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Role of climatic niche models in focal-species-based conservation planning: Assessing potential effects of climate change on Northern Spotted Owl in the Pacific Northwest, USA

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ABSTRACT

Although well-studied vertebrates such as the Northern Spotted Owl (NSO) are often used as focal species in regional conservation plans, range shifts associated with climate change may compromise this role. I used the Maxent (maximum entropy) method to develop NSO distribution models from data on NSO locations, forest age, and an ensemble of climate projections. NSO presence was positively associated with the proportion of old and mature forest at two spatial scales. Winter precipitation was the most important climate variable, consistent with previous studies suggesting negative effects on survival and recruitment. Model results suggest that initial niche expansion may be followed by a contraction as climate change intensifies, but this prediction is uncertain due to variability in predicted changes in precipitation between climate projections. Although new reserves created by the US Northwest Forest Plan prioritized areas with greater biological importance for the NSO than did pre-existing reserves, the latter areas, which lie predominantly at higher elevations, increase in importance under climate change. In contrast with previous analyses of the region's localized old-forest-associated species, vegetation rather than climate dominated NSO distribution models. Rigorous assessment of the implications of climate change for focal species requires development of dynamic vegetation models that incorporate effects of competitor species and altered disturbance regimes. The results suggest that, lacking such data, models that combine climate data with current data on habitat factors such as vegetation can inform conservation planning by providing less-biased estimates of potential range shifts than do niche models based on climate variables alone.

1. Introduction

Focal species are often used in conservation planning to complement efforts to conserve other types of biodiversity targets such as rare-species locations and vegetative communities (Carroll et al., 2003). Planners may intensively focus on habitat and viability requirements of a few well-studied species because they assume such species can serve as "conservation umbrellas", either through overlap in priority habitat with a wider group of poorly-known taxa or by informing design rules on how the size, spacing, and connectivity of reserves affect viability (Noon and Blakesley, 2006; Carroll et al., 2003). Alternately, the focal species approach may arise from legal mandates such as the US Endangered Species Act (ESA) that require detailed consideration of the viability of a few species of highest concern.

The Northern Spotted Owl (NSO; *Strix occidentalis caurina*) was listed in 1990 as a threatened species under the ESA due to declining population trends related to the loss of older coniferous forest habitat to timber harvest (Bart and Forsman, 1992; Noon and Blakesley, 2006). In response, the US federal Northwest Forest Plan (NWFP) was initiated in 1994 to coordinate forest planning at broad spatial scales (the range of the NSO within western Washington, Oregon, and northern California) through a conservation zoning framework that included late-successional reserves (LSR, 2.97 million ha) that emphasize retention and restoration of older forest conditions, adaptive management areas (609,000 ha) where new approaches to forestry would be developed, and the matrix (1.59 million ha) where most timber management would occur (Thomas et al., 2006). The NWFP ultimately evolved into a comprehensive multi-species plan (Thomas et al., 2006). However, because the NWFP initially arose from a legal and policy controversy over the viability of the NSO, the owl remained the *de facto* "umbrella" species for conserving the community of species associated with older forests. In this study, I evaluate the potential effects of climate change on NSO habitat distribution and the efficacy of the NWFP's reserve system at capturing NSO habitat under current and projected future climate. I develop distribution

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models for the NSO using a ‘‘maximum entropy’’ (Maxent) modeling approach developed for use with presence-only data such as NSO nest site locations (Phillips et al., 2006; Phillips and Dudik, 2008).

Species distribution models based solely on climate data, termed ‘‘climatic niche’’ models, allow first approximations of potential effects of global climate change on large suites of taxa (Thomas et al., 2004). Because many of these species are poorly-known, and relevant non-climatic environmental variables may be unavailable over the global or continental extent of analysis, more detailed and biologically-informed models may not be feasible. However, as climatic niche models are increasingly applied to inform single-species conservation strategies, key assumptions, such as that such models adequately describe a species ‘‘fundamental niche’’, have been increasingly questioned (Elith and Leathwick, 2009). Land management agencies in the US and elsewhere increasingly seek to assess climate change impacts in both single- and multi-species conservation plans (USFWS, 2009). An evaluation of the performance of climatic and climate–vegetation niche models for the NSO can suggest how planners can best use available data to assess potential effects of climate change on well-studied focal species while accounting for model uncertainty and retaining adequate skepticism about which components of the niche are represented by model predictions.

2. Materials and methods

The study area was based on the extent of the NWFP, which stretches from the Cascade Range to the Pacific Ocean in Washington and Oregon, and covers portions of northwestern California (Thomas et al., 2006) (Fig. 1). The study region covered 83.9% of the NWFP region’s public lands but, due to limitations in the spatial extent of environmental variables, excludes the extreme southern portions of the NWFP area, an area of predominantly private lands which are not subject to the NWFP’s management mandates (Fig. 1).

I used data from Carroll and Johnson (2008) containing locations of NSO nest sites or activity centers derived from digital databases of surveys of NSO occupancy and reproductive status from the late 1980s through 2000 for Oregon and Washington and primarily (93%) from 1987–2006 for California. Spatially-biased survey effort typical of ‘‘found’’ data presents a major challenge to distribution modeling. To reduce this problem, I thinned data to achieve a minimum separation for each species of 1 km between locations, using a geographic information system (GIS) routine that identified clusters of adjacent records and then reduced the set of such records to one record randomly selected from that set. A 1 km separation threshold made it less likely that multiple records would be included from the same NSO in successive years.

I used data on conifer forest age class developed for the NWFP region through classification of Landsat Thematic Mapper satellite imagery (Strittholt et al., 2006). The vegetation data were aggregated from its original 30 m resolution to 1 ha resolution for use in modeling. Predictor variables were the proportion of old conifer forest (>150 years) and mature conifer forest (50–150 years) at two spatial scales, 1 ha and within a 1 km^2 area centered on each 1 ha cell. Because no dynamic vegetation models have yet been developed that predict forest age class based on changing climate at the spatial resolution and regional extent considered here, the old and mature forest vegetation classes were assumed to remain static during the 50–100 year timeframe of the projections. I further evaluate the implications of this assumption in Section 4.

I represented ‘‘current’’ climate with a model-derived dataset of temperature and precipitation for the conterminous United States and portions of Canada and Mexico (Maurer et al., 2002). The data are closely calibrated to observed climate data (e.g., point observations) but are modeled to maximize comparability of spatial and temporal resolution with those of general circulation model (GCM) simulations of future climate scenarios (Maurer et al., 2002). I maintained compatibility with previous analyses (e.g., Lawler et al., 2009) by using the period 1961–1990 as a standard timeframe to represent ‘‘current’’ climate. I derived the following climate variables from current and projected-future monthly means: mean annual and mean annual standard deviation of temperature and precipitation, as well as mean values for temperature and precipitation from January (wettest, coldest month), ‘‘spring’’ (March, April, May), and July (driest, hottest month).

To analyze potential ‘‘future’’ climate projections, I used an ensemble forecasting approach (Araújo and New, 2007) that fol-

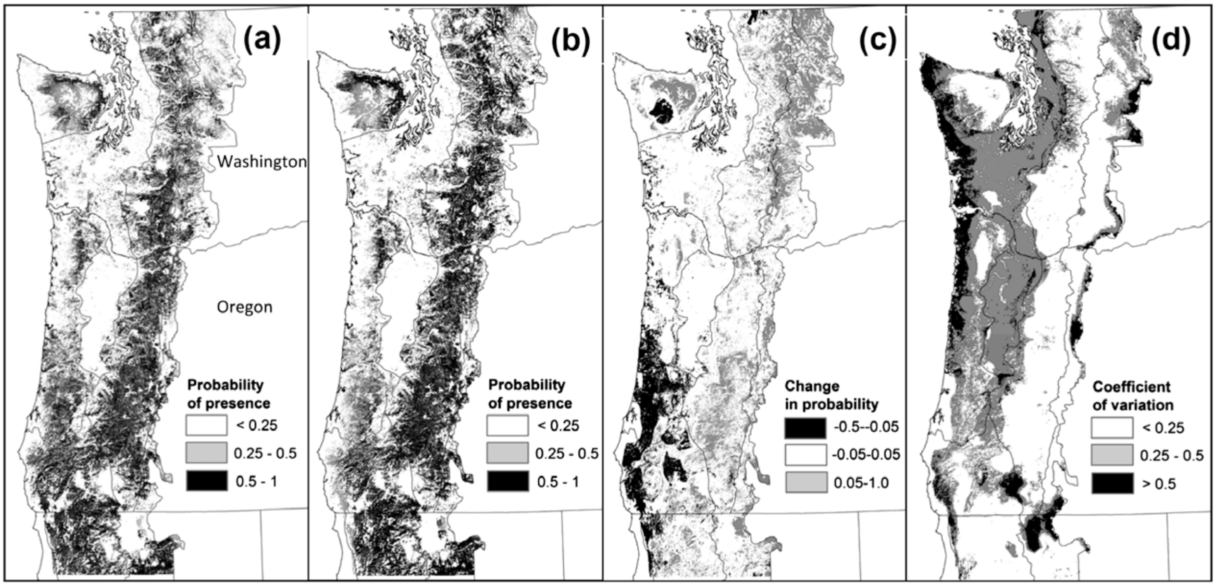

Fig. 1. Results of analysis of habitat suitability for Northern Spotted Owl in the Pacific Northwest, USA, based on maximum entropy (Maxent) models using both climate and vegetation data. Figures show (a) predicted probability under current (1961–1990) climate, (b) mean predicted probability under three representative projections of future (2061–2090) climate, (c) change in probability between current and mean future predictions, and (d) coefficient of variation of future predictions.

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lowed Salathé (2005) in focusing on three representative simulations selected from a group of nine simulations that contrasted in both the GCM and Intergovernmental panel on Climate Change (IPCC) emissions storyline (socioeconomic and population trajectory) used. The three simulations were typified as a lowest warming (GCM GISS_ER with IPCC storyline B1), moderate warming (GCM ECHAM5 SRES with storyline A2), and highest warming scenario (GCM IPSL_CM4 with storyline A2) (Salathé, 2005). The data were produced by statistical downscaling the GCM output to a resolution of 1/8° (approximately 10 by 14 km; Salathé, 2005). I resampled both current and future climate data to 1 ha resolution for the habitat modeling (described below). I selected two time periods for analysis: near-future (2011–2040) and distant-future (2061–2090).

I used Maxent (Phillips et al., 2006; Phillips and Dudik, 2008) to evaluate and model relationships between the climate and the vegetation variables and occurrence of the NSO. Maxent performed well in comparison with 15 alternate methods on a wide variety of taxa in diverse regions (Elith et al., 2006). Although Maxent is designed for use with presence-only data, it qualitatively resembles techniques such as logistic regression in that it compares presence locations to a random subset of ∼10,000 background or available locations (Phillips et al., 2006). Maxent estimates probability distributions that are close to maximum entropy or uniform given constraints derived from the presence data and functions of the environmental variables (Phillips and Dudik, 2008). Model output can be interpreted as the probability of presence under a similar level of sampling effort as was required to obtain the known presence data (Phillips and Dudik, 2008).

I used the set of candidate models (30 climate models and 10 vegetation models) developed by Carroll et al. (2010); (Table S2). I ranked models using the mean rank of AUC and gain and combined the top-ranking climate and vegetation models. AUC evaluates a model's discriminatory ability, whereas gain uses the average log probability of presence samples to evaluate how different, on average, presence locations are to background locations. AUC may range from 0.5 for a model that performs no better than random to near 1 for a perfect model (Phillips et al., 2006). I evaluated AUC for each model on the full data set and also via a cross-validation procedure that divided the data into 10 folds and evaluated the ability of models developed from the remaining samples to predict the holdout data. The highest ranking model among the combination, climate-only, or vegetation-only models was then used to predict distribution throughout the study area under current climate conditions. I compared predictions of the combination model with those of the highest ranked climate-only model. I also evaluated the sensitivity of predictions of NSO habitat value to choice of modeling method by measuring the correlation at a resolution of 1 ha of the Maxent predictions with a previous range-wide model developed using hierarchical Bayesian methods (Carroll and Johnson, 2008).

I extrapolated the best current models using Maxent to predict distribution given projected temperature and precipitation for the three future climate simulations during two future time periods (2011–2040, 2061–2090). I developed a metric of projected future NSO habitat that discounted future presence values to account for uncertainty between Maxent predictions based on the three different climate simulations (Moilanen et al., 2006). I derived this discounted habitat value by subtracting one-half the standard deviation between presence values under the three future climate simulations from the mean of presence values under those simulations.

To measure the change in extent between current range and future predicted range and the geographic shift in range centroid, I transformed continuous probability surfaces by thresholding at a value which maximizes the sum of model specificity and sensitivity (Loarie et al., 2008). I assessed the proportion of NSO "habitat value" (as measured by probability of presence) captured within the four general land management categories, as compared with the proportion expected based on the total area of land in that management category, in order to assess efficacy of the current reserve system in capturing: (1) current, (2) mean near-future (2011–2040), (3) mean distant-future (2061–2090), and (4) distant-future habitat discounted for uncertainty. The management categories were private lands, matrix, LSR, and "congressional" reserves (e.g., parks and wilderness areas primarily established pre-NWFP), which comprise 50.7%, 18.0%, 14.8%, and 16.5% of the analysis area, respectively, and have mean elevations of 408 m, 973 m, 943 m, and 1360 m, respectively.

3. Results

The data thinning process reduced the 6893 initial records of NSO nest or activity locations to 708 presence locations with greater than 1 km separation. The best vegetation model included all four vegetation variables. The best climate model included January and July precipitation and temperature. The best vegetation-only, climate-only, and combined models showed AUC with the full dataset of 0.810, 0.758, and 0.852, respectively. Cross-validation AUC was 0.811, 0.735, and 0.833, respectively. Percent contribution of individual variables for the best combination model (based on the increase in gain; Phillips et al., 2006) was dominated by landscape and local-scale old-growth (55.4% and 17%, respectively), followed by January precipitation (9.6%). Remaining climate variables contributed between 3.1% (July precipitation and January temperature) and 1.2% (July temperature). Predictions of the combination model showed correlations of 0.585 and 0.937 with best climate-only and best vegetation-only models at a resolution of 1 ha. Best climate-only and best vegetation-only models showed a correlation of 0.403. Predictions of the best climate-only, vegetation-only, and combination model showed correlations of 0.267, 0.650, and 0.663, respectively with the NSO model of Carroll and Johnson (2008).

Mean predicted probability of presence was 0.275, 0.286, and 0.285, for current, near-future, and distant-future climate using the combination model (Fig. 1). Mean predicted probability of presence was 0.408, 0.428, and 0.366 for current, near-future, and distant-future climate using the climate-only model (Fig. 2). The binary threshold that maximized the sum of model specificity and sensitivity was 0.319 and 0.466 for the combination and climate-only model, respectively. Given these thresholds, range size under the combination model was 4.60% and 2.52% larger than current range size for mean near-future and distant-future predictions, respectively. Range size under the climate-only model was 14.48% larger and 28.97% smaller than current range size for mean near-future and distant-future predictions, respectively. Under the combination model, the range centroid moved 24.4 km north–northeast over the current to distant-future period. Under the climate-only model, the range centroid (which lay 36.6 km south of that of the combination model) moved 35.3 km northeast over the current to distant-future period.

Under the combination model, habitat suitability was reduced under projected future climates primarily in coastal Oregon (Fig. 1c). Under the climate-only model, reduction in habitat value was more extensive under projected future climates (Fig. 2c). However, a high coefficient of variation, due primarily to variation in predicted precipitation between the three GCMs, made estimates of habitat loss under the climate-only model highly uncertain (Fig. 2d). Under the combination model, LSR and matrix under current climate held 161% and 144% of the habitat value (probability of presence) expected by area, respectively, and this proportion re-

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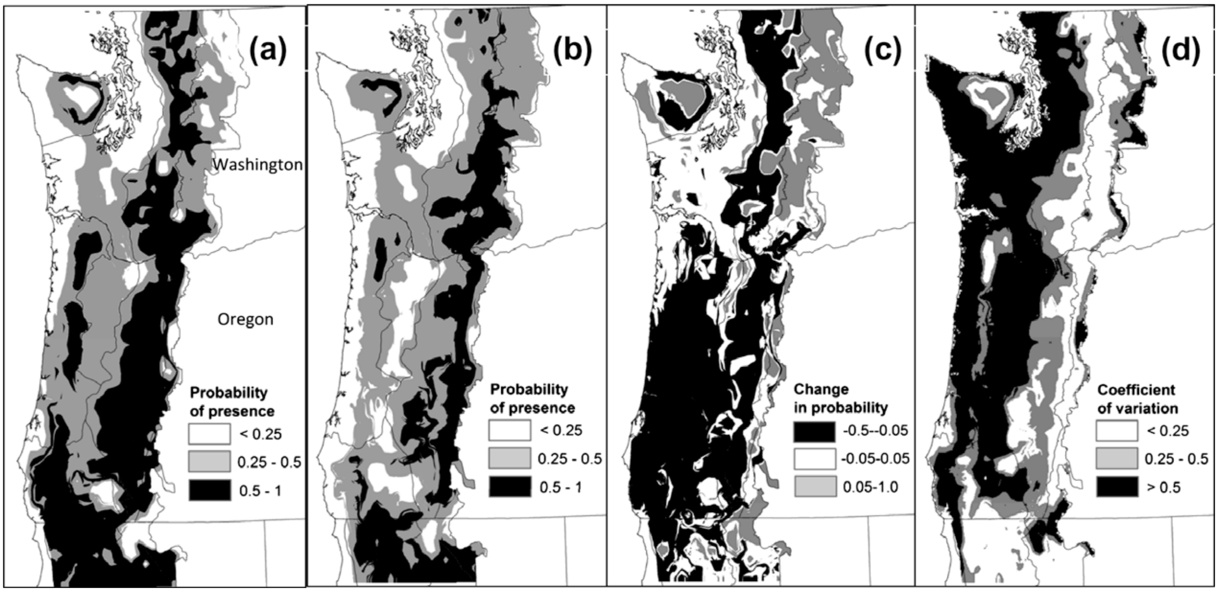

Fig. 2. Results of analysis of habitat suitability for Northern Spotted Owl in the Pacific Northwest, USA, based on maximum entropy (Maxent) models constructed using climate data, but no vegetation data. Figures show (a) predicted probability under current (1961–1990) climate, (b) mean predicted probability under three representative projections of future (2061–2090) climate, (c) change in probability between current and mean future predictions, and (d) coefficient of variation of future predictions.

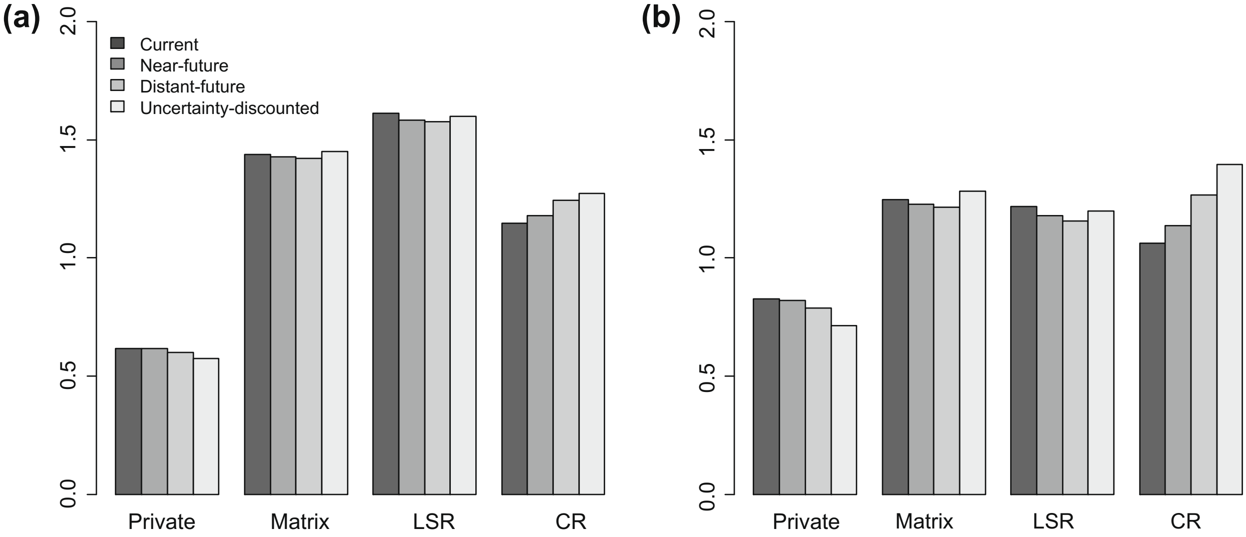

Fig. 3. Proportion of Northern Spotted Owl habitat value captured within four general land management categories under current and future climate, as compared with the proportion expected based on the total area of land in that management category, based on results from the combined vegetation–climate model (a) and best climate-only model (b). The four climate scenarios represent: (1) current, (2) near-future (2011–2040), (3) distant-future (2061–2090), and (4) distant-future discounted for uncertainty between three representative climate projections. Abbreviations: LSR, late-successional reserve, CR, congressional reserve.

mained relatively stable under climate change (Fig. 3). Pre-NWFP reserves held 115% the habitat value expected by area under current climate, a proportion that increased with climate change. Private lands held 62% of the habitat value expected by area under current climate, and this proportion decreased under future climate. Predictions based on the climate-only model differed from those of the combination model in that the value of LSR and matrix were more similar to that expected by area, and the value of pre-NWFP reserves increased to a greater extent under future climates (Fig. 3).

4. Discussion

Well-studied vertebrates such as the Northern Spotted Owl (NSO) are often used as focal species in regional conservation plans such as the Northwest Forest Plan of the US Pacific states (Fig. 1). Land management agencies increasingly seek to assess how climate change may affect both the viability and the focal role of such species (USFWS, 2009). To assess how climate change may affect the NSO's viability and focal species role, I developed distribution models from presence-only data using the Maxent model (Phillips et al., 2006). Vegetation variables retained within the best model were consistent with field studies and previous range-wide modeling that strongly link NSO distribution and abundance to older forest (Bart and Forsman, 1992; Noon and Blakesley, 2006; Carroll and Johnson, 2008). Winter precipitation was the most important climate variable identified, a finding consistent with previous demographic studies that suggest negative effects of winter and spring precipitation on survival, recruitment and dispersal (Frank-

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lin et al., 2000). Extrapolation of the best combination vegetation–climate model to future climates (assuming static vegetation) suggests northward expansion of high suitability NSO habitat. Reduced winter precipitation and increased winter temperature under future climates might be expected to increase winter survival and nesting success and allow range expansion of prey species such as woodrat (*Neotoma* spp.) that currently occur at high densities only in the southern portions of the range (Noon and Blakesley, 2006). However, model results suggest that an initial expansion in the suitable climatic niche may be followed by a contraction as climate change intensifies.

Results from the best model containing both vegetation and climate variables suggest that the NWFP's Late-Successional Reserves successfully prioritized areas with greater biological importance for the NSO than pre-NWFP reserves such as parks and wilderness areas. However, the role of the latter areas, which lie predominantly at higher elevations, is predicted to increase under climate change. NSO populations in coastal areas are already at risk due to their small size and isolation amid a landscape with low proportion of public lands and hence older forest (Noon and Blakesley, 2006). Predicted reductions in habitat quality in coastal areas under future climates may accelerate these threats.

4.1. Role and limitations of climatic niche models in conservation planning

Due to lack of broad-scale data on vegetation and other habitat attributes, assessment of potential climate change impacts on species' distributions must often depend on niche models containing primarily climatic variables (Pearson and Dawson, 2003). Although such models might be expected to suggest overarching limiting factors within which finer-scale habitat relationships operate, the results suggest that conclusions may be misleading in the absence of relevant finer-scale habitat variables (Pearson and Dawson, 2003). For example, when compared with the combination model, the climate-only niche model accentuates projected range shifts (Figs. 1c and 2c). Claims that climate-only species distribution models approximate a species' fundamental niche are problematic without evaluation of the mechanisms by which climate influences physiology and demography of the species of interest (Elith and Leathwick, 2009). Potential mechanisms with which climate change may affect NSO habitat suitability include the direct physiological effect of climate on survival and fecundity (Franklin et al., 2000), and indirect effects via changes in prey abundance, prey community composition, changes in vegetation structure and composition, and altered disturbance regimes.

Additionally, the dominance of precipitation over temperature variables in the NSO models and the high variability in precipitation predictions between alternate GCMs causes predictions of future NSO habitat suitability to be highly uncertain in some regions. Although I evaluated an ensemble of GCMs, additional uncertainty would arise from use of additional niche modeling methods (Elith et al., 2006). Correlative approaches such as niche models also implicitly assume constancy of present with future correlations between climate and spatial distribution, thus ignoring potential changes in the interactive (biotic) component of the NSO's niche (Pearson and Dawson, 2003).

The challenges inherent in predicting climatic effects on distribution may simply be more evident for the well-studied NSO than for lesser-known old-forest-associated taxa (Carroll et al., 2010). Additionally, climate-only models might be expected to show poorer performance for habitat specialists such as the NSO that are often species of concern under endangered-species legislation. The relatively poor performance of the NSO climate-only model contrasts with results for the old-forest-associated localized species, of which 94.6% showed better AUC for climate-only than for vegetation-only models (J. Dunk, unpubl. data). It is encouraging that predictions from the NSO combination model derived from Maxent were relatively similar to those from a recent study using contrasting habitat modeling methods (Carroll and Johnson, 2008). In fact, the contrast between models developed under contrasting methods was less than the contrast between the combination and climate-only Maxent models.

When used as decision-support tools in regional conservation planning, all habitat models can be viewed as inadequate but potentially informative. Although ideally I would have projected future species distributions based on dynamic models that project vegetation response to climate, such models typically predict vegetation response at the biome level, and thus lack the spatial resolution (1 ha), thematic detail (forest age class), and regional geographic extent necessary for my analyses (Purves and Pacala, 2008). Species distribution models built from dynamic vegetation and climate projections represent a "gold standard" that has yet to be achieved for most species due to computational and analytical challenges (Purves and Pacala, 2008). Because of these challenges, niche models used to project range shifts often are based on climatic data alone (Elith and Leathwick, 2009). The NSO model results suggest that niche models combining dynamic climate projections with static vegetation data may represent an improvement over climate-only niche model, especially for short-term (decadal) projections for species associated with long-lived vegetation. In Pacific Northwest forests, stands may remain in the old forest age class (>150 years; Strittholt et al., 2006) for centuries unless harvested or subject to stand-replacing fire disturbance. In these forest types, changes to vegetation attributes will lag significantly behind climatic changes, and long-lived forest structures may buffer effects of climatic change on wildlife. The assumption that old and mature forest vegetation classes remain static under the timeframe of the projections (50–100 years) allows a useful first approximation of climate change impacts with better predictive performance than would niche models based exclusively on climate (Beale et al., 2008).

4.2. Conclusions

The results highlight several areas where progress is needed to increase the ability of conservation planners to evaluate climate change effects. These include integration of climatic niche models with: (1) dynamic vegetation models, especially those accounting for fire and other disturbance, (2) multi-species models, and (3) stochastic population models or population viability analyses (Carroll, 2007). The importance of vegetation variables in the NSO model emphasizes the need to integrate diverse data into climatic niche models and develop finer-resolution dynamic vegetation models (Purves and Pacala, 2008). Shifts in the composition and age of forest stands could mitigate or compound projected shifts in the NSO's climate niche. Vegetation such as the old-growth forests of the Pacific Northwest may stabilize species' distribution under climate change as forests lag in equilibrating to changed climate. Under this scenario, zoning strategies and finer-scale management regimes could be designed to mitigate climate change impacts by allowing greater re-growth of older forest. Alternately, climate-induced change in disturbance regimes (e.g., fire) may destabilize the NSO habitat niche by triggering sudden phase shifts of vegetation to alternative states. Such indirect effects of climate change on habitat via altered disturbance regimes could be evaluated by integrating models of disturbance dynamics into dynamic vegetation models. Although statistical models of fire disturbance project increased fire extent and frequency in portions of the region under future climates (Littell et al., 2009), the effect of such disturbance on NSO habitat is likely to be complex due to uncer-

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tainty in GCM predictions of future precipitation, and in effects of fire on NSO habitat use (Bond et al., 2009).

Development of multi-species models is also necessary to evaluate indirect effects on the NSO of climate effects on competitor species. Although the results project a initial northward movement and expansion of the NSO's optimal climatic range, contemporary data showing increasing displacement of NSO by the congeneric barred owl (*Strix varia*), especially in the northern portion of its range (Noon and Blakesley, 2006). Climate change could enhance the NSO's resiliency to barred owl competition, or alternately, such competition could make the NSO's northern range unavailable before it becomes more climatically favorable. For well-studied focal species such as the NSO, predictions from static niche models may be integrated within stochastic population models to evaluate questions of "how much is enough" habitat for persistence (Carroll, 2007; Keith et al., 2008).

Although the potential effects of climate change do not invalidate strategies such as the NWFP that are based on fixed reserves, they do suggest planners consider potential range shifts in evaluating alternative reserve designs (Carroll et al., 2010). Such efforts should evaluate an ensemble of climate projections (Araújo and New, 2007) and address variation in habitat predictions among alternate climate projections by use of techniques based on info-gap theory that discount habitat values where they show high uncertainty (Moilanen et al., 2006). Proper treatment of uncertainty is a necessary element of the use of niche models as decision-support in regional planning. Until progress is made in developing more complex dynamic multi-species modeling approaches, climatic niche models for habitat-specialist focal species may have limited value as predictive tools. However, they provide a valuable source of hypotheses regarding potential effects of climate change that can inform a precautionary approach to conservation planning.

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