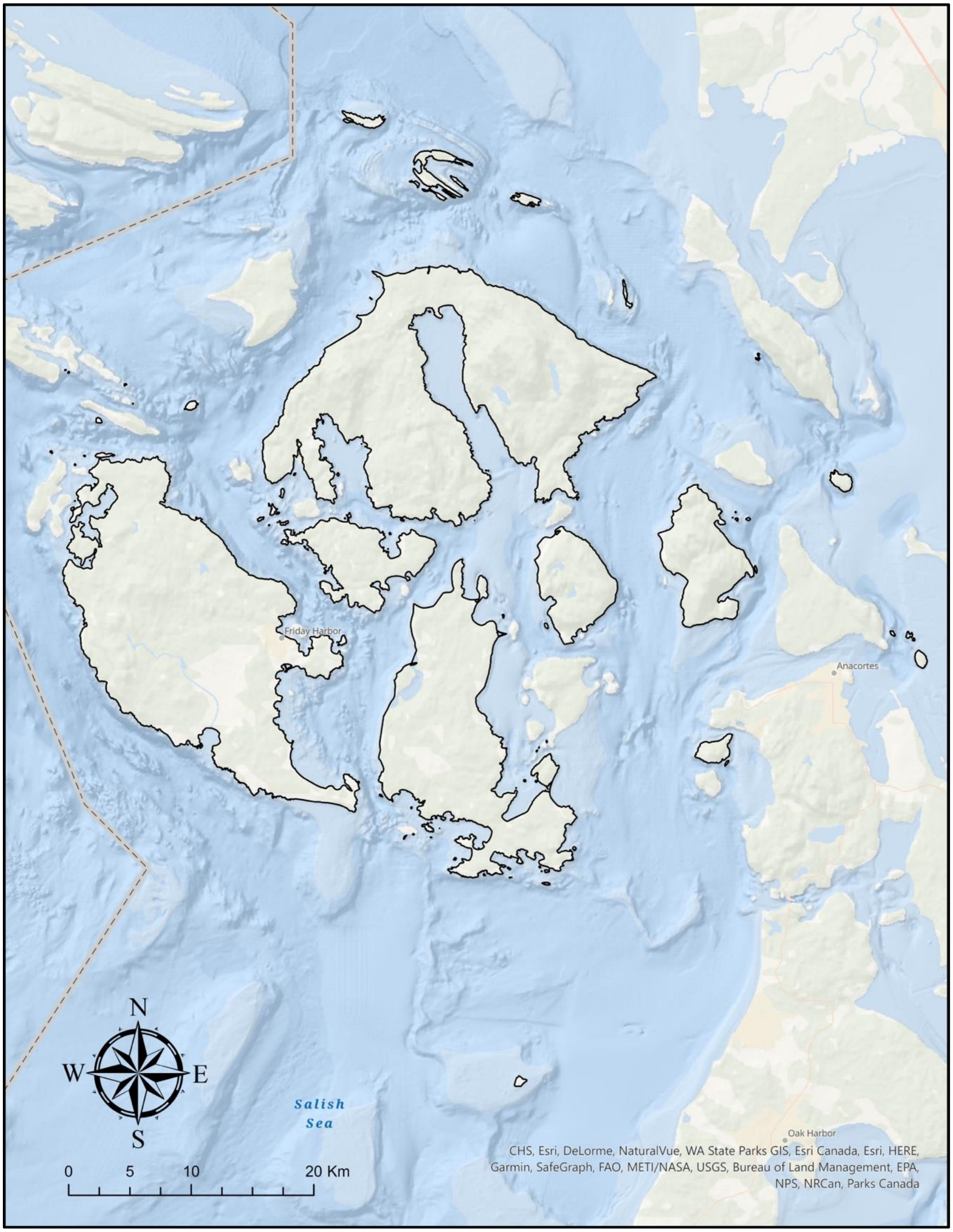
METHODS

STUDY AREA

The study area encompasses 156 islands, 21% of the roughly 740 islands found within San Juan, Whatcom, Skagit, and Island counties in Washington State (Figure 1). The Washington mainland bounds the study region to the East, Boundary Pass and the

Georgia Strait to the North, the Haro Strait to the West, and the Strait of Juan De Fuca to the West.

I considered islands to be areas of land surrounded by salt water at high tide. For islands over 20 hectares, reported hectares were used. Sor smaller islands, perimeters were traced using high-resolution google earth aerial imagery. The perimeter was considered to be where terrestrial vascular plants could conceivably grow (excluding salt-spray rock barrens). When difficult to discern, aerial images overlaid over a 2019 LiDAR of the region was used. The total range of island sizes was between 2.9 m^2 (Boulder Needle) to 14,840.96 hectares (Orcas Island).



CHS, Esri, DeLorme, NaturalVue, WA State Parks GIS, Esri Canada, Esri, HERE, Garmin, SafeGraph, FAO, METI/NASA, USGS, Bureau of Land Management, EPA, NPS, NRCan, Parks Canada

Figure 1-1. The study area, islands that have been surveyed or censused are outlined in black.

LINES OF EVIDENCE

four lines of evidence was used to compile a list of all the species found in the study area: herbarium records, iNaturalist records, species lists, and field surveys. For herbarium records, the consortium of Pacific Northwest Herbaria website (www.pnwherbaria.org) was queried for all collections within the study area based on a traced polygon around all islands in the study area (Figure 1-2).

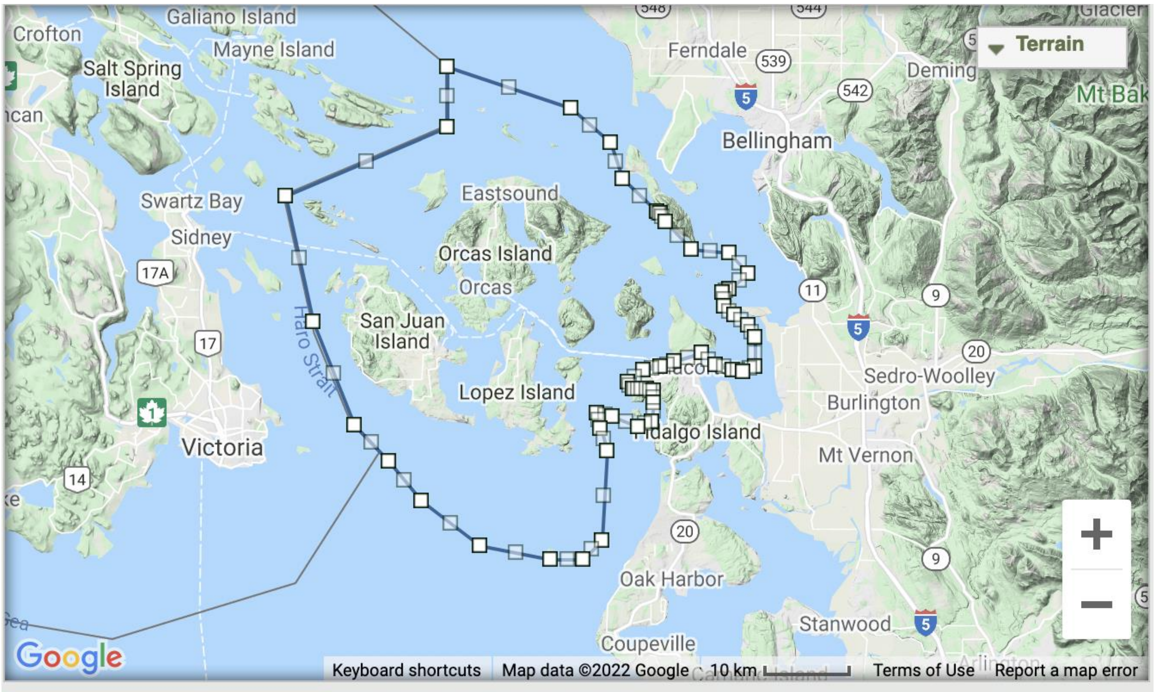


Figure 1-2. Delineation of the search query of the Consortium of Pacific Northwest Herbaria based on a polygon of the study area.

Queries were also based on locality information that included “San Juan Islands” based on a text search to capture potential records that had location errors and may not have been captured in the polygon query. Once queried, all records were collated and reviewed to create island-specific species lists. Species with only one herbarium record were re-examined to determine the plausibility of identification and confirm the accuracy of locality transcriptions. Because several of the earliest collections had broad locality descriptions such as (“San Juan Islands” or “Wasp Islands”), these species were only used to generate the possible regional species pool but not within the island-specific analysis.

For iNaturalist records, photographs were examined for all records up to 2021 and records were included if they were not of cultivated or planted individuals, were definitively identifiable, and were not already documented from a vouchered herbarium specimen. For species lists, all available lists published in the literature and by the Washington Native Plant Society were compiled. Lists were also compiled from local conservation organizations, land management agencies, and local botanists. These lists were then collated by island, and new species were added if herbarium records did not already capture them.

Finally, comprehensive floristic surveys were done of individual unsurveyed islands and islands that have been under-botanized. Floristic surveys of smaller islands involved multiple trained botanists visiting islands one to three times across the growing season, and all habitats were censused for species. If habitats were not accessible on foot (such as cliffs, impenetrable thickets and forests, and unwalkable rocky shorelines), they were surveyed by boat with binoculars.

ESTIMATING TOTAL SPECIES RICHNESS

Since the number of observed species will always be less than the actual total number of species in a flora, the Chao2 estimator (Chao, 1987) was used to determine the minimum estimated number of native and alien species. Estimates were made within four broad habitat types in the archipelago; open habitats (meadows, bald, and developed land), forests (all forest types), wetland (including bogs, marshes, lakes, and ponds), and shoreline habitats. Comparisons of the overall alien and native species pool can inform broad patterns of invasion debt and extinction risk.

QUESTION 1: ARE THE DIFFERENCES IN SPECIES-AREA CURVES BETWEEN ALIEN AND NATIVE TAXA?

Most broadly, alien species could pose a challenge to natural areas if they are less limited than native species by island size and the associated ecological attributes related to island size (habitat diversity, soil diversity, topography, etc.). If the same local biogeographic factors largely constrain native and alien taxa in each of the four habitat species pools, we would expect regressions of island area and richness would explain similar levels of variance (R^2) in both native and alien species within each species pool.

However, because island areas can have a minimal influence on species richness up to a certain island area threshold (*i.e.,* the small island effect; (Burns, Paul McHardy & Pledger, 2009; Dengler, 2010; Wang, Chen & Millien, 2018; Chen et al., 2020; Matthews & Rigal, 2021). I also used breakpoint regression to determine relationships between island size and alien and native species richness (Matthews & Rigal, 2021). For island-area models, semi-log function was used (Arrhenius, 1921), which is a generally more accurate model than the log-log function for smaller islands (Panitsa et al., 2006).

In particular, the small island effect is likely driven by limitations in microhabitats on the smallest islands (Chen et al., 2020). So, suppose alien taxa have fewer barriers to dispersal and are more capable of colonizing and persisting in many habitats and microhabitats. In that case, there should either be no or a very weak small island effect.

To determine differences between native and alien taxa for each nativity and habitat type combination, five regression models were evaluated using multi-model inference (Table 1-1); 1) no small island effect (linear model), 2) a single threshold (small island effect only), or 3) a two-threshold model (small and large island effect). To methods were used for threshold models, continuous and left-horizontal models. Continuous threshold models allow the slope but not intercept of a line to change at a given threshold, while a left-horizontal model maintains a slope of zero before the first breakpoint (Dengler, 2010; Matthews & Rigal, 2021).

Table 1-1. The six models used to assess the relationship between island size and species richness for native and alien species in shoreline, open, forested, and wetland habitats. In each formulation, logS and logA are the base10 log-transformation of species richness and island size, respectively, and the fitted model parameters are ci (intercept), zi (slope), and Ti (threshold). Boolean logic expressions (>, ≤, &) provide either 1 for true or 0 for false.

Model	**Formulation**
Linear	$\mathrm{logS} \sim c + \mathrm{zlogA}$
Continuous one-threshold	$\mathrm{logS} \sim c_1 + (\mathrm{logA} \leq \mathrm{T})\, \mathrm{z_1 logA} + (\mathrm{logA} > \mathrm{T})\, [z_1\mathrm{T} + z_2(\mathrm{logA} - \mathrm{T})]$
Continuous two-threshold	$\mathrm{logS} \sim c_1 + (\mathrm{logA} \leq \mathrm{T})\, \mathrm{z_1 logA} + (\mathrm{logA} > \mathrm{T}\ \&\ \mathrm{logA} \leq \mathrm{T_2})$ $[z_1\mathrm{T_1} + z_2(\mathrm{logA} - \mathrm{T_1})] + (\mathrm{logA} > \mathrm{T_2})\, [z_2(\mathrm{T_2} - \mathrm{T_1}) + z_3(\mathrm{logA} - \mathrm{T_2})]$
Left-horizontal one-threshold	$\mathrm{logS} \sim c_1 + (\mathrm{logA} > \mathrm{T})\, z_2(\mathrm{logA} - \mathrm{T})$
Left-horizontal two-threshold	$\mathrm{logS} \sim c_1 + (\mathrm{logA} > \mathrm{T_1}\ \&\ \mathrm{logA} \leq \mathrm{T_2})\, [z_2(\mathrm{logA} - \mathrm{T_1})] +$ $(\mathrm{logA} > \mathrm{T_2})\, [z_2(\mathrm{T_2} - \mathrm{T_1}) + z_3(\mathrm{logA} - \mathrm{T_2})]$

Once computed, R^2 values for the same model for native and alien species richness were compared. While it is inappropriate to compare R^2 values of different models describing the same response value due to the differences in the parameterization of different models (Dengler, 2010), comparing the same model (and thus the same parameterization) to both alien and native species richness should generally assess if the same biogeographic processes are influencing alien and native species in the same way.

Specifically, if R^2 values for a given model are higher for native species than for alien species, biogeographic variables associated with size are more important for determining species richness for native species than alien species.

Next, AICc and BIC information criteria were used to determine relative model support and if the same general relationship between island size and richness occurs within each nativity and habitat type combination. The debate over the proper information criterion is extensive and beyond the scope of what is presented here. Generally, AIC prioritizes model predictions, and BIC prioritizes correct functional inference (For an introduction to the debate, see Aho et al. (2014) and references therein). Here, models are considered to have sufficient support when both AIC and BIC converge towards a similar top model. When information criteria do not agree, the relative uncertainties between the two rankings for a given nativity and habitat are discussed. Models that have AIC and BIC values with a $\Delta \leq 2$ are considered as having equal support (Harrison et al., 2018). Finally, plots of predicted threshold values were compared to assess if models give reasonable estimates. Models were rejected that had nonsensical threshold values or if regression lines crossed zero (predicting negative species). Thus, it was considered plausible if the top model had the lowest AIC and BIC values and provided ecologically defensible insight.

Finally, island size threshold values were compared between native and alien species. Suppose alien species are less constrained by local biogeographic factors through both increased ability to disperse into habitats and less likely to be extreme habitat specialists. In that case, they should either 1) be less likely to have island size thresholds if they are more capable of being present in even marginally sized habitats (Chen et al., 2020), or 2) if a threshold is present, alien species should have a smaller island threshold size than native species, for the same reason.

QUESTION 2: HOW AT RISK ARE IMPERILED SPECIES BY INVASIVE SPECIES

Invasive species can disproportionately establish in habitats home to many imperiled species (Stadler et al., 2000; Stohlgren, Barnett & Kartesz, 2003; Seabloom et al., 2006). To determine if invasive species are associated with imperiled species in the archipelago, Kendall rank correlations were performed (Whitlock & Schluter, 2015) between imperiled and invasive species richness by island and habitat type. Species found on fewer than five islands were considered imperiled because populations with fewer than five occurrences are at higher risk of extinction (Hartley & Kunin, 2003). Because there should be more species on large islands, invasive and imperiled species richness were divided by island area before performing correlation analysis.

QUESTION 3: WHICH ALIEN PLANTS HAVE THE GREATEST ESTABLISHMENT DEBT?

A core aspect of establishment debt is that the regional prevalence of given alien taxa is related to residence time. In general, alien plants that have been in a region longer will have dispersed to more sites than more recently established taxa (Sorte & Pyšek, 2009). Thus, establishment debt has three main components, how long were taxa in a focal area, what are the plant traits of that species, and what is the number of potentially suitable localities taxa could persist in (Rouget et al., 2016).

To investigate these three components of establishment debt, the question of *how strong the relationship is between invasion history, ecological attributes, and life history* *of alien taxa and the proportion of islands an alien taxon is found on* was examined (Table 1-2).

This study considers five aspects of invasion history related to species prevalence, four related to attributes of a given taxon, and one related to the degree of human impact on an island. The four-taxon attributes are 1) the time since a taxon was first documented, 2) whether a taxon is an archaeophyte or neophyte, 3) how strong an invader is a taxon, and 4) is the taxon an ornamental or horticultural. The fifth landscape attribute is an ordinal score of the degree of human development on an island.

A strong correlation between residence time and prevalence would suggest that recently established alien taxa are likely to spread in the future given enough time. A weak or non-existent association with residence time would suggest other factors, such as dispersal limitation or habitat limitation, could be more important and that the number of alien taxa in the regional species pool, *per se*, is not a good measure of establishment debt.

To assess the relationship between time since introduction and the current distribution of alien taxa, herbarium data from the Consortium of Pacific Northwest Herbaria was used to determine the year of the first record. It was then subtracted it from 2021 to get the time since first seen.

Because collections in the San Juan County have not been uniform throughout time, a larger spatial area was used that included the largest metropolitan areas in the region (Seattle, Washington to the South, Vancouver, BC to the North, Victoria, BC to the West) to help mitigate some of the collection bias. Because for most of its Euro-American history, the San Juan’s has been a destination for people living in the region's urban centers. So, while it is almost certain taxa have been present in a region longer than the first herbarium record, earliest herbarium dates are assumed as a good enough proxy for residence time.

Table 1-2. Candidate predictors of alien plant species frequency in the San Juan Island archipelago.

Component	**Factor**	**Data Type**	**Description**	**Hypothesis**	**References**
Invasion History	Time Since First Seen	Continuous	The earliest year a given taxon was collected in the Salish Sea region.	Taxa present in the region for a longer time will be more prevalent	(Wilson et al., 2007; Sorte & Pyšek, 2009; Pyšek et al., 2015)
	Invasive Type	Categorical	Whether a given taxon is considered a Neophyte, Archaeophyte, or Native in Europe (3 categories).	Taxa associated with human disturbance (Archaeophytes/Neophytes) would be better invaders than Native taxa.	(Sorte & Pyšek, 2009; Kalusová et al., 2013)
	Invasive Status	Categorical	Whether a given taxon is invasive or non-invasive, and an ecosystem transformer or not (4 categories). Transformer status based on field experience, literature, or if listed as allelopathic	Invasive transformers will be the most common taxa, while non-invasive taxa will be the least	(Pyšek et al., 2004; Kalisz, Kivlin & Bialic-Murphy, 2021; Hierro & Callaway, 2021)
	Ornamental	Binary	Whether a given taxon was primarily introduced as an ornamental plant (gardens or landscaping).	Because ornamental plants make up a disproportionate number of invasive species, they should be more common.	(Dehnen-Schmutz et al., 2007; van Kleunen et al., 2018)
	Human Impact Score	Ordinal	A six-point score, see Table 1-3	Islands with a greater human impact score will have more taxa	(Vitousek et al., 1997b)
Ecological	Island Size	Continuous	The smallest island a taxon is currently found on	Taxa found on smaller islands are more likely to be better dispersers and be found on more islands	(Aikio et al., 2020)
	Primary Habitat	Categorical	The primary habitat type a taxon grows in (4 categories; shoreline, open habitats, forest, or wetland).	Species associated with open habitats will be the most frequent	(Rejmánek, Richardson & Pyšek, 2005; Richardson & Pyšek, 2006; Kalusová et al., 2013)
Life History	Dispersal Type	Binary	Whether a taxon is a long or short disperser.	Long-distance dispersers will be more likely to be present on an island	(Bennett et al., 2011)
	Life Span	Categorical	Whether a taxon is an annual, biennial, or perennial.		
	Life Form	Categorical	Whether a taxon is a forb, graminoid, vine, or shrub/tree.		
	Clonality	Binary	Whether a taxon can reproduce vegetatively		

In Europe, while determining the nativity of a taxon is challenging due to the extensive history of human habitation and commerce, biogeographers created a general framework of three broad categories: native, archaeophyte, and neophyte. Archaeophytes are taxa with extensive archeological evidence for human association before 1500, the general date of when global exploration began, while neophytes are taxa generally associated with humans after this date (Preston, Pearman & Hall, 2004).

The general invasiveness of alien species in other parts of the world could help predict how invasive they could be in the San Juan Archipelago. For each taxon, the invasiveness status (invasive/naturalized) was determined as well whether the taxon is an ecosystem transformer or not. Given the uncertainties of climate change, I had a liberal consideration of the potential invasiveness of a taxon, and a species was considered invasive if it is naturalized and recorded as invasive in at least one county in the United States (Invasive Plant Atlas of the United States; Swearingen & Bargeron, 2016). The effect that ecosystem transformers have on ecosystems is well established (Pyšek et al., 2004; Fei, Phillips & Shouse, 2014; Coggan, Hayward & Gibb, 2018; Kalisz, Kivlin & Bialic-Murphy, 2021; Hierro & Callaway, 2021), and native species will likely become extirpated in invaded habitats if alien species transform ecosystems away from habitats that are suitable for native species.

Ornamental garden plants are a common source of invasive species because many are bred for fast-growing competitive traits (Dehnen-Schmutz et al., 2007; van Kleunen et al., 2018). For example, in Ireland, ornamental species were more likely to become established and invasive than other taxa (Milbau & Stout, 2008). However, given how dry many of the natural habitats in the archipelago are, ornamental plants may not comprise a significant proportion of the flora.

The effect of humans on ecosystems is well known and well documented (Vitousek et al., 1997b; Maslin & Lewis, 2015; Young et al., 2016; DellaSala et al., 2018), and alien species are generally thought to do well in human-dominated systems (Vitousek et al., 1997a; McKinney & Lockwood, 1999; McKinney, 2005; Ellis & Ramankutty, 2008; MacDougall et al., 2013; Thomas, 2017, 2019). Thus, alien species are expected to be more frequent in areas with more human disturbance. Because attempting to quantify human impact is multidimensional, an ordinal scale was created in an attempt to create a simple measure of impact based on how accessible an island is if it was settled or not, how developed it is, and how many people visit an island (Table 1-3).

Because species richness and colonization generally increase with area (Arrhenius, 1921; MacArthur & Wilson, 1967; Aikio et al., 2020), I expect alien species to be more probable on larger than smaller islands, especially because the larger islands also have greater human impact and more potential habitats. There is strong evidence that when habitats of a native community are more invadable when they match the source habitats of alien plants (Rejmánek, Richardson & Pyšek, 2005; Richardson & Pyšek, 2006; Chytrý et al., 2008), especially when they are also disturbance-prone. Thus, the archipelago’s coastal meadow habitats are more likely to be invaded because they are the most similar to the meadow habitats of maritime Europe (Kalusová et al., 2013).

Finally, plant traits are often one of the most important factors determining how well a species can colonize an island (Vittoz & Engler, 2007; Milbau & Stout, 2008; Pyšek et al., 2015; Di Musciano et al., 2018; Junaedi & Mutaqien, 2018; Nunez-Mir et al., 2019; Aikio et al., 2020). I chose to use broad life history traits – life span, life form, clonality, and dispersal ability – because they are likely the most basic filters for whether a species can disperse to an island and persist in a specific habitat. For example, short-lived species like annuals are more likely to become extirpated (Saar et al., 2012), while clonal species are more likely to establish (Milbau & Stout, 2008; Aikio et al., 2020).

Table 1-3. Ordinal scale of human impact on islands in the San Juan archipelago

Human Impact Score	Description
0	An inaccessible island with no easily suitable landing location. Islands that were never settled and currently have active restrictions against visiting.
1	Islands with a beach to land on but with no maintained recreation infrastructure and were not historically settled by Europeans. These islands either are publicly owned and have active restrictions against visiting or are privately owned, but illegal visiting is still possible, or limited visiting through permits is allowed.
2	Islands with a beach to land on but no maintained recreation infrastructure, but way trails are present. Island may or may not have been historically occupied or used but is currently unoccupied with low or moderate visitation.
3	Islands with a beach to land on, recreation infrastructure present. Islands are either day-use only or have limited and localized camping with limited trails into the island's interior. Island may or may not have been historically occupied or used but is currently unoccupied with moderate visitation.
4	Islands with a beach to land on. Localized recreation infrastructure is present with maintained trails, toilets, and multiple campsites. Mooring may be present nearby, and islands are moderately to highly visited. Islands with historic European settlement and development.
5	A currently inhabited island with residential development and either year-round or partly year-round occupancy.
6	Islands with a beach to land on. There is widespread recreation infrastructure, with maintained trails, toilets, and multiple campsites. Mooring is present nearby, and islands are heavily visited. Islands with historic European settlement and development.

The published literature and field work were used to compile information on life form, life duration, clonality, and dispersal range. Information provided within the Burke herbarium (https://biology.burke.washington.edu/herbarium/imagecollection.php), the electronic floristic atlas of British Columbia (https://linnet.geog.ubc.ca), and the online flora of Britain and Ireland were used to determine life history traits (https://plantatlas.brc.ac.uk/). For habitat preferences, a mixture of field observation, notes from herbarium labels, and available literature were used and each taxon was coded as likely to be found in shoreline, wetland, open and forested habitats. For dispersal characteristics, the protocol of Bennett et al. (2013) was used to code species as a short or long disperser.

Before running the first model, whether a given alien taxon was a failed introduction was assessed becasue presence in a herbarium does not mean that a species is currently extant in the archipelago. For each taxon, species not seen since 1985 were considered a failed introduction. because the original 1985 publication of the *Wild Plants of the San Juan Islands* was the first systematic and comprehensive flora of the region (Atkinson & Sharpe, 2000).

Once all the above information was compiled ,two modeling exercises were performed using generalized linear mixed models fit with Bayesian reasoning. The first model assessed how invasion history, life history traits, and phylogeny influenced the frequency of alien species across the islands. This model assessed the most important species-level information to put into the second model, which assesses island-specific occurrence probability based on species information, island area, and human impact.

Regression models were run using Bayesian inference using the package *brms* (Bürkner, 2017). predictor variables were centered and standardized before running each model. Each model was run with eight chains, each chain with 5,000 runs (2,500 warm-up), thinned to 100. The intercept was given a prior of mean = 0, standard deviation = 0.5, and parameters a prior probability of mean = 0 and standard deviation of 1 based on prior predictive sampling (McElreath, 2020). Once run, all models were assessed for chain convergence and if $\hat{r}$ <1.03.

To compare model performance and determine variable importance, LOO information criterion was used (LOOIC; Vehtari et al., 2021). Model weights were assessed using the model-stacking approach (Yao et al., 2018). This approach weights the model with the lowest posterior predictive error as more plausible. The relative variable importance was then calculated for each predictor by summing the model weights for each model that the predictor was present. To assess model performance, **compare_performance** function in the *performance* R package was used (Lüdecke et al., 2021). Finally, the model of island-specific occurrence probability was used to predict the island-specific occurrence probability of each alien species in the year 2079 based on the 90% credible interval prediction. Thus, this prediction represents a plausible worst-case scenario of alien species establishment.

QUESTION 4: HOMOGENIZATION DEBT?

To assess current and future homogenization, the Jaccard similarity was calcualted for island pairs currently and in 2079 based on taxonomy (species) and phylogeny using the framework provided by Baselga (2012). The change in pairwise similarity was assessed using paired t-tests based on Bayes Factors using **ggwithinstats()** function in the *ggstatsplot* package (Patil, 2021). All analysis was performed in R version 4.0.4. (R Core Team, 2021).

RESULTS

DESCRIBING THE REGIONAL FLORA

HOW MANY TAXA ARE IN THE FLORA?

Based on herbarium records, species lists, and field observations, there are 1,010 species (1,177 if including infra taxa) in the San Juan archipelago (Appendix 1). The estimated minimum size of the actual flora based on the Chao2 estimate is 1,256 (CI_{95} = 1,134 to 1,575) species. Thus, between 64 to 89% of the San Juan archipelago flora is currently known. Alien species make up 38% of the observed flora (385 species) and 42 to 47% of the estimated flora (Chao2 = 544, CI_{95} = 472 to 747 species).

When partitioned by broad habitat type (Figure 1-3), most species are associated with open habitats (52%), followed by forested (21%), wetland (17%), and then shoreline habitats (10%). Alien taxa dominate the flora of open habitats (62%) but are a much smaller component of shoreline (25%), forest (16%), and wetland (7%) floras.

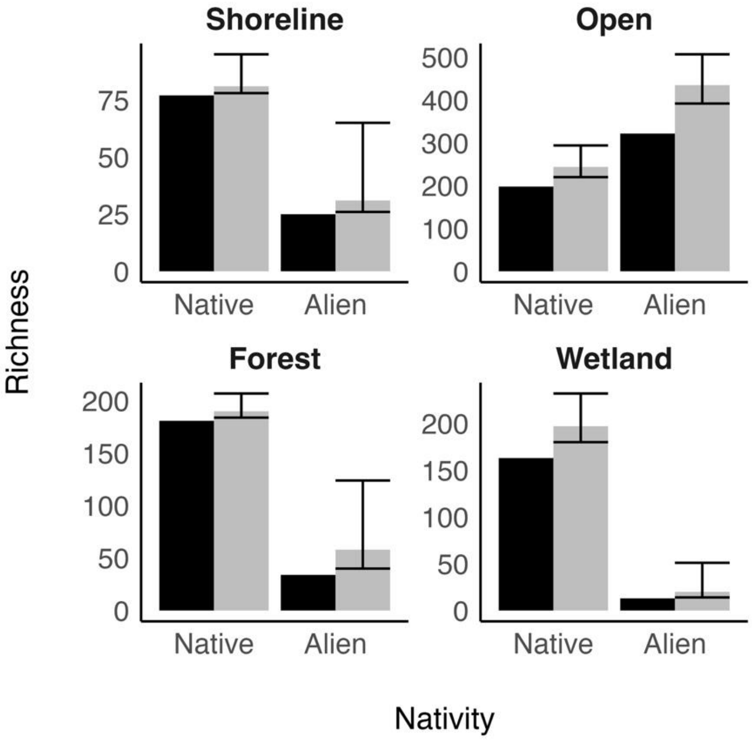


Figure 1-3. The number of observed (black) and estimated (grey) species across four habitat species pools in the San Juan archipelago. Error bars represent 95% confidence intervals for the Chao2 species richness estimate.

HOW MUCH OF THE NATIVE FLORA IS RARE?

Rare species comprise 35% (349 species) of the archipelago's flora (Table 1-4). Most rare species are found only on one (110 species) or two (93) islands. Rare species are mostly found in the two rarer habitats based on land area; wetland (*n* = 134) or open (*n* = 98) habitats. These two habitats had most of the species of conservation concern (18 of 22 species), with open habitats also having the most species of conservation concern (*n* = 14).

Table 1-4. Distribution of rare species across four habitat types found in the San Juan Archipelago

Habitat	Singleton	Doubleton	3-5 islands	WANHP	Total	% of Flora
Shoreline	9	8	14	3	34	43
Open	37	22	25	14	98	49.7
Forest	21	27	34	1	83	45.3

Wetland	43	36	51	4	134	83.8

HOW ESTABLISHED ARE ALIEN PLANTS?

Based on herbarium records, species lists, and field observations, there have been 385 alien plants recorded in the San Juan archipelago, and 90% of these species ($n = 349$) are likely established in the archipelago (Figure 1-4). Open habitats have the most alien species ($n = 321$), and wetland habitats have the fewest (10 species). Across all habitats, invasive species comprise 70% of the alien flora and are more likely to become established.

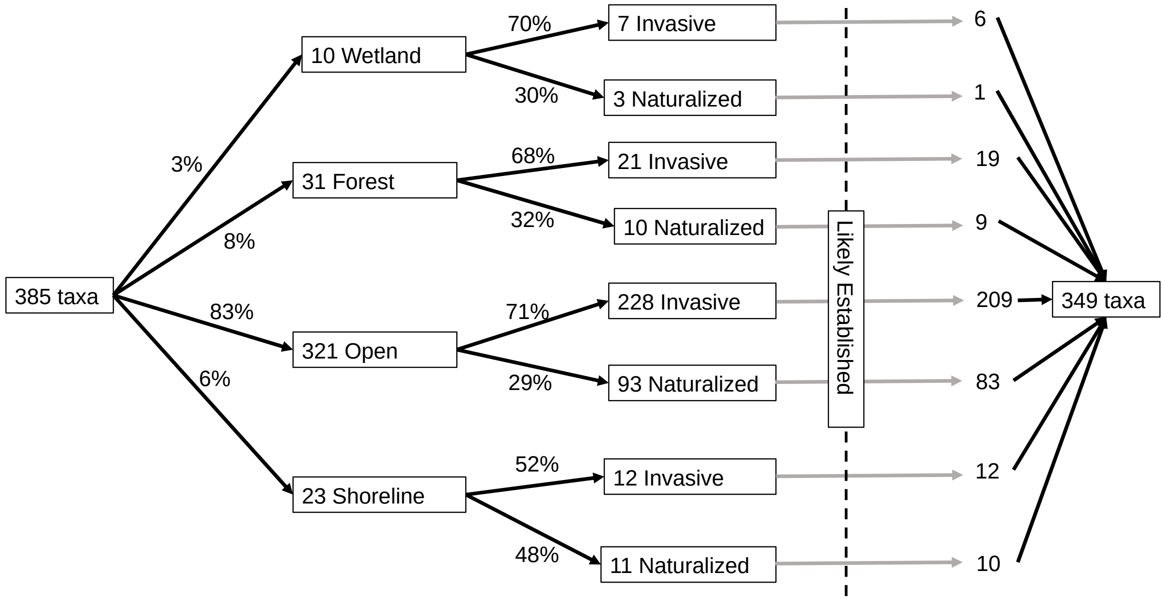


Figure 1-4. The status of 385 alien plant taxa documented within four habitat types found in the San Juan Island archipelago, Washington State, USA. Values in boxes denote the number of taxa in each category; percentages are based on the values from the preceding box. *'Likely Established'* denote taxa recorded in the archipelago and have been seen at least once since 1985.

CURRENT RISKS

In general, invasive alien species are more likely to be present when more rare species are present, even after controlling for island area (Table 1-5). Therefore, rare species associated with open and shoreline habitats have the highest pressure from invasive alien species. In contrast, rare species associated with forest habitats are 53% less likely than open habitats to have high invasive alien species pressure. Currently, invasive alien species are not associated with high numbers of rare native species in wetland habitats.

Table 1-5. Kendall rank correlation coefficients for the relationship between rare native species and invasive alien species across all island habitats (*All*) and among four habitat types. For each habitat type, correlations are only done on islands with rare native species present.

Habitat	**Islands**	**tau**	***p***
All	51	0.837	<0.0001
Shoreline	22	0.607	<0.0001
Open	37	0.883	<0.0001
Forest	24	0.499	0.0050
Wetland	12	-0.032	0.8886

BIOGEOGRAPHIC BARRIERS

Compared to a one-threshold or linear model, a two-threshold model had the greatest support within each habitat and across all habitats (Table 1-6). While both AICc and BIC generally selected the same top models, AICc was more likely to select the two-threshold model that produced nonsensical predictions for the smallest and largest islands (Appendix 2, Table A2-1).

Table 1-6. The top threshold model results for native and alien species across four habitats. '*threshold 1*' and '*threshold 2'* represent the threshold cut-off for their respective models (in hectares). For models ranked by information criteria, see Appendix 2, Table A2-1.

	R2		**Native**		**Alien**	
Habitat	**Native**	**Alien**	**threshold 1**	**threshold 2**	**threshold 1**	**threshold 2**
Overall	0.94	0.86	0.048	1028.3	0.075	4509.5
Shoreline	0.78	0.7	0.002	1153.8	0.030	1637.3
Open	0.88	0.85	0.027	4700.3	0.065	4406.8
Forest	0.93	0.92	0.167	11806.7	1.714	6083.1
Wetland	0.98	0.79	47.003	13247.3	22.087	7658.2

When not separated by habitat types, island area generally explains 8% more variation in native species richness than alien species richness (Figure 1-5, Table 1-6). However, when not considering habitat types, there was a small island effect for both native and alien species, but alien species had a slightly larger small island effect (0.08 hectares, 13 island difference; Figure 4).

The importance of habitat type becomes apparent when separately considering the respective floras of the four broad habitat types. Across all habitat types and nativity, there is generally a large island threshold between the largest small island (Sucia Island, 224 ha) and the smallest large island (Blakely island, 1,685 ha; Figure 1-6). Alien species had a greater large island threshold (4509 hectares) correlated with the three large, highly visited, ferry-served islands (Lopez, San Juan, and Orcas).

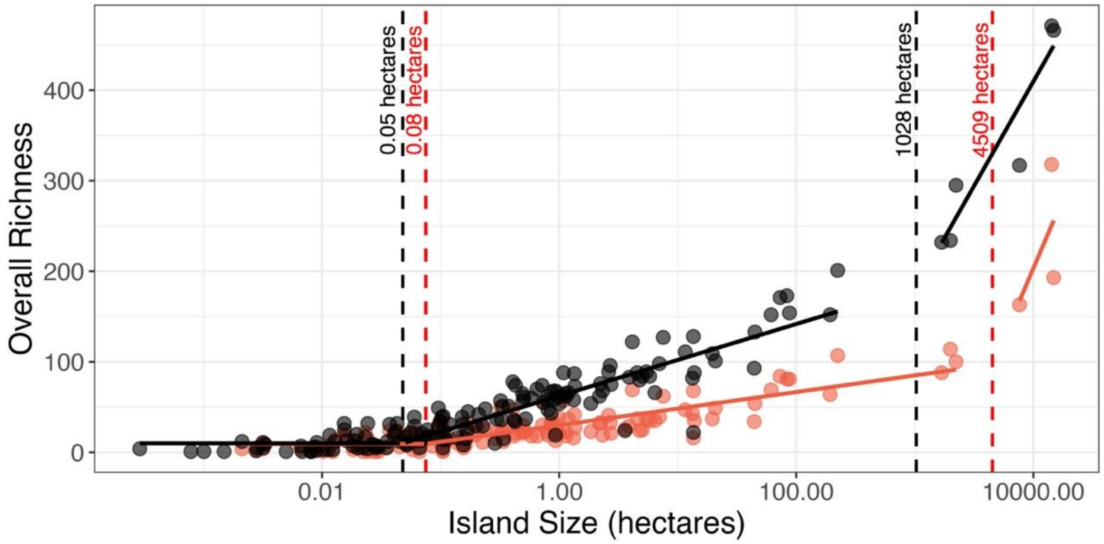


Figure 1-5. Island size and richness relationship between native (black) and alien (red) species. Dotted lines represent island thresholds where the relationship between island area and species richness is statistically different.

Among habitats, the difference in the influence of island size between native and alien species was greater in wetland habitats (19% difference) and shoreline habitats (8%) compared to open (3%) and forested habitats (1%). Small island effect thresholds were generally smaller for native species than alien species (Figure 1-6), except for the alien wetland flora, which had a smaller small island effect threshold (22 ha). However, the slope of the ISAR was greater for native species across all habitats and thresholds except the large island threshold for the alien open habitat flora (Figure 1-6).

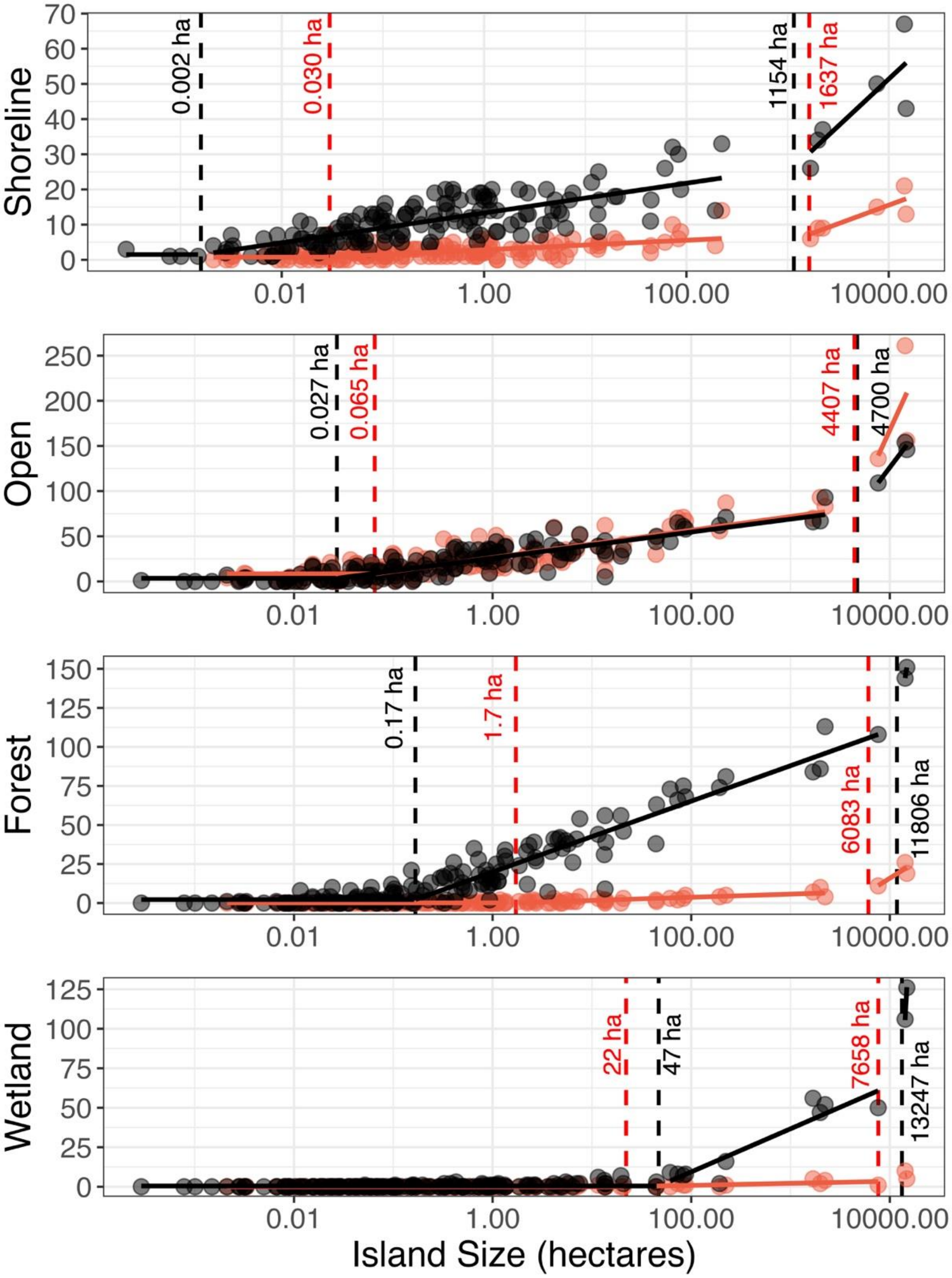


Figure 1-6. Relationship of island size and richness between native (black) and alien (red) species among four species pools; shoreline species, open (meadows and developed land), forests, and wetlands. Dotted lines represent island thresholds where the relationship between island area and species richness is statistically different.

In general, alien species attributes associated with invasiveness categories (residence time, type, invasiveness status, and ornamental status) were more likely to be important factors explaining species frequency across the San Juan archipelago compared to plant traits (Table 1-7). Models that only considered the four invasiveness categories had the best model support (w = 0.46; Appendix 2, Table A2-2). The invasion history categories were used in the next modeling exercise of island-specific incidence probability.

Table 1-7. Importance of nine variables in models predicting the number of islands an alien species is present. Importance values are the sum of model weights found in Table A2-1 in Appendix 2 and represent the probability a given variable is in the most plausible model of the data.

Parameter	Type	Range	Importance
Residence Time	**Continuous**	**0 – 141 years**	**0.70**
Type	**Categorical**	**Native/Archaeophyte/Neophyte**	**0.58**
Status	**Categorical**	**Invasive/InvasiveTransformer/ NonInvasive/NonInvasiveTransformer**	**0.55**
Ornamental	**Categorical**	**Yes/No**	**0.49**
Life Span	Categorical	Annual/Biennial/Perennial	0.19
Clonal?	Categorical	Yes/No	0.10
Life Form	Categorical	Forb/Graminoid/Vine/Woody	0.09
Dispersal Type	Categorical	Short/Long	0.06
Primary Habitat	Categorical	Shoreline/Open/Forest/Wetland	0.08

Phylogeny had a modest influence on alien plant species frequency and explained 19% of the variance of the top model (Appendix2, Table A2-1). Within the phylogeny, Clade explained most of the variance (68%), followed by Family (23%) and then Order (9%).

Due to the long computation times (>14 hours), only the full model of island-specific incidence was run. The full model had moderate support (R^2_{Fixed} = 0.29, R^2_{Random} = 0.17, R^2_{Full} = 0.466). Island identity only explained 14% of the variance in random effects, compared to phylogeny (86%). The relationship of phylogeny to island-specific influence was roughly similar to the relationship of phylogeny to overall frequency. Clade was most important (61%), followed by Family (19%) and Order (6%).

When considering island-specific occurrence, island area and human impact had the largest positive effect on occurrence probability compared to invasion history (Figure 1-7). Alien species were 69% more probable on the largest island (83%) compared to the smallest (14%) and were 55% more probable on the most impacted islands (70%) compared to islands with no human impact (15%).

The residence time of an alien species had the greatest influence on the occurrence probability compared to the other three invasiveness categories. Species that had been in the archipelago longest (141 years) were 31% more likely to occur on an island (34%) compared to the most recently arrived species (3%). The next most important invasion history category was their invasive status. Invasive transformers had the greatest occurrence probability (33%) and were 14% more likely to be on an island than non-invasive alien species (19%). Species native to their source locality were nearly twice as likely to be present on an island (30%) than either archaeophytes (15%) or neophytes (13%). Finally, ornamental species were 10% less likely to occur on an island (5%) than other alien species (15%).

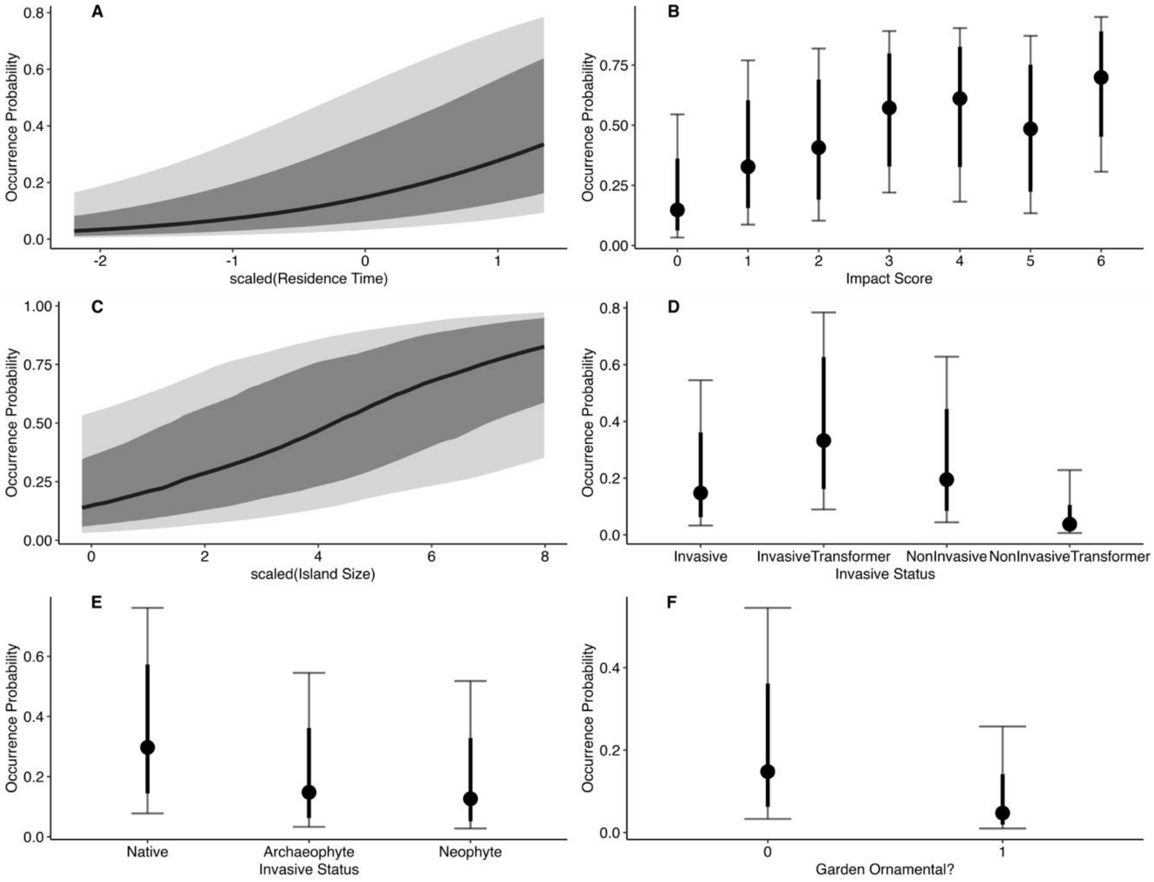


Figure 1-7. Six predictors of island-specific alien species occurrence (probability of occurrence). In panels A and C, shaded areas represent the 68% (dark grey) and 90% (light grey) credible intervals. In panels B, D-F, bars represent 68% (black) and 90% (dark grey) credible intervals.

FUTURE HOMOGENIZATION

When predicting the worst-case distribution of alien species by 2079, alien species are predicted to more than quadruple (average = 4.8x, sd = 2.6x) across islands, and this increase could more than double the flora of each island (average = 2.2x, sd = 2.9x). Larger islands that are more heavily human-impacted are more likely to have larger increases in the number of alien species (Figure 1-8).

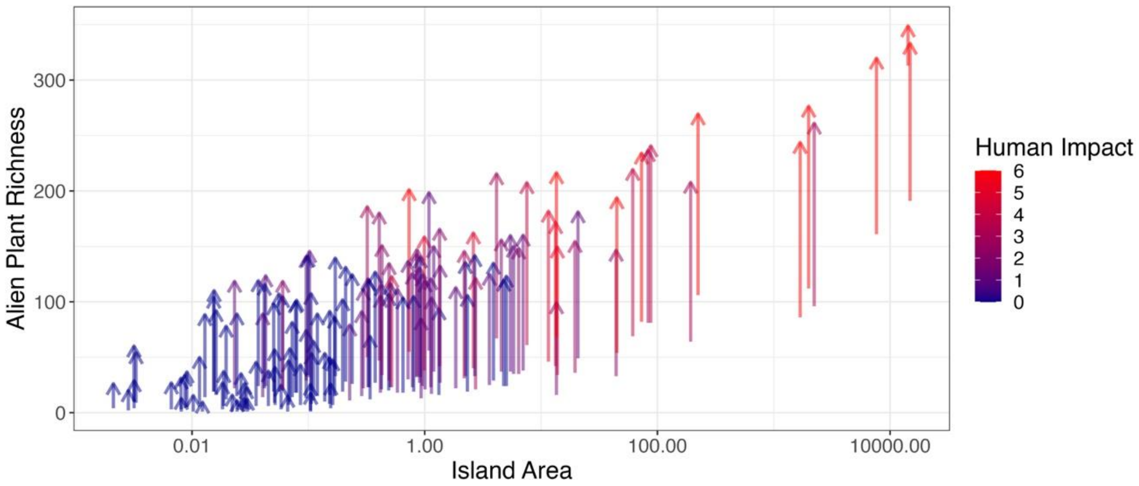


Figure 1-8. Increases in future alien species richness between 2022 and worst-case projection for 2079. Arrows denote the projected number of added species between the two time periods. Arrows are colored based on the human impact score of the island.

Based on the predicted worst-case increase in alien species and loss of rare species, island floras will increase in taxonomic and phylogenetic similarity. In the future, both taxonomic and phylogenetic similarity could increase by 20% across all habitat types (Figure 1-9, Table 1-8). The flora of open habitats will have the greatest increase in taxonomic similarity (24%) but a smaller increase in phylogenetic similarity (12%).

Table 1-8. Bayes Factor t-test summary table.

	Taxonomic		Phylogenetic	
Habitat	Difference	BF	Difference	BF
All Habitats	0.20 (0.20, 0.21)	>1000	0.20 (0.19, 0.20)	>1000
Shoreline	0.14 (0.14, 0.14)	>1000	0.07 (0.07, 0.08)	>1000
Open	0.24 (0.24, 0.25)	>1000	0.12 (0.11, 0.12)	>1000
Forest	0.07 (0.06, 0.07)	-491.35	0.04 (0.04, 0.05)	-180.97
Wetland	0.07 (0.06, 0.09)	-47.4	0 (0, 0.02)	-2.53

The predicted changes in similarity across other habitat floras are more modest, and taxonomic similarity is more likely to increase than phylogenetic similarity. Shoreline floras are expected to increase in taxonomic similarity by 14%, but only phylogenetic similarity will only increase by 7%. Forest and wetland floras are predicted to have the smallest changes in taxonomic similarity (7% each) and insignificant changes in phylogenetic similarity (forest = 4%, wetland = 0%; Table 1-8).

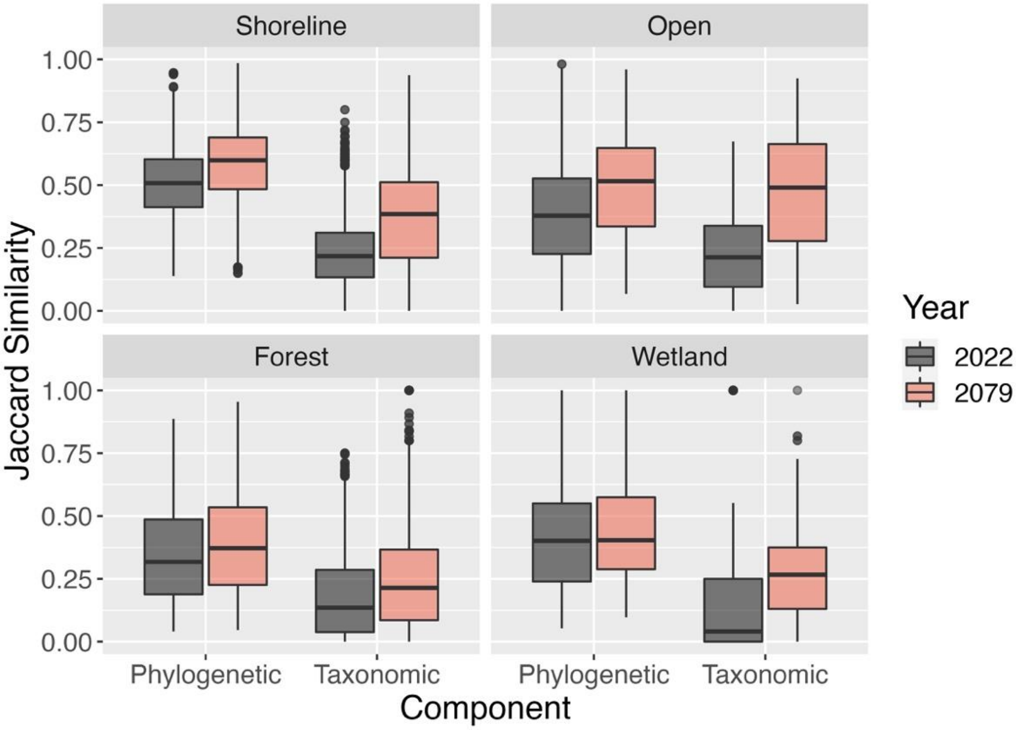


Figure 1-9. Projected changes in the pairwise nestedness component of phylogenetic beta-diversity for alien and native species between 2021 and 2179 (two human generations). Projections are based on the loss of all rare native species and predicted worst-case increases in alien species richness.

DISCUSSION

OVERALL PATTERNS WITHIN THE FLORA

ESTIMATING THE SIZE OF THE FLORA

After the compilation of herbarium records, species lists, iNaturalist observations, and field surveys, a significant number of new species were added to the known flora of the San Juan archipelago. Atkinson and Sharpe (2000), the last comprehensive survey of the archipelago's flora, recorded 970 taxa, which added 141 taxa to their initial work first published in 1985. The new taxa increased the proportion of alien species from 34% in 1985 to 36% by 2000. By 2022, there are 1,010 species (1,177 infra taxa), adding 207 taxa, 38% of which are alien plant species. While this is only an increase of 4% since 1985, if accounting for rates of unseen species, the actual proportion of the flora comprised of alien species is between 42 and 47% and has likely increased by 8 to 13%. When partitioned by nativity, there are fewer unseen native species (estimate = 13%, uncertainty = 6 to 25%), than alien species (estimate = 28%, uncertainty = 16 to 47%).

While Chao2 estimates suggest significant uncertainty in the size of the unseen flora (11 to 36% have yet to be seen), the upper confidence estimates for the number of unseen species are likely improbable. Assessing the accuracy of Chao2 estimates is difficult (Pitman & Jorgensen, 2002; Walther & Moore, 2005), and there are multiple sources of uncertainty. A significant proportion of the native flora has not been seen since 1985 (185 species, 18%), and 55 of those species are only found on a single larger island. The estimated unseen species will likely narrow if those species are instead considered extirpated. Yet, at least one Lazarus species (a species thought to be extirpated but was refound; Keith & Burgman, 2004), *Brodiaea rosea*, was found in recent surveys, even though it was considered historical in Washington and had not been seen in 113 years

Figure 1-10. *Brodiaea rosea* (Indian Valley Brodiaea), a Lazarus taxon not seen since

1908 and thought to be extirpated in Washington State, rediscovered in 2021.. While many of the smaller islands have been systematically surveyed, given the size of the larger islands and how much of the larger islands are private property, it is still probable many more 'missing' taxa are waiting to be rediscovered.

Figure 1-10. *Brodiaea rosea* (Indian Valley Brodiaea), a Lazarus taxon not seen since 1908 and thought to be extirpated in Washington State, rediscovered in 2021.

While Chao2 estimates suggest significant uncertainty in the size of the unseen flora (11 to 36% have yet to be seen), the upper confidence estimates for the number of unseen species are likely improbable.

Another potential uncertainty source is related to whether the recently observed alien taxa are waifs or not, and not including those taxa would also reduce the uncertainty. This uncertainty is likely why the confidence bounds for alien taxa were so broad (16 to 47% remaining to be seen). However, by having a more liberal cutoff for if a species is in the flora, a sizable portion of unobserved alien species could be considered as part of the establishment debt since these are species that could present, but not in numbers large enough to have been seen by observers yet.

BROAD PATTERNS IN FLORA BASED ON HABITAT

The difference in the number of unseen species was also strongly influenced by habitat type. The shoreline flora and forest flora are probably the most completely inventoried (shoreline = 2-9% unseen, forest = 4-13% unseen). However, the shoreline flora is likely the most species-poor (only 101 taxa, 25 alien) due to how extreme the environment is and how few taxa are adapted to the high amounts of salt and sun exposure in littoral environments (Atkinson & Sharpe, 2000). In particular, the alien species that are most frequently found in shoreline habitats are common weeds in urban hardscape environments – sidewalk cracks, parking lots, and rock walls [*Hordeum* sp, *Sagina* sp, *Rumex* sp, *Atriplex* sp; (Frazee et al., 2019)]. Future work could further evaluate the microhabitats of alien taxa that persist in urban environments to assess which species are most likely to persist in shoreline habitats in natural areas.

The forest flora comprised generally regionally common taxa found on the mainland (Hitchcock & Cronquist, 2018) and appears currently resistant to the widespread invasion of alien plants. However, while temperate forests are often considered invasion resistant, forests may just have longer time-lags between the introduction of alien species and invasion (Essl, Mang & Moser, 2012). Furthermore, the small proportion of alien species considered part of the forest flora also might be somewhat underestimated. Alien species that are primarily found in open habitats are present within open forests too – which are frequent habitat types within the archipelago and were once much more common (MacDougall, Beckwith & Maslovat, 2004; Bjorkman & Vellend, 2010; Dunwiddie et al., 2011; Arcese et al., 2018). Thus the invasion debt likely present in forest habitats may only become paid if open forest restoration becomes more frequent.

Wetland and open-habitat floras have more unseen species compared to shoreline forests but likely for different reasons. The wetland flora has the smallest number and proportion of alien species and the highest number of rare native species. Both facts are likely due to how limited this habitat type is across the archipelago and how spatially constrained they are to the largest islands. While some island wetland habitats are likely never to be at much risk from invasive species (such as bogs), the high invasion debt for other habitats, such as ponds, lakes, and freshwater wetlands, is more troubling. Wetland habitats, especially on the larger islands, are probably under-sampled compared to wetland habitats found on smaller islands due to the difficulty of surveying some of the freshwater and wetland habitats on large islands. However, the number of unseen species may be overestimated because there could simply be many singletons because freshwater and wetland habitats are the rarest habitats in the archipelago. It is unknown how such biogeographic patterns bias species estimates (Gotelli et al., 2009) and would be an interesting and useful research problem.

The invasion debt of open habitats has largely been paid, and alien species comprise most of the observed flora, and 18 to 26% of the alien flora remains to be seen.

The open coastal habitats found in the San Juan archipelago are very similar to the coastal grasslands found in Europe, one of the most significant sources of alien species (Kalusová et al., 2013). Native habitats that are similar to habitats from alien source floras are more likely to be invaded by those source habitat species (Rejmánek, Richardson & Pyšek, 2005; Richardson & Pyšek, 2006; Chytrý et al., 2008). In particular, disturbance-prone habitats similar to alien source habitats are especially suspectable to invasion (Kalusová et al., 2013). Not only are habitats similar between the archipelago and maritime Europe, but the microclimate of meadow habitats of the San Juan islands is very similar to summer-dry Mediterranean habitats, making them even more prone to invasion (Kalusová et al., 2013). Meadow habitats in the archipelago hold 83% (n = 78) of the alien species from the Mediterranean, and the most problematic invasive annual grasses (*Bromus*, *Vulpia,* and *Aira spp*) and annual forbs (*Hypochaeris glabra*) are all Mediterranean meadow and grassland species. Finally, when native habitats that match alien habitats are also hotspots of diversity, they can also become hotspots of invasion (Stadler et al., 2000; Seabloom et al., 2006; Kalusová et al., 2013).

The susceptibility of meadow habitats in the archipelago to invasion by alien species is particularly insidious because the coastal meadow habitats also have a disproportionate number of at-risk and rare species compared to other island habitats. Meadow habitats also have many disjunct species associated with dry meadow habitats east of the Cascades or California (Atkinson & Sharpe, 2000). Most of the regional species of conservation concern (14 of 22 taxa) are associated with meadow habitats, and the habitat itself is highly endangered (Bjorkman & Vellend, 2010; Dunwiddie & Bakker, 2011; Arcese et al., 2018). The archipelago's meadows were likely maintained into the modern period through indigenous management (Dunwiddie et al., 2011; Arcese et al., 2014; Turner, 2014; Dick et al., 2022), and current disturbance-based restoration efforts of burning and tree clearing are likely also facilitating alien species establishment.

ISLAND AREA AND HUMAN IMPACT

There is a small to modest difference in how alien species respond to increasing island area compared to native species. Only larger islands (>200 ha) have a strong positive relationship between island area and alien richness. However, it is difficult to disentangle how much of this increase is due to the greater degree of human settlement and visitation compared to island area alone. There is evidence that the dramatic increase could be due to increased human presence and not area per se. For example, Cypress Island (2227 ha) is a largely undeveloped island near Anacortes. It has nearly the same number of alien species ($n = 96$) as Sucia island (223 ha, 106 alien species), a popular State Park island for camping and visitation, which is 10x smaller in size. Another example is San Juan Island (14840 ha), which is only 3% smaller than Orcas Island (14258) but has 1.6x more alien species. This stark difference may be because San Juan gets 2.4 more visitors than Orcas Island, and most visitors visit the islands to hike trails and shorelines (Whittaker, Shelby & Shelby, 2018).

The influence of recreation on alien species introduction and establishment are well known (Wells, Lauenroth & Bradford, 2012; Marion et al., 2016) and is likely the primary driver of increased numbers of alien species on smaller islands that have recreation compared to larger islands without much visitation. The difference due to recreation is likely why human impact score ‘5’ likely had a smaller influence on alien species occurrence than score ‘6’ (Figure 1-7). Islands coded as ‘5’ were privately owned residential islands and are visited by far fewer people than even moderately visited State Park island. For example, Turn Island State Park is a popular 13.6ha forested island near Friday Harbor that has 62% more alien species (68) than the similarly sized, privately-owned forested Charles Island (13.3 ha, 42 species).

SPECIES CHARACTERISTICS AND ESTABLISHMENT

The importance of human impact in facilitating alien species occurrence is more troubling because residence time is the most important variable compared to life history in determining how frequent a species is throughout the archipelago. However, some life history traits may correlate to residence time, even though there was no strong collinearity between life history predictors. For example, long-dispersing annual forbs and grasses were the first to establish in the region compared to short-dispersing perennials (Appendix 2, Figures A2-1 to A2-5), and alien annual grasses are the most common commonly found taxa in the flora.

Besides residence time, invasiveness in other areas in the country and being native to the source region increased the frequency of alien species in the archipelago. However, it may be difficult to tease apart the influence of residence time from a species being an invasive ecosystem transformer because transformers are generally the first species to establish in the area (Appendix 2, figure A2-5). The fact that archaeophytes and neophytes were less frequent than alien species that are native in their home range is likely further evidence confirming that similar habitats across continents are capable of sharing many species when dispersal barriers are removed (Rejmánek, Richardson & Pyšek, 2005; Richardson & Pyšek, 2006; Kalusová et al., 2013).

A HOMOGENIZATION DEBT?

Residence time and human impact primarily drive the number of alien species found in the archipelago. There is likely a significant homogenization debt waiting to be paid in the next few human generations. In the future, islands with the greatest human impacts now could have nearly four times more species, and these species will cause both taxonomic and phylogenetic homogenization. The greatest rates of homogenization will be in meadow habitats that also have the most at-risk species.

Most of the recently introduced alien taxa are associated with the largest ferry-served islands. These taxa represent an establishment debt for the rest of the archipelago. Their overall impact will also depend upon how much area is available to invade in various island habitats (spread debt). Most of these recently introduced alien taxa, regardless of habitat, will likely establish, but the effect this will have on future homogenization rates will depend on the habitat. Shoreline and open habitats (meadows and open forests) will have the greatest homogenization rates, while forests and wetlands are the least likely to become dramatically homogenized in the future.

Because this study does not assess cover as well as incidence, the actual rates of homogenization in the future will likely be higher. While focusing on species presence is easier to do analytically and logistically, the dominance of a species in a habitat is incredibly important. If alien species become the primary common species, the realized homogenization will likely be much greater (Bühler & Roth, 2011), even if rare species persist in small microsites.

Forests and wetlands are not expected to become more homogenized in the future. Many alien species that invade both habitats are neophytes (Chytrý et al., 2008) and are not strong disperses across the islands regardless of residence time. However, I did not consider the introduction debt. There are likely many alien taxa found on the Washington State and British Columbia mainland that could persist in the islands but have not been detected in the region yet. Future work could use the modeling exercises performed in this study to evaluate how likely alien taxa found outside the archipelago (mainland, bioregion, continent, world) could establish within the archipelago. Thus, the homogenization debt predicted in this study should be considered a “minimum” estimate.

CONCLUSION

> This chapter proposed a framework for evaluating conservation needs in the future. I attempted to demonstrate how information-rich species lists and herbarium records are and how novel and informative patterns can emerge when paired with hypotheses and ecological theory. Despite being the basic information of conservation science, accurate lists of the number and distribution of species can be difficult and very time consuming to produce. However, such efforts are worth it. Given the increasing amount of ecological information about species found in published literature and available online in resources like herbaria and

species atlases, such lists can examine pressing questions important to conservation.

The San Juan archipelago is a region with one of the greatest proportions of alien taxa globally (Pyšek et al., 2020) and is also a hotspot of regional plant diversity. Many millions of people visit the archipelago every year from across the world and likely are the source of most of the recent introductions of new alien taxa. The climate and habitats of the archipelago promote high levels of regional native plant diversity and are also like the source regions of alien species from European and Mediterranean source habitats. Thus, habitats with the most imperiled species are also habitats that have the greatest invasive species pressure, similar to patterns found in California (Seabloom et al., 2006).

Without intervention, these imperiled habitats are likely to experience significant biotic homogenization. However, because the most imperiled habitats in the archipelago, meadows and open forests, are dependent upon disturbance, interventions are likely to facilitate continued alien species establishment (Chytrý et al., 2008; Kalusová et al., 2013). Further, these imperiled habitats are some of the most popular hiking and camping destinations in the region and are a vital component of the regional economy (Whittaker, Shelby & Shelby, 2018). Many millions of people visit the archipelago every year from across the world and likely are the source of most of the recent introductions of new alien taxa. Finding a solution to the conundrum of restoring these habitats, reducing alien species pressures, and managing recreation may represent a "wicked problem" (DeFries & Nagendra, 2017), with no straightforward or tractable management solution.

However, managing the seemingly disparate goals of nature conservation and human recreation is a well-known issue in park management (Anderson, Lime & Wang, 1998; Wright, 2003). Future work engaging in this discipline may be a fruitful next step.

CHAPTER 2 – ASSESSING FLORISTIC CHANGE ON SMALL ISLANDS IN THE SOUTHERN SAN JUAN ARCHIPELAGO

INTRODUCTION

THE HOMOGECENE?

Global commerce and its associated economic development across the earth is removing natural biogeographical barriers to species distributions and causing massive changes to ecosystems (Richardson & Pyšek, 2012). The removal of dispersal barriers and the related loss and change to natural habitats is causing floras across the world to lose their biogeographical uniqueness (Olden & Poff, 2003; La Sorte, McKinney & Pyšek, 2007; Yang et al., 2021), a process also known as biotic homogenization (McKinney & Lockwood, 1999). Due to the ubiquity of biotic homogenization across taxons, this current period of the Anthropocene is being dubbed the “Homogecene” (Rejmánek, 2002) or the “New Pangea” (McKinney, 2005).

While biotic homogenization is generally due to the combined effects of both extirpations and introductions (McKinney & Lockwood, 1999), there are varied pathways and patterns of extirpations and introductions that could lead to either biotic homogenization or biotic differentiation (Olden & Poff, 2003). Further, biotic homogenization or differentiation patterns can happen at several levels of biotic organization: taxonomic, phylogenetic, or functional (Olden et al., 2004). Thus, ecologists increasingly urge conservationists to look beyond species richness alone when measuring the impact of human disturbance and also incorporate metrics relating to the composition of species, their phylogenetic history, evolutionary uniqueness, and their trait diversity (Winter et al., 2009; Cadotte & Davies, 2010, 2016; Tucker et al., 2017; Hillebrand et al., 2018). For example, plant colonization generally outpaces plant extirpations on islands, and overall plant species richness has generally doubled (Sax & Gaines, 2008). Because many invasive and alien plant species that invade natural areas are from only a few plant families – primarily Poaceae and Fabaceae (Daehler, 1998), such species additions could cause floras to become simple and highly redundant not due to the loss of unique plant but the addition of many closely related and broadly distributed plants.

In this chapter, I examine four broad and inter-related questions.

1) Is there a directional change in plant community diversity across islands, and how much is due to invasive species compared to island area?
2) Are changes in community diversity due to the differential colonization and extirpation of alien and native species?
3) Are these changes leading to biotic homogenization?
4) Can the patterns found in questions 1-3 be detected in models of individual species persistence on islands?

ISLANDS AT RISK

The San Juan archipelago islands are one of the jewels of Washington’s plant biodiversity. Despite only accounting for 0.26% of Washington’s landmass, botanists can find 30% of Washington’s native plants within the archipelago. Within the archipelago, the hundreds of small islets are a particularly important component of the region’s biodiversity. For example, the small, dry, and windswept islets on the south end of Lopez

Island are home to unique, globally rare coastal meadows. These meadows have populations of globally rare species such as *Castilleja victoriae*, regionally rare species such as *Aphyllon californicum*, and *Ranunculus californicu*s, as well as unique disjunct populations of *Opuntia fragilis, Oxytropis campestris* var. *spicata,* and *Shepherdia canadensis.* There are few places in Washington where a botanist could encounter so many rare and unique species in such a small area.

Yet, while these islands are highly-protected as conservation lands by the State or Federal government, there are several reasons to believe they are at considerable risk of losing their botanical uniqueness. These risks include the synergistic impact of extended drought, the invasion of weedy species, the inherent demographic risks of small populations on small islands, an increase in browsing and disturbance due to the growth and spread of an introduced population of Canada geese, over abundant black-tailed deer, and the regional rarity of many native species that comprise these unique plant assemblages (Table 2-1).

Table 2-1. Summary of Overall demographic and ecological risk of the eight islands in the study. *Overall Risk* is the hypothesized risk of homogenization based upon three demographic risk factors and nine ecological risk factors. The *demographic risk* factors include: 1) the number of native species per island that are regionally rare in the San Juan Islands[2] 2) the number of "species of concern"[3] per island, and 3) the number of native species with small populations[4]. The nine *ecological risk* factors include the presence of nesting Canada geese, mule deer, and seven problematic invasive weeds. For the seven weeds, the recorded cover class value from 2005-2009 is provided. * islands that are comprised of a cluster of rocks.

		Island								
Risk Factor	**Component**	**Goose Island**	**Aleck Rock**	**Castle Island**	**Iceberg Island**	**Boulder Island**	**Flint Beach Island**	**Blind Island**	**Long* Island Rocks**	**Swirl* Rocks**
Overall Risk		High						Moderate		Low
Demographic	Disjunct	3	5	5	3	9	8	6	5	1
	1) Regionally rare spp	2		11	4	8	7	7	8	3
	2) WNAP spp of concern	1	1	2	2	1	2	2	2	1
	3) Native spp w/ small populations	27	8	16	12	8	7	9	7	4
Ecological[1]										
	Canada Geese	Nesting			Nesting	Nesting	Nesting			
	Mule Deer					Present	Present			
	Annual *Bromus* spp	C/F		F/LC	C	A / LC	NR	O	R/F	
	Vulpia spp			O	O	F	R	O		
	Hordeum murinum	C	NR		LC	O	R	O	C	A
	Rubus armeniacus			R						

[1] NR = present but abundance not recorded, R = rare, O = occasional, LC = locally common, F = frequent, C = common; [2] Defined as species that have been recorded on 3 or fewer islands; [3] As defined by the Washington Natural Areas Program; 4 Defined as species that were assigned an ordinal cover of "rare" in the 2005-09 surveys

ABIOTIC STRESSORS

The small islets and rocks on the south end of Lopez are some of the driest and most exposed islands in the archipelago. The average rainfall during the growing season (March – June) is about half an inch less (0.50”) than the rest of the archipelago (PRISM Climate Group). In addition to low rainfall, most islands are dominated by southerly aspects and exposed to the high winds and salt spray from the Strait of Juan de Fuca and Rosario Strait (Figure 2-1).

Figure 2-1. The dry southern face of Boulder Island in early June.

In combination with the harsh conditions on these islands, growing season precipitation has been consecutively below average during the past five of the last ten years, and rainfall ranged from 10% (2018) to 43% (2015) below average (climatetoolbox.org).

The combination of naturally harsh island conditions and repeated summer drought has likely caused considerable stress to most plant species growing on these islands. For example, rain is important for moving salt through soil (Mulder et al., 2011), and extended periods of drought during the growing season may exacerbate salt stress. Further, many small islands are rocky habitats that amplify solar radiation and likely multiply the stress of water-limitation by increasing temperature and evapotranspiration (Atkinson & Sharpe, 2000). Since water scarcity also increases the likelihood of competitive interactions within and among plant species (Kijne, 2006; Tlidi et al., 2020), considerable population reductions and extirpations have likely occurred since initial island surveys in 2005 – 2009.

INVASIVE SPECIES STRESSORS

Invasive alien species can pose significant threats to natural plant communities, even in protected areas with little human impact (Foxcroft et al., 2017). Seabloom et al. (2006) found that invasive and weedy alien species established in natural areas well beyond areas of intense human settlement disproportionally impact areas with high densities of imperiled species.

Several invasive exotic plant species initially detected on these islands have likely increased the risk of biotic homogenization during the past decade. First, drought-adapted invasive annual grasses have likely benefited from the wet winters and dry, droughty summers of the past few years (Abatzoglou & Kolden, 2011). The invasive annual grasses found in the San Juans *Vulpia* (*V.* myuros, *V. bromoides*), *Bromus* (*B. hordeacus, B. sterilis, B. tectorum, B. rigidus*) are likely more competitive than associated species because they are winter annuals that typically complete their life cycle by late spring (for an example with *B. tectorum*, see Garbowski et al., 2021). These annual grasses' different phenology makes them less likely to be impacted by extended summer droughts than native taxa, which typically reproduce and complete their life cycles later in the growing season.

Another potential risk of invasive annual grasses is through altering fire regimes by increasing fire intervals and converting natural areas to near-permanent annual grasslands (D'Antonio & Vitousek, 1992; Balch et al., 2013; Fusco et al., 2019). An increased risk of unplanned fire could lead to species extinctions, especially for plant populations that are already small, not adapted to frequent fire disturbance, or if the fire intensity is greater than typically experienced by a species (Bloom et al., 2018). The invasive shrub, *Rubus bifrons*, is another species that could negatively impact native plant diversity on these islands. At nearby American Camp on San Juan Island, *R. bifrons* has converted significant portions of coastal meadow and bluff habitats into dense shrublands where few other species can persist (Martin & Martin 2021).

Since many native plant species persist in small soil pockets on rocky islets that may only span a few square meters per island, even one established shrub could eliminate entire meadow habitats on some of the smallest islands. *R. bifrons* establishment could also hasten and facilitate the rapid conversion of meadow habitats to shrub thickets when other genera like *Sympocarpus* and *Rosa* are present.

A second threat to the native flora of these islands originated with the introduction of two non-native subspecies of Canada geese to Victoria, BC, and the San Juans in the 1980s (Figure 2-2). These have spread widely throughout the San Juan and Gulf Islands

Figure 2-2. Left Panel: a rocky outcrop heavily impacted by Canada geese (Branta canadensis) loafing, Male geese stand on prominent locations while guarding nest sites. These sites largely devoid of plant life except invasive annual grass, weedy annual forbs and dominated by geese feces. Right Panel: A typical disturbance around a goose nest. Note the sparse vegetation, upturned soil and abundant feces.

and now nest on many smaller islands where they are not disturbed by human visitors and many predators. Unlike the native Canada geese, that were largely migratory and relatively uncommon, the year-round presence of these resident birds is rapidly changing the flora of islands where they nest in abundance through herbivory, nutrient and alien species introductions, and nest building (Bennett et al., 2011; Best & Arcese, 2009; Dawe & Stewart, 2010; Isaac-Renton et al., 2010).

The threat of invasive species amplifies the risks of island extirpations due to small island size (Wilcove et al., 1998), prone to extinction and colonization events (MacArthur & Wilson, 1967). Global and regional rarity compounds the risks of small populations of plants living on small islands. For example, in Washington, the globally rare species *Castilleja victoriae* only grows in an area of a few tens of square meters on a single island in the San Juans. Several other species have regionally disjunct distributions (*Oxytropsis campestris* var. *spicata*, *Ranunculus californicus*). They are only known from a few localities in the San Juans with small to medium-sized populations. Finally, other native taxa have larger regional distributions but are only present as a single or a few individuals, making them the most likely to have become extirpated over the past decade. Some of these species exhibit traits (low stature, lack of clonal growth, absence of substantial storage organs like bulbs or corms) that may make them more susceptible to population declines or extinction (Saar et al., 2012).

METHODS

LOCATION

Seven islands (Boulder, Iceberg, Flint Beach, Goose, Castle, and Blind Island, Blind Island South) and two island clusters (Swirl Rocks and Long Island Rocks) were revisited that were originally surveyed between 2005 and 2009 by Peter Dunwiddie, David Giblin, and others (Figure 2-3).

Figure 2-3. Map of surveyed Islands along the southern shores of Lopez Island, Washington USA.

FIELD SAMPLING

The field sampling methodology follows the protocol used on previous island surveys (Dunwiddie 2018). During the original surveys, botanists visited an island up to three times in early spring, summer and fall and looked for plants until they thoroughly examined all habitat types, and the rate of species detection dramatically slowed. Inaccessible habitats such as cliff faces were surveyed with binoculars by boat. The field protocol involves multiple trained botanists identifying all vascular plant species present on an island in the field or collecting samples of unknown plants to identify later. All identified species were given an ordinal cover class value based on a six-point range from rare to abundant.

In addition to identifying vascular plant species, all Canada goose nests were tallied, and each island was given a three-point ordinal assessment of goose impact based on the number of nests found, how much of the island they were found across, and what proportion of the island was impacted by forage and loafing behavior.

ANALYSIS

I examined five questions to determine if native plant species are declining and if these declines lead to biotic homogenization.

5) Do four components of plant community diversity (nativity, biogeographically-weighted evolutionary distinctiveness, evolutionary importance, and functional richness) within and across the sampled islands change between the initial surveys and 2021?
6) Do native species become extirpated from islands more than alien species, and are they balanced by colonization?
7) How do area, Canada geese, deer herbivory, and invasive annual grass influence rates of community change?
8) Do the changes in species composition lead to biotic homogenization across the sample islands?
9) How does island area, the impact of invasive species, plant traits, plant nativity, and phylogenetic relatedness influence the probability that a species will go extinct from an island?

To first visualize changes in community composition (based on the ordinal cover of species and presence/absence) through time, non-metric multidimensional scaling (NMDS) ordination was used (McCune, Grace & Urban, 2002). Next, differences in composition were visualized by successional arrows to display the direction and magnitude of change. Finally, ordinations were performed using the *vegan* package (Oksanen et al., 2013).

The most basic aspect of biotic homogenization is the loss of native species and their replacement by alien species. Thus, the proportion of the total flora comprised of native species (*nativity*) was calculated for each island. A more nuanced measure of biotic homogenization evaluates the phylogenetic diversity of a flora. To assess the phylogenetic homogenization of an island's flora evolutionary distinctiveness(Faith & Baker, 2006; Redding & Mooers, 2006; Cadotte & Davies, 2010) and evolutionary importance were calculated. Evolutionary distinctiveness measures the number of ancestral lineage branch splits within a given taxon's history – the fewer splits, the more distinct (Redding & Mooers, 2006). However, since a key aspect of biotic homogenization is the replacement of communities by widespread generalists, native species' evolutionary distinctiveness values (Native BED) were weighted by their regional incidence across 156 islands (Dunwiddie 2018, Chapter One).

To generate a phylogenetic tree, the R package *VPhylomaker* was used (Jin & Qian, 2019) based upon the backbone phylogenetic tree of seed plants created by Smith and Brown (2018). Before calculation, the list of all species found within the San Juan archipelago (Chapter One) was first prepared to be consilient with the Smith and Brown tree. First, all infra-taxa were lumped to the species level, and then species names were converted to the accepted name found in The Plant List (www.theplantlist.org). Once the phylogenetic tree of the San Juan archipelago flora was created, the **evol.distinct()** command in the *picante* R package was used to calculate the evolutionary distinctiveness of each species based upon the fair proportions algorithm (Isaac et al., 2007).

Because the loss of phylogenetic diversity could also lead to the loss of functional diversity (Schuldt et al., 2014; Arnan, Cerdá & Retana, 2017), I also examined the change in functional richness based on categorical traits related to dispersal (long or short disperser), life form [forb, grass, shrub, tree, or ancient plant (conifer, fern, lycophyte)] and persistence traits (clonality, annual/perennial, presence of storage organs). Functional traits were compiled from field experience or published literature (Hitchcock & Cronquist, 2018, www.try-db.org). Seed dispersal traits were lumped into either short or long dispersers following methods in Bennett et al. (2013). Finally, to determine if changes in nativity, evolutionary distinctiveness, importance, and functional richness were due to proportional losses in native species, I compared the rates of island extirpations relative to colonizations for both native and alien plants. Paired t-tests using Bayesian inference (Bayes Factors) were performed to assess if the four community components changed between the initial 2005-2009 surveys and 2021 using the **ggwithinstats()** function in the *ggstatsplot* package (Patil, 2021).

Regression analysis using Bayesian inference was used to determine how much of the island-specific change in community composition was related to island area, deer and goose herbivory, and invasive alien grass on the amount of island-specific change between periods. Island areas were determined using aerial imagery to measure the maximum area capable of supporting vascular plants. If islands were small enough, the circumference was mapped using handheld GPS. During visits, each island was given an ordinal goose-deer impact score (DG) based on four values; no impact (0), low impact (1), moderate impact (2), and large impact (3). Impact assessments were based on whether both deer and geese sign was present on an island and how localized the impacts were. Low impact islands had either a highly localized goose presence (one or fewer nests, with limited evidence of loafing damage) or limited deer browse. Moderately impacted islands had at least several goose nests and evidence of several patches of localized goose damage. Moderately impacted islands also had evidence of several deer (multiple deer pellet piles, tracks of multiple sizes, extensively browsed shrubs, and browsed desired forbs *Camassia, Fritillaria*). Large impact islands had widespread evidence of goose nesting and loafing, with many goose nests (> 5) spread across the island with extensive evidence of foraging (turned up soil) and loafing (deep piles of geese feces). The ordinal cover class scores for all annual grasses present were summed to determine invasive annual grass cover. Once summed, the values were normalized by the island with the greatest number and cover of annual grass to create a normalized index score of annual grass cover. Thus, values range from 0 (no annual grass) to 1 (the most annual grass). Finally, because the sample size was too small to model the interaction of grass and the deer-goose impact score, a synergistic impact score was created to determine the relative effect of when both deer or goose impact and annual grass were present. The synergistic impact score (Impact) was calculated by multiplying the IAG index by the DG score. Again, this resulting value was normalized by the island with the greatest synergistic impact value to get a normalized index of 0 (no IAG or deer or geese) and 1 (the most IAG and largest deer and goose impact).

To model the impact of island area and invasive species on the five components of community change (nativity, native evolutionary distinctiveness, evolutionary importance, functional richness, decline rate), I used a multi-model inference approach (Anderson & Burnham, 2004; Millington & Perry, 2011). For each component of community change, I assessed the influence of Area, IAG, DG, and Impact alone, Area with IAG, DG, and Impact, and IAG and DG together for eight candidate regression models total. Regression models were run using Bayesian inference using the package *brms* (Bürkner, 2017). Response and predictor variables were centered and standardized before running each model. Each model was run with eight chains, each chain with 10,000 runs (5,000 warm-up), thinned to 10. Prior predictive sampling was used to determine reasonable, non-flat priors. The intercept was given a prior of mean = 0, standard deviation = 0.5, and parameters a prior probability of mean of – and standard deviation of 1. All models were assessed for chain convergence and $\hat{r}$ <1.03. To compare model performance, the LOO information criterion (LOOIC) was used (Vehtari et al., 2021), and model weights were assessed using the model-stacking approach (Yao et al., 2018). Briefly, this approach weights models as more plausible that have the lowest posterior predictive error. Model performance was calculated using the **compare_performance** function in the *performance* R package (Lüdecke et al., 2021).

To determine the relative importance of each model predictor, the sum of model weights of each model with the parameter was calculated, and parameters with greater weight are more likely to be important. To display model predictions, values from the top model were used to display the mean and 90% credible intervals of predictions. It is important to note that credible intervals are not measures of estimation error around the mean but the probability distribution of the outcome across each level in the respective parameter (McElreath, 2020).

To determine if the changes in community composition between islands resulted in directional change toward homogenization, I assessed changes in the nestedness component of phylogenetic, trait, and taxonomic (based on the ordinal cover) ß-diversity (Baselga, 2010, 2017) using the *betapart* R package (Baselga & Orme, 2012). For each island, the distribution of pairwise nestedness was displayed for each time period, and if the distribution of differences between island pairs was greater than zero, that was evidence for homogenization, while differences less than zero were evidence of divergence.

Finally, to assess if the drivers of community change could be detected in changes in species-level island extirpations, hierarchical logistic mixed-models were used to assess the influence of area, invasive species impact (IAG, DG, Impact), and nativity (native or alien), and plant traits (persistence traits) with phylogenetic relatedness and island as random effects. Like the community change regression models, the same analytical process for multi-model selection was used to compare 31 candidate models assessing various combinations of plant traits, area, and invasive species impact. All analysis was performed in R version 4.0.4. (R Core Team, 2021).

RESULTS

Between the initial surveys and 2021, the degree and direction of community change were mixed across the surveyed islands (Figure 2-4). The greatest change occurred on the smallest rocky islands (Blind South, Swirl East, and West, Long Island Rock 3) compared to the larger meadow-dominated islands. However, the magnitude of change is likely due to the small island floras of the rocky islands (~ < 10 species).

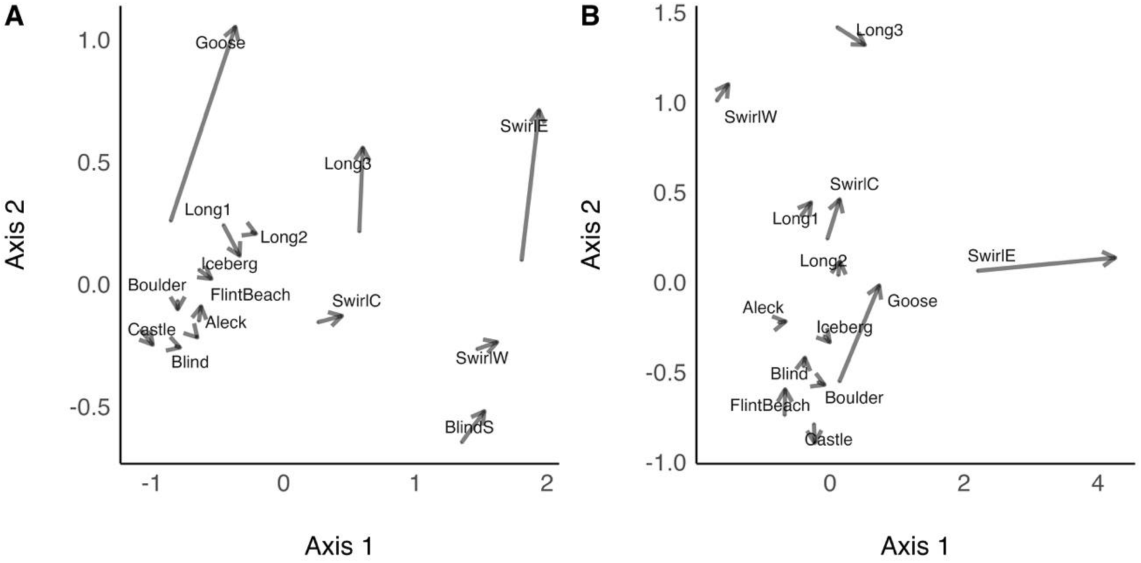


Figure 2-4. NMDS ordination displaying change in plant communities based on species presences and absences (A) and species cover (B) for thirteen islands in the southern San Juan archipelago. The size of points denotes the degree of impact of invasive annual grasses, deer, and geese for each island and visit. Lengths of arrows denote the degree of change in plant composition. (BlindS island did not have cover taken on initial surveys, so it is not in panel B).

QUESTION ONE: DO FOUR COMPONENTS OF PLANT COMMUNITY DIVERSITY WITHIN AND ACROSS THE SAMPLED ISLANDS CHANGE BETWEEN THE INITIAL SURVEYS AND 2021?

Overall, there is weakly-supported evidence (BF values ~ >1) for mean declines in nativity and native biogeographically-weighted evolutionary distinctiveness across all thirteen islands (Table 2-2). There was insufficient evidence suggesting functional richness or evolutionary importance is declining. Still, given that moderately sized declines are possible (within the 90% credible interval), it is likely to occur across some combination of islands (Figure 2-5).

However, declines were more notable in the median values of each community change component. Evolutionary importance had the greatest median decline (-35.6%) from island floras capturing 28.5% of the regional evolutionary history to 18.3%. Native BED had the second greatest median decline (-28.5%) from 30.0% of weighted evolutionary history to 21.5%. The median decline in functional richness was a moderate loss of 2 functional groups (-14.3% change) from 17.5 to 15 groups. Finally, nativity had the smallest median decline (-5.8%) from 76.3% to 71.9%.

Table 2-2. Results of t-tests comparing four community change components between two time periods fit with Bayesian inference. Log(BF) is the log of the Bayes Factor (roughly analogous to a t-statistic). Difference is the mean and 90% highest density interval of the absolute difference between periods for each component. % % difference is the mean percent difference between the two time periods in each component value. *Nativity was rerun, excluding three outliers comprised of the smallest rocks that are primarily shoreline flora and have few alien species present to begin with.

Component	**log(BF)**	**Difference**	**% Difference**
Nativity	1.07	-0.01(-0.05, 0.03)	-2.6
Nativity*	0.51	-0.04(-0.08, -0.004)	-6.85
Functional Richness	0.33	-0.77(-1.72, 0.18)	-6.25
Evolutionary Importance	0.4	-1.82(-4.08, 0.52)	8.46
Native BED	1.36	-5.35(-8.92, -1.57)	-19.44

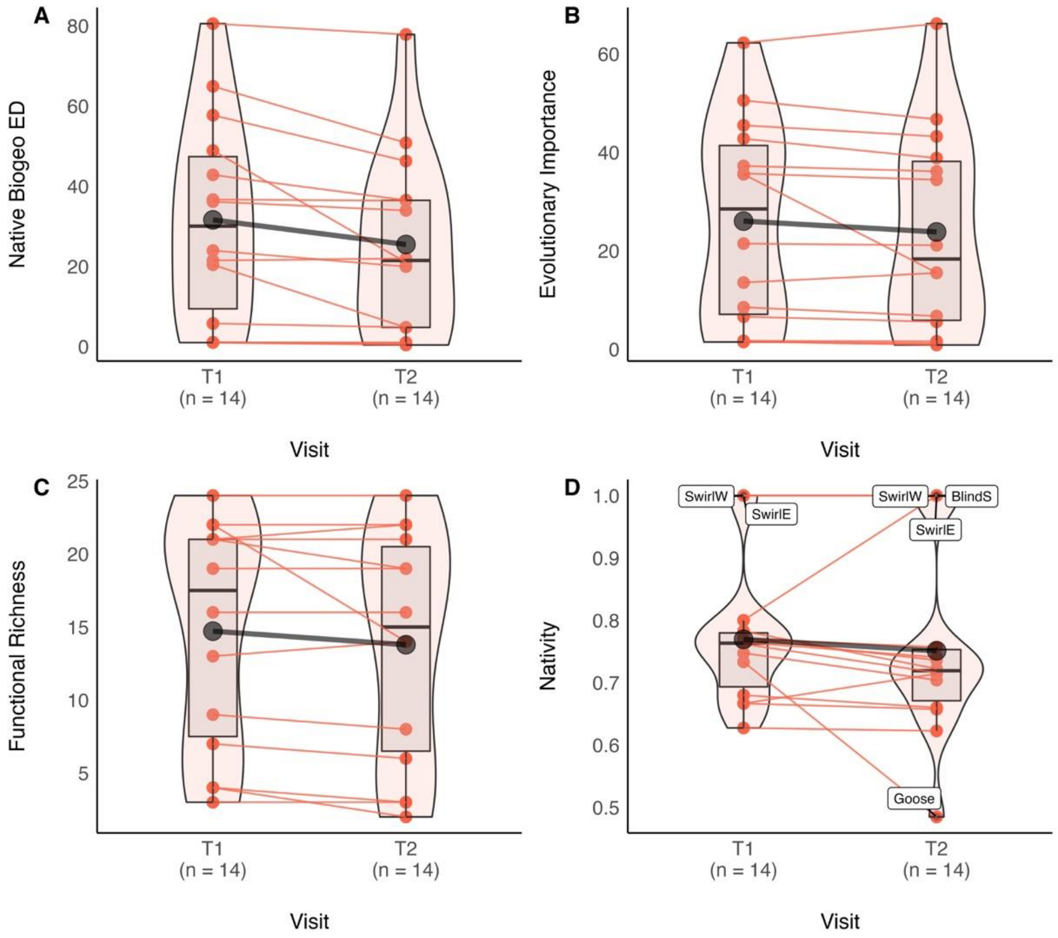


Figure 2-5. Overall change in four components of community composition across 13 islands in the southern San Juan archipelago. A) is the change in the biogeographically-weighted evolutionary distinctiveness of native plants on each island, B) is the change in the total evolutionary importance of the entire plant community of each island, C) Is the island-specific change in functional richness, D) is the change in nativity (the proportion of native plants on each island). Red points and lines denote changes through time in individual islands. Black points and lines denote the change in mean values of each respective community composition component. Labeled islands denote outliers. Box plots denote the minimum, maximum values (black horizontal lines), interquartile range (grey box), and median (thick horizontal line) for each component and period). Violin plots denote the density and distribution of values.

QUESTION TWO: DO MORE NATIVE SPECIES BECOME EXTIRPATED FROM ISLANDS RATE THAN ALIEN SPECIES, AND ARE THEY BALANCED BY COLONIZATION?

Native plants are much more likely to become extirpated compared to alien plants. The overall median change in richness was 3.9 times greater for native plants than alien plants. The median richness of native species declined 21.4% from 42 to 33 species per island, compared to alien species, which only declined 5.6% from 18 to 17 species.

Across all islands, native plants became extirpated at a rate of 2.5 native plants to every one alien plant lost on an island. Further, alien plants were more likely to colonize an island than native plants at an overall rate of 1.6 alien plants for every one native plant (Table 2-3).

Of the meadow islands, Goose Island, which completely burned in a wildfire in June 2015, showed the greatest change in composition, which lost 54 species total, and three native plants became extirpated for every one alien plant, while five alien plants colonized for every one native plant (Table 2-3).

Table 2-3. The change in plant richness and the number of colonizations and extirpations for alien and native plants across 14 islands in the southern San Juan Island archipelago. * islands primarily comprised of shoreline habitat and vegetation.

	Initial Survey		**2021**		**Colonized**			**Extirpated**		
Island	**Alien**	**Native**	**Alien**	**Native**	**Alien**	**Native**	**Total**	**Alien**	**Native**	**Total**
Aleck Rock	20	66	21	60	3	2	5	2	8	10
Blind Island	17	58	18	54	2	1	3		5	5
Blind Island South*	1	4		4				1		1
Boulder Island	24	71	29	69	9	3	12	3	5	8
Castle Island	27	92	33	93	10	4	14	4	3	7
Flint Beach Island	21	64	23	60	4	3	7	2	7	9
Goose Island	21	55	17	16	10	2	12	13	41	54
Iceberg Island	25	51	25	48	2	5	7	2	8	10
Long Island Rock 1	19	32	20	33	4	4	8	3	3	6
Long Island Rock 2	16	34	17	33	2	2	4	1	1	2
Long Island Rock 3*	7	12	4	10	1	3	4	4	5	9
Swirl Rock Central*	5	18	5	13	2		2	2	5	7
Swirl Rock East*		4		3		1	1		2	2
Swirl Rock West*		5		4					1	1

Of the 21 rare species found across the study area, nine (42%) decreased in frequency across the 14 sampled islands (Table 2-4). Three species became extirpated across the islands; the disjunct shrub *Shepherdia canadensis*, the regionally rare perennial grass *Hordeum jubatum*, and the perennial shoreline forb *Sarcocornia pacifica*. The combined declines and extirpations were more frequent for disjunct plants (38%) than the regionally rare plants (20%). The islands with the greatest community change also had the largest decreases in rare species. Swirl Rock lost all its rare species, Goose Island lost 75% of the rare species flora, and Iceberg Island lost half of its rare species flora.

Table 2-4. change in the incidence of rare species across 14 islands along Southern Lopez Island between two survey periods. * species listed as of special concern by the Washington Natural Heritage Program.

Rarity Type	**Taxon**	**2005-2009**	**2021**
Disjunct			
	Aphyllon californicum ssp. californicum	8	5
	Artemisia campestris var. scouleriana	3	3
	Hornungia procumbens	5	3
	*Lepidium oxycarpum**	1	1
	Lupinus microcarpus var. microcarpus	3	2
	Myosurus minimus	2	2
	Olsynium douglasii	1	1
	Opuntia fragilis	7	5
	*Oxytropis campestris var. spicata**	2	1
	*Ranunculus californicus**[1]	6	5
	Sabulina macra	4	3
	Shepherdia canadensis	3	0
	Triteleia grandiflora var. howellii	1	1
Regionally Rare			
	Arctostaphylos media	1	1
	Carex pansa	1	1
	*Castilleja victoriae**	1	1
	Epilobium glandulosum	1	1
	Hordeum jubatum	1	0
	Sarcocornia pacifica	1	0
	Silene scouleri	2	2
	Vaccinium ovatum	1	1

[1] Incidence records also include hybrids with *Ranunculus occidentalis*

HOW DO AREA, CANADA GEESE, DEER HERBIVORY, AND INVASIVE ANNUAL GRASS INFLUENCE RATES OF COMMUNITY CHANGE?

The synergistic impact of invasive annual grasses (IAG) and deer and geese is the strongest predictor of decline across all five community change components compared to either factor individually (Table 2-5). Among the five community change components, the greater the synergistic impact of geese, deer, and IAG, the larger the decline across all four plant community components (Figure 2-6). The relative importance of synergistic impact compared to area suggests that the synergistic influence of invasive species is a more important predictor of species loss than what would be expected due to the expected losses of species on smaller islands. Though, there is some evidence that area is a potentially important predictor of changes in Native BED and the rate of native species losses. There is also evidence that IAG cover alone is important in explaining the loss of nativity.

Table 2-5 Model importance values for four model parameters explaining five community change components. Importance values are the sum of model weights provided in Appendix B, Table B-1 for each model with the parameter present within.

Factor	**Evolutionary Importance**	**Native BED**	**Functional Richness**	**Nativity**	**Decline Rate**
Area	0.080	0.242	0.010	<0.001	0.253
IAG	0.001	<0.001	<0.001	0.390	0.001
DG	<0.001	<0.001	<0.001	0.013	<0.001
Impact	0.918	0.758	0.900	0.610	0.746

Compared to the four islands with no synergistic impact (Castle, Long Island Rock 1, Blind South, Swirl East, and West), Goose Island (the most impacted island; furthest right point in each panel in Figure 2-6) had 1.02 times greater loss in evolutionary importance, 94.6% greater loss in Native BED, 1.12 times greater reduction in nativity, 92.5% greater loss in functional richness and a 96.6% higher decline rate in native species.

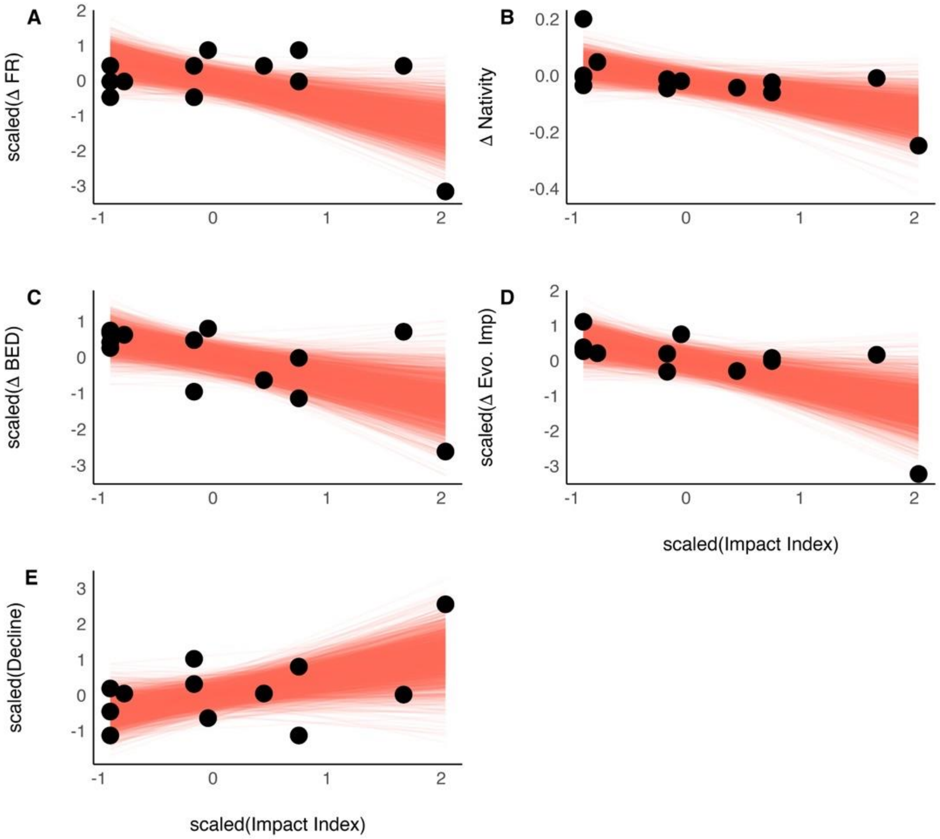


Figure 2-6. Change in five components of community structure within 13 islands in the southern San Juan archipelago. Points represent change values between initial surveys in 2005-2009 and 2021. A) Is the island-specific change in functional richness, B) is the change in nativity (the proportion of native plants on each island), C) is the change in the biogeographically-weighted evolutionary distinctiveness of native plants on each island, D) is the change in the total evolutionary importance of the entire plant community of each island, and E) is the rate of native species decline measured as the ratio of species extirpations to colonizations. Lines represent 2000 draws of the posterior distribution of each model of change. Areas of denser lines indicate more probable fits.

DO THE CHANGES IN SPECIES COMPOSITION LEAD TO BIOTIC HOMOGENIZATION ACROSS THE SAMPLE ISLANDS?

There are no strong directional changes in the mean nestedness component of ß-diversity across phylogeny (mean = -0.48%, sd = 12.41%), traits (mean = -2.99%, sd = 39.37%) or plant cover (mean = -0.88%, sd = 31.24%). Island pairs were as likely to become more related as they were to diverge (Figure 2-7).

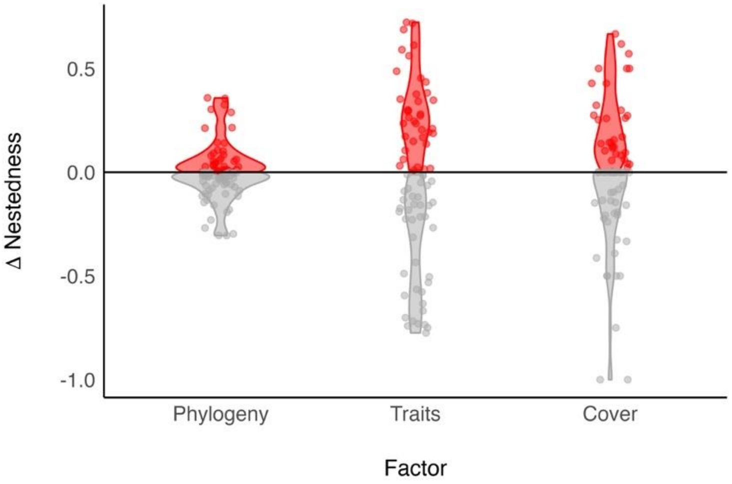


Figure 2-7. The change in plant community nestedness between island pairs (points) among 13 islands between initial surveys in 2005-2009 and 2021. Phylogeny represents the change in the pairwise nestedness component of phylogenetic beta-diversity between island pairs based on their Jaccard similarity. Cover and Traits represent the change in the pairwise balance component of abundance weighted bray Curtis similarity between island pairs. Island pairs are considered homogenized if the nestedness values increase with time.

HOW DOES ISLAND AREA, THE IMPACT OF INVASIVE SPECIES, PLANT TRAITS, PLANT NATIVITY, AND PHYLOGENETIC RELATEDNESS INFLUENCE THE PROBABILITY THAT A SPECIES WILL GO EXTINCT FROM AN ISLAND?

When predicting the individual probability that a species will become extirpated on an island, species-specific traits are generally more important than either area or the synergistic impact of invasive alien grasses, deer, and geese (Table 2-6, Figure 2-8). Further, across all predictors, their interaction with species nativity is more important than a given isolated predictor except for incidence, which could be equally informative alone or interacting with nativity.

Table 2-6. Importance of five model parameters predicting species extirpation. Overall is the sum of model weights in Appendix B Table B-2 for each model with the parameter present. Interaction w/Nativity is the sum of model weights for each model where the parameter is interacting with nativity. Additive is the sum of model weights for each model the parameter is present in isolation.

Factor	**Overall**	**Interaction w/Nativity**	**Additive**
Cover	0.700	0.477	0.223
Incidence	0.648	0.316	0.33
Persistence	0.626	0.382	0.244
Area	0.422	0.308	0.114
Impact	0.259	0.259	0

Species in the rare ordinal cover class are the most likely to become extirpated. On average, rare native species are 12.9% more likely than rare alien species to become extirpated, though there is significant variability (LCL diff = 19%, UCL diff = 5.5%; Figure 2-6, panel A). Though, once species increase in cover, alien plants are slightly more likely to become extirpated. Regionally rare species are also more likely to become extirpated, and regardless of regional incidence, native plants are slightly more likely to become extirpated than alien plants (Figure 2-6, panel B).

Native species without persistence traits are 12.9% more likely to become extirpated on average than alien non-persisters (LCL diff. = 19%, UCL diff. = 5.6%), and 16.4 more likely to become extirpated compared to native persisters (LCL diff. = 18%, UCL diff. = 10%). There is no significant difference between persisters and non-persisters among alien plants (mean diff. = 5.3) or native and alien persisters (mean diff. = 1.7%; Figure 2-6, panel C).

Finally, island area does not significantly impact the probability that an alien plant will become extirpated but has a small influence on native plants, which are more likely to become extirpated on small islands than on larger ones (Figure 2-6, panel D).

There is weak evidence that impact is an informative predictor compared to island area or life history alone. The potential importance of impact is only in interaction with nativity. There was one model that had some support (weighted as the 4th most likely; ~Impact*Nativity+Inc, *w =0.109;* Appendix3, Table A3-2), and there is some evidence that native species are more likely to become extirpated with increasing impact compared to alien species (Appendix 3, Figure A3-1).

DISCUSSION

“We cannot discuss the ecology of islands without making a few disparaging comments on goats.” – Koopowitz & Kaye, 1990

While Koopowitz and Kaye were referring to the dramatic effects of introduced goats on oceanic islands in the quote above, the same sentiment is not difficult to have towards introduced Canada geese and overabundant black-tailed deer. Despite the extensive legal protections designed to conserve the islands and isolation from direct human impacts, the small islands along the southern end of Lopez island have become more degraded since the initial floristic inventories 12 to 16 years ago. During that time, nesting Canada geese have increased in their number and extent across the islands. Such increases have likely ratcheted the cumulative impacts of deer herbivory and other natural island stressors on vascular plants such as nesting gulls and cormorants.

While there was some evidence of community-level declines across all four diversity components (nativity, Native BED, evolutionary importance, and functional richness), declines were generally small for nativity (average 5% loss in nativity) and functional richness (average loss of 2.5 functional groups), the greatest loss was detected in the evolutionary importance and distinctiveness (Native BED) of each island. While the combined losses of native plants and additions of alien plants resulted in small to modest reductions in evolutionary importance in 11 of the 14 islands (mean loss = 1.6%), Goose Island lost 20% of its evolutionary importance. Within native species, the loss of regionally rare species caused evolutionary distinctiveness to decrease across all but two islands by 7.2 million years, with Goose Island losing the equivalence of 27.9 million years of evolutionary history.

The patterns of community-level change were primarily driven by the disproportionate loss of native plants relative to alien plants. While native and alien plants became extirpated across all islands, nearly three times more native plants became extirpated. Further, native species colonized islands less often than alien species. Due to alien plants having an island-specific survival and colonization advantage, the sampled islands are slowly losing their nativity. The loss of nativity and rate of native species decline is likely due to the synergistic impact of Canada geese, deer herbivory, and invasive annual grass. There was moderate to strong evidence that this synergistic impact had a stronger effect than island size or geese, deer, or annual grass alone.

While there was strong to moderate evidence that individual islands are becoming homogenized through the loss of native plants and gaining more alien plants, these changes are not leading to directional community change towards biotic homogenization across and between islands. The lack of inter-island homogenization is likely because the identity of extirpated and colonizing plants is not consistent across islands, and 35% of the flora did not change in frequency across the islands (Appendix 3, Table A3-3). However, two invasive annual grasses (*Bromus sterilis* and *Vulpia myuros*) were the most likely to colonize new islands, though invasive annual grasses were already present on most islands during the initial surveys.

Currently, evidence suggests regionally rare species, which are also rare on individual islands, and do not have a strong suite of persistence traits (woody, storage organs such as bulbs, corms, deep taproots) are more likely to become extirpated, and this likelihood of extirpation is greater for native plants compared to alien plants. Despite the clear evidence of synergistic invasive species impact on community-level change, modeling exercises did not show strong evidence for synergistic impacts as a driver of the extirpation rates of individual taxa compared to knowing the regional incidence, cover, and area of an island. However, there was evidence that synergistic impacts could be a detectable component of species extirpations. At the greatest levels of synergistic impact, native species are predicted to have a 10% greater chance of becoming extirpated (68.7%) compared to alien species (58.3%), though the actual effect on species-level extirpation was highly variable (LCL difference 9.8%, UCL difference = 3.5%; Appendix 3, Figure A3-1). So, while such effects of synergistic impacts are small to modest, the impacts likely add up to meaningful differences when applied across the entire flora of an island and group of islands.

THE CHALLENGE OF SCALE

Some of the difficulty in detecting species-level invasive species impacts is likely due to the broadness of the data collected. While many species did not become extirpated from islands with synergistic impacts, scale-dependent and obvious impacts could be seen visually during visits and captured with photographs (Figure 2-8). A quadrat-based sampling approach within an island comparing the most impacted areas with the least would likely have the power to quantitatively detect change where simple presence-absence could not. These difficult-to-quantify impacts include extensive soil turnover from geese, which forage for rhizomes and roots. Geese can also add nutrients to thin maritime meadow soils through their feces (Figure 2-9). Such additions likely benefit annual competitive species such as grasses compared to native species (Best, 2008; Best & Arcese, 2009). The effects of deer herbivory are well documented in the gulf islands, where they can lead to the loss and significant decline in cover of their preferred forage. In particular, the continued loss of flowering heads and associated seed production will likely lead to a loss of non-clonal and short-lived species in time.

Figure 2-8. Two examples of difficult to capture impacts of deer and geese. In the left image, vegetation has been extensively clipped, and flowers are short-stemmed from extensive deer browse. In addition, the ground has been turned up from goose foraging for plant rhizomes and roots. In the image on the right, geese have clipped and foraged most plant species except those they do not eat, like Dodecatheon pulchellum (center of image). The image on the right was taken in May, and during repeated visits in June, all the flowering heads had been eaten off by deer.

The extensive foraging of geese can also lead to "goose barrens," where vegetation is sparse, and the flora comprises native species the geese do not eat, such as *Sanicula crassicaulis, Toxicoscordion venenosum*, and *Camassia leichtlinii* (Figure 2-9). These barrens often occur in specific habitats where "rock gardens" are present; island meadow microhabitats with rocky outcrops and small-scale soil deposits that are often highly diverse on small scales, especially native annuals such as *Plectritis*, *Collinsia*, and *Trifolium*. Such missing taxa are often still present on a given island in unreachable microhabitats but are no longer significant components of overall flora. Further, such unreachable microhabitats (such as cliff faces and inaccessible rock cracks) tend to have lower protectivity and more risk from other environmental impacts such as winter storm surges. For example, no geese were recorded on Aleck rock during the initial 2005-2009 surveys, but in 2021, at least 17 nests were found filled with 62 eggs total. As a result, we found extensive damage to the coastal meadow community (Figure 2-9 second image).

Figure 2-9. Left image: an example of a 'rock garden' within a maritime meadow not yet impacted by geese. Right image: a rock garden impacted by geese. Such "goose barrens" have been altered from foraging and what remains are species geese do not eat (such as Camassia leichtlini).

THE PARABLE OF GOOSE ISLAND

Finally, two islands in particular – Goose Island and Swirl Rock – demonstrate the concept of the extinction vortex (Gilpin, 1986), and what can happen when small population size, invasive species, and unintentional human impact interact. Goose Island, a small island just off the heavily visited Cattle Point area of San Juan Island, was originally described as one of the highest quality examples of a maritime meadow community (Eaton, 1980). However, nearly 40 years later, more than half the native flora and 75% of the rare flora are now extirpated. While the island was already likely impacted by nesting gulls and cormorants when it was first described, a wildfire burned the entire island in mid-June 2015 due to some setting off a homemade firecracker from nearby Cattle Point. During efforts to put the fire out, up to 100,000 gallons of salt water were also put on the island in an unsuccessful attempt to put out the fire ("Goose Island continues to burn," 2015). While gulls and cormorants continue to nest on the island, several Canada geese were noted in 2021 surveys, as was at least one pile of deer scat. In addition, the island is now a densely grazed lawn of the annual grass *Hordeum murinum*, which covers nearly 100% of the island's area suitable for growing vascular plants (Figure 2-10).

Figure 2-10. Goose Island six years after a wildfire burned the entire island. Note the extensive cover of annual grass and rocky outcrops devoid of plant life.

Swirl Rock is a small collection of three large, jagged rocks that are the most isolated and furthest from larger islands such as Lopez or San Juan. The centermost rock (Swirl Central) is the tallest, and the highest point of the island had several square meters of soil capable of supporting several meadow taxa, including one of the three populations of the WANHP sensitive species *Oxytropis campestris* var. *spicata*. Initial surveys of the island noted no nesting Canada geese or invasive annual grasses. However, in 2021, there was evidence of at least one Canada goose nest and extensive foraging sign. All the meadow taxa, including *O. campestris* var. spicata found in the initial surveys, were gone, and annual grass made a significant component of the flora (Figure 2-11).

Figure 2-11. the view from the top of Swirl Rock in 2021, the site of where a small patch of maritime meadow once persisted, home to one of the three populations of the rare disjunct Oxytropis campestris var. spicata. The area is heavily browsed and impacted by Canada geese (note extensive feces along the top of the island), and the invasive annual grass Hordeum murinum (dried vegetation) dominates the maritime meadow patch.

CONCLUSION

“Flowers as well as weeds follow in the footsteps of man” – Henry David Thoreau, *A Winter Walk*

The patterns of native species decline and alien species colonization and establishment described in this study continue to add to the growing body of evidence that protected natural areas are not protecting biodiversity in light of species invasions (Foxcroft et al., 2013, 2017; Hallmann et al., 2017; De la Fuente & Beck, 2018; Hulme, 2018; Ren et al., 2021). Moreover, invasive species are impacting protected and imperiled ecological communities well beyond the frontier of human settlement and development (Seabloom et al., 2006). In particular, this study supports the detailed evidence demonstrating the negative consequences of introduced Canada geese (Best & Arcese, 2009; Isaac-Renton et al., 2010; Bennett et al., 2011, 2013) as well as the negative consequences of deer herbivory on the native flora of small meadow islands (Martin, Arcese & Scheerder, 2011; Arcese et al., 2014, 2018). Without the rapid and concerted effort to control both deer and Canada goose populations, the long-term viability of these small island meadow communities is in significant doubt.

Studying biodiversity change on islands is a magnifying glass and amplifies the potential patterns and processes happening at larger scales (Whittaker & Fernández-Palacios, 2007). The islands on the southern edge of the San Juan archipelago were some of the most unique and diverse found anywhere in the island chain. Yet, despite their strong protection status and initially high nativity, the indirect impacts of species introductions and human-caused accidents have led to the continued loss of biodiversity. Such patterns highlight the reality that ‘do-nothing’ conservation is a management choice that can still lead to ecological harm, especially in light of concepts of “compassionate conservation” that pushes back against ideas of the lethal control of common invasive species – especially birds and mammals (Hayward et al., 2019; Callen et al., 2020). The small-island meadow communities urge us to revisit the idea of stewardship and the role of humans in an ecosystem.

The idea of the Anthropocene suggests we are having strong, often unintentional impacts on the natural world (Maslin & Lewis, 2015; Bonneuil & Fressoz, 2016), and that the fate of the natural world is dependent upon which direction we choose (Crutzen & Schwägerl, 2011; Sachs, 2011; Hamilton, 2015; Johnson et al., 2017). If we continue to choose to do nothing, most of these small islands will likely continue to degrade and shift towards annual grasslands with fewer species, a facsimile of the historic diversity, the Homogecene will have come.

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APPENDIX 1 VASCULAR FLORA OF THE SAN JUAN ARCHIPELAGO

Table A1-1. The vascular flora of the San Juan Island archipelago, Washington State, USA. ‘*’ alien taxa, *Habitat* is the primary habitat a species is found on, and *Islands* are the number of islands the species has been recorded on.

Family	Full Species	Infra taxa	Habitat	Islands
Adoxaceae	Sambucus cerulea Raf.		Forest	1
Adoxaceae	Sambucus racemosa L.	var. arborescens	Forest	50
Alismataceae	Alisma triviale Pursh		Wetland	1
Amaranthaceae	Amaranthus blitoides S. Watson*		Open	1
Amaranthaceae	Amaranthus powellii S. Watson*		Open	1
Amaranthaceae	Atriplex dioica Raf.		Shoreline	87
Amaranthaceae	Atriplex gmelinii C.A. Mey. ex Bong.	var. gmelinii	Shoreline	26
Amaranthaceae	Atriplex littoralis L.*		Shoreline	1
Amaranthaceae	Atriplex patula L.*		Shoreline	5
Amaranthaceae	Atriplex prostrata Boucher ex DC.*		Shoreline	40
Amaranthaceae	Chenopodiastrum murale (L.) S. Fuentes, Uotila & Borsch*		Open	1
Amaranthaceae	Chenopodium berlandieri Moq.	var. zschackei	Shoreline	19
Amaranthaceae	Chenopodium leptophyllum (Moq.) Nutt. ex S. Watson	var. leptophyllum	Open	1
Amaranthaceae	Chenopodium macrosperma Hook.f		Wetland	1
Amaranthaceae	Oxybasis rubra (L.) S. Fuentes, Uotila & Borsch		Shoreline	2
Amaranthaceae	Salicornia depressa Standl.		Shoreline	3
Amaranthaceae	Salicornia pacifica Standl.		Shoreline	54
Amaranthaceae	Sarcocornia pacifica Standl.		Shoreline	5
Amaryllidaceae	Allium acuminatum Hook.		Open	97
Amaryllidaceae	Allium amplectens Torr.		Open	2
Amaryllidaceae	Allium cernuum Roth		Shoreline	74
Amaryllidaceae	Allium sativum L.*		Open	2
Amaryllidaceae	Allium vineale L.*		Open	2
Amaryllidaceae	Narcissus poeticus L.*		Open	5
Amaryllidaceae	Narcissus pseudonarcissus L.*		Forest	8
Apiaceae	Angelica genuflexa Nutt.		Wetland	1
Apiaceae	Angelica lucida L.		Shoreline	2
Apiaceae	Anthriscus caucalis M. Bieb.*		Open	20
Apiaceae	Carum carvi L.*		Open	1
Apiaceae	Cicuta douglasii (DC.) J.M. Coult. & Rose		Wetland	2
Apiaceae	Conioselinum pacificum (S. Watson) J.M. Coult. & Rose		Wetland	30
Apiaceae	Conium maculatum L.*		Open	3
Apiaceae	Daucus carota L.*		Open	6
Apiaceae	Daucus pusillus Michx.		Open	20

Family	Full Species	Infra taxa	Habitat	Islands
Apiaceae	Foeniculum vulgare Mill.*		Open	3
Apiaceae	Glehnia leiocarpa Mathias		Shoreline	1
Apiaceae	Heracleum mantegazzianum Sommier & Levier*		Forest	3
Apiaceae	Heracleum maximum Bartr.		Open	21
Apiaceae	Lilaeopsis occidentalis J.M. Coult. & Rose		Shoreline	2
Apiaceae	Lomatium nudicaule (Pursh) J.M. Coult. & Rose		Open	43
Apiaceae	Lomatium utriculatum (Nutt. ex Torr. & A. Gray) J.M. Coult. & Rose		Open	29
Apiaceae	Oenanthe sarmentosa C. Presl ex DC.		Wetland	12
Apiaceae	Osmorhiza berteroi DC.		Forest	29
Apiaceae	Osmorhiza purpurea (J.M. Coult. & Rose) Suksd.		Forest	4
Apiaceae	Perideridia montana (Blank.) Dorn		Open	5
Apiaceae	Petrosedum erectum ('t Hart) Grulich*		Shoreline	1
Apiaceae	Petroselinum crispum (Mill.) Fuss*		Open	2
Apiaceae	Pimpinella saxifraga L.*	ssp. nigra	Open	1
Apiaceae	Sanicula bipinnatifida Douglas ex Hook.		Open	12
Apiaceae	Sanicula crassicaulis Poepp. ex DC.	var. crassicaulis	Open	78
Apiaceae	Sium suave Walter		Wetland	1
Apiaceae	Torilis arvensis (Huds.) Link*	ssp. arvensis	Open	7
Apiaceae	Yabea microcarpa (Hook. & Arn.) Koso-Pol.		Wetland	1
Apocynaceae	Apocynum androsaemifolium L.		Open	2
Apocynaceae	Vinca major L.*		Forest	5
Apocynaceae	Vinca minor L.*		Forest	1
Aquifoliaceae	Ilex aquifolium L.*		Open	24
Araceae	Arum italicum Mill.*		Forest	3
Araceae	Lemna minor L.		Wetland	2
Araceae	Lemna trisulca L.		Wetland	3
Araceae	Lemna turionifera Landolt		Wetland	8
Araceae	Lysichiton americanus Hulten & H. St. John		Wetland	5
Araceae	Spirodela polyrhiza (L.) Schleid.		Wetland	3
Araceae	Wolffia borealis (Engelm.) Landolt & Wildi ex Gandhi, Wiersema & Brouillet		Wetland	2
Araceae	Wolffia columbiana H. Karsten		Wetland	2
Araliaceae	Hedera helix L.*		Forest	8
Araliaceae	Hedera hibernica (G. Kirchn.) Bean*		Forest	21
Aristolochiaceae	Asarum caudatum Lindl.		Forest	2
Asparagaceae	Asparagus officinalis L.*		Open	5
Asparagaceae	Brodiaea coronaria (Salisb.) Engl.		Open	62
Asparagaceae	Brodiaea rosea (Greene) Baker	var. rosea	Open	5

Family	Full Species	Infra taxa	Habitat	Islands
Asparagaceae	Camassia leichtlinii (Baker) S. Watson	ssp. suksdorfii	Open	95
Asparagaceae	Camassia quamash (Pursh) Greene	ssp. maxima	Open	15
Asparagaceae	Dichelostemma congestum (Sm.) Kunth		Open	1
Asparagaceae	Hyacinthoides xmassartiana Heist. ex Fabr.*		Open	9
Asparagaceae	Maianthemum dilatatum (Alph. Wood) A. Nelson & J.F. Macbr.		Forest	16
Asparagaceae	Maianthemum racemosum (L.) Link	ssp. amplexicaule	Forest	16
Asparagaceae	Maianthemum stellatum (L.) Link		Forest	7
Asparagaceae	Muscari armeniacum Leichtlin ex Baker*		Open	2
Asparagaceae	Ornithogalum umbellatum L.*		Open	1
Asparagaceae	Scilla forbesii (Baker) Speta*		Open	1
Asparagaceae	Triteleia grandiflora Lindl.	var. howellii	Open	10
Asparagaceae	Triteleia hyacinthina (Lindl.) Greene		Open	23
Aspleniaceae	Asplenium trichomanes L.	ssp. trichomanes	Open	4
Asteraceae	Achillea millefolium L.		Open	107
Asteraceae	Adenocaulon bicolor Hook.		Forest	9
Asteraceae	Agoseris grandiflora (Nutt.) Greene	ssp. grandiflora, ssp. leptophylla	Open	20
Asteraceae	Agoseris heterophylla (Nutt.) Greene	var. heterophylla	Open	3
Asteraceae	Ambrosia chamissonis (Less.) Greene		Shoreline	38
Asteraceae	Anaphalis margaritacea (L.) Benth. & Hook. f.		Open	12
Asteraceae	Anisocarpus madioides Nutt.		Forest	20
Asteraceae	Antennaria racemosa Hook.		Open	1
Asteraceae	Anthemis cotula L.*		Open	2
Asteraceae	Arctium minus (Hill) Bernh.*		Open	4
Asteraceae	Artemisia campestris L.	var. scouleriana	Open	17
Asteraceae	Artemisia suksdorfii Piper		Open	5
Asteraceae	Artemisia vulgaris L.*		Open	1
Asteraceae	Bellis perennis L.*		Open	23
Asteraceae	Bidens beckii Torr. ex Spreng.		Wetland	1
Asteraceae	Bidens frondosa L.		Shoreline	1
Asteraceae	Calendula officinalis L.*		Open	1
Asteraceae	Carduus nutans L.*		Open	1
Asteraceae	Centaurea cyanus L.*		Open	2
Asteraceae	Centaurea diffusa Lam.*		Open	1
Asteraceae	Centaurea gerstlaueri Erdner*		Open	3
Asteraceae	Centaurea jacea L.*		Open	2
Asteraceae	Centaurea melitensis L.*		Open	2
Asteraceae	Centaurea montana L.*		Open	1
Asteraceae	Centaurea stoebe L.*	ssp. australis	Open	3
Asteraceae	Centaurea varnensis Velen.*		Open	1

Family	Full Species	Infra taxa	Habitat	Islands
Asteraceae	Cichorium intybus L.*		Open	2
Asteraceae	Cirsium arvense (L.) Scop.*		Open	32
Asteraceae	Cirsium brevistylum Cronquist		Forest	7
Asteraceae	Cirsium vulgare (Savi) Ten.*		Open	67
Asteraceae	Conyza canadensis (L.) Cronquist		Open	3
Asteraceae	Coreopsis grandiflora x C. lanceolata *		Open	1
Asteraceae	Coreopsis lanceolata L.*		Open	2
Asteraceae	Cotula coronopifolia L.*		Shoreline	2
Asteraceae	Crepis capillaris (L.) Wallr.*		Open	10
Asteraceae	Crepis nicaeensis Balbis ex Pers.*		Open	1
Asteraceae	Crocidium multicaule Hook.		Open	2
Asteraceae	Erigeron philadelphicus L.		Forest	1
Asteraceae	Erigeron speciosus (Lindl.) DC.		Open	1
Asteraceae	Eriophyllum lanatum (Pursh) J. Forbes	var. lanatum, var. leucophyllum	Open	33
Asteraceae	Filago arvensis L.*		Open	1
Asteraceae	Filago vulgaris Lam.*		Open	4
Asteraceae	Gamochaeta ustulata (Nutt.) Holub		Open	26
Asteraceae	Gnaphalium palustre Nutt.		Open	4
Asteraceae	Gnaphalium uliginosum L.*		Open	4
Asteraceae	Grindelia integrifolia DC.		Shoreline	143
Asteraceae	Hemizonella minima (A. Gray) A. Gray		Open	1
Asteraceae	Hieracium albiflorum Hook.		Forest	31
Asteraceae	Hieracium aurantiacum L.*		Open	2
Asteraceae	Hieracium caespitosum Dumort.*		Open	2
Asteraceae	Hieracium flagellare Willd.*		Open	1
Asteraceae	Hieracium stoloniflorum Waldst. & Kit.*		Open	1
Asteraceae	Hypochaeris glabra L.*		Open	24
Asteraceae	Hypochaeris radicata L.*		Open	88
Asteraceae	Jacobaea maritima (L.) Pelser & Meijden		Open	1
Asteraceae	Jacobaea maritima x J. vulgaris *		Open	1
Asteraceae	Jacobaea vulgaris Gaertn.*		Open	14
Asteraceae	Jaumea carnosa (Less.) A. Gray		Shoreline	4
Asteraceae	Lactuca ludoviciana (Nutt.) Riddell		Open	1
Asteraceae	Lactuca serriola L.*		Open	9
Asteraceae	Lapsana communis L.*		Open	13
Asteraceae	Leontodon autumnalis L.*		Open	4
Asteraceae	Leontodon saxatilis Lam.*	ssp. saxatilis	Open	4
Asteraceae	Leucanthemum maximum (Ramond) DC.*		Open	1
Asteraceae	Leucanthemum vulgare Lam.*		Open	7
Asteraceae	Logfia minima (Sm.) Dumort.*		Open	2
Asteraceae	Madia exigua (Sm.) A. Gray		Open	4
Asteraceae	Madia glomerata Hook.		Open	1
Asteraceae	Madia gracilis (Sm.) D.D. Keck		Open	9

Family	Full Species	Infra taxa	Habitat	Islands
Asteraceae	Madia sativa Molina		Open	5
Asteraceae	Matricaria discoidea DC.		Open	6
Asteraceae	Mauranthemum paludosum (Poir.) Vogt & Oberpr.*		Open	1
Asteraceae	Microseris bigelovii (A. Gray) Sch. Bip.		Open	2
Asteraceae	Mycelis muralis (L.) Dumort.*		Forest	28
Asteraceae	Packera indecora (Greene) Á. Löve & D. Löve		Open	1
Asteraceae	Packera macounii (Greene) W.A. Weber & Á. Löve		Open	4
Asteraceae	Petasites frigidus (L.) Fr.	var. palmatus	Wetland	1
Asteraceae	Pseudognaphalium stramineum (Kunth) Anderb.		Open	6
Asteraceae	Pseudognaphalium thermale (E.E. Nelson) G.L. Nesom		Open	6
Asteraceae	Psilocarphus tenellus Nutt.		Open	1
Asteraceae	Senecio sylvaticus L.*		Open	12
Asteraceae	Senecio vulgaris L.*		Open	60
Asteraceae	Sericocarpus rigidus Lindl.		Open	1
Asteraceae	Solidago elongata Nutt.		Open	2
Asteraceae	Solidago lepida DC.	var. salebrosa	Open	12
Asteraceae	Solidago simplex Kunth	var. nana, var. simplex	Open	2
Asteraceae	Soliva sessilis Ruiz & Pav.*		Open	12
Asteraceae	Sonchus arvensis L.*	ssp. arvensis	Open	16
Asteraceae	Sonchus asper (L.) Hill*	ssp. asper	Open	71
Asteraceae	Sonchus oleraceus L.*		Open	102
Asteraceae	Symphyotrichum boreale (Torr. & A. Gray) Á. Löve & D. Löve		Wetland	1
Asteraceae	Symphyotrichum subspicatum (Nees) G.L. Nesom		Open	6
Asteraceae	Tanacetum balsamita L.*		Open	1
Asteraceae	Tanacetum parthenium (L.) Sch. Bip.*		Open	2
Asteraceae	Tanacetum vulgare L.*		Open	3
Asteraceae	Taraxacum erythrospermum Andrz. ex Besser*		Open	14
Asteraceae	Taraxacum officinale F.H. Wigg.*		Open	68
Asteraceae	Tragopogon dubius Scop.*		Open	4
Asteraceae	Tragopogon porrifolius L.*		Open	4
Asteraceae	Tragopogon pratensis L.*		Open	1
Asteraceae	Tripleurospermum inodorum (L.) Sch. Bip.*		Open	4
Athyriaceae	Athyrium filix-femina (L.) Roth ex Mertens	ssp. cyclosorum	Forest	19
Berberidaceae	Berberis aquifolium (Pursh) Nutt.		Open	87
Berberidaceae	Berberis nervosa (Pursh) Nutt.		Forest	20
Betulaceae	Alnus rubra Bong.		Forest	18
Betulaceae	Alnus viridis (Chaix) DC.	ssp. sinuata	Forest	8
Betulaceae	Betula papyrifera Marshall		Forest	5
Betulaceae	Betula pendula Roth*		Forest	1

Family	Full Species	Infra taxa	Habitat	Islands
Betulaceae	Corylus cornuta Marshall	ssp. californica	Forest	3
Blechnaceae	Struthiopteris spicant (L.) Weiss		Forest	5
Boraginaceae	Amsinckia intermedia Fisch. & C.A. Mey.		Open	3
Boraginaceae	Amsinckia menziesii (Lehm.) A. Nelson & J.F. Macbr.		Open	12
Boraginaceae	Amsinckia spectabilis Fisch. & C.A. Mey.	var. spectabilis	Open	5
Boraginaceae	Anchusa azurea Mill.*		Open	2
Boraginaceae	Anchusa officinalis L.*		Open	1
Boraginaceae	Borago officinalis L.*		Open	1
Boraginaceae	Buglossoides arvensis (L.) I.M. Johnst.*		Open	1
Boraginaceae	Lycopsis arvensis L.*		Open	1
Boraginaceae	Myosotis arvensis (L.) Hill*		Open	4
Boraginaceae	Myosotis discolor Pers.*		Open	43
Boraginaceae	Myosotis latifolia Poir.*		Open	1
Boraginaceae	Myosotis laxa Lehm.		Wetland	4
Boraginaceae	Myosotis stricta Link ex Roem. & Schult.*		Open	12
Boraginaceae	Myosotis sylvatica Ehrh. ex Hoffm.*		Forest	1
Boraginaceae	Pentaglottis sempervirens (L.) Tausch ex L.H. Bailey*		Forest	1
Boraginaceae	Plagiobothrys scouleri (Hook. & Arn.) I.M. Johnst.		Shoreline	28
Boraginaceae	Plagiobothrys tenellus (Nutt. ex Hook.) A. Gray		Open	4
Boraginaceae	Symphytum officinale L.*		Open	1
Boraginaceae	Symphytum uplandicum Nyman*		Open	1
Brassicaceae	Alliaria petiolata (M. Bieb.) Cavara & Grande*		Forest	2
Brassicaceae	Arabidopsis thaliana (L.) Heynh.*		Open	8
Brassicaceae	Arabis caucasica Willd.*		Open	1
Brassicaceae	Arabis eschscholtziana Andrz.		Open	23
Brassicaceae	Aubrieta deltoidea (L.) DC.*		Open	1
Brassicaceae	Barbarea orthoceras Ledeb.		Open	15
Brassicaceae	Barbarea vulgaris W.T. Aiton*		Open	1
Brassicaceae	Brassica juncea (L.) Czern.*		Open	4
Brassicaceae	Brassica nigra (L.) W.D.J. Koch*		Open	3
Brassicaceae	Brassica rapa L.*		Open	4
Brassicaceae	Cakile edentula (Bigelow) Hook.*	var. edentula	Shoreline	17
Brassicaceae	Cakile maritima Scop.*	ssp. maritima	Shoreline	44
Brassicaceae	Camelina microcarpa Andrz. ex DC.*		Open	1
Brassicaceae	Capsella bursa-pastoris (L.) Medik.*		Open	10
Brassicaceae	Cardamine flexuosa With.*		Forest	6
Brassicaceae	Cardamine hirsuta L.*		Open	66
Brassicaceae	Cardamine nuttallii Greene		Forest	2
Brassicaceae	Cardamine occidentalis (S. Watson) Howell		Wetland	2
Brassicaceae	Cardamine oligosperma Nutt.		Forest	50

Family	Full Species	Infra taxa	Habitat	Islands
Brassicaceae	Cardamine pensylvanica Muhl. ex Willd.		Forest	4
Brassicaceae	Draba verna L.*		Open	30
Brassicaceae	Erysimum cheiri (L.) Crantz*		Open	1
Brassicaceae	Hesperis matronalis L.*		Open	2
Brassicaceae	Hornungia procumbens (L.) Hayek		Shoreline	11
Brassicaceae	Lepidium campestre (L.) W.T. Aiton*		Open	1
Brassicaceae	Lepidium densiflorum Schrad.		Open	3
Brassicaceae	Lepidium didymum L.*		Open	1
Brassicaceae	Lepidium draba L.*		Open	1
Brassicaceae	Lepidium heterophyllum Benth.*		Open	1
Brassicaceae	Lepidium latifolium L.*		Open	1
Brassicaceae	Lepidium oxycarpum Torr. & A. Gray		Shoreline	2
Brassicaceae	Lepidium perfoliatum L.*		Open	1
Brassicaceae	Lepidium virginicum L.	ssp. menziesii	Shoreline	72
Brassicaceae	Lobularia maritima (L.) Desv.*		Open	2
Brassicaceae	Lunaria annua L.*		Forest	3
Brassicaceae	Nasturtium officinale W.T. Aiton*		Wetland	2
Brassicaceae	Raphanus raphanistrum L.*		Open	3
Brassicaceae	Raphanus sativus L.*		Open	2
Brassicaceae	Rorippa curvisiliqua (Hook.) Bessey ex Britton		Wetland	2
Brassicaceae	Rorippa palustris (L.) Besser	ssp. palustris	Wetland	1
Brassicaceae	Sinapis arvensis L.*		Open	3
Brassicaceae	Sisymbrium altissimum L.*		Open	1
Brassicaceae	Sisymbrium officinale (L.) Scop.*		Open	3
Brassicaceae	Teesdalia nudicaulis (L.) W.T. Aiton*		Open	5
Brassicaceae	Thlaspi arvense L.*		Open	1
Brassicaceae	Turritis glabra L.		Open	49
Buddleja	Buddleja davidii Franch.*		Open	1
Cabombaceae	Brasenia schreberi J.F. Gmel.		Wetland	2
Cactaceae	Opuntia fragilis (Nutt.) Haw.		Shoreline	27
Campanulaceae	Campanula medium L.*		Open	2
Campanulaceae	Campanula persicifolia L.*		Open	1
Campanulaceae	Campanula rapunculoides L.*		Open	1
Campanulaceae	Campanula rotundifolia L.		Open	14
Campanulaceae	Campanula scouleri Hook. ex A. DC.		Forest	4
Campanulaceae	Githopsis specularioides Nutt.		Open	1
Campanulaceae	Lobelia dortmanna L.		Wetland	1
Campanulaceae	Triodanis perfoliata (L.) Nieuwl.		Wetland	6
Caprifoliaceae	Lonicera ciliosa (Pursh) Poir. ex DC.		Forest	52
Caprifoliaceae	Lonicera hispidula (Lindl.) Douglas ex Torr. & A. Gray		Forest	56

Family	Full Species	Infra taxa	Habitat	Islands
Caprifoliaceae	Lonicera involucrata (Richardson) Banks ex Spreng.	var. involucrata	Forest	9
Caprifoliaceae	Symphoricarpos albus (L.) S.F. Blake	var. laevigatus	Forest	94
Caryophyllaceae	Agrostemma githago L.*		Open	1
Caryophyllaceae	Arenaria serpyllifolia L.*	var. serpylilfolia	Open	5
Caryophyllaceae	Cerastium arvense L.	ssp. strictum	Open	106
Caryophyllaceae	Cerastium fontanum Baumg.*	ssp. vulgare	Open	12
Caryophyllaceae	Cerastium glomeratum Thuill.*		Open	82
Caryophyllaceae	Cerastium pumilum Curtis*		Open	71
Caryophyllaceae	Cerastium semidecandrum L.*		Open	47
Caryophyllaceae	Cerastium tomentosum L.*		Open	1
Caryophyllaceae	Dianthus armeria L.*	ssp. armeria	Open	5
Caryophyllaceae	Dianthus barbatus L.*	ssp. barbatus	Open	1
Caryophyllaceae	Holosteum umbellatum L.*	ssp. umbellatum	Open	2
Caryophyllaceae	Honckenya peploides (L.) Ehrh.	ssp. major	Shoreline	11
Caryophyllaceae	Lychnis coronaria (L.) Desr.*		Open	4
Caryophyllaceae	Moehringia macrophylla (Hook.) Fenzl		Forest	5
Caryophyllaceae	Moenchia erecta (L.) P. Gaertn., B. Mey. & Scherbius*		Open	2
Caryophyllaceae	Sabulina macra (A. Nelson & J.F. Macbr.) Dillenb. & Kadereit		Open	17
Caryophyllaceae	Sagina apetala Ard.*		Shoreline	17
Caryophyllaceae	Sagina decumbens (Elliott) Torr. & A. Gray	ssp. occidentalis	Shoreline	88
Caryophyllaceae	Sagina maxima A. Gray	ssp. crassicaulis	Shoreline	31
Caryophyllaceae	Sagina procumbens L.*		Shoreline	12
Caryophyllaceae	Scleranthus annuus L.*		Open	1
Caryophyllaceae	Silene antirrhina L.		Open	16
Caryophyllaceae	Silene douglasii Hook.		Open	1
Caryophyllaceae	Silene gallica L.*		Open	28
Caryophyllaceae	Silene latifolia Poir.*		Open	2
Caryophyllaceae	Silene menziesii Hook.		Forest	12
Caryophyllaceae	Silene scouleri Hook.	ssp. scouleri	Open	5
Caryophyllaceae	Spergula arvensis L.*		Shoreline	2
Caryophyllaceae	Spergularia canadensis (Pers.) G. Don	var. occidentalis	Shoreline	7
Caryophyllaceae	Spergularia macrotheca (Hornem.) Heynh.	var. macrotheca	Shoreline	55
Caryophyllaceae	Spergularia rubra (L.) J. Presl & C. Presl*		Shoreline	35
Caryophyllaceae	Spergularia salina J. Presl & C. Presl		Shoreline	7
Caryophyllaceae	Stellaria borealis Bigelow	ssp. borealis, ssp. sitchana	Wetland	6
Caryophyllaceae	Stellaria crispa Cham. & Schltdl.		Forest	10
Caryophyllaceae	Stellaria graminea L.*		Open	1
Caryophyllaceae	Stellaria longifolia Muhl. ex Willd.		Wetland	2
Caryophyllaceae	Stellaria longipes Goldie	ssp. longipes	Wetland	2
Caryophyllaceae	Stellaria media (L.) Vill.*		Open	86
Caryophyllaceae	Stellaria nitens Nutt.		Open	14

Family	Full Species	Infra taxa	Habitat	Islands
Caryophyllaceae	Stellaria pallida (Dumort.) Crépin*		Open	21
Caryophyllaceae	Vaccaria hispanica (Mill.) Rauschert*		Open	1
Celastraceae	Paxistima myrsinites (Pursh) Raf.		Forest	21
Ceratophyllaceae	Ceratophyllum demersum L.		Wetland	5
Convolvulaceae	Calystegia lucana (Ten.) G. Don*		Open	1
Convolvulaceae	Calystegia sepium (L.) R. Br.		Shoreline	4
Convolvulaceae	Calystegia soldanella (L.) R. Br.		Shoreline	1
Convolvulaceae	Convolvulus arvensis L.*		Open	3
Convolvulaceae	Cuscuta epithymum Murray*	var. epithymum	Shoreline	1
Convolvulaceae	Cuscuta pacifica Costea & M.A.R. Wright	var. pacifica	Shoreline	8
Cornaceae	Cornus occidentalis (Torr. & A. Gray) Coville		Forest	2
Cornaceae	Cornus stolonifera Michx.		Forest	3
Cornaceae	Cornus unalaschkensis Ledeb.		Forest	2
Crassulaceae	Crassula connata (Ruiz & Pav.) A. Berger		Shoreline	2
Crassulaceae	Crassula tillaea Lester-Garl.*		Shoreline	9
Crassulaceae	Sedum acre L.*		Shoreline	3
Crassulaceae	Sedum album L.*		Shoreline	9
Crassulaceae	Sedum divergens S. Watson		Open	1
Crassulaceae	Sedum lanceolatum Torr.		Shoreline	93
Crassulaceae	Sedum oreganum Nutt.		Open	2
Crassulaceae	Sedum spathulifolium Hook.		Shoreline	79
Cucurbitaceae	Marah oregana (Torr. & A. Gray) Howell		Open	5
Cupressaceae	Juniperus scopulorum Sarg.		Open	61
Cupressaceae	Thuja plicata Donn ex D. Don		Forest	24
Cyperaceae	Bolboschoenus maritimus (L.) Palla	ssp. paludosus	Wetland	8
Cyperaceae	Carex aquatilis Wahlenb.	var. aquatilis, var. dives	Wetland	4
Cyperaceae	Carex arcta Boott		Wetland	3
Cyperaceae	Carex aurea Nutt.		Wetland	3
Cyperaceae	Carex canescens L.		Wetland	2
Cyperaceae	Carex canescens L.*		Wetland	2
Cyperaceae	Carex cusickii Mack. ex Piper & Beattie		Wetland	4
Cyperaceae	Carex densa (L.H. Bailey) L.H. Bailey		Open	1
Cyperaceae	Carex echinata Murray	ssp. echinata, ssp. phyllomanica	Wetland	2
Cyperaceae	Carex exsiccata L.H. Bailey		Wetland	5
Cyperaceae	Carex hendersonii L.H. Bailey		Wetland	4
Cyperaceae	Carex hoodii Boott		Open	1
Cyperaceae	Carex inops L.H. Bailey	ssp. Inops	Open	17
Cyperaceae	Carex interior L.H. Bailey		Wetland	2

Family	Full Species	Infra taxa	Habitat	Islands
Cyperaceae	Carex kelloggii W. Boott	var. impressa, var. kelloggii, var. limnophila	Wetland	5
Cyperaceae	Carex laeviculmis Meinsh.		Wetland	1
Cyperaceae	Carex lasiocarpa Ehrh.		Wetland	1
Cyperaceae	Carex leporina L.		Wetland	2
Cyperaceae	Carex leptalea Wahlenb.		Wetland	2
Cyperaceae	Carex leptopoda Mack.		Forest	17
Cyperaceae	Carex leptopoda Mack.		Forest	17
Cyperaceae	Carex lyngbyei Hornem.		Shoreline	15
Cyperaceae	Carex macrocephala Willd. ex Spreng.		Shoreline	5
Cyperaceae	Carex obnupta L.H. Bailey		Wetland	12
Cyperaceae	Carex pachystachya Cham. ex Steud.		Wetland	7
Cyperaceae	Carex pansa L.H. Bailey		Open	3
Cyperaceae	Carex pauciflora Lightf.		Open	1
Cyperaceae	Carex pendula Huds.*		Forest	1
Cyperaceae	Carex praticola Rydb.		Open	2
Cyperaceae	Carex rossii Boott		Open	13
Cyperaceae	Carex stipata Muhl. ex Willd.	var. stipata	Wetland	3
Cyperaceae	Carex subbracteata Mack.		Wetland	1
Cyperaceae	Carex tumulicola Mack.		Open	3
Cyperaceae	Carex unilateralis Mack.		Wetland	1
Cyperaceae	Carex utriculata Boott		Wetland	6
Cyperaceae	Carex vesicaria L.	var. major	Wetland	2
Cyperaceae	Carex viridula Michx.	var. viridula	Shoreline	3
Cyperaceae	Carex vulpinoidea Michx.		Open	1
Cyperaceae	Carex zikae E.H. Roalson & M.J. Waterway		Open	9
Cyperaceae	Dulichium arundinaceum (L.) Britton		Wetland	4
Cyperaceae	Eleocharis acicularis (L.) Roem. & Schult.		Wetland	1
Cyperaceae	Eleocharis macrostachya Britton		Wetland	4
Cyperaceae	Eleocharis obtusa (Willd.) Schult.		Wetland	1
Cyperaceae	Eleocharis palustris (L.) Roem. & Schult.		Wetland	7
Cyperaceae	Eleocharis parvula (Roem. & Schultes) Link ex Bluff Nees, & Schauer		Wetland	1
Cyperaceae	Eriophorum chamissonis C.A. Mey.		Wetland	1
Cyperaceae	Eriophorum gracile W.D.J. Koch ex Roth		Wetland	1
Cyperaceae	Rhynchospora alba (L.) Vahl		Wetland	1
Cyperaceae	Schoenoplectus acutus (Muhl. ex Bigelow) Á. Löve & D. Löve		Wetland	6
Cyperaceae	Schoenoplectus americanus (Pers.) Volkart ex Schinz & R. Keller		Shoreline	2
Cyperaceae	Schoenoplectus subterminalis (Torr.) Soják		Wetland	1

Family	Full Species	Infra taxa	Habitat	Islands
Cyperaceae	Schoenoplectus tabernaemontani (C.C. Gmel.) Palla		Wetland	3
Cyperaceae	Scirpus atrocinctus Fernald		Wetland	1
Cyperaceae	Scirpus cyperinus (L.) Kunth*		Wetland	1
Cyperaceae	Scirpus microcarpus J. Presl & C. Presl		Wetland	5
Cystopteridaceae	Cystopteris fragilis (L.) Bernh.		Forest	7
Dennstaedtiaceae	Pteridium aquilinum (L.) Kuhn	var. pubescens	Forest	30
Dipsacaceae	Dipsacus fullonum L.*		Open	5
Droseraceae	Drosera rotundifolia L.		Wetland	3
Dryopteridaceae	Dryopteris arguta (Kaulf.) Maxon		Forest	1
Dryopteridaceae	Dryopteris expansa (C. Presl) Fraser-Jenk. & Jermy		Forest	14
Dryopteridaceae	Polystichum munitum (Kaulf.) C. Presl		Forest	50
Elaeagnaceae	Elaeagnus umbellata Thunb.*		Open	1
Elaeagnaceae	Shepherdia canadensis (L.) Nutt.		Forest	21
Equisetaceae	Equisetum arvense L.		Open	13
Equisetaceae	Equisetum ferrissii Clute		Open	1
Equisetaceae	Equisetum fluviatile L.		Wetland	3
Equisetaceae	Equisetum hyemale L.	ssp. affine	Wetland	9
Equisetaceae	Equisetum palustre L.		Wetland	5
Equisetaceae	Equisetum telmateia Ehrh.	ssp. braunii	Wetland	13
Ericaceae	Allotropa virgata Torr. & A. Gray		Forest	2
Ericaceae	Arbutus menziesii Pursh		Forest	62
Ericaceae	Arctostaphylos columbiana Piper		Open	2
Ericaceae	Arctostaphylos media Greene		Open	1
Ericaceae	Arctostaphylos uva-ursi (L.) Spreng.		Open	7
Ericaceae	Chimaphila menziesii (R. Br.) Spreng.		Forest	3
Ericaceae	Chimaphila umbellata (L.) W.P.C. Barton	ssp. umellata	Forest	4
Ericaceae	Gaultheria shallon Pursh		Forest	37
Ericaceae	Kalmia microphylla (Hook.) A. Heller	var. occidentalis	Wetland	3
Ericaceae	Moneses uniflora (L.) A. Gray		Forest	1
Ericaceae	Monotropa hypopitys L.		Forest	2
Ericaceae	Monotropa uniflora L.		Forest	13
Ericaceae	Orthilia secunda (L.) House		Forest	2
Ericaceae	Pterospora andromedea Nutt.		Forest	2
Ericaceae	Pyrola aphylla Sm.		Forest	1
Ericaceae	Pyrola asarifolia Michx.	ssp. asarifolia, ssp. bracteata	Forest	4
Ericaceae	Pyrola chlorantha Sw.		Forest	2
Ericaceae	Pyrola dentata Sm.		Forest	1
Ericaceae	Pyrola minor L.		Forest	1
Ericaceae	Pyrola picta Sm.		Forest	3
Ericaceae	Rhododendron columbianum (Piper) Harmaja		Forest	1

Family	Full Species	Infra taxa	Habitat	Islands
Ericaceae	Rhododendron groenlandicum (Oeder) Kron & Judd		Forest	5
Ericaceae	Rhododendron macrophyllum D. Don ex G. Don		Forest	1
Ericaceae	Vaccinium cespitosum Michx.		Forest	1
Ericaceae	Vaccinium ovatum Pursh		Forest	4
Ericaceae	Vaccinium oxycoccos L.		Forest	2
Ericaceae	Vaccinium parvifolium Sm.		Forest	21
Ericaceae	Vaccinium uliginosum L.		Forest	1
Euphorbiaceae	Euphorbia characias L.*		Open	1
Euphorbiaceae	Euphorbia cyparissias L.*		Open	4
Euphorbiaceae	Euphorbia elongata Poir.*		Open	1
Euphorbiaceae	Euphorbia myrsinites L.*		Open	1
Euphorbiaceae	Euphorbia peplus L.*		Open	3
Fabaceae	Acmispon americanus (Nutt.) Rydb.	var. americanus	Open	4
Fabaceae	Acmispon denticulatus (Drew) Sokoloff		Open	10
Fabaceae	Acmispon parviflorus (Benth.) D.D. Sokoloff		Open	17
Fabaceae	Cytisus scoparius (L.) Link*		Open	8
Fabaceae	Laburnum anagyroidis Medik.*		Forest	1
Fabaceae	Lathyrus aphaca L.*		Open	1
Fabaceae	Lathyrus japonicus Willd.		Shoreline	57
Fabaceae	Lathyrus latifolius L.*		Open	4
Fabaceae	Lathyrus littoralis (Nutt.) Endl. ex Walp.		Shoreline	1
Fabaceae	Lathyrus nevadensis S. Watson	var. nevadensis	Forest	47
Fabaceae	Lathyrus palustris L.		Shoreline	5
Fabaceae	Lathyrus sylvestris L.*		Open	1
Fabaceae	Lotus corniculatus L.*		Open	8
Fabaceae	Lotus tenuis Waldst. & Kit. ex Willd.*		Open	2
Fabaceae	Lupinus arboreus Sims*		Open	4
Fabaceae	Lupinus bicolor Lindl.		Open	15
Fabaceae	Lupinus latifolius Lindl. ex J. Agardh	var. latifolius	Open	2
Fabaceae	Lupinus littoralis Douglas	var. littoralis	Open	2
Fabaceae	Lupinus microcarpus Sims	var. microcarpus	Open	7
Fabaceae	Lupinus pachylobus Greene		Open	1
Fabaceae	Lupinus rivularis Douglas ex Lindl.		Open	1
Fabaceae	Medicago arabica (L.) Huds.*		Open	1
Fabaceae	Medicago lupulina L.*		Open	7
Fabaceae	Medicago sativa L.*		Open	2
Fabaceae	Melilotus albus Medik.*		Open	2
Fabaceae	Melilotus officinalis (L.) Lam.*		Open	2
Fabaceae	Oxytropis campestris (L.) DC.	var. spicata	Shoreline	3
Fabaceae	Pisum sativum L.*		Open	1
Fabaceae	Rupertia physodes (Douglas ex Hook.) J.W. Grimes		Open	2
Fabaceae	Trifolium arvense L.*		Open	2

Family	Full Species	Infra taxa	Habitat	Islands
Fabaceae	Trifolium campestre Schreb.*		Open	8
Fabaceae	Trifolium depauperatum Desv.		Open	1
Fabaceae	Trifolium dichotomum Hook. & Arn.		Open	8
Fabaceae	Trifolium dubium Sibth.*		Open	50
Fabaceae	Trifolium fragiferum L.*		Open	1
Fabaceae	Trifolium hybridum L.*		Open	1
Fabaceae	Trifolium incarnatum L.*		Open	2
Fabaceae	Trifolium microcephalum Pursh		Open	58
Fabaceae	Trifolium microdon Hook. & Arn.		Open	53
Fabaceae	Trifolium oliganthum Steud.		Open	43
Fabaceae	Trifolium pratense L.*		Open	14
Fabaceae	Trifolium repens L.*		Open	17
Fabaceae	Trifolium retusum L.*		Open	1
Fabaceae	Trifolium striatum L.*		Open	1
Fabaceae	Trifolium subterraneum L.*		Open	17
Fabaceae	Trifolium suffocatum L.*		Open	2
Fabaceae	Trifolium variegatum Nutt.		Open	40
Fabaceae	Trifolium willdenovii Spreng.		Open	87
Fabaceae	Trifolium wormskioldii Lehm.		Open	2
Fabaceae	Ulex europaeus L.*		Open	1
Fabaceae	Vicia americana Muhl. ex Willd.	var. americana	Forest	76
Fabaceae	Vicia cracca L.*		Open	2
Fabaceae	Vicia hirsuta (L.) Gray*		Open	57
Fabaceae	Vicia lathyroides L.*		Open	1
Fabaceae	Vicia nigricans Hook. & Arn.	var. gigantea	Forest	32
Fabaceae	Vicia sativa L.*	var. angustifolia, var. sativa	Open	71
Fabaceae	Vicia tetrasperma (L.) Schreb.*		Open	1
Fabaceae	Vicia villosa Roth*	var. glabrescens	Open	4
Fagaceae	Quercus garryana Douglas ex Hook.	var. garryana	Open	38
Gentianaceae	Centaurium erythraea Rafn*		Open	5
Gentianaceae	Centaurium pulchellum (Sw.) Hayek ex Hand.-Mazz., Stadlm., Janch. & Faltis*		Open	1
Gentianaceae	Gentianella amarella (L.) Börner	ssp. acuta	Wetland	3
Geraniaceae	Erodium cicutarium (L.) L\\\'Hér. ex Aiton*	ssp. cicutarium	Open	26
Geraniaceae	Geranium bicknellii Britton		Forest	1
Geraniaceae	Geranium carolinianum L.		Forest	5
Geraniaceae	Geranium dissectum L.*		Open	23
Geraniaceae	Geranium lucidum L.*		Open	2
Geraniaceae	Geranium molle L.*		Open	99
Geraniaceae	Geranium pusillum L.*		Open	2
Geraniaceae	Geranium robertianum L.*		Forest	6
Grossulariaceae	Ribes divaricatum Douglas	var. divaricatum	Forest	63
Grossulariaceae	Ribes lacustre (Pers.) Poir.		Forest	10
Grossulariaceae	Ribes sanguineum Pursh	var. sanguineum	Forest	54

Family	Full Species	Infra taxa	Habitat	Islands
Haloragaceae	Myriophyllum sibiricum Kom.		Wetland	4
Haloragaceae	Myriophyllum verticillatum L.		Wetland	3
Hydrangeaceae	Philadelphus lewisii Pursh		Forest	7
Hydrocharitaceae	Egeria densa Planch.*		Wetland	1
Hydrocharitaceae	Elodea canadensis Michx.		Wetland	3
Hydrocharitaceae	Najas canadensis Michx.		Wetland	1
Hydrocharitaceae	Najas flexilis (Willd.) Rostk. & W.L.E. Schmidt		Wetland	3
Hydrophyllaceae	Nemophila parviflora Douglas ex Benth.	var. parviflora, var. austiniae	Forest	14
Hydrophyllaceae	Nemophila pedunculata Douglas ex Benth.		Forest	1
Hydrophyllaceae	Phacelia linearis (Pursh) Holz.		Open	1
Hypericaceae	Hypericum anagalloides Cham. & Schltdl.		Wetland	3
Hypericaceae	Hypericum calycinum L.*		Open	1
Hypericaceae	Hypericum perforatum L.*		Open	7
Hypericaceae	Hypericum scouleri Hook.		Wetland	2
Iridaceae	Crocus stellaris Haw.*		Open	1
Iridaceae	Iris foetidissima L.*		Open	2
Iridaceae	Iris germanica L.*		Open	7
Iridaceae	Iris pseudacorus L.*		Wetland	6
Iridaceae	Olsynium douglasii (A. Dietr.) E.P. Bicknell	var. douglasii	Open	6
Iridaceae	Sisyrinchium californicum (Ker Gawl.) W.T.Aiton		Open	1
Iridaceae	Sisyrinchium idahoense E.P. Bicknell	var. macounii, var. segetum	Open	8
Isoetaceae	Isoetes nuttallii A. Br.		Wetland	1
Isoetaceae	Isoetes occidentalis L.F. Hend.		Wetland	1
Juncaceae	Juncus acuminatus Michx.		Wetland	4
Juncaceae	Juncus alpinoarticulatus Chaix		Wetland	1
Juncaceae	Juncus articulatus L.	ssp. articulata	Wetland	4
Juncaceae	Juncus balticus Willd.	ssp. ater	Shoreline	19
Juncaceae	Juncus bolanderi Engelm.		Shoreline	1
Juncaceae	Juncus breweri Engelm.		Shoreline	2
Juncaceae	Juncus bufonius L.	var. bufonius	Shoreline	23
Juncaceae	Juncus effusus L.	ssp. pacificus, ssp. effusus	Shoreline	13
Juncaceae	Juncus ensifolius Wikstr.		Wetland	7
Juncaceae	Juncus gerardi Loisel.	ssp. gerardi	Shoreline	3
Juncaceae	Juncus hesperius (Piper) Lint		Wetland	8
Juncaceae	Juncus occidentalis (Coville) Wiegand		Wetland	2
Juncaceae	Juncus tenuis Willd.		Wetland	3
Juncaceae	Luzula comosa E. Mey.	var. laxa	Open	24
Juncaceae	Luzula macrantha (S. Watson) Zika & B.L. Wilson		Open	10
Juncaceae	Luzula multiflora (Ehrh.) Lej.		Open	2
Juncaceae	Luzula parviflora (Ehrh.) Desv.		Forest	2
Juncaceae	Luzula subsessilis (S. Watson) Buchenau		Open	58

Family	Full Species	Infra taxa	Habitat	Islands
Juncaginaceae	Triglochin concinna J.B. Davy		Wetland	1
Juncaginaceae	Triglochin maritima L.		Wetland	10
Lamiaceae	Ajuga reptans L.*		Forest	4
Lamiaceae	Clinopodium douglasii (Benth.) Kuntze		Forest	34
Lamiaceae	Glechoma hederacea L.*		Forest	2
Lamiaceae	Lamiastrum galeobdolon (L.) Ehrend. & Polatschek*	ssp. argentatum	Forest	3
Lamiaceae	Lamium amplexicaule L.*		Open	5
Lamiaceae	Lamium hybridum Vill.*		Open	1
Lamiaceae	Lamium purpureum L.*		Open	14
Lamiaceae	Lycopus americanus Muhl. ex W.P.C. Bartr.		Wetland	1
Lamiaceae	Lycopus europaeus L.*		Wetland	2
Lamiaceae	Lycopus uniflorus Michx.		Wetland	5
Lamiaceae	Marrubium vulgare L.*		Open	7
Lamiaceae	Melissa officinalis L.*		Open	1
Lamiaceae	Mentha canadensis L.		Wetland	5
Lamiaceae	Mentha piperita L.*		Open	1
Lamiaceae	Mentha pulegium L.*		Open	1
Lamiaceae	Mentha rotundifolia (L.) Huds.*		Open	1
Lamiaceae	Nepeta cataria L.*		Open	2
Lamiaceae	Prunella vulgaris L.	var. lanceolata, var. vulgaris	Open	11
Lamiaceae	Satureja douglasii (Benth.) Kuntze		Forest	36
Lamiaceae	Scutellaria galericulata L.		Wetland	2
Lamiaceae	Stachys cooleyae A. Heller		Forest	5
Lamiaceae	Stachys mexicana Benth.		Forest	1
Lamiaceae	Thymus pulegioides L.*		Open	1
Lentibulariaceae	Utricularia gibba L.		Wetland	1
Lentibulariaceae	Utricularia minor L.		Wetland	1
Lentibulariaceae	Utricularia vulgaris L.	ssp. macrohiza	Wetland	4
Liliaceae	Erythronium oregonum Applegate	ssp. oregonum	Forest	32
Liliaceae	Fritillaria affinis (Schult. & Schult. f.) Sealy		Open	86
Liliaceae	Lilium columbianum Leichtlin		Forest	19
Liliaceae	Prosartes hookeri Torr.		Forest	1
Liliaceae	Tulipa sp. L.*		Open	1
Linnaeaceae	Linnaea borealis L.	ssp. longiflora	Forest	9
Lycopodiaceae	Lycopodium clavatum L.		Wetland	2
Lythraceae	Lythrum salicaria L.*		Wetland	4
Malvaceae	Alcea rosea L.*		Open	1
Malvaceae	Malva neglecta Wallr.*		Open	1
Malvaceae	Malva sylvestris L.*		Open	1
Malvaceae	Sidalcea hendersonii S. Watson		Shoreline	2
Melanthiaceae	Toxicoscordion venenosum (S. Watson) Rydb.	var. venenosum	Open	61
Menyanthaceae	Menyanthes trifoliata L.		Wetland	2

Family	Full Species	Infra taxa	Habitat	Islands
Montiaceae	Calandrinia ciliata (Ruiz & Pav.) DC.		Shoreline	27
Montiaceae	Claytonia exigua Douglas ex Torr. & A. Gray	ssp. exigua, ssp. glauca	Shoreline	30
Montiaceae	Claytonia parviflora Douglas ex Hook.		Open	21
Montiaceae	Claytonia perfoliata Donn ex Willd.		Forest	91
Montiaceae	Claytonia rubra (Howell) Tidestr.		Shoreline	75
Montiaceae	Claytonia sibirica L.		Forest	7
Montiaceae	Montia dichotoma (Nutt.) Howell		Open	2
Montiaceae	Montia fontana L.		Shoreline	16
Montiaceae	Montia howellii S. Watson		Shoreline	2
Montiaceae	Montia linearis (Douglas) Greene		Open	6
Montiaceae	Montia parvifolia (Moc. ex DC.) Greene		Open	21
Nyctaginaceae	Abronia latifolia Eschsch.		Shoreline	3
Nymphaeaceae	Nuphar polysepala Engelm.		Wetland	6
Nymphaeaceae	Nymphaea odorata Aiton*		Wetland	2
Okay - possible	Solanum americanum Mill.		Open	1
Oleaceae	Ligustrum vulgare L.*		Forest	1
Onagraceae	Camissonia contorta (Douglas) Kearney		Open	1
Onagraceae	Chamaenerion angustifolium (L.) Scop.		Open	26
Onagraceae	Circaea alpina L.	ssp. pacifica	Forest	6
Onagraceae	Clarkia amoena (Lehm.) A. Nelson & J.F. Macbr.		Open	11
Onagraceae	Clarkia gracilis (Piper) A. Nelson & J.F. Macbr.	ssp. gracilis	Open	2
Onagraceae	Epilobium anagallidifolium Lam.		Forest	1
Onagraceae	Epilobium brachycarpum C. Presl		Open	14
Onagraceae	Epilobium ciliatum Raf.		Open	27
Onagraceae	Epilobium densiflorum (Lindl.) Hoch & P.H. Raven		Wetland	2
Onagraceae	Epilobium glandulosum Lehm.		Open	2
Onagraceae	Epilobium hirsutum L.*		Open	2
Onagraceae	Epilobium lactiflorum Hausskn.		Open	1
Onagraceae	Epilobium leptophyllum Raf.		Wetland	2
Onagraceae	Epilobium minutum Lindl.		Open	28
Onagraceae	Epilobium palustre L.		Wetland	1
Onagraceae	Epilobium torreyi (S. Watson) Hoch & P.H. Raven		Wetland	1
Onagraceae	Ludwigia palustris (L.) Elliott		Wetland	3
Onagraceae	Oenothera glazioviana Micheli*		Open	1
Ophioglossaceae	Botrypus virginianus (L.) Michx.		Forest	1
Ophioglossaceae	Ophioglossum pusillum Raf.		Forest	1
Ophioglossaceae	Sceptridium multifidum (Gmel.) Tagawa		Forest	6
Orchidaceae	Calypso bulbosa (L.) Oakes	var. occidentalis	Forest	19
Orchidaceae	Cephalanthera austiniae (A. Gray) A. Heller		Forest	3

Family	Full Species	Infra taxa	Habitat	Islands
Orchidaceae	Corallorhiza maculata (Raf.) Raf.	var. maculata, var. occidentalis	Forest	21
Orchidaceae	Corallorhiza mertensiana Bong.		Forest	3
Orchidaceae	Corallorhiza striata Lindl.	var. striata	Forest	4
Orchidaceae	Epipactis helleborine (L.) Crantz*		Forest	12
Orchidaceae	Goodyera oblongifolia Raf.		Forest	29
Orchidaceae	Neottia banksiana (Lind.) Rchb. f.		Forest	2
Orchidaceae	Neottia convallarioides (Sw.) Richardson		Forest	1
Orchidaceae	Neottia cordata (L.) Richardson*		Forest	7
Orchidaceae	Platanthera dilatata (Pursh) Lindl. ex L.C. Beck	var. albiflora, var. leucostachys	Forest	3
Orchidaceae	Platanthera elegans Lindl.	ssp. elegans	Open	43
Orchidaceae	Platanthera elongata (Rydb.) R.M. Bateman		Forest	4
Orchidaceae	Platanthera orbiculata (Pursh) Lindl.		Forest	2
Orchidaceae	Platanthera stricta Lindl.		Forest	1
Orchidaceae	Platanthera transversa (Suksd.) R.M. Bateman		Forest	6
Orchidaceae	Platanthera unalascensis (Spreng.) Kurtz		Forest	10
Orchidaceae	Spiranthes romanzoffiana Cham.		Open	8
Orobanchaceae	Aphyllon californicum (Cham. & Schltdl.) A. Gray	ssp. californicum	Open	33
Orobanchaceae	Aphyllon purpureum (A. Heller) Holub		Open	29
Orobanchaceae	Bellardia viscosa (L.) Fisch. & C.A. Mey.*		Open	3
Orobanchaceae	Castilleja attenuata (A. Gray) T.I. Chuang & Heckard		Open	10
Orobanchaceae	Castilleja hispida Benth.	var. hispida	Open	47
Orobanchaceae	Castilleja levisecta Greenm.		Open	2
Orobanchaceae	Castilleja victoriae Fairbarns & J.M. Egger		Open	1
Orobanchaceae	Euphrasia nemorosa (Pers.) Wallr.*		Open	3
Orobanchaceae	Kopsiopsis hookeri (Walp.) Govaerts		Forest	2
Orobanchaceae	Orthocarpus bracteosus Benth.		Open	1
Orobanchaceae	Rhinanthus minor L.		Open	1
Orobanchaceae	Triphysaria pusilla (Benth.) T.I. Chuang & Heckard		Open	35
Oxalidaceae	Oxalis corniculata L.*		Open	1
Papaveraceae	Corydalis lutea (L.) DC.*		Forest	1
Papaveraceae	Dicentra formosa (Haw.) Walp.	ssp. formosa	Forest	2
Papaveraceae	Eschscholzia californica Cham.*	ssp. californica	Open	9
Papaveraceae	Fumaria officinalis L.*		Open	1
Papaveraceae	Meconella oregana Nutt.		Open	2
Papaveraceae	Papaver rhoeas L.*		Open	1
Papaveraceae	Papaver somniferum L.*		Open	2

Family	Full Species	Infra taxa	Habitat	Islands
Phrymaceae	Erythranthe alsinoides (Douglas ex Benth.) G.L. Nesom & N.S. Fraga		Forest	26
Phrymaceae	Erythranthe guttata (Fisch. ex DC.) G.L. Nesom		Forest	21
Phrymaceae	Erythranthe microphylla (Benth.) G.L. Nesom		Forest	6
Phrymaceae	Erythranthe moschata (Douglas ex Lindl.) G.L. Nesom		Forest	2
Phrymaceae	Erythranthe nasuta (Greene) G.L. Nesom		Forest	23
Phrymaceae	Erythranthe ptilota G.L. Nesom		Forest	1
Pinaceae	Abies grandis (Douglas ex D. Don) Lindl.		Forest	34
Pinaceae	Picea sitchensis (Bong.) Carrière		Forest	18
Pinaceae	Pinus contorta Douglas ex Loudon	var. contorta, var. latifolia	Forest	27
Pinaceae	Pinus monticola Douglas ex D. Don		Forest	2
Pinaceae	Pseudotsuga menziesii (Mirb.) Franco	var. menziesii	Forest	75
Pinaceae	Tsuga heterophylla (Raf.) Sarg.		Forest	16
Plantaginaceae	Antirrhinum majus L.*		Open	2
Plantaginaceae	Callitriche heterophylla Pursh	var. bolanderi	Wetland	2
Plantaginaceae	Callitriche palustris L.		Wetland	2
Plantaginaceae	Collinsia grandiflora Lindl.		Open	25
Plantaginaceae	Collinsia parviflora Lindl.		Open	84
Plantaginaceae	Cymbalaria muralis G. Gaertn., B. Mey. & Scherb.*	ssp. muralis	Open	2
Plantaginaceae	Digitalis purpurea L.*	var. purpurea	Open	12
Plantaginaceae	Hippuris vulgaris L.		Wetland	5
Plantaginaceae	Linaria dalmatica (L.) Mill.*	ssp. dalmatica	Open	2
Plantaginaceae	Linaria purpurea (L.) Mill.*		Open	1
Plantaginaceae	Linaria vulgaris Mill.*		Open	1
Plantaginaceae	Nuttallanthus texanus (Scheele) D.A. Sutton		Open	1
Plantaginaceae	Plantago elongata Pursh		Shoreline	29
Plantaginaceae	Plantago lanceolata L.*		Open	73
Plantaginaceae	Plantago major L.*		Open	11
Plantaginaceae	Plantago maritima L.		Shoreline	107
Plantaginaceae	Veronica americana Schwein. ex Benth.		Wetland	7
Plantaginaceae	Veronica arvensis L.*		Open	66
Plantaginaceae	Veronica chamaedrys L.*		Open	1
Plantaginaceae	Veronica filiformis Sm.*		Open	1
Plantaginaceae	Veronica officinalis L.*		Open	5
Plantaginaceae	Veronica peregrina L.	var. xalapensis	Wetland	5
Plantaginaceae	Veronica persica Poir.*		Open	1
Plantaginaceae	Veronica scutellata L.		Wetland	4
Plantaginaceae	Veronica serpyllifolia L.	var. humifusa, var. serpyllifolia	Wetland	11
Plumbaginaceae	Armeria maritima (Mill.) Willd.	ssp. californica	Shoreline	42

Family	Full Species	Infra taxa	Habitat	Islands
Poaceae	Achnatherum lemmonii (Vasey) Barkworth	ssp. lemmonii	Open	6
Poaceae	Achnatherum nelsonii (Scribn.) Barkworth	ssp. dorei	Open	2
Poaceae	Agrostis capillaris L.*		Open	9
Poaceae	Agrostis exarata Trin.		Shoreline	28
Poaceae	Agrostis gigantea Roth*		Open	6
Poaceae	Agrostis microphylla Steud.		Wetland	1
Poaceae	Agrostis pallens Trin.		Open	6
Poaceae	Agrostis scabra Willd.		Open	4
Poaceae	Agrostis stolonifera L.*		Open	18
Poaceae	Aira caryophyllea L.*	var. caryophyllea	Open	106
Poaceae	Aira praecox L.*		Open	123
Poaceae	Alopecurus aequalis Sobol.	var. aequalis	Wetland	4
Poaceae	Alopecurus geniculatus L.		Wetland	4
Poaceae	Alopecurus pratensis L.*		Open	5
Poaceae	Anthoxanthum odoratum L.*		Open	25
Poaceae	Arrhenatherum elatius (L.) P. Beauv. ex J. Presl & C. Presl*	var. bulbosum, var. elatius	Open	4
Poaceae	Avena barbata Pott ex Link*		Open	4
Poaceae	Avena fatua L.*		Open	2
Poaceae	Avena sativa L.*		Open	1
Poaceae	Bromus commutatus Schrad.*		Open	4
Poaceae	Bromus diandrus Roth*		Open	106
Poaceae	Bromus hordeaceus L.*		Open	124
Poaceae	Bromus pacificus Shear		Forest	30
Poaceae	Bromus sitchensis Trin.	var. carinatus, var. marginatus, var. sitchensis	Forest	104
Poaceae	Bromus sterilis L.*		Open	77
Poaceae	Bromus tectorum L.*		Open	60
Poaceae	Bromus vulgaris (Hook.) Shear		Forest	16
Poaceae	Calamagrostis canadensis (Michx.) P. Beauv.		Wetland	1
Poaceae	Calamagrostis stricta (Timm) Koeler	ssp. inexpansa	Wetland	1
Poaceae	Cynosurus cristatus L.*		Open	6
Poaceae	Cynosurus echinatus L.*		Open	26
Poaceae	Dactylis glomerata L.*		Open	72
Poaceae	Danthonia californica Bol.		Open	13
Poaceae	Danthonia spicata (L.) P. Beauv. ex Roem. & Schult.		Open	1
Poaceae	Deschampsia caespitosa (L.) P. Beauv.		Wetland	4
Poaceae	Deschampsia danthonioides (Trin.) Munro		Wetland	1
Poaceae	Deschampsia elongata (Hook.) Munro		Wetland	3
Poaceae	Distichlis spicata (L.) Greene		Shoreline	68
Poaceae	Elymus elymoides (Raf.) Swezey	ssp. brevifolius	Open	1

Family	Full Species	Infra taxa	Habitat	Islands
Poaceae	Elymus glaucus Buckley	ssp. glaucus	Open	90
Poaceae	Elymus repens (L.) Gould*		Open	12
Poaceae	Elymus trachycaulus (Link) Gould ex Shinners	ssp. trachycaulus	Open	13
Poaceae	Festuca occidentalis Hook.		Forest	38
Poaceae	Festuca roemeri (Pavlick) E.B. Alexeev	var. roemeri	Open	14
Poaceae	Festuca rubra L.		Open	141
Poaceae	Festuca subulata Trin.		Forest	4
Poaceae	Festuca subuliflora Scribn.		Forest	7
Poaceae	Festuca trachyphylla (Hack.) Krajina*		Open	1
Poaceae	Glyceria borealis (Nash) Batch.		Wetland	3
Poaceae	Glyceria elata (Nash) M.E. Jones		Wetland	2
Poaceae	Glyceria occidentalis (Piper) J.C. Nelson		Wetland	1
Poaceae	Holcus lanatus L.*		Open	78
Poaceae	Holcus mollis L.*	ssp. mollis	Open	1
Poaceae	Hordeum brachyantherum Nevski		Shoreline	43
Poaceae	Hordeum depressum (Scribn. & J.G. Sm.) Rydb.		Shoreline	6
Poaceae	Hordeum jubatum L.	ssp. Intermedium	Shoreline	4
Poaceae	Hordeum marinum Huds.*	ssp. gussoneanum	Shoreline	1
Poaceae	Hordeum murinum L.*	ssp. glaucum, ssp. leporinum, ssp. murinum	Shoreline	66
Poaceae	Koeleria macrantha (Ledeb.) Schult.		Open	61
Poaceae	Leersia oryzoides (L.) Sw.		Wetland	1
Poaceae	Leymus mollis (Trin.) Pilg.	ssp. mollis	Shoreline	66
Poaceae	Leymus vancouverensis (Vasey) Pilg.		Shoreline	1
Poaceae	Lolium multiflorum Lam.*		Open	3
Poaceae	Lolium perenne L.*		Open	19
Poaceae	Melica subulata (Griseb.) Scribn.		Forest	38
Poaceae	Panicum miliaceum L.*	ssp. millaceum	Open	1
Poaceae	Phalaris arundinacea L.*		Open	10
Poaceae	Phleum pratense L.*		Open	6
Poaceae	Poa annua L.*		Open	98
Poaceae	Poa bulbosa L.*	ssp. vivipara	Open	26
Poaceae	Poa compressa L.*		Open	43
Poaceae	Poa confinis Vasey		Shoreline	12
Poaceae	Poa howellii Vasey & Scribn.		Forest	2
Poaceae	Poa infirma Kunth*		Shoreline	1
Poaceae	Poa palustris L.*		Open	3
Poaceae	Poa pratensis L.*		Open	80
Poaceae	Poa secunda J. Presl	ssp. secunda	Open	5
Poaceae	Poa trivialis L.*		Open	5
Poaceae	Polypogon monspeliensis (L.) Desf.*		Shoreline	10

Family	Full Species	Infra taxa	Habitat	Islands
Poaceae	Puccinellia nutkaensis (J. Presl) Fernald & Weath.		Shoreline	91
Poaceae	Puccinellia nuttalliana (Schult.) Hitchc.		Shoreline	5
Poaceae	Puccinellia pumila (Vasey) Hitchc.		Shoreline	1
Poaceae	Schedonorus arundinaceus (Schreb.) Dumort.*		Open	30
Poaceae	Schedonorus pratensis (Huds.) P. Beauv.*		Open	2
Poaceae	Secale cereale L.*		Open	1
Poaceae	Setaria pumila (Poir.) Roem. & Schult.*		Open	1
Poaceae	Thinopyrum ponticum (Podp.) Barkworth & D.R. Dewey*		Open	1
Poaceae	Torreyochloa pallida (Torr.) G.L. Church	var. pauciflora	Wetland	8
Poaceae	Trisetum canescens Buckley		Forest	17
Poaceae	Trisetum cernuum Trin.		Forest	10
Poaceae	Vulpia bromoides (L.) Gray*		Open	107
Poaceae	Vulpia microstachys (Nutt.) Munro	var. pauciflora	Forest	10
Poaceae	Vulpia myuros (L.) C.C. Gmel.*		Open	88
Polemoniaceae	Collomia grandiflora Douglas ex Lindl.		Open	1
Polemoniaceae	Collomia heterophylla Douglas ex Hook.		Forest	5
Polemoniaceae	Collomia linearis Nutt.		Open	1
Polemoniaceae	Gilia capitata Sims		Open	1
Polemoniaceae	Leptosiphon bicolor Nutt.		Open	3
Polemoniaceae	Leptosiphon minimus (H. Mason) Battaglia		Open	6
Polemoniaceae	Microsteris gracilis (Hook.) Greene		Open	1
Polemoniaceae	Navarretia intertexta (Benth.) Hook.		Open	3
Polemoniaceae	Navarretia squarrosa (Eschsch.) Hook. & Arn.		Open	3
Polemoniaceae	Polemonium pulcherrimum Hook.	var. pulcherrimum	Open	2
Polygonaceae	Fallopia bohemica (Chrtek & Chrtková) J.P. Bailey*		Open	3
Polygonaceae	Fallopia convolvulus (L.) Á. Löve*		Open	2
Polygonaceae	Fallopia japonica (Houtt.) Ronse Decr.*		Open	2
Polygonaceae	Persicaria amphibia (L.) Gray		Wetland	5
Polygonaceae	Persicaria hydropiper (L.) Spach*		Wetland	1
Polygonaceae	Persicaria maculosa Gray*		Open	2
Polygonaceae	Polygonum aviculare L.*	ssp. aviculare, ssp.buxiforme, ssp. depressum	Shoreline	56
Polygonaceae	Polygonum douglasii Greene		Shoreline	4
Polygonaceae	Polygonum erectum L.		Shoreline	1
Polygonaceae	Polygonum fowleri B.L. Rob.	ssp. fowleri	Shoreline	6

Family	Full Species	Infra taxa	Habitat	Islands
Polygonaceae	Polygonum minimum S. Watson		Open	1
Polygonaceae	Polygonum nuttallii Small		Open	2
Polygonaceae	Polygonum paronychia Cham. & Schltdl.		Shoreline	1
Polygonaceae	Polygonum spergulariiforme Meisn. ex Small		Shoreline	68
Polygonaceae	Rumex acetosella L.*		Open	78
Polygonaceae	Rumex conglomeratus Murray*		Shoreline	6
Polygonaceae	Rumex crispus L.*		Shoreline	28
Polygonaceae	Rumex maritimus L.	ssp. fueginus	Shoreline	3
Polygonaceae	Rumex obtusifolius L.*		Shoreline	5
Polygonaceae	Rumex occidentalis S. Watson	var. occidentalis	Shoreline	11
Polygonaceae	Rumex salicifolius Weinm.	var. transitorius, var. triangulivalvis	Shoreline	22
Polypodiaceae	Polypodium amorphum Suksd.		Forest	3
Polypodiaceae	Polypodium glycyrrhiza D.C. Eaton		Open	86
Potamogetonaceae	Potamogeton amplifolius Tuck.		Wetland	2
Potamogetonaceae	Potamogeton berchtoldii Fieber		Wetland	1
Potamogetonaceae	Potamogeton crispus L.*		Wetland	1
Potamogetonaceae	Potamogeton epihydrus Raf.		Wetland	2
Potamogetonaceae	Potamogeton foliosus Raf.		Wetland	3
Potamogetonaceae	Potamogeton friesii Rupr.		Wetland	2
Potamogetonaceae	Potamogeton gramineus L.		Wetland	3
Potamogetonaceae	Potamogeton illinoensis Morong		Wetland	1
Potamogetonaceae	Potamogeton natans L.		Wetland	4
Potamogetonaceae	Potamogeton obtusifolius Mertens & W.D.J. Koch		Wetland	2
Potamogetonaceae	Potamogeton praelongus Wulfen		Wetland	4
Potamogetonaceae	Potamogeton pusillus L.		Wetland	1
Potamogetonaceae	Potamogeton richardsonii (A. Benn.) Rydb.		Wetland	2
Potamogetonaceae	Potamogeton robbinsii Oakes		Wetland	2
Potamogetonaceae	Potamogeton zosteriformis Fernald		Wetland	4
Potamogetonaceae	Stuckenia pectinata (L.) Borner		Wetland	2
Primulaceae	Cyclamen hederifolium Aiton*		Forest	1
Primulaceae	Dodecatheon hendersonii A. Gray		Open	3
Primulaceae	Dodecatheon pulchellum (Raf.) Merr.	var. pulchellum	Open	18
Primulaceae	Lysimachia arvensis (L.) U. Manns & Anderb.*		Open	6
Primulaceae	Lysimachia europaea (L.) U. Manns & Anderb.		Forest	4
Primulaceae	Lysimachia latifolia (Hook.) Cholewa		Forest	36
Primulaceae	Lysimachia maritima (L.) Galasso, Banfi & Soldano		Forest	2
Primulaceae	Lysimachia nummularia L.*		Forest	1
Primulaceae	Lysimachia thyrsiflora L.		Forest	2
Pteridaceae	Adiantum aleuticum (Rupr.) Paris	var. aleuticum	Forest	5
Pteridaceae	Aspidotis densa (Brack.) Lellinger		Open	7

Family	Full Species	Infra taxa	Habitat	Islands
Pteridaceae	Cryptogramma acrostichoides R. Br.		Forest	4
Pteridaceae	Pentagramma triangularis (Kaulf.) Yatsk., Windham & E. Wollenw.		Forest	17
Ranunculaceae	Anemone lyallii Britton		Open	2
Ranunculaceae	Aquilegia formosa Fisch. ex DC.	var. formosa	Open	7
Ranunculaceae	Aquilegia vulgaris L.*		Open	3
Ranunculaceae	Clematis vitalba L.*		Open	4
Ranunculaceae	Delphinium consolida L.*		Open	1
Ranunculaceae	Delphinium menziesii DC.		Open	12
Ranunculaceae	Ficaria verna Huds.*		Open	2
Ranunculaceae	Halerpestes cymbalaria (Pursh) Greene		Shoreline	2
Ranunculaceae	Helleborus foetidus L.*		Forest	2
Ranunculaceae	Myosurus minimus L.		Open	28
Ranunculaceae	Ranunculus acris L.*		Open	4
Ranunculaceae	Ranunculus aquatilis L.	var. diffusus	Wetland	2
Ranunculaceae	Ranunculus californicus Benth.		Open	10
Ranunculaceae	Ranunculus californicus x R. occidentalis		Open	8
Ranunculaceae	Ranunculus flammula L.	var. ovalis, var. reptans	Wetland	3
Ranunculaceae	Ranunculus macounii Britton		Wetland	2
Ranunculaceae	Ranunculus occidentalis Nutt.	var. occidentalis	Open	52
Ranunculaceae	Ranunculus repens L.*		Open	8
Ranunculaceae	Ranunculus sardous Crantz*		Open	1
Ranunculaceae	Ranunculus sceleratus L.	var. multifidus	Wetland	2
Ranunculaceae	Ranunculus uncinatus D. Don		Forest	12
Rhamnaceae	Frangula purshiana (DC.) A. Gray ex J.G. Cooper		Forest	3
Rosaceae	Amelanchier alnifolia (Nutt.) Nutt. ex M. Roem.		Forest	77
Rosaceae	Aphanes arvensis L.*		Open	22
Rosaceae	Aphanes australis Rydb.*		Open	40
Rosaceae	Aphanes occidentalis (Nutt.) Rydb.		Open	42
Rosaceae	Comarum palustre L.		Wetland	3
Rosaceae	Cotoneaster dielsianus E. Pritz. ex Diels*		Open	4
Rosaceae	Cotoneaster franchetii Bois*		Open	3
Rosaceae	Cotoneaster horizontalis Decne.*		Open	6
Rosaceae	Cotoneaster lacteus W.W. Sm.*		Open	1
Rosaceae	Cotoneaster rehderi Pojark.*		Open	1
Rosaceae	Cotoneaster simonsii Baker*		Open	3
Rosaceae	Crataegus douglasii Lindl.		Forest	4
Rosaceae	Crataegus gaylussacia A. Heller		Forest	2
Rosaceae	Crataegus monogyna Jacq.*	var. monogyna	Open	20
Rosaceae	Drymocallis glandulosa (Lindl.) Rydb.	ssp. glandulosa	Open	1
Rosaceae	Fragaria chiloensis (L.) Mill.		Shoreline	6
Rosaceae	Fragaria vesca L.	ssp. californica	Forest	31

Family	Full Species	Infra taxa	Habitat	Islands
Rosaceae	Fragaria virginiana Mill.	ssp. glauca	Open	35
Rosaceae	Geum macrophyllum Willd.		Forest	13
Rosaceae	Holodiscus discolor (Pursh) Maxim.	var. discolor	Forest	76
Rosaceae	Malus domestica (Suckow) Borkh.*		Open	17
Rosaceae	Malus fusca (Raf.) C.K. Schneid.		Forest	42
Rosaceae	Malus xdawsoniana Rehder.*		Open	1
Rosaceae	Oemleria cerasiformis (Torr. & A. Gray ex Hook. & Arn.) J.W. Landon		Forest	7
Rosaceae	Physocarpus capitatus (Pursh) Kuntze		Forest	3
Rosaceae	Potentilla anserina L.	ssp. anserina, ssp. pacifica	Wetland	24
Rosaceae	Potentilla argentea L.		Open	1
Rosaceae	Potentilla gracilis Douglas ex Hook.		Open	1
Rosaceae	Potentilla recta L.*		Open	2
Rosaceae	Poterium sanguisorba L.*	var. polygamum	Open	1
Rosaceae	Prunus avium (L.) L.*		Open	10
Rosaceae	Prunus cerasifera Ehrh.*		Open	7
Rosaceae	Prunus cerasus L.*		Open	3
Rosaceae	Prunus domestica L.*		Open	6
Rosaceae	Prunus emarginata (Douglas) Eaton		Forest	39
Rosaceae	Prunus laurocerasus L.*		Open	2
Rosaceae	Prunus lusitanica L.*		Open	1
Rosaceae	Prunus mahaleb L.*		Open	6
Rosaceae	Prunus pugetensis Jacobson & Zika*		Open	1
Rosaceae	Prunus virginiana L.		Forest	10
Rosaceae	Pyracantha coccinea M. Roem.*		Open	2
Rosaceae	Pyrus communis L.*		Open	9
Rosaceae	Pyrus nivalis Jacq.*		Open	1
Rosaceae	Rosa canina L.*		Open	2
Rosaceae	Rosa gymnocarpa Nutt.	ssp. gymnocarpa	Forest	38
Rosaceae	Rosa nutkana C. Presl	ssp. nutkana	Open	106
Rosaceae	Rosa pisocarpa A. Gray	var. pisocarpa	Forest	2
Rosaceae	Rosa rubiginosa L.*		Open	7
Rosaceae	Rosa rugosa Thunb.*		Open	2
Rosaceae	Rubus bifrons Vest*		Open	41
Rosaceae	Rubus laciniatus Willd.*		Open	14
Rosaceae	Rubus leucodermis Douglas ex Torr. & A. Gray		Forest	13
Rosaceae	Rubus nutkanus Moc. ex Ser.		Forest	19
Rosaceae	Rubus spectabilis Pursh		Forest	20
Rosaceae	Rubus ursinus Cham. & Schltdl.		Open	82
Rosaceae	Sorbaria kirilowii (Regel) Maxim.*		Forest	1
Rosaceae	Sorbus aucuparia L.*		Open	9
Rosaceae	Sorbus hybrida L.*		Open	1

Family	Full Species	Infra taxa	Habitat	Islands
Rosaceae	Sorbus intermedia (Ehrh.) Pers.*		Open	7
Rosaceae	Spiraea douglasii Hook.		Wetland	8
Rubiaceae	Galium aparine L.		Forest	95
Rubiaceae	Galium boreale L.		Forest	2
Rubiaceae	Galium divaricatum Pourr. ex Lam.*		Open	2
Rubiaceae	Galium murale (L.) All.*		Open	2
Rubiaceae	Galium odoratum (L.) Scop.*		Forest	3
Rubiaceae	Galium palustre L.		Forest	2
Rubiaceae	Galium trifidum L.		Forest	5
Rubiaceae	Galium triflorum Michx.		Forest	18
Rubiaceae	Sherardia arvensis L.*		Open	8
Ruppiaceae	Ruppia maritima L.		Shoreline	3
Salicaceae	Populus alba L.*		Open	2
Salicaceae	Populus tremuloides Michx.		Forest	8
Salicaceae	Populus trichocarpa Torr. & A. Gray		Forest	7
Salicaceae	Salix geyeriana Andersson		Wetland	1
Salicaceae	Salix hookeriana Barratt ex Hook.		Wetland	8
Salicaceae	Salix lasiandra Benth.	var. lasiandra	Wetland	10
Salicaceae	Salix prolixa Andersson		Wetland	2
Salicaceae	Salix scouleriana Barratt ex Hook.		Forest	47
Salicaceae	Salix sitchensis Sanson ex Bong.		Wetland	7
Santalaceae	Arceuthobium tsugense (Rosend.) G.N. Jones	ssp. contortae	Forest	3
Sapindaceae	Acer glabrum Torr.	ssp. douglasii	Forest	22
Sapindaceae	Acer macrophyllum Pursh		Forest	24
Saxifragaceae	Heuchera micrantha Douglas ex Lindl.	var. diversifolia	Forest	75
Saxifragaceae	Lithophragma glabrum Nutt.		Open	2
Saxifragaceae	Lithophragma parviflorum (Hook.) Nutt.		Open	40
Saxifragaceae	Micranthes integrifolia (Hook.) Small		Open	19
Saxifragaceae	Micranthes rufidula Small		Open	1
Saxifragaceae	Saxifraga austromontana Wiegand		Open	4
Saxifragaceae	Saxifraga cespitosa L.		Shoreline	42
Saxifragaceae	Tellima grandiflora (Pursh) Douglas ex Lindl.		Forest	18
Saxifragaceae	Tiarella trifoliata L.	var. laciniata, var. trifoliata, var. unifoliata	Forest	11
Scrophulariaceae	Verbascum blattaria L.*		Open	1
Scrophulariaceae	Verbascum thapsus L.*		Open	10
Selaginellaceae	Selaginella wallacei Hieron.		Open	78
Solanaceae	Solanum dulcamara L.*		Open	5
Solanaceae	Solanum physalifolium Rusby*		Open	1
Solanaceae	Solanum triflorum Nutt.*		Open	1
Taxaceae	Taxus brevifolia Nutt.		Forest	30
Thymelaeaceae	Daphne laureola L.*		Open	13

Family	Full Species	Infra taxa	Habitat	Islands
Typhaceae	Sparganium angustifolium Michx.		Wetland	4
Typhaceae	Sparganium emersum Rehmann		Wetland	2
Typhaceae	Sparganium eurycarpum Engelm.		Wetland	1
Typhaceae	Typha angustifolia L.*		Wetland	3
Typhaceae	Typha latifolia L.		Wetland	9
Ulmaceae	Ulmus procera Salisb.*		Forest	3
Urticaceae	Urtica dioica L.	ssp. gracilis	Forest	38
Urticaceae	Urtica urens L.*		Open	1
Valerianaceae	Centranthus ruber (L.) DC.*		Open	1
Valerianaceae	Plectritis brachystemon Fisch. & C.A. Mey.		Open	3
Valerianaceae	Plectritis congesta (Lindl.) DC.		Open	68
Valerianaceae	Valeriana scouleri Rydb.		Forest	3
Valerianaceae	Valerianella locusta (L.) Laterr.*		Open	4
Violaceae	Viola adunca Sm.		Open	3
Violaceae	Viola glabella Nutt.		Forest	2
Violaceae	Viola howellii A. Gray		Forest	2
Violaceae	Viola langsdorffii Fisch. ex Ging.		Wetland	1
Violaceae	Viola macloskeyi F.E. Lloyd		Wetland	1
Violaceae	Viola odorata L.*		Forest	1
Violaceae	Viola palustris L.		Wetland	1
Violaceae	Viola sempervirens Greene		Forest	2
Vitaceae	Vitis labrusca L.*		Forest	2
Vitaceae	Vitis vinifera L.*		Open	1
Woodsiaceae	Woodsia oregana D.C. Eaton	ssp. oregana	Forest	1
Woodsiaceae	Woodsia scopulina D.C. Eaton	ssp. laurentiana, ssp. scopulina	Forest	3

APPENDIX 2 – CHAPTER 1 TABLES

Table A2-1. Candidate models explaining the species area curve of islands and native and alien species. *Th1* and *Th2* are the model-derived island size thresholds. *Seg1-3* are the number of islands in each threshold.

Habitat - Nativity	**Model**	**AICc**	**BIC**	**R^2**	**Th1**	**Th2**	**seg1**	**seg2**	**seg3**
All Habitats - Native									
	ContTwo	1339.5	1360.1	0.94	13.56	7114.22	139	14	3
	ZslopeTwo	**1345.6**	**1363.4**	**0.94**	**0.05**	**1028.32**	**46**	**104**	**6**
	ContOne	1385.5	1400.3	0.92	762.30		150	6	
	ZslopeOne	1473.0	1484.9	0.86	0.26		81	75	
	Linear	1559.0	1568.0	0.76					
All Species - Alien									
	ContTwo	1142.2	1162.2	0.9	6984.37	13005.51	142	1	2
	ZslopeTwo	**1181.3**	**1198.5**	**0.86**	**0.08**	**4509.49**	**46**	**96**	**3**
	ContOne	1187.1	1201.6	0.86	1426.03		139	6	

Habitat - Nativity	Model	AICc	BIC	R^2	Th1	Th2	seg1	seg2	seg3
	ZslopeOne	1265.5	1277.2	0.75	3.27		113	32	
	Linear	1318.9	1327.6	0.63					
Shoreline - Native									
	ContTwo	897.1	917.7	0.8	1452.54	14194.73	150	4	2
	ContOne	908.5	923.3	0.78	1127.53		150	6	
	ZslopeTwo	**909.6**	**927.4**	**0.78**	**0.002**	**1153.79**	**4**	**146**	**6**
	ZslopeOne	955.8	967.7	0.7	0.01		15	141	
	Linear	959.2	968.2	0.69					
	Intercept	1139.6	1145.7	0					
Shoreline - Alien									
	ContTwo	561.9	581.9	0.72	1637.3	14260.25	139	5	1
	ContOne	569.7	584.2	0.69	1459.24		139	6	
	ZslopeTwo	**569.3**	**586.5**	**0.7**	**0.03**	**1637.3**	**28**	**111**	**6**
	ZslopeOne	584.1	595.8	0.66	2.3		109	36	
	Linear	614.3	623.0	0.57					
Open - Native									
	ZslopeTwo	**1122**	**1139.7**	**0.88**	**0.03**	**4700.32**	**35**	**118**	**3**
	ContTwo	1123.2	1143.8	0.88	0.03	4700.32	39	114	3
	ContOne	1137.1	1151.9	0.86	1486.37		150	6	
	ZslopeOne	1189.0	1200.9	0.81	0.07		54	102	
	Linear	1221.0	1229.8	0.76					
Open - Alien									
	ContTwo	1105.2	1125.2	0.88	7313.53	11861.16	142	1	2
	ZslopeTwo	**1143.3**	**1160.6**	**0.85**	**0.07**	**4406.84**	**42**	**100**	**3**
	ContOne	1147.2	1161.7	0.84	1528.01		139	6	
	ZslopeOne	1224.3	1235.9	0.73	3.05		113	32	
	Linear	1263.1	1271.9	0.64					
Forest - Native									
	ZslopeTwo	**1071.3**	**1089**	**0.93**	**0.17**	**11806.67**	**75**	**79**	**2**
	ContTwo	1070.1	1090.7	0.93	0.23	11806.67	79	75	2
	ZslopeOne	1095.0	1106.9	0.92	0.22		79	77	
	ContOne	1093.6	1108.4	0.92	0.29		82	74	
	Linear	1232.0	1241.0	0.79					
Forest - Alien									
	ZslopeTwo	**375.5**	**392.7**	**0.92**	**1.71**	**6083.13**	**106**	**36**	**3**
	ContTwo	374.9	394.9	0.92	3.5	6224.83	113	29	3
	ContOne	438.2	452.6	0.88	1106.95		139	6	

Habitat - Nativity	Model	AICc	BIC	R^2	Th1	Th2	seg1	seg2	seg3
	ZslopeOne	485.1	496.7	0.83	820.59		139	6	
	Linear	648.2	657	0.47					
Wetland - Native									
	ContTwo	695.7	716.3	0.98	52.74	13247.3	144	10	2
	ZslopeTwo	**702.5**	**720.3**	**0.98**	**47.0**	**13247.3**	**144**	**10**	**2**
	ContOne	874.3	889.1	0.94	400.1		150	6	
	ZslopeOne	885.8	897.7	0.93	356.56		150	6	
	Linear	1227.9	1236.8	0.36					
Wetland - Alien									
	ZslopeTwo	**217.7**	**234.9**	**0.79**	**22.09**	**7658.21**	**131**	**12**	**2**
	ContTwo	219.1	239.1	0.79	25.36	7658.21	131	12	2
	ZslopeOne	261.7	273.3	0.72	46.15		133	12	
	ContOne	260.7	275.2	0.72	187.99		137	8	
	Linear	382.1	390.9	0.34					

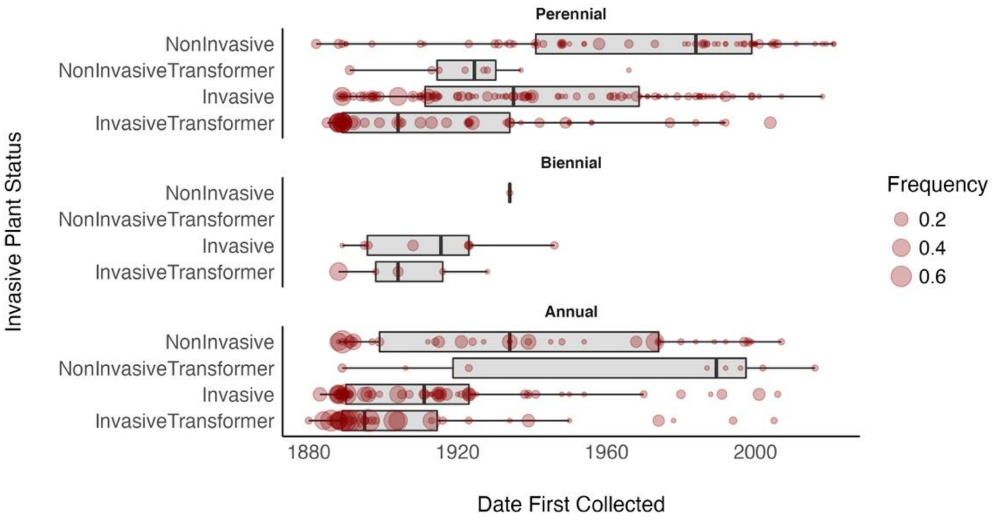

Figure A2-1. The residence time of alien plants in the Salish Sea region of the Pacific Northwest based on their invasive plant status and life span. Each red dot represents an individual plant species, the size of each dot increases with the observed occurrence frequency among surveyed islands. Boxplots represent the 1st and 3rd quartiles (grey box), the minimum and maximum (black horizontal line), and median (bold vertical line).

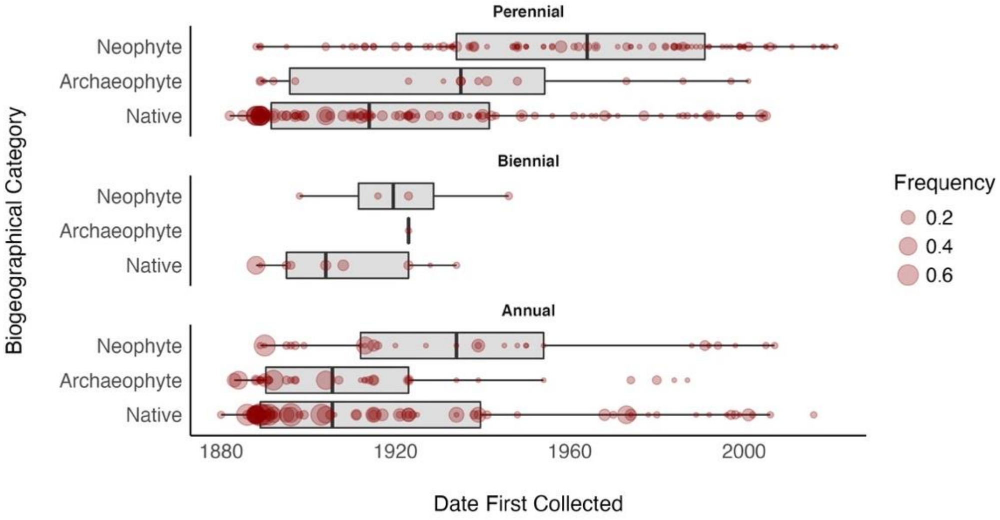

Figure A2-2. The residence time of alien plants in the Salish Sea region of the Pacific Northwest based on their biogeographical category and life span. Each red dot represents an individual plant species, the size of each dot increases with the observed occurrence frequency among surveyed islands. Boxplots represent the 1st and 3rd quartiles (grey box), the minimum and maximum (black horizontal line), and median (bold vertical line).

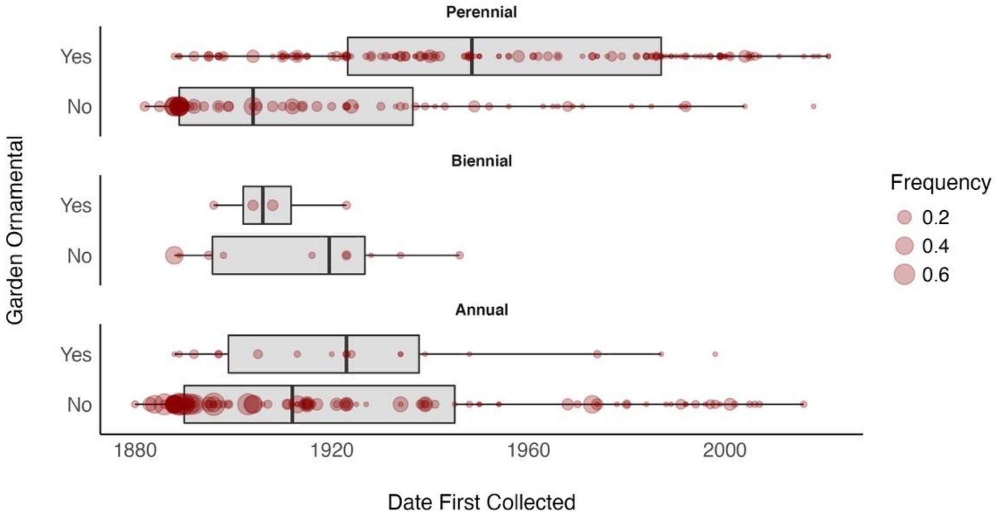

Figure A2-3. The residence time of alien plants in the Salish Sea region of the Pacific Northwest based on whether the species is an horticultural escape and life span. Each red dot represents an individual plant species, the size of each dot increases with the observed occurrence frequency among surveyed islands. Boxplots represent the 1st and 3rd quartiles (grey box), the minimum and maximum (black horizontal line), and median (bold vertical line).

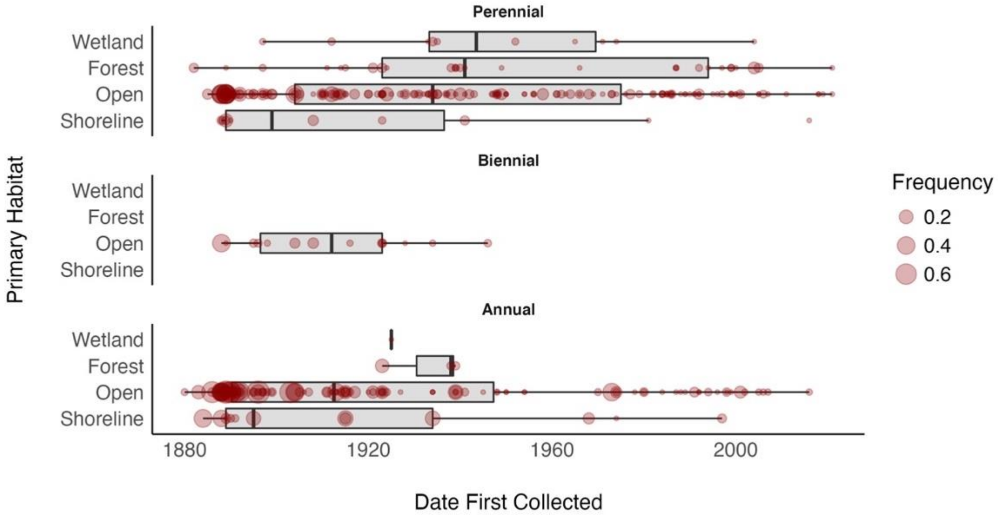

Figure A2-4. The residence time of alien plants in the Salish Sea region of the Pacific Northwest based on the primary habitat a species grows in and life span. Each red dot represents an individual plant species, the size of each dot increases with the observed occurrence frequency among surveyed islands. Boxplots represent the 1st and 3rd quartiles (grey box), the minimum and maximum (black horizontal line), and median (bold vertical line).

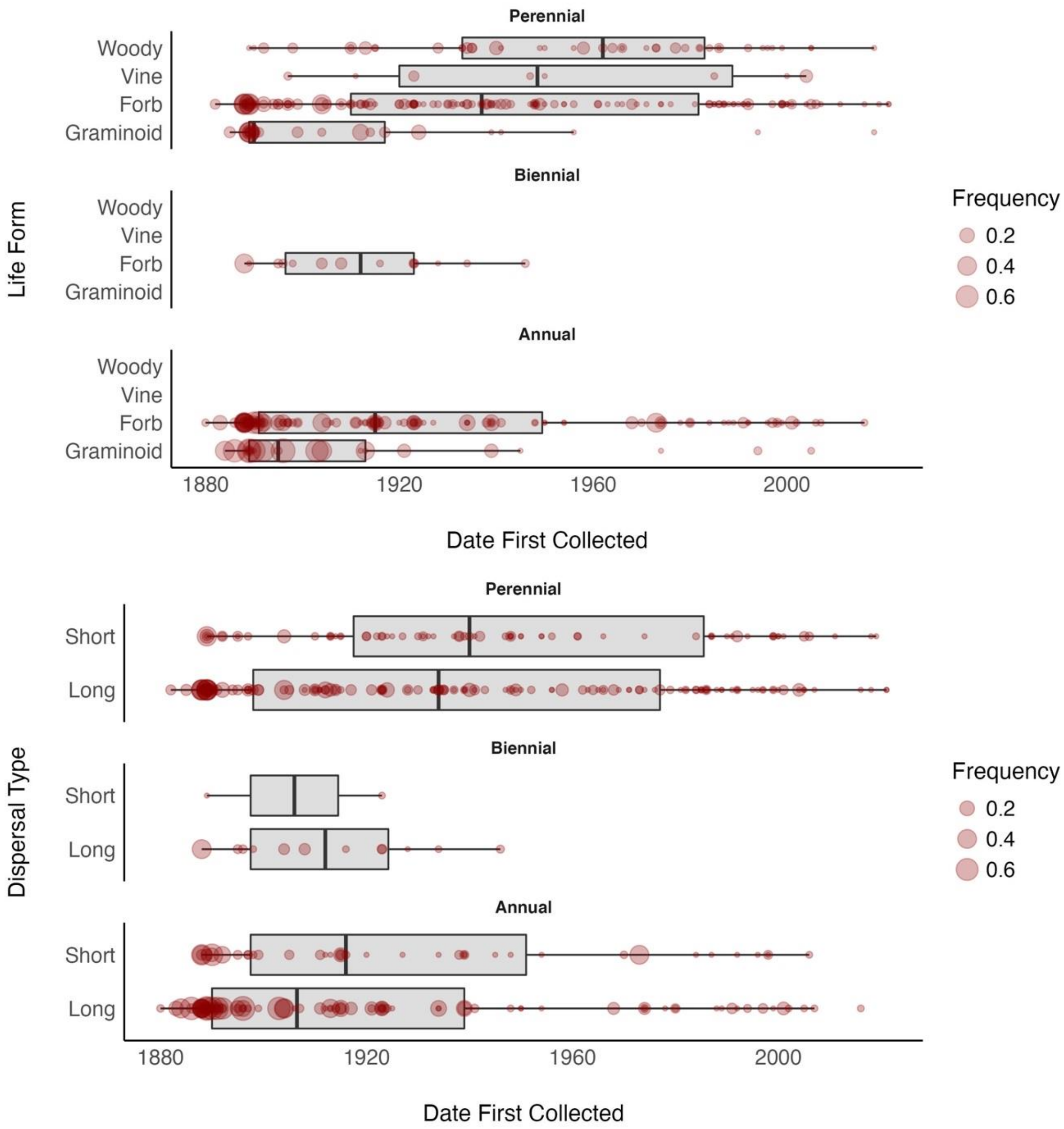

Figure A2-5. The residence time of alien plants in the Salish Sea region of the Pacific Northwest based on the life form, dispersal type and life span. Each red dot represents an individual plant species, the size of each dot increases with the observed occurrence frequency among surveyed islands. Boxplots represent the 1st and 3rd quartiles (grey box), the minimum and maximum (black horizontal line), and median (bold vertical line).

Table A2-2. The 20 candidate models describing the frequency of alien species across 145 islands in the San Juan Island Archipelago. *LOOIC* is the leave-one-out cross-validation information criterion and its standard error, the smaller the value the better relative fit. *W* is the model weight (the probability the model is the optimal model) based on Bayesian stacking of the posterior-predictive densities of each model. Thus, models with the greatest weights have the lowest relative predictive error. R^2 is the variance of each model's predictions divided by the prediction variance and the expected error variance, interpretation is roughly analogous to the classical R^2 value.

Model*	**LOOIC**	***w***	$\mathbf{R^2_{Fixed}}$	$\mathbf{R^2_{Full}}$
TSFS+Ornamental+Status+Type	6438.3 (522.1)	0.46	0.38	0.57
Status+TSFS	7053.8 (573.3)	0.03	0.33	0.51
Ornamental+TSFS	7127.2 (576.7)	<0.01	0.30	0.53
Type+TSFS	7138.5 (583.6)	0.04	0.31	0.50
LifeSpan + TSFS	7186.0 (597.3)	0.07	0.31	0.50
TSFS+Clonal+Form+LifeSpan+Dispersal+Habitat	7212.6 (587.4)	0.06	0.32	0.50
TSFS+Dispersal+Form+LifeSpan	7216 (598.3)	0.01	0.31	0.51
Clonal+TSFS	7405.5 (599.0)	<0.01	0.29	0.45
Form+TSFS	7537.5 (612.1)	<0.01	0.27	0.49
TSFS	7537.5 (615.7)	0.02	0.27	0.46
Habitat+TSFS	7538.2 (607.2)	0.02	0.27	0.46
Dispersal+TSFS	7540.5 (617.6)	<0.01	0.27	0.46
Type	7873.0 (691.9)	0.07	0.24	0.36
Ornamental	7934.0 (658.4)	0.03	0.23	0.43
Status	7989.4 (703.6)	0.06	0.25	0.31
LifeSpan	8331.7 (737.0)	0.07	0.22	0.22
Clonal	8516.1 (725.4)	0.05	0.20	0.14
Dispersal	8660.7 (735.8)	<0.01	0.18	0.07
Form	8674.4 (739.6)	0.02	0.18	0.28
Habitat	8749.4 (738.5)	<0.01	0.18	0.05

*TSFS = residence time, Ornamental = introduced garden ornamental, Status = if invasive, transformer, or naturalized, Type = if native, archaeophyte, or neophyte; Form = grass/forb/shrub/tree/vine; LifeSpan = annual/biennial/perennial; Dispersal = Long/Short; Habitat = primary habitat (shoreline/open/forest/wetland).

APPENDIX 3 CHAPTER TWO TABLES

Table A3-1. Model comparison table of eight candidate models explaining five components of plant diversity across 13 islands in the southern San Juan Island archipelago. *Decline Rate* is the ratio of the number of native plant colonizations to native plant extirpations per island. *Native EDbiogeo* is the change in the sum of evolutionary distinctiveness values for all native species on each island weighted by each species regional incidence in the archipelago. *Evolutionary Importance* is the change in the proportion of total evolutionary history represented on each island. *Nativity* is the change in the proportion of each islands flora comprised of native plants. *Functional Richness* is the sum of the number of unique combinations of dispersal type, lifespan, life form, and root form combinations. *LOOIC* is the leave-one-out cross-validation information criterion and its standard error, the smaller the value the better relative fit. *W* is the model weight (the probability the model is the optimal model) based on Bayesian stacking of the posterior-predictive densities of each model. Thus, models with the greatest weights have the lowest relative predictive error. R^2 is the variance of each model's predictions divided by the prediction variance and the expected error variance, interpretation is roughly analogous to the classical R^2 value. Bolded models comprise ≥ 90% of model weights.

Component	**Model***	**LOOIC**	***w***	**R^2**
Decline Rate				
	Impact	**40.33(5.73)**	**0.746**	**0.3**
	Area	**42.72(7.13)**	**0.253**	**0.14**
	IAG	41.76(5.97)	0.001	0.2
	IAG + Area	43.2(5.73)	0.000	0.26
	Impact + Area	41.81(5.92)	0.000	0.28
	DG	44.63(8.01)	0.000	0.28
	DG + Area	44.9(7.42)	0.000	0.38
	IAG + DG	44.98(6.79)	0.000	0.37
Δ Native ED_{biogeo}				
	Impact	**41.02(8.75)**	**0.758**	**0.38**
	Area	**44.07(7.66)**	**0.242**	**0.08**
	DG	42.79(7.27)	0.000	0.32
	IAG	42.78(6.76)	0.000	0.16
	IAG + Area	43.75(6.01)	0.000	0.21
	DG + Area	44.5(7.11)	0.000	0.39
	Impact + Area	41.92(7.1)	0.000	0.26
	IAG + DG	43.71(7.13)	0.000	0.4
Δ Evo. Importance				
	Impact	**41.25(11.87)**	**0.918**	**0.43**
	Area	48.9(15.28)	0.081	0.049
	IAG	46.86(14.24)	0.001	0.16
	IAG + Area	47.08(12.22)	0.000	0.21
	Impact + Area	42.36(11.56)	0.000	0.44
	DG	46.25(13)	0.000	0.26
	DG + Area	48.23(12.12)	0.000	0.3
	DG + IAG	46.79(11.17)	0.000	0.34
Δ Nativity				
	Impact	**-26.56(7.58)**	**0.610**	**0.42**
	IAG	**-25.98(6.8)**	**0.390**	**0.35**
	Impact + Area	-25.14(6.68)	0.000	0.44
	IAG + Area	-24.62(5.75)	0.000	0.37
	IAG + DG	-23.05(4.39)	0.000	0.48
	Area	-22.19(8.3)	0.000	0.14
	DG + Area	-20.03(5.28)	0.000	0.42
	DG	-20.99(6)	0.000	0.35
Δ Functional Richness				

Component	**Model***	**LOOIC**	***w***	**R^2**
	Impact	**41.25(11.87)**	**0.900**	**0.43**
	Area	49.2(15.19)	0.100	0.038
	IAG	48.3(13.72)	0.000	0.05
	Impact+Area	46.97(11.69)	0.000	0.25
	DG	48.51(12.39)	0.000	0.19
	DG+IAG	50.54(12.03)	0.000	0.22
	IAG+Area	49.42(13.34)	0.000	0.12
	DG+Area	49.34(11.22)	0.000	0.23

**Impact* is an index that accounts for the number and cover of invasive annual grasses (IAG) multiplied by the ordinal deer and goose impact score (DG). The impact index is normalized by the greatest values so all values are between 0 and 1. *Area* is the Log_{10} hectares of each island.

Table A3-2. Model comparison table of 31 candidate models explaining the probability of plant extirpation across 13 islands in the southern San Juan Island archipelago. *LOOIC* is the leave-one-out cross-validation information criterion and its standard error, the smaller the value the better relative fit. *W* is the model weight (the probability the model is the optimal model) based on Bayesian stacking of the posterior-predictive densities of each model. Thus, models with the greatest weights have the lowest relative predictive error. R^2 is the variance of each model's predictions divided by the prediction variance and the expected error variance, interpretation is roughly analogous to the classical R^2 value. Bolded models comprise ≥ 90% of model weights. For explanation of Model abbreviations see * in Table A3-1. * values in parenthesis denote refitted model weights when only considering the top four models.

Model	**LOOIC**	***w****	**R^2_{Fixed}**	**R^2_{Random}**
(N*A)+(N*Inc)+(N*Per)+(N*Cov)	239.67 (23.06)	0.06 (0.42)	0.48	0.13
(N*Cov)+(N*A)	243.25 (23.21)	0.07 (0.38)	0.46	0.15
(N*Inc)+(N*A)	249.68 (23.41)	0.051 (0.20	0.42	0.17
(N*Per)+(N*A)	261.69 (24.28)	0.00 (0.00)	0.4	0.19
N+A+Inc+Per+Cov	405.9 (29.1)	0.112	0.34	0.11
N+Inc+Per+Cov	406.29 (29.14)	0.109	0.33	0.12
(N*Inc)+(N*Per)+(N*Cov)	407.98 (29.72)	0.118	0.34	0.11
A+(N*Impact)+Inc+Per+Cov	409.99 (29.52)	0.002	0.34	0.04
(N*A)+(N*Impact)+(N*Inc)+(N*Per)+(N*Cov)	411.68 (29.86)	0.087	0.35	0.03
N*Cov	412.4 (30.22)	0.142	0.32	0.14
N+Cov	413.7 (29.88)	0.00	0.32	0.16
N+A+Cov	414.02 (29.91)	0.00	0.32	0.14
(N*Impact)+Cov	416.92 (29.94)	0.00	0.32	0.09
N+Inc	418.49 (29.61)	0.00	0.3	0.2
N+A+Inc	418.62 (29.74)	0.00	0.31	0.18
(N*Impact)+(N*A)+(N*Cov)	418.68 (30.71)	0.00	0.33	0.04
(N*Impact)+Inc	418.76 (29.98)	0.109	0.31	0.13
N*Inc	420.53 (29.97)	0.00	0.3	0.2
(N*Impact)+(N*A)+(N*Inc)	424.49 (30.63)	0.00	0.31	0.08
N*Per	428.9 (30.63)	0.077	0.28	0.23
N+Per	429.14 (30.59)	0.00	0.28	0.23
(N*Impact)+Per	430.09 (30.9)	0.021	0.29	0.16
N+A+Per	430.17 (30.87)	0.00	0.28	0.21
N	430.94 (30.64)	0.00	0.28	0.27
A+N	431.47 (30.74)	0.00	0.28	0.24
(N*Impact)+A	431.79 (30.83)	0.00	0.29	0.12
Impact	431.94 (30.91)	0.00	0.29	0.17
(N*Impact)+(N*A)+(N*Per)	432.41 (31.43)	0.04	0.29	0.1
N*A	433.81 (30.91)	0.00	0.28	0.23
Impact+Area	434.44 (31.02)	0.00	0.29	0.12
(N*Impact)+(N*A)	434.82 (31.14)	0.00	0.29	0.12

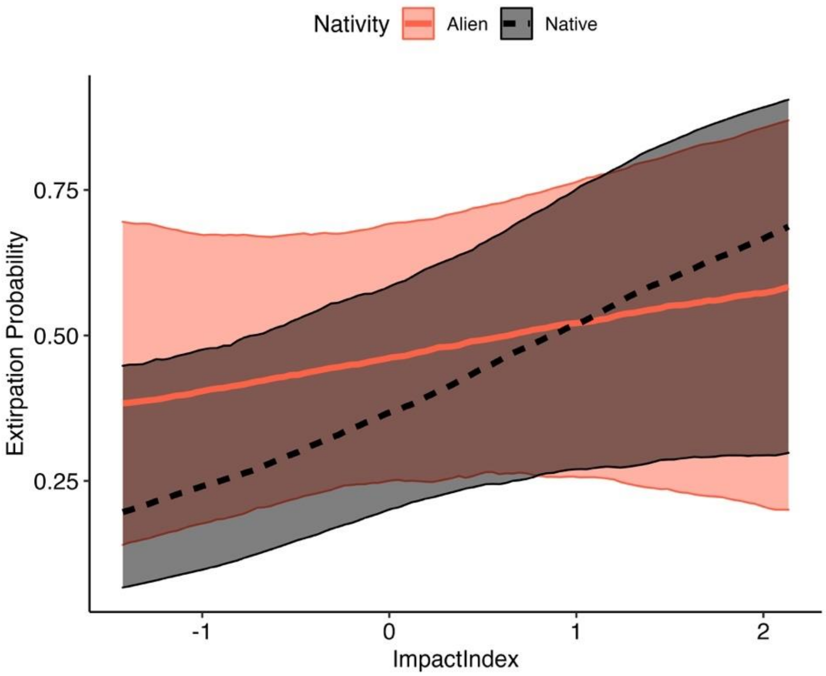

Figure A3-1. Predicted influence of the synergistic impact of IAG, geese and deer on the extirpation probability of alien and native plants. Error bands represent 90% credible intervals.

Table A3-3. The number of colonization and extirpation events among native and alien vascular plants across 14 islands along the Southern end of the San Juan Island archipelago.

Nativity	Taxon	Colonized	Extirpated
Alien			
	Bromus sterilis	4	
	Cerastium pumilum	4	
	Vulpia myuros	4	
	Vicia sativa	3	
	Cakile maritima ssp. maritima	2	2
	Senecio vulgaris	2	2
	Polygonum aviculare	2	1
	Rosa rubiginosa	2	
	Spergularia rubra	2	
	Vulpia bromoides	2	
	Sonchus oleraceus	1	3
	Plantago lanceolata	1	2
	Aira caryophyllea var. caryophyllea	1	1
	Erodium cicutarium	1	1
	Hypochaeris radicata	1	1
	Sonchus asper ssp. asper	1	1
	Cakile edentula	1	
	Cardamine hirsuta	1	
	Cerastium glomeratum	1	
	Dactylis glomerata	1	
	Geranium dissectum	1	
	Gnaphalium uliginosum	1	
	Hordeum murinum	1	
	Ilex aquifolium	1	
	Lepidium latifolium	1	
	Poa annua	1	
	Poa pratensis	1	
	Polypogon monspeliensis	1	
	Rumex crispus	1	
	Schedonorus arundinaceus	1	
	Silene gallica	1	
	Stellaria pallida	1	
	Aira praecox		2
	Oxybasis rubra		2
	Stellaria media		2
	Taraxacum officinale		2

Nativity	Taxon	Colonized	Extirpated
	Atriplex patula		1
	Atriplex prostrata		1
	Brassica juncea		1
	Bromus hordeaceus		1
	Cerastium fontanum ssp. vulgare		1
	Cirsium vulgare		1
	Geranium molle		1
	Leontodon autumnalis		1
	Malus domestica		1
	Rumex acetosella		1
	Sonchus arvensis		1
	Spergularia salina		1
	Taraxacum erythrospermum		1
	Veronica arvensis		1
Native			
	Polygonum spergulariiforme		4
	Claytonia exigua	1	3
	Plantago maritima	1	3
	Aphyllon californicum ssp. californicum		3
	Polystichum munitum		3
	Shepherdia canadensis		3
	Trifolium willdenovii		3
	Achillea millefolium	1	2
	Claytonia perfoliata	1	2
	Spergularia macrotheca var. macrotheca	1	2
	Atriplex dioica		2
	Festuca rubra		2
	Hordeum brachyantherum		2
	Hornungia procumbens		2
	Malus fusca		2
	Montia fontana		2
	Opuntia fragilis		2
	Vicia hirsuta		1
	Brodiaea coronaria	1	1
	Claytonia rubra	1	1
	Conioselinum pacificum	1	1
	Grindelia hirsutula	1	1
	Luzula subsessilis	1	1

Nativity	Taxon	Colonized	Extirpated
	Maianthemum stellatum	1	1
	Trifolium microdon	1	1
	Acer glabrum var. douglasii		1
	Agrostis exarata		1
	Amelanchier alnifolia		1
	Armeria maritima ssp. californica		1
	Berberis aquifolium		1
	Bromus pacificus		1
	Cerastium arvense ssp. strictum		1
	Chamaenerion angustifolium		1
	Collinsia parviflora		1
	Elymus glaucus		1
	Festuca roemeri		1
	Fritillaria affinis		1
	Galium aparine		1
	Gaultheria shallon		1
	Heuchera micrantha		1
	Hordeum depressum		1
	Lepidium virginicum ssp. menziesii		1
	Leymus mollis ssp. mollis		1
	Lomatium utriculatum		1
	Lupinus microcarpus var. microcarpus		1
	Oxytropis campestris var. spicata		1
	Pentagramma triangularis		1
	Platanthera elegans ssp. elegans		1
	Platanthera unalascensis		1
	Plectritis congesta		1
	Polygonum fowleri ssp. fowleri		1
	Polypodium glycyrrhiza		1
	Potentilla anserina		1
	Pseudognaphalium stramineum		1
	Pseudotsuga menziesii var. menziesii		1
	Puccinellia nutkaensis		1
	Quercus garryana var. garryana		1
	Ranunculus californicus × R. occidentalis		1
	Ribes divaricatum var. divaricatum		1
	Rubus nutkanus		1
	Sabulina macra		1
	Sanicula bipinnatifida		1

Nativity	Taxon	Colonized	Extirpated
	Sarcocornia pacifica		1
	Sedum lanceolatum		1
	Sedum spathulifolium		1
	Sisyrinchium idahoense		1
	Trifolium variegatum		1
	Triphysaria pusilla		1
	Turritis glabra		1
	Vicia americana var. americana		1
	Juncus bufonius	2	
	Plagiobothrys scouleri	2	
	Sambucus racemosa var. arborescens	2	
	Ambrosia chamissonis	1	
	Bromus sitchensis var. sitchensis	1	
	Distichlis spicata	1	
	Holodiscus discolor	1	
	Lathyrus japonicus	1	
	Lathyrus nevadensis var. nevadensis	1	
	Ranunculus californicus	1	
	Ribes sanguineum var. sanguineum	1	
	Sagina decumbens ssp. occidentalis	1	
	Sagina maxima	1	
	Salix scouleriana	1	
	Sanicula crassicaulis	1	