Comparison of native and exotic distribution and richness models across scales reveals essential conservation lessons

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Comparing native and exotic plant species distribution and richness models can help to reveal the causes of invasive exotic species proliferation and provide recommendations for preserving native-dominated ecosystems. However, models may have limited applicability if potentially divergent patterns across scales, spatial autocorrelation and correspondence with community-wide patterns such as species richness are not considered. I modeled the distributions of 20 dominant native and 20 dominant exotic species among and within patches in a heavily-invaded and threatened ecosystem in western North America, examining the roles of scale and species origin on variable selection, spatial autocorrelation and model accuracy to determine conditions that favour native over exotic dominants, and derive recommendations for effective management. I also compared distribution models with native and exotic species richness models, to determine the extent to which dominant native and exotic species were representative of synoptic community patterns. Predictability was lower for exotic dominants, possibly because they are environmental generalists, and was lower within than among patches. Predictors were generally shared between distribution and richness models; however, species-specific differences were common within both native and exotic species groups. Predictors for individual species across scales were frequently different and sometimes opposing. Distribution and richness models suggest that management assuming environmental affiliation at one scale may be ineffective at another; that site prioritization to maximize native versus exotic richness may not preserve the habitat of some common native species; and that intensive management to reduce exotics may be difficult due to low predictability and shared affiliations with natives. Comparing native and exotic distribution and richness models at two scales enabled scale-specific conservation recommendations and elucidated trade-offs between management for richness and representation that distribution models at an individual scale would not have allowed.

Species distribution models relating occurrence or abundance of species to environmental or spatial variables (Elith and Leathwick 2009), have been used extensively for conservation applications, including predicting the spread of invasive exotic species (Jones et al. 2010), determining priority areas for land protection (Ortega-Huerta and Peterson 2004), and recommending focused management efforts for areas in which exotics appear to be favoured over natives (Arévalo et al. 2005). Species richness models can also be powerful tools for conservation (Stohlgren et al. 1999), and may be particularly useful for measuring ecological patterns in diverse communities where distributions of all species cannot be modeled (Ferrier and Guisan 2006). Direct comparison of predictions from both distribution and richness models allows inclusive properties of richness models to be complemented by the detail of distribution models, offering a potentially powerful tool to inform conservation (Ferrier and Guisan 2006, Guisan and Rahbek 2011).

However, the inherently multi-scale, spatial nature of ecological processes and data can reduce accuracy and transferability of models, potentially limiting their real-world applicability (Wilson et al. 2005). Although it is generally recognized that scale is a key consideration in ecological models (Levin 1992, Whittaker et al. 2001), nearly all species distribution and richness models make predictions at a single spatial scale (for exceptions, see Schweiger et al. 2005, Nielsen et al. 2008, Jones et al. 2010), and thus may provide incomplete or potentially misleading depictions of factors driving species distributions (Whittaker et al. 2001). This may be particularly the case for comparisons of native versus exotic species, which may have shared or divergent distribution patterns depending on the scale being considered (Fridley et al. 2007).

In addition, both species distributions and richness may be spatially autocorrelated, due to dispersal limitation (Hubbell 2001), mass effects (Cottenie 2005), or spatially autocorrelated environmental variables (Borcard et al. 1992). These signals are often inherently impossible to isolate completely (Gilbert and Bennett 2010), and may affect predictor variable selection (Lennon 2000). Accounting for

spatial autocorrelation may be especially important when modeling species that are dispersal limited (Guisan and Thuiller 2005). Exotic species in particular may lack equilibrium with their environment due to incomplete colonization of new habitats (Seabloom et al. 2006). In addition, considerable controversy persists regarding the influence of spatial autocorrelation on the accuracy of response variable predictions. While some authors argue that spatially explicit models are not necessary for correct estimation of model parameters (Hawkins et al. 2007, Hawkins 2012), others argue that spatial autocorrelation in response variables can lead to inaccurate parameter estimates (Beale et al. 2007, 2010, Kühn and Dormann 2012).

Here, I compare conventional and spatially-explicit species distribution and richness models at two discrete scales (among and within patches), for the 20 dominant native and 20 dominant exotic species (Table 1) in a threatened ecosystem in western North America, to examine the roles of scale and species origin on variable selection, spatial autocorrelation in distributions, and model accuracy. I also compare species distributions with community-level richness patterns among and within patches. In doing so, my aim is twofold: 1) to demonstrate a framework for constructing and comparing species distribution and richness models that addresses the potential problems of scale and spatial autocorrelation outlined above; and 2) to provide recommendations for focussing conservation efforts on the scale at which results are most predictable, and for which the desired response (e.g. decrease target exotic species, preserve largest populations of target native species) is most likely achieved.

Methods

Study area

The study system, known in Canada as the 'Garry oak ecosystem' (GOE), is located on southeast Vancouver Island, British Columbia and adjacent islands, and is considered to be highly diverse, and one of Canada's most endangered ecosystems (GOERT 2011). The climate in this area is sub-Mediterranean, with cool, wet winters and frequent summer drought (MacDougall 2005). Mean annual temperature in the study area ranges from ~9.8 to ~10.6°C; mean annual precipitation (occurring mostly between November and March) ranges from ~670 to ~1100 mm (Wang et al. 2006). GOE meadow patches tend to be located on shallow-soil sites isolated from one another by a combination of forest, salt water and human-dominated landscapes. Since European colonization, ~90% of GOE habitat has been lost, through conversion to farmland and suppression of fires that had prevented encroachment by Douglas-fir *Pseudotsuga menziesii* forest (Bjorkman and Vellend 2010). Remaining patches are often heavily invaded by exotic plant species, which dominate ground cover in some patches (Bennett et al. 2012). A variety of efforts are underway to protect remaining high-priority patches, rehabilitate degraded areas, and monitor and control invasive species among and within patches (GOERT 2011).

Table 1. Occurrences of native and exotic species used in species distribution models, out of 81 patches and 605 quadrats.

	Number of patches	Number of quadrats
Native species		
Camassia leichtlinii	66	231
Festuca rubra	71	216
Brodiaea coronaria	75	213
Galium aparine	79	207
Camassia quamash	46	173
Brodiaea hyacinthina	65	170
Achillea millefolium	74	161
Sanicula crassicaulis	77	160
Plectritis congesta	66	156
Elymus glaucus	70	136
Collinsia parviflora	72	122
Polypodium glycyrrhiza	73	114
Luzula multiflora	62	106
Cerastium arvense	74	93
Lotus micranthus	36	90
Ranunculus occidentalis	56	80
Danthonia californica	44	78
Carex inops	45	75
Trifolium willldenowii	55	70
Lomatium utriculatum	36	69
Exotic species		
Aira praecox	78	262
Hypochaeris radicata	78	249
Anthoxanthum odoratum	53	175
Rumex acetosella	75	159
Vicia sativa	62	150
Holcus lanatus	68	148
Bromus diandrus	55	144
Vulpia bromoides	72	143
Cytisus scoparius	45	140
Stellaria media	70	136
Bromus hordeaceus	68	133
Bromus sterilis	61	128
Geranium molle	67	117
Dactylis glomerata	57	102
Vicia hirsuta	52	99
Veronica arvensis	52	93
Cynosurus echinatus	61	80
Myosotis discolor	49	80
Poa pratensis	62	68
Aphanes arvensis/australis	48	54

Community surveys

I used extensive ('patch-level') and intensive ('intra-patch level') surveys of vascular plant species in the study area (Bennett et al. 2012; P. Giblin and P. Dunwiddie pers. comm.). Patch-level surveys were conducted across 81 meadow patches ranging in size from ~0.2 to 17.7 ha. Patches were systematically surveyed across their full extents for the presence of vascular plant species. Thirty-seven patches occurred on small islands and 44 on Vancouver Island (Supplementary material Appendix 1, Fig. A1). Intra-patch surveys were conducted on 86 meadow patches (including the 81 surveyed extensively). The additional five patches were located on islands for which more than one GOE patch existed, and patch-level survey results had not been separated (D. Giblin and P. Dunwiddie pers. comm.). Intra-patch surveys used 1-m^2

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quadrats located in a stratified random configuration within patches. The number of quadrats per patch was scaled according to patch size and ranged from five to 15. Surveys were conducted from April to June, the time during which most plants are easiest to identify. Plants were identified to the lowest taxonomic level possible using the nomenclature scheme of Douglas et al. (1998–2002). Where necessary, identifications were confirmed at the Univ. of British Columbia or Univ. of Washington herbaria using collected specimens.

Environmental variables

Thirteen environmental variables were collected (Table 2). The variables were chosen based on ecological knowledge of the factors potentially exerting the greatest influence on species distributions in the study area. For the models outlined below, the environmental variables were transformed as necessary to improve fit and conform to model assumptions. In the case of climate, 83 variables provided by the program Climate BC ver. 3.1 (Wang et al. 2006) at 100 m resolution were reduced using principal component analysis (PCA) to a single principal axis, explaining 69% of the total variation in the climate data. Climate PC1 was positively correlated with mean annual temperature ($r = 0.50$, $p < 0.0001$) and negatively correlated with mean annual precipitation ($r = -0.66$, $p < 0.0001$).

Although most environmental variables were not highly correlated, location of a patch on a small island and nearby road length were highly negatively correlated at both scales (Supplementary material Appendix 1, Table A2, A3). Both variables were retained in the distribution model framework because they measure phenomena that are not interchangeable (e.g. nearby road length is low for small islands, and also low for patches surrounded by forest, agriculture and/or other meadows), and because both variables were frequently retained in exploratory (and final) distribution models. However, given their high correlation, selection of one these variables over another was viewed with caution, and it was not possible to determine whether the statistical influence of small-island status in models represents the biological influence of isolation or lack of disturbance or both.

Distribution model framework

To examine species distributions for consistency in patterns across scales, I constructed species distribution models at two scales: 1) the inter-patch scale, using patch-level surveys discussed above and variables collected across the extent of patches ('patch-level' variables); and 2) the intra-patch scale, using quadrat-based, intra-patch surveys discussed above, and variables collected at both the patch-level and at the quadrat ('intra-patch') level. I constructed these models using the 20 most abundant native and 20 most abundant exotic species from my intra-patch surveys (Table 1). The 20 focal native species are among the iconic species in the GOE, while 14 of the 20 focal exotic species are considered among the most important invasive species in the system (GOERT 2011).

Species distribution model development followed the general framework illustrated in Fig. 1. All analyses were conducted using R ver. 2.15.1 (R Development Core Team), and various specialized packages. To address potential problems involving spatial autocorrelation outlined above, I first examined the data for spatial autocorrelation using spline correlograms (Bjørnstad and Falck 2001). This technique is a modification of traditional correlograms that uses a smoothing spline to illustrate consistent patterns in autocorrelation across distances and a bootstrap technique to derive confidence bands for the estimated autocorrelation (Bjørnstad and Falck 2001). These modifications help mitigate problems interpreting patterns and assigning confidence intervals to estimates in traditional correlograms, which approximate continuous spatial autocorrelation using discrete distance intervals. In traditional correlograms, correlations for small distance intervals (and few samples) may be spurious while large distance intervals may result in failure to detect real smaller-scale autocorrelation.

Table 2. Variables examined in models. Variables 1 through 8 were collected at the patch level. Variables 9 through 13 were collected at the intra-patch level.

Variable	Collection method
1. Small island (binary)	
2. Patch area (m^2)	Air photos plus ground truthing with GPS
3. Climate (principal component 1)	First principal component of PCA of 83 closely-related climate variables, estimated using CLIMATE BC*
4. Deer fecal pellets present in at least one quadrat in patch	Presence of pellets in any quadrat in a patch
5. Forest area (500 m buffer; m^2)	Digitization of air photos; calculation of buffer using ArcGIS 10
6. Meadow (500 m buffer; m^2)	Digitization of air photos; calculation of buffer using ArcGIS 10
7. Agricultural land (500 m buffer; m^2)	Digitization of air photos; calculation of buffer using ArcGIS 10
8. Road length (500 m buffer; m)	Digitization of air photos; calculation of buffer using ArcGIS 10
9. Litter (% cover)	Estimation using quadrat
10a. Aspect (northing, degrees)	Compass
10b. Aspect (easting, degrees)	Compass
11. Soil depth (cm)	Soil depth probe, mean of sample per side of quadrat
12. Slope (degrees)	Clinometer
13. Canopy cover (%)	Fish-eye lens photographs (1 m height) and WinSCANOPY 2008a**

*ver. 3.1, Wang et al. (2006).
**Régent Instruments, < www.regentinstruments.com/products/Scanopy/SCANOPYSoftware.html >.
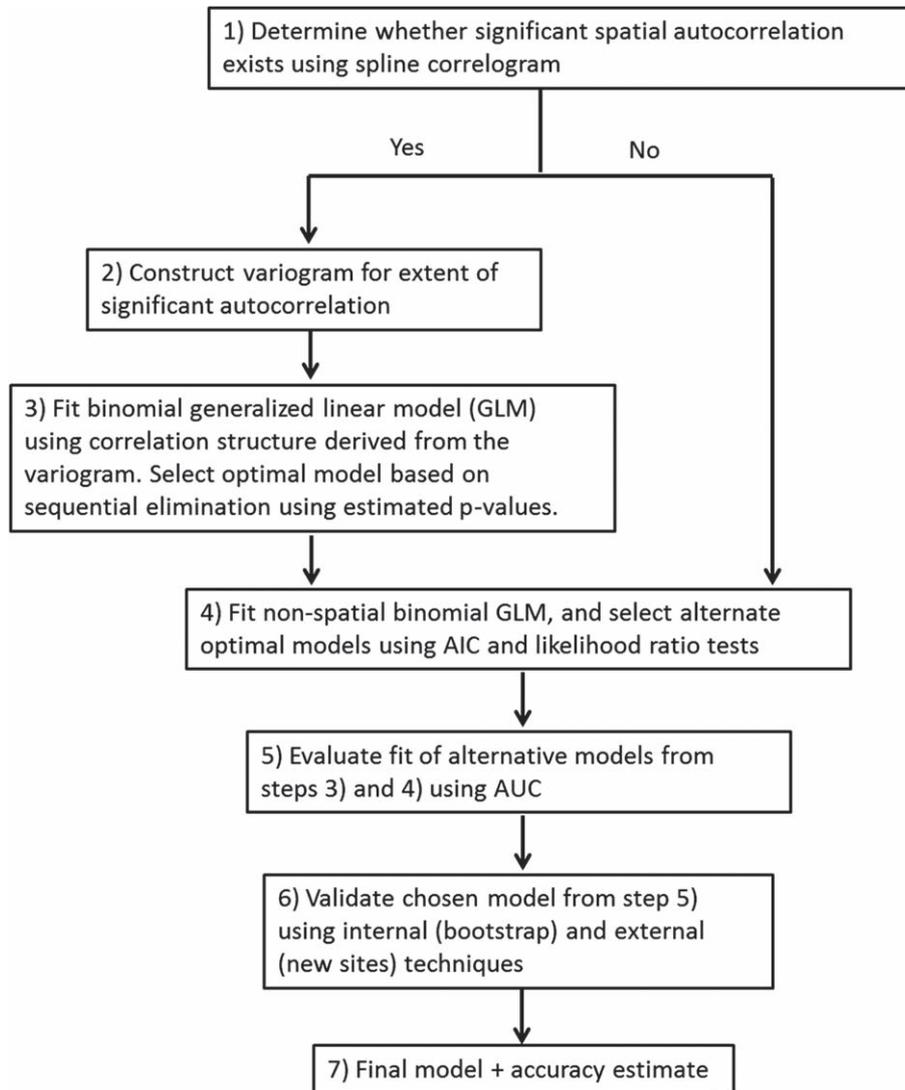
Figure 1. General model framework for species distribution models.

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

At the intra-patch scale, a spatial mixed-model approach was used, with patch identity as a random factor to account for site-specific effects. Intra-patch models used only quadrats from patches where a species was found in patch-level surveys, to restrict prediction of intra-patch distributions to patches where species were known to be present. These models are more appropriate for inferring the determinants of species distributions at the intra-patch scale than models using all quadrats: if a species is not present in a patch, it will always be absent even on compatible microsites. However, models using all quadrats were also constructed, and results were similar to those presented here (Supplementary material Appendix 1, Table A8). All variables, including those measured at the inter-patch scale, were used in the intra-patch models, since patch-level variables may affect presence at the microsite level.

Given the debates outlined above regarding the relative performance of spatially-explicit versus non-spatial models, I constructed conventional, non-spatial logistic models for all species and tested their performance versus the spatial

models. At the intra-patch scale, both non-spatial mixed models (using patch identity as a random factor) and non-spatial conventional models (i.e. no random component) were constructed. For conventional models, optimal models were selected based on backward and forward selection using Akaike's information criterion (AIC) and backward selection using likelihood ratio (LR) tests. Both approaches were used to address different recommendations in the literature (Bolker et al. 2009, Zuur et al. 2009). In all cases, LR-selected variables were either identical to or subsets of AIC-selected models. Both AIC- and LR-selected models were retained for comparison. Fitting spatial binomial models necessitated using penalized quasi-likelihood (cf. Dormann et al. 2007), for which likelihood-based model selection is not feasible. Therefore, backward sequential elimination of variables using estimated p-values was used. In all cases, selected variables were identical to or subsets of AIC-based and LR-based non-spatial models, and in nearly all cases, fixed parameters were similar in magnitude to those of the non-spatial models.

Since spatial models used penalized quasi-likelihood, they could not be compared with non-spatial models using likelihood-based tests. Thus, I compared models for each species for relative accuracy using the area under the receiver operating characteristic curve, or AUC (cf. Fielding and Bell 1997). Although AUC should not be interpreted as an absolute measure of a model's accuracy (Lobo et al. 2008), and should be used with caution to compare among models for species with different prevalences in a dataset (Santika 2011, Jiménez-Valverde 2012), it is nonetheless a useful measure for comparing models of the same species within a single dataset (Santika 2011). Thus, the model with the highest AUC for each species was retained for validation.

Species distribution model validation

Given potential uncertainties affecting performance of species distribution models, including historical factors, biotic interactions and unmeasured environmental variables, careful evaluation of model performance is necessary (Hortal et al. 2012). Thus, I tested the performance of retained distribution models using internal validation via nonparametric bootstrapping (Efron 1983), as well as external validation using independent datasets. In the internal validation bootstrap procedure, I used fixed effects only in intra-patch models for predicting the original dataset from the bootstrap sample. In this way, the use of an external dataset (where patch identities are different from those used in the original models) is more closely simulated.

The external dataset for inter-patch models consisted of 14 patches that had been surveyed at only the patch level and could not be surveyed at the intra-patch scale due to logistical limitations. Eight were located on Vancouver Island (Lilley 2007), and six were located in the San Juan Islands of Washington State (D. Giblin and P. Dunwiddie pers comm.). For intra-patch models, data from 1-m^2 quadrats from Gonzales (2008) were used. Quadrats from patches that were comparable to mine (herbivory classified as 'light' or 'moderate'; no history of intensive human

development) were chosen, resulting in 43 quadrats for external validation. Neither canopy openness nor percent cover of litter was measured by Gonzales (2008). Canopy openness was assumed to be 100%, as the meadows in the external data were all located on small islands with little or no tree cover. Litter cover for these quadrats was estimated using the following linear model from the main dataset: (litter cover) = (soil depth) $\times$ (percent cover all graminoids). This model was highly significant; however, the explained variation was relatively low ($R^2 = 0.16$; $p < 0.0001$).

Species richness models

To examine broader, community-level patterns in native and exotic communities and to determine whether distribution models were representative of these patterns, I constructed richness models to compare with the distribution models. The richness model framework was analogous to that of the individual species models, in that spatial autocorrelation in the response variable was tested with spline correlograms, and then modeled using variograms, which were used to construct error covariance matrices as above. However, species richness was log transformed, and was modeled with a Gaussian distribution, allowing interpretation with respect to biogeographic theory (much of which discusses log-richness relationships), and comparison of spatial models versus non-spatial models using likelihood-based tests. Initial, fully-parameterized spatial and non-spatial models were constructed, and the optimal model framework was chosen using AIC and LR tests (which produced the same results). Subsequent variable selection in the chosen model framework was then undertaken using both AIC- and LR-based selection as above.

Results

Species origin and scale vs variable selection

At the inter-patch scale, models could not be constructed for nine of the 40 species, as I found no significant relationships between their occurrences and environmental variables. These species were generally among the most common in inter-patch data, with too few absences to discern significant links to environmental variables. For the remaining species, selected model terms for native species were in some cases similar to those of exotics (e.g. log patch area was a consistently positive predictor for both natives and exotics; Table 3, Supplementary material Appendix 1, Table A5). However, variables associated with human influence (road length and nearby agricultural area), tended to be negative predictors for presence of native species but positive predictors for exotic species (Table 3). In particular, nearby agricultural area was a positive predictor for four exotic grasses (*Anthoxanthum odoratum, Bromus diandrus, Dactylis glomerata* and *Poa pratensis*). Although location of patches on small islands tended to be a negative predictor of both native and exotic species, four native species (*Camassia leichtlinii, Achillea millefolium, Plectritis congesta* and *Trifolium willdenowii*) were more likely to be found on

Table 3. Variables used in inter-patch scale species distribution models, and percentages of models in which variables were selected.

	Native (n = 15 spp.)		Exotic (n = 16 spp.)	
	Positive	Negative	Positive	Negative
Small island	27	53	0	50
Log patch area	67	0	50	0
Climate (PC1)	7	33	31	13
Deer pellets in ≥ 1 quadrat in patch	47	0	31	13
Forest area (500 m buffer)	40	0	19	19
Meadow (500 m buffer)	27	0	19	0
Log agricultural area (500 m buffer)	0	20	25	6
Log road length (500 m buffer)	7	40	19	13

small-island patches than on Vancouver Island patches (Supplementary material Appendix 1, Table A5).

At the intra-patch scale, percent cover of litter tended to be a negative predictor for both native and exotic species, while canopy openness and soil depth tended to be positive predictors for natives and exotics (Table 4, Supplementary material Appendix 1, Table A7). However, divergent responses predominated for the patch-level variables climate PC1 (negative among natives, positive among exotics), small-island patch location (positive among natives, negative among exotics), deer pellets (no relationship among natives, positive among exotics), and nearby agriculture (negative among natives, positive among exotics).

Variable selection for individual species across scales was not consistent: for 80% of 142 cases among all models where a patch-level variable was selected, the variable was selected at the inter-patch scale for a species but not the intra-patch scale (or vice-versa); and for ~8% of cases, the relationship with the variable was in the opposite direction at the inter- versus intra-patch scale (Supplementary material Appendix 1, Table A5, A7). For

Table 4. Variables used in intra-patch scale species distribution models, and percentages of models in which variables were selected.

	Native (n = 20 spp.)		Exotic (n = 20 spp.)	
	Positive	Negative	Positive	Negative
Small island	25	10	5	30
Log patch area	0	35	10	15
Climate (PC 1)	10	40	35	10
Deer pellets in ≥ 1 quadrat in patch	0	5	30	5
Forest area (500 m buffer)	30	0	15	0
Meadow (500 m buffer)	15	0	10	5
Log agricultural area (500 m buffer)	0	30	10	5
Log road length (500 m buffer)	10	10	15	25
Canopy openness (%)	40	25	45	15
Litter	0	25	0	25
Aspect (easting)	0	10	0	0
Aspect (northing)	5	0	5	10
Log soil depth (cm)	45	15	45	10
Slope	20	15	0	5

example, log patch area was negatively related to intra-patch presence for six species for which it had a positive relationship at the inter-patch scale. In other words, these species were more likely to be present on larger rather than smaller patches, but were less abundant within the larger of the patches where they were present. Intra-patch models constructed using all quadrats exhibited similar differences with inter-patch models: in 78% of cases, a patch-level variable was selected at one scale and not another (Supplementary material Appendix 1, Table A8).

Species origin and scale vs spatial autocorrelation in distribution models

Spatial autocorrelation was generally more pronounced at the intra-patch scale. At the inter-patch scale, significant spatial autocorrelation was observed for one exotic (*Holcus lanatus*) and four native species (*Camassia leichtlinii*, *Plectritis congesta*, *Lotus micranthus*, *Danthonia californica*). For the 31 species modeled at the inter-patch scale, AUC was never highest for the spatially-explicit models. The retained model based on highest AUC was the AIC-selected model in 16 cases and the LR-selected model in one case, while in 14 cases, AIC-selected and LR-selected models were identical. At the intra-patch scale, significant spatial autocorrelation was found for 25 species (12 native and 13 exotic). For 21 of these species (10 native and 11 exotic), spatially-explicit mixed models with patch identity as a random factor had the highest AUC.

Origin and scale vs model performance

Bootstrap cross-validation for inter-patch models indicated slight overfit (Supplementary material Appendix 1, Table A4); however, mean corrected AUC for inter-patch models was 0.83, suggesting high discriminatory power (Hosmer and Lemeshow 2000). For six species, > 5% of bootstrap models failed to converge. External validation of inter-patch models also indicated very good discrimination, with overall concordance of 81.8%. In general, native species models exhibited better predictability than exotic species models (Table 5). The rate of false positives was greater than that of false negatives (Table 5), and was highest for exotic species: 48% (36 of 75) absences were falsely predicted for exotics.

Bootstrap cross-validation of the intra-patch models indicated that overfit was somewhat greater than for inter-patch models (Supplementary material Appendix 1, Table A6), with mean corrected AUC of 0.78, again suggesting good discriminatory power (Hosmer and Lemeshow 2000). However, external evaluation of intra-patch models indicated relatively poorer fit to the external data than for inter-patch models (Table 6). In particular, the rate of false negatives was very high among exotics, at > 90% (Table 6).

Richness models

At the inter-patch scale, spatially-explicit richness models were selected for both native and exotic species using both

Table 5. Confusion matrices comparing predicted versus actual occurrences in external dataset for inter-patch scale distribution models. Prediction threshold = 0.5.

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

AIC and LR criteria. In general, selected variables followed patterns seen in distribution models. Log patch area had a positive relationship with log richness for both native and exotic species, while climate PC1 had a negative relationship with native richness and a positive relationship with exotic richness (Supplementary material Appendix 1, Table A9). However, while small-island status was a negative predictor for 53% of native species at this scale (Table 3), this variable was not selected for native richness (Supplementary material Appendix 1, Table A9). At the intra-patch scale, spatial models were again selected when tested against non-spatial models for native and exotic species, and selected variables reflected patterns seen in distribution models (Supplementary material Appendix 1, Table A10). In intra-patch richness models, relationships with two intra-patch variables, log soil depth (positive) and litter (negative), were shared between native and exotic species (Supplementary material Appendix 1, Table A10).

Discussion

Distribution models exhibited clear differences between dominant native and exotic species and across scales. Comparisons of model results suggested that extrapolating patterns from one scale to another, which has been shown to be problematic when downscaling atlas data (Marcer et al. 2012), would have been unfeasible and prediction at a single scale would have been insufficient for developing appropriate conservation recommendations. In addition, comparison of distribution and richness models across

Table 6. Confusion matrices comparing predicted versus actual occurrences in external dataset for intra-patch distribution models. Prediction threshold = 0.5.

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

scales suggested important trade-offs among potential goals in site prioritization and management.

Origin and scale versus variable selection

Unsurprisingly, the generally positive relationships at the inter-patch scale among exotic species and nearby agricultural areas and roads suggests that human disturbance promotes exotic invasion (cf. Vilà et al. 2007), through a combination of disturbance itself providing resource opportunities, and propagule pressure of ruderal exotics from adjacent developed or disturbed areas. For native species at the inter-patch scale, the fact that small islands were negative predictors for over 50% of species suggests either dispersal limitation has prevented colonization or failed to prevent local extinction for these species thousands of years after their arrival in the area, or some native species are relatively intolerant of environmental conditions (e.g. salt spray) on small islands. At the intra-patch scale, generally positive relationships for native and exotic species between presence and both canopy openness and soil depth, and generally negative relationships with litter (Table 4) suggest that many native and exotic species share similar constraints at small scales (Bennett et al. 2012).

However, considerable variation in selected variables among species indicates species-specific responses in addition to community-wide trends. In addition, the fact that 88% of variables selected for each species (78% in models using all quadrats) were either unshared or opposing at the inter- versus intra-patch scale, indicates caution is necessary when extrapolating the apparent effect of a variable at a single scale to additional scales. For example, log patch area was generally a positive predictor of presence at the inter-patch scale, in line with biogeographic theory predicting greater immigration and less extinction on larger patches (Hanski 1991, Whittaker and Fernández-Pelacios 2007). However, for six species, log patch area was a positive predictor at the inter-patch scale and a negative predictor at the intra-patch scale, suggesting that factors that are positively associated with presence among sites can be negatively associated with abundance within sites. In such cases, if patterns are only known at a single scale, management to promote or diminish a target species across all scales may be ineffective or even counterproductive.

Origin and scale versus spatial autocorrelation

Spatial autocorrelation was not more common for exotics than for natives, with similarly low frequencies at the inter-patch scale and higher frequencies at the intra-patch scale, contrary to the expectation of more prevalent spatial autocorrelation in exotics due to their recent arrival (cf. Jones et al. 2010). Sixteen of the 20 dominant exotics possessed obvious adaptations for long-distance dispersal (e.g. hooked awns, pappus), while only eight of the 20 dominant native species possessed such adaptations. Though evidence of dispersal limitation among exotic species exists in the GOE, it is most prevalent in species lacking means of long-distance dispersal (Bennett et al. 2013). Specialized dispersal mechanisms may have helped the dominant exotics disperse

as widely throughout the study system as the dominant natives, despite their < 140-yr history in western North America (Reichard and White 2001, Bennett et al. 2013).

There has been much debate regarding the relative merits of spatially-explicit versus conventional models (Hawkins et al. 2007, Beale et al. 2010, Hawkins 2012, Kühn and Dormann 2012). My results indicate that the relative accuracy of spatial versus non-spatial models may depend on the scale of analysis. Accounting for spatial autocorrelation in species distributions at the inter-patch scale did not lead to more accurate models, while accounting for the spatial signals in species distributions at the intra-patch scale often improved model fit, as evidenced by the fact that spatially-explicit models had the highest AUC for 84% of species with significant spatial autocorrelation at this scale. However, the average difference in AUC between spatially-explicit and non-spatial models for these species was relatively low (0.02). Whether this difference is important would depend on the specific research question being posed; however, in general the most accurate model possible should be used. Thus, while I agree with recommendations of Beale et al. (2010) that spatial autocorrelation should generally be accounted for in species distribution models, I also recommend testing spatially explicit models against non-spatial models (assuming the latter do not exhibit residual spatial autocorrelation), as non-spatial models allow simpler interpretation and may be sufficient in many cases.

Origin and scale versus distribution model performance

The very good overall performance of inter-patch models was notable given that prevalence (ratio of presences to data points) in the most common species was relatively high (Table 1). High or low prevalence have been thought to negatively affect performance of binomial models (Vaughan and Ormerod 2003). However, recent studies assert the importance of signal strength in predictor variables over prevalence in the performance of binomial models (Vittinghoff and McCulloch 2007, Jiménez-Valverde et al. 2009). However, the high prevalence of some of the most common species meant that relatively limited conditions existed where these species were not found, both in the original and external datasets. This is not necessarily a shortcoming of the models. The fact that statistical associations existed between species distributions and environmental variables suggests that certain site-level conditions exist where even common species are not found. In addition, most absences in the inter-patch external data were correctly predicted (Table 5).

The generally lower performance of exotic species models may have been due to dominant exotics tending to be more generalist than their native counterparts, with less distinct environmental affiliation (Labra et al. 2005, Bennett et al. 2012). Lack of equilibrium with environmental conditions due to dispersal limitation could also have affected model performance for exotic species more than natives. However, as noted above, common exotic species in the GOE appear to have dispersed widely among patches (Bennett et al. 2013).

Lower performance at the intra-patch scale, particularly for exotic species, may have been due to several possible factors. The evaluation dataset lacked measurements of canopy openness or litter, necessitating their estimation. Evaluation data also came entirely from small-island patches. This may explain some of the false negatives for the exotic species in particular, because small-island status was negatively related to the occurrence of 30% of exotic species at the intra-patch scale (Table 4). Although these species were more common on Vancouver Island patches, they were still infrequently found in quadrats on small islands in the main dataset. Such infrequent occurrences of these species in the external dataset composed of small-island patches are necessarily false negatives. In addition, the inherent variability in processes influencing species distributions may be greater at small than at large scales, leading to greater stochasticity in small-scale patterns (Levin 1992).

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

Richness models

Comparison of richness with distribution models was useful in illuminating ecological differences among native and exotic species. In general, selected variables in richness models tended to follow similar patterns to those in distribution models, with native richness at the inter-patch scale being highest in patches more isolated from human development (i.e. less road length, more forest area within 500 m), while exotic richness was highest in areas closer to human development (i.e. more agricultural area, less forest area within 500 m; Supplementary material Appendix 1, Table A9). Such opposing responses to human influence are common and well documented (Vilà et al. 2007). However, similarities in native and exotic richness models with respect to the apparent influence of soil depth and litter (both measured at the intra-patch scale) again suggest that native and exotic species often respond to similar constraints at the microsite level. Although positive relationships between native and exotic richness at small scales in the GOE suggest that such similar constraints are important drivers of community-level patterns (Bennett et al. 2012), future range expansions among less common and slower-dispersing exotics (Bennett et al. 2013), may lead to an ever-greater importance of competition and eventual de-coupling of small scale native and exotic richness patterns. Small islands may offer a partial shelter from threats to native species in the GOE. However, the selection of small island patches as negative predictors for most dominant natives at the intra-patch scale, but as a positive predictor of native richness (and negative predictor of exotic richness) at the intra-patch scale, suggests that while

small islands contain more intra-patch abundance of native species than Vancouver Island patches and are more isolated from human disturbance that particularly threatens rare species (Bennett and Arcese 2013), they may not contain a fully representative native flora of the GOE.

Conclusion and management implications

Patterns in species distributions and richness on landscapes may be complicated by many factors including different responses across scales, species interactions and dispersal limitation (Guisan and Rahbek 2011, Hortal et al. 2012). However, careful choice of spatial scales for modeling species and consideration of potential spatial autocorrelation can help to account for potential complications and improve model applicability. In addition, combining models of species distribution and richness at multiple scales can be a powerful tool to help guide management. Such an approach allows a more comprehensive understanding of the roles of environmental variables and the scales at which patterns are most predictable and management may be most effective, than conventional models at a single scale would allow. For the Garry oak ecosystem, comparing native and exotic species distribution models with richness models illustrated the potential conflicts between conservation goals based on minimizing exotic richness and maximizing native representation, and inherent difficulties in intensive management to control exotic species.

Current conservation efforts in this system are common to many invaded systems, and include site prioritization to preserve native species at the inter-patch scale, and intensive management programs to help control exotic species (GOERT 2011). Richness models indicate that site prioritization to preserve the most intact sites should favour small-island patches, as such patches contain lower richness of exotics with no diminished richness for natives. Such patches would also be favoured if prioritizing for species threatened with extinction (Bennett and Arcese 2013). However, if sites were prioritized for protection to preserve a representative suite of native species, prioritizing islands would not be appropriate, since over 50% of common native species were negatively predicted at the inter-patch scale for small-island patches.

For managing exotic species, overlap among intra-patch environmental predictors for native and exotic species distributions and richness, and the difficulty in predicting intra-patch distributions of exotics, suggest that managing for individual exotic species at this scale may be quite difficult. Intensive management targeting exotic richness hotspots (e.g. weeding programs) should be conducted with great care, as such microsites appear also to be hotspots of native richness. Given these caveats, management and monitoring for exotic species in the study system would most often need to encompass entire patches, and be carefully planned to strike a balance between maximizing coverage and minimizing disturbance to native species. Such important lessons provide examples of how combining distribution and richness models at multiple scales would lead to more effective management in other systems.

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