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Thresholds in forest bird occurrence as a function of the amount of early-seral broadleaf forest at landscape scales

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Abstract. Recent declines in broadleaf-dominated, early-seral forest globally as a function of intensive forest management and/or fire suppression have raised concern about the viability of populations dependent on such forest types. However, quantitative information about the strength and direction of species associations with broadleaf cover at landscape scales are rare. Uncovering such habitat relationships is essential for understanding the demography of species and in developing sound conservation strategies. It is particularly important to detect points in habitat reduction where rates of population decline may accelerate or the likelihood of species occurrence drops rapidly (i.e., thresholds). Here, we use a large avian point-count data set ($N = 4375$) from southwestern and northwestern Oregon along with segmented logistic regression to test for thresholds in forest bird occurrence as a function of broadleaf forest and early-seral broadleaf forest at local (150-m radius) and landscape (500–2000-m radius) scales. All 12 bird species examined showed positive responses to either broadleaf forest in general, and/or early-seral broadleaf forest. However, regional variation in species response to these conditions was high. We found considerable evidence for landscape thresholds in bird species occurrence as a function of broadleaf cover; threshold models received substantially greater support than linear models for eight of 12 species. Landscape thresholds in broadleaf forest ranged broadly from 1.35% to 24.55% mean canopy cover. Early-seral broadleaf thresholds tended to be much lower (0.22–1.87%). We found a strong negative relationship between the strength of species association with early-seral broadleaf forest and 42-year bird population trends; species most associated with this forest type have declined at the greatest rates. Taken together, these results provide the first support for the hypothesis that reductions in broadleaf-dominated early-seral forest due to succession and intensive forest management have led to population declines of constituent species in the Pacific northwestern United States. Forest management treatments that maintain or restore even small amounts of broadleaf vegetation could mitigate further declines.

Key words: broadleaf forest; early-seral forest; ecological thresholds; habitat loss; intensive forest management; landscape ecology; Oregon forest birds; segmented logistic regression; tree plantations.

Introduction

Global demand for wood fiber and products is expected to double within the next 25 years, an increase that is projected to substantially outpace the expected supply (Wood Resources International 1999). Increased demand has prompted intensification of forest management, evident in practices such as short-rotation harvesting, planting genetically improved seedlings, and chemical control of competing vegetation. In addition, maximum efficiency of wood fiber production has been sought through extensive replacement of naturally regenerated forests with conifer plantations in temperate regions around the world (Kittredge 1996, Lindenmayer and Hobbs 2004, Betts et al. 2005, Paquet et al. 2006). In many areas of the world, the practice of intensive production forestry has resulted in a reduction in the complexity and diversity of native vegetation (Franklin et al. 2008), which in turn can have negative consequences for faunal diversity. For example, favoring conifers in production forests of temperate regions neglects the function of broadleaf vegetation, which is expected to be critical habitat for many species of forest wildlife, especially birds (Hagar 2007); broadleaf cover has been shown to influence the composition of songbird communities and species' abundance in the boreal, temperate, and mixed Acadian forests of North America at both stand (Hobson and Bayne 2000) and landscape scales (Drapeau et al. 2000, Young et al. 2005). Declines in populations of species associated with broadleaf vegetation have been observed in regions

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where forest management has favored planted conifers over naturally regenerated broadleaf species (Straw et al. 1994, Enoksson et al. 1995, Carlson 2000, DeGraaf and Yamasaki 2003, Paquet et al. 2006).

In coniferous regions of the Pacific northwestern United States (PNW), broadleaf trees and shrubs occur throughout forest development, but unmanaged, early-seral stages can support a particularly high abundance and diversity of broadleaf vegetation (Franklin and Dyrness 1988, Halpern and Spies 1995, Franklin et al. 2002). Deciduous vegetation in early-seral stands has been associated with greater diversity and abundance of Lepidoptera (butterflies and moths) than in coniferous forest (Hammond and Miller 1998). Because Lepidoptera larvae are an important food resource for many species of birds, availability of deciduous vegetation may have a significant influence on the demography of breeding birds (Nagy and Holmes 2005).

In the absence of management to promote conifer establishment and reduce competing vegetation, broadleaf shrubs can be dominant for a prolonged period in naturally regenerating forest following disturbance (Yang et al. 2005). However, decades of active fire suppression and intensive forest management, and a more recent focus on old-growth conservation on federal lands, have reduced the amount of structurally complex early-seral forest (Kennedy and Spies 2005, Spies and Johnson 2007). Unmanaged early-seral stages of forest development are now considered to be among the most threatened habitat types in coniferous regions of the western United States (Noss et al. 2006, Thomas et al. 2006). Not surprisingly, concern has arisen over viability of populations that use broadleaf vegetation in early-seral forest, particularly as this habitat type contributes disproportionately to forest biodiversity (Halpern and Spies 1997). In the northwestern United States, a number of bird species thought to be strongly associated with early-seral broadleaf habitat have declined and are considered conservation priorities (Altman 1999, U.S. Fish and Wildlife Service 2002). Because the PNW represents a substantial portion of the ranges of these species, loss of quality early-seral habitat could increase risk of extinction.

Although some documented species–habitat associations suggest that loss of broadleaf habitat in conifer-dominated forests will have negative consequences for many vertebrate species (Bunnell et al. 1999, Hagar 2007), quantitative relationships revealing the strength and direction of species associations with broadleaf habitat at landscape scales in the Pacific Northwest are rare. This is troubling because species may respond to habitat loss in a nonlinear fashion (Betts et al. 2007); therefore, qualitative assumptions of an additive effect of increasing habitat amount may be misleading. Indeed, theory predicts the occurrence of threshold levels of habitat in landscapes below which ecological processes change abruptly (With and Crist 1995, Fahrig 2003). As the amount of habitat in a landscape declines, habitat tends to occur in multiple small patches (Gardner and O'Neill 1991). There is also an exponential increase in the average distances between patches (With and Crist 1995). A number of theoretical models predict that below critical thresholds, fragmentation of habitat influences patch occupancy by decreasing colonization rates and increasing rates of local extinction (Lande 1987, With and King 1999).

Qualitative information on species associations, or even quantitative models that assume linearity, are thus likely to be far less informative for understanding the demography of species (Hanski and Ovaskainen 2000) or developing sound conservation strategies (Pulliam and Dunning 1997). Given the decline of broadleaf-dominated, early-seral forest, it is essential to detect points in habitat loss where rates of population decline may accelerate, or the likelihood of species occurrence drops rapidly (Balmford et al. 2003). However, empirical tests for landscape-scale thresholds in either species demography or occurrence are still uncommon (Homan et al. 2004, Radford and Bennett 2004, Betts et al. 2007).

Until recently, there has been a paucity of statistical approaches available to objectively identify ecological thresholds (Guénette and Villard 2005, Huggett 2005). Methods for identifying thresholds in occurrence (i.e., binomial) data have lagged behind those appropriate for continuous data (e.g., Toms and Lesperance 2003). This is problematic because presence/absence data are commonly used in ecology to predict species distributions (Guisan and Thuiller 2005). Receiver operating characteristic analysis and binomial-change point tests have been used to identify statistical cut points (thresholds) in the independent variable that maximize prediction success (i.e., maximized specificity and sensitivity; Homan et al. 2004, Guénette and Villard 2005). Although this is appealing from a management perspective, the identification of statistical cut points does not necessarily imply nonlinear responses to environmental gradients (Betts and Villard 2009).

In this study, our objective was to test for thresholds in forest bird occurrence in relation to broadleaf forest and early-seral broadleaf forest (<20 years old) at multiple scales in Oregon, USA. To accomplish this, we collected data from two broadscale studies on forest bird distribution in Oregon resulting, to our knowledge, in one of the largest point-sampled bird data sets used to date in species distribution modeling ($N = 4375$). We used a new approach (segmented logistic regression; Muggeo 2003, Betts et al. 2007) to detect thresholds in species occurrence. We also sought to determine if decline in broadleaf-dominated, early-seral habitat has had demographic consequences for forest birds. If loss of early-seral broadleaf habitat on the breeding grounds has led to population declines, we expected a negative association between the strength of species association with this forest type and long-term bird population trends.

METHODS

Study areas

We used avian point-count data from two major regions in northwestern (McGarigal and McComb 1995) and southwestern Oregon (Alexander et al. 2004). The northwestern Oregon study area consists of three major hydrological basins (Drift Creek, Lobster Creek, and Nestucca River basins) in the central Oregon Coast Range, USA. Elevation ranges from sea level to 968 m. Climate is maritime with mild, wet winters and cool, dry summers. The study area is characterized by steep slopes and deeply cut drainages and lies almost entirely within the western hemlock (*Tsuga heterophylla*) vegetation zone (Franklin and Dyrness 1988). The natural forest overstory is dominated by Douglas-fir (*Pseudotsuga menziesii*), western hemlock, and western red cedar (*Thuja plicata*). Deciduous, broadleaf trees, primarily red alder (*Alnus rubra*) and bigleaf maple (*Acer macrophyllum*) occur in patches throughout the coniferous matrix, especially in recently disturbed and riparian areas (Franklin and Dyrness 1988). Understory vegetation is variable in composition and distribution. Common species include broadleaf shrubs salmonberry (*Rubus spectabilis*), salal (*Gaultheria shallon*), vine maple (*Acer circinatum*), Oregon grapes (*Berberis* spp.), and huckleberries (*Vaccinium* spp.), and swordfern (*Polystichum munitum*). The entire area experienced a series of catastrophic wildfires in the mid-1800s and regenerated naturally (Spies and Cline 1988). Over the past 45 years, federal land managers have used a dispersed-patch system of clearcut regeneration harvests, which maximizes fragmentation of the late-seral forest matrix (Franklin and Forman 1987). As a result, the area currently has a bimodal age distribution dominated by young forests (40 yr old) and mature forests (100–150 yr old). Mid-aged (40–100 yr old) and old-growth (>150 yr old) forest are poorly represented.

The data from southwestern Oregon were collected as part of an ongoing effort by Klamath Bird Observatory to provide an index to species diversity and abundance in riparian and upland habitats and to maintain a long-term monitoring effort for tracking land bird population trends. The area is characterized by a wide range of ecological types ranging from Cascade slopes where Douglas-fir and mountain hemlock (*Tsuga mertensiana*) are dominant to the much warmer and drier Klamath mountains where Douglas-fir is common at higher elevations, but low elevations are typified by oaks (mostly *Quercus garryana* and *Q. kelloggii*), Pacific madrone (*Arbutus menziesii*), and conifers, predominantly ponderosa pine (*Pinus ponderosa*) and some Douglas-fir. Major components of the shrub layer are buckbrush (*Ceanothus cuneatus*), mountain mahogany (*Cercocarpus betuloides*), whiteleaf manzanita (*Arctostaphylos viscida*), and poison oak (*Toxicodendron diversiloba*). Mesic oak woodlands may show greater canopy closure of black oak or Douglas-fir, while drier nonclay dominated sites show increased domination by the shrub component (Seavy et al. 2008).

Bird sampling

In the northern region, sample points were located in a uniform grid at 200-m intervals along transects spaced 400 m apart in each subbasin. Between 32 and 38 sample points were placed within 30 subbasins (~300 ha each), for a total of 1046 points. In the southwestern region, 3329 sample points were established to capture elevation, forest habitat type and disturbance gradients. In this study, counts were conducted both on- and off-road.

In both study areas, avian data were collected using fixed-radius point counts (Ralph et al. 1995) conducted between 05:30 and10:00 Pacific Standard Time at each sample point. In our analysis, we utilized data for all male birds seen or heard within a 50 m radius. Because the mean bird counts per station tended to be low (<2 males) for most species and because we were interested in estimating probability of occurrence, we reduced relative abundance data to presence–absence data for use in binomial models. In northwestern Oregon, four 8-minute counts were conducted on separate occasions between May and June in the years from 1990 to 1992. Surveys were conducted 15–20 min before sunrise to 4 h after sunrise. Southwestern region point-count data were collected from 2002 to 2005 using the same protocols but points were only visited one to two times. Differences in the number of visits between studies and count duration should result in higher overall probability of detection for the same species in northwestern than southwestern Oregon (Drapeau et al. 1999). However, all other things being equal, the shape of the response of individual species to landscape structure should remain the same (Betts and Villard 2009). Nevertheless, we acknowledge that methodological differences undoubtedly decreased the likelihood of finding similarities in threshold values between study areas. Hence, our results should be considered conservative in this respect.

These combined data sets resulted in a database of 4375 spatial sample points, with 127 164 bird detections representing 110 species. For analysis, we selected the seven most common species that we hypothesized to be associated with either broadleaf forest generally or early-seral broadleaf forest (Black-headed Grosbeak, Black-throated Gray Warbler, MacGillivray's Warbler, Spotted Towhee, Pacific-slope Flycatcher, Warbling Vireo, Western Tanager; see scientific names in Table 1). We also selected five additional species (Rufous Hummingbird, Orange-crowned Warbler, Nashville Warbler, Lazuli Bunting; Olive-sided Flycatcher) that were present in sufficient numbers in one of the two study areas, were expected to be associated with broadleaf cover, or were of conservation concern (Altman 1999).

Quantifying broadleaf cover

To characterize the amount of broadleaf cover surrounding point-count sites we used vegetation data derived from a gradient nearest neighbor method (GNN; Ohmann and Gregory 2002). The GNN method integrates vegetation measurements from regional grids of field plots (Forest Inventory Analysis [FIA] plots), mapped environmental data, and Landsat Thematic Mapper (TM) Imagery to predict vegetation structure and composition at a 30-m pixel resolution. To date, spatial forest inventory data from GNN have not been tested for use in statistical wildlife habitat models. We used GNN data from two different periods (northwestern Oregon, 1995; southwestern Oregon, 2003) to match the differing origin of our point-count data (1990–1992, 2002–2005). At broader spatial scales, vegetation composition predictions from this method closely match those measured in ground-based forest inventory plots (Ohmann and Gregory 2002). At the stand level, correlations between GNN predictions and inventory plots were generally greatest for measures associated with successional status of vegetation. At this fine scale, broadleaf vegetation was predicted with moderate accuracy (Cohen's kappa = 0.49; Landis and Koch 1977, Ohmann and Gregory 2002).

We defined broadleaf cover according to the estimated proportion of broadleaf canopy for each pixel in the GNN. Because stand age per se is not available from GNN data, we defined early-seral broadleaf forest as according to structural criteria; early-seral forest was defined as GNN pixels of any broadleaf vegetation type with quadratic mean diameter (QMD) < 10 cm. We summed the proportion of broadleaf canopy cover and the proportion of early-seral broadleaf canopy cover for all pixels occurring within three spatial extents surrounding sample points: 150 m (7.1 ha), 500 m (78.5 ha), and 2000 m (1256 ha) (after Betts et al. 2006*a*). The smallest spatial scale (150 m) captured variation in broadleaf cover at the scale of individual songbird territories and area sampled by point counts. The two larger spatial extents are scaled to forest passerine habitat use (Drapeau et al. 2000), and likely include the scale relevant to migrant warblers in natal dispersal (Bowman 2003) and extraterritorial movements (Norris and Stutchbury 2001). Averaging percent canopy cover values at broad spatial scales has the drawback of resulting in variables that are somewhat difficult to interpret; for instance, one out of two pixels with 100% broadleaf canopy is equivalent to two pixels with 50% broadleaf canopy. An alternative approach would be to subjectively designate a canopy cover value to qualify as a broadleaf pixel, but the subjective selection of this threshold is problematic because it will vary relative to the species under examination. It is important to note that our landscape vegetation data were not collected at sufficiently high resolution to enable identification of the structural components of early-seral forest (e.g., standing and fallen dead wood).

TABLE 1. Species codes and common names of forest birds of southwestern and northwestern Oregon, USA.

Species	Scientific name	Code
Black-headed Grosbeak	*Pheucticus melanocephalus*	BHGR
Black-throated Gray Warbler	*Dendroica nigrescens*	BGWA
Lazuli Bunting	*Passerina amoena*	LAZB
MacGillivray's Warbler	*Oporornis tolmiei*	MGWA
Nashville Warbler	*Vermivora ruficapilla*	NAWA
Orange-crowned Warbler	*Vermivora celata*	OCWA
Olive-sided Flycatcher	*Contopus cooperi*	OSFL
Pacific-slope Flycatcher	*Empidonax difficilis*	PSFL
Rufous Hummingbird	*Selasphorus rufus*	RUHU
Spotted Towhee	*Pipilo maculatus*	SPTO
Warbling Vireo	*Vireo gilvus*	WAVI
Western Tanager	*Piranga ludoviciana*	WETA

Statistical analysis

We tested for thresholds with segmented logistic regression:

$$\hat{p} = \exp\left(\frac{\beta_0 + \beta_1 x + \beta_2(x - \psi)_+}{1 + \exp\Big(\beta_0 + \beta_1 x + \beta_2(x - \psi)_+\Big)}\right)$$

where $\hat{p}$ is the probability of species occurrence, x is the independent variable, ψ is the break point (threshold), and $(x - \psi)_+ = (x - \psi)\chi I(x > \psi)$ being $I(\mathrm{A}) = 1$, if A is true, β_0 is the intercept, β_1 is the slope of the left line segment (that is, for $x < \psi$), and β_2 is the difference-in-slopes parameter. Thus, $(\beta_1 + \beta_2)$ is the slope of the right line segment ($x > \psi$). Segmented logistic regression relies on an iterative fitting process to estimate ψ, $\beta_0,$ $\beta_1, \ldots, \beta_i$ (Muggeo 2003). Multiple ψ and β are fitted repeatedly until estimates converge at the maximum likelihood estimate. Standard errors and confidence intervals of ψ may be obtained with linear approximation for the ratio of two random variables (Muggeo 2003). This approach to threshold determination has recently been shown to be the most effective at identifying known thresholds in simulated dichotomous data (Ficetola and Denoël 2009). All segmented models were fitted in R 2.0.1 (R Development Core Team 2004) statistical program in the segmented package (Muggeo 2004). Segmented logistic regression requires a starting estimate for ψ. We determined this starting point from examination of both deciles plots (Homan et al. 2004) and fitted values of locally weighted nonparametric models (loess plots, smoothing parameter = 0.75). In instances where the algorithm did not converge (on limited occasions when evidence for a threshold was weak), we searched systematically for a starting point in 5% increments of independent variables.

We determined support for thresholds in occurrence as a function of broadleaf cover variables through the following steps. (1) We used logistic regression (generalized linear models with a logit link function) to test for a linear relationship between probability of occurrence and broadleaf or early-seral broadleaf cover. For each

TABLE 2. Results of generalized linear models and segmented regression testing for relationships between early-seral broadleaf or broadleaf canopy cover at landscape extents and probability of bird species occurrence.

Species and variable†	Study‡	Radius extent (m)	ΔAIC	ΔAIC (auto)	AUC§	AUC auto¶	Ψ (SE)	β (SE)	β (x − ψ) (SE)
BHGR									
BL	N&SOR	2000	−37.9	−38.2	0.77	0.77	15.61 (−1.71)	0.135 (−0.006)	−0.083 (−0.02)
ES BL	S.OR	2000	−14.2	−28.2	0.73	0.86	0.22 (−0.02)	10.059 (−0.774)	−10.963 (−0.806)
ES BL	N.OR	2000	2.9		0.59	0.8		6.33 (−1.409)	
BGWA									
BL	S.OR	2000			0.86	0.89		0.15 (−0.01)	
BL	N.OR	2000	−14.7	3.8	0.64	0.87	25.24 (−0.76)	0.114 (−0.024)	−0.464 (−0.169)
ES BL	S.OR	2000	−269.2	−108.6	0.84	0.89	0.31 (−0.02)	13.28 (−1.21)	−15.535 (−1.375)
LAZB									
BL	S.OR	2000			0.76	0.88		0.089 (−0.005)	
MGWA									
BL	N.OR	2000			0.59	0.91		−0.063 (−0.013)	
ES BL	S.OR	2000			0.63	0.8		1.864 (−0.173)	
ES BL	N.OR	2000	−3.7		0.63	0.92	0.03 (−0.01)	22.579 (−6.156)	−17.34 (−6.288)
NAWA									
BL	S.OR	2000	−172.9	−37.6	0.69	0.82	5.08 (−0.67)	0.26 (−0.017)	−0.244 (−0.019)
ES BL	S.OR	2000			0.63	0.81		0.738 (−0.16)	
OCWA									
ES BL	N.OR	2000	−9.8	2.3	0.6	0.89	0.08 (−0.04)	10.573 (−1.85)	−9.061 (−3.05)
OSFL									
BL	S.OR	500	−10.4	−12.1	0.68	0.82	10.23 (−4.14)	−0.108 (−0.09)	0.071 (−0.091)
ES BL	S.OR	150			0.51	0.77		0.338 (−0.081)	
ES BL	N.OR	150	−13.8	1.9	0.57	0.91	1.17 (−0.32)	1.138 (−0.321)	
RUHU									
ES BL	N.OR	2000			0.58	0.71		3.894 (−0.883)	
SPTO									
BL	S.OR	2000	−43.4	−2.1	0.76	0.82	23.67 (−0.95)	0.069 (−0.007)	0.206 (−0.035)
BL	N.OR	2000	−11.3	2.3	0.65	0.66	15.51 (−3.27)	−0.038 (−0.022)	−0.105 (−0.094)
ES BL	N&SOR	500	−25.1	−4	0.64	0.82	1.65 (−2.44)	2 (−0.145)	−2.272 (−0.37)
WAVI									
BL	S.OR	500	−78.6	−25.4	0.64	0.79	1.26 (−0.2)	1.423 (−0.304)	−1.455 (−0.304)
BL	N.OR	500	3.7	4	0.62	0.85		0.049 (−0.009)	
ES BL	S.OR	2000			0.55	0.79		0.83 (−0.156)	
WETA									
BL	N&SOR	2000			0.53	0.78		−0.007 (−0.003)	
ES BL	N.OR	500			0.65	0.85		6.449 (−1.004)	

Notes: Thresholds (ψ; % cover), regression slopes pre-threshold [β] and post-threshold [β(x − ψ)], and model accuracy (AUC) are reported for each species. Models are reported for the spatial scale that best fits the data. Negative Akaike's Information Criterion (AIC) values indicate support for a threshold rather than a linear model with and without controlling for spatial autocorrelation (auto). Missing values indicate that no model converged.

† Key to abbreviations: BL, broadleaf canopy cover; ES BL, early-seral broadleaf canopy cover.

‡ Key to study areas: S.OR, southwestern Oregon ($N = 3329$); N.OR, northwestern Oregon ($N = 1046$); N&SOR, both study areas combined. The sample sizes refer to point-count sites.

§ Area under the receiver operating characteristic curve.

¶ Models included a spatial autocovariate to control for spatial dependency in sample points. See Table 1 for species codes.

stand type (i.e., broadleaf, early-seral broadleaf), we selected the spatial scale that explained the most deviance in bird occurrence. If 95% confidence intervals for a parameter estimate included zero, we did not consider a variable in subsequent regressions. (2) We tested for statistical interactions between the best variable and study region. If a significant ($P < 0.05$) interaction existed, we modeled each study region separately. As in the interregional analysis, if 95% confidence intervals of the parameter estimates overlapped zero, the variable was not included in later regressions. We do not report linear or threshold parameter estimates for these models with poor explanatory power (Table 2). (3) For remaining models, we used segmented logistic regression to estimate thresholds. (4) We used Akaike's information criterion (AIC) to determine the weight of evidence for threshold models in relation to linear models (Burnham and Anderson 2002). Low AIC values indicate higher degrees of model parsimony. The advantage of the AIC approach is that

Table 2. Extended.

ψ (auto) (SE)¶	β (auto) (SE)¶	$\beta\ (x - \psi)$ (auto) (SE)¶
20.81 (−1.28)	0.124 (−0.007)	−0.112 (−0.017)
0.22 (−0.05)	3.766 (−0.905)	−4.114 (−0.94)
	1.649 (−1.413)	
	0.115 (−0.011)	
	0.028 (−0.02)	
0.25 (−0.02)	12.616 (−1.82)	−13.811 (−1.906)
	0.089 (−0.005)	
	0.005 (−0.019)	
	0.732 (−0.205)	
	−0.062 (−1.2730)	
5.24 (−1.09)	0.168 (−0.024)	−0.165 (−0.026)
	0.618 (−0.172)	
	1.076 (−1.102)	
6.06 (−2.36)	−0.177 (−0.092)	0.129 (−0.092)
	0.213 (−0.091)	
1.25 (−0.56)	0.138 (−0.337)	
	0.35 (−0.19)	
24.55 (−2.48)	0.047 (−0.006)	0.091 (−0.055)
	−0.11 (−0.015)	
1.87 (−0.55)	0.897 (−0.159)	−1.218 (−0.44)
1.35 (−0.37)	0.914 (−0.322)	−0.928 (−0.322)
	0.025 (−0.009)	
	0 (−0.21)	
	−0.003 (−0.003)	
	1.014 (−1.114)	

it penalizes threshold models for the addition of extra parameters (e.g., ψ and β_2) and provides information about the relative amount of support for threshold models.

It is often necessary to account for the potential lack of independence among sample points due to spatial autocorrelation (Legendre and Legendre 1998). We developed additional model terms to account for spatial dependency. These autocovariates were calculated as the probability of observing a species at one sample point conditional on the presence of the same species at a neighboring sample point within a distance class (Augustin et al. 1996). We selected a distance class of 500 m radius because this was the spatial scale below which most species were strongly spatially autocorrelated. We considered there to be support for a threshold in broadleaf cover only if a model contained autocovariates (i.e., accounted for spatial autocorrelation) and if landscape threshold models had a lower AIC than models containing a linear term. Using autocovariates to account for spatial dependency is considered to be a conservative approach; coefficients of environmental predictor variables usually shrink with the inclusion of these terms (Dormann 2007, Betts et al. 2009).

If detection probability is low and correlated with independent variables of interest, results of habitat models may be biased (MacKenzie et al. 2005, Betts et al. 2008). Unfortunately, existing methods for incorporating detection probability into habitat models have no ability to either account for biases due to spatial autocorrelation or to test directly for thresholds. We found evidence for a strong influence of spatial autocorrelation on the parameter estimates of threshold and non-threshold models (see *Results*). We therefore considered it more important to address this issue than to model detection probability. Nevertheless, the multiple-visit structure of the northwestern data set allowed us to calculate detection probability (p) for 11 of the 12 species examined, and to test whether linear models were biased by differential detectability across gradients in amount of broadleaf forest. We calculated p using the methods of MacKenzie et al. (2002) in PRESENCE software. For each species, we modeled both occupancy (Φ) and p as a function of broadleaf forest variables that exhibited the strongest support. Bias was calculated as the difference between coefficients from logistic regression and occupancy models.

Discrimination ability of threshold and linear models was measured using area under the receiver operating characteristic curve (AUC). This was calculated using a continuous scale; evaluation of model performance occurred over the whole range of predicted probabilities (Pearce and Ferrier 2000). AUC values range from 0.5 (random model discrimination) to 1 (perfect model discrimination). As a convention, AUC values > 0.7 are often considered a cut-point above which discrimination success is sufficiently high to be of use in management (Hosmer and Lemeshow 2000, Guénette and Villard 2005). We determined model calibration with the use of calibration plots. These show the relationship between average predicted probability (in fixed group size deciles) and species prevalence (Vaughan and Ormerod 2005).

To test the hypothesis that reduction of early-seral broadleaf cover is affecting population trends of associated bird species, we collected Oregon population trends for each of our 12 focal species and the 13 most common species in our data set from Breeding Bird Survey data (BBS) collected from 1966 to 2007 (Appendix). The BBS relies on highly trained volunteers to collect bird abundance data at 115 50-km sampling routes across Oregon. Trends in bird detections were analyzed using automated generalized estimating equa-

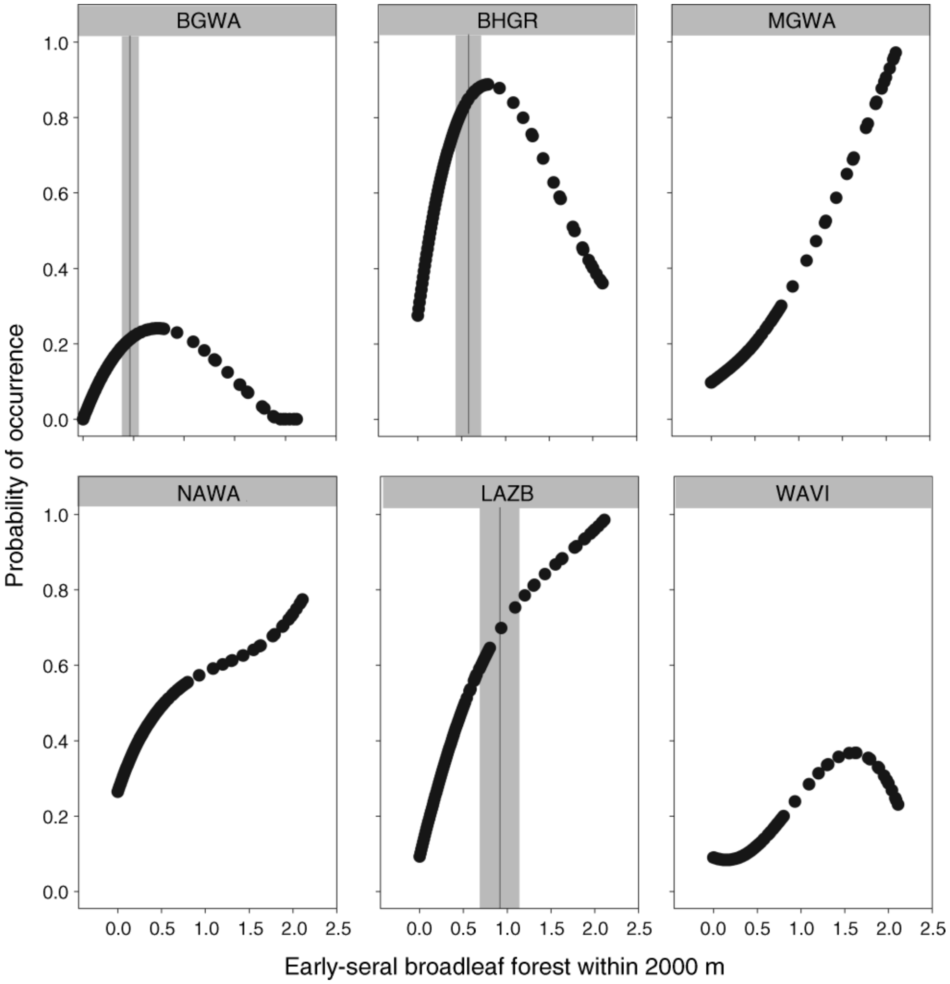

FIG. 1. Effects of the amount of early-seral broadleaf cover in the landscape (%; 2000 m extent) on the occurrence of six species of forest birds in the southwestern Oregon (USA) study area. Thresholds were only plotted if there was support for a nonlinear relationship (ΔAIC to linear model > 2; Table 2). Vertical lines and shaded zones indicate threshold values and associated standard error, respectively. Dots are fitted values from locally weighted regression splines (loess models). Dot density reflects the density of sampling in each part of the broadleaf gradient. See Table 1 for bird species codes.

tions (GEEs) freely available for use (Sauer et al. 2008; *available online*).[6] Logistic regression coefficients from models of species occurrence as a function of amount of broadleaf cover in early-seral habitat (2000 m extent) were used in a linear regression as an independent variable to predict bird population trends.

RESULTS

The occurrence of all 12 species we examined showed positive responses to broadleaf cover in early-seral forest or broadleaf cover generally. However the strength of these relationships (measured as the magnitude of logistic or segmented regression coefficients in relation to standard errors) varied greatly (Table 2). Eight species showed a positive association with early-seral broadleaf cover in at least one of the two study areas (Table 2, Figs. 1 and 2); 95% confidence intervals for these models did not include zero. Lazuli Bunting (southwestern Oregon) and McGillvray's Warbler (both study areas) exhibited the strongest response to this type; model prediction accuracy for both species was relatively high (AUC > 0.75) with broadleaf-dominated, early-seral forest within 2000 m the only independent variable. Seven species were positively influenced by the amount of broadleaf cover, irrespective of age class (Fig. 3). Two species, Spotted Towhee (northwestern Oregon) and McGillivray's Warbler (northwestern Oregon) were negatively influenced by this predictor (Table 2).

For all species except Black-throated Gray Warbler, Western Tanager, and Olive-sided Flycatcher, detection probabilities were >0.8 over four visits. Species with high detection probabilities showed relatively small coefficient biases (1.4–16%; Table 3, Fig. 4). However, if detection probability was low, logistic regression

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[6] ⟨http://www.mbr-pwrc.usgs.gov/bbs/⟩

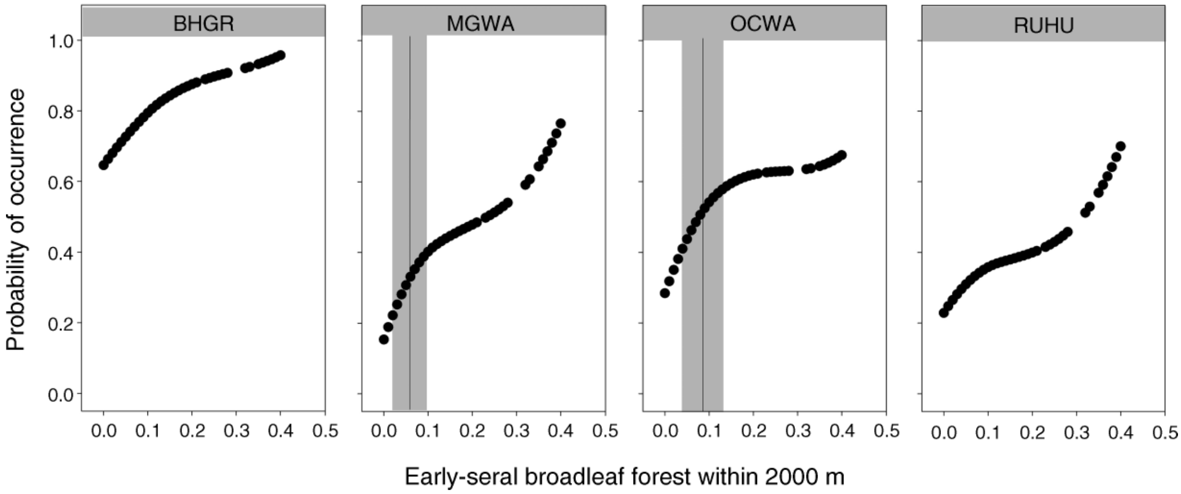

FIG. 2. Effects of the amount of broadleaf-dominated, early-seral forest in the landscape (%; 2000 m extent) on the occurrence of four species of forest birds in the northern Oregon study area. Thresholds were only plotted if there was support for a nonlinear relationship (ΔAIC to linear model > 2; Table 2). Vertical lines and shaded zones indicate threshold values and associated standard error, respectively. Dots are fitted values from locally weighted regression splines (loess models). Dot density reflects the density of sampling in each part of the broadleaf gradient. See Table 1 for species codes.

coefficients were highly conservative; occupancy estimates were 1.6–3.9× greater. Thus, for three species with low p, our results should be considered underestimates of the strength of bird associations with broadleaf forest.

Regional variation in species response to broadleaf cover was large. We detected significant statistical interactions between broadleaf covariates and study region in all but three cases (Table 2). Models for Black-headed Grosbeak, Spotted Towhee, and Warbling Vireo were consistent in both regions. Generally, however, the direction of relationships remained consistent; only in the case of Spotted Towhee did the sign of the response differ between regions.

Though there was some variability in which spatial extents were most useful to predict forest bird occurrence, most variation was consistently explained by the largest extent (2000 m; Table 2). Only Olive-sided Flycatcher distribution was best predicted by the smallest extent (150 m) but models for this species performed poorly (AUC < 0.60).

We found considerable variation among species in model prediction accuracy. Only nine of the 27 univariate models considered had AUC > 0.7 ($\bar{x}$ = 0.66 ± 0.006 SE), the prediction success value considered to be sufficiently high to be of practical utility (Hosmer and Lemeshow 2000). However, when we combined multiple GNN-derived variables prediction success improved (AUC $\bar{x} = 0.71 \pm 0.001$ SE; Table 3). Accounting for spatial dependency with autocovariates substantially improved the discrimination ability of all models (AUC $\bar{x} = 0.83 \pm 0.002$ SE; Table 2). As expected, including autocovariates also reduced the apparent effects of broadleaf cover on bird occurrence. In most cases, model coefficients were reduced with the inclusion of the spatial term (Table 2). Conversely, threshold values tended not to change qualitatively when the autocovariate was added.

We found considerable evidence for thresholds in bird species occurrence as a function of amount and age of broadleaf cover. Threshold models received substantially more support than linear models in 15 of 27 models; ΔAIC in these cases ranged from four to 314 lower than for the equivalent linear model (evidence ratios: 7.53–1.53×10^{68}). Most threshold responses were asymptotic; an initial sharp increase in probability of occurrence leveled off after some threshold value (Table 2, Figs. 1–3). However, in some instances occurrence peaked at a threshold and then dropped (Figs. 1 and 3).

Thresholds of bird species abundance in relation to broadleaf cover ranged widely from 1.35% mean canopy cover (Warbling Vireo, 500 m extent, southwestern Oregon) to 24.55% (Spotted Towhee, 2000 m extent, southwestern Oregon). Early-seral broadleaf thresholds tended to be much lower (0.22 [Black-headed Grosbeak, 2000 m extent, southwestern Oregon]–1.87% [Spotted Towhee, 500 m extent, both study areas]), reflecting the rarity of broadleaf canopy in this age class (Table 2).

Of the 25 common species we considered as a test of whether decline of early-seral broadleaf forest is influencing bird population trends, 16 were significantly positively associated with this cover type, five were negatively associated with this cover type, and we did not detect an effect on four others. We found a strong negative relationship between the strength of species association with broadleaf-dominated, early-seral forest and 42-year bird population trends ($\hat{\beta} = -0.51 \pm 0.14$ SE, $F = 14.26$, $P < 0.001$, $R^2 = 0.38$; Fig. 5). Seven out of nine species with significantly declining populations (range: −3.86% yr^{-1} [Rufous Hummingbird] to −1.05%

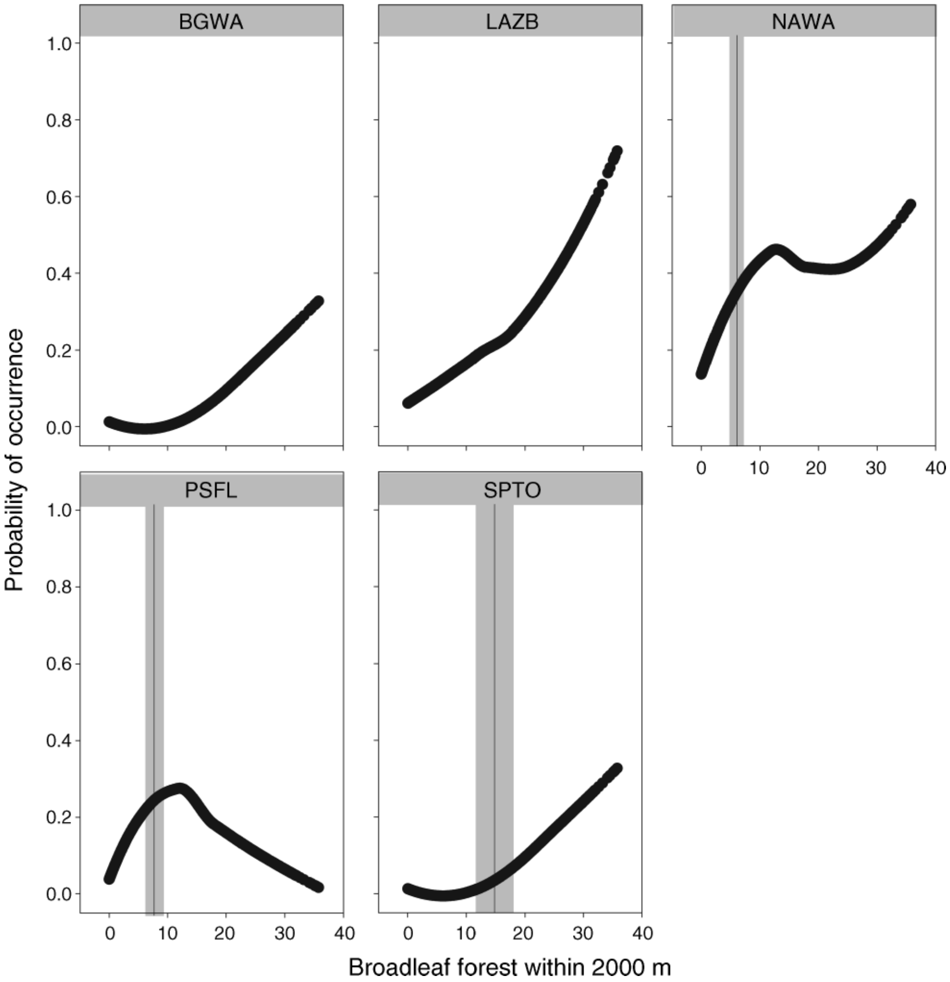

FIG. 3. Effects of the amount of broadleaf cover in the landscape (%; 2000 m extent) on the occurrence of five species of forest birds in the southwestern Oregon study area. Thresholds were only plotted if there was support for a nonlinear relationship (ΔAIC to linear model > 2; Table 2). Vertical lines and shaded zones indicate threshold values and associated standard error, respectively. Dots are fitted values from locally weighted regression splines (loess models). Dot density reflects the density of sampling in each part of the broadleaf gradient. See Table 1 for species codes.

yr^{-1} [Northern Flicker]) were significantly positively associated with early-seral broadleaf forest.

DISCUSSION

We found strong evidence that broadleaf and early-seral broadleaf forest positively influence the distribution of 12 common species of Oregon forest birds. This influence occurs at spatial extents that are relatively large in relation to the home range sizes of the birds examined in this study. At the scale of forest stands, the presence of non-coniferous habitat elements such as broadleaf trees and shrubs has been associated with richness and/or abundance of birds in early-seral (Morrison and Meslow 1983, Easton and Martin 1998, Faaborg 2002) and closed-canopy conifer forests (Huff and Raley 1991, Hagar et al. 1996, Willson and Comet 1996). Similar positive relationships with broadleaf forest have been observed for herpetofaunal (Gomez 1992, DeMaynadier and Hunter 1995) and mammal communities (Gomez and Anthony 1996). So, it is perhaps not surprising that broadleaf cover in early-seral forest positively influences vertebrate biodiversity at broader scales. Interestingly, even some species typically associated with closed-canopy forest (e.g., Western Tanager, Black-throated Gray Warbler) showed a positive response to the broadleaf-dominated, early-seral forest type when it occurred at low amounts in the landscape. This may reflect post-fledging use of these stands by these species, a phenomenon that has been observed in eastern North America (Faaborg 2006, Vitz and Rodewald 2006). The positive response of Olive-sided Flycatcher, often considered a late-seral associate, to the amount of early-seral habitat at a fine spatial scale (150 m) likely reflects this species' use of high-contrast edges (i.e., between late- and early-seral stages) for foraging (Rosenberg and Raphael 1986).

TABLE 3. Model accuracy (AUC) for the best AIC-ranked model with combined landscape variables based on GNN (gradient nearest neighbor) data.

Species	Region†	AUC (SD)	Variables‡
BHGR	OR	0.774 (0.007)	ES2000 + HW150 + HW2000
BGWA	OR	0.807 (0.010)	HW2000
BGWA	S.OR	0.868 (0.014)	HW2000 + ES2000
LAZB	S.OR	0.814 (0.009)	ES2000 + HW2000
MGWA	N.OR	0.660 (0.019)	ES2000 + HW2000
MGWA	S.OR	0.635 (0.014)	ES2000
NAWA	S.OR	0.691 (0.010)	HW2000 + HW150 + ES2000
OCWA	N.OR	0.630 (0.017)	ES2000 + HW2000
OSFL	S.OR	0.698 (0.014)	ES150 + ES2000 + HW500
OSFL	N.OR	0.593 (0.022)	ES150 + HW500
PSFL	S.OR	0.582 (0.014)	ES2000 + HW150 + HW2000
RUHU	N.OR	0.620 (0.019)	ES2000 + ES150 + ES500
SPTO	S.OR	0.772 (0.009)	HW2000 + ES500
SPTO	N.OR	0.693 (0.018)	HW2000 + ES500
WAVI	S.OR	0.547 (0.017)	ES150 + ES2000 + HW150 + HW2000
WAVI	N.OR	0.644 (0.017)	ES2000 + HW150
WETA	N.OR	0.652 (0.018)	ES500

† Key to abbreviations: S.OR, southwestern Oregon study area ($N = 3329$); N.OR, northwestern Oregon ($N = 1046$); OR, Oregon.

‡ Explanation of variables: HW, hardwood canopy cover; ES, early-seral hardwood canopy cover; numbers refer to spatial extent of variable (in meters). See Table 1 for species codes.

The association of many bird species with broadleaf-dominated and structurally complex early-seral conditions is of vital conservation importance because these forest types appear to be in rapid decline on both industrial and public lands in temperate forests globally. In the PNW, active fire suppression and a focus on old-growth conservation on federal lands have reduced the amount of early-seral forest and the broadleaf component of conifer-dominated landscapes (Kennedy and Spies 2005). In addition, the standard silvicultural practice of removing deciduous vegetation from regenerating conifer plantations may have negative effects on both the species richness and nesting success of breeding birds (Easton and Martin 2002). Current policies do not account for the maintenance of early-seral and hard-

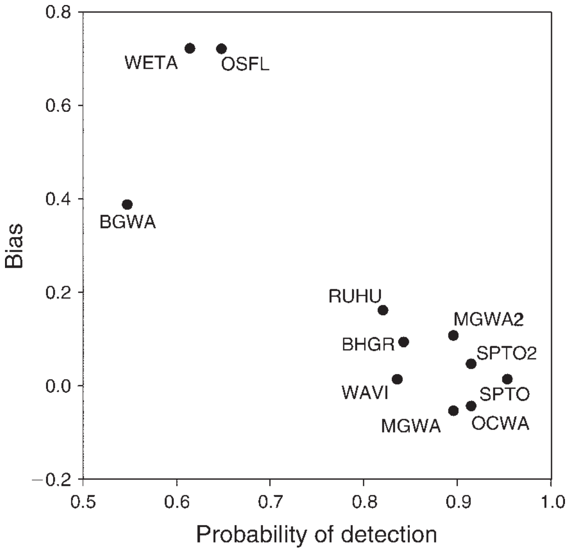

FIG. 4. Bias in logistic regression models in relation to occupancy models as a function of species detection probability. Bias was calculated as: $(\beta_\Phi - \beta)/\beta_\Phi$, where β_Φ is the parameter estimate from occupancy models and β is the coefficient from logistic regression models. See Table 1 for species codes. Species appear twice if they were associated with both early-seral forest (SPTO, MGWA) and broadleaf cover generally (SPTO2, MGWA2).

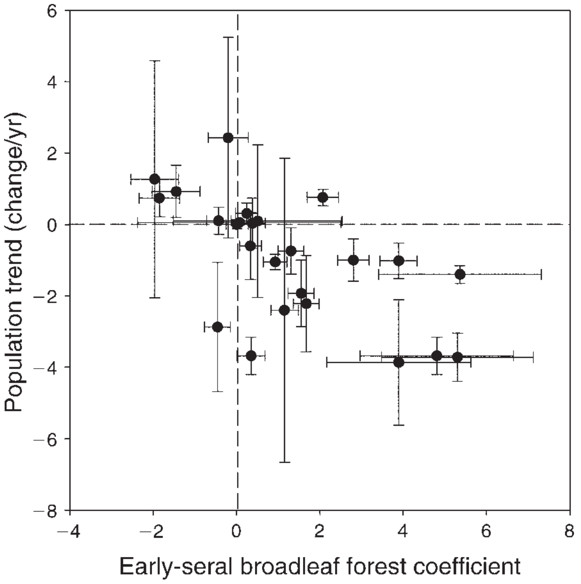

FIG. 5. Population trends in Oregon (% change/yr) for forest-associated bird species as a function of the strength of association with early-seral broadleaf cover. Association strength was measured as the coefficients of logistic regression models with species occurrence as a function of the amount of early-seral broadleaf cover (2000 m spatial extent). Error bars on the x-axis reflect confidence intervals of model coefficients, and y-axis bars are the variances of species population trends.

wood forest, so this decline is projected to continue (Spies et al. 2007*a*). Our results suggest that reduction of compositionally diverse early-seral forest has already had negative effects on the populations of associated birds. With annual rates of population decline >2% per year over 42 years, Rufous Hummingbird, American Goldfinch, Olive-sided Flycatcher, Orange-crowned Warbler, Pacific-slope Flycatcher, Black-throated Gray Warbler, and Purple Finch may all be of potential conservation concern. This list is not exhaustive, as it is drawn only from the common 25 species examined in this study and therefore may represent a conservative estimate of population decline of forest birds in the PNW. Declines in species associated with natural early-seral conditions and broadleaf components of coniferous forests are not isolated to northwest forests, but have been observed globally, including the northeastern United States (Litvaitis 1993, Dettmers 2003), the north central United States (Straw et al. 1994), central Europe (Paquet et al. 2006), Britain (Fuller et al. 2007), and Scandinavia (Enoksson et al. 1995).

Maintenance and enhancement of habitat for species that use early-seral stages and broadleaf vegetation may best be achieved by implementing alternative management strategies early in stand development. For example, controlling density at an early age, before canopy closure, can help to maintain diverse stand composition and structure throughout the life of a stand, and can preserve future management options (e.g., Harrington and Tappeiner 1997, Tappeiner et al. 2002). In forests that regenerate naturally following disturbance, wide spacing of conifers delayed canopy closure and resulted in longer periods of shrub dominance than in densely stocked, managed stands (Tappeiner et al. 1997); in plantations managed for high conifer density, the period of time where broadleaf components exist is thus truncated. Broadleaf vegetation that becomes established early in stand development is more likely to persist under more open conditions, thus contributing structural and functional diversity as the stand matures (MacKinnon and Freedman 1993). If broadleaf components remain in existing plantations, it may be possible to enhance and restore them through active management (Bailey and Tappeiner 1998, Spies et al. 2007*a*). However, before detailed management recommendations can be made, experimental studies are required to confirm and add precision to our results. Such studies would manipulate amounts and configurations of broadleaf cover at stand and landscape scales.

After accounting for spatial autocorrelation, we detected landscape-scale thresholds in response to broadleaf cover for seven of the 12 species examined. Such thresholds in occupancy as a function of habitat loss are predicted to occur in theoretical models (e.g., Fahrig 1998, With and King 1999), but to date have received conflicting empirical support (Andrén 1994, Homan et al. 2004, Radford and Bennett 2004, Lindenmayer et al. 2005). Most studies conducted on forest birds have not reported landscape thresholds (e.g., Lichstein et al. 2002), but this may be due to the lack of adequate methods previously available for threshold detection. For several of the species we examined, model fit and discrimination would have been substantially poorer if the nonlinear nature of species response to the environmental gradient had not been considered (Table 2). Ignoring the existence of potential thresholds could thus mask the influences of landscape composition on site occurrence.

It should be noted that the thresholds we report should not be considered thresholds in habitat below which a population will not persist. We detected thresholds in broadleaf cover below which the likelihood of species occurrence declined more rapidly. These thresholds might be useful to forest managers in the establishment of conservation targets because they may serve as "pre-extinction" thresholds. If landscapes can be managed to increase broadleaf cover to near the thresholds in species occurrence we detected, it is less likely that entire populations will go extinct. Such thresholds may be particularly useful if they triangulate with expected natural ranges of variation in the distribution and abundance of particular forest type (e.g., Drapeau et al. 2009). For instance, in our study system stand-replacing natural disturbances are expected to have been historically infrequent (~100–200 years) and early-seral forest was estimated to occupy approximately 3–12% of the forested landscape (Spies et al. 2007*b*). Presumably early-seral-associated species have evolved physiologies and behaviors to search and settle in patchily distributed and ephemeral forest types. The relatively low thresholds in early-seral broadleaf forest that we detected for Oregon forest birds are congruent with this hypothesis and suggest that in landscapes typically dominated by conifers such as the PNW, even a small broadleaf component can have profound contributions to bird diversity. For certain species, conservation of early-seral broadleaf forest on even only small parcels may provide large conservation benefits.

Quantifying thresholds at the level of individual species is clearly preferable to thresholds in assemblage metrics such as species richness, which potentially obscure compositional changes in the communities and may also mask the loss of species with greater sensitivity to landscape change (Radford et al. 2005). Nevertheless, the detection of thresholds in the occurrence of individual species may still conceal "true" components of habitat quality; future studies should test for thresholds in demographic variables (i.e., survival, reproduction). There is also an inherent danger in managing ecosystems for minimum targets because occurrence thresholds might shift upward in poor years (Betts and Villard 2009).

Asymptotic threshold responses are relatively easy to understand on practical and theoretical grounds. Species may require some minimum amount of habitat on the landscape, below which patches are too difficult to find and/or colonize (With and Crist 1995, Stamps et al. 2005). For species with larger home ranges, there may simply be insufficient resources to warrant territory defense (Dunning et al. 1992). "Humped," or unimodal, patterns in species occurrence as a function of broadleaf cover are more difficult to explain. Pacific-slope Flycatcher and Black-throated Gray Warbler exhibited such responses. Patches of broadleaf vegetation in the Pacific Northwest often occur as a result of natural or anthropogenic disturbance (Kennedy and Spies 2005). Pacific-slope Flycatcher tends to be more associated with mature coniferous forest (Hansen et al. 1995), but may thus find some small amount of edge-associated broadleaf cover of disturbance origin beneficial, particularly in the post-breeding season. However, as mature conifer forest declines below some threshold, the quality of the remaining habitat may decline (Betts et al. 2007). Black-throated Gray Warbler has been reported to use both Douglas-fir and oak in dense mixed stands (Morrison 1982). Thus, the unimodal pattern exhibited by both species may reflect mixed-forest associations at one or several spatial and temporal scales.

We found substantial regional differences in species response to broadleaf cover. In one instance (Spotted Towhee) we found positive effects of broadleaf cover in southwestern Oregon but negative effects in northwestern Oregon. Such differences highlight the importance of understanding that the regression models we apply are statistical correlations and do not imply causation. If the true mechanisms for species distributions shift between regions, models will not be transferable (Betts et al. 2006*b*). We used very coarse-resolution variables "early-seral broadleaf cover" and "broadleaf cover" to predict species distributions. Subcomponents of these variables (e.g., prevalence of particular broadleaf species such as *Quercus* spp.) vary across the state. Species associated with such subcomponents were likely to have been poorly modeled. Different distribution patterns of broadleaf vegetation on landscapes in each region likely influence bird distributions; for instance, bigleaf maple in the north tends to occur as scattered small patches whereas oak in the south occurs as more contiguous stands. Further, our landscape-scale vegetation data were of insufficient resolution to measure the structural components of early-seral forest (e.g., standing and fallen dead wood) that have been shown to be important to some early-seral associated bird species (Saab et al. 2009). Unmeasured variation in complex structure could be a cause of apparent regional variation in species responses and may have reduced the explanatory power of models. Future work should attempt to use finer-resolution vegetation variables to model species distributions. The trade-offs associated with using such variables may be the accuracy of vegetation models, particularly at site scales (Ohmann and Gregory 2002) and the risk of over-fitting distribution models as a function of including many variables (Vaughan and Ormerod 2005).

Conclusions

We found strong positive associations by many PNW songbirds with the amount of broadleaf and early-seral broadleaf forest at broad spatial scales. The majority of these relationships were nonlinear, indicating that conservation of such forest types will have different consequences for bird populations, depending on where a particular landscape happens to occur on the habitat loss gradient. Most previous study and policy in this region and globally has focused on habitat associations of species associated with late seral forest (e.g., Bart and Forsman 1992, Hansen et al. 1995, Villard et al. 1999, Lindenmayer et al. 2002, Betts et al. 2006*a*); this is likely because this forest condition has traditionally been at the greatest risk of decline due to timber exploitation (e.g., Betts et al. 2003). However, the strong negative correlation we observed between dependency on early-seral broadleaf forest and population trends supports the notion that early-seral forest associates are also at high risk of decline due to habitat loss on the breeding grounds. We hypothesize that such declines are due to a combination of forest succession and increasingly intensified forestry that reduces the broadleaf component of early-seral stands. Though early-seral forest in the northwestern United States was probably at a historical high during the 1950s and 1960s (when the BBS began), declines in this forest condition have now likely declined below the historical range of variation (Spies et al. 2007*a*). To maintain species associated with early-seral broadleaved forest, policy makers will need to devise new policies that explicitly favor the creation of this condition.

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APPENDIX

List of bird species used to test the correlation between the strength of early-seral broadleaf association and 42-year population trends for Oregon, USA (*Ecological Archives* A020-079-A1).