Multi-scale comparison of native and exotic communities in the Garry oak ecosystem of British Columbia

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A THESIS SUBMITTED IN PARTIAL FULFILLMENT OF
THE REQUIREMENTS FOR THE DEGREE OF
DOCTOR OF PHILOSOPHY

in

THE FACULTY OF GRADUATE STUDIES

(Forestry)

THE UNIVERSITY OF BRITISH COLUMBIA

(Vancouver)

March 2012

Abstract

Fundamental debates persist regarding the ecology of species invasions, the risk posed by exotic species, and the most effective management to diminish invasion and promote native-dominated ecosystems. Using vascular plant surveys at three scales (between small-island and 'mainland' patches, among patches, within patches) from 86 patches in a threatened meadow ecosystem, I addressed the following questions arising from such debates: 1) Are latent invasions prevalent among exotics, and if so, among which species? 2) What are the relative roles of latent invasions, competition and environmental response in determining native versus exotic biogeographic patterns? 3) How can native and exotic species distribution and richness models at multiple scales be used to improve conservation management? Species-level analyses demonstrated latent invasions among and within patches for short-dispersing exotics, and a positive relationship between exotic species' abundances and minimum residence time in the study region, suggesting that population expansion of some exotic species is at an early stage. A mix of scale-dependent concordant and discordant relationships with environmental variables, rather than competition, appeared to be the primary determinant of native versus exotic species richness and composition patterns. While incomplete invasion of exotics did not produce substantially different community-level biogeographic patterns between native and exotic communities, exotics were dominated by long-dispersing ruderal species more abundant on disturbed patches, while dominant natives were often short-dispersing stress-tolerant species more abundant on isolated patches. Such complexities, overlooked in most previous comparative analyses of native and exotic communities, can be used to predict future patterns and prescribe efficient management. In addition, spatially explicit distribution models revealed greater predictability for native species, and greater predictability among than within patches. Environmental variables related to native and exotic distributions were often shared within patches. Thus, management prescriptions applied among patches are likely to be most successful and predictable. Finally, native species at risk were more common on isolated small-island patches, contrary to biogeographic theory. Protection of small-island patches would be the most efficient conservation strategy for the study system. Interventions to control large exotic species populations, especially where propagule pressure from nearby disturbed areas is high, represent a far less efficient strategy.

Preface

Though I took the lead in study design, collecting and analyzing the data, formulating the conclusions and writing for each chapter, this thesis benefitted greatly from generous advice and data sharing by my colleagues. The following contributions by co-authors and other colleagues are gratefully acknowledged:

Chapter 2: The following co-authors provided valuable assistance: *Mark Vellend* provided the idea of comparing Rabinowitz's 'forms of rarity' for native and exotic species, as well as analytical and editorial advice. *Patrick Lilley* generously allowed me to use his survey data for some of the Vancouver Island sites used in this study. He also provided editorial advice. *Will Cornwell* helped conduct phylogenetic analyses, and provided editorial advice. And *Peter Arcese* provided analytical and editorial advice, as well as logistical assistance, funding and general guidance on framing the arguments used in the paper. Mark Drever is not a co-author; however, he provided helpful assistance on the interpretation of negative binomial models. I collected 75% of the data, designed the analytical framework, conducted the analyses and wrote the paper.

Chapter 3: The following co-authors provided valuable assistance: *David Giblin* generously allowed me to use his survey data from some of the San Juan Island sites. *Peter Dunwiddie* was also responsible for collecting some of the San Juan Island data, and provided ecological and editorial advice. *Peter Arcese* provided editorial advice, logistical assistance, funding and guidance on framing the paper. Though not listed as a co-author, Patrick Lilley provided some data for Vancouver Island surveys. I collected 75% of the data, designed the analytical framework, conducted the analyses and wrote the paper.

Chapter 4: Though not listed as co-authors, the following people provided valuable assistance: Peter Arcese (logistical assistance, editorial advice and general guidance); David Giblin and Peter Dunwiddie (data from some of the San Juan Island sites); Patrick Lilley (data from some of the Vancouver Island sites); and Emily Gonzales (external data for model evaluation). I collected 75% of the data, designed the analytical framework, conducted the analyses and wrote the paper.

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Acknowledgements

I am very grateful for the inspiration and assistance I have received during my time at UBC.

Throughout the course of my studies, my supervisor Dr. Peter Arcese has been an excellent mentor. He is a respected supervisor and close friend; a jam buddy and a tough editor; a skilled and diligent scientist, and an advocate for a balanced lifestyle in his students. He allowed me the latitude to pursue my own ideas, while providing vital advice and guidance on countless occasions.

My supervisory committee has also provided valuable guidance on my thesis, and in general. Mark Vellend has taught me a great deal about plant ecology, through the UBC Florum discussion group (I will always remember the Great Debate between he and Roy), and through numerous conversations. He has also taught me a lot about writing and the scientific process. Andrew MacDougall has provided excellent scientific and career advice. He has also been generous in sharing his phenomenal knowledge of the scientific literature and the ecology of my study system. Sally Aitken has provided scientific advice, guidance, friendship and even some life counselling.

Many other people inspired me and helped me over the past few years. I would like to thank the following people in particular:

-Geurt from Taneum, Laos, for inspiring me to return to academia.

-Emily Gonzales for scientific advice and inspiration on how to live your life.

-Miriam Isaac-Renton and Rebecca Best for being the nicest and toughest field assistants I've ever had, and for helping to see the 'goose project' through.

-Richard Schuster, for political conversations that tended to be more interesting than plant ecology, and for being a statistical sounding board.

-Valerie LeMay, Mark Drever and David Tait, also for being statistical sounding boards.

-Roy Turkington and other Florum members for sharing knowledge of plant ecology.

-Ben Gilbert, John Smol, Ken Reimer, Claire Kaufman, Brian Cumming and Emily Young for assistance on side projects that helped to shape the analytical framework of my thesis. Thanks especially to Ben, for patience and determination when our 'quick stats note' exploded into a major project.

-Peter Dunwiddie for ecological and taxonomic advice, logistical support and friendship throughout my PhD.

-David Giblin for ecological and taxonomic advice, as well as data sharing.

Chapter 1: Introduction

Background

As the pace of human trade and rate of migration have accelerated, so has the rate of human-assisted introduction of species (hereafter, 'exotic species') to new environments (Robbins 2004; Ding et al. 2008). Invasive exotic species, defined herein as those that have a profound impact on their new environments (cf. Davis and Thompson 2000), can have far-reaching and destructive ecological and economic effects (Elton 1958). Several invasive species have been implicated in the collapse of native ecosystems and the extinction of native species (reviewed in Elton 1958; Mack et al. 2000; Simberloff 2000); and economic costs in the USA from invasive species have been estimated at ~$120 billion per year (Pimentel et al. 2005).

However, the vast majority of exotic species do not have profound ecological impacts, and in fact most fail to establish viable populations (Williamson and Fitter 1996). Indeed, considerable debate exists regarding the threats posed by species introductions. Some argue that the threats posed by exotic species are relatively small compared to other threats to ecosystems, and that 'invasions' are best viewed as extensions of processes that naturally occur in all ecosystems (e.g., Davis 2003; Davis et al. 2011). Others cite examples of invasive species that have caused ecological damage, and call for strong precautionary measures to limit species introductions and eradicate those exotic invasives that are present wherever possible (e.g., Mack et al. 2000; Lambertini et al. 2011). Such general debate about the ecological effects of exotic species is rooted in differing concepts of how native and exotic species interact with each other and their environments.

For terrestrial plants in particular, the direct ecological effects of exotic species, even those that become invasive, have been difficult to assess, and to separate from other anthropogenic ecological changes. Specific evidence exists that enhanced competitive ability may allow some exotic species to become dominant invasives. Callaway and Aschehoug (2000), for example, found evidence supporting the 'novel weapons' hypothesis: root exudates from *Centaurea diffusa* were shown to suppress the growth of other species in this invasive weed's introduced range, but in not its native range. Presumably, the plants in its native range have evolved tolerances of its allelopathic exudate. The invasive grass *Anthoxanthum odoratum* also appears to produce allelopathic exudate that may aid in its invasion (Yamamoto 1995). Callaway et al. (2004) also found evidence supporting the 'enemy release' hypothesis, whereby the exotic invader *Centaurea maculosa* is released from some of its natural enemies (in this case, soil biota) from its native habitat when it enters a new range.

However, beyond several specific examples, there is relatively little evidence for greater competitive ability of exotic plant species, even those that become invasive. Indeed, there is virtually no evidence for competition-driven extinction of native plants by exotic invasive plants (Davis 2003; Sax and Gaines 2008). And there is as yet no evidence for an upper limit of plant species richness at large (e.g., regional) scales (Stohlgren et al. 2008a), such that the addition of new exotic species does not appear to have precipitated the extirpation of natives at these scales.

Several studies have indicated that factors other than competition may be key to exotic species dominance. Experimental seeding of native species by Seabloom et al. (2003) indicated that subordinate perennial native grassland species appear to draw down resources

faster than dominant annual exotics, and suppress their growth when sown directly into the exotic swards. MacDougall and Turkington (2005) found that exotic dominants suppress growth of native species, but that recruitment limitation appears to have a stronger negative effect on native populations. In many cases, a profound anthropogenic environmental or ecological change may be the catalyst that allows exotic invasive species to dominate. Increased herbivory due to cessation of traditional hunting practices and/or diminished natural predator populations is an example of such a change. Experimental isolation of the effects of herbivory and competition by Gonzales and Arcese (2008) indicated that herbivory rather than competition was responsible for exotic plant species dominance in meadows where herbivores were abundant. Likewise, a study on the effects of herbivore removal versus nutrient drawdown by native and exotic plants in an exotic-dominated grassland (HilleRisLambers et al. 2010), suggested that resistance to herbivory, not competitive ability, was responsible for the exotic dominance.

Human disturbance is another common associate with exotic species dominance (e.g., Hobbs and Huenneke 1992; Hobbs and Humphries 1995; Vilà et al. 2007). Many exotic species are ruderals, adapted to growth in resource-rich environments (Daehler 2003), which are common in disturbed areas where vegetation removal provides resource opportunities for invaders (Davis et al. 2000). Thus, exotic invasive species may be opportunistic 'passengers' of human-induced ecological changes, rather than the engineers of changes themselves (cf. MacDougall and Turkington 2005). Whether ruderal exotic species populations may diminish once the disturbance is removed, as noted by Meiners (2007) in a long-term study of abandoned agricultural fields, or whether the exotic invasives will be 'transformative species' (cf. Richardson et al. 2000), engineering conditions for continued exotic dominance

(cf. Seabloom et al. 2003; Badano et al. 2007), is an important question requiring long-term research.

Predictability of invasiveness in exotic plant species has proven difficult. Some analyses indicate that invasiveness is predictable using traits such as dispersal ability (e.g., Rejmánek and Richardson 1996; Hamilton et al. 2005) or vegetative growth (e.g., van Kleunen et al. 2010), while others indicate that characteristics of native and invasive species largely overlap (Thompson et al. 1995; Daehler 2003; Leishman et al. 2010). While invasiveness may be broadly predictable using abundances and ranges of species in their native continents (Firn et al. 2011), analysis of exotic species across oceanic islands (Kueffer et al. 2010) indicates that invasiveness in one location does not guarantee invasiveness in another, and may instead depend critically on local conditions in new habitats. Propagule pressure, or the number of individuals released into a new environment, may also be an important indicator of invasion success (Lockwood et al. 2005; Pemberton and Liu 2009; Simberloff 2009).

The dominant themes and debates in invasion ecology both reflect and influence current debates in community ecology as a whole. Much of theoretical ecology has been devoted to understanding community assembly; and exotic species invasions offer opportunities to test community assembly theories. For example, niche theory suggests that species must differ in either niche or competitive ability from the currently-established species in order to establish themselves (e.g., Tilman 1980; MacDougall et al. 2009). On a community level, the differences between the functional traits of novel species and those of previously-established species may determine colonization success (Fargione et al. 2003; Strauss et al. 2006), and the impact of novel species on established communities (Wardle et

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al. 2011). However, invasibility theory suggests that community assembly depends not on species characteristics but on a kaleidoscopic pattern of spatiotemporal fluctuations in resource availability, which, depending on their frequency and amplitude, can promote varying levels of diversity (Davis et al. 2000; Davis 2003; Melbourne et al. 2007). Stochastic niche theory (Tilman 2004) allows for openings based on fluctuations in resources, but maintains that diminishing opportunities for colonization exist as species accumulate and critical resources are usurped. And the intermediate disturbance hypothesis (Grime 1973; Connell 1978) predicts that extremely high disturbance may lead to a lack of diversity, and by implication low colonization by all but the most disturbance-adapted species.

Parallel debate regarding the importance of environmental niches versus competition versus dispersal-related processes in determining richness and diversity of communities also informs and is informed by invasion ecology. Neutral theory (Hubbell 2001; Bell 2001) posits that community composition is determined based on stochastic dispersal of individuals within a metacommunity, with colonization of new sites and community composition changes arising from spatially-weighted dispersal of propagules from nearby individuals. Niche-based theories (e.g., Hutchinson 1957; Grime 1977) predict that community composition reflects the local environment, in that species must be adapted to their environments to maintain populations, and dominant species are particularly well-adapted to their environments. The contrasting predictions of dispersal-based neutral vs. niche-based models of community assembly have spawned many tests of the predictions of neutral theory (e.g., Tuomisto et al. 2003; Gilbert and Lechowicz 2004; Muneepeerakul et al. 2008) and the role of dispersal versus environment in general in communities (e.g., Pither and Aarsen 2005; Bennett et al. 2010). The effects of competition have also frequently been emphasized in

small-scale experiments (e.g., Tilman 1997; Fargione et al. 2003; Hautier et al. 2009). Such contrasting explanations for community assembly parallel the contrasting explanations for native versus exotic richness ratios at different scales (e.g., Lonsdale 1999; Stachowicz and Tilman 2005), whereby shared environmental tolerances are assumed to lead to positive richness ratios at larger scales and competition is assumed to lead to negative richness ratios at smaller scales (Shea and Chesson 2002; Davies et al. 2005).

A central conundrum in community ecology is that different ecological theories make similar predictions about some of the most common biogeographic patterns. For example, island biogeography theory (MacArthur and Wilson 1967) is essentially 'neutral', in that it predicts the species-area relationship that is near-ubiquitous in ecology, without the need to invoke species differences, relying instead on the notion that patches of a given size will have a saturation-level number of species (Hubbell 2001). However, niche-based processes, whereby islands of increased size are likely to have a greater number of habitats, can also be invoked to explain the species-area relationship (Whittaker and Fernandez-Pelacios 2007). Likewise, the 'hollow-curve' species abundance distribution, whereby a very small number of species are dominant while a great many are rare, can be explained by the stochastic assembly of communities (Hubbell 2001). However, the neutral 'explanation' of species abundance distributions has been criticized for its use of flexible and difficult to determine ecological parameters (McGill et al. 2006), and the hollow-curve species abundance distribution can also be explained by invoking niches (Sugihara 1980).

In general, community composition has been shown to be more closely related to niches than to neutral processes (Cottenie 2005). Competition also does not appear to be as important as environmental factors in determining community composition in general (e.g.,

Houlahan et al. 2007; Ricklefs 2011). However, despite the apparent robustness of niche-based interpretations of community assembly, the extent of equilibrium of communities with their environments is a matter of debate. In changing environments, species dispersal to newly-favourable conditions may take considerable time (Svenning and Skov 2004, 2007). Exotic species' ranges in particular have been shown to be related to residence time (e.g., Williamson et al. 2009), and 'invasion debt', or a latent expansion of exotic species populations, has been inferred at larger (e.g., state, national) scales (Seabloom et al. 2006; Essl et al. 2011).

The study of exotic species and their native counterparts has the potential to contribute greatly to the resolution of these and other debates in community ecology (Sax et al. 2005; Callaway and Maron 2006; Daleo et al. 2009). The characteristics and biogeographic patterns of native and exotic species can be compared to examine theories on the roles of dispersal, competition and environment in determining community composition. And the environmental correlates of richness for native and exotic species can be compared, to examine whether the roles of environmental characteristics and dispersal-related processes can vary depending on the stage of community assembly and the identity of species.

Answering theoretical questions regarding community assembly also has profound implications for the management and preservation of native diversity. If the roles of species traits, environment, dispersal and competition can be better understood, the trajectory of native and exotic diversity over time can be better predicted. Thus, the theoretical and practical aspects of ecology coincide in the study of invasions. There is little doubt that ecosystems are under threat in many parts of the world, and the contribution of exotic species to this threat is important to understand. However, as noted above, it has been difficult to

generalize regarding the patterns in exotic species invasions. The number of hypotheses regarding species invasions has proliferated (Mitchell et al. 2006; Catford et al. 2009), and there are many remaining questions regarding the roles of dispersal, competition and environmental niches in species invasions (Fridley et al. 2007). The paucity of basic 'rules' of invasion biology appears to parallel that of community ecology as a whole (Simberloff 2010). Perhaps the greatest reason for the lack of coherent rules in invasion ecology is that despite the truncated process of community assembly that may result from the large number of anthropogenic species introductions, it is still very difficult to examine patterns on both the spatial and temporal scales necessary to understand the causes of community assembly via species invasions (Fridley et al. 2007). Examinations at multiple spatial scales are relatively rare, and those that exist often reveal contrasting effects at different scales (Shea and Chesson 2002; Davies et al. 2005; Pauchard and Shea 2006). Autocorrelation of potential explanatory factors driving species distributions can also make attributing causation to patterns on the landscape particularly difficult (Legendre 1993; Gilbert and Bennett 2010); and many of the most important and least-understood patterns occur at scales that essentially preclude experimental analysis (Fridley et al. 2007).

The Garry oak ecosystem – a natural laboratory

To address many of the inherently difficult questions in invasion ecology, it is necessary to isolate the potential factors that influence the trajectory of species invasions. I chose to examine some of the key questions above using a study system where the spatial and environmental characteristics disconnect potential influential factors. The system represents the northern portion of a savanna ecosystem ranging from California north to British Columbia (Garry Oak Ecosystems Recovery Team (GOERT) 2011a). In Canada, this

ecosystem is commonly referred to as the Garry oak ecosystem (GOE), due to its frequent

association with Garry oak (*Quercus garryana*) trees. The GOE is composed of a network of

discrete meadow patches located on the southeast rainshadow of Vancouver Island and

adjacent islands, and tends to be located in low-elevation, shallow-soil areas (Lea 2006;

Dunwiddie and Bakker 2011). The GOE is considered to be floristically diverse, and to

contain many plant species adapted to open, Mediterranean environments that are subject to

frequent summer drought (Fuchs 2001).

Palynological evidence of Garry oak trees in Canada dates from >9500 a BP, and

evidence for the presence of *Camassia spp.* (iconic species of the GOE) dates from ~11 000

a BP, shortly after deglaciation (Pellatt et al. 2001). The GOE appears to have once occupied

a larger and more environmentally diverse portion of Vancouver Island, as well as other

areas of southwestern British Columbia (Lea 2006; Vellend et al. 2008; Bjorkman and

Vellend 2010). Assuming oak pollen can be considered a proxy of the extent of GOE

meadows, the GOE appears to have reached its maximum extent on and near Vancouver

Island during the Hypsithermal period (~8500 to 6000 a BP; Pellatt et al. 2001). After this

time, GOE meadows may have diminished in extent, but were likely maintained to a large

degree by deliberate landscape manipulation by Aboriginal people using fire, especially in

areas of deeper soil that otherwise tend to revert to Douglas-fir woodland (MacDougall et al.

2004; Vellend et al. 2008). Subsequent European colonization led to the cessation of

Aboriginal land management practices and loss of GOE meadows. In both Canada and

western Washington State, the GOE occupies less than 10% of its former extent (Lea 2006;

Dunwiddie and Bakker 2011), having been largely supplanted by direct conversion to

developed areas and farmland as well as forest encroachment (Lea 2006; Gedalof et al. 2006; Dunwiddie and Bakker 2011).

GOE meadows have also been invaded by a diverse assemblage of exotic species. At least 150 exotic vascular plant species have been identified in GOE meadows (Fuchs 2001). The extent of invasion among individual meadows is highly variable: exotics dominate the vegetation cover of some meadows (MacDougall and Turkington 2005; Gonzales 2008; data presented herein), while in others (data presented herein) native species cover is >90%. Compared to Europe and eastern North America, for which the history of anthropogenic species invasions spans >300 years (e.g., Pyšek 1998; Long et al. 2009), the GOE is relatively recently invaded, with a ≤140-year history of post-colonial species invasions (Reichard and White 2001), compared to >300 years in eastern North America (Mack 2003).

Several features make the GOE an excellent natural laboratory for studying community assembly through species invasions. The GOE is composed of disjunct patches, which offer discrete, nested scales for analyzing patterns in species distribution and community diversity. The patches themselves are surrounded by different matrices: some patches are located on small islands, surrounded largely or entirely by water; others are located in urban environments; and others are surrounded by forests. The level of human disturbance also varies greatly among patches. Within the patches themselves, a high degree of environmental heterogeneity creates a variety of microhabitats (cf. MacDougall et al. 2006; Pinto and MacDougall 2010). The diversity of both native and exotic species allows statistical power sufficient to compare communities based on species characteristics.

The GOE is a hotspot for biodiversity in Canada and in the Pacific Northwest region of North America, but also an imperilled one due to a range of factors including invasion. As such, this system is considered to be highly important for conservation (GEORT 2011a), and therefore biogeographic questions that are addressed in this ecosystem are important for conservation management. Understanding the factors that promote native or exotic species dominance can greatly help efforts to preserve the remnants of this ecosystem.

Thesis chapters

My thesis chapters analyze community patterns in the GOE to address several specific questions regarding the comparative biogeography of native and exotic species.

Chapter 2 uses species-level analyses of native and exotic communities, to determine whether abundance patterns among species grouped by origin (native versus exotic), life form and dispersal mechanism are indicative of 'invasion debt' (incomplete expansion of populations) in exotic species. Specifically, the following questions are asked: 1) Are exotic short-dispersing species underrepresented compared to other species groups, organized by life form, origin and dispersal mechanisms? 2) Are frequencies of exotic species in general related to minimum residence time in the region? 3) Considering invasiveness in other parts of North America, do short-dispersing exotic species show proportionally more evidence of latent invasiveness than their long-dispersing counterparts? And 4) are exotic species of all types underrepresented on small, isolated and relatively undisturbed island patches?

In Chapter 3, I systematically explore the scale-dependent patterns in richness, abundance and community composition for native and exotic communities in the GOE, to address the following specific questions arising from debates in the literature: 1) Do exotic

species competitively limit native species abundance and richness? 2) Do native and exotic communities exhibit shared or divergent responses to environmental variation? 3) Are community-level biogeographic patterns in native versus exotic communities reflective of incomplete population expansions in exotics? I use systematic analyses of native/exotic richness ratios, and scale-specific models of richness, cover and community composition, as well as comparison of species-pair correlations and species-area and abundance relationships, to outline the importance of habitat characteristics in determining native and exotic community assembly across scales.

In Chapter 4, I examine the influence of spatial autocorrelation and scale in native and exotic species distribution models, and use distribution and richness models at two scales to address critical conservation questions in the GOE regarding protected area site selection, remediation of degraded sites and monitoring of invasive species. I present spatially-explicit distribution models at two scales for the twenty dominant native and twenty dominant exotic species in the study area, to aid management practices including monitoring, site rehabilitation and protected area site selection. I also present richness models for native and exotic species designed to focus specifically on predicting richness both among and within patches (as opposed to models in Chapter 3, which focus on the influence of environmental factors specific to each scale). And I present models to predict the presence of species that are provincially- and nationally-recognized to be at risk of extinction. Finally, I demonstrate the utility of such models for site selection, site rehabilitation and prioritizing of invasive species monitoring, using example sites located within the study area.

In Chapter 5, I summarize conclusions from the previous chapters, as well as general conclusions that can be drawn from this study. I also examine the limitations of this study,

and provide recommendations for future work. Finally, I provide some recommendations for conservation and management of the GOE, in light of the findings presented in this thesis.

Chapter 2: Abundance, rarity and invasion debt among exotic species in a patchy ecosystem

Introduction

Predicting the impact of invasive exotic species has become an important goal of ecological research. Species invasions also provide ecologists with opportunities to witness community assembly at easily observable temporal and geographic scales, facilitating tests of ecological theory (Callaway and Maron 2006; Daleo et al. 2009). A common approach to understanding species invasions is to identify characteristics that differentiate invasive exotic species from native or non-invasive exotic species, and then to infer that these distinguishing qualities are predictors of invasiveness. Results of such studies have been mixed, with several analyses revealing characteristics linked to invasiveness (e.g., Callaway & Aschehoug 2000; van Kleunen et al. 2010), while others indicate that the characteristics of native and invasive species largely overlap (e.g., Daehler 2003; Leishman et al. 2010), or that changes in externalities such as resource availability (Davis et al. 2000) and disturbance (MacDougall and Turkington 2005; Vilà et al. 2007), rather than species characteristics, are the main drivers of invasion.

Much of the discrepancy in such comparisons may be due to the focus of most analyses on a single geographic scale (Shea & Chesson 2002; Strayer et al. 2006) and on currently dominant species, while neglecting potential indications of long-term change via species that have yet to reach their potential distributions. Recent colonists or relatively slow dispersers may not appear to be invasive when in fact they are in the process of initial range or population expansion (Strayer et al. 2006). Indeed, latent range expansions potentially exist for many exotic species that are currently uncommon, representing an 'invasion debt'

(*sensu* Seabloom et al. 2006; Essl et al. 2011). Thus, it is important to determine what the current patterns among native and exotic species can tell us about long-term trends.

Here, we test for patterns in native and exotic species occurrences at different scales that are predicted by an invasion debt hypothesis, in vascular plant communities from 67 discrete meadow patches located on Vancouver Island, British Columbia, and adjacent smaller islands. We use a multi-faceted approach to determine the statistical relationships between the abundance of species and their origin, dispersal ability and life form, and then use detailed analyses of these patterns to test for indicators of invasion debt in exotic species assemblages. High diversity of both native and exotic species in our study system, the discreteness of individual patches (including some located on isolated, relatively undisturbed islands), and the comparatively recent history of species introductions, make it ideal for examining the process of species invasion.

An area experiencing invasion debt will display differences in abundance patterns between exotic species and long-term native residents that are reflective of the relatively recent arrival of the exotics. Thus we predicted the following: 1) Exotic short-dispersing species would be underrepresented compared to other species, because they have not had sufficient time to disperse to all suitable habitat; 2) frequencies of exotic species in general would be related to minimum residence time in the region; 3) among exotic species identified as being invasive elsewhere in North America, a smaller proportion of short dispersers than long dispersers would be common in the study area (and a greater proportion would be rare); and 4) exotic species of all types would be underrepresented on small, isolated island patches, reflecting the relative inaccessibility of the most isolated patches, the recent arrival of exotic species in the study region, and the possible role of disturbance agents in aiding

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propagule spread of exotic species (cf. MacDougall and Turkington 2005). While fulfilment of any one of the predictions above does not allow firm conclusions to be made, fulfilment of all or most of them provides strong weight of evidence for the existence of invasion debt.

In contrast to the large scale (e.g., national, province/state) of most analyses of the roles of time and species characteristics in invasion (e.g., Lloret et al. 2004; Seabloom et al. 2006; Williamson et al. 2009; Ahern et al. 2010), we examined patterns of commonness and rarity at two ecologically-distinct spatial scales: first, by surveying the frequency of occurrence of 188 native and 113 exotic species among discrete habitat patches, and second by sampling their occurrence among small plots located within patches. We report multiple lines of evidence supporting the invasion debt hypothesis, strongly suggesting incipient changes in community composition in the study area. We also demonstrate the existence of a suite of exotic species that appear to possess distinctly high dispersal capacity in addition to the ability to establish substantial populations among sites throughout the study area.

Methods

Study area

Our study sites were comprised of discrete lowland meadow patches on south-eastern Vancouver Island, British Columbia, and adjacent smaller islands in the Strait of Georgia. The climate in the study area is sub-Mediterranean, with cool, wet winters and frequent summer drought. The meadow patches in the study area are collectively referred to as the Garry oak ecosystem, due to the common occurrence of Garry oak (*Quercus garryana*) trees within them. These meadow patches tend to be located on shallow-soil areas isolated from one another by a combination of forest, ocean and human development. They are considered

to be floristically diverse, and a high priority for conservation (Fuchs 2001), but are also highly invaded by many exotic plant species. In some areas, exotic species occupy most of the ground cover, and are thought to threaten populations of native species (Fuchs 2001). Various factors have been proposed as causes of exotic species abundance in the study system, including altered fire regimes (MacDougall 2005), human disturbance (Lilley & Vellend 2009), increased herbivory of native plants (Gonzales & Arcese 2008), and propagule pressure from neighbouring farms and roadsides (MacDougall & Turkington 2005). Our sites were chosen from among the best-preserved examples of these meadow patches, within a representative range of their current distribution in Canada.

Community surveys

In 2006, 2007 and 2008, 67 meadow patches on Vancouver Island and the southern Gulf Islands of British Columbia, ranging in size from ~0.2 to 17.7 ha, were surveyed for vascular plants (see Appendix 1 for details). Surveys took place from April to June, when most plants in the study system are easiest to identify. In patch-level surveys for abundances among patches (i.e., the 'inter-patch' scale), the patches were systematically surveyed across their full extents. For quadrat-based, intra-patch surveys for abundances within patches, we used a stratified-random selection of quadrats with the number of quadrats per patch ranging from 5 to 15, depending on patch size. A total of 484 1-m^2 quadrats were surveyed. Plants were identified to the species level or lower in 95% of cases, using the nomenclature scheme of Douglas et al. (1998-2002).

Species characteristics

Dispersal capability for plant species was treated as a binary variable and determined based on presence ('long dispersers') or absence ('short dispersers') of widely recognised

dispersal-aiding adaptations (e.g., hooked awns, pappus, edible fruit, adhesive seeds). For all

species not possessing obvious characteristics facilitating long-distance dispersal, the

primary literature was searched for evidence of long-distance dispersal capacity (e.g.,

consumption by animals and survival in their guts). Fifty-two of 353 species that could not

be unambiguously categorised were eliminated from analysis, resulting in a pool of 301

species classified by origin, dispersal ability and life form (Table 2.1). These classifications

were the predictor variables in the generalised linear model (GLM) framework described

below, with the number of occurrences of a species across either patches or quadrats being

the response variable.

Table 2.1: Number of species according origin, dispersal and life form category

		Native	Exotic
Short Dispersers	Forb	81	40
	Graminoid	3	0
	Shrub	1	1
	Tree	0	1
Long Dispersers	Forb	52	40
	Graminoid	15	22
	Shrub	22	8
	Tree	14	1

Rarity and commonness at combined scales

The relative abundances of species do not necessarily translate across scales: some

species may be common at one scale and rare at another (Rabinowitz 1981). Therefore, to

simultaneously compare abundances at both the inter- and intra-patch scales, we used a

modified version of Rabinowitz's "Forms of Rarity" framework (Rabinowitz 1981), which

permitted analysis of factors associated with commonness or rarity at both the inter- and

intra-patch scales together, as well as focused examination of the factors associated with

extremities of distribution patterns ('common', 'rare'). In her original framework, Rabinowitz (1981) included seven forms of rarity and one form of commonness, based on local abundance, regional distribution and environmental specialization. Since environmental specialization could not have been reasonably determined for rare species in the dataset (due to too few occurrences) and thus the environmental specialization component of the Rabinowitz framework could not be reliably determined for such species, we limited our characterisations to the following: rarity at both inter- and intra-patch scales; rarity at the intra-patch scale but commonness at the inter-patch scale; rarity at the inter-patch scale but commonness at the intra-patch scale; and commonness at both scales. For the inter-patch scale, we defined 'common' as presence in at least 15 patches, and 'rare' as presence in two or fewer patches. For the intra-patch scale, 'common' was defined as presence in two or more quadrats in at least one patch, and 'rare' as presence in one or fewer quadrats in any patch. Note that 149 of 301 species were found in patch-level surveys but not in any quadrats. Since our definitions of commonness and rarity were necessarily arbitrary, we conducted analyses on more liberal or conservative classification schemes. These yielded similar results (see Appendix 4).

Minimum residence time and invasiveness in other regions

To estimate minimum residence time for exotic species, records from the two largest herbaria in the Pacific Northwest of North America, at the Universities of Washington and British Columbia, were searched for the year of the earliest naturalised specimen (i.e., outside of human cultivation according to voucher labels) in the region (defined as the Coast Mountains westward, within Washington State and British Columbia). Collections at the UBC Herbarium were hand-searched, as the online records were incomplete at the time of

writing. Even in a well-collected locale such as the study area, estimates of arrival time based on herbarium specimens represent minima, as time elapses between establishment and collection. The earliest recorded date from either herbarium was used to minimise the potential for collection lag times to bias results. To determine the proportions of exotic short and long dispersers known to be invasive elsewhere and common or rare in our study area, we examined the North American database of invasive species (invasive.org) to identify species independently classified as 'invasive' by provincial or state management agencies elsewhere in North America.

Patterns on isolated/least-disturbed patches

To determine whether invasion debt is indicated by underrepresentation of all exotic species on the isolated and least-disturbed patches, a subset 22 patches located on small islands in the study area was analysed separately. All 22 patches are under federal or provincial protection, or are in the legislative process of becoming protected, due to their relatively pristine condition and conservation value, and they have no history of agricultural use (e.g., grazing), nor current evidence of human trails. Within 1000 m buffers around these patches, the mean area of agricultural land and mean length of roads were each ~100 times less than for the Vancouver Island patches (J. Bennett, unpublished data). While the effects of isolation and low disturbance cannot be separated for these islands, both their relative isolation and low disturbance were predicted to decrease the representation of exotic species of all types.

Statistical analyses

Tests for species' attributes associated with differences in number of occurrences or rarity and commonness designation were conducted in a generalized linear model (GLM)

framework. All species were considered in each model, with the response variable being the number of occurrences of every species, and origin, dispersal ability and life form being the categorical predictor variables. This framework allowed us to test for differences in abundances among species grouped according to predictor variables. Nested models were produced using all possible combinations of variables, beginning with complex models using all possible interaction terms and proceeding to simple, single-term models. Models were compared using likelihood ratio tests to determine whether additional factors resulted in significantly greater fit, with the most parsimonious model retained as the best set of predictors for each response variable.

To explore the role of minimum residence time, models were created using exotic species only, and including estimated minimum residence time as an additional (continuous) predictor variable. To assess whether minimum residence time was related to the spatial extent of exotic species distributions in the study area, additional models were run for exotic species only, with predictor variables as above, and the response variable being range estimates among sample sites using minimum convex polygons of occurrences at the inter-patch scale.

Appropriate error distributions were used for all models. Numbers of occurrences in patches and quadrats were overdispersed counts, so models for number of occurrences used a negative binomial error distribution (as opposed to quasi-Poisson, which precludes likelihood ratio tests); forms of rarity and commonness models used a binomial distribution. In the most parsimonious models, t-tests of individual terms of the categorical variables were used to determine their significance. All statistical analyses were conducted using R v.2.12.0 (R Development Core Team 2010).

Phylogenetic analyses

      If phylogenetic relationships among species being compared are themselves related to the response variable of interest, species may demonstrate a lack of independence as data points (cf. Harvey et al. 1995). Phylogenetic relationships may also reveal testable patterns that can allow generation of new hypotheses that could not be derived using species themselves (e.g., Cadotte *et al*. 2010). We therefore examined the potential influence of phylogeny in our data using two approaches. To determine whether phylogenetic distances were smaller within than among groups selected in the most parsimonious models outlined above, we used permutation tests, randomly rearranging group identities to compare intra-group phylogenetic differences to inter-group differences (see Appendix 2 details). Next, to determine whether there was a phylogenetic signal related to abundance itself (our response variable in the models above), we generated matrices of abundance differences among species at the inter- and intra-patch scales and tested for a phylogenetic signal in abundance data, using a Mantel test with Spearman rank correlation to compare the phylogenetic and abundance differences. The former analysis indicated slightly lower phylogenetic distances within than outside selected groups, except for native long dispersers (Appendix 2), while the Mantel test indicated a very weak phylogenetic signal in abundance (inter-patch scale: $R^2 =$ 0.002, P = 0.035; intra-patch scale: $R^2 = 0.004$, P = 0.045). Thus, while some groups are comprised of species more closely related than random samples of species, there is a negligible connection between phylogeny and abundances of species themselves. We therefore interpreted the differences in abundance among groups in terms of their ecological traits, rather than their phylogenetic relatedness.

Results

In models testing for correlates of species' abundances at both inter- and intra-patch scales, the model with origin interacting with dispersal mode was most parsimonious (Table 2.2), and exotic short dispersers were significantly underrepresented at both scales (Fig. 2.1a,b). In addition, exotic long dispersers were overrepresented at the inter-patch scale (Table 2.2, Fig. 2.1a).

Table 2.2: Significant parameters from the most parsimonious models for numbers of occurrences and forms of rarity and commonness. See Appendix 3 for full results (including non-significant parameters)

Response Variable	Predictor Variables	Final Model	Parameter	Parameter Value	Standard Error	t	P
Number of Occurrences in Patches	O, D, G_f	O × D	EL	0.364	0.169	2.16	0.0342
			ES	-0.756	0.192	3.95	0.0003
Number of Occurrences in Quadrats	O, D, G_f	O × D	ES	-1.109	0.418	2.65	0.0114
Commonness on Both Inter- and Intra-Patch Scales	O, D, G_f	O × D	ES	-1.626	0.472	3.44	0.0014
Rarity on Both Inter- and Intra-Patch Scales	O, D, G_f	O × D	EL	-1.008	0.365	2.77	0.0073
Number of Occurrences in Patches (Exotic spp. only; including estim. time since arrival)	D, G_f, T_a	D + T_a	T_a	0.453	0.103	4.40	<0.0001
Number of Occurrences in Quadrats (Exotic spp. only; including estim. time since arrival)	D, G_f, T_a	D + T_a	T_a	1.479	0.280	5.28	<0.0001
Minimum Convex Polygon Size (Exotic spp. only; including estim. time since arrival)	D, G_f, T_a	D + T_a	T_a	0.210	0.095	2.22	0.0292
Number of Occurrences in Patches (22 Small-Island Patches Only)	O, D, G_f	O × D	ES	-1.500	0.259	5.798	<0.0001
Number of Occurrences in Quadrats (22 Small-Island Patches Only)	O, D, G_f	O × D	ES	-2.003	0.484	4.135	0.0002

Predictor variables: O = origin (native or exotic); D = dispersal ability (short or long); G_f = growth form (forb, grass, shrub, tree); T_a = estimated minimum residence time

Predictor variable categories: E = exotic; N = Native; S = short dispersers; L = long dispersers (i.e., EL = exotic long dispersers)

Figure 2.1: Frequencies of long- and short- dispersing exotic and native species. a) number of patches per species for each origin and dispersal category in full patch surveys; b) number of quadrats per species for each origin and dispersal category in quadrat-level surveys; c) percent of species in each origin and dispersal category, according to form of rarity and commonness. Error bars indicate ±1 standard error.
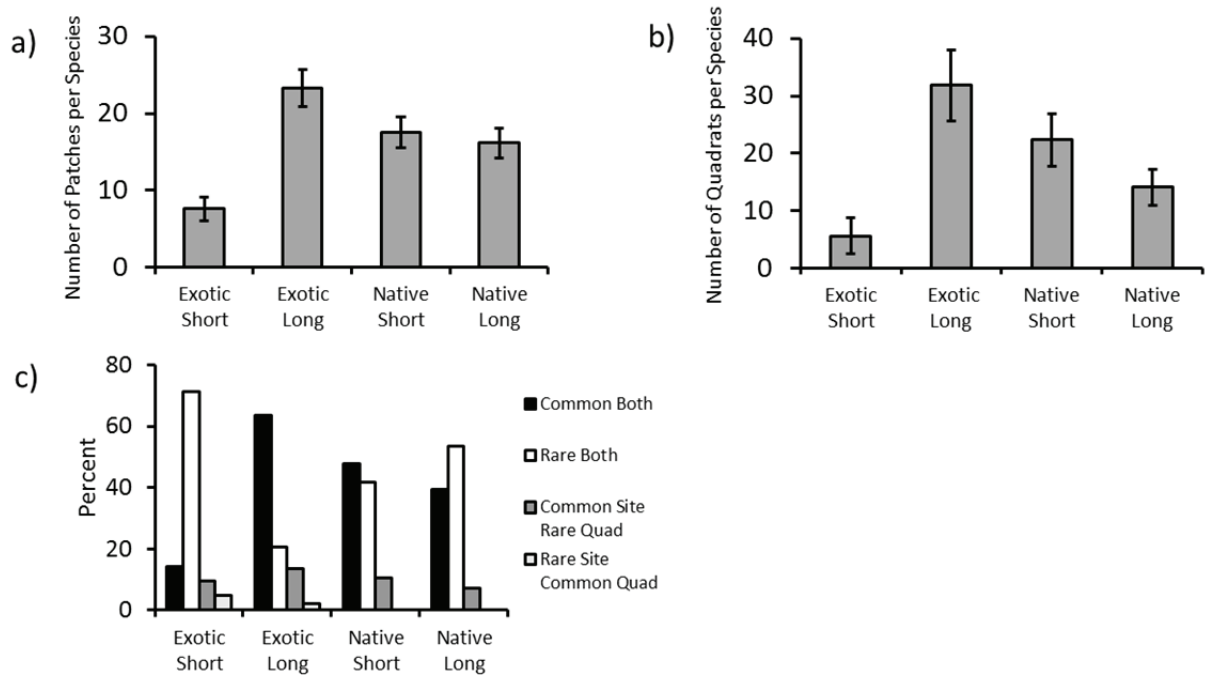
Models of commonness and rarity in our modified Rabinowitz framework followed similar patterns to those of single-scale models. Our classification scheme yielded 203 species which could be categorised by form of commonness or rarity, while the remaining 98 species of intermediate abundance were not classified. Ninety percent of the 203 classified species were categorised as rare (n = 90) or common (n = 91) at both inter- and intra-patch scales, and thus either well or poorly represented both within and among patches. In contrast, 20 species were common at the inter-patch scale but rare at the intra-patch scale, and two were rare at the inter-patch scale and common at the intra-patch scale. Sufficient data existed to model the species categories related to commonness at the two scales and rarity at the two scales. In both cases, the model with origin interacting with dispersal ability was most parsimonious. Exotic short dispersers were a significant negative predictor of commonness at

both scales combined, while exotic long dispersers were a significant negative predictor of combined-scale rarity (Table 2.2, Fig. 2.1c).

Estimated minimum residence time was included as a variable in the most parsimonious models for exotic species only at the inter- and intra-patch scales, in addition to dispersal ability, but not the interaction term (Table 2.2). Using minimum convex polygon range estimates as the response variable also resulted in estimated minimum residence time and dispersal ability being retained in the most parsimonious model. Though exotic short dispersers appear to have been introduced later than exotic long dispersers on average (t=4.23, DF = 64, P<0.0001), the independent significant term for arrival time in the model indicates an independent effect of arrival time on abundance and range size of all exotic species. Interestingly, all species present in ≥10 quadrats are reported to have been present in the region for ≥70 years (Fig. 2.2).

Figure 2.2: Number of quadrats in which an exotic species was found versus estimated minimum residence time in the region.
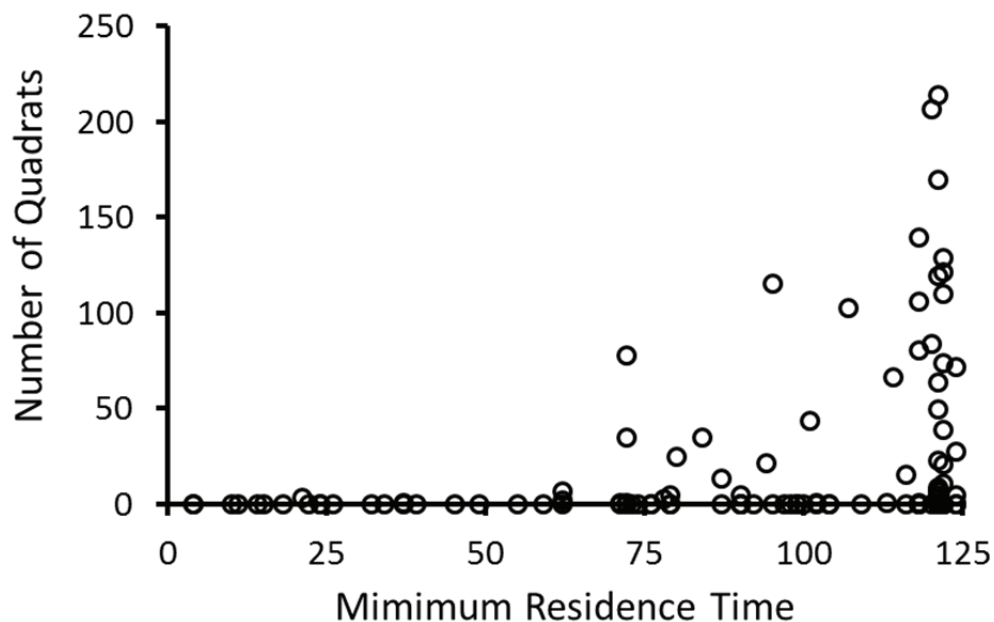
Comparison with North American provinces and states indicates that exotic short dispersers are currently less often identified as invasive than exotic long dispersers: 22 of 42 (55%) exotic short dispersers identified in our study area are considered invasive elsewhere in North America, whereas 61 of 71 (86%) exotic long dispersers are considered invasive elsewhere in North America. However, as predicted, among species that are considered invasive elsewhere in North America, a greater proportion of exotic long dispersers (25 of 61 species) than short dispersers (2 of 22 species) were common at both scales in the study area (Fisher Exact Test, one-tail, $P = 0.028$). In addition, among species that are considered invasive elsewhere in North America, a greater proportion of exotic short dispersers (12 of 22 species) than long dispersers (6 of 61 species) were rare at both scales in the study area (Fisher Exact Test, one-tail, $P = 0.002$).

In the subset of 22 small-island patches, the pattern of representation was very similar to the full dataset (Table 2.2; Fig. 2.3). Exotic short dispersers were underrepresented at both scales compared to other species, while exotic long dispersers remained slightly but not significantly overrepresented on a per-species basis.

Figure 2.3: Frequencies of long- and short-dispersing exotic and native species in the subset of 22 small-island patches. a) number of patches per species in full patch surveys; b) number of quadrats per species in quadrat-level surveys. Error bars indicate ±1 standard error.
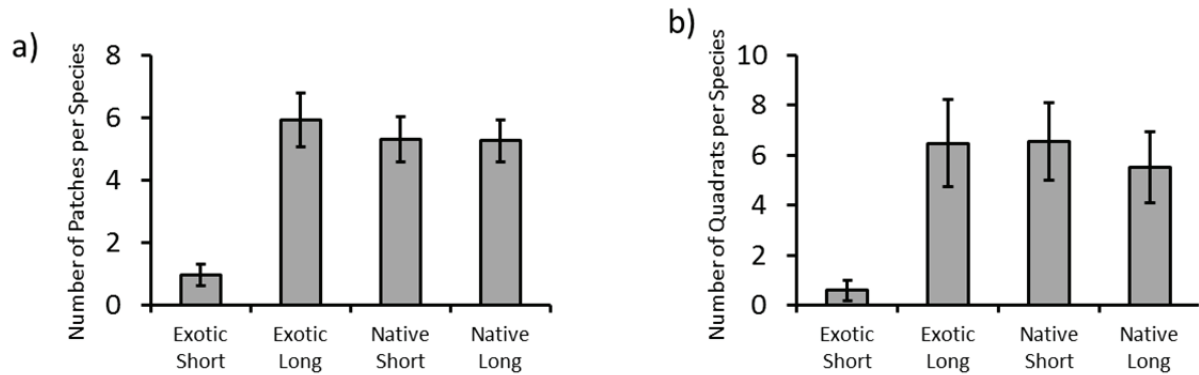
Discussion

While several previous analyses have clearly shown that incipient invasions exist among exotic species at broad (e.g., national, province/state) scales (e.g., Seabloom et al. 2006; Williamson et al. 2009; Ahern et al. 2010), our analyses utilized smaller, ecologically-distinct scales, and explored the effects of dispersal ability, life form, disturbance/isolation and residence time in species invasions. At both inter- and intra-patch scales, our results supported the prediction that exotic short dispersers would be underrepresented, and strongly suggested invasion debt among slower-dispersing species at these scales. In contrast, native short dispersers were neither over- nor underrepresented (Fig. 2.1), and presumably have had time to disperse to much of the suitable habitat in the study area. The importance of arrival time in predicting numbers of occurrences of exotic species at the inter- and intra-patch scales as well as estimated range sizes in the study area, also indicates that invasions in our study area are in an early stage, strongly suggesting invasion debt, particularly among exotic short dispersers.

While exotic short dispersers appear to be somewhat less invasive as a group than exotic long dispersers based on continent-wide comparisons, among the species that are considered invasive elsewhere in North America, a higher proportion of the short dispersers were rare in our study area. In addition, a higher proportion of the exotic long dispersers that were identified as invasive elsewhere were common in the study area. Both of these patterns suggest that a greater proportion of latent dominant species currently exist among the exotic short dispersers.

The history of species introductions in the study region is relatively short, at ≤140 years (Reichard & White 2001), compared to >300 years in eastern North America (Mack 2003). In time, some of the exotic short dispersers that have become prevalent in other areas of North America appear likely to become common in the study region, and the relative abundances of long and short dispersers may more closely reflect those of native species, for which long-distance dispersal ability did not significantly relate to abundance. While predicting which exotic short dispersers are most likely to proliferate in our study area in the future is difficult, several species that are currently rare in our surveys are recent arrivals to the region and considered to be invasive in many jurisdictions of North America, including: *Alliaria petiolata* (first naturalised specimen: 1988); *Allium vineale* (first naturalised specimen: 1961); *Vinca minor* (first naturalised specimen: 1939); and *Hesperis matronalis* (first naturalised specimen: 1937). In addition, there are several exotic short dispersing species that have very close ecological analogues among the native short dispersers that are presently common on drier, shallow-soil microsites. Examples include *Allium vineale* vs. *A. cernuum*; *Hyacinthoides hispanica* vs. *Camassia* spp.; *Sedum album* vs. *S. spathulifolium*.

The slight overrepresentation of exotic long dispersers on the 22 relatively isolated and undisturbed island patches did not support our prediction that all exotics would be underrepresented on these patches. We had expected that even the exotic long dispersers would have had relatively limited opportunity to establish in such places. Though only 48 of 71 exotic long dispersers were found on this group of patches, and average plant cover of natives in quadrats on these patches was ~80% (versus ~54% in all other patches), exotic long dispersers were slightly more represented on a per-species basis than native short or long dispersers. A similar phenomenon was observed by Lloret et al. (2004) at a larger scale on Mediterranean islands, whereby exotic wind-dispersed species were overrepresented compared to other species. While disturbance and human-induced propagule pressure are potential facilitators of the spread of invasive species in our study area (MacDougall & Turkington 2005; Lilley & Vellend 2009), it also appears likely that intrinsic species characteristics such as dispersal ability and perhaps pre-adaptation to environmental conditions in the study system have been important in the establishment of exotic long dispersers on even the most isolated and undisturbed patches in our study area.

The fact that exotic long dispersers were less likely to be rare in the combined scales of the Rabinowitz framework than other species, in addition to being overrepresented at the inter-patch scale, is also notable, since the native counterparts to these species have apparently been present in our study area for several thousand years (Pellatt et al. 2001). Indeed, the two most common species at the intra-patch scale, and the first and third most common species at the inter-patch scale (*Aira praecox* and *Hypochaeris radicata*, respectively), are both exotic long dispersers. These findings were unexpected in our study system, because we assumed that the patches and islands represented in our data were

substantially isolated from one another by inhospitable dispersal barriers with the potential to delay colonization. However, several exotic long dispersers have rapidly overcome these barriers and colonized even the most isolated patches, despite their relatively recent (≤140 years) arrival in the region.

The specific life history strategies of some exotic long dispersers may contribute to their invasion success in our study area, particularly if they are occupying previously-unfilled niches (Emery 2007). For example, native annual grasses are rare in our study region (MacDougall & Turkington 2006), whereas several common exotic long dispersers are annual grasses (e.g., *Aira praecox*, *Bromus diandrus*). Exotic grasses in our dataset were all long dispersers and thus were overrepresented in the most parsimonious models. However, life form was not a predictor in the most parsimonious models, and thus exotic grasses were not distinguished from long-dispersing exotic forbs or shrubs in these models. While further research on the detailed morphological and physiological traits of exotic dominants may help to understand the causes of invasiveness, the common exotic long dispersers in this system appear to represent a variety of growth forms and life history strategies that are largely shared with native species. Several of these exotic long dispersers correspond to Daehler's (2003) concept of a 'super-invader', with ability to both disperse to and persist in remote patches. While disturbance probably facilitates the spread of such species, they do not appear to be dependent on disturbance for establishment among and within patches, as indicated by their presence on even the relatively undisturbed patches. Such species appear to be both dispersive and tolerant of environmental conditions in the study system.

While several lines of evidence strongly suggest that an invasion debt exists within our study system, the exact details of future trends are difficult to predict. Our data represent

a snapshot in time, so they cannot be used to forecast quantitative trends. However, the results of previous broad-scale studies within countries or provinces/states point to likely directions. Analyses in Europe, where many invasions occurred much earlier than in western North America, have shown that minimum residence time is a good predictor of species' range on national scales (e.g., Williamson et al. 2009; Essl et al. 2011). Williamson et al. (2009) suggested that the maximum range within a country of an exotic species may be achieved ~150 to 300 years after arrival, though infilling within this range would presumably take place over longer time periods. While disturbance may promote range expansion of some exotics, Seabloom et al. (2006) noted that ranges of exotic annual grasses in California are likely expanding ahead of the front of human disturbance. Such a scenario appears to be the case in our study system, despite it being composed of isolated patches, some of which have experienced little direct human impact. Several of the dominant exotic species possess both highly effective means of long-distance dispersal and the ability to establish populations throughout the study area, despite seasonal drought that could limit the establishment and persistence of some species (MacDougall 2005). In addition, the abiotic environment has changed considerably since the first exotic species were introduced in the 1800's, including climate warming (Canadian Climate Change Scenarios Network (CCCSN) 2011) and the fragmentation of Garry oak meadow patches (Lilley & Vellend 2009), both of which will likely continue in future. Some of the exotic species in our study system originate in warmer, drier climates (Lilley & Vellend 2009), and their invasion may be facilitated by climate change. Thus, even assuming that large areas are protected from human development or 'restored' by management, propagule pressure from already-invaded areas is likely to continue to facilitate invasion, requiring diligent monitoring of even the best-conserved sites.

Invasion in our system (and likely others) appears to be a continuous process whereby some highly dispersive species spread rapidly upon arrival, while populations of other species expand more slowly due to lack of long-distance dispersal mechanisms or habitat requirements. While newly-arrived species possessing mechanisms for long-distance dispersal should clearly be treated as potential rapid invaders, the exotic short dispersers that possess mechanisms for persistence in Mediterranean climates may be just as important to monitor from management and ecological standpoints. Native species may still outcompete exotic ruderal species in areas requiring specialized adaptations (e.g., shallow-soil, seasonally dry areas; MacDougall & Turkington 2006), and preservation of native diversity in such habitats could be vital to maintaining native biodiversity in this system as a whole. Therefore, removing slower-dispersing exotics that possess adaptations to tolerate these conditions may be an important additional management strategy. Proactive removal of species that are known to be invasive elsewhere would also be an efficient management technique. Populations of both of these species groups are generally still low enough in the study system that they can conceivably be controlled or eradicated, without the monumental effort associated with removal of the most common exotic species.

Chapter 3: Native versus exotic community patterns across three scales: roles of environment, competition and incomplete invasion

Introduction

Understanding how native and exotic species interact with their environment and each other is profoundly important to conservation biology. The degree to which exotics impact native species and modify ecosystem properties can determine whether long-term conservation or restoration goals are met. However, consensus on the biogeographic consequences of species invasions has been difficult to achieve (Fridley et al. 2007), and the conservation implications of species invasions continue to be vigorously debated (e.g., Davis et al. 2011; Lambertini et al. 2011).

Three of the fundamental questions in invasion ecology are: 1) To what extent do exotic species outcompete and (eventually) exclude natives? 2) Do native and exotic communities respond to their environments in similar or different ways (i.e., are they functionally similar or different)? 3) Can current patterns predict future trajectories in invasions? Niche and coexistence theories suggest that differences in niche or competitive ability must exist between established species and new arrivals for the latter to successfully colonize (MacDougall et al. 2009). Meta-analysis of native and exotic plant species traits by van Kleunen et al. (2010) revealed some evidence of different strategies between native species and invasive exotics. In addition, small-scale seed-addition experiments (e.g., Tilman 1997; Levine 2000; Corbin and D'Antonio 2004) and observed negative relationships between native and exotic richness at small scales (Shea and Chesson 2002; Davies et al. 2005; Stachowicz and Tilman 2005; Chen et al. 2010) have suggested that competitive

ability plays a role in promoting establishment and dominance of exotics. Some exotic species indeed appear to possess physiological advantages that facilitate their super-abundance (e.g., Callaway and Aschehoug 2000; Callaway et al. 2004; Ridenour et al. 2008).

However, evidence for competition among native and exotic plant species in natural communities is limited, especially at larger scales, where competitive exclusion of native by exotic plants has very rarely been observed (Davis 2003; Stohlgren et al. 2008a,b; Sax and Gaines 2008). Moreover, at broad regional scales, native and exotic species often exhibit positive richness relationships (e.g., Lonsdale 1999) and similarly-shaped species-area curves (Stark et al. 2006), implying that factors promoting native species diversity also promote exotic diversity (Stohlgren et al. 2008a). Invasibility theory (Davis et al. 2000; Melbourne et al. 2007) and considerable empirical evidence also suggest that native and exotic species often share similar strategies and constraints (Daehler 2003; Leishman et al. 2010; Tecco et al. 2010).

A logical explanation for such contrasting patterns at different scales is that extrinsic factors determine native and exotic richness at large scales, while competition is more influential at smaller scales (Shea and Chesson 2002; Davies et al. 2005). However, multiple causes may in fact lead to such patterns (Fridley et al. 2007). Extrinsic factors such as disturbance may in some cases drive negative richness relationships at larger scales (Lilley and Vellend 2009), with invasive species being 'passengers' rather than 'drivers' of ecological changes (MacDougall and Turkington 2005). In addition, the stage of invasion can affect many biogeographic measures of native and exotic species, such as species-area and species-abundance relationships (Labra et al. 2005; Hulme 2008), since signals of environmental preference and competition may not appear in the initial stages of invasion.

Spatial and temporal scales of observation are central to the ongoing debate regarding the critical questions raised above. While most analyses consider only a single scale, it seems clear that native and exotic species can interact with their environments and each other in different ways at different scales (Shea and Chesson 2002; Davies et al. 2005; Pauchard and Shea 2006). Despite the advantage of an experimental approach in isolating and testing alternative hypotheses of community assembly via species invasions, such an approach is virtually impossible at the larger scales needed to develop a comprehensive understanding of the invasion process. Thus, careful analysis and inference using a combination of biological and extrinsic data gathered from multiple, ecologically-relevant spatial scales may be necessary to examine the roles of competition and environmental response in native and exotic community assembly (Fridley et al. 2007).

We utilized such an approach to address the following questions in a species-rich, recently-invaded ecosystem: 1) Do patterns in native and exotic community richness and cover indicate competitive limitation of natives by exotics? 2) Do native and exotic species exhibit shared or divergent responses to environmental variation across scales? 3) Are community-level biogeographic patterns in native versus exotic communities reflective of incomplete population expansions in exotics?

To answer these questions, we sampled plant communities at discrete, nested scales from the landscape to microsite to test specific biogeographic predictions relevant to each question (Table 3.1). Specifically, we examined correlations in abundance among individual species pairs for native and exotic species, including separate analyses focussing on: 1) pairs of closely-related species; 2) native-exotic species richness relationships at three scales; 3) native versus exotic percent cover relationships at the microsite scale; 4) species richness

models based on environmental variables at two scales; and 5) partial canonical ordinations to compare environmental influences at all three scales on native versus exotic community composition. We also tested species-area and species-abundance relationships against predicted patterns based on stage of invasion and assumed community assembly processes, and we examined the dispersal abilities and environmental tolerances of hyper-abundant species in the 'tails' of abundance distributions. While demonstrating a single pattern cannot lead to strong conclusions about the mechanisms of native and exotic community assembly, taken together our results illustrate several scale-dependent differences and similarities among native and exotic assemblages and allow us to prescribe efficient conservation actions to minimize exotic invasions and conserve native diversity.

Methods

Study area

Our study sites were composed of 86 discrete, lowland meadow patches on southeast Vancouver Island, British Columbia, as well as smaller islands in the Strait of Georgia (See Appendix 1 for details). The climate in the study area is sub-Mediterranean, with cool, wet winters and frequent summer drought (MacDougall 2005). The meadow patches in the study area tend to be located on shallow-soil areas isolated from one another by a combination of forest, salt water and human-dominated landscapes. The patches are part of what is regionally referred to as the Garry oak ecosystem (GOERT 2011a), a floristically diverse vegetation type that is dominated by grasses and forbs. Approximately 390 native and 180 exotic vascular plant species have been reported in this vegetation type (Fuchs 2001). Garry oak ecosystem meadows represent an excellent laboratory for testing spatial and environmental components of community variation, as the meadow patches are spatially

distinct from one another; some are located on Vancouver Island, while others are located on small, relatively isolated islands in the Georgia Basin. A high degree of environmental heterogeneity also exists both among and within patches (MacDougall et al. 2006; Pinto and MacDougall 2010).

Community surveys

We used both extensive (patch-level) and intensive (microsite-level) surveys of vascular plant species in the study area. Patch-level surveys were conducted on 81 meadow patches ranging in size from ~0.2 to 17.7 ha. These patches were systematically surveyed across their full extents for presence of vascular plant species. Thirty-seven of these patches occurred on small islands and 44 on Vancouver Island. Intensive surveys were conducted on 86 meadow patches (including the 81 surveyed extensively) using percent cover estimates of vascular plants in 1-m^2 quadrats located in a stratified random configuration within patches. A total of 605 quadrats were surveyed; the number of quadrats per patch ranged from 5 to 15, depending on patch size. This sampling scheme facilitated comparisons of native and exotic communities at three ecologically distinct scales. The largest - the 'landscape' scale - was represented by all patches. At this scale, we distinguished two types of patches: those located on Vancouver Island and those located on nearby small islands. Those located on small islands have the commonality of being surrounded on all sides by the ocean as a dispersal barrier, while those on Vancouver Island are individually isolated by a matrix of forest, agriculture and development. The middle, 'inter-patch' scale represented differences among individual patches across the study area; and the smallest, 'intra-patch' scale represented microsite variation within patches. All surveys took place from April to June, the time of peak biomass in the study area, during which most plants are easiest to identify. Plants were

identified to the lowest taxonomic level possible; those that could not be identified *in situ* were collected for later identification at the University of British Columbia or University of Washington Herbarium. In patch-level surveys, a total of 394 taxa (257 native, 137 exotic) were identified, in >95% of cases to the species level. In quadrat-based surveys, 192 (127 native, 65 exotic) of these species were found.

Environmental variables

A total of 13 environmental variables were used in species richness and community composition models to assess the influence of environmental factors at different scales. Variable descriptions, collection and calculation methods appear in Appendix 5. In the case of climate, 83 variables recorded in Climate BC v.3.1 (Wang et al. 2006) were reduced using principal component analysis (PCA) to a single principal axis, explaining 69% of the total variation in the climate data. Climate PC1 was positively correlated with mean annual temperature ($r = 0.50$, $P<0.0001$) and negatively correlated with mean annual precipitation ($r = -0.66$, $P<0.0001$). Location of patches on small islands versus Vancouver Island was coded as a binary variable. In addition, soil samples were collected from each quadrat location and an initial representative group of 120 samples was analyzed for total carbon and nitrogen. However, soil data were omitted from final analyses because neither variable was significant in preliminary native and exotic richness models and canonical ordinations.

Table 3.1: Predicted patterns regarding the role of competition in native versus exotic community patterns; shared versus divergent environmental response; and evidence for incomplete invasion, with examples of references used to derive to predictions

Prediction	Predicted Pattern	Evidence For (+) or Against (-) Prediction	Test
Competitive limitation of natives by exotics	Negative native vs. exotic richness relationship at small scales, due to competition (Shea and Chesson 2002; Davies et al. 2005; Chen et al. 2010)	+	Ordinary least-squares (OLS) regression (native richness vs. exotic richness)
	Negative native vs. exotic % cover relationship stronger than random expectation; competitive invaders out-compete natives (Callaway and Aschehoug 2000; Ridenour et al. 2008)	+	OLS regression plus permutation of species origin to determine effect of origin on relationship
	Negative native vs. exotic % cover relationship, not different from that expected by chance (due to limited space at small scale; Fridley et al. 2004)	(+/-)	
	Correlations in percent cover among native vs. exotic species pairs predominantly negative due to competition (Tilman 1997; Stachowitz and Tilman 2005); negative correlations most prevalent among related species due to limiting similarity (Fargione et al. 2003; Vilà and Weiner 2004; Emery 2007; Diez et al. 2008)	+	Compare positive/negative significant correlations among species pairs (cf. Ricklefs 2011)
	Correlations in percent cover among native vs. exotic species pairs no different from random expectation (Hubbell 2001; Daleo et al. 2009)	-	
	Positive correlations predominate due to shared responses to environmental constraints (Thompson et al. 1995)	-	
Native vs. exotic shared environmental response	Native vs. exotic richness relationship positive at larger scales only, due to similar response to factors at broad scales (Lonsdale 1999; Stohlgren et al. 1999; Shea and Chesson 2002; Davies et al. 2005; Chen et al. 2010; others)	+	OLS regression of native vs. exotic richness
	Native vs. exotic richness relationship may be positive at smaller scales as well, due to shared response to invasible environments (Davis et al. 2000; Melbourne et al. 2007)	+	
	Native vs. exotic richness relationships negative at either large or small scales, due to greater response of exotics to disturbance (Vilà et al. 2007)	-	
	Native and exotic richness both related to similar environmental variables (Davis et al. 2000; Daehler 2003; Leishman et al. 2010; Tecco et al. 2010)	+	Mixed models, isolating influence at relevant scales
	Native and exotic richness respond to different variables, due to different strategies (MacDougall et al. 2009; van Kleunen et al. 2010)	-	

Prediction	Predicted Pattern	Evidence For (+) or Against (-) Prediction	Test
	Community composition relationship with environmental/spatial variables across scales similar due to similar environmental constraints of natives and exotics (Davis et al. 2000; Gilbert and Lechowicz 2005)	+	Decomposition of variation using partial ordination; bootstrapped ordinations for individual variables
	Exotic communities respond to different variables due to different strategies (MacDougall et al. 2009; van Kleunen et al. 2010)	-	
Exotic community biogeographic patterns reflect incomplete invasion	Exotic species not at equilibrium with environment (Welk 2004; Labra et al. 2005; Qian and Ricklefs 2006)	+	Redundancy analyses (RDAs); determine whether compositional change in exotics is more weakly related to environment than in natives
	Species-area curves of exotics have lower intercepts and steeper slopes, due to recent colonization (Hulme 2008)	+	ANCOVA comparing species-area relationships for natives and exotics
	Species-area relationships similar for natives and exotics, due to similar biogeographic constraints (Stark et al. 2006)	-	
	Exotics have proportionally more rare species, due to recent introduction (Lloret et al. 2004; Hulme 2008)	+	Test for differences in species-abundance relationship
	Dominant exotics in 'tails' of species abundance distributions (SAD) have long-distance dispersal ability, as populations of short dispersers will not have had sufficient time to spread (cf. Chapter 2)	+	Comparison of dispersal abilities of dominant exotics in 'tails' of SAD with exotics in general and with dominant natives
	Dominant exotics in 'tails' of SAD have broader environmental tolerances than natives (Labra et al. 2005); species with more specialized niches have not had time to reach potential distributions	+	Comparison of environmental specialization of dominant natives vs. exotics in 'tails' of SAD

Data analysis

Role of competition

      Competitive suppression of native by exotic species should lead to negative native versus exotic species richness relationships, particularly at smaller scales (Shea and Chesson 2002; Davies et al. 2005; Table 3.1). To test this prediction we used ordinary least-squares (OLS) regression of native versus exotic species richness per patch or quadrat. In addition, we used OLS regression to examine the relationship between native and exotic percent cover in quadrats. While the expected native versus exotic percent cover relationship at this level would be negative among any group of species, due to filling of limited space within the small sample area (cf. Fridley et al. 2004), highly-competitive invasives (cf. Callaway et al. 2004; van Kleunen et al. 2010) would create a native versus exotic cover relationship that was more strongly negative than expected by chance. To determine whether the observed percent cover relationships were more negative than expected by chance, we randomly permuted native/exotic status among species 1000 times, retaining the original numbers of 'natives' and 'exotics', re-testing the relationship each time to determine whether the slopes with randomized origin were more or less steep than the original slope.

      To assess the relative evidence of competition versus other potential determinants of community patterns (Table 3.1), a correlation matrix of percent cover for species pairs across all quadrats was generated, and proportions of correlation coefficients among species pairs that were above critical ($P = 0.05$) positive values and below critical negative values were then compared using Z-tests (cf. Ricklefs 2011). As the data for quadrat surveys were non-normal, Spearman rank correlation coefficients were used. To diminish the possibility of spurious correlations among the multiple comparisons, only species with 10 or more

occurrences among all quadrats were used. While tests of individual correlation coefficients are not interpretable due to potential Type-I error inflation from multiple tests, the general trends themselves are testable, and comparable to random expectations. Under a predominant influence of competition, negative associations would be greater than either positive associations or the random expectation (cf. Ricklefs 2011); if shared species associations due to shared environmental affiliations or facilitation were predominant, positive associations would be greater than the random expectation; under a neutral pattern, where species identity would be unimportant, no difference from the random expectation would be predicted. Random expectations for proportions of significant correlations were generated by randomly shuffling the percent cover entries within each species across all quadrats and then re-calculating the correlation matrix 1000 times. Proportions of significant positive and negative correlations for native versus other native species, exotic versus other exotic species, and exotic versus native species, were compared after correction for the random expectation. Since limiting similarity may affect invasion patterns whereby physically and phylogenetically distinct exotics may be better invaders due to greater competition among close relatives (Fargione et al. 2003; Emery 2007; Diez et al. 2008), we also compared a subset of correlation coefficients for the nearest confamilial relatives of native versus exotic species, to determine whether negative correlations were greater than positive among these species. Phylogenetic relationships were determined using the Phylomatic online phylogenetic analytical tool (phylodiversity.net).

Responses to environment

To test predictions regarding shared versus divergent environmental responses in native and exotic species (Table 3.1), we analyzed relationships between native and exotic

richness and environmental variables at all three scales. At the landscape scale, we compared

the two distinct groups of patches (those on small islands and those on Vancouver Island) for

average richness per patch using t-tests. We then tested for differences among environmental

variables for the two groups of patches using a permutation test. At the inter-patch scale, we

used linear mixed models to predict relationships of species richness to environmental

variables measured at this scale. The potential influence of patch location on small islands

(versus Vancouver Island) at this scale was controlled by using small island/Vancouver

Island status as a random factor in models. Similar models were constructed using variables

at the intra-patch scale, using both small island versus Vancouver Island status and patch

identity as random factors to isolate the intra-patch signal. In both cases, species richness was

log-transformed to improve fit, and predictor variables were transformed as necessary based

on residual patterns in initial exploratory models. We also created models for total percent

cover (arcsine square root transformed) of native and exotic species at the intra-patch scale,

in order to compare patterns in dominance with those of richness. In all cases, final models

were selected based on sequential elimination of nested candidate models using likelihood

ratio tests (Zuur et al. 2009). Estimates of P-values for comparison of selected parameters

were derived using Markov-chain Monte Carlo sampling (Baayen et al. 2008). All statistical

analyses were performed using R v. 2.12.0 (R Development Core Team 2010); mixed models

were created using the lme4 package (Bates et al. 2011).

To examine whether abiotic factors might influence native versus exotic species

richness relationships outlined above (e.g., shared positive influences masking competitive

effects), we re-ran the original OLS native versus exotic richness models, removing the

effects of important external variables. At the inter-patch scale, the effect of log area was

removed as a first step, since patch area is well-recognized to be positively related to species richness in general (Rosenzweig 1995), and indeed log area was the strongest positive predictor at this scale for both native and exotic species. This allowed us to partition the native versus exotic richness relationship that was independent of the species-area relationship shared by both groups. Next, for native versus exotic richness models at both scales we removed the effects of variables that were selected in the separate native species richness models and exotic species richness models described above, to determine whether there was an independent negative relationship between native and exotic richness that would suggest competitive dominance of one group over the other.

To assess changes in native versus exotic community composition with respect to environmental variables measured at the three observed scales, we used a series of redundancy analyses (RDAs) using intra-patch percent cover data and both environmental and spatial variables. Initial ordinations using all variables were constructed for native and exotic species separately, and the main axes of variation for the two groups were compared. We then used variation partitioning of partial ordination fractions (Borcard et al. 1992) to decompose variation explained by ordinations into conditional (including covariation) and marginal (independent) signals with respect to variables measured at each of the three scales. Spatial relationships among patches were represented by third-order polynomial transformations of centered UTM coordinates as per Borcard et al. (1992), as opposed to eigenvectors (e.g., Borcard and Legendre 2002), which can suffer from statistical artefacts that inflate both the spatial signal and covariation with environmental signals (Gilbert and Bennett 2010). Polynomials were not orthogonalized since orthogonal polynomials explain the same total variation as non-orthogonal polynomials, and are more difficult to interpret in

terms of a spatial signal; individual polynomial terms were not interpreted due to high

covariation among them. Measured in this way, the spatial relationships among patches may

be related to either dispersal limitation or unmeasured, spatially-autocorrelated

environmental variables.

Species data were transformed using the Hellinger transformation (Legendre and

Gallagher 2001), and variation explained by ordinations was corrected according to Peres-

Neto et al. (2006). Although exploratory ordinations indicated that variation explained was

insensitive to changes in the number of species included, we chose to include only species

found in 10 or more quadrats, to avoid the risk of spurious associations.

To decompose the components of community variation into independent fractions

corresponding to variables at each scale, a total of 11 partial RDAs was required (see

Appendix 6 for details). Covariation with variables at other levels was subtracted at each

scale, to obtain the independent variation explained. At the inter-patch scale, the signal of

spatial polynomials was analyzed separately from that of the environmental variables, to

obtain an estimate of inter-patch spatial patterns. All variables included in the analyses were

individually tested *a priori* for a statistically-significant signal: two variables at the intra-

patch scale (northing and easting) were eliminated for both native and exotic species due to a

lack of significant signal. It is important to note that the ordination fractions explained at

each scale do not account for the absolute fraction of variation that could possibly be

explained at this level, as not all possible variables (or interactions) were measured. For

example, unmeasured factors potentially responsible for differences among patches could not

be accounted for using patch identity as a categorical variable, due to the 85 individual

predictor variables that would have been added. Thus, comparisons among the measured spatial and environmental variables in native and exotic assemblages are relative.

To determine the relative importance of single variables in ordinations, individual ordinations of both conditional and marginal variation explained for each variable were compared for native and exotic species. The absolute values of variation explained in individual ordinations must be interpreted with caution (Økland 1999; Gilbert and Bennett 2010); therefore we used a bootstrap technique to assess the robustness of the general relative patterns. Patch data were subsampled randomly with replacement 1000 times, and then each ordination was re-run. This process generated confidence intervals for mean values of variation explained for individual variables and the ranks of their relative importance in ordinations.

Incomplete invasion

Incomplete dispersal of exotic species to suitable patches would result in a lack of equilibrium with the environment among exotic species (Welk 2004; Labra et al. 2005; Qian and Ricklefs 2006; Table 3.1), and thus a weaker environmental component of variation in community composition than for natives. To assess this prediction, we compared the total variation explained by environmental variables for native and exotic species in RDAs above.

We also compared species-area relationships and species abundance distributions of native and exotic species based on additional predictions of biogeographic patterns arising from incomplete expansion of exotic populations (Table 3.1). We tested for differences in the slopes and intercepts of native and exotic species-area relationships using analysis of covariance (ANCOVA) in log-transformed species-area OLS regressions. To test for

differences between species abundance relationships of native and exotic species, we created histograms of species abundances, and tested for the difference between the ratio of native to exotic species in each bin and that of the dataset as a whole, using Fisher Exact tests. Several configurations of histograms, using bin sizes of five, 10 and 20 occurrences for full surveys, and 20, 40 and 80 occurrences for quadrats, as well as log (base 2) bins were tested, to ensure that configuration choice did not affect results.

Species whose abundances fell within 50% of the most abundant species (representing the few super-abundant species in the dataset, or the 'tails' of the species-abundance distributions), were compared for differences in long-distance dispersal capacity, as well as environmental specialization, to assess the prediction that long dispersers and generalists would dominate among the newly-arrived exotics (Table 3.1). Long-distance dispersal capacity was determined based on presence of dispersal-aiding adaptations (e.g., hooked awns, pappus, edible fruit, adhesive seeds). For all species not possessing obvious characteristics facilitating long-distance dispersal, the primary literature was searched for evidence of long-distance dispersal capacity (e.g., consumption by animals and survival in their guts), and species were classified accordingly. Ratios of long-dispersing species to short-dispersing species were compared for native and exotic species in the tails of abundance distributions at the inter- and intra-patch scales, using Fisher Exact tests. Environmental specialization was estimated using the range of species occurrences among quadrats, correcting for the total number of occurrences using null estimates based on random sampling (see Appendix 7 for details). Environmental specialization estimates were compared for the most common native and exotic species at the intra-patch scale using a t-test.

Results

Role of competition

Native versus exotic richness and cover relationships

At the inter-patch scale we found no linear relationship between native and exotic species richness (Fig. 3.1a), while the relationship at the intra-patch scale was weak but positive and significant (Fig. 3.1b). Percent cover of native species at the intra-patch scale was negatively related to percent cover of exotic species (B_1 = -0.344; R^2=0.22; P<0.0001). Randomization of origin in species also resulted in significant negative slopes in all cases, with 231 of 1000 random runs having a steeper negative slope than the real data, indicating that the observed negative relationship was independent of origin.

Correlations among species pairs

The proportion of significant correlations in percent cover was greater than the random expectation among native versus native species pairs, exotic versus exotic species pairs, and native versus exotic species pairs (see Appendix 8 for details). In each set of comparisons, positive correlations were more common than the random expectation (Fig. 3.2). Among 125 pairs of native and exotic closest confamilial relatives, there were 26 significant positive correlations and 24 significant negative correlations.

Figure 3.1: Native versus exotic species richness relationships: a) inter-patch scale; b) intra-patch scale.
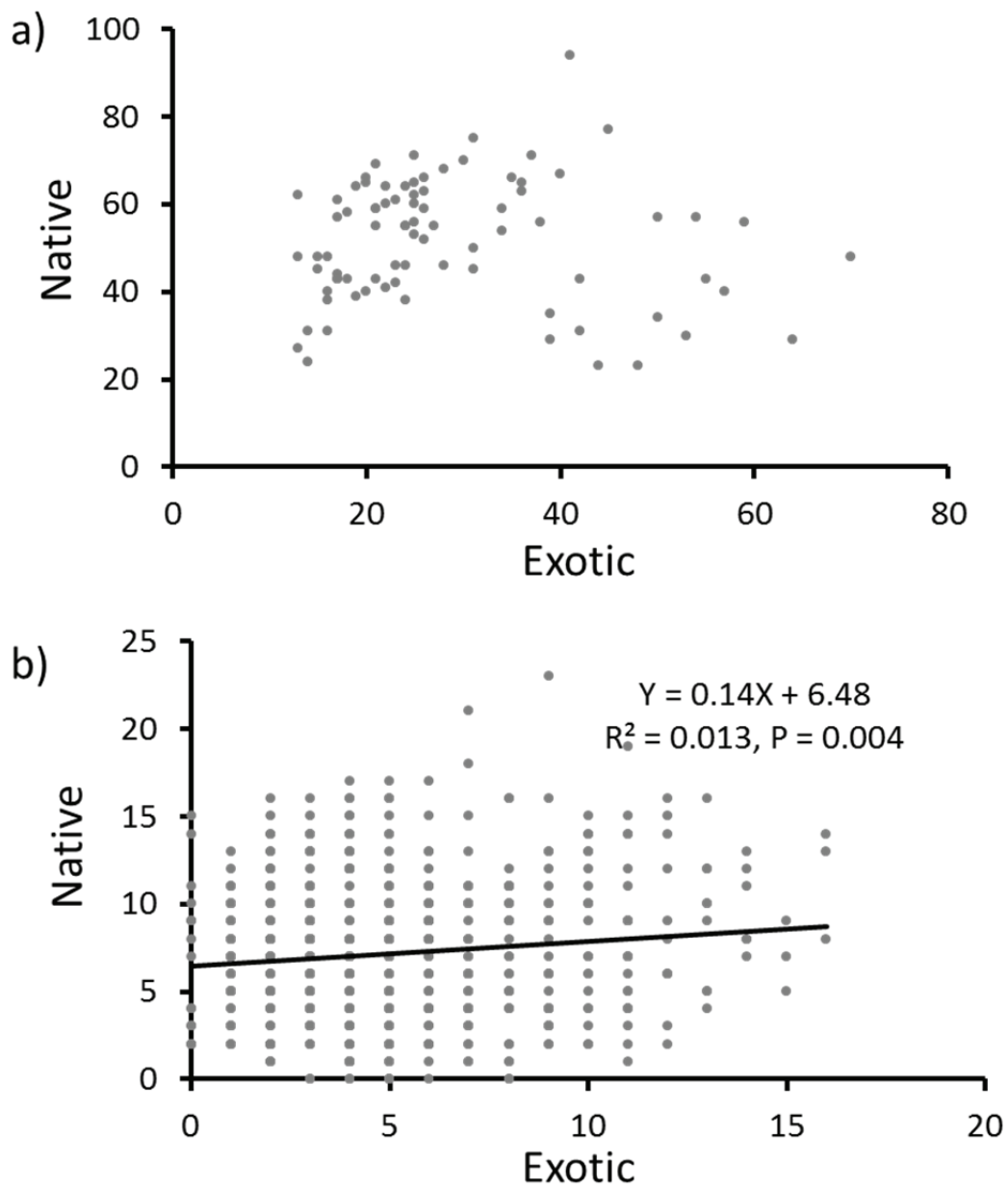
Figure 3.2: Proportions of Spearman rank correlations in percent covers among species pairs that were significant. White bars = significant positive correlations; black bars = significant negative correlations. In all cases, the proportion of significant positive correlations is significantly higher than negative correlations (native-native: Z = 20.2, P<0.0001; exotic-exotic: Z = 27.0, P<0.0001; native-exotic: Z = 3.5, P=0.0003).
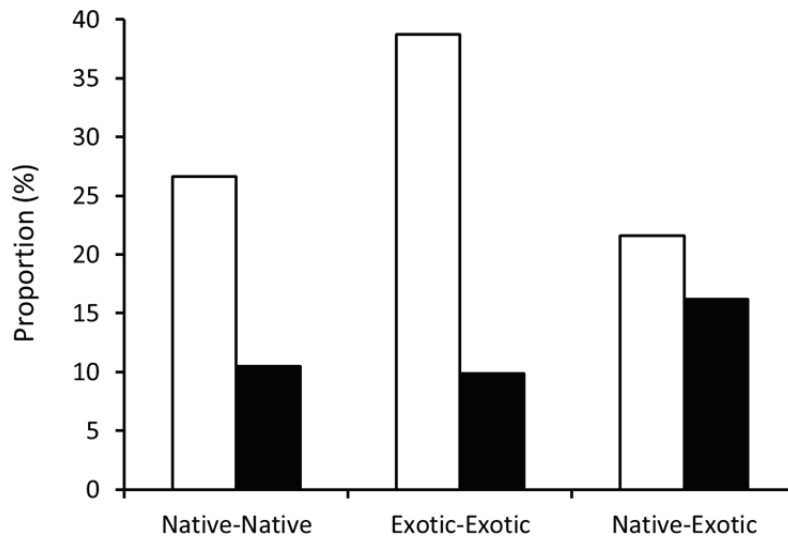
Responses to environment

Richness versus environment

At the landscape scale, the two groups of patches (those on Vancouver Island and those on small islands) differed significantly in their average exotic species richness (mean exotic richness on small islands = 21.9 ±1.1 SE; mean exotic richness on Vancouver Island = 34.8 ±2.2 SE; t = 5.0, P>0.0001). However, there was no significant difference in the average richness of native species between small-island patches and Vancouver Island patches (mean native richness on small islands = 50.6 ±2.3 SE; mean native richness on Vancouver Island = 52.6 ±2.1 SE; t = 1.6, P = 0.52). Standardization by log area did not affect this pattern

(results not shown). At this scale, several variables differed in mean value from Vancouver Island to small-island patches (see Appendix 9 for details).

At the inter-patch scale, models predicting native and exotic species richness also differed, with log area being the only positive predictor variable shared between the two groups (Table 3.2). When the effect of log area was removed from the native versus exotic species richness model at the inter-patch scale, native and exotic richness were negatively related to each other (log native versus log exotic, $B_1 = -0.2827$, $R^2 = 0.30$, P<0.0001). However, when the effects of other parameters selected during the development of richness models for native and exotic species (Table 3.2) were also removed, the richness relationship became non-significant, as per the original native versus exotic richness relationship ($B_1 = 0.048$, $R^2 = 0.003$, P = 0.61).

At the intra-patch scale, parameters in the final native and exotic richness models were a mix of unshared (negative relationship with litter for exotics only), concordant (shared positive relationships with log soil depth), and discordant (opposite relationships with canopy openness; Table 3.2). If the effects of parameters selected to develop richness models were removed from the native versus exotic richness model, the weak positive richness relationship seen in Fig. 3.1b remained statistically significant (log native versus log exotic, $B_1=0.084$, $R^2=0.007$, P=0.036). In predictive models of native and exotic species cover at the intra-patch scale, the same variables were selected for native and exotic species, with a mixture of concordant and discordant responses (Table 3.2).

Table 3.2: Selected parameters based from models of: a) log species richness for native and exotic species at both the inter- and intra-patch scales, and b) arcsine square root cover at the intra-patch scale.

a) Richness

Inter-patch Scale	Variable	Estimate	Standard Error	t	P (est.)
Native	Forest Area (ha; within 500 m)	0.00207	0.000382	5.43	<0.00001
	Log Road Length (log m; within 500 m)	-0.0299	0.00706	-4.24	0.0001
	Log Area (log m^2)	0.119	0.0263	4.53	<0.00001
Exotic	Forest Area (ha; within 500 m)	-0.00297	0.000462	-6.44	<0.00001
	Climate PC1	0.0363	0.0121	3.01	0.0035
	Log Area (log ha)	0.205	-0.0267	7.66	<0.00001
Intra-patch Scale					
Native	Log Soil Depth (log cm)	0.101	0.0241	4.21	<0.0001
	Canopy Openness (%)	-0.00190	0.000486	-3.91	<0.0001
Exotic	Litter (% cover)	-0.00229	0.000822	-2.79	0.0055
	Log Soil Depth (log cm)	0.0790	0.0246	3.21	0.0014
	Canopy Openness (%)	0.00217	0.000477	4.55	<0.0001

b) Cover

Intra-patch Scale	Variable	Estimate	Standard Error	t	P (est.)
Native	Log Soil Depth (log cm)	0.198	0.0296	6.68	<0.0001
	litter (% cover)	-0.00537	0.000990	-5.42	<0.0001
	Canopy Openness (%)	-0.00200	0.000574	-3.48	0.0005
Exotic	Log Soil Depth (log cm)	0.135	0.0236	5.71	<0.0001
	Litter (% cover)	-0.00179	0.000789	-2.26	0.024
	Canopy Openness (%)	0.00157	0.000455	3.45	0.0006

Constrained ordinations

Biplot scores in RDAs using all variables indicated that the primary axis of variation was most closely associated with patches on small islands (negative eigenvalues in both cases) and log road length within a 500-m buffer (positive eigenvalues), for both native and exotic communities (see Appendix 6 for details). Decomposition of community change

across scales using variation partitioning revealed broadly similar patterns among native and exotic species, suggesting that each responded similarly to the environment and spatial structure across scales (Fig. 3.3). The most striking differences occurred between small-island and Vancouver Island patches, whereby the native community showed greater differentiation (i.e., greater variation explained) than the exotic community. Though much of the variation explained at this level was shared with other levels and could not be unambiguously partitioned, the pattern is reasonably clear. Several native species were very common on islands but rarely encountered on Vancouver Island (e.g., *Rosa nutkana*, which was present in 20% of small island quadrats and 3% of Vancouver Island quadrats), while others were very common on Vancouver Island but rarely encountered on islands (e.g., *Camassia quamash*, which was present in 49% of Vancouver Island quadrats and 4% of small island quadrats). Indeed, abundance of individual native species in quadrats on small islands was only weakly related to their abundance on Vancouver Island ($R^2 = 0.08$, P=0.03), meaning that many species were common on either smaller islands or Vancouver Island but not both. The abundance of exotic species on small islands versus Vancouver Island was much more strongly related ($R^2 = 0.31$, P<0.0001), meaning that species that were common on Vancouver Island also tended to be common on small islands.

Bootstrap analyses of individual variables also revealed broadly similar profiles of explained variation between native and exotic communities, with small island versus Vancouver Island status and log road length being the most important variables for both native and exotic species (see Appendix 6). Again, differentiation was stronger between small-island and Vancouver Island patches for native than exotic species (see Appendix 6).

Figure 3.3: Decomposition of community change related to variables measured at three spatial scales. Total variation (leftmost diagram) is decomposed into marginal (unique; black segments) and conditional (shared; white segments) variation explained by variables at each scale (white segments). Marginal variation from each level sums to the total variation in the leftmost diagram. At the inter-patch scale, spatial polynomial terms of UTM coordinates are separated from environmental variables.
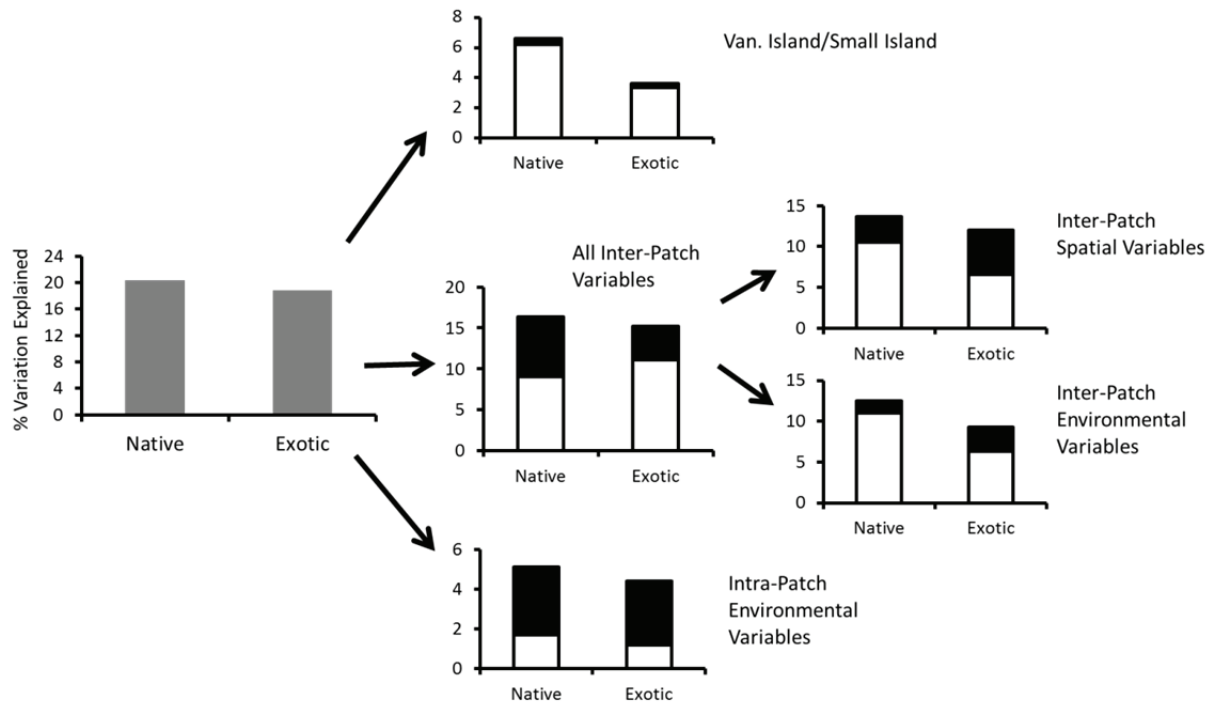
Incomplete invasion

Ordinations

As indicated above, variation explained by ordinations across scales was similar for native and exotic communities, with slightly weaker environmental signals for exotics (Fig. 3.3). However, ordinations indicated that long-distance dispersers were overrepresented among exotic (but not native) species that were abundant on small-island patches. Twelve exotic species were common on small-island patches, as indicated by negative axis 1 scores in the RDA with all variables. These 12 exotic species were all long dispersers. Of the 32

native species with negative axis 1 scores, only 13 were long dispersers, whereas 19 were short dispersers. The difference between the two ratios is highly significant (Fisher Exact test, P = 0.0003). The ratio of long to short dispersers in exotic species with negative axis 1 scores was also significantly different than that of the full set of exotic species (Fisher Exact test, P = 0.008), while the ratio of long to short dispersers for natives with negative axis 1 scores was not significantly different from that of the full set of native species (Fisher Exact test, P = 0.184).

Species-area relationships and species abundance distributions

Comparison of species-area relationships between native and exotic species suggested influence of incomplete invasion on the exotic species-area relationship. The intercept of the species-area relationship for exotic species was significantly lower than for native species (t = 12.7, P<0.0001; Fig. 3.4), while the slope was qualitatively but only marginally significantly steeper (t = 1.83, P = 0.072).

Species abundance distributions were remarkably similar for native and exotic species (Fig. 3.5), regardless of bin size (Appendix 10). At the inter-patch scale, no ratio in any histogram bin, regardless of bin size, was significantly different from the total ratio of native to exotic species. At the intra-patch scale, only one bin (160 to 199 quadrats) in the 40-interval histogram and one bin (79 to 160 quadrats) in the 80-interval histogram exhibited ratios that were significantly different from the expected ratio, with a higher proportion of exotic species (Fisher Exact test, P = 0.043 and P = 0.037, respectively).

However, among the super-abundant species in the 'tails' of inter- and intra-patch species abundance distributions, a significantly higher ratio of exotic species were long

dispersers (Table 3.3). Ratios of long versus short dispersers for native and exotic species were not significantly different in the full dataset. Environmental specialization of super-abundant exotic species at the intra-patch scale was also marginally significantly lower than that of super-abundant native species ($t = 2.05$, $P = 0.053$), suggesting that generalists were more common among super-abundant exotics than among super-abundant natives.

Figure 3.4: Log-transformed species-area relationships for native (A) and exotic (B) species.
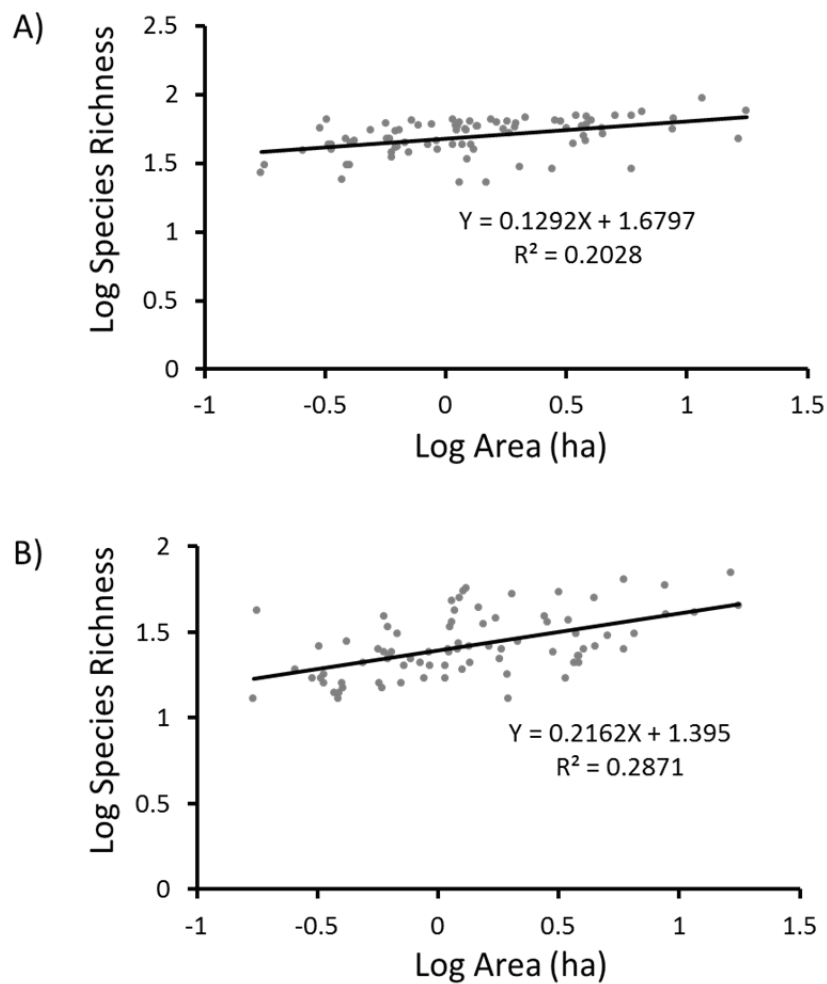
Figure 3.5: Species-abundances of native (black bars) and exotic (white bars) species, as proportions of total abundance in full patch surveys (inter-patch scale). See Appendix 10 for species-abundance relationships for quadrat surveys, as well as additional bin sizes.
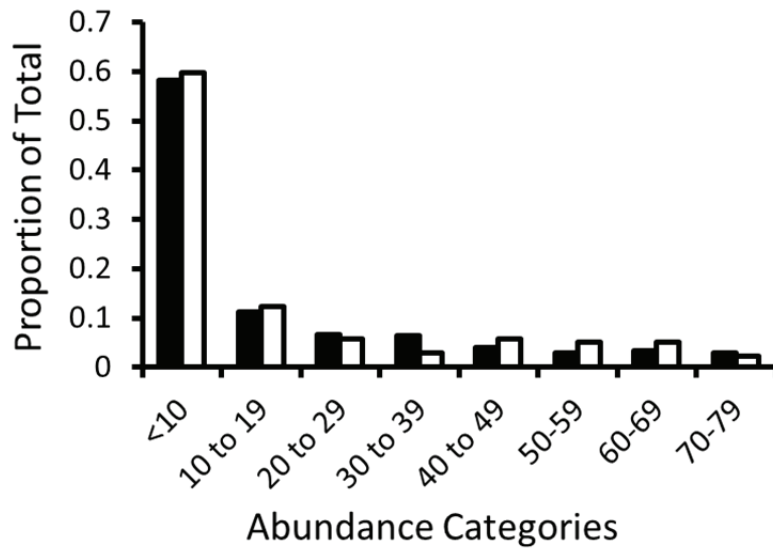
Table 3.3: Number of long and short dispersing species in the full dataset, and in super-abundant species at the inter- and intra-patch scales

		Long Dispersers	Short Dispersers	Fisher Exact Test, P
All Species	Native	109	93	0.198
	Exotic	72	45	
Super-Abundant, Inter-patch Scale	Native	20	17	0.0017
	Exotic	24	2	
Super-Abundant, Intra-patch Scale	Native	5	7	0.027
	Exotic	10	1	

Discussion

None of our tests for competition as a determinant of native and exotic community patterns (Table 3.1) yielded positive evidence. However, tests for shared versus divergent environmental response at the inter-patch and intra-patch scales (Table 3.1) demonstrated a

mixture of concordant and discordant responses (Table 3.2). And tests for the influence of

incomplete invasion on biogeographic patterns were generally positive once species dispersal

and specialization characteristics were considered. Thus, community patterns demonstrated

the following: a lack of evidence for competition as a primary determinant of native versus

exotic community patterns; scale-dependent similarities and differences in native and exotic

species' responses to the environment; and a community assembly process that is ongoing,

suggesting the development of novel native and exotic communities in the future. Moreover,

our results suggest that if our analyses had focused on a single scale, or used fewer

explanatory parameters, different conclusions would likely have been drawn, underlining the

importance of addressing such complexities in native and exotic community comparisons.

Indeed, we found that complex responses to external factors at different scales may underlie

many of the synoptic patterns that have been interpreted in isolation in the literature to date,

indicating that such patterns may be difficult to interpret in the absence of a more thorough

comparison of native and exotic communities at multiple scales. Below, we examine in detail

the evidence for competition, concordant versus discordant environmental response, and

incomplete invasion in determining biogeographic patterns in native and exotic communities.

Role of competition

While some theory and small-scale experimental results predict that competition

among native and exotic species will be common in nature (e.g., Elton 1958; Tilman 1997;

Corbin and D'Antonio 2004; Table 3.1), several lines of evidence indicate that competition

has played a relatively minor and perhaps negligible role in determining present native

versus exotic community patterns among our study patches. First, we found a positive

relationship between native and exotic species richness at the 1-m^2 scale (Fig. 3.1b), even

after removing the effect of environmental variables. Second, the negative cover relationship between native and exotic species was not stronger than the random expectation, suggesting that native versus exotic competition was not greater than would be expected among native species themselves. Third, positive correlations predominated among individual native/exotic species pairs (Fig. 3.2), even among the closest confamilial relatives. While the presence of more positive than negative correlations does not eliminate the possibility of competition or some degree of limiting similarity among species, it does strongly suggest that shared environmental tolerances are mainly responsible for determining present patterns in native versus exotic species co-occurrences, and that competition plays a subordinate role. Indeed, those negative correlations that were significant may have been at least partly due to different habitat affiliations between species.

There is a growing body of evidence indicating that competition is often of limited importance in determining the relative abundances of native and exotic plant species (e.g., Gilbert and Lechowicz 2005; Gonzales and Arcese 2008; Lilley and Vellend 2009; Simberloff 2010), and that exotic species tend to be "passengers" rather than "drivers" of ecological change, generally responding to external factors rather than engineering changes through competition (MacDougall and Turkington 2005). Some degree of competition between native and exotic plants presumably exists, and some exotic species in our study area are apparently highly effective competitors (e.g., *Anthoxanthum odoratum*, which may suppress other species via allelopathic exudate; Newman and Rovira 1975; Yamamoto 1995). However, our results, and indeed the predominant findings of previous community-level analyses, indicate no obvious compensatory relationship among native and exotic species, instead implying that other factors have been essential in structuring communities.

While the potential for exotic species to competitively exclude natives at larger scales is debated (e.g., Stohlgren et al. 2008a,b; Harrison 2008), the phenomenon appears to be rare at present (Stohlgren et al. 2008a; Sax and Gaines 2008). Indeed, there is virtually no evidence of contemporary extinctions of plants based solely on competition with invasive species (Davis 2003; Sax and Gaines 2008), and species saturation may not exist for plants at larger scales (Stohlgren et al. 2008a), or may not be obvious for hundreds to even thousands of years. At our geographic scales of analysis and at the present time, abiotic factors such as isolation and disturbance appear to exert greater control on native and exotic flora. Our lack of evidence for negative richness relationships at the 1-m^2 level is particularly revealing, and is contrary to predictions of negative richness relationships at small scales due to competition (Shea and Chesson 2002; Davies et al. 2005). The microsite scale is presumably the point at which competition among species would first be observed. However, in our study system, native richness does not currently appear to be driven by exotic species, even at the microsite scale.

Environmental heterogeneity at small spatial and temporal scales has been hypothesized to promote both species invasions and the persistence of existing species (Foster and Tilman 2003; Melbourne et al. 2007). Thus, given the high degree of habitat heterogeneity in our study system, both in terms of microsite-level variability (Pinto and MacDougall 2010) and temporal climatic fluctuations (Zhang and Hebda 2005), we expect natives to continue to persist in the absence of increased disturbance or novel ecological stressors. While animals may exhibit saturation and extinction based on competition (Mack et al. 2000), the fact that plants do not as yet reveal such patterns may be due to their ability

to persist in microsites, and their tendency to interact over smaller spaces than motile creatures, which may compete over larger distances.

However, while the negative percent cover relationship we observed at the microsite level was not related to species origin, it does indicate that exotic species are usurping space and, presumably, resources. Foster and Tilman (2003) similarly noted a lack of evidence for saturation among native and exotic species in a speciose and environmentally diverse savanna, but cautioned that the full effect of competitive interactions may not be observable for many years. In our study system, 67 native plant species are currently at risk of extinction (GOERT 2011a). Although our results suggest that competition with exotic species is not a primary cause of their rarity, it may diminish their fecundity (Pinto and MacDougall 2010), further jeopardizing a tenuous position. Whether exotic species have more deleterious competitive effects on rare natives than do other native species remains an open question. However, if the general level of competition does indeed increase with the addition of novel species (cf. Tilman 1997), then competition may in the future interact more strongly with environmental factors that, given our current results, appear to have predominantly affected community composition and species abundance in our study system.

Environmental response

At the landscape scale, lower richness of exotic species on small islands may have been due to a number of factors. Road length and agricultural land within 500 m buffers of patches, both proxies of human disturbance and exotic propagule pressure, were significantly lower for small-island patches than Vancouver Island patches. Human disturbance, a known promoter of species invasions (Hobbs and Huenneke 1992; Davis et al. 2000) is likely to be considerably higher on the Vancouver Island patches, as is propagule pressure from adjacent

disturbed areas. Incomplete dispersal of exotics across the biogeographic barrier of the ocean likely also contributed to this difference in exotic richness between Vancouver Island and small-island patches.

Patterns in native versus exotic species richness relationships at the inter-patch and intra-patch scales did not correspond to the positive relationship at large scales and negative relationship at small scales predicted by many theoretical and empirical analyses (e.g., Shea and Chesson 2002; Davies et al. 2005; Fridley et al. 2007; Chen et al. 2010). While exceptions to the generally-recognized common patterns have been demonstrated (Fridley et al. 2007; Lilley and Vellend 2009), we observed them across many study patches and at more than one scale, in addition to clear differences in native and exotic richness patterns in two types of patches at the broadest (landscape) scale. Fridley et al. (2007) noted several mechanisms capable of producing positive or negative relationships among species, with biotic factors driving negative relationships and either abiotic or biotic factors driving positive relationships. Lilley and Vellend (2009) reported a negative native versus exotic richness relationship at the inter-patch scale in a sub-region of our study area, and inferred that this was based on abiotic factors. In contrast, our results from a larger study group that is more representative of the GOE indicate that abiotic factors can contribute to positive, negative or no apparent richness relationship at different scales, through a combination of concordant and discordant influences on native and exotic species richness.

Specific variables related to native and exotic richness across scales indicate that, in general, exotic species in our study area are more common in more disturbed, less isolated patches and more open microsites (Table 3.2). This result is unsurprising and commonly reported (e.g., McIntyre and Lavorel 1994; Davis et al. 2000; Vilà et al. 2007). Nevertheless,

it reinforces growing evidence that external factors are strong determinants of native and exotic species patterns (e.g., MacDougall and Turkington 2005; Lilley and Vellend 2009; Simberloff 2010). Responses to these external influences may be shared or divergent between natives and exotics. For example, the strong positive influence of soil depth in richness and percent cover models of both native and exotic species (Table 3.2) suggests a common constraint at the microsite level. In our study system, the summer growing season receives little precipitation, and deeper soils allow greater access to moisture (MacDougall and Turkington 2006). Likewise, the negative effect of litter illustrates its suppressive influence on both native and exotic communities (Table 3.2).

Incomplete invasion

While redundancy analyses of community composition revealed broad similarities between native and exotic species in the percentage of variation explained across scales (Fig. 3.3), the slightly lower fraction of variation explained by environment among exotics may indicate a comparative lack of equilibrium with the environment. However, comparisons among native and exotic species that were common on the small-island patches were more striking. Common exotics on small-island patches were nearly all long dispersers, while natives that were common on small-island patches frequently possess relatively large seeds for which there is no known dispersal mechanism (e.g., *Camassia leichtlinii*, *Brodiaea coronaria*, *Allium cernuum, Sedum spathulifolium*). Many such species also possess adaptive structures for tolerating drought and thus appear to follow a strategy of tolerance and persistence amid fluctuating conditions. While some common exotic species also possess obvious morphological characteristics for surviving fluctuations in moisture regime (e.g., *Hypochaeris radicata*; succulent leaves and taproot), others (e.g., *Aira praecox, Bromus*

diandrus) do not possess such structures. Such species may rely on a combination of frequent dispersal and seedbank to establish and survive in patches more removed from source populations.

While species-area relationships were consistent with lower representation of exotics on smaller patches due to incomplete invasion (Hulme 2008), abundance distributions of exotic species did not reveal proportionally more rares than those of natives, as would be predicted for incomplete invasion (Lloret et al. 2004; Hulme 2008). However, the hyper-abundant exotics in the 'tails' of species-abundance distributions were predominantly long dispersers and generalists, which was not the case for hyper-abundant natives. Thus, despite displaying superficially similar species abundance distributions, key differences in life history between dominant native and exotic species imply that dispersal ability is an important factor affecting dominance among exotics but not natives.

Over time, we suggest that the slower-dispersing exotic species will likely become more common, eventually leading to more similar biogeographic patterns in native and exotic species. For example, Long et al. (2009) found very similar species-area curves for native and exotic species on coastal islands of eastern North America that were located in closer proximity to one another (within 15 km), and had a ~150 year longer history of post-colonial occupation than our study area. In the absence of management to prevent species invasions, our study system may in the future display similar patterns.

In addition, exotic species whose characteristics resemble the drought-tolerant short-dispersing native dominants more closely (e.g. *Allium vineale*; *Hyacinthoides hispanica*; *Sedum album*) may increase in dominance, while ruderal, disturbance-dependent species may

currently be overrepresented in the exotic flora (MacDougall and Turkington 2006), and may

diminish somewhat over time. Seasonal and interannual droughts have characterized the

study system for thousands of years (Zhang and Hebda 2005). Over time, some of the less

frequent and more severe droughts could conceivably reduce the abundance of exotic long

dispersers that do not possess the means of surviving large fluctuations in conditions, while

populations of more drought-tolerant exotics may increase. Alternatively, if some of the

currently-common exotics (several of which originated in the Mediterranean region; Lilley

and Vellend 2009) possess both long-distance dispersal ability and drought tolerance, these

species may compete with natives more intensively in the future and potentially dominate

many patches within our study area.

It is also possible that niche partitioning in space and time may occur such that native

and exotic species sharing the same habitat will tend to reflect different phenologies. Spatial

and temporal fluctuations in resources likely lead to coexistence of many species (Davis et

al. 2000; Melbourne et al. 2007). In addition, different life-history strategies may lead to

post-invasion coexistence, such that requirements for various resources may differ (cf. Byers

and Noonburg 2003), or species may partition resources in time, differing in their phenology

such that competition is reduced. For example, small native winter annual species such as

Collinsia parviflora, as well as perennial natives with underground nutrient stores that give

them a head-start on spring growth (e.g., *Olsynium douglasii, Erythronium oregonum,*

Lomatium utriculatum), may be able to grow and produce seed before larger exotic grasses

outcompete them for light. Future analyses exploring possible tradeoffs between drought

tolerance and long-distance dispersal ability, as well as the long-term roles of competition

and spatial/temporal niche partitioning among native and exotic dominants, will improve the

predictability of future trends in native and exotic communities for this and other study systems.

Conclusion and conservation recommendations

The contrasting evidence in the literature regarding the relative competitive abilities and environmental responses of native and exotic species (e.g., Daehler 2003; van Kleunen et al. 2010) can be summarised in the following question: "Are there fundamental ecological differences between native and exotic species?" We have shown that the answer can be either "yes" or "no", depending on the scale of observation and parameters measured. Native and exotic communities may respond in both concordant and discordant ways to specific influences at different scales, sharing some biogeographic patterns, but differing in some specific drivers of richness and composition, as well as characteristics of dominant species. Understanding native versus exotic community responses across scales is crucial to predicting future trends and to recommending conservation actions aimed at maintaining viable and species-rich native communities.

While exotic species can generally be understood as "passengers" of environmental changes (cf. MacDougall and Turkington 2005), successful exotics appear to be different from their native counterparts, likely because characteristics that are different from those possessed by the original inhabitants are favoured when environments are fundamentally changed. In areas where the environment has recently changed, species that are able to disperse quickly to newly-available microsites will tend to proliferate (Rejmánek and Richardson 1996). Such highly-dispersive, ruderal species are more readily introduced by humans, and thrive in areas where human disturbance is an important factor (Moles et al.

2008), such as several of our sites on Vancouver Island that exhibit higher-than-average exotic richness and cover.

Given that the diversity of native and exotic species in our study system presently appears to depend largely on abiotic factors, conservation efforts could focus on the specific factors and scales for which native and exotic species responses are discordant, and then take advantage of those factors that favour natives over exotics. For example, small islands appear to be generally better protected from invasion than patches on Vancouver Island. Though some highly-dispersive exotics have successfully colonized small-island patches (Chapter 2), they are far less abundant on small-island patches than on Vancouver Island patches. Adding small-island patches to protected area networks thus may represent a more efficient conservation strategy than adding more heavily-invaded patches on Vancouver Island. In addition, human disturbance at the inter-patch scale also appears to be a key factor that can negatively influence native richness; therefore limiting disturbance particularly around patches that are relatively intact should be an effective means of preserving native richness. At the intra-patch scale, however, we found weak positive richness relationships and a predominance of positive correlations in percent cover among individual native and exotic species pairs. Thus, at the smallest scale, it may be difficult to manage conditions favouring one group over the other. In addition, attempting to reduce competition from exotic species at the intra-patch scale, for example via selective weeding, may not be sufficient to save rare native species, since there is a high likelihood that ruderal exotics will re-colonize (Kettenring and Adams 2011), and common native species may be equally competitive with their rare counterparts.

Although the most common exotic species in our study area appear to have benefited from a strategy of long-distance dispersal, some of the more dispersal-limited and as yet uncommon exotic species may have the greatest future potential for range expansion (Chapter 2). For the less common exotics, vigilant monitoring and removal will likely be key to preventing future expansion among those that are tolerant of long-term environmental fluctuations, and may reduce the possibility of competition with exotics becoming an important determinant of native species survival.

Chapter 4: Spatially-explicit predictions of native and exotic species distributions and richness in a patchy ecosystem

Introduction

Predictive models of species richness and distributions can be powerful tools for biological conservation. Species richness models have been used in a variety of conservation applications, such as predicting the effects of anthropogenic environmental changes (e.g., McIntyre and Lavorel 1994; Findlay and Houlahan 1997), predicting the environmental correlates of exotic species invasions (e.g., Stohlgren et al. 1999), and deriving criteria for protected area selection (e.g., Honnay et al. 1999). Species distribution models have also been used to guide land management prescriptions (e.g., Milsom et al. 2000; Ortega-Huerta and Peterson 2004), guide the rehabilitation of disturbed sites (e.g., Grosvernier and Matthey 1997), and predict species invasions (e.g., Zhu et al. 2007; Evangelista et al. 2008; Jones et al. 2010). As a consequence, it is widely recognized that well-designed and validated species distribution and richness models have the potential to greatly increase the efficiency of conservation efforts through focussed monitoring and proactive management (Rodríguez et al. 2007).

Three major goals of protected area managers are to: 1) select optimal sites to conserve; 2) rehabilitate disturbed sites; and 3) monitor emerging threats such as invasive species. Each goal requires managers to predict patterns in species distributions and diversity as accurately as possible (Rodríguez et al. 2007). Species richness and distribution models can therefore be vital tools for protected area management (Guisan and Thuiller 2005; Peterson 2006; Rodríguez et al. 2007).

However, several difficulties arise when modeling species distributions and richness. While statistical models of any type may be limited by inadequate parameterization, insufficient sample size, or violation of model assumptions (Kutner et al. 2005), ecological models often have the added challenge of characterizing environmental processes that are inherently spatial (Legendre 1993). This can lead to two general problems. First, species distributions may be spatially autocorrelated, due to dispersal limitation (Hubbell 2001), mass effects (Cottenie 2005), or spatially autocorrelated environmental variables (Borcard et al. 1992). These signals are often inherently impossible to isolate completely (Gilbert and Bennett 2010). Spatial autocorrelation may occlude the signal of environmental niches, and can lead to pseudoreplication, whereby nearby sites violate the assumption of randomness in sampling (Fortin and Dale 2005). Selection and interpretation of model parameters may therefore be influenced by spatial autocorrelation, as biotic processes may lead to statistical relationships between spatially autocorrelated species distributions and environmental variables (Legendre 1993; Keitt et al. 2002; Gilbert and Bennett 2010). Accounting for spatial autocorrelation may be especially important when modelling species that are dispersal limited (Guisan and Thuiller 2005). Exotic species in particular may lack equilibrium with their environment due to incomplete colonization of new habitats (Seabloom et al. 2006; Jones et al. 2010; Chapter 2). However, despite known potential problems with predictor variable selection in models for spatially autocorrelated species, considerable controversy persists regarding the influence of spatial autocorrelation on the accuracy of response variable predictions (e.g., Hawkins et al. 2007; Beale et al. 2007; Diniz-Filho et al. 2007; Betts et al. 2009; Dorman 2009).

A second potential problem is the choice of spatial scale for predictions. Although it is generally recognized that scale is a key consideration in ecological models (e.g., Levin 1992; Whittaker et al. 2001; Münzbergová 2004; Belmaker and Jetz 2011), nearly all species distribution models make predictions at a single spatial scale (for exceptions, see Schweiger et al. 2005; Nielsen et al. 2008), and thus may miss influential factors that affect distribution patterns across scales, or differences in the effect of factors at different scales (Whittaker et al. 2001). Choosing an appropriate scale for modeling can be particularly difficult across continuous landscapes, where the choice of scale can be arbitrary (Levin 1992; Elith and Leathwick 2009).

Here, I derive a framework to compare conventional and spatially-explicit richness and distribution models at the inter- and intra-patch scales (i.e., among and within patches), for native and exotic species in a threatened ecosystem. I model distributions of 20 dominant native and 20 dominant exotic species, as well as native and exotic richness and presence of native species at risk of extinction, to answer the following questions: 1) Are spatially-explicit distribution models more accurate, particularly for exotic species? 2) What are the influences of scale and species origin on variable selection and model accuracy? And 3) how can richness and distribution models at different scales be used to guide: a) site prioritization for protection; b) site rehabilitation; and c) invasive species monitoring?

The study system, known in Canada as the 'Garry oak ecosystem' (GOE), is located on southeast Vancouver Island, British Columbia and adjacent islands, and is considered to be highly diverse, and one of Canada's most endangered ecosystems (GOERT 2011a). A variety of efforts are underway to protect remaining high-priority sites, rehabilitate degraded sites, and monitor and control invasive species (e.g., Rook et al. 2011; Stanley et al. 2011;

GOERT 2011a,b). Such efforts have had mixed success (e.g., Rook et al. 2011; GOERT 2011a,b), and would greatly benefit from quantitative predictions for distributions of the species and communities managers are attempting to preserve or control. The ability to predict native richness and the presence of rare species at different scales would allow prioritization of sites and portions of sites for protection. In addition, the ability to predict common native species could improve the success of remedial planting efforts; and the ability to predict invasive species presence at different scales would help to inform monitoring and control efforts.

Methods

Study area

My study sites were composed of GOE patches on southeast Vancouver Island, British Columbia, as well as smaller islands in the Strait of Georgia. The climate in the study area is sub-Mediterranean, with cool, wet winters and frequent summer drought (MacDougall 2005). The mean annual temperature ranges from ~9.8 to ~10.6 degrees C; mean annual precipitation (occurring mostly between November and March) ranges from ~670 to ~1100 mm (Wang et al. 2006). The meadow patches in the study area tend to be located on shallow-soil sites isolated from one another by a combination of forest, salt water and human-dominated landscapes. Sixty-seven provincially- or federally-recognized vascular plant species at risk of extinction have been found in the study system (GOERT 2011a,b).

Community surveys

I used extensive (patch-level) and intensive (microsite-level) surveys of vascular plant species in the study area. Patch-level surveys, to be used in inter-patch scale models,

were conducted on 81 meadow patches ranging in size from ~0.2 to 17.7 ha. Patches were

systematically surveyed across their full extents for the presence of vascular plant species.

Thirty-seven patches occurred on small islands and 44 on Vancouver Island. Microsite-level

surveys, to be used in intra-patch scale models, were conducted on 86 meadow patches

(including the 81 surveyed extensively), using 1-m^2 quadrats located in a stratified random

configuration within patches to determine presence of vascular plants. The number of

quadrats ranged from five to 15, depending on patch size. All surveys took place from April

to June, the time of peak biomass in the study area, during which most plants are easiest to

identify. Plants were identified to the lowest taxonomic level possible; those that could not

be identified *in situ* were collected for later identification at the University of British

Columbia or University of Washington Herbarium. In patch-level surveys, a total of 394 taxa

(257 native, 137 exotic) were identified, in >95% of cases to the species level. In quadrat-

based surveys, 192 (127 native, 65 exotic) of these species were found.

Environmental variables

Thirteen environmental variables were collected at the inter-patch and intra-patch

scales (Appendices 5,11). The variables were chosen primarily based on ecological

knowledge of the factors potentially exerting the greatest influence on species distributions in

the study area, and secondarily on relative ease of collection, to facilitate model application

by land managers interested in predicting species distributions on their sites. For the models

outlined below, the environmental variables were transformed as necessary to improve fit

and conform to model assumptions (Appendix 5). In the case of climate, 83 variables

recorded in Climate BC v.3.1 (Wang et al. 2006) were reduced using principal component

analysis (PCA) to a single principal axis, explaining 69% of the total variation in the climate

data. Climate PC1 was positively correlated with mean annual temperature ($r = 0.50$,

P<0.0001) and negatively correlated with mean annual precipitation ($r = -0.66$, P<0.0001).

Distribution model framework

I constructed species distribution models at two scales for the 20 most abundant

native and 20 most abundant exotic species from my intra-patch surveys (Table 4.1). I chose

the most abundant species from my intra-patch surveys for the species distribution models,

because these species are likely the most abundant over the aerial extent of my sites.

Species distribution model development followed the general framework illustrated

in Fig. 4.1. All analyses were conducted using R v.2.12.0 (R Development Core Team 2010),

and various specialized packages. In the first step, I examined the data for spatial

autocorrelation using spline correlograms (Bjørnstad et al. 1999; Bjørnstad and Falck 2001;

Seabloom et al. 2005; Zuur et al. 2009). This technique is a modification of traditional

correlograms that uses a smoothing spline to illustrate consistent patterns in autocorrelation

across distances (Bjørnstad et al. 1999), and a bootstrap technique to derive confidence

Table 4.1: Occurrences of a) native species and b) exotic species used in species distribution models, out of 81 patches and 605 quadrats

a) Native Species

Species	Number of Patches	Number of Quadrats
Camassia leichtlinii	66	231
Festuca rubra	71	216
Brodiaea coronaria	75	213
Galium aparine	79	207
Camassia quamash	46	173
Brodiaea hyacinthina	65	170
Achillea millefolium	74	161
Sanicula crassicaulis	77	160

Species	Number of Patches	Number of Quadrats
Plectritis congesta	66	156
Elymus glaucus	70	136
Collinsia parviflora	72	122
Polypodium glycyrrhiza	73	114
Luzula multiflora	62	106
Cerastium arvense	74	93
Lotus micranthus	36	90
Ranunculus occidentalis	56	80
Danthonia californica	44	78
Carex inops	45	75
Trifolium willdenowii	55	70
Lomatium utriculatum	36	69

b) Exotic Species

Species	Number of Patches	Number of Quadrats
Aira praecox	78	262
Hypochaeris radicata	78	249
Anthoxanthum odoratum	53	175
Rumex acetosella	75	159
Vicia sativa	62	150
Holcus lanatus	68	148
Bromus diandrus	55	144
Vulpia bromoides	72	143
Cytisus scoparius	45	140
Stellaria media	70	136
Bromus hordeaceus	68	133
Bromus sterilis	61	128
Geranium molle	67	117
Dactylis glomerata	57	102
Vicia hirsuta	52	99
Veronica arvensis	52	93
Cynosurus echinatus	61	80
Myosotis discolor	49	80
Poa pratensis	62	68
Aphanes arvensis/australis	48	54

Figure 4.1: General model framework for species distribution models
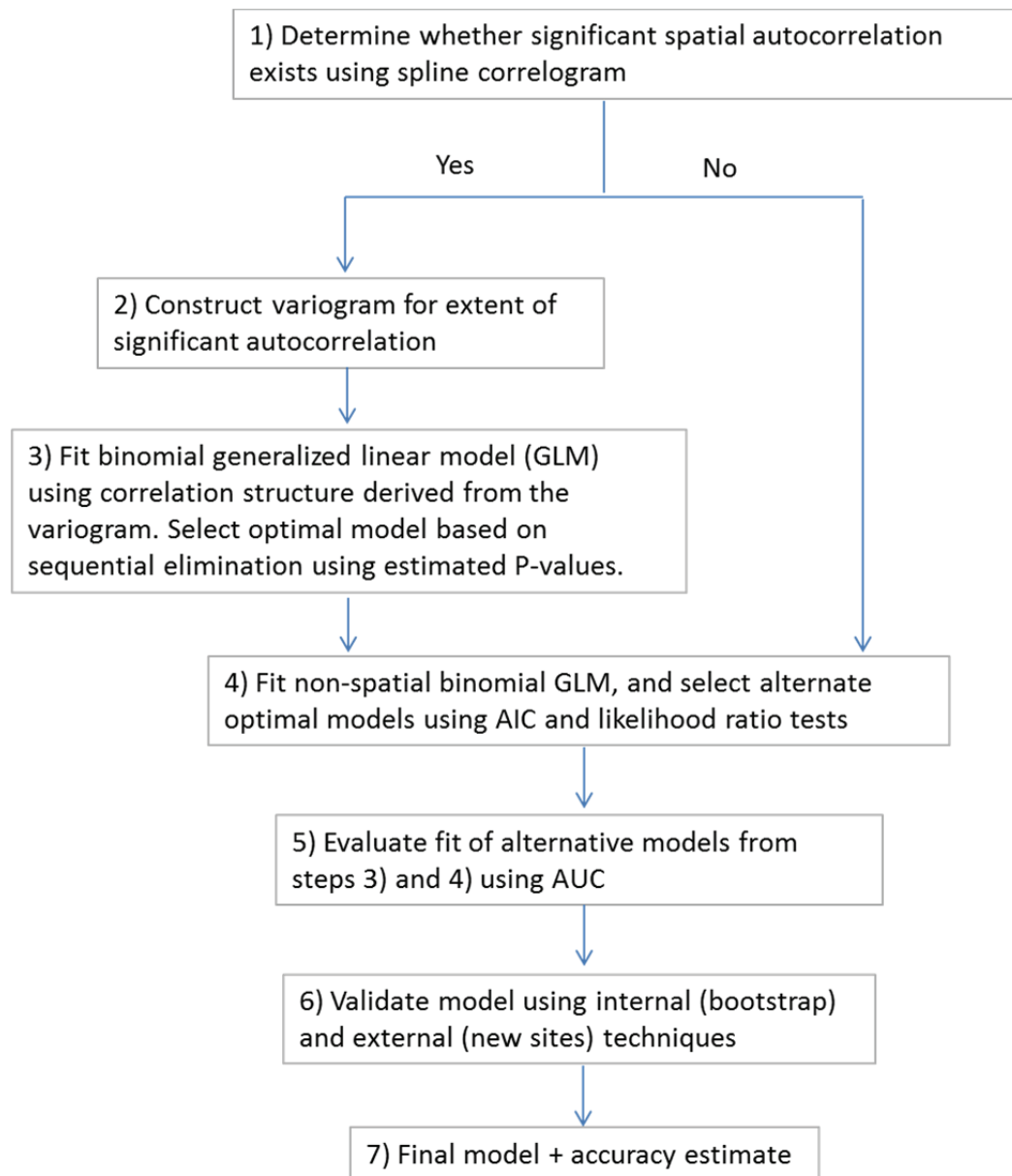
bands for the estimated autocorrelation (Bjørnstad and Falck 2001). These modifications help

mitigate the problems of interpreting patterns and assigning confidence to estimates in

traditional correlograms, which approximate continuous spatial autocorrelation using discrete

distance intervals. In traditional correlograms, correlations for small distance intervals (and few samples) may be spurious while large distance intervals may result in failure to detect real smaller-scale autocorrelation.

If significant positive spatial autocorrelation was detected using spline correlograms, I next constructed variograms to model the spatial correlation structure in the data over the distances in which significant autocorrelation was detected. Based on spatial decay patterns in plant dispersal (e.g., Clark et al. 1999; Nathan and Muller-Landau 2000), I used an exponential variogram with no nugget. The variogram was then used to construct the error covariance matrix for a generalized linear binomial model (cf. Dorman et al. 2007; Beale et al. 2010). Several types of generalized linear models constructed with a spatial error covariance structure appear to perform well in comparisons using spatially autocorrelated data (e.g., Dorman et al. 2007; Kissling and Carl 2008; Beale et al. 2010), and to avoid biases potentially introduced by covariates (Dorman 2007; Beale et al. 2010; Gilbert and Bennett 2010). However, using variograms to account for spatial autocorrelation in the response variable is a theoretically more flexible and accurate technique than arbitrary choice of spatial weights based on neighbours (e.g., Kissling and Carl 2008), especially for irregularly-spaced data (Wall 2004).

At the intra-patch scale, a spatial mixed-model approach was used, with patch identity as a random factor, to account for site-specific effects. Only quadrats from patches where a species was found in patch-level surveys were used in intra-patch models, to restrict prediction of intra-patch distributions to patches where the species were known to be present. If a species is not present in a patch, it will always be absent on even compatible microsites.

All variables, including those measured at the inter-patch scale, were used in the intra-patch models, since patch-level variables may affect presence at the microsite level.

To test the performance of spatial models against less complex models, I also constructed non-spatial logistic models, regardless of whether spatial autocorrelation was detected. At the intra-patch scale, both non-spatial mixed models (using patch identity as a random factor) and non-spatial conventional models (i.e., no random component) were constructed. I fitted these models to all species, to address debates on whether spatial models may more accurately predict species distributions than non-spatial models. For conventional models, optimal models were selected based on forward and backward elimination using Akaike's Information Criterion (AIC) and backward elimination using likelihood ratio (LR) tests. Both approaches were used to address different recommendations in the literature (e.g., Bolker et al. 2009; Zuur et al. 2009). AIC-based model selection was automated, whereas LR tests were non-automated, and model assumptions were checked at each step. In all cases, LR-selected variables were either identical to or subsets of AIC-selected models. Both AIC- and LR-selected models were retained for comparison. Fitting spatial binomial models necessitated using penalized quasi-likelihood (cf. Dorman et al. 2007), for which likelihood-based model selection is not feasible. Therefore, sequential elimination of variables using estimated P-values was used. In all cases, selected variables were identical to or subsets of AIC-based and LR-based non-spatial models, and in nearly all cases, fixed parameters were very similar in magnitude to those of the non-spatial models.

For each species, the retained models were compared for accuracy using the area under the receiver operating characteristic curve, or AUC (cf. Fielding and Bell 1997; Pearce and Ferrier 2000). Although AUC should not be interpreted as an absolute measure of a

model's accuracy (Lobo et al. 2008), and should be used with caution to compare among models for species with different prevalences in a dataset (Santika 2011; Jiménez-Valverde *in press*), it is nonetheless a useful measure for comparing models of the same species within a single dataset (Wisz et al. 2008; Santika 2011). In my case, the model with the highest AUC for each species was retained for validation.

Model validation

I tested the performance of retained distribution models using internal validation via nonparametric bootstrapping (Efron 1983; Vaughan and Ormerod 2005), as well as external validation using independent datasets. In the bootstrap procedure, I used fixed effects only in intra-patch models for predicting the original dataset from the bootstrap sample. In this way, the use of an external dataset (where patch identities are different from those used in the original models) is more closely simulated.

The external dataset for inter-patch models consisted of 14 patches that had been surveyed at only the inter-patch scale. Eight were located on Vancouver Island (Lilley 2007), and six were located in the San Juan Islands of Washington State (D. Giblin and P. Dunwiddie, unpublished data). For intra-patch models, data from 1-m^2 quadrats from Gonzales (2008) were used. Patches in this dataset that were comparable to mine (i.e., light to moderate herbivory, no history of intensive human development) were chosen, resulting in 43 quadrats for external validation. Neither canopy openness nor percent cover of litter was measured by Gonzales (2008). Canopy openness was assumed to be 100%, as the meadows in the external data were all located on small islands with little or no tree cover. Litter cover for these quadrats was estimated using the following linear model from the main dataset:

(litter cover) = (soil depth) × (percent cover all graminoids). This model was highly significant; however, the explained variation was relatively low ($R^2 = 0.16$; $P<0.0001$).

Models of species richness and presence of rare species

To facilitate conservation decisions based on species richness, I constructed additional models for richness of native and exotic species at the inter-patch and intra-patch scales. The model framework was analogous to that of the individual species models, in that spatial autocorrelation in the response variable was tested with spline correlograms, and then modeled using variograms, which were used to construct error covariance matrices as above. However, species richness (log transformed) was modeled with a Gaussian distribution, which allowed me to use maximum likelihood models and likelihood-based model selection. Initial, fully-parameterized spatial and non-spatial models were constructed, and the optimal model framework was chosen using AIC and an LR test (which produced the same result). Subsequent variable elimination in the chosen model framework was then undertaken using both AIC- and LR-based selection as above.

Since protection and monitoring priorities frequently revolve around the presence of species at risk of extinction, I also modeled federally- or provincially-listed rare native species from the Canadian Committee on the Status of Endangered Wildlife in Canada (COSEWIC) and British Columbia Red and Blue lists of "species at risk" (http://www.env.gov.bc.ca/atrisk/red-blue.htm). Modeling such species individually was precluded by their rarity in the dataset. Therefore, presence of at least one of the vascular plant species from these lists in a patch was modeled using a binomial distribution as per the species distribution models above. Even using this metric, modeling rare native species was precluded at the intra-patch scale due to species' rarity.

Results

Spatial autocorrelation in distribution models

Spatial autocorrelation varied among species, and was generally more pronounced at the intra-patch scale. At the inter-patch scale, significant positive spatial autocorrelation was observed for one exotic (*Holcus lanatus*) and four native species (*Camassia leichtlinii, Plectritis congesta, Lotus micranthus, Danthonia californica*). Models could not be constructed for nine of the 40 species, as I found no significant relationships between their occurrences and environmental variables. These species were generally among the most common in inter-patch data, with too few absences to discern significant links to environmental variables. For the 31 species modeled at the inter-patch scale, AUC was never highest for the spatially-explicit models. Instead, the retained model based on highest AUC was the AIC-selected model in 16 cases and the LR-selected model in one case, while in 14 cases, AIC-selected and LR-selected models were identical.

At the intra-patch scale, significant positive spatial autocorrelation was found for 25 species (12 native and 13 exotic). For 21 of these species (10 native and 11 exotic), spatially-explicit mixed models with patch identity as a random factor had the highest AUC. For 18 other species, AIC- or LR-selected non-spatial mixed models had the highest AUC, while for a single taxon (*Aphanes arvensis/australis*), the non-spatial, non-mixed model had the highest AUC. Full results for models at both scales are found in Appendix 12.

Variable selection

At the inter-patch scale, selected model terms for native species were in some cases similar to those of exotics (e.g., log patch area was a consistently positive predictor for both

81

natives and exotics; Table 4.2, A.12.3, A.12.4). However, variables associated with human

influence (road length and nearby agricultural area), tended to be negative predictors for

presence of native species but positive predictors for exotic species (Table 4.2). In particular,

nearby agricultural area was a positive predictor for four exotic grasses (*Anthoxanthum*

odoratum, *Bromus diandrus*, *Dactylis glomerata* and *Poa pratensis*). Although location of

patches on small islands tended to be a negative predictor of both native and exotic species,

due presumably to biogeographic isolation, four native species (*Camassia leichtlinii*,

Achillea millefolium, *Plectritis congesta* and *Trifolium willdenowii*) were more likely to be

found on small-island patches than on Vancouver Island patches (Table A.12.3).

Table 4.2: Variables used in inter-patch scale models of species distributions, and percentages of models in which variables were selected.

	Native		Exotic	
	Positive	Negative	Positive	Negative
Small Island	27	53	0	50
Log Patch Area	67	0	50	0
Climate (PC1)	7	33	31	13
Deer Pellets in ≥1 Quadrat/ in Patch	47	0	31	13
Forest Area (500 m buffer)	40	0	19	19
Meadow (500 m buffer)	27	0	19	0
Log Agricultural Area (500 m buffer)	0	20	25	6
Log Road Length (500 m buffer)	7	40	19	13

At the intra-patch scale, retained model terms indicated a mix of similar and

dissimilar responses among native and exotic species, with considerable variation among

species (Tables 4.3, A.12.7, A.12.8). Percent cover of litter tended to be a negative predictor

for both native and exotic species, while canopy openness and soil depth tended to be

positive predictors for natives and exotics. However, divergent responses predominated for

climate PC1 (negative among natives, positive among exotics); small-island patch location

(positive among natives, negative among exotics); deer pellets (no relationship among

natives, positive among exotics), and nearby agriculture (negative among natives, positive among exotics).

Table 4.3: Variables used in intra-patch scale models of species distributions, and percentages of models in which variables were selected.

	Native		Exotic	
	Positive	Negative	Positive	Negative
Island	25	10	5	30
Log Area (m^2)	0	35	10	15
Climate (PC 1)	10	40	35	10
Deer Pellets in ≥1 Quadrat/ in Patch	0	5	30	5
Forest Area (500 m buffer)	30	0	15	0
Meadow (500 m buffer)	15	0	10	5
Log Agricultural Area (500 m buffer)	0	30	10	5
Log Road Length (500 m buffer)	10	10	15	25
Canopy Openness (%)	40	25	45	15
Litter	0	25	0	25
Aspect (Easting)	0	10	0	0
Log Soil Depth (cm)	45	15	45	10
Aspect (Northing)	5	0	5	10
Slope	20	15	0	5

Relationships between variables and presence for individual species were not always similar at the inter- and intra-patch scales. In several cases, a variable was selected at the inter-patch scale and not the intra-patch scale (or vice-versa), and for ~10% of selected variables, the relationship was in the opposite direction at the inter- versus intra-patch scale (Tables A.12.3, A.12.4, A.12.7, A.12.8). For example, log patch area was negatively related to intra-patch presence for seven species for which it had a positive relationship at the inter-patch scale. In other words, these species were more likely to be found on larger rather than smaller patches in extensive surveys, but in intensive surveys were less common within the larger of the patches where they were present.

Model accuracy

Bootstrap cross-validation for inter-patch models indicated slight overfit (Table A.12.1, A.12.2); however, mean corrected AUC for inter-patch models was 0.83. For six species, >5% of bootstrap models failed to converge. However, in all cases, model discriminatory power appeared to be very good, using AUC = 0.7 as a general guideline indicating high discriminatory power (Hosmer and Lemeshow 2000).

External validation of inter-patch models also indicated very good discrimination, with overall concordance of 81.8% (Table 4.4). In general, native species models exhibited better predictability than exotic species models. The rate of false positives was greater than that of false negatives (Table 4.4), and was highest for exotic species: 48% (36 of 75) negative occurrences were falsely predicted for exotics.

Table 4.4: Confusion matrices comparing predicted versus actual occurrences in external dataset for inter-patch scale models

		Predicted		
				Percent
	Actual	Positive	Negative	Concordance
All	*Positive*	273	24	81.8
	Negative	55	82	
Native	*Positive*	138	10	86.2
	Negative	19	43	
Exotic	*Positive*	135	14	77.7
	Negative	36	39	

Bootstrap cross-validation of the intra-patch models indicated that overfit was somewhat greater than for inter-patch models (Table A.12.6, A.12.6). Overfit was higher for non-spatial mixed models (average ΔAUC 0.11), than for spatial mixed models (average ΔAUC 0.04). External evaluation of intra-patch models also indicated somewhat poorer fit to

the external data than for inter-patch models (Table 4.5). In particular, false negatives were high: whereas inter-patch models had a false-negative rate of ~8% (24 of 297 positive species occurrences; Table 4.4), the intra-patch models had a false-negative rate of ~75% (268 of 355 occurrences).

Table 4.5: Confusion matrices comparing predicted versus actual occurrences in external dataset for intra-patch models

		Predicted		
				Percent
	Actual	Positive	Negative	Concordance
All	*Positive*	87	268	75.7
	Negative	141	1184	
Native	*Positive*	73	101	76.9
	Negative	93	573	
Exotic	*Positive*	14	167	74.4
	Negative	48	611	

Native and exotic species richness models

At the inter-patch scale, spatially-explicit richness models were selected for both native and exotic species in initial AIC/LR tests. Log patch area had a positive relationship with log richness for both native and exotic species, while climate PC1 had a negative relationship with native richness and a positive relationship with exotic richness (Appendix 13; Table A.13.1). At the intra-patch scale, spatial models were again selected when tested against non-spatial models using LR tests, and subsequent selection yielded LR-selected models that were subsets of AIC-selected models. In intra-patch richness models, relationships with two variables, log soil depth (positive) and litter (negative), were shared between native and exotic species (Table A.13.2).

Distribution of rare native species

Twenty-three federally- or provincially-recognized rare native species were found in the study patches (Appendix 14; Table A.14.1). For rare species' presence at the inter-patch scale, the spline correlogram indicated no significant spatial autocorrelation. Therefore, a standard GLM was used, with LR- and AIC-based model selection. AIC-based results are presented in Table 4.6.

Table 4.6: AIC-selected parameters for presence of one or more rare species at the inter-patch scale

	B_1	SE	Z	P
Island	1.918	0.789	2.432	0.015
Forest Area (ha; 500 m buffer)	0.0502	0.015	3.353	0.0008
Deer Pellets in ≥1 Quadrat/Patch	-0.947	0.62	-1.528	0.127

Discussion

Despite the generally-recognized phenomenon of spatial autocorrelation in species distributions, spatially-explicit species distribution models are still relatively uncommon in ecology, due to their greater complexity than standard models, the bewildering number of possible techniques (Elith and Leathwick 2009; Beale et al. 2010), as well as persistent debates regarding the relative accuracy of spatially-explicit versus conventional models (e.g., Hawkins et al. 2007; Beale et al. 2007; Diniz-Filho et al. 2007; Betts et al. 2009; Dorman 2009). The framework I used allows direct comparison of spatially-explicit and non-explicit models as well as comparison of models at different scales. Modeling species distributions at more than one scale allowed a more comprehensive understanding of the roles of variables associated with species distributions and of the scales at which management interventions

may be most effective, than conventional models at a single scale would have allowed. Below, I discuss the implications of the model results for predicting spatially autocorrelated native and exotic species distributions and richness, and for protected area site selection, site rehabilitation and invasive species monitoring in the study area.

Spatial autocorrelation and model construction

Spatial autocorrelation in species distributions was much more prevalent at the intra-patch than the inter-patch scale. At the inter-patch scale, 30 of 35 modeled species distributions lacked significant spatial autocorrelation, and non-spatial models had the highest AUC for the other five species. This suggests that biogeographic factors other than distance between populations may have been important at this scale. For dominant native species, enough time may have elapsed since colonization of the region that distances among patches are not influential on their current distributions at the inter-patch scale. For exotics, the prevalence of dispersal facilitators such as roadsides and human visitors may be more important than distances in determining inter-patch distributions of at least the 20 dominant species. At the intra-patch scale, the similar number of native and exotic species with significant positive spatial autocorrelation (12 versus 13, respectively), was somewhat surprising. I expected greater spatial clustering in the exotics due to their recent arrival in the study system (Hulme 2008; Jones et al. 2010). Among the 20 dominant exotics, dispersal limitation or spatial clumping due to unmeasured variables may be similar to that of the dominant natives within patches.

There has been much debate on the relative accuracy of spatially-explicit versus conventional models (e.g., Betts et al. 2009; Dorman 2009). My results indicate that the relative accuracy of spatial versus non-spatial models may depend on the scale of analysis.

Accounting for the spatial signals in species distributions at the intra-patch scale often improved model fit, as evidenced by the fact that spatially-explicit models had the highest AUC for 84% (21 of 25) species with significant positive spatial autocorrelation at this scale. For these species, the average difference in AUC between spatially-explicit and non-spatial models was relatively low (0.02). Whether this difference is of practical importance would depend on the specific research question; however, in general the most accurate model possible should be used.

Accounting for the relatively weak spatial signals in species distributions at the inter-patch scale did not lead to more accurate models. Thus, while I agree with recommendations of Beale et al. (2010) that spatial autocorrelation should be accounted for in species distribution models, I also recommend testing spatially explicit models against non-spatial models (assuming the latter do not exhibit residual spatial autocorrelation), as non-spatial models may be equally or more accurate in some cases.

Origin and scale versus variable selection

Unsurprisingly, the generally positive relationships in exotic species between presence and nearby agricultural areas or roads suggests that human disturbance promotes exotic invasion (cf. Hobbs and Huenneke 1992; Vilà et al. 2007; Chapter 3), through some combination of disturbance itself providing resource opportunities, and propagule pressure of ruderal exotics from adjacent developed or disturbed areas. At the intra-patch scale, generally positive relationships for native and exotic species between presence and both canopy openness and soil depth, and generally negative relationships with litter (Table 4.3) suggest that many native and exotic species share similar constraints at small scales (see Chapter 3 for additional details). Considerable variation among species also suggests species-specific

responses in addition to community-wide trends. In addition, opposing relationships for some variables (Tables A.12.3, A.12.4, A.12.7, A.12.8) at the inter- versus intra-patch scale, suggest caution in extrapolating the effect of a variable at a single scale to additional scales. The selection of log patch area as a positive predictor at the inter-patch scale and a negative predictor at the intra-patch scale may have been related to unmeasured environmental variables that covaried with area.

Origin and scale versus distribution model performance

At both scales, model performance varied among species (Tables A.12.1, A.12.2, A.12.5, A.12.6). In general, model performance was lower for exotic species, perhaps reflecting either generalist strategies or relative lack of equilibrium with the environment. Since spatial autocorrelation was equally common among the 20 modeled exotic and 20 modeled native species at the intra-patch scale, the former is perhaps more likely. Overall model performance was very good for inter-patch scale models (Table 4.4, A.12.1, A.12.2). Intra-patch scale models also generally performed well in internal evaluation (Table 4.5, A.12.5, A.12.6), but had a poor rate of false negatives when applied to external data, particularly for exotic species (Table 4.5).

The relative importance of false negatives and false positives in species distribution models depends on the specific research question. However, false negatives are generally viewed with greater concern in ecology (Anderson et al. 2003; Peterson et al. 2008). For example, when predicting presence of invasive exotic species in new patches, it may be more important to avoid missing actual occurrences than to predict occurrences that do not exist. For such questions, prediction at the inter-patch scale only may be appropriate.

Several possible factors may have affected intra-patch model performance when applied to external data. First, the evaluation dataset lacked estimates of canopy openness or litter, necessitating their estimation. Evaluation data also came entirely from small-island patches. This may explain some of the false negatives for the exotic species in particular, because small-island status was negatively related to the occurrence of 30% of exotic species at the intra-patch scale (Table 4.3). Although these species were more common on Vancouver Island patches, they were still infrequently found in quadrats on small islands in the main dataset. Such infrequent occurrences of these species in the external dataset composed of small-island patches are necessarily false negatives. In addition, mass effects (Kunin 1998) may also have led to false negatives. Finally, the inherent variability in processes leading to species distributions may be greater at small than at large scales, leading to greater stochasticity in small-scale patterns (Levin 1992).

Though the intra-patch models are not generally accurate at predicting absences, especially for exotic species, they nevertheless provide valuable information on the factors leading to higher likelihood of finding a given species. Such information can be used to help prioritize monitoring for exotic species toward microsites where they are more likely to be found, or to guide remedial planting of native species on the most compatible microsites. For example, the exotic *Dactylis glomerata* was common on microsites with greater canopy cover and deeper soil (Table A.12.8). Monitoring or removal efforts within a patch could initially focus on such areas. Likewise, the native *Elymus glaucus* was more common on microsites with greater soil depth (Table A.12.7), suggesting that this species is a candidate for remedial planting in deeper-soil microsites. Even if soil depths and canopy covers are not

quantitatively known for a given site, a manager can prioritize monitoring or planting based on knowledge of relative soil depths and canopy covers.

Native/exotic richness and distribution of rare native species

Spatially explicit richness models were similar to conventional models focussing on variables at single scales presented in Chapter 3. In general, native richness at the inter-patch scale was highest in patches more isolated from human development (i.e., furthest from roads, nearest to forests; Table A.13.1), while exotic richness was highest in areas in closer proximity to human development (i.e., nearest to agriculture, furthest from forests; Table A.13.1). Such opposing responses to human influence are common and well documented (see Chapter 3 for details). At the intra-patch scale, native species richness was also highest in patches located on small islands or surrounded by forest (Table A.13.2). However, similarities in native and exotic species models with respect to the apparent influence of soil depth and litter (both measured at the quadrat level) again suggest that native and exotic species often respond to similar constraints at the microsite level (Chapter 3).

In contrast to biogeographic theory (e.g., Diamond 1975; Hanski 1991; Hubbell 2001), which predicts that rare species should be encountered less often on more isolated patches, my model predicting the presence of federally- or provincially-listed species at risk of extinction indicated that such species were more likely to be encountered on small-island patches than on Vancouver Island patches. Lower disturbance on the small-island patches may be the primary cause of this pattern; indeed, some populations of rare species have been extirpated on patches near human settlements on Vancouver Island (A. Ceska, pers. comm). While such isolated patches appear to offer refuge to rare meadow species the Georgia Basin, the long-term viability of populations may require assisted migration among refuge patches,

due to the risks of inbreeding depression. However, in the Georgia Basin and likely other heavily impacted habitats, long-term demographic and genetic threats to isolated populations are less severe than the immediate threats now causing extirpation in core habitats.

Model applications

Below, I apply the species distribution and richness models to specific conservation management questions regarding: a) site selection; b) site rehabilitation; and c) invasive species monitoring.

a) Site selection

The area occupied by the GOE in Canada is less than 10% of its original extent (Lea 2006), and there is an ongoing interest among land agencies in protecting high-quality GOE sites (GOERT 2011). My models for native and exotic species richness and presence of federally- or provincially-listed rare species can be used to derive profiles of ideal GOE sites for protection.

To maximize native richness at the inter-patch scale, model terms (Table A.13.1) suggest that patches that are isolated from development; those with forest nearby; and those in cooler, drier portions of the study area, should be priorities for protection. For maximum native species richness at the intra-patch scale, similar patches are suggested, with island patches and those isolated from agricultural land also being favoured (Table A.13.2). For federally- and provincially-recognized rare species, models indicate that protecting small-island patches and those with nearby forest would be most beneficial, as such patches are more likely to harbour rare native species. Transplantation of rare species may also be more appropriate on small-island patches, where human disturbance is minimized. Patches with

relatively low deer density (65% of sites) are also preferable for protection to preserve or promote rare species, as the model (Table 4.6) indicates a negative relationship between presence of rare native species and deer pellets.

b) Site rehabilitation

Due to the paucity of intact GOE meadows in Canada and the northwest USA, there is great interest in rehabilitating patches that once harboured healthy GOE communities (Dunwiddie and Bakker 2011). Although several degraded sites exist as urban parks, long-term restoration of these sites is likely to be difficult with continuing human disturbance and propagule pressure of exotics. However, Colville Island, WA (lat/long: 48.42°, -122.82°) is an example of a site that may be an ideal candidate for restoration. Colville Island is part of the San Juan Islands National Wildlife Refuge, and as such is closed to public access. It is also a former glaucus-winged gull (*Larus glaucescens*) colony that was abandoned prior to 1999 (Amlaner 1977; Hayward and Verbeek 2008). Because of this history of heavy gull disturbance, Colville Island was not included in my external model evaluation for inter-patch scale models, though it had been surveyed along with the other islands.

When inter-patch scale models of species distributions were fit to Colville Island, there were nine false positives and zero false negatives for native species (Appendix 15; Table A.15.1). The native richness on Colville Island (26 species) was also less than half the predicted value (54 species; Table A.15.2). The potential detrimental effects of gulls on island vegetation via nitrogen enrichment and disturbance are well known (e.g., Sobey and Kenworthy 1979; Hogg and Morton 1983), and it is highly likely that gull disturbance led to the extirpation of at least some of these species on the island.

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Assuming the gull colony does not return, Colville Island is a good candidate for site rehabilitation. Several native species (e.g., *Camassia leichtlinii*, *Achillea millefolium*, *Cerastium arvense*) that are widespread on small-islands are highly likely to have been present on Colville Island historically. These and other under-predicted native species (Table A.15.1) could be planted to help create a diverse native community that is relatively protected from human disturbance and herbivory. Intra-patch models could also be used to guide remedial planting to match species to microsites with higher predicted probabilities of occurrence.

c) Invasive species monitoring

A ~5.7 ha patch located in Mount Wells Regional Park, BC (48.44°, -123.56°) is an excellent example site to demonstrate the utility of exotic species distribution models for guiding monitoring programmes. This patch is surrounded mostly by forest; however, it is also located near the rapidly-developing city of Langford and has road access within 500m. Fitting the exotic species distribution models to this patch resulted in seven false positives and zero false negatives. In addition, exotic species richness for this patch (19 species) was significantly lower than the predicted value (27 species; Table A.15.4).

Though exotics appear to be underrepresented on this patch, it is likely that increased human use will promote their invasion. Model predictions for common exotic species (Table A.15.3) provide likely candidates for monitoring and proactive removal of small populations that may be encountered. These species can be prioritized in terms of their presence at the intra-patch scale among all study patches (Table 2b), which provides a first-order indication

of the ability of exotic species to spread throughout the patches they invade, or by their

predicted probability of occurrence on the site (Table A.15.3).

Conclusion

Models of species distribution and richness at multiple scales can be powerful tools to

guide management, especially if they are constructed using a framework that tests for spatial

autocorrelation and incorporates it where necessary in the error covariance matrix. Models of

species distributions at multiple scales also allow management prescription at scales for

which distributions are most predictable. In this study, native and exotic species distribution

and richness models at the inter- and intra-patch scales allowed me to address pressing

questions regarding site prioritization, site rehabilitation and invasive species monitoring in a

threatened ecosystem.

However, even with great care in model construction, accurately predicting species

distributions is difficult, especially at small scales. The 75% rate of false negatives in my

intra-patch scale models exemplifies this issue. For specific questions depending on accurate

depiction of species absences, such a rate would be unacceptable. Such questions are best

addressed at the larger, inter-patch scale, where the rate of false negatives was much lower.

For certain research questions, a relatively low fit may still be interpretable and

useful, with appropriate caution (e.g., Jones et al. 2010). For applications requiring greater

accuracy, researchers may need to gather more distribution data and/or more environmental

variables in the hopes of achieving a more accurate model. However, low fit may sometimes

be inherent: generalist species and species that are not at equilibrium with their environments

may both exhibit relatively low predictability in distribution models (e.g., Evangelista et al.

2008; Jones et al. 2010), even if spatial autocorrelation is accounted for. In all cases, the research question at hand and the ecological knowledge of the researcher are vital in interpreting a model and choosing the subsequent course of action.

Chapter 5: Conclusion

Invasion ecology is an intensive area of research[1], because of the profound ecological and economic damage that can be caused by invasive exotic species, and because studying invasions offers opportunities for advancing ecological theory. Despite this attention, neither generally-applicable predictions nor universal principles regarding species invasions have been attained (Simberloff 2010), and fundamental debates persist regarding the ecology of species invasions (e.g., Stohlgren et al. 2008a,b; Harrison 2008) and the risks posed by exotic species to native species and ecosystems (e.g., Davis et al. 2011; Lambertini et al. 2011).

Contrasting patterns in exotic communities at different spatial scales (e.g., Shea and Chesson 2002; Davies et al. 2005), in different environments (e.g., Brown and Carter 1998; Martin et al. 2008) and across time (e.g., Evans et al. 2001; Meiners 2007), have at least partly been responsible for a lack of generalizability and a proliferation of hypotheses regarding species invasions (reviewed in Catford et al. 2009). Such contrasts and associated debates are reflective of community ecology as a whole (Simberloff 2010). However, while the proliferation of hypotheses and alternate explanations of patterns in invasion ecology is daunting, this complexity also offers opportunities to find hidden commonalities in the diverse patterns reported to date, as well as biological causes of discrepancies among analyses.

I used a study system that provides an excellent landscape-level laboratory for studying invasion ecology, in addition to sophisticated analyses at multiple scales, to address some of the dominant questions regarding the trajectories and ecological effects of exotic

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[1] In November 2011, A Google Scholar search of the exact phrase "exotic species" for the period of 2001-2011 returned ~21 000 references. A similar search for the phrase "invasive species" returned >30 000 references.

species invasions. Broadly, the questions I addressed were: 1) Are latent invasions prevalent among exotic species, and if so, among which species? 2) What are the relative roles of latent invasions, competition and shared versus divergent environmental response in determining native versus exotic community-level biogeographic patterns? And 3) how can models of native and exotic species distributions and richness at multiple scales be used to improve conservation management? Each chapter addresses one of these questions at either two or three scales. Below, I summarize the results and conclusions of each chapter, and then summarize the general conclusions that can be drawn from this study. I also examine the limitations of this study, and provide recommendations regarding future research and management of the study ecosystem based on my findings and those of previous studies.

Chapter 2: 'Invasion debt' in exotic species

'Invasion debt', the latent expansion of exotic species populations, has been demonstrated at state and national scales (Seabloom et al. 2006; Essl et al. 2011), but has not previously been explored in detail at smaller scales (e.g., among and within patches). Nor has the role of dispersal mechanism as a predictor of latent exotic species invasions among and within patches. In Chapter 2, I sought to address these gaps by asking the following specific questions: 1) Are exotic short-dispersing species underrepresented compared to other species groups? 2) Are the abundances of exotic species related to minimum residence time in the region? 3) Do short-dispersing exotic species considered to be invasive elsewhere in North America show proportionally more evidence of latent invasiveness than their long-dispersing counterparts? And 4) are exotic species of all types underrepresented in relatively isolated and undisturbed island patches?

Analyses to address these questions suggest that invasion debt exists primarily among exotic short-dispersing species, at both the inter- and intra-patch scales (i.e., among and within patches). Exotic short dispersers were underrepresented at both scales compared to exotic long dispersers and native short and long dispersers. Among species classed as invasive elsewhere in North America, more exotic short dispersers appear to have the potential for latent population expansion than do exotic long dispersers. Finally, populations of all exotic species both within and among patches appear to be related to minimum residence time in the study region.

Surprisingly, despite being present in the area ≤140 years, exotic long dispersers were slightly (though not significantly) overrepresented on a per-species basis, even on the most isolated and least disturbed small-island patches. Thus, while small-island patches exhibited lower exotic richness and cover at both the inter- and intra-patch scales, they do harbour populations of a suite of apparent 'super-invaders' (cf. Daehler 2003) that are able to disperse to and establish on the most isolated and least disturbed patches. Although several of these species are graminoids, several are forbs, and dispersal ability was a better predictor than life form (or interactions) of species abundances at both scales. Dispersal ability was thus a key factor affecting the rapid spread of these exotic species and may undermine attempts to eradicate them from patches that are in close proximity to propagule sources.

In contrast, native short dispersers were slightly overrepresented versus long dispersers on a per-species basis, perhaps due to tradeoffs favouring environmental tolerance over colonization ability, via persistent but larger seeds (cf. Muller-Landau 2010) or somatic adaptation to environmental stress (cf. Grime 1977). Several analogues of currently-

dominant native short dispersers exist in the exotic flora. Over time, these species may increase in dominance, such that the exotic flora may more closely resemble the native flora.

Williamson et al. (2009) suggested that an exotic species might reach its maximum range 150 to 300 years after arrival in a new region, while infilling within this range takes longer. My results, and those of McCune and Vellend (in prep), suggest that the infilling process is ongoing in the study region. The pace of this process will likely depend in part on species' dispersal mechanisms, as well as tolerance (via somatic structures, phenology or seedbank) of the sub-Mediterranean conditions of the study area. Monitoring and removal of slower-dispersing exotic species that may proliferate in the future may be a more efficient strategy than removal of currently dominant exotics. Additional conservation implications for 'invasion debt' in the study system as well as the role of incomplete dispersal of exotics in determining community-level biogeographic patterns are outlined below.

Chapter 3: Roles of competition, environment and incomplete invasion in native/exotic biogeographic patterns

Three of the major questions in invasion ecology are: 1) How much of a competitive threat is posed by exotic species? 2) How different are exotic species from native species, in terms of environmental response? 3) Are latent exotic population expansions responsible for different community-level biogeographic patterns in exotics versus natives? These questions are analogous to those regarding the roles of competition, environment and dispersal limitation in community ecology as a whole (e.g., Gilbert and Lechowicz 2004; Seabloom et al. 2005). Previous analyses (e.g., Shea and Chesson 2002; Davies et al. 2005) have suggested that different mechanisms may predominate at large versus small scales. Chapter 3 therefore used biogeographic analyses of patterns in GOE plant communities at the following

discrete scales to test theoretical predictions related to the questions above: 1) the 'landscape'

scale, representing all patches (and divided into Vancouver Island and small-island patches);

2) the inter-patch scale; and 3) the intra-patch scale.

Two key results suggest that competition is not a primary determinant of native

versus exotic species distribution and abundance patterns in the GOE: 1) Contrary to many

studies (e.g., Shea and Chesson 2002; Davies et al. 2005; Chen et al. 2010), I found a weak

positive correlation between native and exotic species richness at the smallest (intra-patch; 1

m^2 quadrats) scale; and 2) significant correlations among native and exotic species pairs

(even closely-related species) were predominantly positive.

Instead, detailed analysis of richness versus environmental parameters at the inter-

and intra-patch scales suggested that native and exotic communities are influenced by a mix

of concordant and discordant responses to environmental factors at each scale. In general,

exotic richness was positively associated with factors related to disturbance and propagule

pressure, while native richness was negatively associated with disturbance and positively

associated with nearby forest area. However, the intra-patch scale variables soil depth and

litter both had similar associations with native and exotic richness and cover.

Likewise, partial redundancy analyses suggested a mix of shared and dissimilar

responses to environmental variables in native and exotic communities. However, although

ordination plots and species abundance distributions were superficially similar between

native and exotic species, the 'outliers' in the exotic species ordination that were common on

small-island patches were all long dispersers, and the dominant exotic species in the 'tails' of

abundance distributions were long dispersers and environmental generalists. Neither of these

patterns occurred in native species. Thus, while native and exotic species exhibit superficially similar biogeographic patterns in my study system, the exotics are currently dominated by long-dispersing, ruderal species, while many dominant natives are short dispersers.

The above results suggest that many interpretations of observed patterns in native and exotic communities in terms of fundamental differences in competitive ability or environmental response are oversimplifications. Native and exotic community patterns may reflect a mix of concordant and discordant environmental responses that depend on the scale of analysis and variables considered. Though the dominant exotic species appear to be more ruderal in nature in the GOE (as anthropogenic landscape change has likely promoted colonization by such species), both communities also share some of the same fundamental constraints (cf. Thompson et al. 1995). Focussing on the specific scales and environmental variables for which native and exotic community responses are divergent (e.g., protecting small-island patches with less exotic richness or cover, rather than trying to protect or restore microsites where native and exotic richness are correlated), can be used to make conservation efforts more efficient, and curtail activities that may elicit similar responses in native and exotic communities.

Chapter 4: Spatially explicit distribution and richness models at two scales

My goals in Chapter 4 were to examine the influence of spatial autocorrelation and scale in native and exotic species distribution models, and use distribution and richness models at two scales to address key conservation issues in the GOE. Distribution and richness models are extremely important for conservation management, for predicting invasions (e.g., Zhu et al. 2007; Evangelista et al. 2008; Jones et al. 2010), as well as site

selection (e.g., Milsom et al. 2000; Ortega-Huerta and Peterson 2004) and rehabilitation (e.g., Grosvernier and Matthey 1997). However, as they usually deal with only one scale, distribution models often have limited applicability (Elith and Leathwick 2009). There is also considerable debate regarding the relative accuracy of spatially-explicit and conventional distribution models (e.g., Hawkins et al. 2007; Beale et al. 2007; Diniz-Filho et al. 2007; Betts et al. 2009; Dorman 2009). To address these general problems in distribution modelling and to guide conservation management in the GOE, I used a framework that tested for spatial autocorrelation, incorporated it into models, and then tested spatially-explicit versus conventional models. In particular, I modeled distributions for 20 dominant native and 20 dominant exotic species as well as native and exotic species richness at the inter-patch and intra-patch scales, plus the presence of native 'species at risk' at the inter-patch scale.

Among both native and exotic species, spatial autocorrelation occurred most often at the intra-patch scale, and its incorporation into models at this scale generally improved model accuracy. In general, distribution models indicated that dominant exotics occurred more often in relatively disturbed patches, whereas dominant natives occurred more often in more isolated patches. However, there was considerable variation among species, and several variables (in particular, patch area) sometimes had opposing relationships with species distributions at the inter- versus intra-patch scales, suggesting scale-dependent effects on species populations.

The model for native 'species at risk' distribution showed that, contrary to biogeographic theory that predicts that rare species will be rarest in more isolated sites (e.g., MacArthur and Wilson 1967; Hanski 1991; Hubbell 2001), small-island patches and those buffered by forest were more likely to harbour rare species in the study area. Isolation

probably provides protection from human disturbance, herbivory and, potentially, competition with exotics that are still uncommon in relatively isolated patches. The effects of disturbance and herbivory in particular may be more detrimental to rare native species' populations than to native species in general, since rare populations are likely to be more spatially clustered (Condit 2000), and thus more vulnerable to small-scale stochastic events.

The models presented in Chapter 4 have a wide variety of potential uses, including: 1) deriving criteria for protected area site selection; 2) rehabilitating degraded sites using compatible species; and 3) monitoring for exotic species that are under-predicted in inter-patch models. I demonstrated each of these applications using examples from the study area. For site selection, models indicated that isolated small-island patches would be the best candidates for protection, based on predicted high levels of native richness and low levels of exotic richness at both scales, as well as higher predicted probability of harbouring rare species. For site rehabilitation, models suggested native species for remedial planting, using the example of a former gull colony. And on a site for which several exotic species and exotic richness were underpredicted, a list of high-probability invaders was derived to inform a potential monitoring programme.

General conclusions and the future of the GOE

Several general conclusions regarding the ecology of species invasions may be drawn from this study. First, 'invasion debt', or lags in species invasions, which have been explicitly recognized on larger scales (e.g., Seabloom et al. 2006; Williamson et al. 2009; Essl et al. 2011), are probably important determinants of dominance and rarity patterns in exotic species at all scales in recently-invaded systems. These species-level patterns appear to be dependent on both time since colonization and dispersal abilities. Second, competition,

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which has been attributed to negative native versus exotic richness ratios at small scales (e.g., Shea and Chesson 2002; Davies et al. 2005), may in fact be a relatively minor determinant of native versus exotic community patterns at all scales (cf. Gilbert and Lechowicz 2005; Fridley et al. 2007; Gonzales and Arcese 2008; Simberloff 2010). Dominance by exotic over native species (or *vice versa*) may instead be related to environmental response or propagule pressure (e.g., MacDougall and Turkington 2005; Seabloom et al. 2006; HilleRisLambers et al. 2010), the effects of which may vary across spatial scales. Finally, explicit recognition of the spatial and temporal scale-dependence of all the above factors is key to understanding community assembly through species invasions. Competition, dispersal limitation and environmental response all vary across space and time. Without acknowledging such complexities, and explicitly accounting for them as much as possible, comparative analyses of native and exotic communities have limited generalizability. This issue may be largely responsible for the divergent conclusions that are common among studies comparing native and exotic communities (Fridley et al. 2007; Catford et al. 2009). Complexities and contingencies are common in both invasion ecology and in community ecology in general (e.g. Lawton 1999; Lange 2005; O'Hara 2005). However, through careful analyses of patterns at different scales, hidden commonalities among seemingly divergent patterns can be found, and prescription for appropriate conservation management at scales that are most predictable can be achieved. Below, I discuss the implications of such complexities for predicting future ecological changes in the study system.

Despite common conceptions that the GOE is dominated by exotic species (e.g., Fuchs 2001; MacDougall and Turkington 2006; GOERT 2011a), the data used in my thesis, which to my knowledge represent the most comprehensive survey of BC and Washington

State GOE meadows to date, indicate that native plant species still dominate this ecosystem, at least among patches that are not heavily impacted by deer herbivory. Mean percent cover across 605 quadrats for native vascular plants was ~40%, nearly double that of exotics (~21.5%). However, it is safe to assume that the relative abundance of exotic species within communities will increase as new invaders and already-established exotics spread into compatible environments at rates depending on their dispersal abilities (Chapter 2). Indeed, re-surveys of historical GOE monitoring plots on Vancouver Island (McCune and Vellend, in prep) suggest that the proportion of exotic species cover is rising. On small-island patches this process will likely proceed at a slower pace, potentially offering opportunities for targeted removal of small populations of exotics before they invade beyond the capacity of feasible removal efforts.

In the short term, this increase in exotic abundance may not come at the cost of native diversity. In the GOE and elsewhere, environmental variation in time (Davis et al. 2000) and space (Melbourne et al. 2007) may create opportunities for exotic colonization while leaving opportunities for native species, thus promoting a diverse flora in general (cf. Adler et al. 2006). Indeed, on a global scale, such processes may explain the fact that no extinctions of native plants have been shown to be directly caused by competition with exotics (Sax and Gaines 2008). However, competition may play a role at the smallest scales ($<1m^2$; cf. Brown and Peet 2003), and over time may scale up to larger, more easily-observable scales (Harrison 2008), resulting in negative native versus exotic richness relationships and species abundance correlations at the inter- and intra-patch scales. In theory, the intensity of competition in a community should accumulate as species accumulate, making new colonization progressively more difficult (Tilman 1980; 2004). Whether species

accumulation rates will slow, or whether niche partitioning amid fluctuating environments will be sufficient to suppress competition over the long term, are open questions in the GOE and in other systems (Sax and Gaines 2008).

Limitations of this study

Through direct comparison of native and exotic flora using species-level analyses (Chapter 2), multi-scale decomposition of community patterns (Chapter 3), and innovative distribution and richness models (Chapter 4), my thesis advances invasion ecology in several ways, and contributes vital new information to help guide conservation in the GOE. However, my research also has several potential limitations, some of which may be addressed in the future, while others may be difficult to address due to logistical limitations and the uncertainties inherent in ecological research.

In general, my strategy of surveying plant distributions and collecting environmental data both among and within two groups of distinct patches (i.e., those on Vancouver Island and those on small islands), allowed good separation of statistical effects at the landscape, inter- and intra-patch scales. However, my sampling did not allow full separation of isolation and disturbance because patches more isolated from exotic propagules (e.g., small-island patches, those surrounded by forests) were necessarily also isolated from proximity to humans. Thus, I can only strongly conclude that human disturbance and/or exotic propagule pressure was associated with higher exotic richness and dominant exotic species presence. Separating these effects within the study system, especially at the inter-patch scale, would be very difficult.

While ancillary studies have explored the possible roles of avian herbivores and frugivores in exotic species invasions in the study system (Isaac-Renton et al. 2010; Bennett et al. *in press*), the potentially more detrimental effects on native species via herbivory by deer were not addressed in detail here. My metric of herbivory (deer pellets in ≥1 quadrat/patch) was not significantly different for Vancouver Island versus small-island patches (Fisher Exact test, $P = 0.67$). However, some small-island patches with high levels of deer herbivory were purposefully excluded from my study because, based on previous studies (Gonzales and Arcese 2008; Gonzales 2008) and personal observations, sites with high deer densities appeared to have fundamentally different communities than seen in most GOE meadows, and thus would have appeared as strong outliers in my analyses, potentially trivializing the influence of variables of broader general interest. Given that the detrimental effects of high herbivory in GOE patches are well-documented (Gonzales 2008), my conclusions and recommendations refer to sites that are not highly degraded by deer herbivory. Future work to explore the full range of deer impact in the study system, including more accurate measures of deer densities and herbivory, may reveal threshold deer densities below which native-dominated communities can be sustained, and may inform the restoration of herbivory-degraded sites.

A third potential limitation involves the long-term influence of climate on community composition in my study area. Most data presented in this thesis were collected in two field seasons; therefore the effects of temporal climate fluctuations on community composition (e.g., Hobbs et al. 2007) cannot be discerned. Climate predictions for the study area exhibit considerable uncertainty depending on the model and emission scenario used, but generally point to a ~1 degree rise in mean annual temperature over the next 25 years and no clear

trend in precipitation (CCCSN 2011). Naturally-occurring interannual- to century-scale

climate fluctuations in the study region (e.g., Cumming et al. 2002; Zhang and Hebda 2005;

Harley and Paine 2009) may also intensify with anthropogenic climate change (Meehl and

Tebaldi 2004). Understanding how interannual- to decadal-scale climate changes could

influence plant community composition in the GOE will also depend on many as yet

uncertain factors, including land-use practices, dispersal limitation, and environmental

tolerances of existing species and new invaders.

Fourth, although the data represent perhaps the most comprehensive survey of the

GOE to date, additional species and environmental data at the inter- and intra-patch scales

would have allowed a more complete comparison of native and exotic community

composition and richness. Additional variables (e.g., NO_3, P, K and micronutrients, which

may affect fine-scale species distributions in the GOE; Pinto and MacDougall 2010), might

also have been gathered and analyzed, and interactions among them examined given

sufficiently intensive sampling. However, the choice of variables reflected my best

judgement on the potential variables that could determine community richness and

composition in the GOE, as well as statistical and logistical limitations.

Future work

The key findings as well as the limitations of this study suggest several possible

avenues for future work. The spatial patterns in native and exotic species that were

thoroughly explored in Chapters 3 and 4 are likely to interact with temporal trends that could

not be fully explored, including climate fluctuations. Environmental fluctuations in both

space (Melbourne et al. 2007) and time (Davis et al. 2000) are likely to promote coexistence

and diversity. A relatively unexplored question, however is: how do these spatial and

temporal environmental fluctuations interact? Directly analyzing the role of spatiotemporal environmental fluctuations in determining native and exotic community composition would potentially allow a much greater understanding of the mechanisms of coexistence, in the study area and in general. MacDougall et al. (in prep) are currently exploring community responses to climate fluctuations and other environmental parameters, using a long term dataset from a GOE site. Given the logistical difficulties in expanding such efforts to multiple sites, I intend to pursue the topic in general through a simulation exercise, devising a stochastic model quantifying the effects of spatiotemporal resource fluctuations on species richness for simulated patches of different sizes.

The potential longer-term roles of competition and population expansion of exotic species also require further exploration via targeted long-term vegetation monitoring. My own finding that competition is not a primary determinant of native versus exotic community patterns, along with similar findings in other areas (e.g., Gilbert and Lechowicz 2005; Simberloff 2010), may not be applicable in the longer term, as competition may become more important over time (Harrison 2008). Likewise, it is unknown whether future population expansions of exotic species among and within patches will depend on disturbance (Hobbs and Huenneke 1992; Vilà et al. 2007), or will proceed without disturbance given sufficient propagule pressure (Seabloom et al. 2006). The presence of several exotic species on the most isolated small-island sites (Chapter 2) suggests anthropogenic disturbance is unnecessary for these species to colonize; however, the greater presence of exotics in disturbed areas (Chapters 3 and 4) suggests that disturbance may be a key factor leading to exotic dominance. Longer-term monitoring, particularly to compare exotic populations on disturbed and relatively undisturbed sites, would help to further

untangle these issues. Similarly, on more heavily-invaded sites, longer-term monitoring of exotic communities would help to determine whether the exotic long dispersers will continue to dominate, or whether the populations of exotic short dispersers that currently appear to exhibit 'invasion debt' will expand.

My research also suggests potential projects that would more directly inform local and regional conservation agendas. First, the prediction that small islands harbour more federally- and provincially-listed rare species should be tested with more plant surveys of small islands in the southern Strait of Georgia. These surveys would help to redefine population distributions of species at risk of extinction, and may lead to the establishment of new protected areas or conservation covenants. Second, plant surveys could be integrated with breeding bird surveys (Arcese and Schuster, in prep) to derive a ranking system for high-value sites, in order to inform conservation site prioritization and land-use practices. GOE meadows are considered important areas for both plant and animal conservation (GOERT 2011a). Integrating predictions for these communities would allow more holistic ranking of sites for conservation management.

Management implications of results

The GOE is considered one of Canada's most endangered ecosystems (GOERT 2011a), and is also the subject of intense conservation effort, including measures to promote the protection of remaining GOE sites, and restoration activities to rehabilitate degraded sites. The Garry Oak Ecosystem Recovery Team (GOERT), the organization that coordinates much of the GOE conservation effort in Canada, aims (in principle) to prioritize protection over restoration (GOERT 2011b).

The results of my thesis strongly support this aim. While restoration activities to remove certain invasive shrub species (e.g., *Cytisus scoparius* removal in parks; CRD 2011) have shown some degree of success, the vast majority of invasive exotic species remain beyond the reach of such projects. Experimental efforts to diminish exotic dominance using combinations of mowing, fire and herbicides, have shown mixed success at small scales (e.g., MacDougall and Turkington 2007; Gonzales and Clements 2010; Rook et al. 2011; Stanley et al. 2011). Long-term results, where available (A. MacDougall pers. comm.), show that reductions in exotic species cover and gains in native species cover may diminish over time. This is perhaps unsurprising: a recent meta-analysis of invasive plant control experiments (Ketterning and Adams 2011) indicated a relatively low long-term success rate. Interventions such as herbicides and fire, even if they did function in the long term, are likely to be politically difficult and expensive, and in sites near large sources of invasive propagules such interventions would probably be required on a continuing basis.

Based on experimental disturbances at a deep-soil GOE site, MacDougall and Turkington (2007) recommended combining protection with re-introducing disturbance, to mimic intentional burning by First Nations that appears to have helped create or maintain GOE meadows (MacDougall et al. 2004). However, it is clear from my study that the *least* disturbed GOE sites (i.e., those on isolated small islands) now harbour the healthiest native ecosystems. Although Aboriginal fire was very likely responsible for maintaining meadows on deeper-soil sites (MacDougall et al. 2004), it is highly unlikely that fire was common on the small islands that are now among the best-preserved remnants of the GOE. Introducing fire to such native-dominated, small-island sites is probably unnecessary.

Targeting the geographic scale at which invasions can be most controlled is key to mitigating the effects of invasive species (Pauchard and Shea 2006). My results indicate that patch-level protection is probably the key to conserving native biodiversity in the GOE. Isolated patches, particularly on small islands, appear to be at early stages of invasion, and are dominated by native species at both the inter-patch and intra-patch scales. In contrast, similarities in intra-patch scale models for native and exotic percent cover suggest that conditions favouring native over exotic dominance at this scale may be difficult to isolate or engineer. In heavily-invaded sites, interventions that temporarily diminish exotic cover (e.g., weeding), would probably not be able to create conditions that favour native over exotic species cover, since continuing propagule pressure from adjacent disturbed areas would allow exotics to return.

Thus, while the potential beneficial effects of disturbance such as fire and mowing on deeper-soil sites are worth exploring, the most efficient conservation strategy is to preserve (without disturbance) those isolated sites that are dominated by native communities. Such sites on small islands have previously received little attention compared to their conservation value. In fact, commonly-accepted maps and areal estimates of the extent of GOE meadows (e.g., GOERT 2011b) are not representative of the true extent of meadows among the small islands; some small-island patches are accounted for but other, relatively large patches are not. And several small-island patches on which I found provincially- or federally-recognized species at risk of extinction are either Crown land (i.e., non-protected government land) or in private hands, without conservation covenants. One of the largest and most intact GOE patches remaining in Canada (Ballenas Island, ~30-35 ha), is for sale at the time of writing. The opportunity cost of preserving a single hectare of degraded GOE in Victoria, where

prices for single detached homes often exceed $1M, would likely be considerably higher than the asking price of Ballenas Island ($1.75M).

Protected small-island patches would still require monitoring, and, potentially, removal of exotic species. Given the low predictability of presence for exotic species at the intra-patch scale (Chapter 4), monitoring would need to take place across entire patches. In microsites where known invasives were relatively common, longer-term monitoring of cover using quadrats would help determine whether these species pose a competitive threat to natives, or whether their populations remain stable or diminish over time on such undisturbed sites. Monitoring at this scale would also determine whether removal programs are successful or even necessary on small-island sites. Regardless, potential removal programs would be much more feasible on the less-invaded, small-island patches than on heavily-invaded sites.

Despite their relative inefficiency as direct conservation measures, attempts at restoration of heavily-invaded sites may have ancillary benefits. For example, there is increasing interest in reconstituting GOE sites from urban parks, forests, or agricultural land that was once GOE (Dunwiddie and Bakker 2011). If this is done to create dioramas that help to raise awareness of GOE conservation or to inculcate a conservation ethic in urban environments, it perhaps is a sound strategy. Likewise, public involvement in removal of iconic weeds, if it is conducted such that it does not disturb sensitive sites, is also beneficial for awareness of GOE conservation issues. And removal of newly-arrived exotic species, especially those that are invasive elsewhere, may be very important, and far more efficient than intensive invasive removal projects on degraded sites. However, if decisions must be made to partition scarce resources in the most efficient manner possible, then preserving

additional isolated, native-dominated small-island patches is almost certainly the best

conservation strategy for the GOE.

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Appendices

Appendix 1: Study area

Figure A.1.1: Map showing location of study patches with respect to Vancouver Island, BC (inset, top), and detail of the northern (inset, A) and southern (B) study patch locations. Patches numbered 1-46 and 66-86 were used in Chapter 2; all patches were used in Chapters 3 and 4.
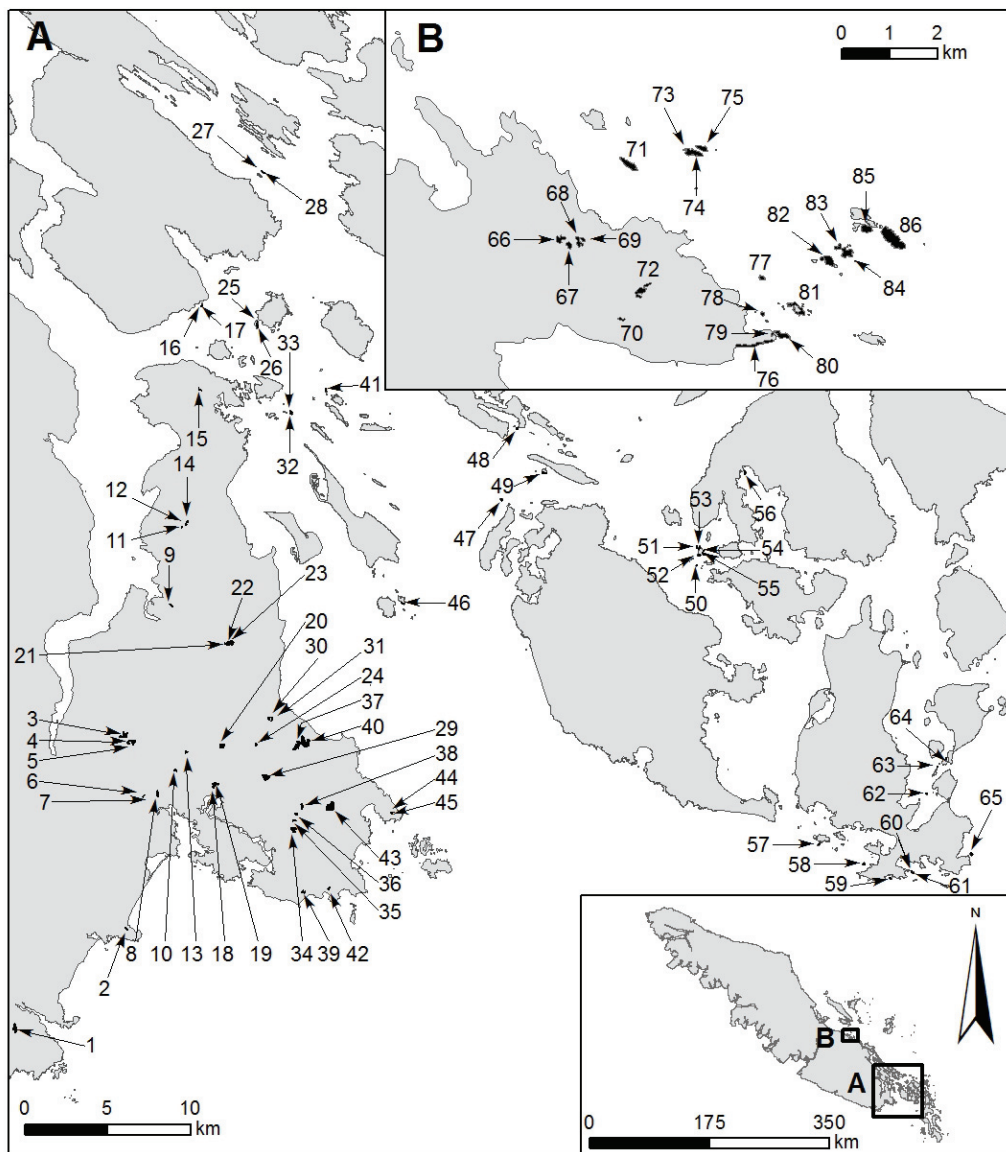
Table A.1.1: Study patch locations and areas

Site Number	UTM E	UTM N	Patch Area (ha)	Site Number	UTM E	UTM N	Patch Area (ha)
1	457038	5353912	5.89	44	479738	5366852	0.60
2	463606	5371544	6.52	45	479840	5366913	0.18
3	463731	5359888	1.17	46	480408	5379481	1.07
4	463862	5371087	1.84	47	486342	5385734	1.34
5	464131	5371151	5.03	48	487290	5390016	0.92
6	464755	5367830	0.30	49	488939	5387348	2.34
7	464815	5367931	0.39	50	498094	5381777	0.37
8	465620	5368016	3.48	51	498112	5382883	0.62
9	466429	5379377	1.55	52	498243	5382377	1.46
10	466710	5369442	1.20	53	498262	5382845	0.75
11	467091	5384080	0.49	54	498497	5382594	0.50
12	467329	5384239	0.72	55	498572	5382428	1.13
13	467360	5370524	1.35	56	501013	5387344	1.14
14	467424	5384396	0.77	57	505472	5364996	0.40
15	468176	5392362	1.22	58	508172	5363805	0.92
16	468243	5397383	0.26	59	509755	5362946	0.88
17	468323	5397411	0.34	60	511053	5363329	0.33
18	468998	5368462	1.27	61	511129	5363265	0.47
19	469142	5368624	3.19	62	511945	5368033	0.70
20	469516	5370901	4.43	63	512592	5369629	0.33
21	469683	5377042	4.48	64	513136	5370141	0.39
22	469831	5377080	0.32	65	514652	5364391	1.81
23	470076	5377102	2.15	66	414789	5460188	1.96
24	471560	5370989	1.22	67	414972	5460057	1.26
25	471624	5396376	0.57	68	415177	5460132	1.62
26	471634	5396182	1.10	69	415271	5460182	0.56
27	471928	5405471	0.59	70	416081	5458504	0.68
28	471950	5405459	0.34	71	416236	5461763	4.02
29	472145	5369016	8.72	72	416504	5459107	3.37
30	472319	5372549	1.11	73	417399	5462070	0.17
31	472510	5372537	1.73	74	417587	5462008	3.83
32	473662	5390915	0.62	75	417774	5462102	1.93
33	473670	5391022	0.63	76	418879	5457985	3.72
34	473817	5365881	5.88	77	419033	5459377	0.84
35	473863	5366401	1.15	78	419042	5458617	0.59
36	473985	5366808	1.48	79	419249	5458193	0.42
37	474043	5370939	8.82	80	419459	5458174	2.84
38	474316	5367260	2.77	81	419766	5458728	3.81
39	474408	5362108	2.03	82	420424	5459740	3.83
40	474493	5371123	17.68	83	420639	5460024	1.07
41	475757	5392324	0.64	84	420820	5459904	3.66
42	475945	5362321	1.31	85	421229	5460411	3.01
43	476045	5367242	16.38	86	421783	5460202	11.54

Appendix 2: Phylogenetic analyses

Creation of phylogenetic tree

We created a phylogenetic tree of our species using the Angiosperm Phylogeny Group III (2009) phylogeny. Where there was no sub-family phylogenetic information, species within genera were assumed to be more closely related than genera within families. Internal nodes were dated using fossil evidence where available (Wikstrom et al. 2001), and the branch lengths for the tree were scaled to the dated nodes and made ultrametric via Bladj software (Webb 2000). Phylogenetic distances among species were subsequently used to test intra- versus inter-group distances and to test for a phylogenetic signal in abundance differences.

Tests for phylogenetic relatedness within and among groups

We tested for significant differences in intra- versus inter-group phylogenetic distances using permutation tests (permuting group identities 10 000 times) of mean within-group distances versus means of all other distances. Apart from native long dispersers, selected groups exhibited lower intra-group than inter-group phylogenetic distances (Table A.2.1). As reported in the Chapter 2, we also tested for a phylogenetic signal in abundance differences at both scales, using Mantel tests.

Table A.2.1: Permutation test results for intra- versus inter-group phylogenetic distances

Group	Intra-Group vs. Inter-Group Difference (%)	Z	P
Exotic Long Dispersers	-3.1	-7.82	<0.0001
Exotic Short Dispersers	-5.9	-8.55	<0.0001
Native Long Dispersers	0.2	0.53	0.60
Native Short Dispersers	-1.0	-3.01	0.0032

Appendix 3: Tests for all variables from most parsimonious models

Table A.3.1: Significant and non-significant parameters from the most parsimonious models for numbers of occurrences and forms of rarity and commonness.

Response Variable	Predictor Variables	Final Model	Tested Parameter	Parameter Value	Standard Error	T	P
Number of Occurrences in Patches	O, D, G_f	O × D	EL	0.364	0.169	2.161	*0.0342*
			ES	-0.756	0.192	3.948	*0.0003*
			NL	-0.010	0.143	0.070	0.9443
			NS	0.081	0.254	0.321	0.7491
Number of Occurrences in Quadrats	O, D, G_f	O × D	EL	0.626	0.368	1.698	0.0940
			ES	-1.109	0.418	2.654	*0.0114*
			NL	-0.202	0.312	0.649	0.5176
			NS	0.271	0.553	0.490	0.6256
Commonness on Both Inter- and Intra-Patch Scales	O, D, G_f	O × D	EL	0.510	0.397	1.283	0.2037
			ES	-1.626	0.472	3.443	*0.0014*
			NL	-0.047	0.362	0.129	0.8979
			NS	0.434	0.649	0.669	0.5053
Rarity on Both Inter- and Intra-Patch Scales	O, D, G_f	O × D	EL	-1.008	0.365	2.765	*0.0073*
			ES	0.334	0.411	0.812	0.4216
			NL	0.385	0.302	1.276	0.2047
			NS	0.211	0.518	0.407	0.6853
Number of Occurrences in Full Surveys (Exotic spp. only; including estim. minimum residence time)	D, G_f, T_a	D + T_a	T_a	0.453	0.103	4.399	*<0.0001*
Number of Occurrences in Quadrats (Exotic spp. only; including estim. minimum residence time)	D, G_f, T_a	D + T_a	T_a	1.479	0.280	5.275	*<0.0001*
Minimum Convex Polygon Size (Exotic spp. only; including estim. minimum residence time)	D, G_f, T_a	D + T_a	T_a	0.210	0.095	2.218	*0.0292*
Number of Occurrences on Patches (22 Small-Island Patches Only)	O, D, G_f	O × D	EL	0.326	0.225	1.448	0.1522
			ES	-1.500	0.259	5.798	*<0.0001*
			NL	0.207	0.194	1.066	0.2888
			NS	0.217	0.346	0.629	0.5312
Number of Occurrences in Quadrats (22 Small-Island Patches Only	O, D, G_f	O × D	EL	0.385	0.425	0.906	0.3682
			ES	-2.003	0.484	4.135	*0.0002*
			NL	0.223	0.362	0.616	0.5391
			NS	0.398	0.644	0.618	0.5383

Notes:

-Predictor variables: O = origin (native or exotic); D = dispersal ability (short or long); G_f = growth form (forb, grass, shrub, tree); T_a = estimated minimum residence time

-Predictor variable categories: E = exotic; N = Native; S = short dispersers; L = long dispersers (i.e., EL = exotic long dispersers)

Appendix 4: Alternate forms of rarity and commonness

Conservative estimate (fewer common, more rare):

Common (patch-level) = 20 or more patches

Rare (patch-level) = 4 or fewer patches

Common (quadrat-level) = greater than one occurrence in quadrats from at least one patch

Rare (quadrat-level) = never found in more than one quadrat per patch

Liberal estimate (more common, fewer rare):

Common (patch-level) = 10 or more patches

Rare (patch-level) = 1 or 0 patches

Common (quadrat-level) = greater than one occurrence in quadrats from at least one patch

Rare (quadrat-level) = never found in more than one quadrat per patch

Table A.4.1: Most parsimonious models for rarity and commonness (conservative estimate)

Response Variable	Predictor Variables	Final Model	Tested Parameter	Parameter Value	Standard Error	T	P
Commonness	O, D, G_f	$O \times D + G_f$	EL	0.389	0.414	0.940	0.3507
			ES	-1.330	0.490	2.714	*0.0098*
			NL	-0.066	0.374	0.177	0.8601
			NS	0.413	0.669	0.617	0.5393
			F	-0.198	0.095	2.080	*0.0388*
			G	0.760	0.324	2.343	*0.0244*
			S	0.563	0.374	1.504	0.1432
			T	-0.375	0.642	0.584	0.5686
Rarity	O, D, G_f	$O \times D$	EL	-0.803	0.311	2.580	*0.0120*
			ES	0.448	0.352	1.274	0.2099
			NL	0.334	0.260	1.281	0.2032
			NS	0.045	0.456	0.098	0.9221

Table A.4.2: Most parsimonious models for rarity and commonness (liberal estimate)

Response Variable	Predictor Variables	Final Model	Tested Parameter	Parameter Value	Standard Error	T	P
Commonness	O, D, G_f	$O \times D + G_f$	EL	0.433	0.380	1.141	0.2576
			ES	-1.342	0.446	3.009	*0.0045*
			NL	-0.163	0.339	0.481	0.6316
			NS	0.499	0.605	0.825	0.4115
			F	-0.180	0.093	1.943	0.0534
			G	0.757	0.321	2.355	*0.0238*
			S	0.567	0.365	1.554	0.1307
			T	-0.605	0.638	0.948	0.3590
Rarity	O, D, G_f	O	E	-0.536	0.207	2.587	*0.0110*
			N	0.322	0.124	2.587	*0.0105*

Notes:

-Predictor variables: O = origin (native or exotic); D = dispersal ability (short or long); G_f = growth form (forb, graminoid, shrub, tree)

-Predictor variable categories: E = exotic; N = native; S = short dispersers; L = long dispersers; F = forb; G = graminoid; S = shrub; T = tree

Appendix 5: Variables examined in models and RDAs in Chapters 3 and 4.

Table A.5.1: **Variables examined in models and RDAs. Variables 1 through 8 were collected at the patch scale. Variables 9 through 13 were collected at the intra-patch scale.**

Variable	Justification	Collection Method
1. Island (binary)	-dispersal barriers (MacArthur and Wilson 1967; Cody 2006)	
2. Patch area (m^2)	-may affect colonization directly (MacArthur and Wilson 1967), or through availability of microhabitats (Whittaker and Fernández-Palacios 2007; Melbourne et al. 2007)	Air photos plus ground truthing with GPS
3. Climate (Principal Component 1)	-several climate variables may affect species distributions at different scales (Ohlemüller et al. 2006; Morin and Lechowicz 2008; Lilley and Vellend 2009; Austin and Van Neil 2011)	First Principal Component of PCA of 83 closely-related climate variables, estimated using CLIMATE BC* (variance explained by first axis = 69%)
4. Deer Feces Present in at least one Quadrat in patch	-herbivory may promote exotics and/or diminish natives (Gonzales and Arcese 2008; MacDougall 2008)	Presence of pellets in any quadrat in a patch
5. Forest Area (500 m buffer; ha)	-forests may serve as a buffer to reduce invasion (Martin et al. 2008)	Digitization of air photos; calculation of buffer using ArcGIS 10
6. Meadow (500 m buffer; ha)	-proximity of similar ecosystems may affect dispersal (Vellend 2003; Harrison et al. 2006)	Digitization of air photos; calculation of buffer using ArcGIS 10
7. Agricultural land (500 m buffer; ha)	-includes lawns; agricultural land may be a source of exotic propagules (Daehler 1998; Seabloom et al. 2006) and is a proxy for disturbance	Digitization of air photos; calculation of buffer using ArcGIS 10
8. Road length (500 m buffer;	-road length is a proxy for disturbance and propagule pressure (Lilley and Vellend 2009),	Digitization of air photos; calculation of

Variable	Justification	Collection Method
m)	which can both promote species invasions (e.g., Davis et al. 2000; Lockwood et al. 2005; Vilà et al. 2007)	buffer using ArcGIS 10
9. Litter (% cover)	-litter may affect plant communities in a variety of ways, potentially promoting or inhibiting plant growth and survival (Facelli and Pickett 1991)	Estimation using quadrat
10a. Aspect (Northing, degrees)	-Aspect can influence moisture regime and therefore vegetation communities (Gilbert and Lechowicz 2004; Bennie et al. 2006; Austin and Van Neil 2011)	Compass
10b. Aspect (Easting, degrees)		Compass
11. Soil Depth (cm)	-shallow soils have limited moisture availability (MacDougall and Turkington 2006)	Soil depth probe, one sample per side of quadrat
12. Slope (degrees)	-Slope can influence moisture regime and therefore vegetation communities by increasing drainage (Gilbert and Lechowicz 2004; Bennie et al. 2006; Austin and Van Neil 2011)	Clinometer
13. Canopy Cover (%)	-shading can influence community composition through light, moisture regimes, creating conditions that may promote or inhibit certain species (Callaway 1995; Scholes and Archer 1997)	Fish-eye lens photographs (1 m height) and WinSCANOPY 2008a**

*v. 3.1, Wang et al. (2006).

**Régent Instruments Inc. http://www.regentinstruments.com/products/Scanopy/SCANOPYSoftware.html

Appendix 6: Partial ordinations

Table A.6.1: Partial ordinations required for decomposition of community variation explained by variables at each scale

RDA Number	Predictor Variables
1	All Variables
2	Small Island vs. Vancouver Island
3	All Variables but Island vs. Vancouver Island
4	All Patch-Level
5	All Variables but Patch-Level
6	Patch-Level Spatial Polynomials
7	Patch-Level Environmental Variables
8	All Variables but Patch-Level Polynomials
9	All Variables but Patch-Level Environment
10	All Quadrat-Level
11	All Variables but Quadrat-Level

Table A.6.2: Algebra for determining variability in community data at different levels, using results of partial RDAs, numbered according to Table A.7. Covariation is obtained by subtracting the marginal from the conditional variation explained.

Level of Variability	Conditional	Marginal
Island vs. Vancouver Island	2	1-3
All Inter-Patch Variables	4	1-5
Inter-Patch Spatial Variables	6	1-7
Inter-Patch Environmental Variables	8	1-9
Intra-Patch Environmental Variables	10	1-11

Figure A.6.1: RDA – Native species including all variables
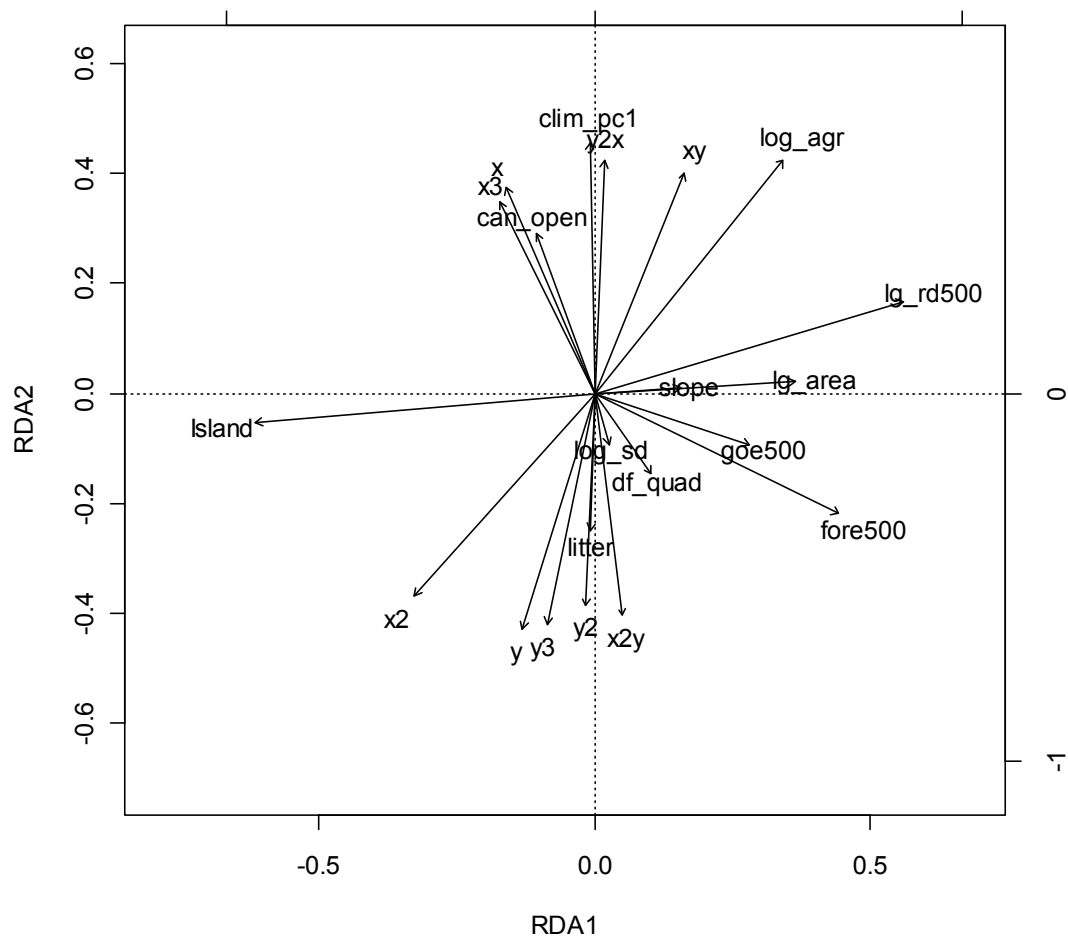
Figure A.6.2: RDA – Exotic species including all variables
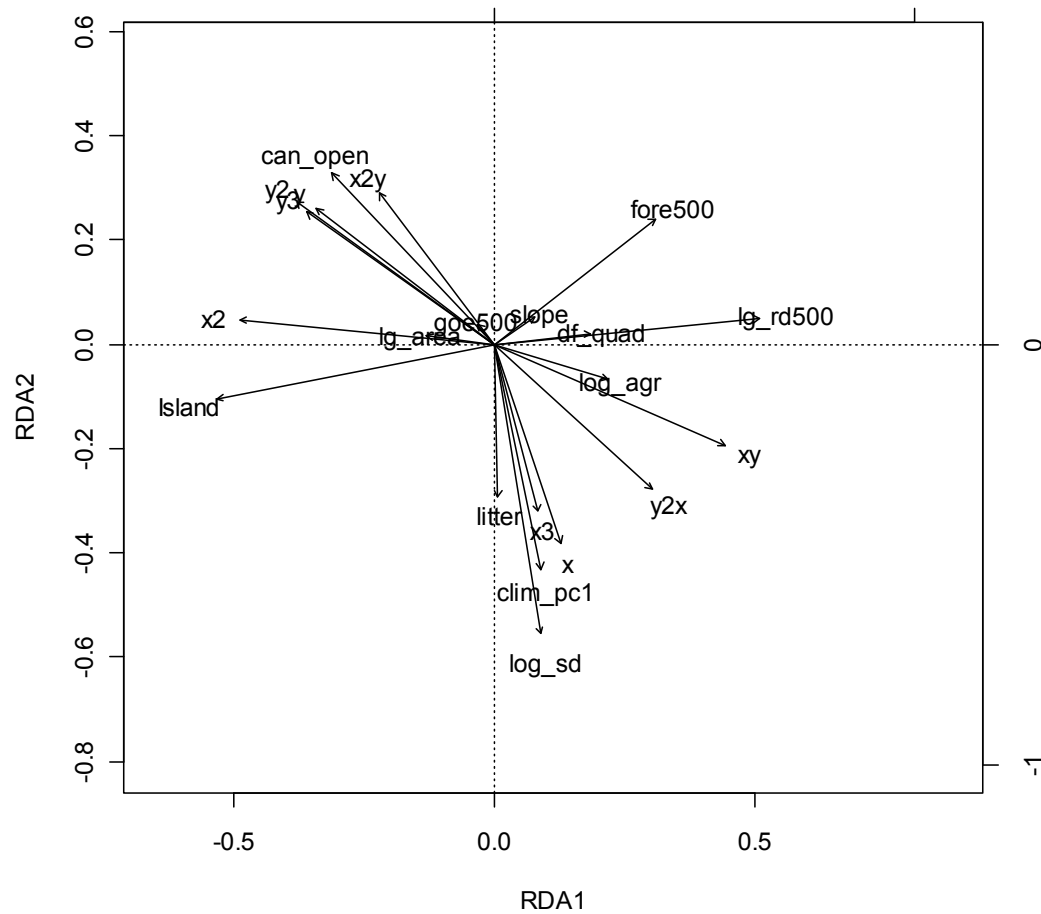
Table A.6.3: Codes from ordination plots above

Code	Variable
Island	Island (binary)
lg_area	Patch area (m^2 - log transformed)
clim_pc1	Climate (Principal Component 1)
df_quad	Deer Feces (Pellets) Present in ≤1 Quadrat in patch
fore500	Forest Area (500 m buffer; ha)
goe500	Meadow (500 m buffer; ha)

Code	Variable
log_agr	Agricultural land (500 m buffer; ha- log transformed)
lg_rd500	Road length (500 m buffer; m - log transformed)
Litter	Litter (% cover)
log_sd	Soil Depth (cm - log transformed)
Slope	Slope (degrees)
can_open	Canopy Cover (%)
x	Centered, standardized UTM easting
y	Centered, standardized UTM northing
xy	$x \times y$
x2	x^2
y2	y^2
x2y	$x^2 y$
y2x	$y^2 x$
x3	x^3
y3	y^3

Figure A.6.3: Conditional (non-independent) percent variation explained in individual variables in RDAs. Ninety-five percent confidence intervals are based on a bootstrap procedure described in Chapter 3. Variables are defined in Table A.9.
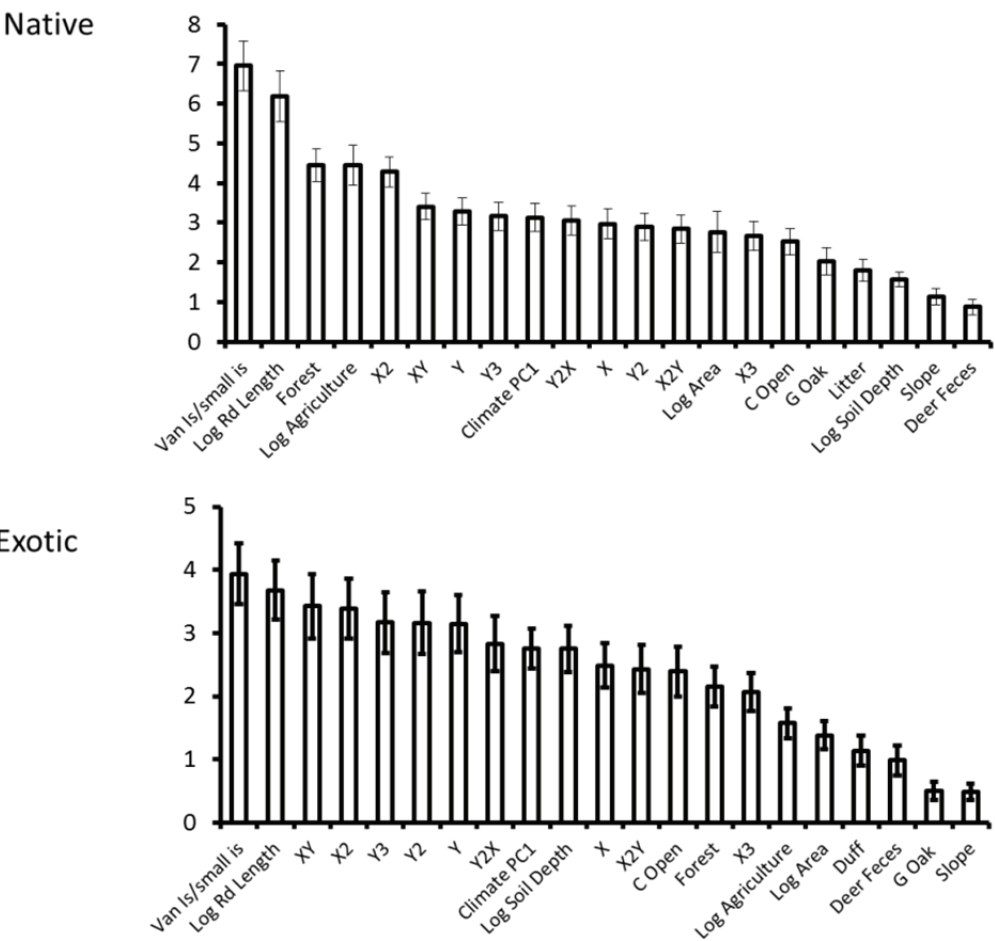
Figure A.6.4: Marginal (independent) percent variation explained in individual variables in RDAs. Ninety-five percent confidence intervals are based on a bootstrap procedure described in Chapter 3. Variables are defined in Table A.9
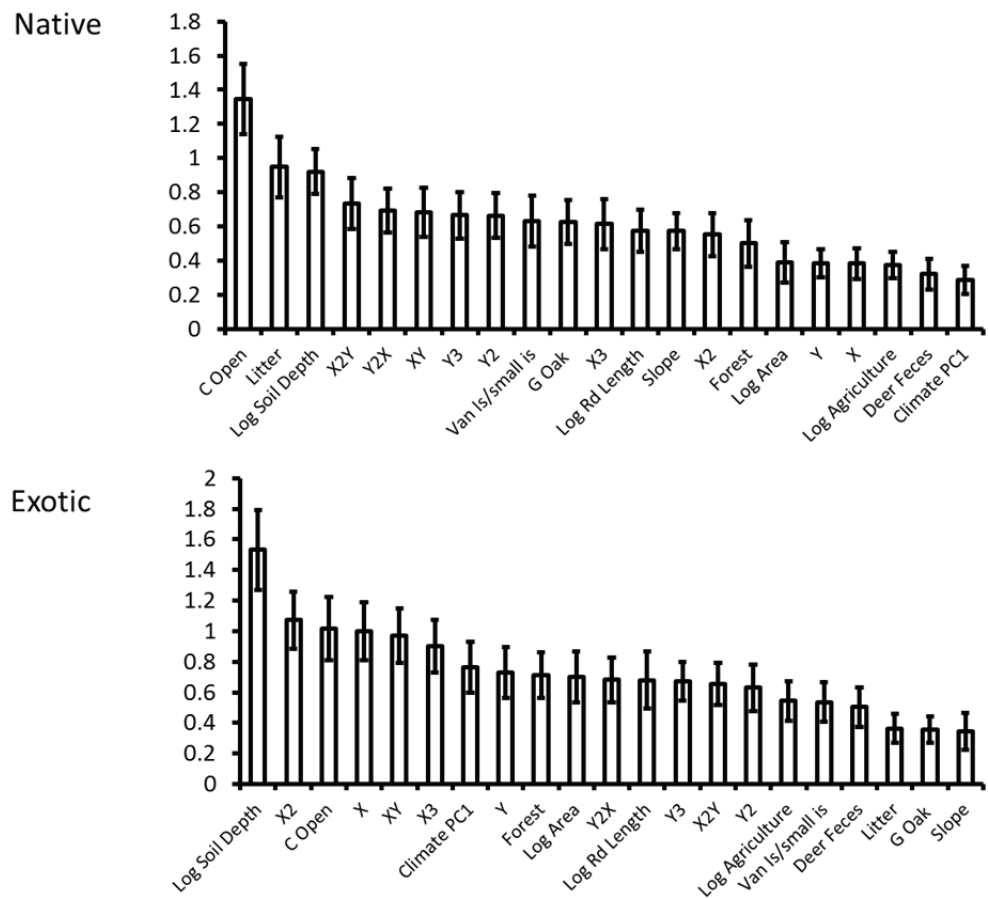
Appendix 7: Environmental specialization calculation

Environmental specialization was estimated using a multivariate measure of environmental factors within which a given species was found to occur. At each quadrat location, a total of six environmental variables that were reflective of the general characteristics of the local environment were measured. These were then used to estimate the range of conditions in which species were found within the study patches. Since the range of environmental conditions in which a species is found is necessarily correlated with the number of quadrats in which it is found, we expressed specialization as a deviation from the null expectation based on number of occurrences. Null expectations for each species i found in $n \geq 5$ quadrats and ≥ 2 sites, were derived using averages of variables taken from 1000 random draws of N quadrats from the dataset, using the following algorithm:

1) Convert all environmental variables to z-scores to equalise their contributions.

2) Sample each quadrat-level environmental variable from N randomly-chosen quadrats from the full dataset;

3) Calculate the range of each variable across the N samples;

4) Sum the ranges of every variable across the N samples;

5) Repeat steps 3-4, 1000 times;

6) Take the average sum across the 1000 random samples to get an estimate of the null specialization estimate for N samples;

7) Subtract the null estimate from the summed range of environmental variables from the N quadrats actually containing the focal species i.

For species whose ranges within the study area were highly constrained by dispersal limitation (e.g., shorter-dispersing and recently-arrived exotics), this measurement could be biased upwards due to spatial autocorrelation in species distributions and environmental variables. However, as the most common exotic species in the 'tails' of abundance distributions were compared for exotic and native species and spatial autocorrelation was not different among these species (see Chapter 4 for details), there is unlikely to be a bias towards either group.

Appendix 8: Percent cover correlations

Table A.8.5: Tests for proportions of correlations among individual native and other native species (1770 species pairs), exotic and other exotic species (630 species pairs), and native and exotic species (2160 species pairs).

	Native-Native		Exotic-Exotic		Native-Exotic	
	Positive	Negative	Positive	Negative	Positive	Negative
PCS* - real data	0.27	0.10	0.39	0.10	0.22	0.16
PCS - randomized data	0.06	0.03	0.06	0.03	0.06	0.03
PCS - Corrected	0.20	0.08	0.33	0.06	0.16	0.13
Z (PCS positive vs. negative)	20.17		27.02		3.45	
P	<0.0001		<0.0001		0.0003	

*PCS = proportion of correlations that are significant ($|r|>0.067$ for all groups)

Appendix 9: Environmental differences between small-island and Vancouver Island patches

Table A.9.1: Differences in mean values for environmental variables on Vancouver Island versus small-island patches. P-values are derived from a permutation test.

	Vancouver Island		Small Island		P
	Mean	SD	Mean	SD	
Log (Agr. 500 m)	2.64	2.46	0.46	1.35	**<0.0001**
Forest (500m)	46.16	35.32	5.66	7.55	**<0.0001**
Meadow (500 m)	2.83	3.42	1.50	2.20	**0.043**
Log Road Length (500 m)	3.36	0.90	0.071	0.043	**<0.0001**
Log Area	4.24	0.46	3.99	0.41	**0.015**
Climate PC1	-0.20	1.02	0.07	1.01	0.23
Deer Pellets (in quad)	0.43	0.50	0.27	0.45	0.16

Appendix 10: Species abundance distributions

Table A.10.1: Species abundance distribution at inter-patch scale, bin size = 20 occurrences.

Bin	Exotic	Native	Ratio Exo/Nat	P*
1-20	100	186	0.537634	1
21-40	12	35	0.254	0.257
41-60	15	19	0.35	0.264
61-80	10	17	0.588235	0.836
All	137	257	0.533074	---

* 2-tailed Fisher exact test of exotic:native ratio between individual bins and all data

Table A.10.2: Species abundance distribution at inter-patch scale, bin size = 10 occurrences. The bin size for this table corresponds to the histogram in Fig. 3.5

Bin	Exotic	Native	Ratio Exo/Nat	P
1-10	83	156	0.53	1.00
11-20	17	30	0.57	0.87
21-30	8	18	0.44	0.83
31-40	4	17	0.24	0.16
41-50	8	11	0.73	0.62
51-60	7	8	0.88	0.41
61-70	7	9	0.78	0.59
71-80	3	8	0.38	0.76
All	137	257	0.53	---

Table A.10.3: Species abundance distribution at inter-patch scale, bin size = 5 occurrences.

Bin	Exotic	Native	Ratio Exo/Nat	P
1-5	59	131	0.45	0.40
6-10	24	25	0.96	0.06
11-15	11	16	0.69	0.54
16-20	6	14	0.43	0.81
21-25	6	11	0.55	1.00
26-30	2	7	0.29	0.72

Bin	Exotic	Native	Ratio Exo/Nat	P
31-35	0	8	0.00	0.06
36-40	4	9	0.44	1.00
41-45	4	6	0.67	0.75
46-50	4	5	0.80	0.73
51-55	2	3	0.67	1.00
56-60	5	5	1.00	0.33
64-65	4	7	0.57	1.00
66-70	3	2	1.50	0.35
71-75	1	6	0.17	0.43
76-80	2	2	1.00	0.61
All	137	257	0.53	---

Table A.10.4: Species abundance distribution at inter-patch scale, log base-2 bins

Bin	Exotic	Native	Ratio Exo/Nat	P
1	25	61	0.41	0.38
2	13	32	0.41	0.51
3-4	15	24	0.63	0.73
5-8	21	27	0.78	0.26
9-16	21	30	0.70	0.44
17-32	13	33	0.39	0.42
33-64	23	38	0.61	0.67
65-128	6	12	0.50	1.00
All	137	257	0.53	---

Table A.10.5: Species abundance distribution at intra-patch scale, bin size = 80 occurrences.

Bin	Exotic	Native	Ratio Exo/Nat	P
1-80	121	241	0.50	0.70
81-160	13	9	1.44	*0.037*
161-240	1	7	0.14	0.27
241-320	2	0	Na	0.12
All	137	257	0.53	---

Table A.10.6: Species abundance distribution at intra-patch scale, bin size = 40 occurrences.

Bin	Exotic	Native	Ratio Exo/Nat	P
1-40	113	225	0.50	0.75
41-80	8	16	0.5	1.00
81-120	4	4	1	0.46
121-160	9	5	1.8	*0.043*
161-200	1	3	0.33	1
201-240	0	4	0	0.30
241-280	2	0	na	0.12
All	137	257	0.53	---

Table A.10.7: Species abundance distribution at intra-patch scale, bin size = 20 occurrences.

Bin	Exotic	Native	Ratio Exo/Nat	P
1-20	108	208	0.52	0.87
21-40	5	17	0.29	0.36
41-60	5	9	0.56	1.00
61-80	3	7	0.43	1.00
81-100	2	2	1.00	0.28
101-120	2	2	1.00	0.28
121-140	4	2	2.00	0.61
141-160	5	3	1.67	0.13
161-180	1	3	0.33	1.00
181-200	0	0	na	1.00
201-220	0	3	0.00	0.55
221-240	0	1	0.00	1.00
241-260	1	0	na	0.34
261-280	1	0	na	0.34
All	137	257	0.53	---

Table A.10.8: Species abundance distribution at intra-patch scale, log base 2 bins

Bin	Exotic	Native	Ratio Exo/Nat	P
1	75	139	0.54	1
2	4	9	0.44	1
3-4	5	17	0.29	0.36

Bin	Exotic	Native	Ratio Exo/Nat	P
5-8	9	16	0.56	1
9-16	5	15	0.33	0.47
17-32	5	12	0.42	0.80
33-64	7	19	0.37	0.52
65-128	8	10	0.8	0.45
129-256	10	11	0.91	0.25
257-512	1	0	na	0.35
All	137	257	0.53	---

Appendix 11: Variable correlation matrices

Table A.11.1: Correlation matrix of variables at the inter-patch level

	Log(AGR500)	FOREST(500)	GOE(500)	Log(RD500)	Log(Area)	Island	DP(q/s)
FOREST(500)	0.087						
GOE(500)	0.024	0.290					
Log(RD500)	0.534	0.421	0.151				
Log(Area)	0.311	0.263	0.201	0.266			
Island	-0.476	-0.610	-0.224	-0.916	-0.276		
DP(q/s)	-0.047	0.381	0.050	0.126	0.097	-0.168	
Climate (PC1)	0.365	-0.163	-0.199	0.233	-0.053	-0.134	0.0258

Table A.11.6: Correlation matrix of variables at the intra-patch level

	Northness	Eastness	Island	DP(q/s)	Litter	Log(Soil Depth)	Slope	Canopy Openness	Log(Area)	Climate (PC1)	Log(AGR500)	FOREST(500)	GOE(500)
Eastness	0.070												
Island	-0.034	0.062											
DP(q/s)	-0.007	0.015	-0.119										
Litter	0.010	0.004	-0.010	0.075									
Log(Soil Depth)	0.044	-0.003	-0.047	-0.013	0.373								
Slope	0.019	0.020	-0.218	0.135	-0.012	-0.118							
Canopy Openness	0.020	-0.009	0.127	-0.183	-0.227	-0.191	0.003						
Log(Area)	0.025	-0.027	-0.342	0.024	0.053	0.061	0.161	0.051					
Climate (PC1)	0.061	-0.023	-0.131	0.042	0.062	0.143	0.041	0.024	-0.010				
Log(AGR500)	0.054	-0.012	-0.549	-0.049	-0.110	0.024	0.122	0.112	0.370	0.395			
FOREST(500)	0.012	-0.020	-0.595	0.362	0.011	-0.080	0.319	-0.131	0.312	-0.152	0.150		
GOE(500)	0.038	0.017	-0.205	0.159	0.053	-0.073	0.139	-0.044	0.232	-0.135	0.073	0.348	
Log(RD500)	0.043	-0.065	-0.924	0.082	-0.005	0.081	0.206	-0.072	0.341	0.238	0.603	0.397	0.146

Note that although most environmental variables in my models were not highly correlated, location of a patch on a small island and nearby road length were highly negatively correlated at both scales. Both variables were retained in the distribution model framework because they measure phenomena that are not interchangeable (e.g., nearby road length is low for small islands, and also low for patches surrounded by forest, agriculture and/or other meadows). Indeed, both variables were retained in models of five species at the inter-patch scale and five species at the intra-patch scale. However, given their high correlation, the selection of one of them over the other in any given model should be viewed with a degree of caution. Thus it is not possible to determine whether the statistical influence of small-island status or road length in models represents the biological influence of isolation or disturbance or both.

Appendix 12: Distribution model results

Table A.12.1: Overfit (initial minus bootstrap-corrected AUC) and bootstrap-corrected AUC for inter-patch models of native species. Italicized numbers indicate bootstrap datasets where >5% models did not converge.

Latin Name	Common Name	Overfit	Corrected AUC
Camassia leichtlinii	great camas	0.015	0.94
Festuca rubra	red fescue	0.017	0.88
Brodiaea coronaria	harvest brodiaea	Na	Na
Galium aparine	cleavers	Na	Na
Camassia quamash	common camas	*0.003*	*0.99*
Brodiaea hyacinthina	white brodiaea	0.033	0.84
Achillea millefolium	yarrow	*0.061*	*0.84*
Sanicula crassicaulis	Pacific sanicle	Na	Na
Plectritis congesta	sea blush	0.036	0.82
Elymus glaucus	blue wildrye	0.063	0.74
Collinsia parviflora	small-flowered blue-eyed Mary	Na	Na
Polypodium glycyrrhiza	licorice fern	Na	Na
Luzula multiflora	many-flowered wood-rush	*0.043*	*0.93*
Cerastium arvense	field chickweed	0.068	0.78
Lotus micranthus	desert deervetch	0.020	0.89
Ranunculus occidentalis	western buttercup	0.019	0.86
Danthonia californica	California oatgrass	0.017	0.87
Carex inops	long-stoloned sedge	0.022	0.91
Trifolium willldenowii	tomcat clover	0.045	0.76
Lomatium utriculatum	spring gold	0.015	0.71

Table A.12.2: Overfit (initial minus bootstrap-corrected AUC) and bootstrap-corrected AUC for inter-patch models of exotic species. Italicized numbers indicate bootstrap datasets where >5% models did not converge.

Latin Name	Common Name	Overfit	Corrected AUC
Aira praecox	early hairgrass	Na	Na
Hypochaeris radicata	hairy cat's-ear	Na	Na
Anthoxanthum odoratum	sweet vernalgrass	0.027	0.75
Rumex acetosella	green sorrel	Na	Na
Vicia sativa	common vetch	Na	Na
Holcus lanatus	common velvetgrass	*0.048*	*0.83*
Bromus diandrus	rip-gut brome	*0.037*	*0.91*
Vulpia bromoides	barren fescue	0.014	0.77
Cytisus scoparius	Scotch broom	*0.021*	*0.96*
Stellaria media	common chickweed	0.004	0.71
Bromus hordeaceus	soft brome	0.042	0.85
Bromus sterilis	barren brome	0.029	0.77
Geranium molle	dovefoot geranium	-0.001	0.77
Dactylis glomerata	orchard grass	0.031	0.78
Vicia hirsuta	tiny vetch	0.007	0.75
Veronica arvensis	wall speedwell	0.002	0.87
Cynosurus echinatus	hedgehog dogtail	0.011	0.71
Myosotis discolor	common forget-me-not	0.012	0.83
Poa pratensis	Kentucky bluegrass	*0.019*	*0.85*
Aphanes arvensis/australis	parsley-piert	0.006	0.78

Table A.12.3: Terms from final native species distribution models at the inter-patch scale

		B_1	SE	Z	P
Camassia leichtlinii	Intercept	1.3965	0.5596	2.4960	0.0126
	Island	6.2068	2.3738	2.6150	0.0089
	Climate (PC1)	4.3462	1.6443	2.6430	0.0082
Festuca rubra	Intercept	6.9439	3.2487	2.1370	0.0326
	GOE(500)	0.3364	0.2342	1.4360	0.1509
	Log(RD500)	-1.7478	0.8543	-2.0460	0.0408
Brodiaea coronaria	(No model)				
Galium aparine	(No model)				
Camassia quamash	Intercept	-23.8886	16.5069	-1.4470	0.1478
	Island	-13.8110	7.2503	-1.9050	0.0568
	Log(Area)	7.9683	4.3824	1.8180	0.0690
	Log(AGR500)	-1.6249	1.3020	-1.2480	0.2120
	FOREST(500)	0.1598	0.1074	1.4870	0.1369
Brodiaea hyacinthina	Intercept	-5.1820	3.9663	-1.3060	0.1914
	Island	-2.2899	0.9086	-2.5200	0.0117
	DP(q/s)	1.4343	0.9086	1.5790	0.1144
	Log(Area)	1.9469	0.9823	1.9820	0.0475
	Climate (PC1)	-0.9463	0.4045	-2.3390	0.0193
Achillea millefolium	Intercept	-30.6646	13.8412	-2.2150	0.0267
	Island	4.9736	2.1713	2.2910	0.0220
	Log(Area)	7.5492	3.3075	2.2820	0.0225
	FOREST(500)	0.0411	0.0250	1.6460	0.0997
	GOE(500)	0.5631	0.3099	1.8170	0.0692
Sanicula crassicaulis	(No model)				
Plectritis congesta	Intercept	-1.3809	0.7143	-1.9330	0.0532
	Island	2.7915	0.8102	3.4450	0.0006
	FOREST(500)	0.0537	0.0197	2.7310	0.0063
	GOE(500)	0.4480	0.2365	1.8940	0.0582
Elymus glaucus	Intercept	-0.6208	5.3655	-0.1160	0.9079
	Island	-5.5965	4.4437	-1.2590	0.2079
	DP(q/s)	1.4116	1.1199	1.2600	0.2075
	Log(Area)	1.8818	0.9694	1.9410	0.0522

		B$_1$	SE	Z	P
	Log(RD500)	-1.3296	1.1851	-1.1220	0.2619
Collinsia parviflora	(No model)				
Polypodium glycyrrhiza	(No model)				
Luzula multiflora	Intercept	-31.5033	10.3037	-3.0570	0.0022
	DP(q/s)	2.6268	1.4317	1.8350	0.0665
	Log(Area)	8.4457	2.7560	3.0650	0.0022
	Climate (PC1)	-1.1660	0.6204	-1.8790	0.0602
	Log(AGR500)	-0.4661	0.2853	-1.6340	0.1023
	FOREST(500)	0.1372	0.0555	2.4720	0.0134
	Log(RD500)	-0.9877	0.5224	-1.8910	0.0587
Cerastium arvense	Intercept	-8.1089	5.2409	-1.5470	0.1218
	Log(Area)	2.8097	1.4016	2.0050	0.0450
	FOREST(500)	0.0548	0.0291	1.8830	0.0597
	Log(RD500)	-0.7592	0.3006	-2.5250	0.0116
Lotus micranthus	Intercept	13.0584	6.5580	1.9910	0.0465
	Island	-15.3407	6.5091	-2.3570	0.0184
	DP(q/s)	1.7379	0.7742	2.2450	0.0248
	Climate (PC1)	-0.9884	0.4554	-2.1700	0.0300
	Log(RD500)	-3.4712	1.7482	-1.9860	0.0471
Ranunculus occidentalis	Intercept	-1.6195	3.0569	-0.5300	0.5963
	Island	-3.1117	1.0833	-2.8730	0.0041
	DP(q/s)	3.4045	1.1714	2.9060	0.0037
	Log(Area)	1.0717	0.7351	1.4580	0.1449
	Log(AGR500)	-0.5307	0.2318	-2.2900	0.0220
Danthonia californica	Intercept	-5.3771	2.9250	-1.8380	0.0660
	Island	-2.6555	0.7903	-3.3600	0.0008
	Log(Area)	1.6204	0.6921	2.3410	0.0192
	Climate (PC1)	-1.5497	0.4259	-3.6390	0.0003
Carex inops	Intercept	8.6753	9.5853	0.9050	0.3654
	Island	-24.9072	12.6059	-1.9760	0.0482
	DP(q/s)	2.7504	1.2833	2.1430	0.0321
	Log(Area)	3.4199	1.2842	2.6630	0.0077

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		B_1	SE	Z	P
	Climate (PC1)	-0.8954	0.6347	-1.4110	0.1583
	Log(RD500)	-5.6533	3.2661	-1.7310	0.0835
Trifolium willdenowii	Intercept	-15.4384	5.4297	-2.8430	0.0045
	Island	6.8436	3.3107	2.0670	0.0387
	Log(Area)	2.4107	0.8715	2.7660	0.0057
	FOREST(500)	0.0404	0.0180	2.2510	0.0244
	GOE(500)	0.2464	0.1416	1.7400	0.0819
	Log(RD500)	0.9927	0.7628	1.3010	0.1931
Lomatium utriculatum	Intercept	0.1594	0.3703	0.4300	0.6670
	Island	-1.5213	0.4996	-3.0450	0.0023
	DP(q/s)	0.7402	0.5067	1.4610	0.1441

Table A.12.4: Terms from final exotic species distribution models at the inter-patch scale

		B₁	SE	Z	P
Aira praecox	(No model)				
Hypochaeris radicata	(No model)				
Anthoxanthum odoratum	Intercept	-0.3958	0.3651	-1.0840	0.2783
	Climate (PC1)	-0.6422	0.2787	-2.3040	0.0212
	Log(AGR500)	0.4490	0.1701	2.6400	0.0083
	Log(RD500)	0.2620	0.1717	1.5260	0.1269
Rumex acetosella	(No model)				
Vicia sativa	(No model)				
Holcus lanatus	Intercept	-11.5957	4.5374	-2.5560	0.0106
	DP(q/s)	-1.4022	0.8919	-1.5720	0.1159
	Log(Area)	3.9775	1.3038	3.0510	0.0023
	Climate (PC1)	0.8730	0.4605	1.8960	0.0580
	Log(AGR500)	-0.3243	0.1917	-1.6920	0.0907
	FOREST(500)	-0.0340	0.0140	-2.4210	0.0155
Bromus diandrus	Intercept	-0.8317	7.2261	-0.1150	0.9084
	Island	-15.8178	7.8349	-2.0190	0.0435
	Log(Area)	4.9296	1.6137	3.0550	0.0023
	Climate (PC1)	2.1835	0.7666	2.8480	0.0044
	Log(AGR500)	0.6136	0.3026	2.0280	0.0426
	FOREST(500)	-0.1156	0.0400	-2.8920	0.0038
	GOE(500)	0.8476	0.3480	2.4350	0.0149
	Log(RD500)	-5.5154	2.3948	-2.3030	0.0213
Vulpia bromoides	Intercept	-8.6000	4.2740	-2.0120	0.0442
	Log(Area)	2.7090	1.1190	2.4200	0.0155
Cytisus scoparius	Intercept	-17.1567	7.3308	-2.3400	0.0193
	DP(q/s)	-2.2125	1.4651	-1.5100	0.1310
	Log(Area)	3.4726	1.7288	2.0090	0.0446
	Climate (PC1)	1.7521	0.7938	2.2070	0.0273
	FOREST(500)	0.0506	0.0338	1.4960	0.1348
	GOE(500)	0.4915	0.2822	1.7420	0.0816

		B$_1$	SE	Z	P
	Log(RD500)	1.4085	0.5699	2.4720	0.0134
Stellaria media	Intercept	2.6150	0.5981	4.3720	0.0000
	Island	-1.6217	0.7034	-2.3060	0.0211
Bromus hordeaceus	Intercept	-7.0199	4.2293	-1.6600	0.0970
	Island	-1.2599	0.8625	-1.4610	0.1441
	Log(Area)	2.3804	1.0504	2.2660	0.0234
	Climate (PC1)	1.6177	0.4952	3.2660	0.0011
	GOE(500)	0.3319	0.2002	1.6580	0.0973
Bromus sterilis	Intercept	-6.1447	3.1885	-1.9270	0.0540
	Island	-1.3903	0.6104	-2.2780	0.0227
	Log(Area)	2.0046	0.7945	2.5230	0.0116
Geranium molle	Intercept	1.9221	0.3843	5.0020	0.0000
	Climate (PC1)	0.9796	0.3480	2.8150	0.0049
Dactylis glomerata	Intercept	2.8277	1.2709	2.2250	0.0261
	Island	-3.2137	1.2483	-2.5740	0.0100
	DP(q/s)	1.2932	0.6535	1.9790	0.0478
	Log(AGR500)	0.3849	0.2049	1.8780	0.0603
	FOREST(500)	-0.0326	0.0168	-1.9420	0.0521
Vicia hirsuta	Intercept	0.6910	0.3988	1.7320	0.0832
	Island	-1.1671	0.5136	-2.2720	0.0231
	DP(q/s)	1.6589	0.6215	2.6690	0.0076
Veronica arvensis	Intercept	-0.5848	0.3417	-1.7120	0.0870
	DP(q/s)	2.1746	0.8151	2.6680	0.0076
	FOREST(500)	0.0320	0.0136	2.3560	0.0185
Cynosurus echinatus	Intercept	0.4460	0.3514	1.2690	0.2044
	Climate (PC1)	-0.6626	0.2977	-2.2260	0.0260
	Log(RD500)	0.4413	0.1649	2.6760	0.0075
Myosotis discolor	Intercept	-4.8965	3.1102	-1.5740	0.1154
	Island	-1.7570	0.7340	-2.3940	0.0167
	DP(q/s)	1.9255	0.7564	2.5460	0.0109
	Log(Area)	1.2820	0.7235	1.7720	0.0764
	FOREST(500)	0.0245	0.0185	1.3270	0.1846
Poa pratensis	Intercept	1.7261	0.8056	2.1430	0.0322
	Island	-2.1841	0.8508	-2.5670	0.0103
	DP(q/s)	1.9374	0.8553	2.2650	0.0235

		B_1	SE	Z	P
	Log(AGR500)	0.4403	0.2602	1.6920	0.0907
Aphanes arvensis/australis	Intercept	-2.8154	2.4906	-1.1300	0.2583
	Log(Area)	1.1138	0.6332	1.7590	0.0786
	Log(RD500)	-0.6839	0.1674	-4.0850	0.0000

Table A.12.5: Overfit (initial minus bootstrap-corrected AUC) and bootstrap-corrected AUC for intra-patch scale models of native species.

	Model Type*	Overfit	Corrected AUC
Camassia leichtlinii	MXSP	0.019	0.89
Festuca rubra	MXSP	0.029	0.89
Brodiaea coronaria	MXLR	0.145	0.66
Galium aparine	MXSP	0.018	0.83
Camassia quamash	MXAIC/LR	0.121	0.72
Brodiaea hyacinthina	MXSP	0.010	0.81
Achillea millefolium	MXSP	0.058	0.83
Sanicula crassicaulis	MXLR	0.126	0.75
Plectritis congesta	MXSP	0.083	0.80
Elymus glaucus	MXSP	0.114	0.72
Collinsia parviflora	MXAIC	0.005	0.76
Polypodium glycyrrhiza	MXSP	0.009	0.88
Luzula multiflora	MXSP	0.001	0.77
Cerastium arvense	MXLR	0.106	0.73
Lotus micranthus	MXAIC	0.068	0.76
Ranunculus occidentalis	MXAIC	0.175	0.69
Danthonia californica	MXAIC	0.038	0.84
Carex inops	MXLR	0.057	0.89
Trifolium willdenowii	MXAIC/LR	0.116	0.71
Lomatium utriculatum	MXSP	Na	Na

*Model Type: AIC = non-spatial, AIC selected; MXAIC = non-spatial mixed model, AIC-selected; MXLR = non-spatial mixed model, LR test selected; MXAIC/LR = both MXAIC and MXLR are identical; MXSP = spatial mixed model

Table A.12.6: Overfit (initial minus bootstrap-corrected AUC) and bootstrap-corrected AUC for intra-patch scale models of exotic species.

	Model Type	Overfit	Corrected AUC
Aira praecox	MXSP	0.039	0.83
Hypochaeris radicata	MXAIC/LR	0.148	0.65
Anthoxanthum odoratum	MXSP	0.184	0.78
Rumex acetosella	MXSP	0.011	0.82
Vicia sativa	MXSP	0.038	0.82
Holcus lanatus	MXAIC/LR	0.111	0.74
Bromus diandrus	MXSP	0.041	0.82
Vulpia bromoides	MXSP	Na	Na
Cytisus scoparius	MXAIC	0.077	0.78
Stellaria media	MXLR	0.139	0.68
Bromus hordeaceus	MXLR	0.137	0.64
Bromus sterilis	MXSP	0.035	0.82
Geranium molle	MXSP	0.031	0.83
Dactylis glomerata	MXSP	0.035	0.87
Vicia hirsuta	MXLR	0.186	0.68
Veronica arvensis	MXAIC	0.151	0.65
Cynosurus echinatus	MXSP	0.018	0.90
Myosotis discolor	MXSP	0.009	0.86
Poa pratensis	MXLR	0.150	0.74
Aphanes arvensis/australis	AIC	0.013	0.73

Table A.12.7: Terms from final native species distribution models at the intra-patch scale

		B_1	SE	t	P
Camassia leichtlinii	Intercept	-8.2110	3.8625	-2.1258	0.0341
	Island	16.7377	3.9661	4.2202	0.0001
	Litter	-0.0329	0.0094	-3.4802	0.0006
	Log(Area)	-1.7043	0.4668	-3.6508	0.0003
	Log(RD500)	3.9645	1.0287	3.8539	0.0003
Festuca rubra	Intercept	-1.7658	0.6817	-2.5901	0.0099
	Northness	0.2615	0.1468	1.7811	0.0756
	Island	2.3489	0.3848	6.1045	0.0000
	Log(Soil Depth)	-0.5339	0.2985	-1.7890	0.0743
	Canopy Openness	0.0109	0.0058	1.8685	0.0624
	Log(AGR500)	-0.3498	0.1013	-3.4536	0.0009
Brodiaea coronaria	Intercept	-0.1219	0.7558	-0.1610	0.8718
	Island	-2.8507	0.6966	-4.0920	0.0000
	Canopy Openness	0.0187	0.0054	3.4760	0.0005
	Log(RD500)	-0.4581	0.1897	-2.4150	0.0157
Galium aparine	Intercept	0.2303	0.5829	0.3951	0.6929
	Log(Soil Depth)	1.1669	0.2727	4.2795	0.0000
	Canopy Openness	-0.0319	0.0049	-6.5569	0.0000
	FOREST(500)	0.0000	0.0000	4.0369	0.0001
Camassia quamash	Intercept	-3.2710	0.7066	-4.6280	0.0000
	Slope	-0.0429	0.0153	-2.8030	0.0051
	Canopy Openness	0.0199	0.0064	3.1300	0.0017
	GOE(500)	0.0000	0.0000	2.1490	0.0317
	Log(RD500)	0.4993	0.1423	3.5080	0.0005
Brodiaea hyacinthina	Intercept	-0.5343	0.3013	-1.7734	0.0769
	Litter	-0.0259	0.0093	-2.7945	0.0054
	FOREST(500)	0.0000	0.0000	3.9369	0.0002

		B_1	SE	t	P
Achillea millefolium	Intercept	0.5562	1.9198	0.2897	0.7721
	Island	1.0870	0.4060	2.6777	0.0091
	Log(Soil Depth)	1.0176	0.2993	3.4003	0.0007
	Canopy Openness	0.0141	0.0056	2.5324	0.0116
	Log(Area)	-1.0441	0.4445	-2.3492	0.0192
	Climate (PC1)	-0.5529	0.1936	-2.8560	0.0045
	Log(AGR500)	-0.2638	0.1039	-2.5390	0.0132
Sanicula crassicaulis	Intercept	-0.7514	0.6662	-1.1280	0.2594
	Log(Soil Depth)	1.9831	0.3457	5.7360	0.0000
	Canopy Openness	-0.0331	0.0056	-5.8780	0.0000
	Climate (PC1)	-0.4153	0.1711	-2.4280	0.0152
Plectritis congesta	Intercept	3.6146	1.8407	1.9637	0.0502
	Litter	-0.0390	0.0098	-3.9599	0.0001
	Slope	0.0438	0.0146	2.9976	0.0029
	Log(Area)	-0.9905	0.4474	-2.2136	0.0274
	Climate (PC1)	-0.7337	0.2116	-3.4681	0.0006
Collinsia parviflora	Intercept	-2.8450	0.8617	-3.3010	0.0010
	Island	0.9518	0.3994	2.3830	0.0172
	Litter	-0.0248	0.0112	-2.2120	0.0270
	Log(Soil Depth)	-0.7136	0.3234	-2.2070	0.0273
	Slope	0.0227	0.0145	1.5700	0.1165
	Canopy Openness	0.0204	0.0070	2.9120	0.0036
	FOREST(500)	0.0000	0.0000	2.7790	0.0054
Elymus glaucus	Intercept	-0.8608	0.5587	-1.5408	0.1241
	Log(Soil Depth)	1.1672	0.2899	4.0262	0.0001
	Slope	0.0322	0.0125	2.5828	0.0101
	Canopy Openness	-0.0229	0.0046	-5.0278	0.0000

		B_1	SE	t	P
	Climate (PC1)	0.2321	0.1160	2.0014	0.0459
Polypodium glycyrrhiza	Intercept	0.0101	0.6540	0.0155	0.9876
	Log(Soil Depth)	-0.8027	0.2849	-2.8180	0.0050
	Slope	0.0483	0.0130	3.7311	0.0002
	Canopy Openness	-0.0150	0.0056	-2.6758	0.0077
	Climate (PC1)	0.5578	0.2021	2.7598	0.0060
Luzula multiflora	Intercept	-2.5572	0.4129	-6.1935	0.0000
	Log(Soil Depth)	1.3129	0.3222	4.0754	0.0001
	Climate (PC1)	-0.3380	0.1334	-2.5330	0.0117
	Log(AGR500)	-0.3254	0.0790	-4.1184	0.0001
Cerastium arvense	Intercept	0.8108	1.6942	0.4780	0.6323
	Canopy Openness	0.0174	0.0074	2.3650	0.0180
	Log(Area)	-0.8271	0.3905	-2.1180	0.0342
	Log(AGR500)	-0.2138	0.1007	-2.1230	0.0337
	Log(RD500)	-0.3461	0.1131	-3.0600	0.0022
Lotus micranthus	Intercept	-0.5999	2.0430	-0.2940	0.7691
	Log(Soil Depth)	0.9460	0.4175	2.2660	0.0234
	Slope	-0.0349	0.0194	-1.7990	0.0720
	Canopy Openness	0.0137	0.0073	1.8710	0.0613
	Log(Area)	-0.8310	0.4829	-1.7210	0.0853
	Climate (PC1)	-0.7411	0.2046	-3.6220	0.0003
	FOREST(500)	0.0000	0.0000	2.6230	0.0087
	GOE(500)	0.0000	0.0000	2.9000	0.0037
Ranunculus occidentalis	Intercept	5.3453	2.1002	2.5450	0.0109
	Eastness	-0.3121	0.2132	-1.4630	0.1434
	Litter	-0.0266	0.0146	-1.8280	0.0676
	Log(Soil	0.8598	0.4484	1.9170	0.0552

		B_1	SE	t	P
	Depth)				
	Slope	-0.0617	0.0263	-2.3480	0.0189
	Canopy Openness	-0.0116	0.0070	-1.6510	0.0988
	Log(Area)	-1.4490	0.4832	-2.9990	0.0027
	Climate (PC1)	-0.4603	0.1937	-2.3770	0.0175
Danthonia californica	Intercept	-0.5599	2.1000	-0.2670	0.7898
	DP(q/s)	-1.1480	0.4330	-2.6520	0.0080
	Log(Soil Depth)	1.0160	0.4592	2.2120	0.0270
	Log(Area)	-0.7650	0.4721	-1.6200	0.1051
	Climate (PC1)	-1.2860	0.2962	-4.3420	0.0000
	Log(AGR500)	-0.1958	0.1253	-1.5630	0.1182
	FOREST(500)	0.0000	0.0000	2.7610	0.0058
	GOE(500)	0.0000	0.0000	2.9090	0.0036
Carex inops	Intercept	-5.3518	0.9772	-5.4760	0.0000
	Island	-3.1332	0.6973	-4.4930	0.0000
	Log(Soil Depth)	4.0235	0.7053	5.7050	0.0000
	Climate (PC1)	-1.1847	0.3543	-3.3440	0.0008
	Log(AGR500)	-0.6302	0.1594	-3.9540	0.0001
Trifolium willdenowii	Intercept	-7.5890	1.3840	-5.4830	0.0000
	Eastness	-0.4173	0.2055	-2.0300	0.0423
	Island	1.7850	0.5749	3.1050	0.0019
	Canopy Openness	0.0460	0.0132	3.4780	0.0005
	FOREST(500)	0.0000	0.0000	2.9520	0.0032
Lomatium utriculatum	Intercept	-1.4407	0.2679	-5.3785	0.0000

Table A.12.8: Terms from final exotic species distribution models at the intra-patch scale

		B$_1$	SE	t	P
Aira praecox	Intercept	-4.2881	1.3976	-3.0681	0.0023
	DP(q/s)	0.6724	0.2887	2.3293	0.0224
	Log(Soil Depth)	-2.6221	0.2989	-8.7725	0.0000
	Slope	-0.0299	0.0135	-2.2106	0.0275
	Canopy Openness	0.0389	0.0060	6.4807	0.0000
	Log(Area)	0.7705	0.3115	2.4735	0.0137
	GOE(500)	0.0000	0.0000	2.2402	0.0279
Hypochaeris radicata	Intercept	-2.7061	1.3249	-2.0430	0.0411
	Island	-0.9944	0.3037	-3.2740	0.0011
	Litter	-0.0273	0.0092	-2.9660	0.0030
	Log(Soil Depth)	-0.6316	0.2682	-2.3550	0.0185
	Canopy Openness	0.0240	0.0055	4.3950	0.0000
	Log(Area)	0.6147	0.2970	2.0700	0.0385
	Climate (PC1)	0.3478	0.1368	2.5430	0.0110
	Log(AGR500)	-0.2735	0.0734	-3.7270	0.0002
Anthoxanthum odoratum	Intercept	8.6509	3.6552	2.3667	0.0185
	Northness	0.4028	0.1738	2.3183	0.0210
	Canopy Openness	0.0263	0.0078	3.3901	0.0008
	Log(Area)	-3.2958	0.9069	-3.6342	0.0003
	FOREST(500)	0.0000	0.0000	2.3022	0.0252
	Log(RD500)	0.7224	0.2289	3.1561	0.0026
Rumex acetosella	Intercept	-3.8610	0.5751	-6.7142	0.0000
	Island	-1.0397	0.2771	-3.7527	0.0003
	DP(q/s)	0.9024	0.2708	3.3326	0.0013
	Canopy Openness	0.0317	0.0060	5.2929	0.0000
	Climate (PC1)	0.4818	0.1389	3.4694	0.0006

		B_1	SE	t	P
Vicia sativa	Intercept	-2.9030	0.4092	-7.0951	0.0000
	Log(Soil Depth)	1.6947	0.3091	5.4824	0.0000
Holcus lanatus	Intercept	-0.6036	0.2226	-2.7120	0.0067
	Climate (PC1)	-0.6646	0.1703	-3.9040	0.0001
	Log(RD500)	-0.3986	0.1018	-3.9160	0.0001
Bromus diandrus	Intercept	-3.8376	0.7600	-5.0494	0.0000
	Northness	-0.3318	0.1576	-2.1051	0.0359
	Island	0.7936	0.3992	1.9882	0.0516
	DP(q/s)	0.8304	0.4084	2.0332	0.0467
	Canopy Openness	0.0237	0.0073	3.2377	0.0013
	Climate (PC1)	0.4610	0.2084	2.2120	0.0276
Vulpia bromoides	Intercept	-1.0782	0.1388	-7.7675	0.0000
Cytisus scoparius	Intercept	-3.4450	0.5941	-5.7980	0.0000
	Canopy Openness	0.0148	0.0063	2.3410	0.0192
	Climate (PC1)	0.8599	0.2360	3.6440	0.0003
	Log(AGR500)	0.1879	0.0691	2.7190	0.0066
	FOREST(500)	0.0000	0.0000	3.3030	0.0010
	GOE(500)	0.0000	0.0000	1.7320	0.0833
Stellaria media	Intercept	-3.5254	0.4430	-7.9590	0.0000
	Log(Soil Depth)	1.5104	0.3186	4.7410	0.0000
	Climate (PC1)	0.2598	0.1566	1.6590	0.0970
	Log(RD500)	0.2574	0.0850	3.0270	0.0025
Bromus hordeaceus	Intercept	-1.3280	0.7842	-1.6930	0.0905
	Island	-1.7920	0.6325	-2.8330	0.0046
	Canopy Openness	0.0220	0.0064	3.4190	0.0006
	GOE(500)	0.0000	0.0000	-2.3880	0.0169
	Log(RD500)	-0.3564	0.1674	-2.1290	0.0333
Bromus sterilis	Intercept	-2.8886	0.4271	-6.7638	0.0000
	Log(Soil Depth)	0.8377	0.2800	2.9923	0.0029

		B_1	SE	t	P
	Log(RD500)	0.3138	0.0957	3.2806	0.0017
Geranium molle	Intercept	0.0002	0.8774	0.0002	0.9998
	Island	-2.1357	0.8397	-2.5436	0.0133
	DP(q/s)	0.9284	0.3588	2.5874	0.0118
	Litter	-0.0328	0.0110	-2.9738	0.0031
	Log(Soil Depth)	0.8358	0.3136	2.6651	0.0080
	Log(RD500)	-0.5066	0.2294	-2.2085	0.0306
Dactylis glomerata	Intercept	-1.7701	0.7011	-2.5247	0.0120
	Log(Soil Depth)	1.9615	0.3490	5.6201	0.0000
	Canopy Openness	-0.0288	0.0059	-4.8439	0.0000
	Climate (PC1)	0.9942	0.2255	4.4081	0.0000
Vicia hirsuta	Intercept	-2.2525	0.8213	-2.7420	0.0061
	Log(Soil Depth)	1.7725	0.4141	4.2800	0.0000
	Canopy Openness	-0.0155	0.0066	-2.3540	0.0186
Veronica arvensis	Intercept	-0.3438	0.8175	-0.4210	0.6740
	Island	-3.0767	0.8478	-3.6290	0.0003
	DP(q/s)	0.5454	0.3301	1.6530	0.0984
	Litter	-0.0405	0.0134	-3.0120	0.0026
	Log(Soil Depth)	1.8413	0.3965	4.6440	0.0000
	Climate (PC1)	0.3050	0.1986	1.5360	0.1247
	Log(RD500)	-0.6210	0.2171	-2.8610	0.0042
Cynosurus echinatus	Intercept	-2.2756	0.2392	-9.5145	0.0000
	Northness	-0.3453	0.1697	-2.0347	0.0425
	Climate (PC1)	-0.9575	0.2258	-4.2397	0.0000
Myosotis discolor	Intercept	0.3246	2.0422	0.1590	0.8738
	DP(q/s)	-0.9982	0.3919	-2.5474	0.0140
	Litter	-0.0308	0.0150	-2.0588	0.0403
	Log(Soil	2.6451	0.4839	5.4659	0.0000

		B_1	SE	t	P
	Depth)				
	Canopy Openness	0.0220	0.0080	2.7387	0.0065
	Log(Area)	-1.3528	0.4551	-2.9726	0.0032
	FOREST(500)	0.0000	0.0000	4.4177	0.0001
	Log(RD500)	-0.3284	0.1233	-2.6640	0.0104
Poa pratensis	Intercept	-3.8757	0.9846	-3.9360	0.0001
	Log(Soil Depth)	2.4625	0.5054	4.8720	0.0000
	Canopy Openness	-0.0176	0.0074	-2.3720	0.0177
Aphanes arvensis/australis	Intercept	1.7111	2.0227	0.8460	0.3976
	Island	-1.1067	0.4167	-2.6560	0.0079
	DP(q/s)	0.7988	0.3409	2.3430	0.0191
	Litter	-0.0212	0.0136	-1.5560	0.1196
	Canopy Openness	0.0334	0.0117	2.8490	0.0044
	Log(Area)	-1.4198	0.4345	-3.2680	0.0011
	Log(AGR500)	0.1246	0.0791	1.5770	0.1149

Appendix 13: Richness model results

Table A.13.1: AIC-selected variables from species richness models at the inter-patch scale

Native	B_1	SE	t	P
Forest Area (ha; 500 m buffer)	0.00122	0.000463	2.647	0.0099
Log Road Length (m; 500 m buffer)	-0.0238	0.00851	-2.802	0.0064
Log Patch Area (m^2)	0.127	0.0248	5.122	<0.0001
Climate (PC1)	-0.0256	0.0153	-1.668	0.0994
Exotic	B_1	SE	t	P
Island	-0.211	0.0374	-5.629	<0.0001
Log Agricultural Area (500 m buffer)	0.0127	0.00742	1.71	0.0914
Forest Area (ha; 500 m buffer)	-0.0027	0.000507	-5.331	<0.0001
Log Patch Area (m^2)	0.177	0.0273	6.474	<0.0001
Climate (PC1)	0.0256	0.0144	1.784	0.0784

Table A.13.2: AIC-selected variables from species richness models at the intra-patch scale

Native	B_1	SE	T	P
Island	1.579	0.815	1.938	0.0561
Litter (% cover)	-0.0322	0.0127	-2.532	0.0116
Log Soil Depth (cm)	2.187	0.389	5.625	<0.0001
Slope (degrees)	0.0391	0.019	2.0503	0.0408
Canopy Openness (%)	-0.0239	0.00752	-3.183	0.0015
Log Patch Area (m^2)	-1.0957	0.648	-1.692	0.0913
Climate (PC1)	-0.44	0.294	-1.494	0.136
Log Agricultural Area (ha; 500 m buffer)	-0.226	0.156	-1.448	0.151
Forest Area (ha; 500 m buffer)	0.03	0.011	3.0151	0.0034
Exotic	B_1	SE	T	P
Island	-3.576	1.162	-3.077	0.0028
Litter (% cover)	-0.0333	0.0103	-3.219	0.0014
Log Soil Depth (cm)	1.172	0.313	3.741	0.0002
Canopy Openness (%)	0.0239	0.00614	3.886	0.0001
Deer Pellets in ≥1 Quadrat/Patch	1.0535	0.451	2.335	0.022
Climate (PC1)	0.356	0.226	1.575	0.116
Log Road Length (m; 500 m buffer)	-0.547	0.325	-1.682	0.0964

Appendix 14: Species at risk

Table A.14.1: Federally- and provincially-recognized species at risk found in study sites

	COSEWIC	BC Red/Blue[1]
Allium amplectens		Blue
Allium geyeri		Blue
Aster curtus		Red
Balsamorhiza deltoidea	Endangered	Red
Callitriche heterophylla		Blue
Castilleja victoriae	Endangered	Red
Clarkia amoena		Blue
Hutchinsia procumbens		Blue
Juncus arcticus ssp. *alaskanus*[2]		Blue
Lomatium dissectum		Red
Lotus cf. *formosissimus*	Endangered	Red
Lupinus densiflorus var. *densiflorus*	Endangered	Red
Melica harfordii		Blue
Ranunculus californicus	Endangered	Red
Sanicula arctopoides	Endangered	Red
Sanicula bipinnatifida	Threatened	Red
Silene scouleri ssp. *grandis*	Endangered	Red
Thysanocarpus curvipes		Blue
Trifolium depauperatum		Blue
Triteleia howellii	Endangered	Red
Viola howellii		Blue
Viola praemorsa spp. praemorsa	Endangered	Red
Yabea microcarpa		Red

Notes:

1 - British Columbia species at risk designations: blue = 'special concern', or sensitive to declines due to human or environmental factors; red = 'endangered' or 'threatened' with extinction. For further details, see http://www.env.gov.bc.ca/atrisk/red-blue.htm

2 – Taxonomy of this species is uncertain. Specimens were not collected (because of subspecies status). Field observations indicate a strong possibility that observations were ssp. *alaskanus*.

Appendix 15: Tables for conservation applications of models

Table A.15.1: Native species that were false positives for Colville Island

Species	Predicted Probability of Occurrence
Camassia leichtlinii	99%
Brodiaea hyacinthina	63%
Achillea millefolium	99%
Plectritis congesta	82%
Elymus glaucus	93%
Luzula multiflora	99%
Cerastium arvense	99%
Ranunculus occidentalis	56%
Trifolium willdenowii	93%

Table A.15.2: Predicted native richness – Colville Island

Predicted log richness	Lower 95% confidence interval	Upper 95% confidence interval	Real log richness	Back-transformed predicted	Back-transformed real richness	P
1.7326	1.6625	1.8332	1.4150	26	54	<0.001

NOTE: Confidence intervals and P-values are based on ordered bootstrap replicates

Table A.15.3: Exotic species that were false positives for Mount Wells Regional Park patch

Species	Predicted Probability of Occurrence
Holcus lanatus	81%
Bromus sterilis	94%
Vicia hirsuta	67%
Veronica arvensis	92%
Myosotis discolor	75%
Poa pratensis	84%
Aphanes arvensis/australis	55%

Table A.15.4: Predicted exotic richness – Mount Wells Regional Park patch

Predicted log richness	Lower 95% confidence interval	Upper 95% confidence interval	Real log richness	Back-transformed predicted	Back-transformed real richness	P
1.4322	1.3139	1.4803	1.2788	27.0536	19	0.005