Research

Negative native–exotic diversity relationship in oak savannas explained by human influence and climate

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Recent research has proposed a scale-dependence to relationships between native diversity and exotic invasions. At fine spatial scales, native–exotic richness relationships should be negative as higher native richness confers resistance to invasion. At broad scales, relationships should be positive if natives and exotics respond similarly to extrinsic factors. Yet few studies have examined both native and exotic richness patterns across gradients of human influence, where impacts could affect native and exotic species differently. We examined native–exotic richness relationships and extrinsic drivers of plant species richness and distributions across an urban development gradient in remnant oak savanna patches. In sharp contrast to most reported results, we found a negative relationship at the regional scale, and no relationship at the local scale. The negative regional-scale relationship was best explained by extrinsic factors, surrounding road density and climate, affecting natives and exotics in opposite ways, rather than a direct effect of native on exotic richness, or vice versa. Models of individual species distributions also support the result that road density and climate have largely opposite effects on native and exotic species, although simple life history traits (life form, dispersal mode) do not predict which habitat characteristics are important for particular species. Roads likely influence distributions and species richness by increasing both exotic propagule pressure and disturbance to native species. Climate may partially explain the negative relationship due to differing climatic preferences within the native and exotic species pools. As gradients of human influence are increasingly common, negative broad-scale native–exotic richness relationships may be frequent in such landscapes.

Theories of interspecific competition suggest that communities with high native species diversity use resources more efficiently than low diversity communities, thereby reducing resource availability and increasing the community's resistance to invasion (Elton 1958, 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 (Vila et al. 2007). 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 (Stohlgren et al. 1999, Maskell et al. 2006). 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) 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 if native and exotic richness respond similarly to the same extrinsic factors (Levine 2000, Gilbert and Lechowicz 2005).

While the mechanisms responsible for negative native–exotic richness relationships at fine scales are well-established, mechanisms behind 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 favor native diversity also favor invasion success (Shea and Chesson 2002) and (2) increased heterogeneity of conditions within sites favors both natives and exotics by allowing more species of both 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 extrinsic gradients favoring native richness also favor exotic richness. Yet, given the lack of a shared evolutionary history of the native and exotic species pools, we might expect different responses across local environmental gradients that reflect differences in this history (Pärtel 2002). Furthermore, biogeographical and historical

factors affecting regional processes can also be important determinants of richness patterns (Ricklefs and Schluter 1993) and may impact native and exotic richness differently. More generally, individual species – both native and exotic – may show substantial variation in how their distributions correspond to habitat characteristics, with some of this variation potentially predictable based on species' traits (Goodwin et al. 1999, Verheyen et al. 2004). 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, and the contribution of different species to such patterns.

Extrinsic local and regional factors can filter species at three different life history stages: dispersal, establishment, and persistence (including reproduction). Diversity–invasibility research to date has focused largely on how existing diversity, environment, and heterogeneity in the receiving environment affect species establishment (Stohlgren et al. 1999, Davies et al. 2005). However, seed dispersal often limits local diversity (Zobel et al. 2000), and in fragmented landscapes, the size and spatial arrangement of remnant habitat patches can affect the relative frequencies of arrival and 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 in the surrounding landscape that influence exotic propagule pressure, such as agriculture, horticulture, and increased transport activity (di Castri 1989). Conversely, human-mediated disturbance, such as soil perturbation, hydrological changes and vegetation trampling, may affect many 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 (urban development) 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. In addition, to assess the potential role of species' traits in explaining the contrasting richness patterns observed for natives versus exotics, we modeled individual species distributions at the regional scale, and tested whether easily measured species traits could predict the importance of particular predictor variables in determining species' patch occupancy.

Methods

The study was conducted in remnant patches of fragmented Garry oak *Quercus garryana* savanna habitat situated across an urban development gradient near Victoria, British Columbia, Canada (48°26′N, 123°22′W), on southeastern Vancouver Island (Fig. 1). This region is the northern range limit of a complex of oak prairies and woodlands extending from northern California to southwestern British Columbia. The climate is sub-Mediterranean, with a significant summer drought (Fuchs 2001). Soils are generally shallow, post-glacial, and moderately infertile (Roemer 1972). Due to habitat loss from urbanization, agriculture and forestry since European settlement, less than 10% of the historical extent of oak savanna habitat is this region remains in a near-natural state (Lea 2006, Vellend et al. 2008). Remnant patches occur in a matrix consisting mostly of urban development and second-growth coastal Douglas-fir *Pseudotsuga menziesii* forest. While these patches are crucial reservoirs for the high native plant diversity characteristic of this ecosystem, they are also invaded by a diverse flora of exotic species, the majority of which have been resident in the region for several decades (Roemer 1972).

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, were traversed across the entire extent of each patch and all
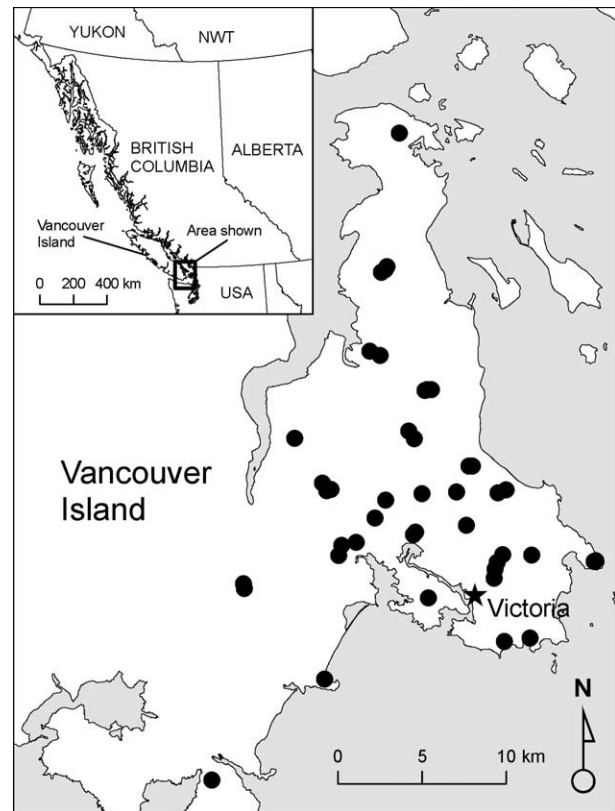

Figure 1. Map showing locations (black circles) of 43 remnant oak savanna study patches on southeastern Vancouver Island, near Victoria, British Columbia, Canada.

vascular plant species observed from the transects were recorded. Surveys were conducted twice, once in spring (12 April – 5 June) and once in 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 (log-transformed and used as a covariate), connectivity, surrounding road density, slope, aspect, canopy cover, soil depth, variation (CV) in soil depth, soil pH and climate. Connectivity of each patch i (S_i) was calculated using maps in ArcView GIS 3.2 as a distance-weighted sum of surrounding oak savanna patches:

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

where A_j is the area of patch j (in m^2), d_{ij} is the minimum edge-to-edge distances (in m) between patches i and j, and α is the parameter setting the influence of distance on connectivity (Moilanen and Nieminen 2002). We used $\alpha = 0.002$ which represents a realistic average migration range for most grassland species (Johansson and Ehrlen 2003, Verheyen et al. 2004). Surrounding road density was calculated as the length of roads per unit area in a 500 m buffer around each patch. Road density was interpreted as indicative both of exotic species propagule pressure via human-mediated dispersal, and of anthropogenic disturbances, which are most likely manifested in this system as soil perturbation, vegetation trampling, and hydrological changes created by trails. We initially calculated road density within buffers ranging in size from 100 m to 1 km, and found that values were strongly correlated across this range of buffer sizes (r > 0.8). We chose 500 m as most likely to capture the relevant surrounding areas with influence on the focal patch. Mean annual precipitation varied from 727–1135 mm, mean annual temperature from 8.9–10°C, and elevation from 20–298 m. Because of strong correlations in climate and topography across the landscape, 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 (Hamann and Wang 2005, Wang et al. 2006) to represent 'climate' in subsequent analyses. These three 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. After our initial analysis was conducted more recent averages for climate data became available (1971–2000), but variables were so strongly correlated across the two data sets (r > 0.98) that we did not alter the original analysis.

Stratified random sampling was used to characterize slope, aspect, canopy cover, and soil pH within patches. Sample points were selected by dividing each patch into four approximately equal area sections and generating random points within each quarter-section. We sampled 32–40 points (8–10 per quarter-section) in each patch, and slope, aspect (expressed as degrees from north), canopy cover, and soil depth were measured at each point. 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; 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 in each patch. One 6-cm diameter soil core was taken to 10 cm depth at a randomly-selected subset of ten of the sampling points (2–3 per quarter-section). One hundred and twenty ml of soil was collected from each core and combined into a single sample. Composite samples were uniformly mixed, dried, sifted, and pH measured in a 1:4 soil-to-water mixture.

To compare regional and local scales, we conducted a survey of 52 1-m^2 plots in our largest habitat patch (Mill Hill Regional Park, 31.7 ha), which was broadly representative of habitat patches across the region, and had a relatively high degree of environmental heterogeneity. Plots locations were selected from an initial set of 100 stratified-random positions to cover as broad a range of conditions as possible, and surveyed for vascular plant species twice in 2006 (16–19 May and 5–6 July). Where possible, environmental variables measured at the local plot scale were similar to those measured in the regional survey. 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 local plots as described above 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 reflectometer.

Statistical analyses

Because of the high number of potential predictor variables, we used forward selection in generalized linear models to find the best extrinsic predictors of native and exotic richness at both regional and local scales. 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 (at the regional scale) by including it as a covariate (entered first into the GLM after checking that the assumption of linearity of dependent variables versus log area was met), as species–area effects were not a focus of this study. Area may influence species richness both through a sampling effect (the length of transect surveyed was proportional to patch area) and through the biogeographic effect of reduced extinction risk. Because of potential overdispersion in the count data, we included a variance inflation factor or scale parameter (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 versus 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 ver. 9.1.3.

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) based on key word analysis of habitat descriptions from the published provincial flora (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. Keywords used were as follows: 4 – 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 – none of the above. Our field experience and knowledge of the regional flora indicate that category 1 represents species that are rarely, if ever, found associated with roadsides, rather than simply representing species for which there is no information. Five exotic species were left out of the analysis as they were not found in Douglas et al. (1998–2002). We compared the distribution of species across these categories for natives versus exotics using a G-test.

The presence–absence of each species at the regional scale was modeled using multiple logistic regression (Hosmer and Lemeshow 1989) using the above explanatory variables, excluding soil depth heterogeneity 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 20–80% 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. The relatively small number of species (nine natives, four 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 Supplementary material Appendix 1). Habitat specialists were species with >80% of their occurrences within oak savanna habitats versus other habitat types, as determined from an analysis of 228 vegetation releves previously sampled across a wide range of habitat types within the same study area (Roemer 1972). We then used further logistic regressions to test whether these traits could predict the existence 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.

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 (*Matricaria discoidea*). There was a negative relationship between the richness of natives and exotics across the 43 patches at the regional scale (Fig. 2a, 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. 2b, 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, with the highest native richness occurring in wet, cool, high elevation patches (Table 1, Fig. 2). 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 1, Fig. 2).

At the regional scale, more variation in native species richness was explained by surrounding road density and climate than by exotic species richness ($\Delta QAIC_C =$ −19.02). 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; $\Delta QAIC_C = +0.42$; $R^{2*}_{adj} = 0.946$). Surrounding road density and climate also outperformed native species richness as predictors of exotic species richness at the regional scale ($\Delta QAIC_C = −23.64$), and adding native species richness as a predictor, after accounting for these patch characteristics, yielded no improvement in predictive power (likelihood ratio test: $\chi^2 = 0.621$, DF = 1, p = 0.43; $\Delta QAIC_C = −0.10$; $R^{2*}_{adj} = 0.962$).

Due to correlations in the pattern of development and regional topography, there was significant shared variation in the regional models attributable to either road density or climate. Variation partitioning using partial linear regression indicates that, of the variation in native species richness accounted for by road density and climate together, 21% is uniquely explained by road density, 13% is uniquely explained by climate, and the 66% is shared. Exotic species richness showed almost identical trends. Yet, despite the high levels of shared variation, both road density and
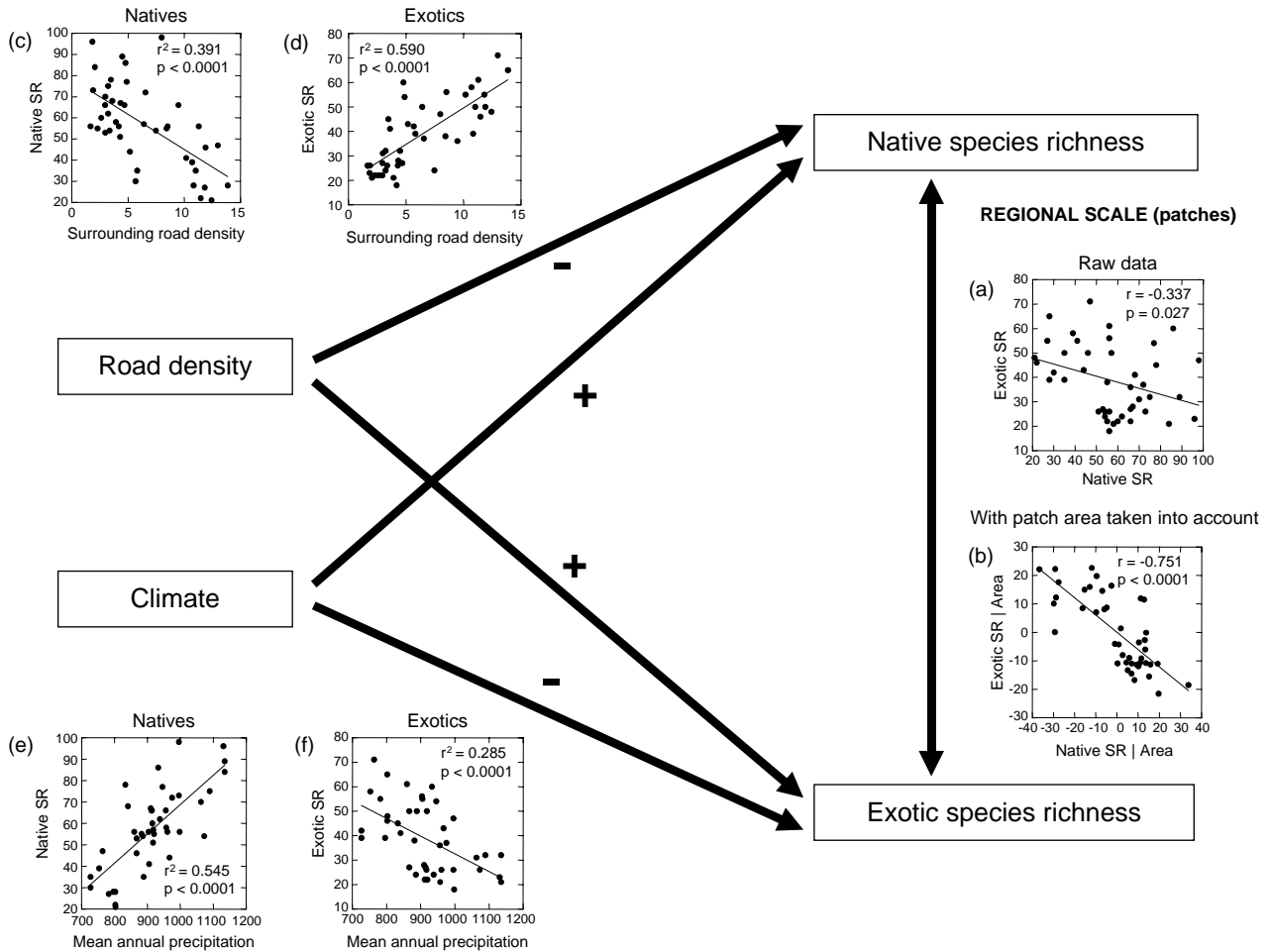
Figure 2. The relationships between native and exotic species richness (SR) may be due to a direct effect of natives on exotics (or vice versa) or to similar responses to historical, landscape, or environmental variables. The relationship between native and exotic species richness at the regional scale 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 (in km/km^2). (e) and (f) show the relationship between native and exotic richness and mean annual precipitation (in mm, shown here instead of the synthetic climate variable for ease of interpretation). The signs accompanying the arrows summarize the direction of the relationships.

climate explain significant variation in the final model (Table 1).

At the local scale, there was no relationship between native and exotic richness ($r = 0.006$, $p = 0.966$). In 1-m^2 plots, higher native richness was significantly associated with sites with more canopy cover, higher soil pH and higher soil moisture (Table 1). Only aspect (degrees from north) significantly predicted patterns of exotic species richness at the local scale with more south-facing sites having higher exotic richness (Table 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 ($R^{2*}_{adj} = 0.493$ for native model, $R^{2*}_{adj} = 0.119$ for exotic model).

Based on their habitat descriptions, a higher proportion of native species are associated with 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, $p < 0.0001$; Fig. 3).

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 (Supplementary material Appendix 2). 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. 4a). 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. 4a).

Table 1. Results of forward stepwise model selection for selecting significant spatial, human influence, and environmental variables. 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				Local			
	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 (%)	n/a	n/a	n/a	n/a	[3] +0.1539	6.01, 0.0142		
(scale parameter c)	1.2615		1.1502		1.3076		0.871	

*Wald test used as test statistic for intercept instead of likelihood ratio test.
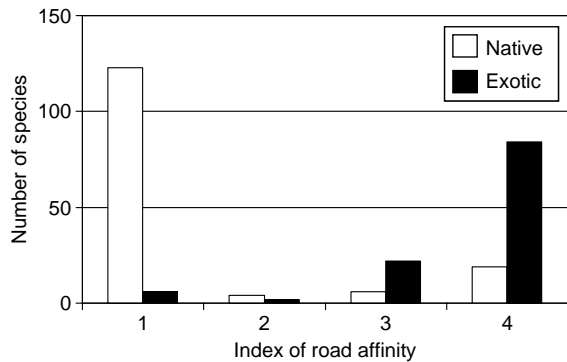
Figure 3. Distributions of the road affinities of native and exotic species classified using keyword analysis of their habitat descriptions in Douglas et al. (1998–2002). Low values indicate species with no suggested association with roads while high values indicate a high degree of association with roads or roadside habitats. Keywords used were as follows: 4 – 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 – none of the above. Five exotic species were left out of the analysis as they were not found in Douglas et al. (1998–2002).

Similar to native species, climate, road density, and patch area showed the most significant effects on patch occupancy of exotics (Fig. 4b). For exotics, road density (20 species, 40%) showed more significant effects than climate (13 species, 26%). 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.

We found few predictive relationships between life history traits and the existence of effects of the explanatory variables. Only one of the 36 potential trait-environment relationships was significant ($p < 0.05$): native species for which area effects were found tended to be habitat specialists. Two other relationships were marginally significant ($p < 0.1$): road density effects were more common in native habitat generalists and native species for which slope effects were found were more often woody than forbs. At an α-level of 0.1, based on the type I error rate and the number of tests made, based on chance alone we would expect two to three significant relationships (i.e. the number observed here), so we interpret these analyses only as exploratory.

Discussion

The 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 favor native species richness should also increase invasion success creating positive relationships between native and exotic species richness (Shea and Chesson 2002). Biotic resistance, if present, should operate mostly at the spatial scale of competitive interactions, such as 1-m^2 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. Shared variation by road density and climate limit our ability to specify precisely the relative contributions of these variables, but this has no influence on our most general result that the negative regional relationship was likely created by extrinsic rather than intrinsic drivers. Native and exotic species respond in opposite ways to the key gradients in this landscape. In addition, it seems clear that road density and climate both made significant contributions to determining the richness and distributions of native and exotic species (Fig. 2, 4). Furthermore, these effects are robust to our choices about the appropriate scale of influence from surrounding areas (i.e. buffer width used to calculate road density) and the period of climate data used.
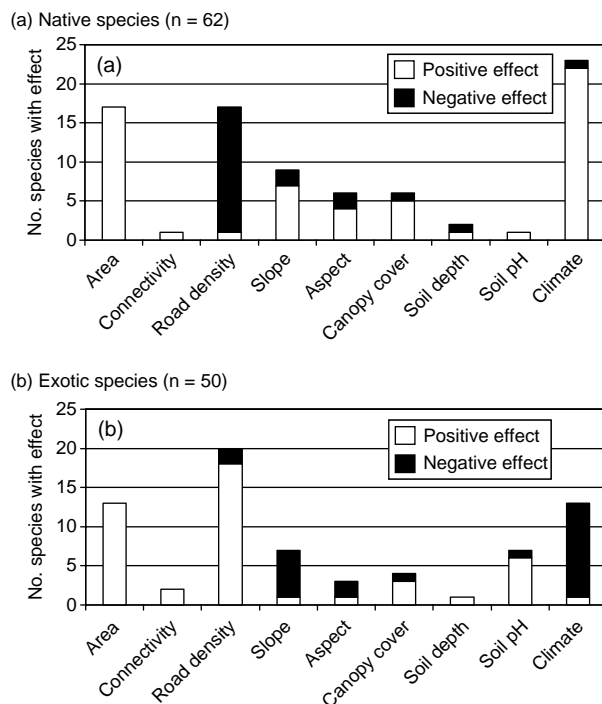

Figure 4. Bar graphs showing number of significant effects for each explanatory variable across all multiple logistic regression models for (a) native species and (b) exotic species at the regional scale.

Two possible mechanisms likely underlie the effect of road density on native and exotic species: (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 are consistent with a possible role of propagule pressure from roads and associated development as a driver of exotic richness in this system.

While exotic propagule pressure may help explain patterns of exotic richness, human disturbance that accompanies roads is likely a contributing factor, or even the sole factor, accounting for the observed effects of road density on both native and exotic richness. Previous studies suggest that disturbances from surrounding land use, such as hydrological changes, nutrient inputs, grazing and trampling, can extend into natural areas (Hobbs and Huenneke 1992), and that such disturbances negatively affect many native species (McIntyre and Lavorel 1994). Williams et al. (2006) found that road density around remnant Australian grasslands correlated strongly with native plant extirpation. In our system, the disturbances most likely associated with high surrounding road density stem from increased foot traffic and dense trail networks, which increase vegetation trampling, soil perturbation, and localized hydrological changes (Lilley and Vellend unpubl.). Many native species in North America may be poorly adapted to the nature, frequency, and intensity of such human-mediated disturbances (Hobbs and Huenneke 1992). Conversely, disturbance is generally thought to increase the success of many exotic species, which are often ruderal or weedy species (Hobbs 1989). Many of these species have experienced selection in disturbed habitats in Europe for many generations, and are therefore adapted to exogenous disturbance to a greater degree than most native North American species (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 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 via mediating interactions, we would expect exotic and native species richness to be more strongly correlated with each other than with extrinsic factors but this was not the case. Differences in the affinities of native and exotic species for roads in our dataset (Fig. 3) support our assertion of direct and opposite effects of roads on natives and exotics.

Differences in the distributions of climatic affinities 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 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 (Pärtel 2002). Oak savannas in 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) suggest that 50% of present-day California species have their evolutionary history in wet, cool north-temperate environments. If the majority of our species pool evolved in 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 across the climatic gradient in this region may reflect opposite distributions in climatic preferences in the regional species pool, though further analyses are needed to explore this hypothesis.

While species responses to habitat attributes and landscape structure are expected to depend on life history traits (Verheyen 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. However, the strikingly different response of native and exotic species to various habitat characteristics (Fig. 4) itself suggests important functional differences between the native and exotic species pools. As such, it seems that in this landscape easy-to-measure traits such as growth form and dispersal mode are not indicative of the key functional attributes that determine how species respond to habitat characteristics. For the 62 native and 50 exotic species for which we gathered trait data, natives and exotics do not differ in the proportion of species with different life forms ($\chi^2 = 5.9$, p $= 0.11$) or dispersal modes ($\chi^2 = 0.77$, p $= 0.68$), and although there are relatively more annuals than perennials in the exotic species pool ($\chi^2 = 8.3$, p $= 0.02$), both sets of species are dominated by perennials (50% of exotics, 76% of natives). Simple traits do not strongly distinguish native from exotic species in this landscape.

In conclusion, our results have important implications for understanding the fundamental drivers of community change, of native–exotic 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 favor exotic species adversely affect native species. If extrinsic factors control native and exotic richness independently then exotic species are only passengers and not drivers of regional-scale biodiversity declines (sensu Mac-Dougall 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.

References

Axelrod, D. I. 1973. History of the Mediterranean ecosystem in California. – In: di Castri, F. and Mooney, H. A. (eds), Mediterranean-type ecosystems: origin and structure. Springer, pp. 225–277.

British Columbia Conservation Data Centre. 2007. BC species and ecosystems explorer. – B.C. Ministry of Environment, Victoria, BC, Canada <www.env.gov.bc.ca/atrisk/toolintro.html>, accessed 12 July 2007.

Burnham, K. P. and Anderson, D. R. 2002. Model selection and multimodel inference: a practical information-theoretic approach (2nd ed.). – Springer.

Davies, K. F. et al. 2005. Spatial heterogeneity explains the scale dependence of the native–exotic diversity relationship. – Ecology 86: 1602–1610.

Davies, K. F. et al. 2007. Productivity alters the scale dependence of the diversity–invasibility relationship. – Ecology 88: 1940–1947.

Davis, M. A. et al. 2000. Fluctuating resources in plant communities: a general theory of invasibility. – J. Ecol. 88: 528–534.

di Castri, F. 1989. History of biological invasions with special emphasis on the Old World. – In: Drake, J. A. et al. (eds), Biological invasions: a global perspective. Wiley, pp. 1–30.

Douglas, G. W. et al. (eds) 1998–2002. Illustrated flora of British Columbia. Vol. 1–8. – B.C. Ministry of Environment, Lands, and Parks and B.C. Ministry of Forests.

Elton, C. 1958. The ecology of invasions by animals and plants. – Methuen.

Fridley, J. D. et al. 2004. Null models of exotic invasion and scale-dependent patterns of native and exotic species richness. – Ecology 85: 3215–3222.

Fridley, J. D. et al. 2007. The invasion paradox: reconciling pattern and process in species invasions. – Ecology 88: 3–17.

Fuchs, M. A. 2001. Towards a recovery strategy for Garry oak and associated ecosystems in Canada: ecological assessment and literature review. Tech. Rep. GBEI/EC-00-030. – Environment Canada, Canadian Wildlife Service.

Gelbard, J. L. and Belnap, J. 2003. Roads as conduits for exotic plant invasions in a semiarid landscape. – Conserv. Biol. 17: 420–432.

Gilbert, B. and Lechowicz, M. J. 2005. Invasibility and abiotic gradients: the positive correlation between native and exotic plant diversity. – Ecology 86: 1848–1855.

Goodwin, B. J. et al. 1999. Predicting invasiveness of plant species based on biological information. – Conserv. Biol. 13: 422–426.

Hamann, A. and Wang, T. L. 2005. Models of climatic normals for genecology and climate change studies in British Columbia. – Agr. For. Meteorol. 128: 211–221.

Hobbs, R. J. 1989. The nature and effects of disturbance relative to invasions. – In: Drake, J. A. et al. (eds), Biological invasions: a global perspective. Wiley, pp. 389–406.

Hobbs, R. J. and Huenneke, L. F. 1992. Disturbance, diversity, and invasion: implications for conservation. – Conserv. Biol. 6: 324–337.

Hosmer, D. W. and Lemeshow, S. 1989. Applied logistic regression. – Wiley.

Johansson, P. and Ehrlen, J. 2003. Influence of habitat quantity, quality and isolation on the distribution and abundance of two epiphytic lichens. – J. Ecol. 91: 213–221.

Kolb, A. and Diekmann, M. 2005. Effects of life-history traits on responses of plant species to forest fragmentation. – Conserv. Biol. 19: 929–938.

Lea, T. 2006. Historical Garry oak ecosystems of Vancouver Island, British Columbia, pre-European contact to the present. – Davidsonia 17: 34–50.

Lemmon, P. E. 1956. A spherical densiometer for estimating overstorey density. – For. Sci. 2: 314–320.

Levine, J. M. 2000. Species diversity and biological invasions: relating local process to community pattern. – Science 288: 852–854.

Lonsdale, W. M. 1999. Global patterns of plant invasions and the concept of invasibility. – Ecology 80: 1522–1536.

MacArthur, R. H. and Wilson, E. O. 1967. The theory of island biogeography. – Princeton Univ. Press.

MacDougall, A. S. and Turkington, R. 2005. Are invasive species the drivers or passengers of change in degraded ecosystems? – Ecology 86: 42–55.

Maskell, L. C. et al. 2006. Interactions between non-native plant species and the floristic composition of common habitats. – J. Ecol. 94: 1052–1060.

McIntyre, S. and Lavorel, S. 1994. Predicting richness of native, rare, and exotic plants in response to habitat and disturbance variables across a variegated landscape. – Conserv. Biol. 8: 521–531.

Meidinger, D. and Pojar, J. 1991. Ecosystems of British Columbia. – B.C. Ministry of Forests.

Moilanen, A. and Nieminen, M. 2002. Simple connectivity measures in spatial ecology. – Ecology 83: 1131–1145.

Nagelkerke, N. J. D. 1991. A note on a general definition of the coefficient of determination. – Biometrika 78: 691–692.

Pärtel, M. 2002. Local plant diversity patterns and evolutionary history at the regional scale. – Ecology 83: 2361–2366.

Raven, P. J. and Axelrod, D. 1978. Origin and relationships of the California flora. – Univ. Calif. Publ. Bot. 72: 1–134.

Reichard, S. H. and White, P. 2001. Horticulture as a pathway of invasive plant introductions in the United States. – Bioscience 51: 103–113.

Richerson, P. J. and Lum, K. 1980. Patterns of plant–species diversity in California – relation to weather and topography. – Am. Nat. 116: 504–536.

Ricklefs, R. E. and Schluter, D. (eds) 1993. Species diversity in ecological communities: historical and geographical perspectives. – Univ. of Chicago Press.

Roemer, H. L. 1972. Forest vegetation and environments of the Saanich Peninsula, Vancouver Island. PhD thesis. – Univ. of Victoria.

Shea, K. and Chesson, P. 2002. Community ecology theory as a framework for biological invasions. – Trends Ecol. Evol. 17: 170–176.

Stachowicz, J. J. et al. 2002. Biodiversity, invasion resistance, and marine ecosystem function: reconciling pattern and process. – Ecology 83: 2575–2590.

Stohlgren, T. J. et al. 1999. Exotic plant species invade hot spots of native plant diversity. – Ecol. Monogr. 69: 25–46.

Taylor, B. W. and Irwin, R. E. 2004. Linking economic activities to the distribution of exotic plants. – Proc. Natl Acad. Sci. USA 101: 17725–17730.

Tilman, D. 2004. Niche tradeoffs, neutrality, and community structure: a stochastic theory of resource competition, inva-sion, and community assembly. – Proc. Natl Acad. Sci. USA 101: 10854–10861.

Vila, M. et al. 2007. Regional assessment of plant invasions across different habitat types. – J. Veg. Sci. 18: 35–42.

Vellend, M. et al. 2008. Environmentally biased fragmentation of oak savanna habitat on southeastern Vancouver Island, Canada. – Biol. Conserv. 141: 2576–2584.

Verheyen, K. et al. 2004. Metapopulation dynamics in changing landscapes: a new spatially realistic model for forest plants. – Ecology 85: 3302–3312.

Wang, T. et al. 2006. Development of scalefree climate data for western Canada for use in resource management. – Int. J. Climatol. 26: 383–397.

Williams, N. S. et al. 2006. Local extinction of grassland plants: the landscape matrix is more important than patch attributes. – Ecology 87: 3000–3006.

Zobel, M. et al. 2000. Is small-scale species richness limited by seed availability or microsite availability? – Ecology 81: 3274–3282.