Conservation Biology

Contributed Paper

A Multispecies Framework for Landscape Conservation Planning

W. SCOTT SCHWENK* AND THERESE M. DONOVAN‡

*Vermont Cooperative Fish and Wildlife Research Unit, University of Vermont, Burlington, VT, 05405, U.S.A., scott.schwenk@uvm.edu
‡U.S. Geological Survey, Vermont Cooperative Fish and Wildlife Research Unit, University of Vermont, Burlington, VT, 05405, U.S.A.

Abstract: *Rapidly changing landscapes have spurred the need for quantitative methods for conservation assessment and planning that encompass large spatial extents. We devised and tested a multispecies framework for conservation planning to complement single-species assessments and ecosystem-level approaches. Our framework consisted of 4 elements: sampling to effectively estimate population parameters, measuring how human activity affects landscapes at multiple scales, analyzing the relation between landscape characteristics and individual species occurrences, and evaluating and comparing the responses of multiple species to landscape modification. We applied the approach to a community of terrestrial birds across 25,000 km^2 with a range of intensities of human development. Human modification of land cover, road density, and other elements of the landscape, measured at multiple spatial extents, had large effects on occupancy of the 67 species studied. Forest composition within 1 km of points had a strong effect on occupancy of many species and a range of negative, intermediate, and positive associations. Road density within 1 km of points, percent evergreen forest within 300 m, and distance from patch edge were also strongly associated with occupancy for many species. We used the occupancy results to group species into 11 guilds that shared patterns of association with landscape characteristics. Our multispecies approach to conservation planning allowed us to quantify the trade-offs of different scenarios of land-cover change in terms of species occupancy.*

Keywords: biodiversity, forests, habitat loss, landbirds, landscape conservation, multispecies assessment, occupancy modeling, Vermont

Un Marco de Referencia con Múltiples Especies para la Planificación de la Conservación del Paisaje

Resumen: *Los paisajes con cambios rápidos han generado la necesidad de métodos cuantitativos para la evaluación y planificación de la conservación de grandes extensiones espaciales. Diseñamos y probamos un marco de referencia con especies múltiples para planificar la conservación para complementar las evaluaciones de especies individuales y enfoques a nivel de ecosistema. Nuestro marco consistió de 4 elementos: muestreo para estimar parámetros poblacionales efectivamente, medición del efecto de actividades humanas en el paisaje a escalas múltiples, análisis de la relación entre características del paisaje y la presencia de especies individuales y evaluación y comparación de las respuestas de especies múltiples a la modificación del paisaje. Aplicamos el método a una comunidad de aves terrestres en 25,000 km^2 con un rango de intensidades de desarrollo humano. La modificación humana de la cobertura de suelo, la densidad de caminos y otros elementos del paisaje, medidos en escalas espaciales múltiples, tuvieron gran efecto sobre la ocupación de las 67 especies estudiadas. La composición del bosque a 1 km de los puntos tuvo un fuerte efecto sobre la ocupación de muchas especies y un rango de asociaciones negativas, intermedias y positivas. La densidad de caminos a 1 km de los puntos, el porcentaje de bosques siempre verdes a 300 m, y la distancia al borde del parche también se asociaron estrechamente con la ocupación de muchas especies. Utilizamos los resultados de ocupación para agrupar a las especies en 11 gremios que compartieron patrones de asociación con las*

Paper submitted September 1, 2010; revised manuscript accepted March 28, 2011.

Conservation Biology, Volume 25, No. 5, 1010–1021

DOI: 10.1111/j.1523-1739.2011.01723.x

características del paisaje. Nuestro método con especies múltiples para planificar la conservación nos permitió cuantificar los pros y contras de escenarios diferentes de cambio de cobertura de suelo en términos de la ocupación de especies.

Palabras Clave: aves, biodiversidad, bosques, conservación del paisaje, evaluación de múltiples especies, modelo de ocupación, pérdida de hábitat, Vermont

Introduction

Rapid changes in land cover, road density, and other landscape elements (hereafter landscape changes) have spurred a growing desire to conserve biological diversity at large extents (Groves et al. 2000; North American Bird Conservation Initiative 2010) and have led to a proliferation of regional and national conservation plans worldwide. Planning over such large areas, however, poses substantial challenges given the many species, ecosystems, and effects of human activities that must be considered (Poiani et al. 2000). Methods that encompass multiple species and large geographic areas, but that are not overly difficult, time consuming, or expensive to implement are highly relevant for conservation planning.

A major challenge in conservation planning is to determine the targets of conservation action and to address their responses to landscape change and management in a unified conceptual framework. Given the impossibility of monitoring all species present within a large area, one approach is to consider entire ecosystems (Franklin 1993), but determining reliable measures of ecosystem condition remains difficult (Dale & Beyeler 2001; Carpenter et al. 2006). Focal species (Lambeck 1997) and other surrogate-species approaches (Wiens et al. 2008) can narrow the list of species that are targeted for management, but whether the response of surrogate species to human activity, including management, is indicative of the responses of other species they are intended to represent is unclear (Lindenmayer et al. 2002; Cushman et al. 2010). Multispecies assessments therefore have potential to complement ecosystem and single-species approaches, yet they present analytical challenges. Frequently, different environmental variables are selected to define habitat requirements for each species or multiple variables are collapsed into a few aggregated variables to define habitat requirements. Although these approaches have advantages, they also make it difficult to predict trade-offs among species in response to management and to understand the collective response of species to human-induced landscape changes.

It is also difficult to account for composition and configuration of land cover and to monitor species across large areas. Historically, many researchers focused only on the effects of loss of a particular land-cover type (such as forest) to species known to depend on it and did not consider the surrounding matrix and species that may benefit from that change in land cover (Kupfer et al. 2006). Additionally, inferences from regional monitoring data are often inaccurate because many analyses do not account for variability in detection probability or lack a defined geographic sampling frame (MacKenzie et al. 2002; Rosenstock et al. 2002). Collectively, these challenges have hindered the gathering of information needed for conservation planning across large areas.

To maximize the effectiveness of conservation efforts for large areas, a cohesive, rigorous approach that simultaneously evaluates the response of multiple species to landscape characteristics is needed. We propose that such an approach include sampling that effectively estimates population parameters for multiple species; measuring the ways in which human activity affects landscapes at multiple spatial extents relevant to the study species; analyzing the relation between landscape characteristics and individual species occurrences; and evaluating and comparing the responses of multiple species to landscape modification. Such an approach would allow systematic evaluation of how species occurrence is related to major human-induced landscape changes and generation of testable predictions of species' responses to future landscape change. We applied this multispecies framework for conservation planning to a community of terrestrial birds occurring across a large area.

Methods

Study Area and Sampling Design

Our study area was the entire state of Vermont (U.S.A.), 25,000 km^2, which was 73% forested at the time of the study (MRLC 2001). Agricultural area covered approximately 15% and developed areas (residential, commercial) approximately 2% of the state, respectively. Birds were observed at 693 points throughout the state (Supporting Information). We selected the locations of points at random from among forested (70% of points), agricultural or grassland (15%), or developed (15%) areas, and points were at least 500 m apart (methods are further described in Long et al. [2007] and Mitchell & Donovan [2008]). The resulting set of points was broadly representative of the gradient of human development and forest fragmentation across the state (Table 1). Three, single

Table 1. Descriptive statistics and correlation matrix for covariates used in modeling occupancy of bird species.[a]

Environmental covariates	*Data set minimum, mean, maximum (693 points)*	*Study area (Vermont) minimum, mean, maximum*	*Topographic wetness index*	*Distance to edge*	*Percent evergreen forest*	*Percent forest*	*Road density*
Forest dominant within 25 m of point (binary variable)	74% of points within forest	73% of study area forested					
Topographic wetness index, 30-m pixel	1.0, 4.4, 23.7	−0.2, 5.0, 29.3	1.00	−0.18	−0.07	−0.36	0.09
Distance (m) from point to edge of nearest different land cover[b]	0, 198, 2030	(not calculated)		1.00	−0.16	0.39	−0.32
Percent evergreen forest within 300 m of point	0, 13, 81	0, 15, 100			1.00	0.15	0.01
Percent forest within 1 km of point	0, 75, 100	0, 75, 100				1.00	−0.51
Road density (km/km^2) within 1 km of point	0, 1.3, 10.8	0, 1.1, 13.8					1.00

[a] *Statistics are presented for the data set (693 points) and for the entire study area in which the points were located (Vermont, U.S.A.).*
[b] *Distance to edge was truncated at 1000 m (9 of 693 points affected) to improve model convergence.*

observer, 10-min point counts were made at each point during the breeding season (20 May to 16 July). Observations were made within a 75-m radius of the point, and counts were separated by 2-min intervals. During the third count, a recording of alarm calls of Black-capped Chickadees (*Poecile atricapillus*) and other birds was played to increase the probability of bird detection. Points were visited once (3 counts) in either 2003 or 2004. Point counts were conducted by 1 of 4 experienced observers who recorded all bird species heard or seen.

Measurement of Landscape Characteristics at Multiple Spatial Extents

We selected a small number of covariates that reflected major habitat features likely to be associated with occupancy of many species, measured human influences on the landscape, and were not highly correlated (Table 1). At a local extent (i.e., less than the size of a breeding bird's territory), we used the binary variable of whether land cover within a 25-m radius of the point-count location was predominantly forest, given the effect of trees on habitat structure for birds. We chose 25 m because observers could reliably classify land-cover types at this distance without leaving the point, which was advantageous for logistical reasons. We expected forest status within 25 m to be representative of forest status within the 75-m radius of the bird count. As a measure of local landform, which can influence vegetation structure and composition and bird distributions (Lichstein et al. 2002; Mitchell et al. 2006), we computed topographic wetness index values. The index was a continuous variable. Values of the index ranged from 1.0 (little accumulation of water, e.g., ridge tops) to 23.7 (substantial flow accumulation, e.g., basins, valley floors).

At greater than local extents, the 3rd and 4th covariates were distance from the point to the edge of the nearest different land cover and percent evergreen forest within 300 m, given numerous avian studies documenting associations of edges and evergreen trees with distributions of birds (e.g., Robbins et al. 1989; Mitchell et al. 2001). Our rationale for using 300 m was that we expected this distance to coincide with the extent of habitat used by many terrestrial species of birds (Betts et al. 2006). We calculated covariates with ArcGIS software (ESRI, Redlands, California). Calculating distance to edge, the distance from the point to where land-cover type changed, required a series of steps. First, we modified land-cover data from the 2001 National Land Cover Database (NLCD) (MRLC 2001) by overlaying roads, which we classified as developed land, and power lines, which we classified as scrub or shrub, on 30-m pixels classified as forest in the NLCD. Second, we reclassified Vermont's 18 NLCD land-cover classes into 6 classes that we expected birds to perceive as distinct: developed and bare land; agricultural area or grassland; forest; scrub or shrub; nonforested wetland; and open water. For each point, we then recorded the distance to the edge of the nearest pixel of a different land-cover class.

The 5th and 6th covariates measured percent forest and road density (kilometers of roads per square kilometer) within a 1-km radius around survey points. Percent forest is affected by removal and fragmentation of forests by human activity, particularly agriculture; it has been estimated that Vermont was 95% forested prior to European settlement (Thompson & Sorenson 2000). Percent forest was strongly and negatively correlated with percent agriculture within 1 km of points ($R = -0.83$). Road density is a measure of human development and in Vermont is closely related to developed land cover. We used a 1-km distance because this distance has been strongly associated with avian occurrence in other studies (Bakermans & Rodewald 2006) and because of evidence that birds use areas considerably larger than breeding territories in selecting habitat for nesting and when acquiring resources (Whitaker & Warkentin 2010).

Relating Landscape Characteristics to Species Occupancy

We developed occupancy models for territorial, terrestrial birds with relatively small home ranges and for which number of points with detections was sufficient for modeling (>10 points). We implemented single-season occupancy models in MARK 5.1 (White & Burnham 1999), which provided an estimate of ψ, the probability that a site is occupied by a species (MacKenzie et al. 2002). We defined a site as a circle with a 75-m radius (the point-count distance) centered on a study point. For each species, we generated 32 a priori models. The binary covariate forest was included in all models. The 32 models collectively included all possible combinations of the other 5 environmental covariates (Supporting Information). The following equation is for the model containing all occupancy covariates:

$$\begin{aligned}\text{logit}(\psi) &= \beta_0 + \beta_1(\text{forest}) + \beta_2(\text{topographic witness}) \\ &+ \beta_3(\text{topographic witness})^2 + \beta_4(\text{distance to edge}) \\ &+ \beta_5(\text{distance to edge} \times \text{forest}) + \beta_6(\%\,\text{evergreen}) \\ &+ \beta_7(\%\,\text{evergreen})^2 + \beta_8(\%\,\text{forest}) + \beta_9(\%\,\text{forest})^2 \\ &+ \beta_{10}(\text{road density}) + \beta_{11}(\text{road density})^2. \end{aligned} \tag{1}$$

The quadratic terms, which were always paired with their corresponding unsquared terms, allowed assessment of a nonlinear relation between the covariates and occupancy. The distance to edge × forest interaction term, always paired with distance to edge, allowed the relation between occupancy and distance to edge to vary as a function of whether the point was located in a forest patch.

The approach we adopted improves occupancy estimates by accounting for detection probability (p), the probability that a species present at a site was detected by the observer. We modeled detection probability as a function of visit-specific covariates that affected detection probability in other studies (Alldredge et al. 2007): time of day, day from initiation of sampling, observer (categorical), road density (greater traffic noise and development may reduce detection probability), and whether the point was in a forested or nonforested patch.

We then used MARK to estimate for each site ψ and 2 values of the detection parameter, 1 for the first 2 visits ($p_1 = p_2$, where p is the probability the species is detected if present) and 1 for the third visit (p_3) with the alarm-call recording. We assessed model fit by running bootstrap goodness-of-fit tests (MacKenzie & Bailey 2004) for each species in program PRESENCE (MacKenzie et al. 2006). In some cases, primarily for species detected at few sites, we reduced the number of covariates or categories within a covariate. The most frequent modification (29 species) was to remove one or more observers from the model set in which limited numbers of detections precluded reliable estimation of observer effects.

For each species, we evaluated models in a multimodel inference framework with Akaike's information criterion (AIC) (Burnham & Anderson 2002). Rather than identifying one best model, we drew inferences from the full model set. The support for each model i was represented by its AIC weight w_i; the sum of w_i for all models equaled 1. We used the weights to calculate model-weighted average occupancy for individual sites and for the entire study area (for the models with the top 95% of model weight). Because each occupancy covariate j (% forest, distance to edge, road density, % evergreen forest, and topographic wetness, including its quadratic term or distance to edge × forest in the case of distance to edge) was equally represented in the model set and included in 16 of 32 models, we estimated the relative importance of each covariate $w_+(j)$ by summing w_i for the 16 models containing the covariate. The larger the value of $w_+(j)$, the greater the evidence that covariate j was influential in accounting for occupancy patterns relative to other covariates in the model set. Where $w_+(j) > 0.5$, which indicated j was strongly associated with occupancy, we assessed the direction and magnitude of species association with model-averaged β values for the covariate. We included the binary covariate forest in all models because it is well established that presence of forest affects occurrence of most terrestrial birds; this covariate therefore was not included in the analysis of relative importance. Because we used the same covariate set for all species, we were able to compare and summarize results across species. To estimate the relative importance of each covariate for the entire bird community, we averaged the values of relative variable importance, $w_+(j)$, for each species.

So that we could interpret results across multiple species, we divided species into guilds that had similar associations with covariates on the basis of occupancy modeling results. Primarily, we used cluster analysis to assign species to groups. First, we estimated probability of occupancy for each species at each site. We then calculated relative occupancy for each species by dividing the site-specific predicted occupancy by the average species-specific predicted occupancy for all sites. Calculating relative occupancy allowed us to compare species on the basis of the strengths of association with covariates rather than on the number of sites they were predicted to occupy. We applied Proc Distance of SAS (SAS Institute, Cary, North Carolina) to the relative occupancy estimates to calculate a matrix of Euclidean distances, which then served as the input for hierarchical agglomerative cluster analysis of the species set with Proc Cluster. We visually examined the resulting dendrogram to identify clusters of species with similar responses.

Scenarios of Landscape Change

To demonstrate how use of a common set of covariates can be applied to evaluate how human modifications of the landscape may affect multiple species, we developed 4 scenarios of landscape change and used the occupancy models to predict species occurrence. The scenarios were a highly forested landscape (% forest = 100, % evergreen forest = 20, road density = 0); a mostly forested landscape, which represented average covariate values for the dataset (% forest = 75, % evergreen forest = 13, road density = 1.3); a less forested and more developed landscape (% forest = 25, % evergreen forest = 13, road density = 5); and a highly developed landscape (% forest = 10, % evergreen forest = 5, road density = 10). For each scenario, we estimated occupancy for forested and nonforested sites.

Results

Occupancy Models

We developed models for 67 species based on 12,764 detections, which was most of the detections in the data set. An additional 45 terrestrial bird species were detected (413 detections, 244 points), but the number of detections was insufficient to develop models for those species. Estimated probability of occupancy for modeled species (Supporting Information) ranged from 2.4% for House Finch (*Carpodacus mexicanus*) to 83% for Black-capped Chickadee (*Poecile atricapillus*). Estimated average probability of being detected at least once at a site (Supporting Information) ranged from 40% for Cedar Waxwing (*Bombycilla cedrorum*) to 97% for Black-capped Chickadee. The average for all species was 73% (SD 13).

Across the species set, relations between covariates and occupancy ranged from positive, to quadratic, to negative forms (Fig. 1 & Supporting Information). The association with percent forest within 1 km varied across species (Fig. 1a). Twenty-one species had the highest probability of occupancy at sites with >80% forest, whereas 7 species had the highest probability of occupancy at sites with <20% forest. Of the 37 species for which $w_+(j)$ for percent evergreen forest exceeded 0.5, 19 species had the highest probability of occupancy at sites with <40% evergreen forest and 18 species had the highest probability of occupancy at sites with >40% evergreen forest (Fig. 1b). Different species had negative or positive associations with road density (Fig. 1c) and topographic wetness (Fig. 1d).

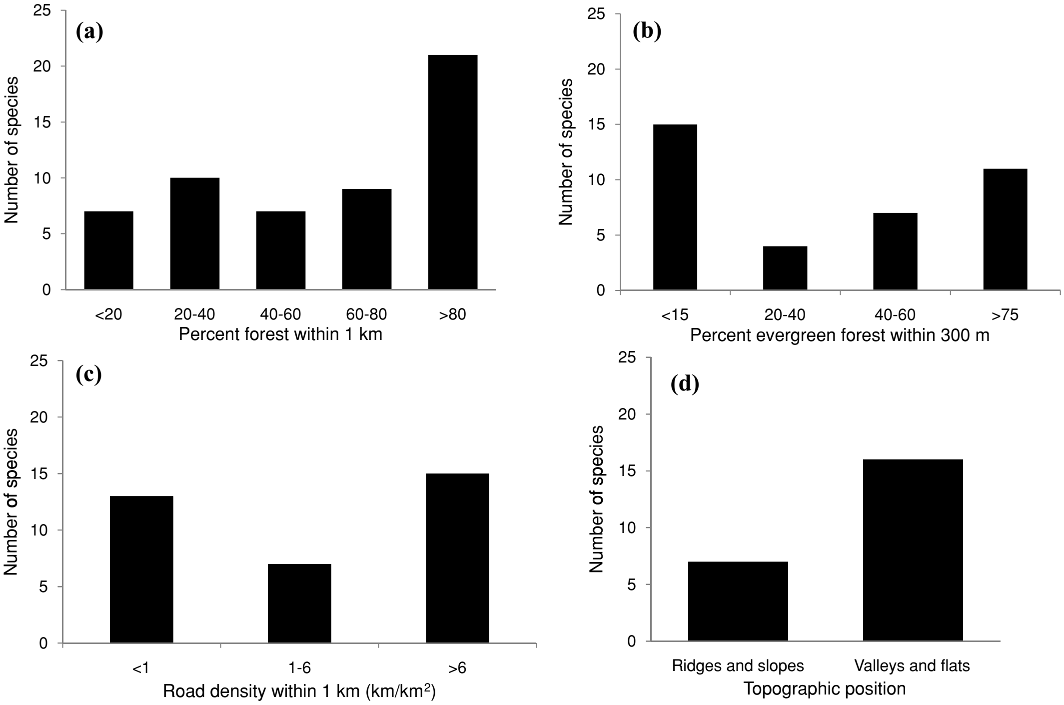

Figure. 1. Values of covariates at which maximum occupancy of individual bird species occurred: (a) percent forest within 1 km of point, (b) percent evergreen forest within 300 m of point, (c) road density (kilometers of roads per square kilometer), and (d) topographic position (from topographic wetness index). Only those species for which the relative variable importance, as assessed by multimodel selection, was > 0.5 for a given covariate are included.

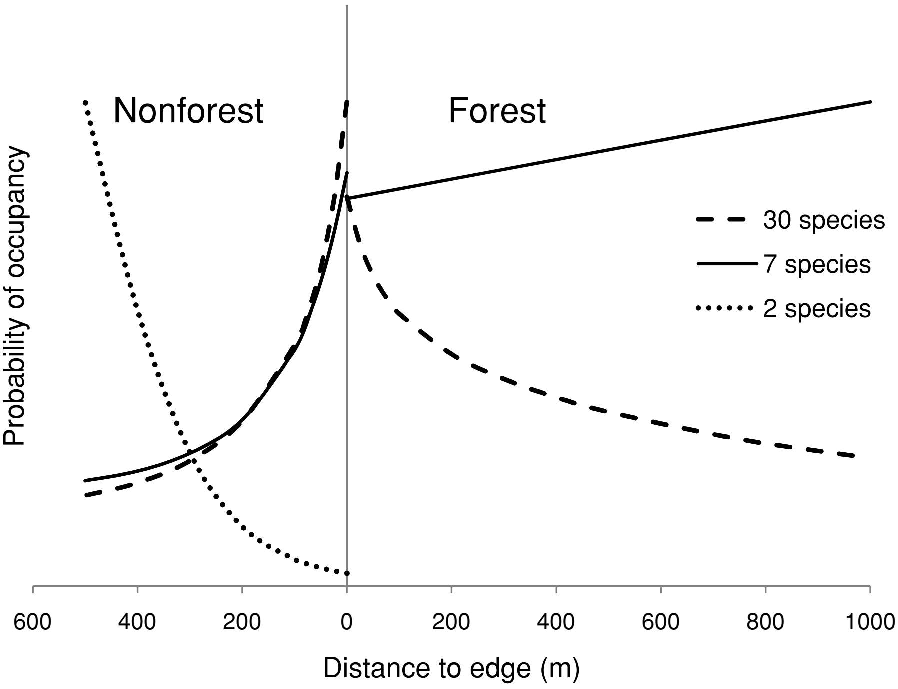

Figure 2. Three types of relations between distance to edge and probability (increasing from bottom to top) of bird occupancy (vertical line, edge between a nonforest patch and a forest patch; dashed line, decreasing occupancy as distance to edges increased in both nonforested and forested landscapes; solid line, decreasing occupancy as distance to edges increased in nonforested landscapes but as distance to edges decreased in forests; dotted line, increasing occupancy as distance to edges increased in nonforested landscapes with no occupancy in forests away from edges) (1 detection at a point within a forested patch for both species). Lines are average responses of all species within each category for which relative variable importance for distance to edge was >0.5 in the multimodel selection.

Occupancy of 28 species was positively associated with sites that were predominantly forested within 25 m, and 39 species were negatively associated (Supporting Information) with this variable. The associations between forest within 25 m and occupancy were not always similar to the associations between percent forest within 1 km and occupancy. For example, Dark-eyed Junco (*Junco hyemalis*) was associated with nonforested sites within areas with >80% forest.

We identified 3 categories of associations between occupancy and distance to edge (Fig. 2). The most common association was decreasing occupancy away from edges both within and outside forest (30 species) (Supporting Information). For 20 of these species, occupancy away from edges decreased more rapidly for nonforested sites than forested sites. For 7 species, such as Red-eyed Vireo (*Vireo olivaceus*), probability of occupancy was greater within forest more distant from edges (i.e., in forest interiors).

Of the 5 covariates ranked with multimodel selection (Table 2), percent forest received the strongest support across all species (average $w_{+}[j] = 0.78$). Edge, evergreen, and roads had similar weights of support (average $w_{+}[j]$ 0.55–0.63). Values of the topographic wetness index were less supported than the other covariates (average $w_{+}[j] = 0.42$), but there was evidence that it was important for 23 species ($w_{+}[j] > 0.5$).

Bird Guilds

We assigned species to 11 guilds (Table 3). Birds in guilds 1, 2, and 3 were distinct from birds in other guilds, and these guilds contained species with the highest probabilities of occupancy in predominantly nonforested areas. Probabilities of occupancy of species in guild 1 (grassland species) increased as distance to edge increased, whereas probabilities of occupancy of species in guilds 2 and 3 were greatest near edges. Associations of occupancy of species in guild 3 with road density were more strongly positive than those of species in guild 2. Species in guilds 4, 5, 7, and 8 tended to be associated with deciduous forests that constituted intermediate percentages of the landscape within 1 km. Species in guild 6 were associated with interior forests because occupancy probability was greatest in mostly forested areas and away from forest edges. Probabilities of occupancy of species in guilds 9 and 10 were greatest in forests with

Table 2. Summary of relative importance of covariates ranked with multimodel selection for occupancy of 67 bird species.[a]

Covariates	*Average relative variable importance*[b]	*Number of species for which variable was most strongly associated with occupancy*	*Number of species for which relative variable importance*		
			>0.5	>0.75	>0.9
Percent forest within 1 km of point	0.78	27	54	45	36
Distance to edge of nearest different land cover type	0.63	14	39	28	19
Percent evergreen forest within 300 m of point	0.61	13	37	27	21
Road density within 1 km of point	0.55	11	35	22	14
Topographic wetness index	0.42	2	23	13	10

[a] *Larger values indicate greater importance in accounting for occupancy patterns, according to Akaike's information criterion (AIC), relative to other modeled variables. Three threshold values (0.5, 0.75, 0.9) are presented to illustrate a range from moderate to strong support for the covariates.*

[b] *Total* AIC_c *weight* $w_{+}(j)$ *for models containing the covariate j, averaged across all bird species (all covariates appeared in 16 of 32 models).*

a considerable proportion of evergreen trees. Species in guild 11 were quite distinct from the other guilds. The 2 species in this guild occurred at the edge of lowland forests that had intermediate percentages of evergreen trees (most likely pine, *Pinus* sp.). In several cases, shared occupancy associations resulted in uncertainty in guild assignments.

Scenarios of Landscape Change

The magnitude and direction of changes in predicted probabilities of occurrence given different scenarios of landscape change varied among species (examples in Table 4; complete results in Supporting Information). Progressing from completely forested landscapes without roads (scenarios 1a and 1b) to 90% nonforested, developed landscapes (scenarios 4a and 4b) resulted in a decrease in occupancy by forest species (guilds 6 and 10), but an increase in occupancy by edge species (guilds 2 and 4). For example, Ovenbird (*Seiurus aurocapilla*, guild 6) occupancy at forested sites was predicted to be 0.84 in a completely forested landscape compared with 0.08 in the most highly developed landscape. By contrast, American Robin (*Turdus migratorius*, guild 4) occupancy was predicted to be 0.31 in a completely forested landscape and 0.95 in the most highly developed landscape. Predicted probabilities of occupancy of grassland species (guild 1) were greatest in scenario 3b, which had intermediate proportions of forest (25%) and road density.

Discussion

Applications of the Multispecies Framework

Our multispecies framework for conservation planning has the potential to complement single-species assessments and thereby to improve understanding and management of the effects of landscape change on species. Coordinated multispecies monitoring has been proposed as an element in assessing ecosystems at large extents (Manley et al. 2004), but to be useful in conservation planning there must be a way to relate monitoring results to the influences of humans on landscapes. Our framework illustrates an effective way to link these elements. By considering associations between occupancy of many species and covariates measured at multiple spatial extents, it is straightforward to compare the predicted response of species to different combinations of landscape characteristics. By quantifying trade-offs among management actions, an approach that includes scenarios of landscape change can meet critical information needs of conservation planners. Additionally, drawing on species-landscape relations to define guilds may be a useful way to understand similar responses among groups of species without precluding the ability to examine species-specific associations with environmental covariates.

Human Landscape Modification and Bird Occupancy

Our sampling across a gradient of forest, agricultural, and developed cover provided more information on associations between covariates and species occurrences than sampling in only one type of land cover, such as forests, would have. Landscapes associated with human activity, such as urban areas, roads, and agriculture, occurring at multiple spatial extents, had strong associations with occupancy, but they were not uniformly negative. The highest probabilities of occupancy for many species occurred at intermediate values of percent forest and road density. Some species of conservation concern within the study area, such as the Bobolink (*Dolichonyx oryzivorus*) and other grassland-dependent species, now occur almost exclusively on human-modified landscapes (Shustack et al. 2010).

Table 3. Guilds of modeled species of birds, defined primarily through cluster analysis of estimated probability of occupancy at 693 study points.

Guild	*Relation of occupancy with covariates*	*Species*
1. Grassland species	increases as distance from forest increases; peaks at intermediate road density	Bobolink, Savannah Sparrow
2. Species associated with edge and open areas (nonforest species)	increases near edges; intermediate or inverse association with percent forest; peaks at intermediate or low (valley) topographic position	Alder Flycatcher, American Crow, American Goldfinch, Baltimore Oriole, Barn Swallow, Chipping Sparrow, Common Grackle, Common Yellowthroat, Eastern Kingbird, Eastern Phoebe, Tufted Titmouse, Gray Catbird, House Finch, Indigo Bunting, Mourning Dove, Northern Cardinal, Red-winged Blackbird, Song Sparrow, Tree Swallow, Yellow Warbler
3. Species associated with human structures (nonforest species)	intermediate or negative association with percent forest; positive or intermediate association with road density; negative or intermediate association with percent evergreen forest	European Starling, House Sparrow, House Wren, Rock Pigeon
4. Deciduous forest and forest-edge species, road tolerant	increases near edges and as road density increases; peaks at intermediate percent forest; negative or intermediate association with percent evergreen forest	American Robin, Black-capped Chickadee, Blue Jay, Cedar Waxwing, Downy Woodpecker
5. Deciduous forest species tolerant of edges	increases near edges; peaks in mostly forested areas	American Redstart, Rose-breasted Grosbeak, Ruby-throated Hummingbird, Veery, White-breasted Nuthatch
6. Forest interior species	increases as percent forest cover and distance to edges increases; inconsistent associations with percent evergreen forest	Black-throated Blue Warbler, Black-throated Green Warbler, Hairy Woodpecker, Hermit Thrush, Ovenbird, Red-eyed Vireo, Yellow-bellied Sapsucker
7. Forest species of intermediate forest landscapes	peaks at intermediate percent forest cover; not strongly associated with distance to edges	Black-and-white Warbler, Eastern Wood-Pewee, Scarlet Tanager, Wood Thrush
8. Forest-edge species not associated with roads	decreases as road density increases	Chestnut-sided Warbler, Least Flycatcher, Mourning Warbler
9. Mixed-forest species	increases as percent forest cover increases; positive or intermediate association with increasing percent of evergreen forest; negative or intermediate association with increasing road density; not strongly associated with distance to edge	Blue-headed Vireo, Blackburnian Warbler, Brown Creeper, Canada Warbler, Northern Parula, Yellow-rumped Warbler
10. Evergreen and mixed-forest species	increases near edges and as percent forest increases; positive or intermediate response to increasing percent cover of evergreen forest; not strongly associated with road density	Dark-eyed Junco, Golden-crowned Kinglet, Magnolia Warbler, Nashville Warbler, Purple Finch, Red-breasted Nuthatch, Swainson's Thrush, Winter Wren, White-throated Sparrow
11. Species of lowland edge forests with pine	peaks at intermediate percent forest and intermediate percent evergreen forest	Great-Crested Flycatcher, Pine Warbler

Use of a shared set of covariates and evaluation of the relative variable importance of covariates allowed us to draw inferences about which covariates were most strongly associated with occurrence of many terrestrial species of birds. The human alterations to landscape that appeared to have the largest effects operated at 2 extents: changes in land-cover composition at large extents, as measured by percent forest within 1 km of sites, and local changes that influenced whether the patch surrounding the site was forested. Percent forest represented a gradient from highly agricultural landscapes to highly forested (and less developed)

Table 4. Scenarios of landscape change and predicted changes in patterns of bird occupancy.[*]

	Covariate values				*Example species, types of sites occupied*				
Scenario	*% forest within 1 km of point*	*road density (km/km^2) within 1 km of point*	*distance to edge of nearest different land cover type (m)*	*% evergreen forest within 300 m of point*	*Savannah Sparrow, grassland*	*American Goldfinch, edge and open areas*	*American Robin, forest edge*	*Ovenbird, forest interior*	*Dark-eyed Junco, evergreen and mixed forest*
1a. Highly forested site and landscape	100	0	500	20	0.00	0.13	0.31	0.84	0.34
1b. Nonforested site within highly forested landscape	100	0	20	20	0.00	0.36	0.49	0.50	0.44
2a. Forested site, mostly forested landscape (data set mean)	75	1.3	198	13	0.00	0.43	0.55	0.74	0.05
2b. Nonforested site, mostly forested landscape (data set mean)	75	1.3	198	13	0.04	0.31	0.40	0.13	0.05
3a. Forested site; landscape less forested and more developed	25	5	198	13	0.01	0.93	0.68	0.31	0.00
3b. Nonforested site; landscape less forested and more developed	25	5	198	13	0.12	0.90	0.54	0.03	0.00
4a. Forested site; highly developed landscape	10	10	20	5	0.00	0.95	0.95	0.08	0.00
4b. Nonforested site; highly developed landscape	10	10	20	5	0.06	0.98	0.97	0.03	0.00

[*] *Four scenarios are applied to 5 representative species. Each scenario is replicated for a forested and a nonforested point. Approach can be readily extended to more species and other types of landscapes and scenarios.*

landscapes. The importance of percent forest in occupancy models is consistent with substantial evidence that landscape composition is a principal factor in the occurrence of many species (Turner 2005) and with the hierarchical theory of habitat selection (Johnson 1980). Forest cover within a 25-m radius also affected occupancy, but not enough to base predictions of effects at larger extents (e.g., forest species with highest occupancy in partially forested landscapes). Distance to edge (a patch metric) had a strong association with occupancy (positive relation for some species, negative for others).

Several mechanisms may explain species' edge-occupancy patterns, such as preference for shrub patches that frequently occur near forest edges, attraction to areas with multiple types of land cover, and avoidance of edges by species that use only forests or grasslands (McCollin 1998). Negative associations with road density, which we considered a measure of the potential effects of roads and of the overall intensity of human development (Forman & Alexander 1998), may reflect adverse effects of habitat fragmentation. Positive associations probably do not indicate a beneficial effect of roads per se, but rather reflect new habitats and food sources made available by suburban and exurban development (Hansen et al. 2005).

A comparison of our results with other studies of associations between gradients of human development and multiple species is difficult because many researchers focused on only one major land-cover type (such as forest) and used different sets of covariates for different species. Results of such studies show that loss and fragmentation of a given type of land cover is associated with reduction of abundance or occurrence (Donovan & Flather 2002; Fahrig 2003). Typically, however, most researchers have not considered whether amount or quality of habitat for some species increases as a result of the same changes in land cover. A study by Lepczyk et al. (2008) is perhaps most directly comparable to our work. They examined human influence on abundance of 132 bird species across the mid-western United States in 408 landscapes of approximately 1200 km^2 each (3.1 km^2 in our study). Lepczyk et al. found that the abundance in 63% of species is associated with 2 measures of human influence on the landscape (percent anthropogenic land cover and housing density). In contrast, our analysis of relative variable importance showed occurrence was related to 2 comparable covariates (percent forest and road density) for 96% of species (64 of 67) evaluated. Although we and Lepczyk et al. found similar percentages of species with primarily positive (9% vs. 6%, respectively) and negative (33% vs. 40%) associations with human-influenced changes in landscape characteristics as measured by these covariates, we found a greater percentage of species with intermediate associations with one or both covariates (53% vs. 31%).

Associations between Individual Covariates and Probability of Occupancy

The associations with covariates that we found for some species are similar to published descriptions of breeding habitat (Poole 2010), but other associations were unexpected. For example, Red-eyed Vireo and Scarlet Tanager (*Piranga olivacea*) nest in mature forests and are more likely to occur in large than in small forest patches (Mowbray 1999; Cimprich et al. 2000). Therefore, we expected that probability of occupancy of these species would increase as proportion of forest cover increased, but the highest probability of occupancy for both species was associated with intermediate percentages of forest (i.e., a quadratic function). One possible explanation for this is that landscapes with intermediate percentages of forest cover provide greater access to early successional forests, which are used after the breeding period but before migration (e.g., Marshall et al. 2003). Alternatively, heavily forested landscapes in Vermont include areas of high elevation and high proportions of evergreen trees that may correspond to lower habitat quality.

Eleven species associated with evergreen or mixed deciduous-evergreen forests (Poole 2010), such as Swainson's Thrush (*Catharus ustulatus*) and Black-throated Green Warbler (*Dendroica virens*), had the highest probabilities of occurrence at sites with $>50\%$ evergreen forest in the surrounding area. However, some forest species associated with evergreen or mixed forests elsewhere, such as the Red-eyed Vireo (Cimprich et al. 2000), did not show such associations in Vermont. Other species with the greatest probability of occupancy at sites with evergreen forest $<50\%$ included those associated with agricultural or residential areas (Poole 2010).

Although most of the 13 species negatively associated with roads were also positively associated with percent forest or percent evergreen forest, exceptions included Eastern Kingbird (*Tyrannus tyrannus*), a species typically associated with open types of land cover (Murphy 1996). Many of the 15 species with strongest positive associations with roads are commonly associated with human activity or suburban areas (Poole 2010). Six species with maximum probability of occupancy at intermediate road densities are not found in large forest tracts, but also may avoid dense concentrations of roads and human development (Poole 2010) (e.g., Red-winged Blackbird [*Agelaius phoeniceus*]).

Study Uncertainties

Several uncertainties remain, some of which are inherent in studies conducted at a large spatial extent. It is not possible to determine whether the relations we observed between covariates and occupancy are causal, although we believe that plausible mechanisms link these variables. Limiting the number of a priori covariates may have resulted in the omission of variables that were associated with occupancy for certain species. The restricted number of covariates and the lack of fine-resolution vegetation measures for the entire study area mean our findings are most relevant to coarse-resolution patterns of occupancy. Use of occupancy as a population parameter is not as direct an indicator of habitat quality as survival probability or reproductive rate (MacKenzie et al. 2006), but we found that occupancy can be feasibly and reliably estimated with brief visits to a given point if detection probabilities are relatively high. Because each point was visited in only 1 out of 2 years, we could not assess the degree to which covariate associations and occupancy varied by year. Although we present static associations between occupancy and covariates, these associations establish baseline conditions that could be incorporated into multiseason monitoring of populations or metapopulations over the long term. Overall, our findings and our approach to the study of extensive areas complement more intensive, small-scale studies.

Acknowledgments

We thank T. Collingwood, R. DeMots, C. Eiseman, and S. Wilson for conducting bird surveys. We also appreciate assistance from C. Bettigole, E. Buford, N. Charney, G. Clark, A. Gregor, S Harris, K. Manaras, K. McFarland, R. Long, B. Mitchell, J. O'Neil-Dunne, J. Panek, R. Renfrew, A. Strong, and T. Yuta and the access to properties granted by many landowners. E. Fleishman, and 2 anonymous reviewers provided helpful comments on the manuscript. Funding was provided by the U.S. Department of Agriculture Northeastern States Research Cooperative, the McIntire-Stennis Cooperative Forestry Program, the U.S. Forest Service, and the U.S. Geological Survey, Vermont Cooperative Fish and Wildlife Research Unit. Use of trade names in this article does not imply endorsement by the federal government. The Vermont Cooperative Fish and Wildlife Research Unit is jointly supported by the U.S. Geological Survey, the University of Vermont, the Vermont Department of Fish and Wildlife, and the Wildlife Management Institute.

Supporting Information

Additional information on sampling locations (Appendix S1), occupancy model structure (Appendix S2), occupancy estimates and covariate associations (Appendix S3), species models (Appendix S4), and scenarios of landscape change (Appendix S5) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than the absence of the material) should be directed to the corresponding author.

Literature Cited

Alldredge, M. W., T. R. Simons, and K. H. Pollock. 2007. Factors affecting aural detections of songbirds. Ecological Applications **17:**948–955.

Bakermans, M. H., and A. D. Rodewald. 2006. Scale-dependent habitat use of Acadian Flycatcher (*Empidonax virescens*) in central Ohio. Auk **123:**368–382.

Betts, M. G., G. J. Forbes, A. W. Diamond, and P. D. Taylor. 2006. Independent effects of fragmentation on forest songbirds: an organism-based approach. Ecological Applications **16:**1076–1089.

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

Carpenter, S. R., R. DeFries, T. Dietz, H. A. Mooney, S. Polasky, W. V. Reid, and R. J. Scholes. 2006. Millennium ecosystem assessment: research needs. Science **314:**257–258.

Cimprich, D. A., F. R. Moore, and M. P. Guilfoyle. 2000. Red-eyed Vireo (*Vireo olivaceus*). In A. Poole, editor. The birds of North America online. Cornell Lab of Ornithology, Ithaca, New York. Available from http://bna.birds.cornell.edu/bna/species/527 (accessed March 2010).

Cushman, S. A., K. S. McKelvey, B. R. Noon, and K. McGarigal. 2010. Use of abundance of one species as a surrogate for abundance of others. Conservation Biology **24:**830–840.

Dale, V. H., and S. C. Beyeler. 2001. Challenges in the development and use of ecological indicators. Ecological Indicators **1:**3–10.

Donovan, T. M., and C. H. Flather. 2002. Relationships among North American songbird trends, habitat fragmentation, and landscape occupancy. Ecological Applications **12:**364–374.

Fahrig, L. 2003. Effects of habitat fragmentation on biodiversity. Annual Review of Ecology, Evolution, and Systematics **34:**487–515.

Forman, R. T. T., and L. E. Alexander. 1998. Roads and their major ecological effects. Annual Review of Ecology and Systematics **29:**207–231.

Franklin, J. F. 1993. Preserving biodiversity: species, ecosystems, or landscapes? Ecological Applications **3:**202–205.

Groves, C., L. Valutis, D. Vosick, B. Neely, K. Wheaton, J. Touval, and B. Runnels. 2000. Designing a geography of hope: a practitioner's handbook for ecoregional conservation planning. 2nd edition. The Nature Conservancy, Arlington, Virginia.

Hansen, A. J., R. L. Knight, J. M. Marzluff, S. Powell, K. Brown, P. H. Gude, and K. Jones. 2005. Effects of exurban development on biodiversity: patterns, mechanisms, and research needs. Ecological Applications **15:**1893–1905.

Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology **61:**65–71.

Kupfer, J. A., G. P. Malanson, and S. B. Franklin. 2006. Not seeing the ocean for the islands: the mediating influence of matrix-based processes on forest fragmentation effects. Global Ecology and Biogeography **15:**8–20.

Lambeck, R. J. 1997. Focal species: a multi-species umbrella for nature conservation. Conservation Biology **11:**849–856.

Lepczyk, C. A., C. H. Flather, V. C. Radeloff, A. M. Pidgeon, R. B. Hammer, and J. Liu. 2008. Human impacts on regional avian diversity and abundance. Conservation Biology **22:**405–416.

Lichstein, J. W., T. R. Simons, and K. E. Franzreb. 2002. Landscape effects on breeding songbird abundance in managed forests. Ecological Applications **12:**836–857.

Lindenmayer, D. B., A. D. Manning, P. L. Smith, H. P. Possingham, J. Fischer, I. Oliver, and M. A. McCarthy. 2002. The focal-species approach and landscape restoration: a critique. Conservation Biology **16:**338–345.

Long, R. A., T. M. Donovan, P. MacKay, W. J. Zielinski, and J. S. Buzas. 2007. Effectiveness of scat detection dogs for detecting forest carnivores. Journal of Wildlife Management **71:**2007–2017.

MacKenzie, D. I., and L. L. Bailey. 2004. Assessing the fit of site-occupancy models. Journal of Agricultural, Biological, and Environmental Statistics **9:**300–318.

MacKenzie, D. I., J. D. Nichols, G. B. Lachman, S. Droege, J. A. Royle, and C. A. Langtimm. 2002. Estimating site occupancy rates when detection probabilities are less than one. Ecology **83:**2248–2255.

MacKenzie, D. I., J. D. Nichols, J. A. Royle, K. H. Pollock, L. L. Bailey, and J. E. Hines. 2006. Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence. Elsevier Academic Press, San Diego, California.

Manley, P. N., W. J. Zielinski, M. D. Schlesinger, and S. R. Mori. 2004. Evaluation of a multiple-species approach to monitoring species at the ecoregional scale. Ecological Applications **14:**296–310.

Marshall, M. R., J. A. DeCecco, A. B. Williams, G. A. Gale, and R. J. Cooper. 2003. Use of regenerating clearcuts by late-successional bird species and their young during the post-fledging period. Forest Ecology and Management **183:**127–135.

McCollin, D. 1998. Forest edges and habitat selection in birds: a functional approach. Ecography **21:**247–260.

Mitchell, B. R., and T. Donovan. 2008. Mob mentality: effect of a mobbing playback on avian detection probabilities during point count surveys. The Open Ornithology Journal **1:**8–19.

Mitchell, M. S., R. A. Lancia, and J. A. Gerwin. 2001. Using landscape-level data to predict the distribution of birds on a managed forest: effects of scale. Ecological Applications **11:**1692–1708.

Mitchell, M. S., et al. 2006. Relationships between avian richness and landscape structure at multiple scales using multiple landscapes. Forest Ecology and Management **221:**155–169.

Mowbray, T. B. 1999. Scarlet Tanager (*Piranga olivacea*). In A. Poole, editor. The birds of North America online. Cornell Lab of Ornithology, Ithaca, New York. Available from http://bna.birds.cornell.edu/bna/species/479 (accessed March 2010).

MRLC (Multi-Resolution Land Characteristics Consortium). 2001. National land cover database 2001. U.S. Geological Survey, MRLC Project, Sioux Falls, South Dakota. Available from www.mrlc.gov (accessed April 2008).

Murphy, M. T. 1996. Eastern Kingbird (*Tyrannus tyrannus*). In A. Poole, editor. The birds of North America online. Cornell Lab of Ornithology, Ithaca, New York. Available from http://bna.birds.cornell.edu/bna/species/253 (accessed March 2010).

North American Bird Conservation Initiative. 2010. The state of the birds 2010 report on climate change, United States of America. U. S. Department of the Interior, Washington, D.C.

Poiani, K. A., B. D. Richter, M. G. Anderson, and H. E. Richter. 2000. Biodiversity conservation at multiple scales: functional sites, landscapes, and networks. BioScience **50:**133–146.

Poole, A., editor. 2010. The birds of North America online. Cornell Laboratory of Ornithology, Ithaca, New York. Available from http://bna.birds.cornell.edu/BNA/ (accessed March 2010).

Robbins, C. S., D. K. Dawson, and B. A. Dowell. 1989. Habitat area requirements of breeding forest birds of the middle Atlantic states. Wildlife Monographs **103:**3–34.

Rosenstock, S. S., D. R. Anderson, K. M. Giesen, T. Leukering, and M. F. Carter. 2002. Land bird counting techniques: current practices and an alternative. The Auk **119:**46–53.

Shustack, D. P., A. M. Strong, and T. M. Donovan. 2010. Habitat use patterns of Bobolinks and Savannah Sparrows in the northeastern United States. Avian Conservation and Ecology **5:** http://www.ace-eco.org/vol5/iss2/art11/.

Thompson, E. H., and E. R. Sorenson. 2000. Wetland, woodland, wildland: a guide to the natural communities of Vermont. The Nature Conservancy, Montpelier, Vermont, and Vermont Department of Fish and Wildlife, Waterbury, Connecticut.

Turner, M. G. 2005. Landscape ecology: what is the state of the science? Annual Review of Ecology, Evolution, and Systematics **36:**319–344.

Whitaker, D. M., and I. G. Warkentin. 2010. Spatial ecology of migratory passerines on temperate and boreal forest breeding grounds. Auk **127:**471–484.

White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study **46:**S120–S139.

Wiens, J. A., G. D. Hayward, R. S. Holthausen, and M. J. Wisdom. 2008. Using surrogate species and groups for conservation planning and management. BioScience **58:**241–252.