

**DETERMINANTS OF NATIVE AND EXOTIC PLANT DIVERSITY
AND COMPOSITION IN REMNANT OAK SAVANNAS ON
SOUTHEASTERN VANCOUVER ISLAND**

by

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Abstract

Many regional and local factors can influence the distribution of native and exotic species in ecological communities. I examined the regional- and local-scale determinants of native and exotic vascular plant species richness and composition in a highly fragmented oak savanna ecosystem on southeastern Vancouver Island. In sharp contrast to most reported results, I found a negative relationship between native and exotic richness at the regional scale, and no relationship at the local scale. Two extrinsic factors, surrounding road density and climate, best explained the regional-scale relationship by each affecting natives and exotics in opposite ways. Road density and climate were also the dominant predictors of native and exotic composition at the regional scale. Patterns in the patch occupancy of individual species confirmed the importance of these factors but I found that low surrounding road densities and cool, wet conditions predicted the presence of many natives and the absence of many exotics. Environmental factors explained variation in richness and composition at the local scale, but these factors were different for natives and exotics. My results suggest that natives and exotics respond to roads and climate in fundamentally different ways. Roads increase both exotic propagule pressure and disturbance, which may facilitate exotic invasion. In contrast, disturbance from roads may increase the likelihood of local extinction for particular natives. Differing climatic preferences within the native and exotic species pools may also partially explain the observed patterns. There was no evidence that native diversity directly affects exotic diversity (or vice versa). Surprisingly, I found that connectivity was not an important predictor of richness or composition despite the high degree of habitat fragmentation in this ecosystem.

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1 Introduction

Modern community ecology is the study of patterns in the distribution and abundance of species and the processes that produce and maintain these patterns (Morin 1999). In many communities, observed species distribution patterns vary with spatial scale, which suggests that different processes may be at work at different scales (Levin 1992, Rosenzweig 1995). While local environmental conditions and interactions between species (e.g., competition, predation, facilitation) have long been recognized as important determinants of species found at a given location (Huston 1979, Ricklefs 1987), there has been a recent recognition that regional processes, historical events, and geographical circumstances may interact with these local processes to determine distributions of species (Ricklefs and Schluter 1993, Cottenie et al. 2003). In plant communities, for example, habitat fragmentation and disturbance due to human development can influence the dispersal, establishment, and persistence of species in local remnant communities. Despite their importance to biodiversity conservation, the relative influence of these regional and local factors on species distributions at different scales is not well-studied in many landscapes.

Species introduced by humans outside their native range are widely seen as a threat to the persistence of native biodiversity (Wilcove et al. 1998). In many locations, assemblages of exotic species are a significant component of the diversity in the ecosystems they have invaded (Qian and Ricklefs 2006). While the evidence of exotics causing native extinctions is infrequent and equivocal in some cases (Gurevitch and Padilla 2004), exotic species are undoubtedly increasing “biotic homogenization” among ecosystems (Lockwood and McKinney 2001, Rooney et al. 2004). Understanding the

success of exotic species and what makes habitats more or less “invasible”, or susceptible to invasions, is essential to minimizing their impacts (Lonsdale 1999).

There is a growing movement to use community ecology as a framework for studying biological invasions (Shea and Chesson 2002). So far, research on invasive species has taken many varied approaches, studying the biogeographical spread of exotic species (di Castri 1989, Mack et al. 2000), the life history traits of invaders (Rejmanek and Richardson 1996, Goodwin et al. 1999), characteristics of the resident community (Tilman 1997, Levine and D’Antonio 1999), and factors in the receiving environment (Richardson and Bond 1991, Milberg et al. 1999). However, research questions about native species and introduced species are often similar, such as “how do species map onto their environment?” and “what traits make species more or less susceptible to the effects of disturbance?” It is important to recognize similarities in the potential determinants of the distribution and abundance of native and exotic species (Thompson et al. 1995). While we often lack before and after data to directly study how exotic species alter communities in natural landscapes, understanding current co-occurrence patterns of natives and exotics can help to elucidate whether the processes determining patterns of native diversity and exotic success are similar or different. Integrating invasion research into community ecology will help in this regard. Invasions also represent large-scale opportunities to study fundamental questions in community ecology that would not be otherwise feasible (Sax et al. 2007).

Resident species diversity or richness is one characteristic of a community that has been proposed to increase resistance to invasion from new species (Elton 1958, Tilman 2004). Studies showing how native species richness (the number of species)

affects the invasibility of communities to exotic species have sought to characterize the relationship between native and exotic richness. Experiments and observations at small scales have largely found negative relationships between native and exotic richness, supporting the hypothesis that communities with more species are often less invaded (Tilman 1997, Stachowicz et al. 2002). In contrast, in many ecosystems, positive relationships have been observed at large scales between native and exotic richness and the hotspots of native diversity are often those most invaded by exotic species (Stohlgren et al. 1999, Lonsdale 1999, Sax 2002, Brown and Peet 2003). To resolve this apparent paradox, several authors have suggested that the relationship between native and exotic species is scale-dependent (Levine and D'Antonio 1999, Fridley et al. 2007). Negative relationships are expected at the scale where individual plants interact and compete for limited resources, such as 1-m² plots (Tilman 2004). In contrast, positive relationships will arise at large scales (e.g., across landscapes > 100 km²) because the same extrinsic factors that favour native species, such as overall resource availability (Shea and Chesson 2002) or heterogeneity (Davies et al. 2005), also favour invasion success. There is a need to test this scale-dependence in the relationship between natives and exotics across a wider variety of extrinsic conditions.

While resident diversity may play a role in limiting invasion at small scales, many extrinsic factors can also determine the species diversity and composition of native and exotic plant communities. Local environmental or abiotic conditions that influence the availability of resources such as light, nutrients, moisture, and space place limits on the species that can inhabit a particular location. These resource gradients mediate competitive interactions and often lead to the separation of species into distinct niches as

they map onto available environmental conditions in different ways (Leibold et al. 2004). In this view of the local environment as the dominant determinant of species distributions, dispersal allows species to move to suitable environments when local conditions change (Leibold et al. 2004).

In a regional context, habitat is heterogeneous and dispersal is often spatially limited (Foster and Tilman 2003). For example, in order for a plant species to inhabit a given site, seeds (or other propagules) must arrive at that site via dispersal and find suitable conditions to be able to establish and maintain a viable population that can avoid going extinct. In developing landscapes around the world, human land use patterns are converting natural ecosystems to fragmented networks of discrete habitat patches (Fahrig 2003, Vellend 2003). When habitat is fragmented, connectivity between habitat patches is often reduced and seed dispersal between patches becomes less frequent (Dupre and Ehrlen 2002). This is because the probability of seed dispersal between patches decreases with increasing distance between patches. Likewise, the size of the remaining habitat patches can limit how many individuals make up a population and small populations are more vulnerable to stochastic extinction than large populations (Thomas 2000). Thus, both the spatial configuration and the size of the remaining fragments can limit dispersal and population sizes, influencing the relative frequencies of colonization and extinction among habitat patches (MacArthur and Wilson 1967, Hanski 1999, Bastin and Thomas 1999). However, species may be present at sites with habitat unsuitable to sustain a viable population (sink habitats) because of repeated and frequent immigration (Dias 1996) or because their habitat size has only recently decreased and the population has not yet had time to become extinct (Helm et al. 2006, Vellend et al. 2006). Species may also be

affected differently by connectivity and space based on individual traits they possess that may facilitate (or conversely, hinder) their dispersal or persistence abilities (Dupre and Ehrlén 2002, Verheyen et al. 2004).

The distribution and abundance of species within habitat patches can be affected by human influence from activities within the adjacent landscape matrix. Introductions of many exotic species (whether intentional or accidental) are facilitated by human activity (Lonsdale 1999, Duguay et al. 2007). Disturbance associated with human activity, such as fire suppression, can also alter natural disturbance regimes to which native species are well-adapted, leading to local extirpations (Hobbs and Huenneke 1992, Leach and Givnish 1996). Conversely, new human-mediated disturbance regimes can favour introduced species from ecosystems where human influence has been a regular part of the ecosystem on evolutionary time scales (di Castri 1989). Thus, spatial context, human influence, and local environmental conditions represent different filters capable of influencing species diversity and composition. Their relative importance will vary depending on the nature of the landscape, species characteristics, and spatial scale.

Plants in Garry oak (*Quercus garryana* Dougl. ex Hook.) ecosystems of southwestern British Columbia represent an ideal system for studying the relative importance of factors that influence the distribution and abundance of native and exotic species in plant communities. Garry oak plant communities, characterized by meadows of scattered Garry oak trees, forbs, grasses, and bryophytes, harbour more plant species than any other terrestrial ecosystem in coastal British Columbia (Ward et al. 1998). Since European settlement in the mid 19th century, oak savanna habitat has been altered and fragmented by development, agriculture, and forestry such that less than 10% of the

ecosystem remains in a near-natural state (Lea 2006). Remnant patches are distributed across a human influence gradient; land use around habitat patches ranges from urban development to second-growth coastal Douglas-fir (*Pseudotsuga menziesii* (Mirbel) Franco *var. menziesii*) forest. Garry oak ecosystems also include many exotic plant species, whose effects on the ecosystem are poorly understood (Roemer 1995). Understanding the relative importance of spatial context, human influence, and environmental factors is also of vital importance to conservation: sixty-one of the native plant species in Garry oak habitats are classified as ‘at risk’ of extinction in Canada, and twelve species are at risk globally (Fuchs 2001) .

Comparisons to historical accounts of Garry oak savannas show that contemporary plant communities are significantly altered (MacDougall et al. 2004). Exotic plants, particularly grasses, have invaded many of the remaining oak savanna habitat patches to varying degrees. Correlations between invasions by exotic species and declines in some native species point to possible competitive pressure from exotics, facilitated by the absence of low-intensity aboriginal burning (MacDougall and Turkington 2004). Increased herbivory from native deer populations and grazing by introduced livestock may also mediate these interactions by selectively impacting native plants and avoiding exotic grasses (Gonzales and Arcese, in preparation). Recent studies have found that seed production and subsequent dispersal by native species is limited by the strong competitive effects of exotic species on fecundity, thereby allowing exotic grasses to dominate (MacDougall and Turkington 2005). Many oak savanna species are poorly adapted for dispersal in fragmented landscapes. Therefore, regionally, effects of area and isolation may be expected for some of these dispersal-limited native species

(Dupre and Ehrlén 2002, Foster and Tilman 2003). Other disturbances, such as human trampling, may also mediate the apparent interactions between native and exotic species.

Historically, scientific research in Canadian Garry oak plant communities has focused largely on community classification (e.g., Roemer 1972, Erickson 1995) and rare species ecology. Recent experimental work has begun to look at some of the underlying processes determining vegetation communities at the local scale (MacDougall and Turkington 2004, 2005, 2006) and to characterize the role of disturbance (MacDougall 2005, MacDougall and Turkington 2007). Some of this work suggests that heterogeneity of environmental conditions, soil depth, soil moisture, nutrients, and availability of light are significant factors in determining the distribution of plant species (MacDougall et al. 2006). However, despite recognition of the relevance of spatial context in the conservation of this heavily fragmented ecosystem (Fuchs 2001), no community-level studies have looked at the relative importance of human influence, landscape context, and local conditions to plant communities across the landscape. Studying patches at the landscape scale is important to conservation efforts as this is the scale at which conservation in this ecosystem occurs.

My research investigated the relative influence of spatial context, human influence, and environmental conditions on vascular plant species distributions in remnant Garry oak savannas on southeastern Vancouver Island. To do this, I made empirical observations of the number, identity, and abundance of native and exotic vascular plant species in forty-three Garry oak habitat patches varying in their environmental characteristics (e.g., soil, light, and topography), human influence, and landscape context (e.g., patch size and connectivity) near Victoria, British Columbia,

Canada (48°26' N 123°22' W). These patches were distributed in parks and protected areas across a region extending approximately 40 km north to south and 25 km west to east (Fig. 1.1). I looked for the main predictors of native and exotic species *richness* (the number of species) and *composition* (the particular set of species and their abundances) at two different spatial scales - among remnant habitat patches (regional scale), and among small plots within a single habitat patch (local scale). I also looked at the predictors of the patch occupancy or presence-absence of individual species and whether plants are affected differently according to particular life history traits, such as dispersal mode and degree of habitat specialization, which may confer certain advantages in the face of habitat fragmentation or other conditions. All analyses examine whether exotic plant species show different responses to habitat factors than native species, which may indicate that exotics possess characteristics that facilitate their invasions or persistence abilities under certain conditions.

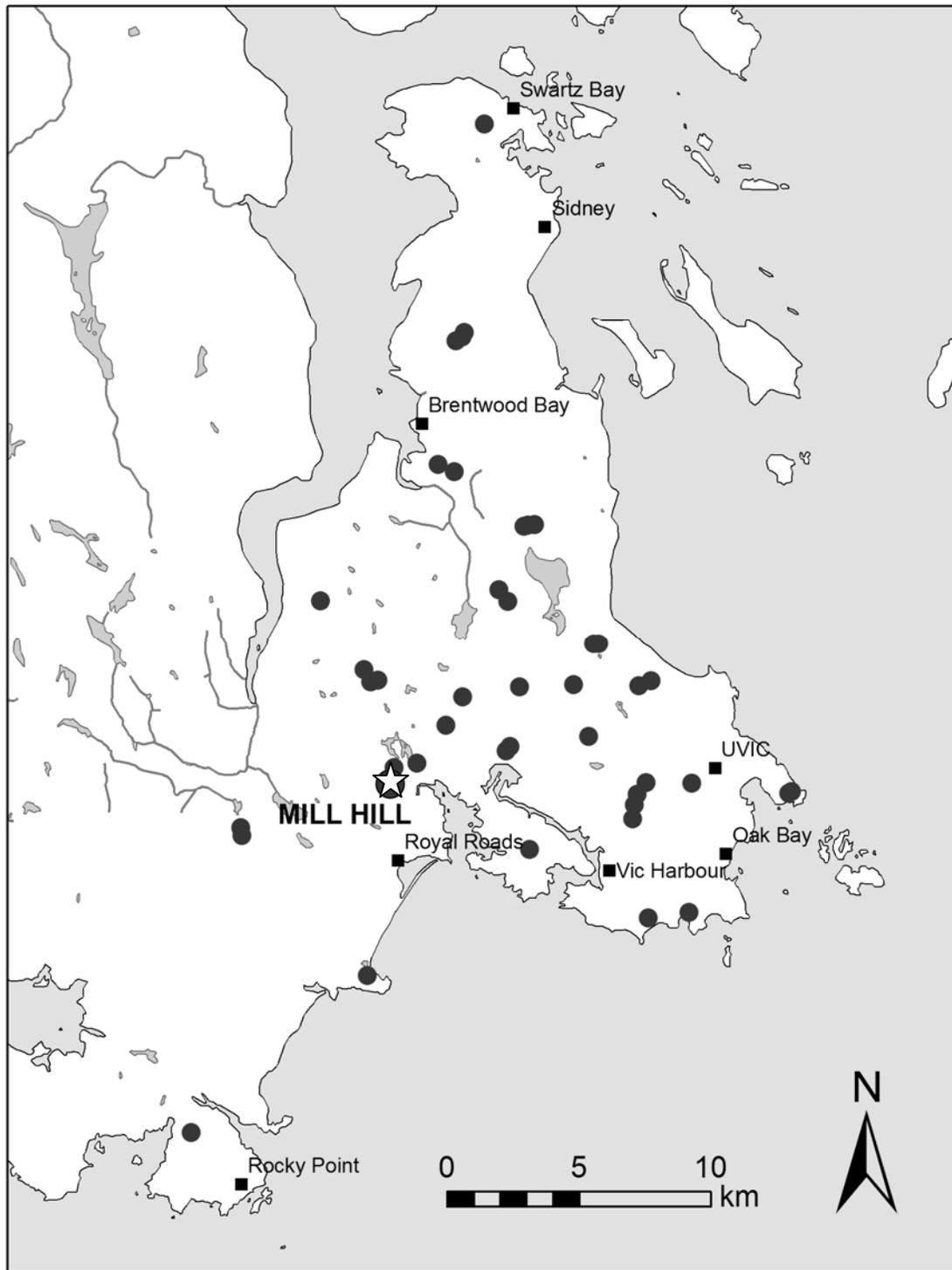
My data and analyses are presented in two parts, written as manuscripts. Species richness and composition are two fundamentally different metrics of how communities respond to their natural environments and human-induced change. Therefore, I look at patterns in richness and composition separately. Chapter 2 addresses the relationships between native and exotic species richness at regional and local spatial scales. By studying patterns in the number of native and exotic species, I determine whether the relationship between natives and exotics at each scale is best explained by a direct interaction between native and exotic richness or by similar (or different) responses to extrinsic factors at each scale. Chapter 3 focuses on similarities and differences in the patterns and predictors of native and exotic species composition and the predictors of

patch occupancy of individual species. Here, I also address whether simple life history traits can help to further explain patch occupancy patterns within the native and exotic species pools.

The goal of my analyses is to explore the mechanisms that drive native diversity and exotic success and to provide interesting new insights into the relative influences of regional processes on local biodiversity. Understanding the extent to which different factors determine plant distributions should help to establish their importance in conservation planning in this ecosystem and provide a basis for a quantitative predictive framework for identifying priority sites for conservation.

Figure 1.1. Map showing remnant oak savanna sampling sites around Victoria, British Columbia, Canada.

Patches sampled for the regional-scale study are denoted by the dark circles. Mill Hill Regional Park, site of the local-scale study (1-m² plot sampling), is denoted by the white star.



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2 Negative native-exotic diversity relationship in oak savannas explained by human influence and climate¹

2.1 Introduction

Community ecology theory suggests that native species diversity should increase a community's resistance to invasion from exotic species (Elton 1958). Higher numbers of native species should more efficiently use resources reducing those available to newly arrived exotics and thereby decreasing their probability of establishment (Tilman 2004). While such a mechanism would predict negative relationships between native and exotic species richness, empirical relationships observed in natural systems are often not negative (Levine and D'Antonio 1999). In fact, many diversity-invasibility studies have found that exotics disproportionately invade the hotspots of native diversity and native and exotic richness are positively correlated (e.g., Stohlgren et al. 1999). Several authors have proposed a scale dependence to both the direction and underlying causes of native-exotic richness relationships based on empirical observations at different scales within the same system (Levine 2000, Brown and Peet 2003) and across different systems (Fridley et al. 2007). At fine spatial scales where individuals interact (such as 1-m² plots), negative relationships are expected because the strength of competitive exclusion increases with diversity (Stachowicz et al. 2002) or because of statistical artifacts related to limits on numbers of organisms in small plots (Fridley et al. 2004). At broad spatial scales (e.g., landscapes >100 km²) extrinsic factors overwhelm such resistance effects and positive relationships are expected because native and exotic richness respond similarly to the same extrinsic factors (Levine 2000, Gilbert and Lechowicz 2005).

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While mechanisms for negative native-exotic richness relationships at fine scales are well-established, mechanisms behind the broad-scale positive relationships and the scale dependence are uncertain (Davies et al. 2007). So far, broad-scale positive relationships have been generally attributed to two different causes: (1) average environmental conditions at the site level that favour native diversity also favour invasion success (Shea and Chesson 2002) and (2) increased heterogeneity of conditions within sites favours both natives and exotics by allowing more species of both natives and exotics to coexist (Davies et al. 2005). However, should a positive relationship at broad scales be generally expected? Such a generality depends on an implicit assumption that the dominant extrinsic gradients favouring native richness will also favour exotic richness. Yet, given the lack of a shared evolutionary history of the native and exotic species pools, we might not expect a similar response across local environmental gradients that reflect differences in this history (c.f., Partel 2002). Furthermore, biogeographical and historical factors affecting regional processes can also be important determinants of richness patterns (Ricklefs and Schluter 1993) and may potentially impact native and exotic richness differently. To better understand native-exotic richness relationships, there is a need to examine the relative importance of a wider range of extrinsic factors capable of driving patterns of native and exotic species diversity at local (fine) and regional (broad) scales.

Extrinsic local and regional factors can filter species at three different life history stages: (1) dispersal, (2) establishment, and (3) persistence. Diversity-invasibility research to date has focused largely on how existing diversity, environment, and heterogeneity in the local receiving environment affects species establishment (e.g.,

Stohlgren et al. 1999, Davies et al. 2005). However, seed dispersal is often a limiting factor for local diversity (Tilman 1997), and in fragmented landscapes, the size and spatial arrangement of remnant habitat patches can affect species richness by influencing relative frequencies of arrival as well as extinction (MacArthur and Wilson 1967). While these biogeographical factors may affect natives and exotics similarly (Levine 2000), arrival of exotics is often a function of human activities influencing exotic propagule pressure (di Castri 1989). Conversely, human-mediated disturbance may affect native species negatively, increasing local extinctions (McIntyre and Lavorel 1994). These opposing effects of human influence could, in theory, result in a negative relationship between native and exotic richness at a broad scale. However, of the studies cited in support of the generality of positive broad-scale native-exotic richness relationships by Fridley et al. (2007), none examined how native and exotic richness vary across gradients of human influence.

Here we examine the regional-scale relationship between native and exotic plant species richness across a gradient of human influence in remnant patches of a fragmented oak savanna ecosystem in southwestern British Columbia, Canada. In sharp contrast to most reported broad-scale results, we found a negative native-exotic richness relationship at this scale, and no relationship at the local scale. We test for extrinsic drivers of native and exotic species richness, and whether the relationship between natives and exotics is best explained by those drivers or through a direct interaction between native and exotic richness.

2.2 Methods

The study was conducted in remnant patches of fragmented Garry oak (*Quercus*

garryana Dougl. ex Hook.) savanna habitat situated across a development gradient near Victoria, British Columbia, Canada (48°26' N 123°22' W), on southeastern Vancouver Island. This region is the northern range limit of a complex of oak prairies and woodlands extending from northern California to southwestern British Columbia (details given in Appendix A). To understand the drivers of native and exotic plant species richness among these oak savannas, we assessed the occurrence of native and exotic species in patches as well as a suite of potentially important extrinsic patch attributes representing spatial context, human influence, and environment.

We surveyed 43 habitat patches for their vascular plant diversity in 2006. Patches were selected to vary widely in their area (0.2-30 ha), isolation, surrounding land use, and environmental conditions. Transects, spaced 25 m apart and covering the entire patch area, were surveyed for species (forbs, grasses, shrubs and trees) twice, once in early spring (12 April – 5 June) and once in late spring/early summer (7 June – 27 July) to capture plants with early and later phenologies. Species origins (native, exotic, or unknown) were designated using the BC Species and Ecosystems Explorer (British Columbia Conservation Data Centre 2007).

Characterization of each patch included a number of geographical and environmental variables: patch area (used as a covariate), connectivity, surrounding road density (used as an index of human influence), slope, aspect (degrees from north), canopy cover, soil depth, variation (CV) in soil depth, soil pH, and climate (details in Appendix A). Connectivity was calculated as a distance-weighted sum of surrounding oak savanna patches. Surrounding road density was the length of roads per unit area in a 500 m buffer around each patch. We used the first axis of a principal components analysis (PCA) of

elevation and interpolated 1961-1990 climate normals for mean annual precipitation and temperature to represent “climate” in subsequent analyses. These variables were highly correlated ($|r| = 0.471-0.851$) and the first axis of the PCA explained 86.5% of the variation in the data. Full details of the sampling and GIS tools used are given in Appendix A.

To compare the regional results with species richness patterns at a local scale, we conducted a stratified-random survey of plots in our largest habitat patch (31.7 ha; see Appendix A), which is broadly representative of habitat patches across the region, and has a relatively high degree of environmental heterogeneity. Fifty-two 1-m² circular plots were surveyed for vascular plant species twice in 2006 (16-19 May and 5-6 July). Environmental variables measured at the local plot scale were similar to those measured in the regional survey (Appendix A).

STATISTICAL ANALYSES

We conducted four kinds of analyses. First, we calculated correlations and partial correlations (controlling for patch area) between native and exotic richness. Second, because of the high number of potential predictor variables, we used forward selection in generalized linear models (Poisson distribution, log link) to find the best extrinsic predictors of native and exotic richness. Third, we used information-theoretic model comparisons (Burnham and Anderson 2002) to compare the predictive ability of these variables with the ability of native richness to predict exotic richness (and vice versa). Fourth, to compare across scales, we conducted similar analyses among fifty-two 1-m² plots within our largest patch. All details for these analyses are given in Appendix A.

2.3 Results

Across the 43 patches we found 272 species: 153 (56.3%) natives, 118 (43.4%) exotics, and one species (0.4%) of unknown origin. There was a negative relationship between natives and exotics across the 43 patches at the regional scale (Fig. 2.1a, $r = -0.337$, $P = 0.027$). When patch area was taken into account, the partial correlation between native and exotic richness was still negative and even stronger (Fig. 2.1b, $r = -0.751$, $P < 0.0001$).

With patch area as a covariate, the best predictors of native species richness at the regional scale were surrounding road density (negative effect) and climate (positive effect), with the highest native richness occurring in wet, cool, high elevation patches (Table 2.1; Fig. 2.1). Similarly, with area taken into account, exotic richness at the regional scale was best predicted by climate and road density, but in opposite directions compared to the model for native species (Table 2.1; Fig. 2.1).

At the regional scale, more variation in native species richness was explained by surrounding road density and climate than by exotic species richness ($\Delta\text{QAIC}_C = -19.02$; see Appendix B for more details). Furthermore, once road density and climate had been accounted for, exotic species richness did not explain any additional variation in native species richness (likelihood ratio test: $\chi^2 = 0.026$, $df = 1$, $P = 0.87$; $\Delta\text{QAIC}_C = +0.42$). The high adjusted R^2 value ($R^2_{\text{adj}} = 0.946$) shows that roads and climate explained much of the variation in native species richness. Surrounding road density and climate also outperformed native species richness as predictors of exotic species richness at the regional scale ($\Delta\text{QAIC}_C = -23.64$). Furthermore, adding native species richness as a predictor, once these patch characteristics had been accounted for, yielded no

improvement in the model's predictive power (likelihood ratio test: $\chi^2 = 0.621$, $df = 1$, $P = 0.43$; $\Delta\text{QAIC}_C = -0.10$; $R^2_{\text{adj}} = 0.962$).

At the local scale, there was no relationship between native and exotic richness ($r = 0.006$, $P = 0.966$). In 1-m² plots, higher native richness was significantly associated with sites with more canopy cover, higher soil pH, and higher soil moisture (Table 2.1). Only aspect significantly predicted patterns of exotic species richness at the local scale with more south-facing sites having higher exotic richness (Table 2.1). At the local scale, using native richness to predict exotic richness (and vice versa) did not improve on the null intercept-only models (likelihood ratio tests: $\chi^2 = 0.0024$, $df = 1$, $P = 0.96$ (natives); $\chi^2 = 0.0018$, $df = 1$, $P = 0.97$ (exotics)) which confirms that native and exotic richness were unrelated at the local scale. While the abiotic models were statistically significant (likelihood ratio tests: $\chi^2 = 35.29$, $df = 3$, $P < 0.0001$ (natives); $\chi^2 = 6.54$, $df = 1$, $P = 0.0105$ (exotics)), abiotic variables explained far less variation in richness at the local scale than at the regional scale, especially for exotics ($R^2_{\text{adj}} = 0.493$ for native model, $R^2_{\text{adj}} = 0.119$ for exotic model).

2.4 Discussion

The observed negative relationship between native and exotic species richness at the regional scale represents an important exception to the empirical generalization that broad-scale native-exotic richness relationships are positive (see Fig. 1 in Fridley et al. 2007). At relatively broad scales, current theory predicts that extrinsic factors that favour native species richness should also increase invasion success creating positive relationships between native and exotic species richness (Naeem et al. 2000, Shea and Chesson 2002). Biotic resistance, if present, should operate mostly at the spatial scale of

competitive interactions, such as 1-m² plots for plants (Fridley et al. 2007). While our negative relationship may, in the absence of further analysis, be taken to suggest that biotic resistance operates even at the regional or patch scale, surrounding road density and climate better predicted both measures of species richness independently, but in opposite directions in both cases. Once these variables were accounted for, there was no evidence that high native diversity confers invasion resistance. Furthermore, if diversity was conferring resistance at the patch scale, we would also expect this effect at the local plot scale; however, no relationship between native and exotic richness was observed locally. While our analysis does not preclude a direct effect of certain exotic species on native species declines, our results suggest that richness *per se* is not a driving factor in native declines at either scale. Our data provide support for extrinsic controls on native and exotic richness at the regional scale, and suggests that native-exotic richness relationships at broad scales can be negative if the directions of influence of these factors on natives and exotics are different.

Two possible mechanisms likely underlie the effect of road density on native and exotic richness: (1) increased exotic propagule pressure and (2) opposite effects of disturbance on native and exotic species. Roads can increase propagule pressure for many exotic species by acting as corridors for dispersal and allowing easier movement of potential vectors, such as humans or vehicles (Gelbard and Belnap 2003). Land conversion and development associated with roads also brings intentional introductions of exotic species for agricultural, horticultural, or other purposes which can subsequently become naturalized in adjacent natural habitats (Reichard and White 2001). In general, human activity has been shown to correlate with exotic introductions using a broad range

of surrogate variables (Taylor and Irwin 2004). Patterns of exotic richness in other studies have been shown to be immigration-driven at regional scales (Lonsdale 1999, Levine 2000). Thus, our data also suggest an important role of propagule pressure from roads and development as a driver of exotic richness in this system.

While exotic propagule pressure may explain patterns of exotic richness, disturbance associated with roads seems more likely to underlie the negative effect of road density on native richness. Previous studies suggest that altering natural disturbance regimes may adversely affect native species (McIntyre and Lavorel 1994, Leach and Givnish 1996). Disturbance from surrounding land use can extend into natural areas via changes in fire regimes, hydrology, nutrient inputs, grazing, and trampling (Hobbs and Huenneke 1992, Trombulak and Frissell 2000) with the magnitude of these effects related to the level of surrounding development. Williams et al. (2006) found that road density around patches of remnant Australian grasslands was a strong correlate of native plant extirpation. Native species in our system may also be poorly adapted to the type and/or frequency of human-mediated disturbance associated with roads and increased development (Hobbs and Huenneke 1992). Conversely, disturbance is generally thought to increase the success of exotic species, which are often ruderals (Hobbs 1989) or species adapted to exogenous disturbance in their native range (di Castri 1989). While the opposite effects of disturbance on natives and exotics could be taken to suggest that disturbance mediates competitive interactions between native and exotic species richness by initially facilitating exotic establishment (Davis et al. 2000), disturbance effects on natives appear to be independent of exotic richness. If the effect of disturbance was only to mediate interactions, we would expect exotic and native richness to be more strongly

correlated with each other than with extrinsic factors but this was not the case. General differences in the affinities of native and exotic species for roads in our dataset assessed from habitat descriptions in the published regional flora (Douglas et al. 1998-2002) support our assertion of direct and opposite effects of roads on natives and exotics. A much higher proportion of native species prefer habitats with little or no association with roads, while exotics are dominated by species with known road affinities (Appendix C).

Differences in the distributions of climatic preferences within native and exotic species pools may also contribute to the negative native-exotic richness relationship. In our study, higher native and lower exotic richness was associated with higher precipitation and elevation, and lower temperatures. Species pool hypotheses propose that the distribution of habitat preferences of species along environmental gradients within the regional species pool, and therefore richness patterns along these gradients, are related to the availability of environments where those species evolved (Partel 2002). Oak savannas in southwestern British Columbia are most closely related to the Mediterranean (dry) grasslands of California and Oregon (Meidinger and Pojar 1991). The Mediterranean-type flora of California is of relatively recent origin as the present-day Mediterranean climate in that region arose only in the Quaternary period (Axelrod 1973). Wetter, cooler environments were likely more common in western North America over evolutionary time scales. Raven and Axelrod (1978) suggests that 50% of present-day California species have their evolutionary history in wet, cool north-temperate environments. If similar patterns are reflected within our study region and the majority of our species pool evolved in more available wetter and cooler climates, this could produce strong species richness – climate relationships within the native flora. In California, climate variables

have been found to be strong predictors of regional richness patterns and mean annual precipitation was the most predictive variable showing a positive relationship to richness (Richerson and Lum 1980). Conversely, many of the exotic species in our system may prefer drier conditions, having come from other Mediterranean regions of the world (Roemer 1972). Thus, we can hypothesize that richness patterns seen across the climatic gradient in this region reflect opposite distributions in climatic preferences in the regional species pool, though further analyses are needed to fully explore this hypothesis.

While the above mechanistic explanations can potentially explain the relationships of road density and climate to native and exotic richness patterns, our data are limited in allowing comparison of their relative effects. Due to correlations in the pattern of development and regional topography in our study area, there is significant shared variation in our models attributable to either road density or climate. Variation partitioning using partial linear regression (Legendre and Legendre 1998) indicates that, of the 77% of the variation in native species richness accounted for by road density and climate together, 20.6% is uniquely explained by road density, 13.4% is uniquely explained by climate, and 70.0% is shared. Exotic species richness showed almost identical trends. Yet, despite the high levels of shared variation, both road density and climate explain significant variation in the final model (Table 2.1) indicating independent contributions to the negative native-exotic richness relationship. It is also possible that the observed effect attributed to climate represents a disturbance effect related to elevation that was not captured by road density; lower elevation sites are more likely to be disturbed by human activities. However, while this suggestion may somewhat temper our confidence for climate as a dominant driver in our study system, we still have a

strong argument that potential mechanisms related to human influence and possibly climate are capable of producing negative native-exotic richness relationships at a broad scale, which represents an important modification to the empirical generalities found in the literature to date (Fridley et al. 2007).

In conclusion, our results have important implications for understanding the fundamental drivers of community change, of native-exotic richness relationships, and for biodiversity conservation more generally. First, biodiversity hotspots can be the least invaded on a regional scale without invoking a biotic resistance explanation if extrinsic factors influencing invasion success, such as propagule pressure, vary oppositely to the main gradients driving patterns of native richness, or if the same factors drive native and exotic richness in opposite directions. In our study system, the same factors that favour exotic richness adversely affect native richness. If extrinsic factors control native and exotic richness independently then exotic species are only passengers and not drivers of regional-scale biodiversity declines (*sensu* MacDougall and Turkington 2005). Consequently, an appropriate generalization of native-exotic richness relationships might be not how the direction of the relationship (positive or negative) changes with scale (Fridley et al. 2007) but how the factors that control richness (intrinsic or extrinsic) vary with scale. Second, we hypothesize that human-mediated disturbance gradients, which are ubiquitous across the globe, have the potential to create negative native-exotic richness relationships in a variety of systems. Further examination of native and exotic richness simultaneously along such gradients is needed. Negative native-exotic richness relationships at the regional scale are not only possible, but could be more common than previously thought.

Table 2.1. Results of forward selection of variables for generalized linear models of native and exotic species richness at regional and local scales.

Estimated coefficients, χ^2 significance statistics, and P -values are reported from a Type III analysis. Order of variable selection is indicated in square brackets. For the regional models, (log) patch area was used as a covariate and forced into the model first. Empty boxes indicate that variables that were not selected as they were not significant in the presence of the other variables. “n/a” denotes where a variable was not included because it was either not relevant or difficult to measure at that scale.

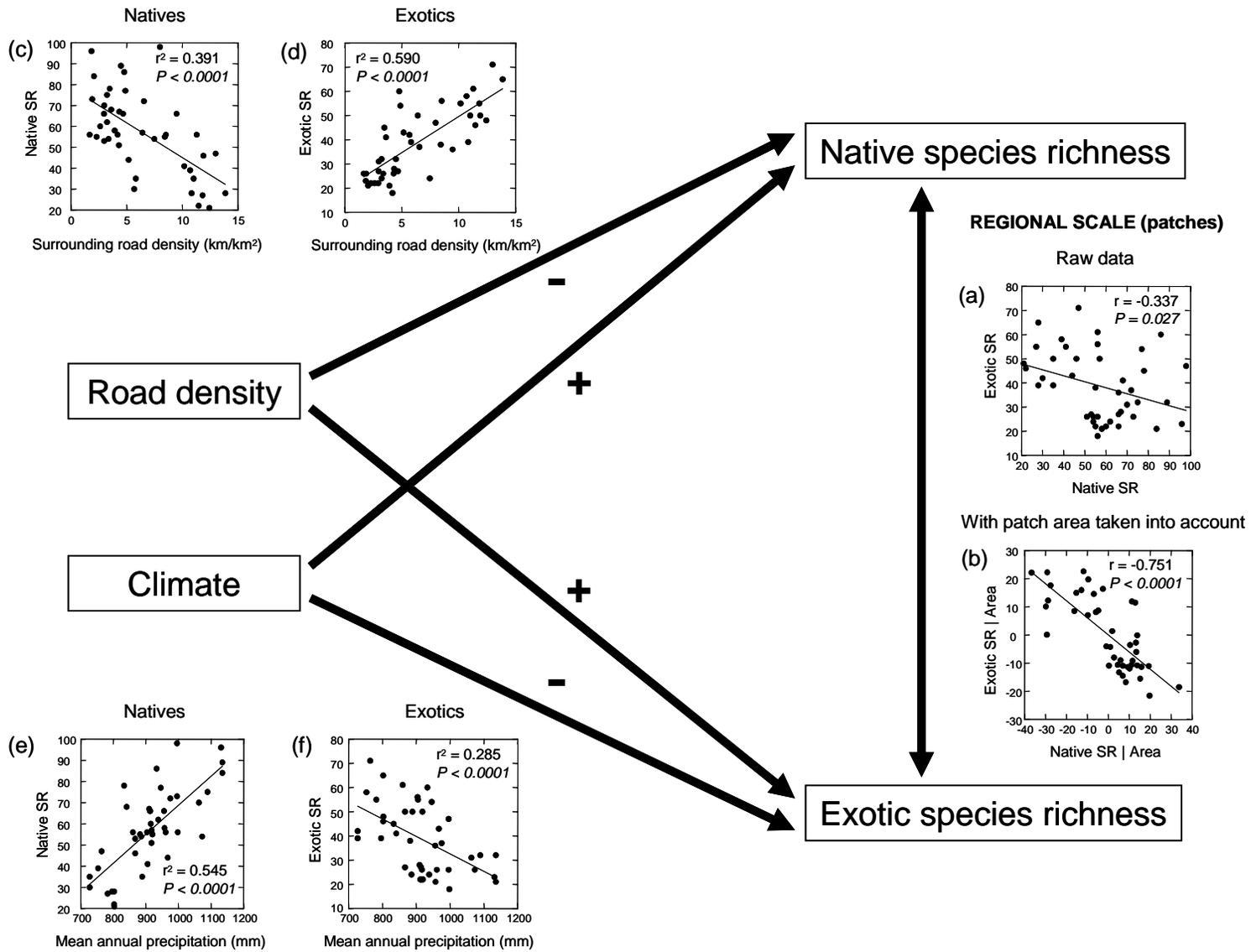
Parameter	Regional scale				Local scale			
	Native SR*		Exotic SR*		Native SR*		Exotic SR*	
	Est. coeff.	χ^2 , P -value	Est. coeff.	χ^2 , P -value	Est. coeff.	χ^2 , P -value	Est. coeff.	χ^2 , P -value
Intercept**	+2.8356	139.85, <0.0001	+1.8529	49.67, <0.0001	-2.5385	5.61, 0.0178	+1.3243	114.39, <0.0001
Log patch area	+0.3295	33.34, <0.0001	+0.3441	29.82, <0.0001	n/a	n/a	n/a	n/a
Log connectivity					n/a	n/a	n/a	n/a
Surrounding road density	[1] -0.0444	17.81, <0.0001	[2] +0.0382	12.7, 0.0004	n/a	n/a	n/a	n/a
Distance to nearest road	n/a	n/a	n/a	n/a				
Slope (degrees)								
Aspect (degrees from N)							[1] +0.0032	8.19, 0.0042
Soil depth (cm)								
Soil depth heterogeneity (cm)								
Canopy cover (%)					[1] +0.1142	12.19, 0.0005		
Soil pH					[2] +0.5951	10.15, 0.0014		
Climate (PCA1)	[2] +0.0009	9.41, 0.0022	[1] -0.0014	14.36, 0.0002	n/a	n/a	n/a	n/a
Soil moisture (%) (scale parameter c)	n/a	n/a	n/a	n/a	[3] +0.1539	6.01, 0.0142		
		1.2615		1.1502		1.3076		0.871

* SR = species richness.

** Wald test used as test statistic for intercept instead of likelihood ratio test.

Figure 2.1. Diagram showing relationships among native species richness, exotic species richness, road density, and climate at the regional scale.

The relationships between native and exotic species richness (SR) across patches may be due to a direct effect of natives on exotics (or vice versa) or to similar responses to spatial, human influence, or environmental variables. The relationship between native and exotic species richness at the regional scale in 43 remnant habitat patches is shown (a) with no correction for patch area and (b) once an area effect has been statistically controlled for. (c) and (d) show the relationship between native and exotic richness and surrounding road density. (e) and (f) show the relationship between native and exotic richness and climate (here, represented by mean annual precipitation). The signs accompanying the arrows summarize the direction of the relationships.



2.5 References

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3 Native and exotic plant species composition in oak savannas at local and regional scales²

3.1 Introduction

Exotic species are of increasing interest both because of their potential negative impacts on native biota (Wilcove et al. 1998, Mack et al. 2000) and their applicability to investigating fundamental questions in community ecology (Sax et al. 2007).

Understanding patterns of species invasions and their underlying mechanisms can provide insight into how species interact with each other and their environment and, by doing so, inform our ability to conserve and restore natural ecosystems (Seabloom et al. 2003, MacDougall and Turkington 2007). A key question of invasion biology is whether native and exotic species are “different” (Sax et al. 2005); that is, do exotics share unique traits or responses that make them ecologically different from native species and potentially facilitate success in their naturalized range? One area of research has examined whether successful invaders possess certain life history traits (e.g., stem height, seed size, and seed number for plants) that can increase their probability of invasion or competitive ability in new environments (Williamson and Fitter 1996, Goodwin et al. 1999, Kolar and Lodge 2001). Results have been mixed with some studies finding potential relationships between traits of exotic species and their invasion ability (e.g., Rejmanek and Richardson 1996, Reichard and Hamilton 1997) while others suggest prediction of species invasiveness based on traits may be difficult or even futile (e.g., Williamson 1999).

In addition to the traits of the exotic species themselves, the success of exotic

² A version of this chapter will be submitted for publication. Lilley, P. L., and M. Vellend. Native and exotic plant species composition in oak savannas at local and regional scales.

species in new habitats also depends on the characteristics of the receiving community and environment. The diversity of resident native species can influence the invasibility of plant communities to exotic species (Tilman 1997, Levine and D'Antonio 1999).

Environmental conditions, while often recognized as a determinant of native species distributions, can also contribute to exotic distributions and be a primary control on invasibility (Richardson and Bond 1991). Changes to disturbance regime or resource availability also seem to be key mechanisms promoting invasion (Davis et al. 2000).

Thus, invasion and its effects are often context-dependent (Milberg et al. 1999, Rejmanek 1999) and studies must also look at how natives and exotics may respond similarly or differently to habitat attributes, such as environmental gradients, within the invaded ecosystem (Kolar and Lodge 2001, Daehler 2003). Such work could help reveal general habitat characteristics that make communities more or less susceptible to invasions.

Several filters operating at different scales can influence the distribution of plant species within ecosystems. While local environmental factors (water, nutrients, light, and space) and resident species determine the suitability of sites for the establishment, growth, and survival of vascular plants, spatial and historical factors operating at regional scales are being increasingly recognized to also control plant distributions and impact plant community composition (Ricklefs and Schluter 1993, Bastin and Thomas 1999). Throughout the globe, habitat loss and fragmentation due to land conversion and development is restricting natural plant communities to discrete habitat patches (Fahrig 2003, Vellend 2003). By limiting dispersal and population sizes, the spatial arrangement and size of these remnant patches can affect the likelihood of colonization by new species from nearby occupied patches and increase the probability of extinction of existing

populations (MacArthur and Wilson 1967, Hanski 1999, Bastin and Thomas 1999). Additionally, human influence from activities within the adjacent landscape matrix can also influence patch occupancy and abundance by facilitating introductions of exotic species (Lonsdale 1999, Duguay et al. 2007) and altering natural disturbance regimes (Hobbs and Huenneke 1992). Thus, spatial factors, human influence and environment represent a series of filters which can determine the distribution patterns of both newly arrived exotic species and resident native species. Their relative importance will vary depending on the species characteristics and the nature of the ecosystem, as well as spatial scale (Fridley et al. 2007).

While some authors have suggested there is little difference between how native and exotic species respond to gradients (McKinney and Lockwood 2005), there are several reasons why we may expect native and exotic species to respond differently to some of the above-mentioned factors, especially at the landscape scale. First, initial dispersal of exotics is often human-assisted (either intentionally or accidentally). Consequently, distributions of exotic species are often strongly related to human activity (Lonsdale 1999). In landscapes with gradients of human activity, early in the invasion process, exotic species may occupy only a small subset of potentially suitable sites where propagule pressure is higher (Wiser et al. 1998). However, this effect may be short-lived as more sites become occupied over time, dispersal becomes less limiting, and species are limited only by the suitability of site conditions (Wiser et al. 1998, Gilbert and Lechowicz 2005). In contrast, native species, being in the landscape for longer, are perhaps closer to equilibrium with their environment and already distributed according to environmental and other gradients (Guo 2006). Second, disturbance is known to facilitate

invasion (Crawley 1987, Hobbs 1989). Therefore, exotic species may be more tolerant of, or even promoted by, human-mediated alterations to natural disturbance regimes because of their evolutionary history in ranges subject to such regular exogenous disturbances (di Castri 1989). Natives, which lack a long history of evolution in the context of anthropogenic disturbance, may be negatively impacted by such disturbance regime changes (McIntyre and Lavorel 1994). Third, exotic species may be less sensitive to certain environmental factors due to greater ecological niche breadth relative to native species (Richards et al. 2006). For example, if specific native species are generally more specialized on habitat conditions found only within remnant habitat patches, they may show strong effects of patch area and isolation. Effective patch sizes and connectivity may be much different for habitat generalists or exotics, where populations can exist within matrix habitats between patches. On the other hand, research has shown that response times of plants to fragmentation can occur over long periods of time with extinction debts persisting for many years (Vellend et al. 2006). Consequently, patterns of native species may relate more strongly to past rather than current-day habitat configuration (Lindborg and Eriksson 2004, Helm et al. 2006) and effects may only emerge over time. Thus, the factors that predict native and exotic species composition may be quite different (Wiser et al. 1998).

Species traits may also influence a species' response to habitat factors regardless of whether the species is native or exotic. For example, life history traits are known to predict species responses to fragmentation (Henle et al. 2004). For plants, species with shorter average seed dispersal distances, as predicted by dispersal mode, may be more likely to show effects of patch area and isolation (Verheyen et al. 2004). This is because

patch colonization rates are lower for such species. Similarly, habitat configuration may also have different effects on specialist and generalist species. As mentioned earlier, native species specialized on a specific, highly fragmented habitat type may be more sensitive to area and isolation effects than generalists that can also inhabit matrix habitats (Dupre and Ehrlén 2002, Kolb and Diekmann 2005). Examining the nature and strength of the trait-environment relationships may also help to understand differences between native and exotic species further and improve predictions of species-specific responses to changes in landscape structure, disturbance regimes, or environmental conditions.

In this study, we examine the similarities and differences in native and exotic species responses to spatial context, human influence, and environmental factors in remnant oak savannas in southwestern British Columbia. To do so, we take a three-part approach. First, we begin by comparing the predictors of native and exotic species community composition at two different spatial scales – among habitat patches (regional) and within a single habitat patch (local). Second, we examine patterns in the predictors of patch occupancy (i.e., presence-absence) of individual native and exotic species to gain further insights into the important drivers of distribution patterns. Finally, we test whether several simple life-history traits (life form, life span, dispersal mode, and habitat specialization) can explain differences among species in their response to different habitat characteristics.

3.2 Methods

STUDY AREA AND REGIONAL (PATCH) PLANT SURVEYS

Our study took place at the northern range limit of Garry oak (*Quercus garryana* Dougl. ex Hook.) savanna habitat on southeastern Vancouver Island near Victoria, British

Columbia, Canada (48°26' N 123°22' W). This ecosystem extends from northern California to southwestern British Columbia in the lee of the coastal mountain ranges of western North America. The ecosystem has a sub-Mediterranean climate in British Columbia, with a significant summer drought (Fuchs 2001). Soils are generally shallow, post-glacial, and moderately infertile (Roemer 1972, Erickson 2002). Due to habitat loss from urbanization, agriculture, and forestry since European settlement, less than 10% of the historical extent of oak savanna habitat in this region remains in a near-natural state (Lea 2006). Remnant patches are distributed across a human influence gradient, with surrounding conditions ranging from urban development to second-growth coastal Douglas-fir (*Pseudotsuga menziesii* (Mirbel) Franco var. *menziesii*) forest.

Forty-three oak savanna habitat patches ranging broadly in their size (0.2-30 ha), connectivity, surrounding land use, and environmental conditions were surveyed for vascular plant species composition (trees, shrubs, forbs, graminoids, ferns) in 2006. We surveyed for both native and exotic species (classified using British Columbia Conservation Data Centre 2007) along parallel transects spaced at 25 m intervals. Patches were surveyed at two different times during the spring flowering period, once in early spring (12 April – 5 June) and once in late spring/early summer (7 June – 27 July) to maximize detectability of species with early and later phenologies. Most plants were identified *in situ* although specimens were collected for some species requiring microscopic examination, comparison to herbarium records, or consultation with experienced botanists. Abundance was coarsely estimated using a modified Braun-Blanquet abundance/dominance scale where rankings were based on approximate spatial distribution within the patch: r (0-2%), + (2-10%), 1 (11-40%), 2 (41-70%), 3 (71-100%).

We eliminated or combined a small percentage of species (<5%) from the study due to difficulties with detection (i.e., cryptic species), taxonomy, or short flowering time relative to the length of the survey periods. While there is a loss of information in using only a subset of total species in our study, this loss is offset by shorter sampling times and a resulting increase in the number of sites we were able to sample (Vellend et al. in press). All patches surveyed were found in parks or other protected areas.

PATCH ATTRIBUTES

To test for relationships between patch attributes and species composition or patch occupancy, we characterized the spatial context, human influence, and environmental conditions of each patch using the following variables:

Spatial variables

- a) Patch area: Patch area was estimated by delineating patch boundaries on high-resolution colour orthophoto images using ArcView GIS 3.2 (ESRI, Redlands, California, USA). Images were created from aerial photos taken in July 2005.
- b) Patch connectivity: We used a patch-based weighted sum approach and a regional database of spatially-delineated oak savanna habitat patches (from Ward et al. 1998, updated June 2005) to find the connectivity of each patch. The connectivity of patch i was calculated as follows (Moilanen and Nieminen 2002, Eq. 3):

$$S_i = \sum_{i \neq j} \exp(-\alpha d_{ij}) A_j$$

where A_j is the area of patch j (in m^2), d_{ij} is the minimum edge-to-edge distance (in m) between patches i and j , and α is the parameter setting the influence of distance on connectivity. We used $\alpha = 0.002$ to scale our effect of distance on dispersal. This represents a realistic average migration range for many grassland

species (Bastin and Thomas 1999, Verheyen et al. 2004). Minimum edge-to-edge-distances were found using the “Distances and Bearings between Matched Features v. 2.1” extension for ArcView (Jenness Enterprises, Flagstaff, Arizona, USA).

Human influence variable

- c) Surrounding road density: As an index of human influence, representing both the propagule pressure of exotic species and degree of potential human-mediated disturbance, we calculated surrounding road density as the length of roads per km² within a 500 m buffer around each patch. Road mapping was from a 1:20,000 Terrain Resource Inventory Mapping (TRIM) roads layer provided by the Province of British Columbia.

Environmental variables

- d) Slope: Slope was measured using a clinometer at 32-40 randomly sampled points stratified across quarter-sections within each patch (see Appendix A).
- e) Aspect: Aspect was measured using a compass at the same randomly sampled points. As aspect is a circular variable, it was converted to degrees from north.
- f) Canopy cover: Canopy cover was also assessed at the same 32-40 points in each patch using a spherical densiometer (Lemmon 1956).
- g) Soil depth: Soil depth was estimated by pushing a 70-cm small diameter steel probe to bedrock at the same 32-40 points in each patch. To ensure measurements reflected bedrock depth and were minimally affected by the rocky soils, five depth measurements (at the centre and at 40-cm from centre in each of the four cardinal directions) were taken at each point and averaged.

- h) Soil depth heterogeneity: The coefficient of variation (CV) in soil depth was used to quantify within-patch habitat heterogeneity. We selected soil depth as our heterogeneity measure because it was the only variable measured at multiple points within sites for which the mean-CV correlation was less than 0.5 ($r = -0.479$, $P = 0.001$).
- i) Soil pH: Soil pH was measured from a composite sample of soil cores taken at a stratified random subset of ten of the above sampling points used for other environmental variables. Cores were 6 cm in diameter and taken to 10 cm depth. 120 ml of soil was collected from each core and combined into the composite sample for the patch. Composite samples were uniformly mixed, dried, sifted, and pH measured using an ion-exchange membrane probe in a 1:4 soil-to-water mixture (5 g of soil, 20 ml of water).
- j) Climate: Mean annual precipitation and temperature for each patch were interpolated from 1961-1990 climate normals using the Climate BC database (Hamann and Wang 2005, Wang et al. 2006). Because mean temperature, precipitation, and elevation were highly correlated across the landscape ($|r| = 0.471-0.851$), we used the first axis of a principal components analysis (PCA) based on these three variables as a synthetic variable to represent “climate” in subsequent analyses. This axis explained 86.5% of the variation in the data.

LOCAL-SCALE (1-M²) PLOT SURVEYS

To compare the regional results with species composition patterns at a local scale, we conducted a stratified-random survey of fifty-two 1-m² circular plots in our largest habitat patch (31.7 ha) at Mill Hill Regional Park in Langford, British Columbia, Canada

(48°27' N 123°30' W). This patch is broadly representative of habitat patches across the region, and has a relatively high degree of environmental heterogeneity. Plot locations were chosen from an initial set of 100 stratified randomly-generated points (see Appendix D) to ensure the sampled plots covered a broad range of conditions. Each plot was surveyed for vascular plant species twice in 2006 (16-19 May and 5-6 July) using the same abundance/dominance scale as for the patch surveys. For the 1-m² plots, we measured the same or similar predictor variables as in the regional-scale study where possible. Slope, aspect, canopy cover, soil depth, and soil pH were measured for the plots as at sampling points for the regional-scale data except that soil pH was measured from a single soil core at the plot centre. We also added the following variables at the local scale:

- a) Distance to nearest road: We used distance from each plot to the nearest road as an index of proximity to urbanization and an analog for road density at the regional scale.
- b) Soil moisture: As fine-scale climate data for each plot was unavailable, soil moisture (% volumetric water content) was added as an additional environmental predictor at the local scale and measured using a Hydrosense Time Domain Reflectometer (TDR) (Campbell Scientific, Logan, Utah, USA).

Area, connectivity, and soil depth heterogeneity did not have local-scale analogs. Where necessary at both scales, predictor variables were log- or square root-transformed to reduce skew.

STATISTICAL ANALYSES

First, we used Canonical Correspondence Analysis (CCA; ter Braak 1986, Legendre and Legendre 1998) to model variation in native and exotic species abundances along spatial, human influence, and environmental gradients at the regional and local scale. CCA was performed on native and exotic species separately at each scale. Prior to the analyses, within each dataset, we excluded species that occurred in fewer than two patches or plots and converted our abundance ranks to the midpoints of the coverage range represented by each rank to reflect relative abundance. To look at whether the CCA results differed if we used this ‘abundance’ data vs. presence-absence data, we compared results using each type of input data. The two analyses gave similar results; therefore, we report results using only the abundance data here. We used the patch attributes listed above (ten at the regional scale, seven at the local scale) as potential explanatory variables in each CCA. To understand their relative importance and remove highly correlated variables, we subjected the explanatory variables to forward selection ($\alpha = 0.05$), testing for additional significant variation explained (conditional or partial effect) with each variable added using Monte Carlo permutation tests (999 permutations). Final models included only those variables that were significant. To interpret the ordination axes, we used ordination diagrams (species-environment biplots) and the intraset correlations (ter Braak 1986). CCA analyses were carried out in Canoco for Windows 4.5 (Biometris – Plant Research International, Wageningen, The Netherlands).

Second, at the regional scale, the presence-absence of each species was modeled using multiple logistic regression (Hosmer and Lemeshow 1989) using nine of the above explanatory variables, excluding soil depth heterogeneity. We excluded soil depth

heterogeneity from this analysis because there is no theoretical basis for relevance of this variable when predicting individual species distributions. For statistical reasons, we restricted our analyses to species found in between 20% and 80% of patches (9-34 patches inclusive). We used a forward stepwise variable selection approach with the probabilities for variable entry or removal both set at 0.05. Across the native and exotic species analyzed, we assessed the frequency of significant effects and direction of prediction of each variable in the selected models. The relatively small number of species (9 natives, 4 exotics) found in 20-80% of the local-scale plots precluded a similar analysis at the local scale.

Finally, for the species whose individual distributions were modeled using logistic regressions at the regional scale, we collected information on four life history traits: life form (tree/shrub, forb, graminoid, or fern), life span (annual, biennial, or perennial), dispersal mode (wind, vertebrate, or ants/ballistic/none), and habitat specialization (generalist or specialist; native species only) (see Appendix E). We then used further logistic regressions to test whether these traits could predict the presence-absence of significant effects of each explanatory variable: for example, do species with different dispersal modes vary systematically in the likelihood that their distributions will be influenced by a variable such as connectivity? Because very few exotic species could be classified as true oak savanna habitat specialists in our landscape, we did not use habitat specialization for exotic species. As all traits examined were nominal variables, these were categorized into x “design” variables, where x is one less than the number of levels for each variable (Hosmer and Lemeshow 1989). Because both sets of logistic regressions were largely exploratory, no corrections were made for multiple statistical

tests on the same data. We based conclusions largely on the results as a whole, and interpreted the individual significance tests cautiously. All logistic regressions were carried out using PROC LOGISTIC in SAS 9.1.3 (SAS Institute Inc., Cary, North Carolina, USA).

3.3 Results

At the regional scale, across our 43 study patches, we found 153 native species and 118 exotic species. One species of unknown origin was also identified (*Matricaria discoidea* DC.) and was excluded from further analysis. One hundred and thirty of the natives and 107 of the exotics were found in more than one patch and were thus included in the CCA analyses. At the local scale, within our fifty-two 1-m² plots, we found 54 native species and 23 exotic species. Thirty-nine natives and 20 exotics were found in two or more plots.

PREDICTING COMPOSITION USING CCA ORDINATION

Selected explanatory variables accounted for 36.5% of the variation in native species composition among patches (sum of eigenvalues = 0.480, total inertia = 1.316). Climate accounted for 29.8% of this explained variation and was the single best predictor of native composition (Table 3.1). Canopy cover, surrounding road density, connectivity, aspect, soil depth heterogeneity, and soil depth were added in order after climate by the forward selection process, and accounted for unique additional significant variation in native composition (Table 3.1). Once variation was attributed to climate, canopy cover explained an additional 15.3% of the variation explained by the CCA and other variables accounted for about 10% or less of the variation (Table 3.1). Because climate and road density were strongly correlated ($r = -0.663$), the major (first) axis of variation in native

species composition was essentially a combined climate-road density gradient (Fig. 3.1a, Table 3.2a). Due to this collinearity, we used conditional and marginal effects (Leps and Smilauer 2003) to compare the predictive power of each variable independently (marginal effect) and when added in the presence of the other variables during the forward selection process (conditional effect). Comparison of the marginal effects of climate and road density suggests their explanatory abilities are similar (Table 3.1). However, the conditional effects indicate both variables explain unique significant variation in composition and were therefore selected for inclusion in the model. The second axis of the CCA is a canopy cover gradient (Fig. 3.1a, Table 3.2a).

Selected explanatory variables accounted for 30.6% of the variation in exotic species composition among patches (sum of eigenvalues = 0.508, total inertia = 1.658). Surrounding road density was the single best predictor of exotic composition, explaining 34.5% of the total variation explained by the CCA (Table 3.1). Climate, soil pH, area, and canopy cover explained decreasing amounts of significant additional variation. Once variation was attributed to road density, climate explained an additional 13.6% of the variation and other variables about 10% or less of the variation (Table 3.1). Again, since climate and road density were correlated, both variables correlated strongly and similarly with the first axis of the CCA (Fig. 3.1b, Table 3.2b). However, as above, roads and climate also explain significant unique variation in exotic composition. The second axis of the CCA was a soil pH gradient and the third axis an effect of patch area on exotic composition (Fig. 3.1b, Table 3.2b).

At the local scale, selected explanatory variables accounted for lower amounts of variation in native and exotic species composition, 9.0% and 17.6% respectively (natives:

sum of eigenvalues = 0.473, total inertia = 5.244; exotics: sum of eigenvalues = 0.636, total inertia = 3.617), relative to the regional analyses. The main gradients explaining significant variation in native species composition were canopy cover (29.4%) and slope (17.0%; Table 3.3). No other variables explained significant additional unique variation in the data. Slope was uncorrelated with canopy cover ($r = -0.157$). Consequently, the first axis of the CCA was a canopy cover gradient and the second axis was strongly related to slope (Fig. 3.2a, Table 3.4a). Environmental variables also accounted for local-scale variation in exotic species composition as well but the most important environmental gradients differed. Soil depth, soil pH, canopy cover, and slope, in decreasing order of importance, accounted for patterns in exotic species across the sampled 1-m² plots (Table 3.3). The first axis of the CCA was a soil depth gradient and the second axis represented an effect of soil pH (Fig. 3.2b, Table 3.4b). Further axes were more difficult to attribute to specific explanatory variables.

PREDICTING SPECIES PRESENCE-ABSENCE

Of the 112 species (62 natives, 50 exotics) for which regional-scale logistic regression models were fit, eight species had no significant effects of any of the explanatory variables (see Appendix F). All variables were significant predictors of species presence-absence for at least one species. The most frequent variables predicting the patch occupancy of native species at the regional scale were climate, road density, and patch area (Fig. 3.3a). Of the 62 native species examined, significant effects of climate were obtained for 23 (37.1%) species. Significant effects of surrounding road density and patch area were obtained for 17 (27.4%) species each. Generally, climate effects were positive (higher rainfall, lower temperatures, and higher elevations predict

native species presence) and road effects were negative. Patch area effects were consistently positive. Other variables showed significant effects but for far fewer (nine or less) species (Fig. 3.3a).

Similar to native species, climate, road density, and patch area showed the most significant effects on patch occupancy of exotics (Fig. 3.3b). For exotics, road density (20 species, 40.0%) showed more significant effects than climate (13 species, 26.0%). However, in contrast to native species, the general direction of road density and climate effects were opposite to that seen for most native species: road density effects were positive and climate effects were negative (higher rainfall, lower temperatures, and higher elevations predict species absence). Significant effects of patch area were obtained for 13 exotics (26.0%) and these patch area effects were consistently positive.

PREDICTING PATCH ATTRIBUTE EFFECTS USING SPECIES TRAITS

We found few predictive relationships between life history traits and the presence-absence of effects of the explanatory variables. Only one of the 36 potential trait-environment relationships was significant for native species (Table 3.5): species for which area effects were found tended to be habitat specialists (Fig. 3.4a). Two other relationships were marginally significant: road density effects were more common in habitat generalists (Fig. 3.4b) and species for which slope effects were found were more often woody species and less often forbs (Fig. 3.4c). As we mentioned earlier, these results should be interpreted with caution as, at an α -level of 0.1, based on the Type I error rate and the number of tests made, we would expect two to three significant relationships based on chance alone. None of the life history traits helped to predict significant effects of the explanatory variables for exotics.

3.4 Discussion

For both native and exotic species, surrounding road density and climate emerged as the dominant gradients predicting changes in species composition among remnant habitat patches at the regional scale. Patterns of community change along a shared road density-climate gradient are the most predictable in our data. Despite a strong correlation and shared variation between road density and climate in this landscape, both factors explain unique variation in composition of natives and exotics in patches. However, while the same gradients are important, the directionality of effects in the patch occupancy data suggest that, for many species, natives and exotics reach their optimal abundance towards opposite ends of these gradients. Furthermore, environmental conditions that explain additional variation in composition are different for natives and exotics in the regional analysis. At the local scale, native and exotic species abundances respond to different dominant habitat attributes. In our study system, despite a shared importance of road density and climate, natives and exotics respond to these dominant regional-scale gradients in fundamentally different ways across patches and map onto different aspects of their local environment within patches.

Many studies have suggested that trait differences between native and exotic species can explain the apparent success of exotic species in their naturalized range (Rejmanek and Richardson 1996, Kolar and Lodge 2001, Hamilton et al. 2005). However, other studies have found little difference in the actual performance of native and exotic species within ecosystems (Daehler 2003, Meiners 2007). We looked directly at how natives and exotics respond to their habitat context and found that they generally respond quite differently. Our results support the idea that invasion success within a

region may be context-dependent (Thompson et al. 1995, Daehler 2003) and that habitat characteristics are an important driver of exotic species success (Milberg et al. 1999). This suggests that any conceptual framework for understanding plant invasions needs to consider the characteristics of the habitat being invaded as well as traits of the invading species (Moles et al. 2008). We found that important habitat factors can be both landscape factors (such as road density) and local environmental conditions. Furthermore, the separation we observed in the preferences of exotics and natives along environmental gradients may indicate that natives and exotics occupy different niches (Lambdon et al. in press), possibly suggesting a mechanism of success or coexistence for some species.

In addition to native and exotic species *composition*, native and exotic species *richness* are also correlated most strongly with road density and climate in this ecosystem (Chapter 2). However, an effect on diversity of a given habitat variable does not predetermine an effect on species composition if species are added or removed at random along the richness gradient. Road density and climate predicted patch occupancy for only 30-40% of native and exotic species. Other species did not show significant effects. This suggests that species are differentially sensitive to these gradients, rather than being added or removed at random along the richness gradient, which would indicate similar sensitivity across species. Our data show that the species richness effects observed previously (Chapter 2) are the result of species-specific responses to the road density and climate gradients.

Two different underlying mechanisms may account for the effect of surrounding road density on plant communities (see also Chapter 2). Changes in road density can: (1) impact the relative dispersal or propagule supply of species from adjacent habitats

(Bartuszevige et al. 2006) and (2) alter natural disturbance regimes (e.g., via changes to fire regimes, nutrient inputs, grazing) or change rates of exogenous disturbance (e.g., human trampling) (Hobbs and Huenneke 1992). For exotics, dispersal has been proposed as a key factor limiting invasion success in ecosystems (D'Antonio et al. 2001). In human-altered landscapes, roads facilitate human movement which increases the dispersal of exotics (Trombulak and Frissell 2000, Gelbard and Belnap 2003). As development increases, exotic composition may shift because propagule pressure shifts from agronomic or weedy species (introduced early during European settlement) to horticultural and garden species associated with more recent urban development (Lambdon and Hulme 2006). In our study system, the current distributions of some exotics may be dispersal-limited while others may not, either because they are easily dispersed (e.g., wind-dispersed seeds, berries dispersed by birds) or because they were introduced to the landscape earlier and have had more time to spread. Because dispersal mode is not an important predictor of a road density effect in our data, time since introduction may be a more important factor underlying the effect of roads on exotic species composition (Cadotte et al. 2006). Many of the exotics that are found only in sites with the highest road densities appear to be garden ornamental species (P. Lilley, personal observation), many of which are likely recent introductions. We did not test time since introduction as a potential life history trait to predict effects because documented histories of introduction in our landscape are not known for most species. Disturbance may also interact with propagule supply to facilitate exotic establishment (Hobbs 1989). Many species introduced in North America have evolved in landscapes with much longer histories of human-mediated disturbance as intense as we see at present (di Castri 1989).

For native species in this ecosystem, disturbance associated with increased human influence, such as soil disturbance and trampling, seems more likely to be the dominant mechanism by which road density leads to changes in native composition. Other alterations to natural disturbance regimes, such as fire suppression (MacDougall and Turkington 2007) and increased herbivory (Gonzales and Arcese, in preparation) play a role in native species declines in other parts of this ecosystem. Roads or other measures of human influence, such as population density, have been shown to correlate with local extirpation of natives in other landscapes (Thompson and Jones 1999, Williams et al. 2006). In our landscape, significant road effects were generally negative also suggesting high road density may lead to species extirpations from patches. However, patch occupancy for the majority of native species (roughly 60%) is not related to road density. Also, for the species that do show effects, the distribution of species along the road density gradient (Fig. 3.1a) shows that species are differentially influenced by the effects of disturbance.

Climate also contributes to native and exotic plant composition at the regional scale across our study patches. Climatic conditions can influence resource availability (water, light, etc.), place physiological limits on species growth, and mediate competitive interactions among species (Davis et al. 2000). In oak savanna habitat on southeastern Vancouver Island, moisture availability has been previously thought to drive native species distributions at the regional scale (Roemer 1972). Our study patches range over a fairly wide climatic gradient despite the relatively short distances involved (mean annual precipitation varies from 727-1135 mm and elevation above sea level varies from 20-298 m over a 40 km by 25 km study area) such that climate likely contributes to some form of

species sorting (Leibold et al. 2004). Furthermore, paleoecological data on Garry oak distributions in British Columbia suggests that climate has defined the boundaries between oak savanna habitat and surrounding coniferous forest over the last 12,000 years (Hebda 1995, Pellatt et al. 2001). Given that forest encroachment is occurring into deeper soil oak savannas in the absence of fire (Gedalof et al. 2006), encroachment of forest understory species into oak savanna habitats may be more likely to occur under wetter conditions. This encroachment may represent an additional source of variation in native richness (Chapter 2) and composition along the climatic gradient. Because of their longer history within the landscape, native species distributions may be more climatically-controlled while exotics are more dispersal-limited. However, due to correlations between road density and climate, we cannot disentangle the majority of the variation and thus, the relative effects of these two variables for each of the species pools.

Once road density and climate effects are accounted for, local environmental conditions explain additional variation among patches; environmental conditions were the only significant predictors among 1-m² plots within our single habitat patch. The importance of canopy cover at the regional scale is likely simply a scaling up of the main effect of canopy cover on natives observed at the local scale. Light has previously been suggested to be the primary limiting resource at the local scale for native species in this ecosystem (MacDougall 2005, MacDougall and Turkington 2007). The importance of soil depth to exotic distributions is also consistent with previous findings (MacDougall et al. 2006). Certain exotics, such as exotic perennial grasses, tend to do better in deeper soils and may be better competitors against natives in these less stressful environments (MacDougall et al. 2006).

Despite the highly fragmented nature of Garry oak savanna habitat and the hypothesized importance of spatial integrity to native biodiversity (Fuchs 2001), we found that spatial habitat structure was not a dominant driver of regional-scale biodiversity patterns. We expected greater explanatory power of connectivity for composition and individual species distributions but our habitat connectivity index explained only small amounts of variation in native composition, and few native or exotic species show patch occupancy effects attributable to connectivity. On the other hand, patch area significantly predicted patch occupancy for about 30% of native and exotic species. The positive effects were consistent with lower probabilities of extinction within large patches (Bastin and Thomas 1999). Other studies have found that habitat quality (i.e., environmental conditions) is usually a more important factor driving the distributions of species and that habitat configuration only explains distributions of a subset of species (Dupre and Ehrlén 2002). Connectivity may be difficult to generalize across species since plant dispersal is not well understood for most species and the metapopulation description of plant populations may not be appropriate for many species (Freckleton and Watkinson 2002, Lindenmayer et al. 2008). Although the response time of plant populations to fragmentation may be slow (Helm et al. 2006, Vellend et al. 2006), the relative importance of human influence factors suggests that disturbance effects currently overwhelm any effects due to spatial habitat structure.

While species responses to habitat attributes and landscape structure are expected to depend on life history traits (Henle et al. 2004, Kolb and Diekmann 2005), we found that the traits we examined provided few insights into why responses to key habitat variables varied among species. Our finding that native habitat specialists were more

sensitive to area effects is consistent with recent assertions that metapopulation models are best suited for species where habitat can be well-defined within patches (Freckleton and Watkinson 2002). Explanations for trait effects that were marginally significant are more speculative. For example, most of the habitat generalists with significant road density effects are also coniferous forest understory species and found outside Garry oak habitats. The higher sensitivity of habitat generalists to increasing road density may be because populations of these species found within oak savanna patches represent sink populations dependent on nearby forested habitats for continued recruitment. We only observed trait-environment relationships for native species. This may be because native species distributions are in closer equilibrium with environment conditions than exotic species, which have only recently arrived and have not yet had time to distribute themselves with respect to their traits and environmental gradients (Guo 2006). These possibilities are in need of future testing.

Finally, our results have several important implications for conservation and management of remnant oak savanna patches. First, the importance of road density in predicting species composition among patches suggests that surrounding human development plays a dominant role in compositional shifts of plant communities in adjacent patches even when patches are seemingly protected in parks or protected areas. Consequently, management activities should seek to limit these impacts to avoid further declines in native plant species populations. Additional research could help to understand the particular mechanisms behind such effects so that human influence effects can be most appropriately mitigated. Second, the lack of observed connectivity effects suggests that planning measures to promote connectivity in conservation planning will be less

effective than site-specific actions that limit human influence. Third, a general lack of predictive ability of our selected species traits suggest that common traits, at least the ones we tested, provide little help in predicting responses of certain species, such as those of conservation concern, to further habitat change.

Table 3.1. Results of forward selection of variables for canonical correspondence analyses (CCA) of native and exotic species composition at the regional scale.

Selection order is shown for each CCA with conditional (or partial) effects showing additive contributions to variance explained (relative to total variation explained by all explanatory variables). “-“ indicates variables that were not selected because they did not explain additional significant variation once other variables were already in the CCA. Marginal (independent) effects show the amount of variation explained by a CCA using that variable alone (relative to the total variation explained by all explanatory variables). Marginal effects do not add to 100% because of shared variation between variables.

Variable (N=43)	CCA of native species – regional scale			CCA of exotic species – regional scale		
	Selection order	Variance explained (%)		Selection order	Variance explained (%)	
		Conditional effects	Marginal effects		Conditional effects	Marginal effects
Patch area (log ₁₀)	-		10.2	4	8.8	9.3
Connectivity (log ₁₀)	4	8.5	15.4	-		19.4
Surrounding road density	3	9.5	24.6	1	34.5	34.5
Mean slope	-		20.1	-		23.6
Mean degrees from north	5	7.3	9.5	-		9.9
Mean canopy cover	2	15.3	15.3	5	6.9	15.5
Mean soil depth (log ₁₀)	7	6.1	10.6	-		7.2
Soil depth heterogeneity (CV)	6	6.8	14.7	-		7.3
Soil pH	-		9.2	3	10.7	13.7
Climate	1	29.8	29.8	2	13.6	33.9
Total variation explained by selected variables		83.2			74.2	

Table 3.2. Canonical coefficients and intraset correlations for significant variables with axes of canonical correspondence analyses (CCA) of composition at the regional scale.

The environmental variables were standardized to make the canonical coefficients of different variables comparable.

(a) Native species composition – regional scale (N=43)

Axis variable	Canonical coefficients				Intraset correlations			
	Axis 1	Axis 2	Axis 3	Axis 4	Axis 1	Axis 2	Axis 3	Axis 4
Climate (PCA1)	-0.65	0.32	-0.83	0.11	-0.95	0.10	-0.19	0.063
Mean canopy cover	0.010	-0.65	0.58	0.19	-0.066	-0.91	0.069	-0.047
Surrounding road density	0.37	0.27	-0.39	0.85	0.81	0.33	-0.18	0.38
Log connectivity	-0.089	-0.30	0.26	0.90	-0.56	-0.026	0.29	0.67
Mean degrees from north	0.025	-0.18	-0.55	0.25	-0.11	-0.51	-0.47	0.014
CV soil depth	-0.11	0.28	0.58	0.19	-0.43	0.55	0.43	0.24
Log soil depth	-0.054	-0.090	-0.35	0.15	0.29	-0.42	-0.41	0.23

(b) Exotic species composition – regional scale (N=43)

Axis variable	Canonical coefficients				Intraset correlations			
	Axis 1	Axis 2	Axis 3	Axis 4	Axis 1	Axis 2	Axis 3	Axis 4
Surrounding road density	-0.47	0.71	-0.28	-1.05	-0.91	0.19	-0.23	-0.22
Climate (PCA1)	0.56	0.35	-0.25	-1.41	0.90	0.23	-0.15	-0.31
Soil pH	-0.15	0.71	0.12	0.40	0.21	0.83	-0.17	0.20
Log area	0.11	-0.21	-0.91	0.52	0.15	0.072	-0.95	0.25
Mean canopy cover	0.17	0.44	0.16	0.31	0.48	0.47	0.33	0.40

Table 3.3. Results of forward selection of variables for canonical correspondence analyses (CCA) of native and exotic species composition at the local scale.

Selection order is shown for each CCA with conditional (or partial) effects showing additive contributions to variance explained (relative to total variation explained by all explanatory variables). “-“ indicates variables that were not selected because they did not explain additional significant variation once other variables were already in the CCA. Marginal (independent) effects show the amount of variation explained by a CCA using that variable alone (relative to the total variation explained by all explanatory variables). Marginal effects do not add to 100% because of shared variation between variables.

Variable (N=52)	CCA of native species – local scale			CCA of exotic species – local scale		
	Selection order	Variance explained (%)		Selection order	Variance explained (%)	
		Partial effects	Marginal effects		Partial effects	Marginal effects
Distance to nearest road	-		12.4	-		6.5
Slope (square root)	2	17.0	16.9	4	11.0	10.3
Degrees from north	-		12.8	-		8.7
Canopy cover (square root)	1	29.4	29.4	3	14.4	20.9
Soil depth (square root)	-		16.9	1	22.5	28.3
Soil pH	-		13.2	2	15.8	19.9
Soil moisture	-		15.9	-		26.6
Total variation explained by selected variables		46.4			80.1	

Table 3.4. Canonical coefficients and intraset correlations for significant variables with axes of canonical correspondence analyses (CCA) of composition at the local scale.

The environmental variables were standardized to make the canonical coefficients of different variables comparable.

(a) Native species composition – local scale (N=52)

Axis variable	Canonical coefficients				Intraset correlations			
	Axis 1	Axis 2	Axis 3	Axis 4	Axis 1	Axis 2	Axis 3	Axis 4
Canopy cover (square root)	-1.00	0.022	-	-	-1.00	0.080	-	-
Slope (square root)	-0.080	-1.00	-	-	-0.022	-1.00	-	-

(b) Exotic species composition – local scale (N=52)

Axis variable	Canonical coefficients				Intraset correlations			
	Axis 1	Axis 2	Axis 3	Axis 4	Axis 1	Axis 2	Axis 3	Axis 4
Soil depth (square root)	-1.02	0.15	0.30	0.26	-0.88	-0.070	-0.03	0.46
Soil pH	-0.080	0.65	-0.78	0.19	-0.084	-0.74	-0.67	-0.019
Canopy cover (square root)	-0.16	-0.63	-0.69	-0.45	-0.33	-0.67	-0.64	-0.18
Slope (square root)	-0.51	0.23	0.29	-0.92	-0.10	0.46	0.17	-0.87

Table 3.5. Results of logistic regression analyses testing whether species traits predict the presence-absence of effects of explanatory variables across 62 native species at the regional scale.

Nine explanatory variables were tested and numbers in bold represent significant (or near significant) relationships between traits and particular variables.

	Area		Connectivity		Road density		Slope		Aspect		Canopy cover		Soil depth		Soil pH		Climate	
	β^\dagger	Sign.	β^\dagger	Sign.	β^\dagger	Sign.	β^\dagger	Sign.	β^\dagger	Sign.	β^\dagger	Sign.	β^\dagger	Sign.	β^\dagger	Sign.	β^\dagger	Sign.
Life form		NS		NS		NS		(*)		NS								
Tree/shrub	-		-		-				-		-		-		-		-	
Forb	-		-		-			-1.1423		-		-		-		-		-
Graminoid	-		-		-			1.2091		-		-		-		-		-
Fern	-		-		-			0.5159		-		-		-		-		-
Life span		NS		NS		NS		NS		NS		NS		NS		NS		NS
Annual	-		-		-		-		-		-		-		-		-	
Biennial	-		-		-		-		-		-		-		-		-	
Perennial	-		-		-		-		-		-		-		-		-	
Dispersal mode		NS		NS		NS		NS		NS		NS		NS		NS		NS
Wind	-		-		-		-		-		-		-		-		-	
Vertebrate	-		-		-		-		-		-		-		-		-	
Ants/ballistic/none	-		-		-		-		-		-		-		-		-	
Habitat specialization		*		NS		(*)		NS		NS		NS		NS		NS		NS
Specialist																		
Generalist	-0.6561				0.5526													

Notes: Refer to Appendix E for trait classifications of each species. One statistical test was conducted for each species trait (listed as the major heading). “-“ denotes no effect.

* Significance (Sign.) is indicated as: (*), $0.05 \leq P < 0.1$; *, $P < 0.05$; NS, not significant.

$\dagger \beta$ is the maximum likelihood value of the coefficient for each variable in the fitted logistic regression model. Because one less design variable than the number of levels of each nominal variable was used in the model.

Figure 3.1. Biplots of CCA output for native and exotic species composition at the regional scale.

Data is from forty-three remnant oak savanna patches. Select plant species (triangles) and explanatory variables selected by forward selection (arrows) are shown. Plant species shown are key oak savanna species found at both scales and the same species as shown in Fig. 3.2 for purposes for comparison. Percent variation in species composition explained by each axis is shown in brackets.

(a) Native species – regional scale

Plant species shown are: ACHIMIL = *Achillea millefolium*, ACHNLEM = *Achnatherum lemmonii* var. *lemmonii*, ALLIACU = *Allium acuminatum*, BRODCOR = *Brodiaea coronaria* ssp. *coronaria*, CAMASSI = *Camassia* sp., CAREINO = *Carex inops* ssp. *inops*, CERAARV = *Cerastium arvense*, COLLPAR = *Collinsia parviflora*, DANTCAL = *Danthonia californica*, LOMANUD = *Lomatium nudicaule*, LOMAURT = *Lomatium urticulatum*, MELISUB = *Melica subulata*, MIMUALS = *Mimulus alsinoides*, MONTPAR = *Montia parviflora*, OLYSDOU = *Olysnium douglasii* var. *douglasii*, PENTTRI = *Pentagramma triangularis*, PLECCON = *Plectritis congesta*, RANUOCC = *Ranunculus occidentalis* var. *occidentalis*, SANICRA = *Sanicula crassicaulis*, SEDUSPA = *Sedum spathifolium*.

Explanatory variables shown are: climate = first axis of climate PCA, canopy = mean canopy cover, roads = surrounding road density, connect = log connectivity, aspect = mean degrees from north, CV_depth = coefficient of variation in soil depth, depth = log mean soil depth.

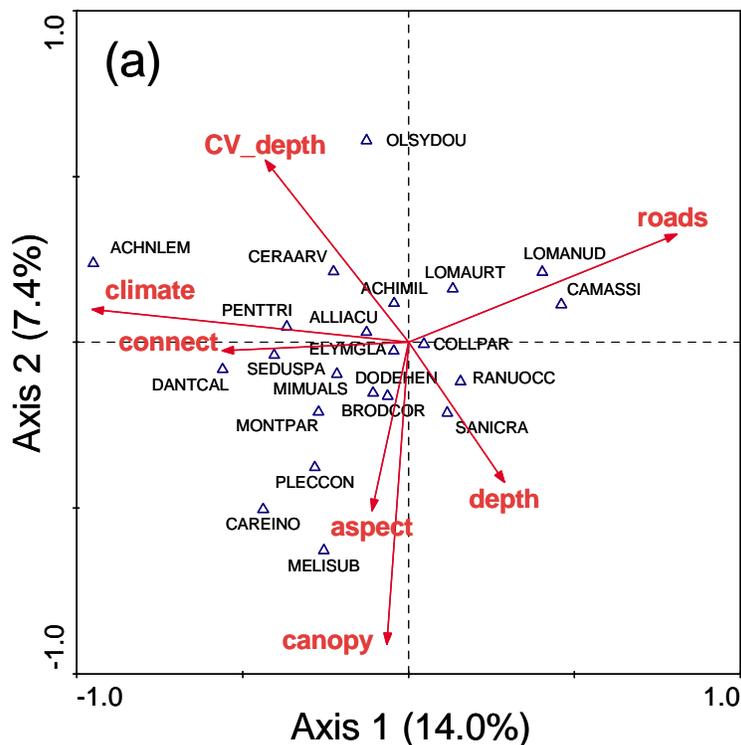


Figure 3.1 cont'd.

(b) Exotic species – regional scale

Plant species shown are: AIRACAR = *Aira caryophyllea*, AIRAPRA = *Aira praecox*, ANTHODO = *Anthoxanthum odoratum*, BROMHOR = *Bromus hordaceus*, BROMSTE = *Bromus sterilis*, CYNOECH = *Cynosurus echinatus*, CYTISCO = *Cytisus scoparius*, DACTGLO = *Dactylis glomerata*, HYPEPER = *Hypericum perforatum*, HYPOGLA = *Hypochaeris glabra*, HYPORAD = *Hypochaeris radicata*, MYOSDIS = *Myosotis discolor*, POA_PRA = *Poa pratensis*, STELMED = *Stellaria media*, TEESNUD = *Teesdalia nudicaulis*, VEROARV = *Veronica arvensis*, VICIHIR = *Vicia hirsuta*, VICISAT = *Vicia sativa*, VULPBRO = *Vulpia bromoides*, VULPMYU = *Vulpia myuros*.

Explanatory variables shown are: roads = surrounding road density, climate = first axis of climate PCA, pH = soil pH, area = log area, canopy = mean canopy cover.

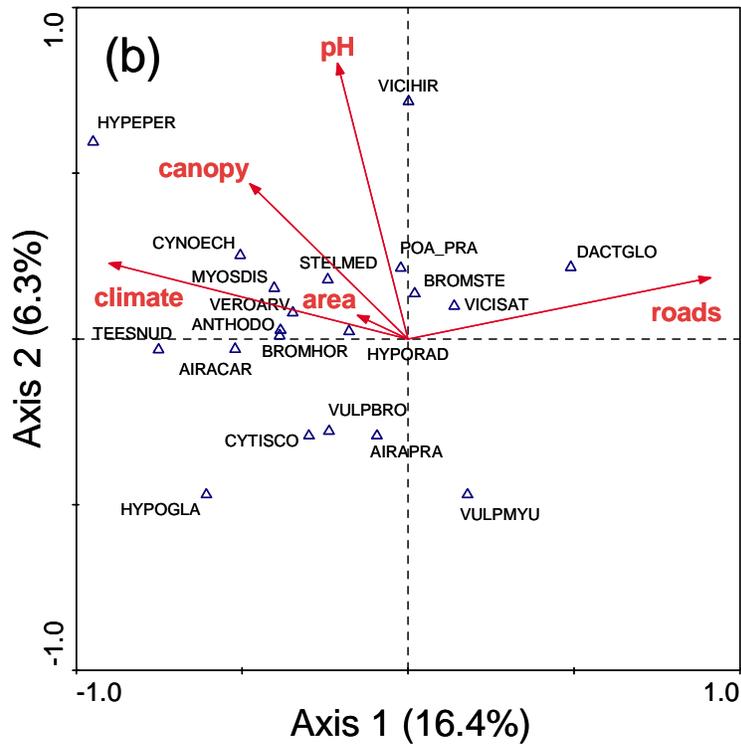


Figure 3.2. Biplots of CCA output for native and exotic species composition at the local scale.

Abundance data is from fifty-two 1-m² circular plots at Mill Hill Regional Park. Select plant species (triangles) and explanatory variables selected by forward selection (arrows) are shown. Plant species shown are key oak savanna species found at both scales and the same species as shown in Fig. 3.1 for purposes for comparison. Percent variation in species composition explained by each axis is shown in brackets.

(a) Native species – local scale

For abbreviations for the plant species shown, see the caption for Fig. 3.1a.

Explanatory variables shown are: canopy = canopy cover, slope = square root slope.

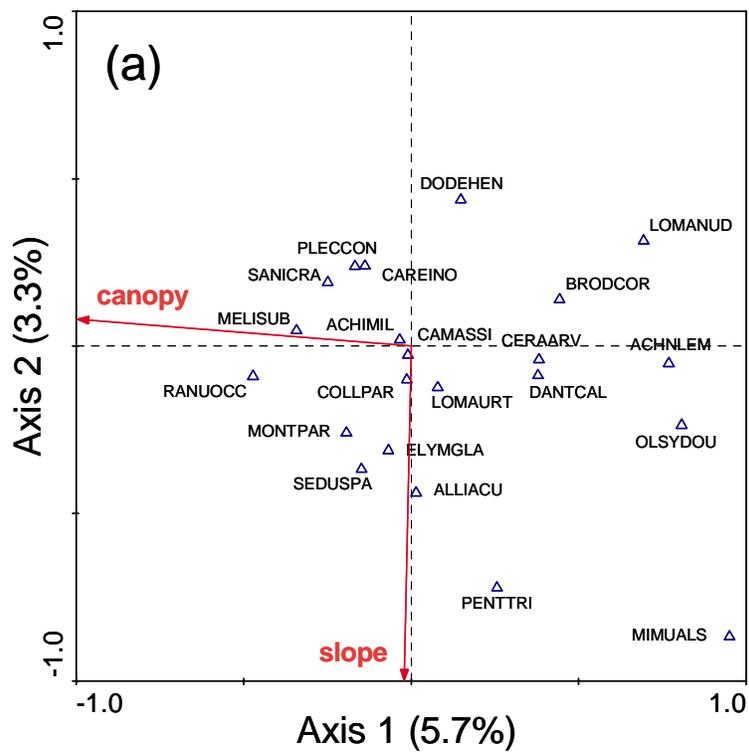


Figure 3.2 cont'd.

(b) Exotic species – local scale

For abbreviations for the plant species codes shown, see the caption for Fig. 3.1b.

Explanatory variables shown are: depth = soil depth, pH = soil pH, canopy = square root canopy cover, slope = square root slope.

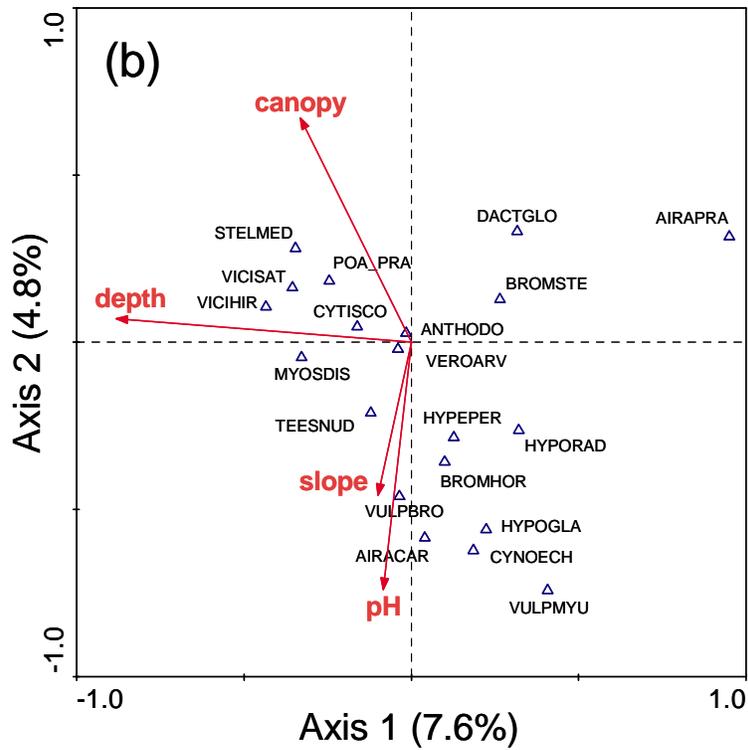
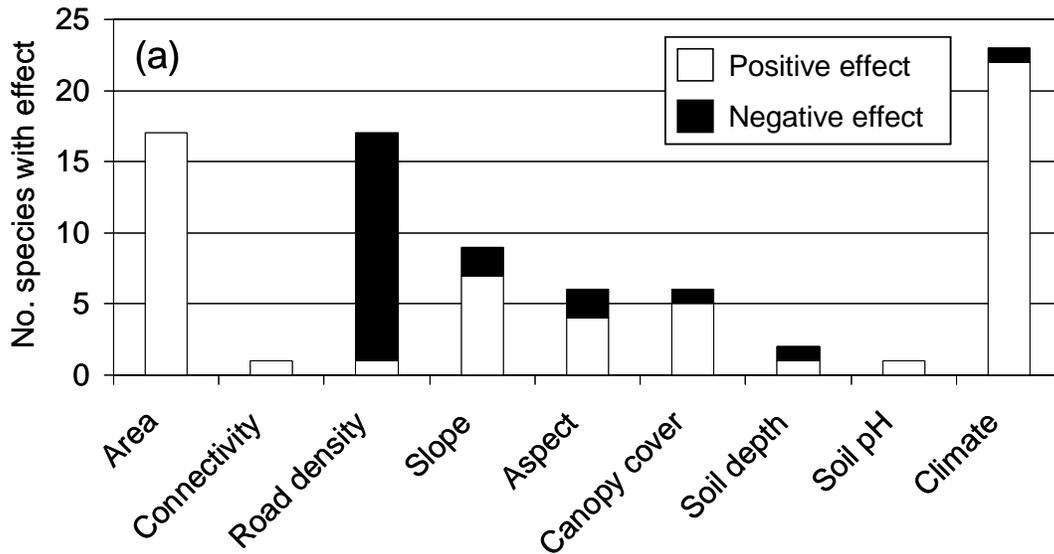


Figure 3.3. Bar graphs showing number of significant effects for each explanatory variable across all multiple logistic regression models for native species and exotic species at the regional scale.

Variables were selected for inclusion in each model using forward stepwise selection (α for entry = 0.05, α to stay = 0.05). Colours indicate the direction of effect: open bars indicate positive effects (i.e., increasing values of variable predicts species presence) and solid bars indicate negative effects (i.e., increasing values of variable predicts species absence). For example, the bar for road density in (a) indicates that a significant effect of roads on patch occupancy was found for 17 of 62 native species tested, with 1 positive effect and 16 negative effects.

(a) Native species – regional scale (62 natives)



(b) Exotic species – regional scale (50 exotics)

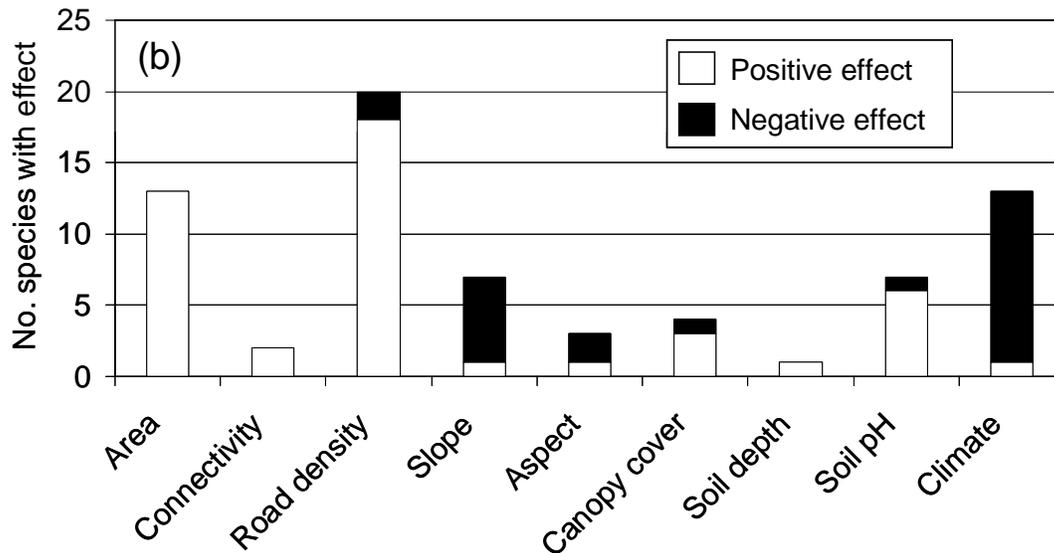
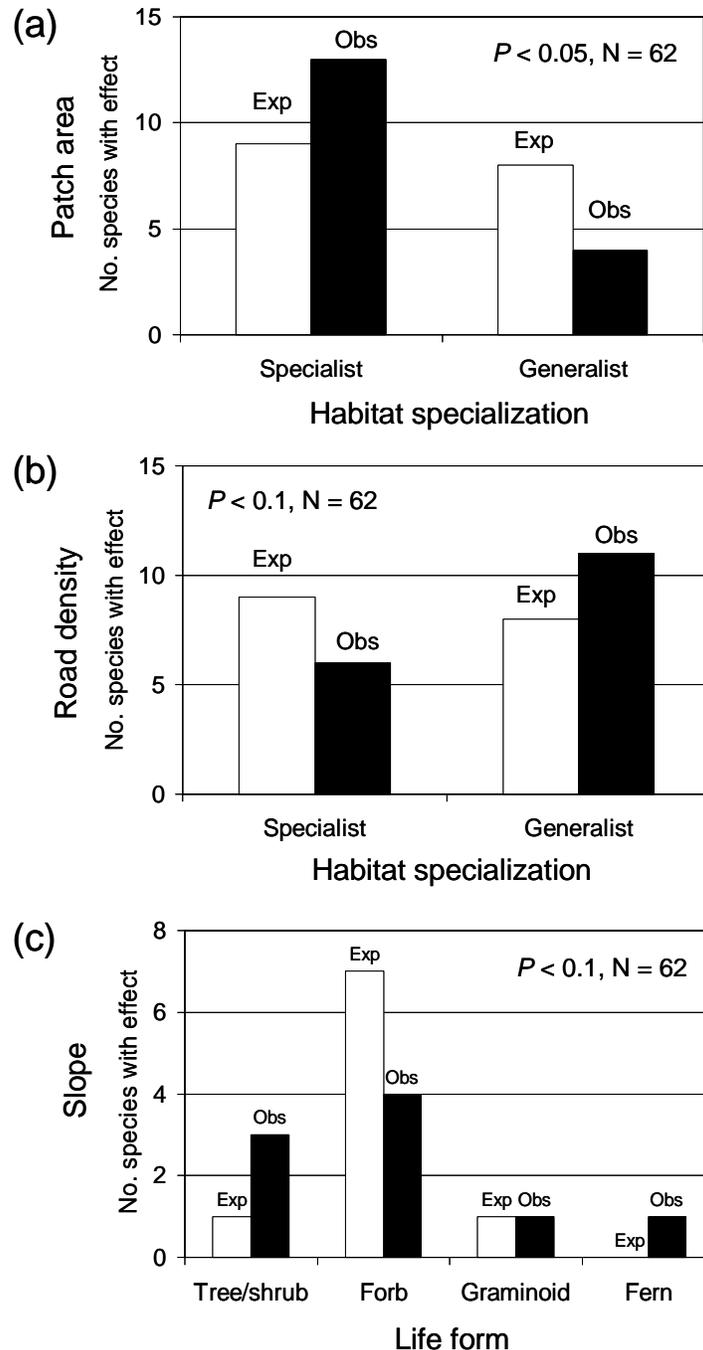


Figure 3.4. Bar graphs showing the one significant and two marginally significant relationships between life history traits and frequency of effects for explanatory variables.

In each case, the observed number of species exhibiting effects (solid bars) are compared to the expected number of species exhibiting effects (open bars) based only on the proportion of species with that trait in the data (i.e., if there was no relationship between the trait and the explanatory variable). (a) Habitat specialists are more likely to show effects of patch area ($P = 0.042$), (b) habitat generalists are more likely to show effects of surrounding road density ($P = 0.063$), and (c) woody species were more likely to show effects of slope than forb species ($P = 0.090$). Logistic regressions were used to conduct the statistical tests.



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4 Conclusion

Biodiversity conservation depends on research into the basic processes that produce and maintain patterns of species diversity and composition in ecological communities. Identifying the relative importance of different factors that determine species distributions in specific landscapes is also essential to conserving particular threatened ecosystems. My research, focused on the determinants of plant species diversity and composition in remnants oak savannas on southeastern Vancouver Island, was aimed at furthering both of these goals. Consequently, in this final chapter, I will review how my research has contributed to knowledge of plant communities and exotic plant invasions in general, as well as how it applies to conserving and managing remaining Garry oak habitats specifically. I will highlight where information may still be limited and further speculate about what other mechanisms may be important to structuring plant communities in this ecosystem but which were not the focus of my study. In these ways, I will generate ideas of how future research could build upon the progress I have made.

My research confirms the importance of considering both *local* and *regional* factors as potential determinants of species diversity and composition in plant communities (Menge and Olson 1990, Ricklefs and Schluter 1993). It also shows how the relative importance of factors can change with the scale of observation (Levin 1992). Both regional and local factors, road density and climate respectively, were the dominant extrinsic drivers of native and exotic richness (Chapter 2) and composition (Chapter 3) at the regional scale among remnant oak savanna patches. However, environmental conditions, such as canopy cover and soil depth, largely explained the composition of

natives and exotics at local scales within patches. Therefore, considering habitats in both their regional and local context and at different scales, as I have done here, is vital to understanding patterns of both native and exotic species.

In Chapter 2, I addressed the observed patterns in native and exotic species richness in oak savanna habitat. Elton (1958) hypothesized that native species diversity should increase a community's resistance to invasion from exotic species producing a negative relationship between native and exotic species richness. However, recent research has suggested a spatial scale-dependence to the direction of the relationship: negative relationships are often seen at the fine scales at which species interact (e.g., 1-m² plots; Tilman 1997, Stachowicz et al. 2002) while positive relationships are found at broad scales (e.g., landscapes) because of similar extrinsic controls on native richness and exotic richness (Sax 2002, Shea and Chesson 2002). In contrast to most reported results at broad scales (Fridley et al. 2007), I found that native and exotic species richness were negatively correlated at the regional scale (landscape scale > 100 km²). However, this broad-scale negative relationship was best explained by opposite responses of natives and exotics to extrinsic factors (road density and climate) rather than resident diversity resisting invasion. While extrinsic factors are expected to affect native and exotic diversity similarly in some situations (e.g., Brown and Peet 2003, Davies et al. 2005), I found that extrinsic factors may also affect natives and exotics oppositely (see also McIntyre and Lavorel 1994). Future research can assess the generality of this result by examining native and exotic richness at multiple scales in landscapes with factors potentially influencing natives and exotics in opposite ways, such as development

gradients. This work would help to clarify what extrinsic factors can produce negative native-exotic richness relationships and whether such relationships are common or not.

In Chapter 3, I looked at whether native and exotic species composition is affected similarly or differently by habitat context. Like species richness, I found native and exotic community composition also changed most strongly with road density and climate. However, these factors generally had opposite effects on the patch occupancy of individual native and exotic species. Decreasing road density and wetter, cooler climates predicted presences for many natives and absences for many exotics. I have proposed potential mechanisms for how these factors could affect native and exotic species differently. For example, road density may increase exotic propagule pressure and disturbance. Disturbance may negatively impact native species while promoting exotics because of evolutionary differences in their tolerance for anthropogenic disturbance (di Castri 1989). These mechanisms represent testable hypotheses for future research. Soil disturbance, trampling, nutrient inputs, fire suppression, and changes in moisture, light, and grazing regimes are possible changes brought about by roads (Trombulak and Frissell 2000). Understanding what particular effects on habitat are most responsible for plant community change will improve understanding of how human influence, in a broad sense, can alter ecological communities.

Taken together, Chapters 2 and 3 showed that the changes in species richness I observed across the landscape were not due to random gains or losses of species along the species richness gradients; road density and climate predicted changes in both richness and composition. Only 30-40% of native and exotic species show effects of these factors (Chapter 3), and simple life history traits accounted for few of the

differences among species. Other traits that are more difficult to measure, or complex combinations of traits, must determine the differential responses observed. For example, species' physiological tolerances or plastic responses to different factors may determine differential environmental controls on distribution, and these traits may be unrelated to the simple traits I measured. Species-specific studies could begin to explore how and why different species are capable of tolerating disturbance or wider climatic niches while other species are not.

As mentioned in chapters 2 and 3, because road density and climate are correlated, a large proportion of variation in species richness and composition is attributable to either factor and it is difficult to determine their relative effects. While multicollinearity can limit what interpretations can be made from data (James and McCulloch 1990, Graham 2003), the correlation between these factors in the data also reflects their correlation in the field. I have attempted to use statistics to account for and acknowledge multicollinearity and report shared variation where appropriate using methods such as variance partitioning (Legendre and Legendre 1998). Given that climate is an intrinsic feature of the local environment and road density is human-caused, each factor has different implications for prescribing conservation actions. Future studies could use targeted sampling methods to break the correlations among explanatory variables (e.g., Gilbert and Lechowicz 2005). Experiments that test the success of species under different disturbance and climate regimes may also help disentangle the effects of human influence and climate.

My work has shown that human influence is an important driver of diversity pattern in this landscape and can help explain current diversity and composition patterns.

In my research, I used predictor variables derived from present-day landscapes, such as current road density. However, the variables that influence plant communities can change over time and factors acting in the past may also have shaped patterns seen today. Two historical factors in particular may affect native and exotic plant species distributions in both in my study system and other ecosystems more broadly. First, for exotics, time since introduction can be an important predictor of exotic success (Scott and Panetta 1993, Lambdon and Hulme 2006). This factor could explain why only some species show sensitivity to road density while other species are more widely distributed. The number of exotic species in oak savannas on southeastern Vancouver Island has increased over time (Roemer 1995), undoubtedly due to newly arriving non-native species. Some species, such as many forage plant species, are thought to have arrived soon after European settlement of the region in the 1840's. Many garden or horticultural escapees have likely arrived only as urbanization increased in the mid 20th century. These recent arrivals may be more likely to show dispersal-limited distributions because they have not had time to distribute themselves in response to other gradients (Wiser et al. 1998). While quantitative records of introduction dates do not exist, it may be possible to develop surrogate indices to help resolve species-specific differences. For example, assessing differences between agricultural-introduced species vs. horticultural species, or species introduced with greater or lesser numbers of propagules (few introductions vs. broadcast seeding), could provide indirect tests of the importance of time since introduction or mode of introduction.

A second historical factor that may influence current-day plant communities is when human influence began to occur around remnant patches. Deferrari and Naiman

(1994) found that species distributions may relate more to cumulative disturbance over time than to current-day disturbance patterns. Past habitat connectivity has been found to predict species distribution patterns in other systems better than current-day landscape metrics (Lindborg and Eriksson 2004). Effects of historical connectivity have been shown to persist as extinction debts for more than a century (Vellend et al. 2006). While easy to measure, current road density may not capture some of the variation in human influence that has occurred because of variation in the times at which roads were constructed and differences in particular land uses around patches. Further characterizing the disturbance history of patches may improve explanations for variation in richness and composition among remnant patches and is an exciting possibility for future research.

My results have several interesting implications for the conservation and management of remaining Garry oak habitat on southeastern Vancouver Island. First, protecting oak savanna habitat patches with low surrounding road density and cool, wet climatic conditions will conserve the highest native diversity sites while minimizing levels of exotic invasion. Thus, road density and climate should be important criteria for selecting future protected areas if the goal is maximizing native plant biodiversity at individual sites. These site selection criteria, though they may not adequately protect individual species of conservation concern, will conserve the most diverse and intact remnant plant communities, and represent an important broad-level approach for plant conservation in this ecosystem. The importance of road density also suggests minimizing future road development around existing sites should be considered.

Second, while spatial integrity has been noted as an important consideration for conservation planning (Fuchs 2001), my data showed that the connectivity of patches

does not seem to be an important consideration for plants in this ecosystem. I found connectivity effects for very few species. On the other hand, patch size did influence native diversity and composition positively. The lack of connectivity effects may indicate a true lack of sensitivity of the plant community to this variable, or that habitat loss and fragmentation is severe enough that all sites are similarly dispersal-limited (i.e., there is little variation among sites in connectivity). It is possible these effects may emerge over time as fragmentation in this ecosystem is somewhat recent (i.e., last 150 years). However, at present, my analyses suggest that factors other than connectivity are more appropriate criteria for selecting sites for protection.

Third, even though my research sites were situated in parks or protected areas, I still observed a strong effect of surrounding development context (as measured by road density) on native and exotic richness and composition. As a result, simply establishing a park appears inadequate to protect plant communities from exotic propagule pressure and human disturbance. Human disturbances, such as trampling, appear quite heavy in parks that receive many visitors (personal observation). Specific mechanisms underlying the effect of road density are not entirely known but locating trails appropriately and limiting human access to certain areas may be key management tools. Minimum-width development buffers around Garry oak sites may provide some protection as well.

In conclusion, the ecological patterns I have observed have provided a new perspective on how local and regional factors act to determine the distribution and abundance of species within ecosystems and how human impacts, such as disturbance and the introduction of exotic species, may alter these patterns. My analysis has identified human influence and climate as key factors driving of plant distributions in Garry oak

ecosystems for both native and exotic species. However, their opposite effects on natives and exotics suggest that native and exotic species are fundamentally different in their responses to these factors. The documented patterns of species with respect to road density and climate suggest these factors should be used to identify priority sites for Garry oak savanna conservation, to guide surrounding land-use decisions, and to manage existing protected sites. Concurrently, researchers also need to better evaluate the relative effects of these two factors and the mechanisms by which these factors may affect specific species. These approaches will improve the effectiveness of conservation actions for the Garry oak plant communities on southeastern Vancouver Island and other threatened ecosystems.

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Appendices

Appendix A

Methodological details, including characterization of patch attributes, environmental parameters, and statistical testing (Chapter 2)

FURTHER DESCRIPTION OF STUDY AREA

Garry oak (*Quercus garryana* Dougl. ex Hook.) savannas on southeastern Vancouver Island and across their range exist in the lee of the coastal mountain ranges of western North America. In British Columbia, the climate in these ecosystems is sub-Mediterranean, with a significant summer drought (Fuchs 2001). Soils are post-glacial, moderately infertile, and generally less than 1 m deep (Roemer 1972, Erickson 2002). Since European settlement in the mid 19th century, oak savanna habitat on Vancouver Island has been altered and fragmented by development, agriculture and forestry such that less than 10% remains in a near-natural state (Lea 2006). We sampled patches in these remaining habitats. Patches lie across an urban-rural gradient. Current land use intensity around these patches varies from dense urbanization to second-growth Douglas-fir (*Pseudotsuga menziesii* (Mirbel) Franco var. *menziesii*) forest. All patches sampled were in parks or other protected areas.

DERIVATION OF GEOGRAPHIC AND ENVIRONMENTAL PATCH CHARACTERISTICS

Patch area, connectivity and surrounding road density

To characterize spatial context, patch area and connectivity were derived from GIS analysis in ArcView GIS 3.2 (Environmental Research Systems Institute, Redlands, California, USA). Patch area (used as a covariate) was calculated by differentiating habitat patches from surrounding vegetation or development on high-resolution colour

orthophoto images from July 2005 provided by the Capital Regional District (regional government). Groundtruthing was completed during plant surveys and boundaries were adjusted as necessary. Connectivity to surrounding similar habitats was found using a regional database of spatially-delineated oak savanna habitat patches for the region (excluding our study patches) updated in June 2005 (Ward et al. 1998). The connectivity of patch i was calculated as follows (Moilanen and Nieminen 2002, Eq. 3):

$$S_i = \sum_{i \neq j} \exp(-\alpha d_{ij}) A_j$$

where A_j is the area of patch j (in m^2), d_{ij} is the minimum edge-to-edge distance (in m) between patches i and j , and α is the parameter setting the influence of distance on connectivity. We used $\alpha = 0.002$ which represents a realistic average migration range for most grassland species (Verheyen et al. 2004, Bastin and Thomas 1999, Johansson and Ehrlén 2003). Minimum edge-to-edge-distances were calculated using the “Distances and Bearings between Matched Features v. 2.1” extension for ArcView (Jenness Enterprises, Flagstaff, Arizona, USA).

As an index of human influence, representing both the propagule pressure of exotic species and degree of potential human-mediated disturbance, we calculated surrounding road density as the length of roads per km^2 within a 500 m buffer around each patch. Road mapping was from a 1:20,000 Terrain Resource Inventory Mapping (TRIM) roads layer provided by the Province of British Columbia.

Environmental variables

Stratified random sampling was used to characterize mean environmental conditions within patches. Sample points were selected by dividing each patch into four approximately equal area sections and generating random points within each quarter-

section using the “DNR Random Sample Generator” extension for ArcView (Minnesota Department of Natural Resources, St. Paul, Minnesota, USA). Sampling points were located in the field using a handheld GPS. At least 32 (8 per quarter-section) and no more than 40 points (10 per quarter-section) were sampled in each patch.

Slope, aspect, canopy cover, and soil depth were measured at each sampling point. Slope and aspect were measured using a clinometer and compass, respectively. As aspect is a circular variable, it was converted to degrees from north. Canopy cover was assessed using a spherical densiometer (Lemmon 1956). Soil depth was found by pushing a 70-cm small diameter steel probe to bedrock. Measurements were taken at the plot centre and 40-cm from plot centre in each of the four cardinal directions and averaged. We also calculated a coefficient of variation (CV) in soil depth to quantify within-patch habitat heterogeneity. We selected soil depth as our heterogeneity measure because it was the only variable measured at multiple points within sites for which the mean-CV correlation was less than 0.5 ($r = -0.479$, $P = 0.001$).

Soil pH was measured from a composite soil sample. A 6-cm diameter soil core was taken to 10 cm depth at a randomly-selected subset of ten of the above sampling points (2-3 per quarter-section). 120 ml of soil was collected from each core and combined into a single sample for the patch. Composite samples were uniformly mixed, dried, sifted, and pH measured using an ion-exchange membrane probe in a 1:4 soil-to-water mixture (5 g of soil, 20 ml of water).

Mean annual precipitation and temperature for each patch were interpolated from 1961-1990 climate normals using the Climate BC database (Hamann and Wang 2005, Wang et al. 2006). Because mean temperature, precipitation, and elevation were highly

correlated across the landscape ($|r| = 0.471-0.851$), we used the first axis of a principal components analysis (PCA) based on these three variables as a synthetic variable to represent “climate” in subsequent analyses. This axis explained 86.5% of the variation in the data.

LOCAL-SCALE (1-m²) PLOT SURVEYS

The local-scale study was located in our largest habitat patch at Mill Hill Regional Park in Langford, British Columbia, Canada (48°27' N 123°30' W). This site, approximately 30 ha in size, was chosen for its regional representativeness and range of environmental conditions covered within the patch. Plot locations were chosen from an initial set of 100 stratified randomly-generated points (see methods above) to ensure the sampled plots covered a broad range of conditions.

For the 1-m² plots, we measured the same or similar predictor variables as in the regional-scale study where possible. While area and connectivity do not have local-scale analogs, we used distance from each plot to the nearest road as an index of proximity to urbanization and an analog for road density at the regional scale. Slope, aspect, canopy cover, soil depth, and soil pH were measured for the plots as in the regional scale except that soil pH was measured from a single soil core at the plot centre. As fine-scale climate data for each plot was unavailable, soil moisture (% volumetric water content) was added as an additional environmental predictor at the local scale and measured using a Hydrosense Time Domain Reflectometer (TDR) (Campbell Scientific, Logan, Utah, USA). Where necessary at both scales, predictor variables were log- or square root-transformed to reduce skew.

STATISTICAL TESTING

The correlation between native and exotic species richness was tested using Pearson's correlation coefficient at each scale. Given the obvious and ubiquitous effect of area on species richness (Rosenzweig 1995), at the regional scale we also examined the partial correlation between native and exotic richness, controlling for patch area.

We fit separate generalized linear models (GLM) for exotic and native species richness, using a Poisson distribution with a log-link function. We first removed the effect of area by including it as a covariate (entered first into the GLM), as species-area effects were not a focus of this study. Because of potential overdispersion in the count data, we included a variance inflation factor or scale parameter c (Burnham and Anderson 2002). Variables were added sequentially through forward selection by adding the variable that provided the largest increase in the log-likelihood until further addition of variables did not yield a significantly better model fit (likelihood ratio test, $\alpha=0.05$). Significance of individual predictor variables in the final models was assessed using likelihood ratio tests.

To assess the relative predictive abilities of extrinsic variables vs. native richness to predict exotic richness and vice versa, we compared three models for each species type with an intercept-only null model: (1) a model using only exotic or native richness as a predictor, (2) a model using only the selected extrinsic predictors, and (3) a global model combining both types of predictors. Models were compared using a variant of Akaike's Information Criterion, the QAIC_C (Burnham and Anderson 2002) and, where models were nested, likelihood ratio tests. Adjusted generalized coefficients of determination, R^2_{adj} (Nagelkerke 1991), were calculated to compare model fits to a saturated model.

Analyses were carried out in SAS version 9.1.3 (SAS Institute Inc., Cary, North Carolina, USA).

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Appendix B

Full results of model comparisons for predicting native and exotic species richness at regional and local scales (Chapter 2)

Table B.1. Full model comparison results for generalized linear models predicting native and exotic species richness at regional and local scales.

Patch area was used as a covariate in the regional models. Log-likelihood tests were used to compare nested models. Asterisks (*) with log L values denote significantly different models. QAIC_c and adjusted (max-rescaled) generalized coefficients of determination (R^{2*}) were used to compare non-nested models. A single scale parameter c is used for each set of models and is estimated from the global model (model 3) (Burnham and Anderson 2002).

(a) Native species richness - regional scale

Model	Variables included	Deviance	df	log L	QAIC _c	Adjusted R ^{2*}
Intercept only (null)	-	292.3800	42	4585.0218*	-7178.116	0
Richness only	patch area, exotic SR	102.3772	40	4643.2333**	-7268.95	0.9333
Extrinsic factors only	patch area, road density, climate	62.0630	39	4655.5844***	-7287.971	0.9624
Richness + extrinsic factors (global)	patch area, road density, climate, exotic SR	62.0209	38	4655.5973***	-7287.554	0.9625

Global scale parameter = c = 1.2775

(b) Exotic species richness - regional scale

Model	Variables included	Deviance	df	log L	QAIC _c	Adjusted R ^{2*}
Intercept only (null)	-	219.6796	42	3308.1101*	-5724.364	0
Richness only	patch area, native SR	88.5867	40	3357.1765**	-5808.969	0.8979
Extrinsic factors only	patch area, climate, road density	51.5964	39	3371.0215***	-5832.611	0.9464
Richness + extrinsic factors (global)	patch area, climate, road density, native SR	50.7667	38	3371.332***	-5832.711	0.9472

Global scale parameter = c = 1.1558

Table B.1 cont'd.

(c) Native species richness - local scale

Model	Variables included	Deviance	df	log L	QAIC_C	Adjusted R^{2*}
Intercept only (null)	-	137.9740	51	183.8264*	-284.9801	0
Richness only	exotic SR	137.9700	50	183.8276*	-284.9019	< 0.0001
Extrinsic factors only	canopy cover, pH, soil moisture	79.2361	48	201.4722**	-311.8358	0.4931
Richness + extrinsic factors (global)	canopy cover, pH, soil moisture, exotic SR	78.2298	47	201.7745**	-311.9534	0.4990

Global scale parameter = c = 1.2901

(d) Exotic species richness - local scale

Model	Variables included	Deviance	df	log L	QAIC_C	Adjusted R^{2*}
Intercept only (null)	-	51.5736	51	119.4603*	-238.9206	0
Richness only	native SR	51.5719	50	119.4612*	-238.8424	< 0.0001
Extrinsic factors only	aspect	45.0331	50	122.7306**	-245.3812	0.1194
Richness + extrinsic factors (global)	aspect, native SR	45.0250	49	122.7346**	-245.2243	0.1195

Global scale parameter = c = 1

REFERENCE

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: A practical information-theoretic approach, 2nd edition. Springer-Verlag, New York, New York, USA.

Appendix C

Road affinity analysis using keywords from habitat descriptions in Douglas et al. (1998-2002) (Chapter 2)

To independently test the importance of human influence (as measured by surrounding road density) as a driver of native and exotic species diversity in this ecosystem, we assigned each species in our dataset an index of affinity for roadsides and disturbed areas (1 to 4, where 1 is low road affinity, 4 is highest road affinity) based on key word analysis of habitat descriptions from the published provincial flora (Douglas et al. 1998-2002) (Table C.1). We compared the distribution of species across these categories for natives vs. exotics. Based on their habitat descriptions, a higher proportion of native species prefer habitats with little or no association with roads, while exotics were dominated by species with known road affinities (G test: $G = 179.5$, $df = 3$, $P < 0.0001$; Figure C.1). This ancillary analysis provides support for the relationship of native and exotic species richness with road density.

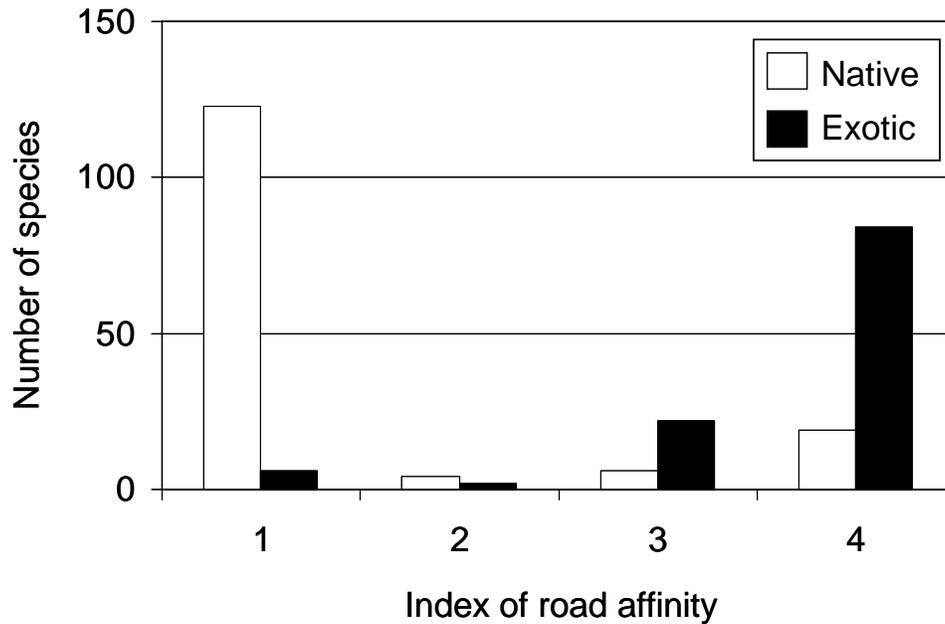
Table C.1. Associated road affinity rankings for keywords from habitat descriptions in Douglas et al. (1998-2002).

Ranking for each species was based on the highest road affinity ranking of all keywords found in the habitat description.

Road affinity ranking	Keywords
4 (highest)	Roadsides, ditches, railways, powerline rights-of-way, lawns, gardens, rare garden escapee
3	Disturbed places, disturbed sites, waste areas, waste places
2	Logging units, pastures, recent burns, fields
1 (lowest)	None of the above

Figure C.1. Distributions of the road affinities of native and exotic species classified using keyword analysis of their habitat descriptions in Douglas et al. (1998-2002).

Low values indicate species with no suggested association with roads while high values indicate a high degree of association with roads or roadside habitats. Five exotic species were left out of the analysis as they were not found in the regional flora.



REFERENCE

Douglas, G. W., G. B. Straley, D. V. Meidinger, and J. Pojar, editors. 1998-2002. Illustrated flora of British Columbia, volumes 1-8. B.C. Ministry of Environment, Lands, and Parks and B.C. Ministry of Forests, Victoria, British Columbia, Canada.

Appendix D

Details of random sampling methods for characterizing mean environmental conditions of study patches (Chapter 3)

For several local-scale environmental variables, mean conditions within patches were characterized using stratified random sampling. Sample points were selected by dividing each patch into four approximately equal area sections and generating random points within each quarter-section using the “DNR Random Sample Generator” extension for ArcView (Minnesota Department of Natural Resources, St. Paul, Minnesota, USA). Sampling points were located in the field using a handheld GPS. At least 32 (8 per quarter-section) and no more than 40 points (10 per quarter-section) were sampled in each patch.

Appendix E

Species traits classifications for species used in logistic regression analysis (Chapter 3)

Table E.1. Species traits classifications for 62 native species used in logistic regression analysis.

Native species

Species†	Origin	Life form	Life span	Dispersal mode	Habitat specialization
<i>Acer macrophyllum</i>	native	tree/shrub	perennial	wind	generalist
<i>Achnatherum lemmonii</i> var. <i>lemmonii</i>	native	graminoid	perennial	vertebrate	specialist
<i>Agoseris grandiflora</i>	native	forb	perennial	wind	specialist
<i>Allium acuminatum</i>	native	forb	perennial	ants/ballistic/none	specialist
<i>Amelanchier alnifolia</i>	native	tree/shrub	perennial	vertebrate	generalist
<i>Arabis glabra</i>	native	forb	biennial	ants/ballistic/none	specialist
<i>Arctostaphylos uva-ursi</i>	native	tree/shrub	perennial	vertebrate	generalist
<i>Aster curtus</i>	native	forb	perennial	wind	specialist
<i>Barbarea orthoceras</i>	native	forb	biennial	ants/ballistic/none	generalist
<i>Brodiaea coronaria</i> ssp. <i>coronaria</i>	native	forb	perennial	ants/ballistic/none	specialist
<i>Carex inops</i> ssp. <i>inops</i>	native	graminoid	perennial	ants/ballistic/none	specialist
<i>Clinopodium douglasii</i>	native	forb	perennial	ants/ballistic/none	generalist
<i>Cystopteris fragilis</i>	native	fern	perennial	wind	generalist
<i>Danthonia californica</i>	native	graminoid	perennial	vertebrate	specialist
<i>Daucus pusillus</i>	native	forb	annual	vertebrate	specialist
<i>Delphinium menziesii</i> ssp. <i>menziesii</i>	native	forb	perennial	wind	specialist
<i>Dodacatheon pulchellum</i>	native	forb	perennial	ants/ballistic/none	specialist
<i>Epilobium</i> sp.*	native	forb	annual	ants/ballistic/none	specialist
<i>Eriophyllum lanatum</i> var. <i>lanatum</i>	native	forb	perennial	wind	specialist
<i>Festuca idahoensis/rubra</i> *	native	graminoid	perennial	ants/ballistic/none	specialist
<i>Fragaria vesca</i>	native	forb	perennial	vertebrate	generalist
<i>Fragaria virginiana</i>	native	forb	perennial	vertebrate	generalist
<i>Fritillaria affinis</i> var. <i>affinis</i>	native	forb	perennial	ants/ballistic/none	specialist
<i>Geranium</i> <i>bicknellii/carolinianum</i> *	native	forb	annual	ants/ballistic/none	specialist
<i>Goodyera oblongifolia</i>	native	forb	perennial	ants/ballistic/none	generalist
<i>Grindelia integrifolia</i>	native	forb	perennial	wind	specialist
<i>Heuchera micrantha</i> var. <i>diversifolia</i>	native	forb	perennial	ants/ballistic/none	generalist

Table E.1 cont'd.

Species†	Origin	Life form	Life span	Dispersal mode	Habitat specialization
<i>Hieracium albiflorum</i>	native	forb	perennial	wind	generalist
<i>Lathyrus nevadensis</i> var. <i>pilosellus</i>	native	forb	perennial	ants/ballistic/none	generalist
<i>Lithophragma parviflorum</i>	native	forb	perennial	ants/ballistic/none	specialist
<i>Lomatium nudicaule</i>	native	forb	perennial	ants/ballistic/none	specialist
<i>Lomatium urticulatum</i>	native	forb	perennial	ants/ballistic/none	specialist
<i>Lonicera hispidula</i>	native	tree/shrub	perennial	vertebrate	generalist
<i>Lotus micranthus</i>	native	forb	annual	ants/ballistic/none	specialist
<i>Lupinus bicolor/polycarpus</i> *	native	forb	annual	ants/ballistic/none	specialist
<i>Luzula multiflora</i>	native	graminoid	perennial	ants/ballistic/none	generalist
<i>Madia madioides</i>	native	forb	biennial	ants/ballistic/none	generalist
<i>Mahonia nervosa</i>	native	tree/shrub	perennial	vertebrate	generalist
<i>Melica harfordii</i>	native	graminoid	perennial	ants/ballistic/none	generalist
<i>Mimulus alsinoides</i>	native	forb	annual	ants/ballistic/none	specialist
<i>Mimulus guttatus</i>	native	forb	annual	ants/ballistic/none	specialist
<i>Moehringia macrophylla</i>	native	forb	perennial	ants/ballistic/none	generalist
<i>Montia parvifolia</i>	native	forb	perennial	ants/ballistic/none	specialist
<i>Nemophila parviflora</i> var. <i>parviflora</i>	native	forb	annual	ants/ballistic/none	generalist
<i>Oemleria cerasiformis</i>	native	tree/shrub	perennial	vertebrate	generalist
<i>Olsynium douglasii</i> var. <i>douglasii</i>	native	forb	perennial	ants/ballistic/none	specialist
<i>Osmorhiza berteroi</i>	native	forb	perennial	vertebrate	generalist
<i>Pentagramma triangularis</i>	native	fern	perennial	wind	specialist
<i>Piperia sp.</i> *	native	forb	perennial	ants/ballistic/none	generalist
<i>Plectritis congesta</i>	native	forb	annual	ants/ballistic/none	specialist
<i>Plectritis macrocera</i>	native	forb	annual	ants/ballistic/none	specialist
<i>Polystichum minutum/imbricans</i> *	native	fern	perennial	wind	generalist
<i>Prunella vulgaris</i>	native	forb	perennial	ants/ballistic/none	generalist
<i>Ranunculus occidentalis</i> var. <i>occidentalis</i>	native	forb	perennial	ants/ballistic/none	specialist
<i>Rumex aquaticus</i> var. <i>fenestratus</i>	native	forb	perennial	ants/ballistic/none	generalist
<i>Salix sp.</i> *	native	tree/shrub	perennial	wind	generalist
<i>Sanicula graveolens</i>	native	forb	perennial	vertebrate	generalist
<i>Sedum spathifolium</i>	native	forb	perennial	ants/ballistic/none	specialist
<i>Trientalis borealis</i> ssp. <i>latifolia</i>	native	forb	perennial	ants/ballistic/none	generalist
<i>Trifolium microcephalum</i>	native	forb	annual	ants/ballistic/none	specialist
<i>Trifolium willdenowii</i>	native	forb	annual	ants/ballistic/none	specialist
<i>Zigadenus venenosus</i> var. <i>venenosus</i>	native	forb	perennial	ants/ballistic/none	specialist

Table E.2. Species traits classifications for 50 exotic species used in logistic regression analysis.

Exotic species

Species†	Origin	Life form	Life span	Dispersal mode	Habitat specialization
<i>Anthriscus caucalis</i>	exotic	forb	biennial	vertebrate	-
<i>Arrhenatherum elatius</i>	exotic	graminoid	perennial	vertebrate	-
<i>Avena fatua</i>	exotic	graminoid	annual	vertebrate	-
<i>Bellis perennis</i>	exotic	forb	perennial	ants/ballistic/none	-
<i>Bromus rigidus</i>	exotic	graminoid	annual	vertebrate	-
<i>Centaurea cyanus</i>	exotic	forb	annual	wind	-
<i>Cirsium vulgare</i>	exotic	forb	perennial	wind	-
<i>Convolvulus sepium</i>	exotic	tree/shrub	perennial	ants/ballistic/none	-
<i>Cotoneaster</i> sp.*	exotic	tree/shrub	perennial	vertebrate	-
<i>Crataegus monogyna</i>	exotic	tree/shrub	perennial	vertebrate	-
<i>Daphne laureola</i>	exotic	tree/shrub	perennial	vertebrate	-
<i>Daucus carota</i>	exotic	forb	biennial	vertebrate	-
<i>Elymus repens</i>	exotic	graminoid	perennial	ants/ballistic/none	-
<i>Erodium cicutarium</i> ssp. <i>cuticularium</i>	exotic	forb	annual	ants/ballistic/none	-
<i>Geranium dissectum</i>	exotic	forb	annual	ants/ballistic/none	-
<i>Geranium robertianum</i>	exotic	forb	annual	ants/ballistic/none	-
<i>Hedera helix</i>	exotic	tree/shrub	perennial	vertebrate	-
<i>Holcus lanatus</i>	exotic	graminoid	perennial	wind	-
<i>Hordeum murinum</i>	exotic	graminoid	annual	vertebrate	-
<i>Hyacinthoides hispanica</i>	exotic	forb	perennial	ants/ballistic/none	-
<i>Hypericum perforatum</i>	exotic	forb	perennial	ants/ballistic/none	-
<i>Hypochaeris glabra</i>	exotic	forb	perennial	wind	-
<i>Ilex aquifolium</i>	exotic	tree/shrub	perennial	vertebrate	-
<i>Lamium purpureum</i>	exotic	forb	perennial	ants/ballistic/none	-
<i>Lapsana communis</i>	exotic	forb	annual	ants/ballistic/none	-
<i>Lepidium</i> sp.*	exotic	forb	biennial	ants/ballistic/none	-
<i>Leucanthemum vulgare</i>	exotic	forb	perennial	ants/ballistic/none	-
<i>Ligustrum vulgare</i>	exotic	tree/shrub	perennial	vertebrate	-
<i>Lolium perenne</i>	exotic	graminoid	perennial	ants/ballistic/none	-
<i>Lunaria annua</i>	exotic	forb	biennial	wind	-
<i>Madia sativa</i>	exotic	forb	annual	ants/ballistic/none	-
<i>Mycelia muralis</i>	exotic	forb	biennial	wind	-
<i>Myosotis discolor</i>	exotic	forb	annual	ants/ballistic/none	-
<i>Narcissus pseudo-narcissus</i>	exotic	forb	perennial	ants/ballistic/none	-
<i>Poa annua</i>	exotic	graminoid	annual	ants/ballistic/none	-
<i>Poa bulbosa</i> var. <i>vivipara</i>	exotic	graminoid	perennial	ants/ballistic/none	-
<i>Poa compressa</i>	exotic	graminoid	perennial	ants/ballistic/none	-
<i>Rubus armeniacus</i>	exotic	tree/shrub	perennial	vertebrate	-

Table E.2 cont'd.

Species†	Origin	Life form	Life span	Dispersal mode	Habitat specialization
<i>Rumex crispus</i>	exotic	forb	perennial	ants/ballistic/none	-
<i>Senecio sylvaticus</i>	exotic	forb	annual	wind	-
<i>Senecio vulgaris</i>	exotic	forb	biennial	wind	-
<i>Silene gallica</i>	exotic	forb	annual	ants/ballistic/none	-
<i>Sisymbrium officinale</i>	exotic	forb	annual	ants/ballistic/none	-
<i>Sonchus asper/oleraceus*</i>	exotic	forb	biennial	wind	-
<i>Teesdalia nudicaulis</i>	exotic	forb	annual	ants/ballistic/none	-
<i>Trifolium dubium</i>	exotic	forb	annual	ants/ballistic/none	-
<i>Trifolium repens</i>	exotic	forb	perennial	ants/ballistic/none	-
<i>Veronica arvensis</i>	exotic	forb	annual	ants/ballistic/none	-
<i>Vicia hirsuta</i>	exotic	forb	annual	ants/ballistic/none	-
<i>Vinca major</i>	exotic	tree/shrub	perennial	ants/ballistic/none	-

†Nomenclature according to Douglas et al. 1998-2002 except where noted by asterisk (*) which denotes species lumped together for purposes of this study.

REFERENCE

Douglas, G. W., G. B. Straley, D. V. Meidinger, and J. Pojar, editors. 1998-2002. Illustrated flora of British Columbia, volumes 1-8. B.C. Ministry of Environment, Lands, and Parks and B.C. Ministry of Forests, Victoria, British Columbia, Canada.

Appendix F

Results of logistic regression analyses for predicting patch occupancy at the regional scale (Chapter 3)

Table F.1. Results of regional-scale multiple logistic regression models for 62 native species including % patch occupancy, R^2 goodness-of-fit values, and parameter estimates for significant variables.

Native species

Species†	PO‡ (%)	R^2 §	Parameter estimates (β_n) from logistic regression models								
			Area	Connectivity	Road density	Slope	Aspect	Canopy cover	Soil depth	pH	Climate
<i>Acer macrophyllum</i>	39.5	0.152				0.122					
<i>Achnatherum lemmonii</i> var. <i>lemmonii</i>	25.6	0.464	2.241			0.234					
<i>Agoseris grandiflora</i>	32.6	0.590	2.852				0.316				
<i>Allium acuminatum</i>	79.1	0.498	2.923			-0.536					
<i>Amelanchier alnifolia</i>	60.5	0.266	2.237								
<i>Arabis glabra</i>	30.2	0.155					0.129				
<i>Arctostaphylos uva-ursi</i>	41.9	0.373									0.013
<i>Aster curtus</i>	20.9	0.163									0.007
<i>Barbarea orthoceras</i>	23.3										
<i>Brodiaea coronaria</i> ssp. <i>coronaria</i>	72.1										
<i>Carex inops</i> ssp. <i>inops</i>	76.7	0.524				-0.290	0.242				
<i>Clinopodium douglasii</i>	62.8	0.459				-0.431					
<i>Cystopteris fragilis</i>	25.6	0.508									0.018
<i>Danthonia californica</i>	69.8	0.198				-0.239					
<i>Daucus pusillus</i>	25.6	0.668	3.196			-0.621		0.073			

Table F.1 cont'd.

Species†	PO‡ (%)	R²§	Parameter estimates (β_n) from logistic regression models								
			Area	Connectivity	Road density	Slope	Aspect	Canopy cover	Soil depth	pH	Climate
<i>Delphinium menziesii</i> ssp. <i>menziesii</i>	72.1	0.826	5.972								0.059
<i>Dodacatheon pulchellum</i>	20.9	0.223	2.162								
<i>Epilobium</i> sp.*	41.9	0.365									0.012
<i>Eriophyllum lanatum</i> var. <i>lanatum</i>	48.8	0.458									0.016
<i>Festuca idahoensis/rubra</i> *	74.4	0.191				0.154					
<i>Fragaria vesca</i>	34.9	0.386						0.065			0.009
<i>Fragaria virginiana</i>	34.9	0.453						-0.049			0.013
<i>Fritillaria affinis</i> var. <i>affinis</i>	41.9										
<i>Geranium bicknellii/carolinianum</i> *	30.2	0.558	3.929				-0.279				
<i>Goodyera oblongifolia</i>	39.5	0.421				-0.475					
<i>Grindelia integrifolia</i>	25.6	0.444		2.486				0.062			
<i>Heuchera micrantha</i> var. <i>diversifolia</i>	72.1	0.328				-0.336					
<i>Hieracium albiflorum</i>	37.2	0.473				-0.570					
<i>Lathyrus nevadensis</i> var. <i>pilosellus</i>	60.5	0.313					-0.201				
<i>Lithophragma parviflorum</i>	69.8	0.543									0.021
<i>Lomatium nudicaule</i>	32.6	0.222	1.987								
<i>Lomatium urticulatum</i>	55.8										
<i>Lonicera hispidula</i>	72.1	0.679				-0.689					
<i>Lotus micranthus</i>	62.8	0.768						0.089			0.046
<i>Lupinus bicolor/polycarpus</i> *	46.5	0.156	1.523								
<i>Luzula multiflora</i>	67.4	0.721	4.400			-0.804					
<i>Madia madioides</i>	25.6	0.514								4.750	0.013
<i>Mahonia nervosa</i>	27.9	0.371	1.785			-0.358					
<i>Melica harfordii</i>	39.5	0.423				-0.477					

Table F.1 cont'd.

Species†	PO‡ (%)	R ² §	Parameter estimates (β_n) from logistic regression models								
			Area	Connectivity	Road density	Slope	Aspect	Canopy cover	Soil depth	pH	Climate
<i>Mimulus alsinoides</i>	79.1	0.522									0.022
<i>Mimulus guttatus</i>	34.9	0.626	3.886		-0.447						
<i>Moehringia macrophylla</i>	65.1	0.503	1.939		-0.459						
<i>Montia parvifolia</i>	79.1	0.650									0.029
<i>Nemophila parviflora</i> var. <i>parviflora</i>	76.7	0.746			-0.577			0.162			
<i>Oemleria cerasiformis</i>	58.1	0.464							12.418		-0.010
<i>Olsynium douglasii</i> var. <i>douglasii</i>	60.5	0.322	2.604								
<i>Osmorhiza berteroi</i>	55.8										
<i>Pentagramma triangularis</i>	69.8	0.407				0.263					
<i>Piperia</i> sp.*	69.8	0.554									0.022
<i>Plectritis congesta</i>	76.7	0.389						0.132			
<i>Plectritis macrocera</i>	37.2	0.175									0.007
<i>Polystichum minutum/imbricans</i> *	72.1	0.495									0.019
<i>Prunella vulgaris</i>	27.9	0.379					-0.044				0.010
<i>Ranunculus occidentalis</i> var. <i>occidentalis</i>	79.1	0.535						0.193			
<i>Rumex aquaticus</i> var. <i>fenestratus</i>	20.9	0.640			0.880		0.088				
<i>Salix</i> sp.*	23.3	0.265							-10.561		
<i>Sanicula graveolens</i>	27.9	0.738						0.113			0.027
<i>Sedum spathifolium</i>	79.1	0.614	6.169		-0.566						
<i>Trientalis borealis</i> ssp. <i>latifolia</i>	44.2	0.395									0.014
<i>Trifolium microcephalum</i>	25.6	0.365									0.012
<i>Trifolium willdenowii</i>	62.8	0.831	9.286					-0.124			0.075
<i>Zigadenus venenosus</i> var. <i>venenosus</i>	53.5	0.349									0.012

Table F.2. Results of regional-scale multiple logistic regression models for 50 exotic species including % patch occupancy, R² goodness-of-fit values, and parameter estimates for significant variables.

Exotic species

Species†	PO‡ (%)	R ² §	Parameter estimates (β_n) from logistic regression models								
			Area	Connectivity	Road density	Slope	Aspect	Canopy cover	Soil depth	pH	Climate
<i>Anthriscus caucalis</i>	25.6	0.478				-0.270				4.662	
<i>Arrhenatherum elatius</i>	27.9	0.380			0.375						
<i>Avena fatua</i>	23.3	0.585	3.699		0.520						
<i>Bellis perennis</i>	44.2	0.525	4.201						0.091		-0.018
<i>Bromus rigidus</i>	51.2	0.648	4.078								-0.021
<i>Centaurea cyanus</i>	25.6	0.362									-0.014
<i>Cirsium vulgare</i>	46.5	0.578		1.673				-0.065		4.652	
<i>Convolvulus sepium</i>	20.9	0.676			0.957		0.087				
<i>Cotoneaster</i> sp.*	27.9	0.303			0.318						
<i>Crataegus monogyna</i>	34.9	0.345					-0.221				
<i>Daphne laureola</i>	55.8	0.516					-0.323				
<i>Daucus carota</i>	25.6	0.277			0.303						
<i>Elymus repens</i>	30.2	0.625			0.603						
<i>Erodium cicutarium</i> ssp. <i>cutarium</i>	51.2	0.353	1.961				-0.175				
<i>Geranium dissectum</i>	34.9	0.185					-0.141				
<i>Geranium robertianum</i>	32.6	0.388			0.375						
<i>Hedera helix</i>	37.2	0.681									-0.031
<i>Holcus lanatus</i>	74.4	0.695	5.586							-9.119	-0.019
<i>Hordeum murinum</i>	34.9	0.691			0.691						
<i>Hyacinthoides hispanica</i>	20.9	0.759			0.598						-0.023
<i>Hypericum perforatum</i>	23.3	0.357	3.025								
<i>Hypochaeris glabra</i>	30.2	0.588	2.629				0.307			11.773	

Table F.2 cont'd.

Species†	PO‡ (%)	R²§	Parameter estimates (β_n) from logistic regression models								
			Area	Connectivity	Road density	Slope	Aspect	Canopy cover	Soil depth	pH	Climate
<i>Ilex aquifolium</i>	23.3	0.316									-0.013
<i>Lamium purpureum</i>	58.1	0.697			1.069						
<i>Lapsana communis</i>	27.9	0.235									-0.010
<i>Lepidium</i> sp.*	23.3										
<i>Leucanthemum vulgare</i>	20.9										
<i>Ligustrum vulgare</i>	25.6	0.628	3.632		0.615						
<i>Lolium perenne</i>	44.2	0.633	2.545								-0.023
<i>Lunaria annua</i>	20.9	0.512									-0.021
<i>Madia sativa</i>	41.9	0.759									0.045
<i>Mycelia muralis</i>	62.8	0.137								2.564	
<i>Myosotis discolor</i>	74.4	0.365			-0.239					4.096	
<i>Narcissus pseudo-narcissus</i>	23.3	0.419					-0.290				
<i>Poa annua</i>	58.1	0.718	3.196					-0.053	0.193		-0.034
<i>Poa bulbosa</i> var. <i>vivipara</i>	20.9	0.181			0.240						
<i>Poa compressa</i>	34.9	0.201							0.065		
<i>Rubus armeniacus</i>	55.8	0.560			0.637						
<i>Rumex crispus</i>	27.9	0.604			0.586						
<i>Senecio sylvaticus</i>	34.9	0.400	2.012		-0.330						
<i>Senecio vulgaris</i>	34.9	0.384			0.371						
<i>Silene gallica</i>	25.6										
<i>Sisymbrium officinale</i>	44.2	0.299									-0.011
<i>Sonchus asper/oleraceus</i> *	65.1	0.210							-0.066		
<i>Teesdalia nudicaulis</i>	39.5	0.674	3.466	3.038							
<i>Trifolium dubium</i>	58.1	0.346	1.960		0.237						
<i>Trifolium repens</i>	20.9	0.349			0.371						
<i>Veronica arvensis</i>	65.1	0.185								3.127	
<i>Vicia hirsuta</i>	74.4	0.214								3.650	
<i>Vinca major</i>	23.3	0.675			0.732						

† Nomenclature according to Douglas et al. 1998-2002 except where noted by asterisk (*) which denotes species lumped together for purposes of this study.

‡ PO = patch occupancy

§ Nagelkerke R^2 or max-rescaled generalized coefficient of determination (Hosmer and Lemeshow 1989).

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