

Stand-Level Forest Structure and Avian Habitat: Scale Dependencies in Predicting Occurrence in a Heterogeneous Forest

Katherine Manaras Smith, William S. Keeton, Therese M. Donovan, and Brian Mitchell

Abstract: We explored the role of stand-level forest structure and spatial extent of forest sampling in models of avian occurrence in northern hardwood-conifer forests for two species: black-throated blue warbler (*Dendroica caerulescens*) and ovenbird (*Seiurus aurocapillus*). We estimated site occupancy from point counts at 20 sites and characterized the forest structure at these sites at three spatial extents (0.2, 3.0, and 12.0 ha). Weight of evidence was greatest for habitat models using forest stand structure at the 12.0-ha extent and diminished only slightly at the 3.0-ha extent, a scale that was slightly larger than the average territory size of both species. Habitat models characterized at the 0.2-ha extent had low support, yet are the closest in design to those used in many of the habitat studies we reviewed. These results suggest that the role of stand-level vegetation may have been underestimated in the past, which will be of interest to land managers who use habitat models to assess the suitability of habitat for species of concern. FOR. SCI. 54(1):36–46.

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SUCCESSFUL BIODIVERSITY CONSERVATION hinges on our ability to understand wildlife-habitat relationships at multiple spatial scales (Grand and Cushman 2003, Storch 2003). Ecological scale can be defined as a combination of its two components: extent and grain (Forman and Godron 1986, Turner 1989, Wiens 1989). Extent is the area considered at each study plot or the entire study area. Grain is the resolution, or size of individual units of observation (McGarigal and Marks 1995). Based on data collected at a specified grain and extent, habitat models represent wildlife habitat relationships mathematically and are widely used by wildlife managers and conservation planners to predict the likely distribution of species in different scenarios of landscape and forest stand structure (Vernier et al. 2002).

Because patterns change depending on the scale at which they are measured (Gardner et al. 1987, Wiens 1989, Trani (Griep) 2002, Bissonette 2003), spatial scale choices for habitat model development are critical. For instance, if habitat is characterized at a scale that is not relevant to a target species, the resulting habitat models will not reflect the true habitat needs of the species (MacFaden and Capen 2002), potentially leading to ill-informed management practices.

We explored scale dependencies associated with habitat modeling for two neotropical migrant species in northern hardwood-conifer forests. Our study analyzes the relative predictive strength of occupancy models based on forest

habitat characterization across three spatial extents. We measured individual trees (live and dead), saplings, and shrubs to describe the physical structure of the forest environment. Hereafter, we refer to habitat structure at this fine grain as “stand-level structure” and to coarser-grained descriptions of habitat structure, such as remotely sensed forest cover, as “landscape-level structure.” On a landscape level, habitat structure generally refers to coarser-grained phenomena, such as the percentage of forest cover, measured in 1-km² pixels. In this example, the grain is equivalent to pixel size, or 1 km². The extent is the area classified as either forest or nonforest. The specific extent and grain that constitute landscape versus stand-level habitat are arbitrary and may differ among studies. Defining and bounding these levels are necessary for discussing, testing, and identifying biologically relevant scales and are incumbent on the authors of each study (McGarigal and Marks 1995).

The importance of stand-level avian habitat was the focus of many investigations in the 1960s and 1970s (e.g., MacArthur and MacArthur 1961). These studies show, for example, that foliage height diversity is predictive of bird species diversity. Specific elements of stand-level structure have also been repeatedly shown to explain an important component of the variation among bird communities (Renken and Wiggers 1993, Hansen et al. 1995, Rhim and Lee 2000, Hagan and Meehan 2002, MacFaden and Capen 2002, Storch 2002).

Starting in the 1980s, concern about the cumulative

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effects of habitat loss and fragmentation prompted landscape ecologists and conservation biologists to investigate the effect of habitat structure on wildlife communities over larger areas (Gustafson 1998, Stauffer 2002). Indeed, landscape-level habitat structure is an important predictor of bird occurrence in many systems (Maurer and Heywood 1993, McGarigal and McComb 1995, Flather and Sauer 1996, Saab 1999, Penhollow and Stauffer 2000, Mitchell et al. 2001, Grand and Cushman 2003). Most of these studies evaluated species distribution across very large spatial extents in which landscape composition varied. Such landscape-level analyses have been stimulated by advances in the discipline of landscape ecology, as well as advances in geographic information system (GIS) technology (Gustafson 1998, Storch 2003).

Despite evidence that certain species rely on specific structural attributes, such as logs, snags, and cavities (Haney and Schaadt 1996, Paragi et al. 1996, Pelton 1996, DeGraaf and Yamasaki 2001), these attributes are often not included in many modeling efforts because inventorying them on the ground is expensive and time-consuming (Hagan and Meehan 2002). Additionally, a number of researchers, after assessing the relative importance of landscape versus stand-level vegetation, concluded that the former is a stronger predictor of avian abundance (Saab 1999, Mitchell et al. 2001). Thus, there is a growing trend for researchers to use data that can be collected remotely in modeling efforts and to forgo data that require intensive, on the ground, collection.

One reason that stand-level vegetation does not explain the observed patterns of abundance as well as landscape-level vegetation may be that data collection protocols for vegetation are mismatched with those used for surveying birds. We reviewed literature that assessed stand-level forest structure in modeling bird habitat and found that it is not uncommon to see a mismatch between the extent at which birds are surveyed and the extent at which vegetation structure is characterized. For example, Mitchell et al. (2001) paired a 50-m radius (0.78-ha) point count for birds with a single point sample of vegetation structure. Canopy closure and canopy height were measured at a single point, and only the five closest trees to the point count station were measured for estimates of basal area and species composition. Similarly, MacFaden and Capen (2002) paired a 50+-m radius point count with a single, variable radius plot. Hagan and Meehan (2002) and Grand and Cushman (2002) paired bird data from fixed-area point counts with forest structure data from much smaller fixed-area plots. In the first example, a 50-m radius point count (0.78-ha) was paired with a 10-m \times 50-m (0.005-ha) vegetation plot (Hagan and Meehan 2002). In the second example, a 1.8-ha point count area (elliptical in shape) was paired with a 100-m \times 6-m (0.06-ha) belt transect (Grand and Cushman 2002).

Sampling is an efficient way to estimate habitat structure and composition across the point count area. However, measuring stand structure at a single point maximizes the risk that that point will not be representative of the habitat used by individuals detected there. This is especially true in a heterogeneous forest that consists of disturbance-originated patches that vary with respect to successional stage,

species composition, and so on (see Seymour et al. 2002). We hypothesize that this mismatch of extent between bird sampling and stand-level vegetation sampling may result in underestimations of the importance of stand level forest structure to species occurrence and habitat suitability.

In this study, we used a hierarchical vegetation sampling design to compare the explanatory power of habitat models built from stand-level forest structure data gathered at three nested extents. We used occupancy models (MacKenzie et al. 2002) to determine habitat characteristics for two neotropical migrant forest songbirds, black-throated blue warbler (*Dendroica caerulescens*) and ovenbird (*Seiurus aurocapillus*). Occupancy modeling enabled estimation of ψ (the probability that a site will be occupied, given the vegetation metrics at a given extent), as well as p (the probability of detecting an animal, given it was present on the site). We compared occupancy models in a priori model sets with Akaike's information criterion (AIC). The AIC model selection approach allowed us to evaluate information from multiple models, rather than a single strongest model alone (Burnham and Anderson 2002). Ovenbird and black-throated blue warbler were chosen as focal species because they have well-established relationships with stand-level habitat attributes that can be easily measured and quantified. Ovenbirds preferentially select deciduous forests with open understories because they forage in leaf litter and nest on the ground (Van Horn and Donovan 1994). Black-throated blue warblers prefer deciduous forests with dense understories because they forage by gleaning lepidopteran larvae off broad leaves and nest in low saplings or shrubs (Holmes 1994).

We tested a series of related predictions: (1) the explanatory power of habitat models will be sensitive to the spatial extent at which stand-level habitat is characterized; (2) models will fit data poorly when vegetation structure is characterized in a 0.2-ha area around each point count station; (3) model fit will improve when vegetation structure is characterized within the intermediate area of 3 ha around each point count station; and (4) models will have the best fit when vegetation structure is characterized in a 12-ha area around each point count station. This area is equivalent to that within which birds were heard and recorded in point counts. We predicted that these models will be the strongest because the habitat within this 12-ha extent is most likely to be visited and defended by the detected birds.

STUDY AREA AND METHODS

Study Area

Our study was conducted in central Vermont, USA. This region is dominated (79%) by forest, with small towns and agricultural land at lower elevations embedded in a forested matrix that extends across the Green Mountains, a northern extension of the Appalachian Range. Forests are dominated by sugar maple (*Acer saccharum*), American beech (*Fagus grandifolia*), and yellow birch (*Betula alleghenensis*), with an important conifer component including white pine (*Pinus strobus*), eastern hemlock (*Tsuga canadensis*), and red spruce (*Picea rubens*). Our study area included only stands that have been unmanaged or minimally managed in the

recent past. Sites with evidence of recent (e.g., within the past 50 years) timber management were excluded.

Study Sites

We conducted bird and vegetation surveys at 20 sites. Sites were selected from a set of points randomly selected from a GIS layer of publicly owned land, providing the vegetation was forested according to LANDSAT imagery from 2002 (UVM Spatial Lab 2005). We restricted the study to the Northern and Southern Green Mountain and Northern and Southern Vermont Piedmont biophysical regions (Thompson 2002) and a 1,000–2,400-ft elevation zone to control for coarse-scale physical factors such as geology and climate, which are hypothesized to affect the composition of avian communities (Thompson and Sorenson 2000). This design nevertheless allowed us to sample across a broad range of northern hardwood, conifer, and mixed hardwood-conifer forest types, while excluding bottomland/floodplain and high elevation forests dominated by different species assemblages (Marchand 1987). We also attempted to control for landscape configuration at our sites. For instance, the 28.44-ha area around all point count stations was at least 90% forested.

Bird Surveys

We located point count locations in the field with a global positioning system. Birds were surveyed under the assumption of population closure, as described by MacKenzie et al. (2002). At each point count station three 10-minute point counts were conducted on the same day between 5:00 am and 12:00 pm during the 2003 or 2004 breeding season. The first two counts were silent, and a playback of chickadee mobbing was played during the third count to potentially increase the detection probability (Gunn et al. 2000, Betts et al. 2005). The radius of point counts was unlimited, and technicians recorded estimated distances to each individual bird. The vast majority of detections were within 200 m of the survey location, which means they were also within the largest area used for forest sampling (12 ha).

Vegetation Surveys

At each study site, we used 0.2-ha forest inventory plots to characterize the forest structure associated with each point count location. We organized plots to sample three concentric circles representing the three spatial extents (0.2, 3, and 12 ha) of interest. The first forest inventory plot was centered at the point count station. This center plot was used to describe habitat structure at the smallest extent (0.2 ha). Thus, the smallest spatial extent (0.2 ha) represented a 100% census, such that estimates of habitat characteristics at that extent contain no sampling variation. At the two larger spatial extents, estimates of habitat characteristics were obtained through sampling. The number of additional sample plots was proportionate to the area in each of the two larger spatial extents. There were a total of four plots for the 3-ha extent and nine plots for the 12-ha extent. We located the second plot (3-ha extent) by walking the appropriate distance from the point count station on a randomly selected

bearing. The remaining seven plots were spaced equally relative to each other. The statistical sample was thus randomized, while the plot dispersion increased the likelihood of capturing spatially variable forest conditions.

We used variable radius prism (2.3 metric basal area factor) plots to inventory forest structure and composition. Species, status (live or dead), and dbh (1.37 m) were recorded for stems >5 cm dbh included in each plot. We estimated vertical shrub density in three vertical tiers using 3-m × 1-m density boards. Saplings were counted by species in a 0.0172-ha fixed area plot. These methods allowed us to estimate mean basal area and understory density to describe the habitat associated with each point count location for each of the three spatial extents.

Our sampling design allowed us to evaluate the relative utility of three different methodological approaches for modeling habitat. The use of proportionate sampling allowed us to hold sampling intensity/density constant, while altering the variable of interest, which was spatial extent. An alternative research question could be: “If we keep the spatial extent constant, what is the effect of sampling density?” However, the answer to that question is well established. If the forest is more homogeneous in structure or composition, few samples are needed to get an unbiased estimate of the mean, whereas if the forest is more heterogeneous, a greater number of samples would be required to get an accurate estimate of the mean. This is a basic sampling problem that has been well researched (see review in Shivers and Borders 1996) but differs fundamentally from the objectives of our study.

Analysis

We used an occupancy model described by MacKenzie et al. (2002) to analyze our data. This likelihood-based method of estimating site occupancy uses detection/nondetection data from multiple sampling occasions to derive site-specific encounter histories.

The occupancy model framework allows for the estimation of two key parameters: the probability that a site will be occupied, which can be a function of the site’s vegetation structure at a selected extent (ψ); and the probability of detection, given an animal is present (p). Both ψ and p can be modeled as functions of covariates within the framework of the occupancy model. Detection probability can increase during playbacks. Thus, we modeled p as equal between the first two sampling occasions, without playbacks ($p_1 = p_2$) and allowed detection probability during playbacks (p_3) to be different. We modeled ψ as a function of habitat covariates.

The encounter history for each site was used to estimate occupancy and detection probability on a site-by-site basis in a multinomial, maximum likelihood framework. For instance, an encounter history “111” indicated that the species of interest was encountered on each of three sampling occasions. An encounter history of “001” means that the species of interest was not detected in the first two sampling occasions, but was detected on the third sampling occasion. With three sampling occasions, there were 2³, or 8, possible encounter histories for each site (111, 110, 101, 011, 001,

100, 010, and 000). The probability of realizing each history is dependent on a combination of probabilities. For example, the probability of realizing a 101 history is $\psi[p(1)] [1 - p(2)] [p(3)]$, where $p(1) = p(2) = p(3)$, or detection probability is constant over time. The probability of realizing a 000 history, $\psi[1 - p(1)] [1 - p(2)] [1 - p(3)] + (1 - \psi)$, is additive, because the site may have been unoccupied, $(1 - \psi)$, or occupied with no detection, $(\psi[1 - p(1)] [1 - p(2)] [1 - p(3)])$. A logistic submodel was substituted for ψ , which reflected a habitat model ($\psi = \exp(Bx)/(1 + \exp(Bx))$).

We chose candidate habitat models based on ovenbird and black-throated blue warbler biology. We chose not to include a model with no covariates because our focal species are known to respond to stand-level forest structure. To avoid overparameterizing our models, we chose the two habitat variables that were most likely to be predictive of occupancy for each species, according to literature about their habitat preferences and biology. The same two variables were used for both species. The first variable, called "understory density" and abbreviated in tables as "understory," described the vertical density of the shrub and low sapling canopy layer and the horizontal density of saplings. Shrub and sapling cover were assumed to be functionally equivalent from the perspective of our focal species. Understory density was calculated as the mean of the z scores of vertical shrub density and horizontal sapling density.

The second variable, called "% BA conifer" and abbreviated in model tables as "conifer," provides a coarse description of species composition at each site. We used the Northeast Ecosystem Management Decision Model (NED-2) (Twery et al. 2005) to calculate the species-specific basal areas based on forest inventory plot data. The variable was calculated as the coniferous basal area divided by the total basal area of live trees at each site, and then rescaled to z scores. We expected occupancy by both species to respond negatively to % BA conifer. We expected ovenbird to respond negatively and black-throated blue warbler to respond positively to understory density.

For each species, we evaluated 10 occupancy models in the program MARK (White and Burnham 1999) and then compared the evidence of each model using the information-theoretic approach (Burnham and Anderson 2002). The model set for each species included models that estimated occupancy as a function of understory density, % BA conifer, and a combination of understory density and % BA conifer at each of three extents (0.2, 3, and 12 ha), as well as a null model that estimated only the probability of occupancy and detection probability (Tables 1–4).

We followed Burnham and Anderson's (2002) guidelines to evaluate the relative strength of models in our model sets using AICc, a version of AIC adjusted for small sample size. Models with lower AICc values were considered more parsimonious. The difference between the AICc of the best model in the set and that of each subsequent model is denoted Δ AICc. Models with Δ AICc of <2 were considered to have substantial support, those with Δ AICc of between 2 and 7 were considered to have considerably less support, and those with Δ AICc >10 were considered to have virtually no support. Finally, we combined the weights

for all models for each species by extent to provide a basis for the overall effectiveness of models using habitat variables characterized at each extent. We calculated the model averaged detection probabilities for each species across all models using the program MARK (White and Burnham 1999). Model averaged results were plotted by extent, with the second covariate set to zero.

As previously stated, 10 models were evaluated for each species. An important assumption of the information theoretic approach is that at least one model adequately fits the observed data. To test this assumption, we tested the fit of the model in which occupancy is a function of understory density and % BA conifer at the 12-ha extent for both bird species: We used the bootstrap test developed by MacKenzie and Bailey (2002) specifically for testing the fit of occupancy models. Fit is considered good for a model as long as the observed χ^2 value is below the 95th percentile of bootstrapped χ^2 values.

Results

Bird Occurrence and Detection Probability

Ovenbirds were detected at 12 of 20 sites. Black-throated blue warblers were detected at 10 of 20 sites. The model averaged detection probability for black-throated blue warbler was 0.38 (95% confidence interval: 0.14–0.68) without playbacks and 0.66 (95% confidence interval: 0.40–0.85) with playbacks. Model averaged ovenbird detection probabilities were 0.54 (95% confidence interval: 0.28–0.77) without playbacks and 0.88 (95% confidence interval: 0.68–0.96) with playbacks.

Habitat

Stands ranged from 1 to 85% coniferous by basal area at the 12-ha (largest) extent (mean = 31.4%, SD = 24.4%). Stands ranged from 0 to 87% coniferous by basal area at the 3-ha extent (mean = 35.2%, SD = 28.4%). Stands ranged from 0 to 100% at the 0.2-ha extent (mean = 31.3%, SD = 37.7%). Average vertical understory cover was 28.1% (SD = 16.1) at the 12-ha extent, 25.35% (SD = 16.3%) at the 3-ha extent, and 20.8% (SD = 21.6%) at the 0.2-ha extent. At the 12-ha extent average sapling density was 2,555 saplings/ha (SD = 1,548), or 1 sapling for every 4 m²; it was 2,331 saplings/ha at the 3-ha extent and 2,195 saplings at the 0.2-ha extent. These SD values indicate high spatial variability within the 12-ha area.

Occupancy Models

Ovenbird

Our most highly parameterized model was well supported by our data, according to a bootstrap goodness-of fit test (MacKenzie and Bailey 2002; model $\chi^2 = 4.58$). The model χ^2 value was in the 76th percentile of χ^2 values from 1,000 bootstrap iterations of simulated site history information, indicating no evidence of lack of fit.

The best supported models in the set were those that predicted ovenbird occupancy as a function of understory density at the larger two extents (12- and 3-ha) (Table 1).

Table 1. Comparison and ranking of ten models (based on AICc) used to relate the probability of ovenbird (*S. aurocapillus*) occupancy to habitat features measured at multiple spatial scales in ($n = 20$) forested study sites in central Vermont, USA 2003–2004

Model	AICc	Δ AICc	Weight	K	Deviance	Evidence ratio	Cumulative weight
Understory 12 ha	68.97	0.00	0.30	4	58.31	1.00	0.30
Understory 3 ha	69.68	0.70	0.21	4	59.01	1.43	0.51
Null model	69.77	0.80	0.20	3	62.27	1.50	0.71
Conifer 12 ha	72.28	3.31	0.06	4	61.62	5.00	0.77
Conifer 0.2 ha	72.53	3.56	0.05	4	61.87	6.00	0.82
Understory 12 ha and conifer 12 ha	72.59	3.62	0.05	5	58.30	6.00	0.87
Conifer 3 ha	72.63	3.66	0.05	4	61.69	6.00	0.92
Understory 0.2 ha	72.67	3.69	0.04	4	62.00	7.50	0.96
Understory 3 ha and conifer 3 ha	73.10	4.13	0.04	5	58.81	7.50	1.00
Understory 0.2 ha and conifer 0.2 ha	75.97	7.00	0.01	5	61.68	30.00	1.01

AICc is Akaike Information Criteria, adjusted for small sample size. The difference between the model with the lowest AICc and each other candidate model (Δ AICc) is reported as a measure of comparison. Weight is the probability that the model is the best model in the set. K is the number of parameters in a model. Deviance is a measure of the current model's ability to explain the field data, compared with a saturated model that fits the data perfectly by design. Evidence ratio is the degree to which the best model is better than any given model. For example, understory 12 ha is 1.43 times more likely to be the best model than understory 3 ha.

Modeling ovenbird occupancy as a function of understory density at the smallest extent was only slightly supported by the data, with a weight of 0.04 (Table 1). For ovenbirds, % conifer was less important than understory structure, but still contributed some information. We base this inference on the fact that the variable “conifer” is included in three models with Δ AICc between 2 and 4, but not in the best two models. The cumulative weights of models at the 12-, 3-, and 0.2-ha extents were 0.41, 0.30, and 0.10, respectively. The null model ranked third with a weight of 0.20 (Table 1).

The effect of understory density on ovenbird occupancy was negative, as expected (Figure 1; Table 3). This trend was sustained at smaller extents but was obscured at the smallest extent where only a single vegetation plot was sampled. This indicates that understory density was not a reliable predictor of occupancy when measured by a single forest inventory plot. In contrast, when habitat was characterized at the 3- and 12-ha extents, a clearer pattern emerged. In summary, models that evaluated understory vegetation at the largest spatial extent were more strongly

supported by the data than models evaluating the understory at the smallest spatial extent, where only a single forest inventory plot was used in the analysis.

Black-Throated Blue Warbler

We ran a bootstrap goodness-of fit test on the model predicting black-throated blue warbler occupancy as a function of % conifer at the 12-ha extent. The model χ^2 value (model $\chi^2 = 9.36$) was in the 94th percentile of χ^2 values from 1,000 bootstrap iterations of simulated site history information, indicating no evidence of lack of fit.

The best supported models for black-throated blue warbler occupancy were those that estimated occupancy as a function of species composition (% BA conifer) at the larger two extents, and other models had considerably less support (Table 2). Understory density was less important than relative conifer abundance in predicting black-throated blue warbler occupancy based on these results. Δ AICc was always >4 for models that predicted black-throated blue

Table 2. Comparison and ranking of 10 models (based on AICc) used to relate the probability of black-throated blue warbler (*D. caerulescens*) occupancy to habitat features measured at multiple spatial scales in ($n = 20$) forested study sites in central Vermont, USA 2003–2004

Model	AICc	Δ AICc	Weight	K	Deviance	Evidence ratio	Cumulative weight
Conifer 12 ha	66.52	0	0.34	4	55.85	1.00	0.34
Conifer 3 ha	66.76	0.24	0.30	4	56.09	1.13	0.64
Conifer 3 ha and understory 3 ha	69.19	2.67	0.09	5	54.90	3.78	0.73
Understory 3 ha	69.55	3.03	0.08	4	58.88	4.25	0.81
Conifer 12 ha and understory 12 ha	69.96	3.44	0.06	5	55.68	5.67	0.87
Conifer 0.2 ha	70.66	4.14	0.04	4	59.99	8.50	0.91
Null model	71.78	5.26	0.02	3	64.28	17.00	0.93
Understory 0.2 ha	71.88	5.36	0.02	4	61.21	17.00	0.95
Understory 12 ha	72.28	5.76	0.02	4	61.61	17.00	0.97
Conifer 0.2 ha and understory 0.2 ha	72.33	5.81	0.02	5	58.04	17.00	0.99

AICc is Akaike Information Criteria, adjusted for small sample size. The difference between the model with the lowest AICc and each other candidate model (Δ AICc) is reported as a measure of comparison. Weight is the probability that the model is the best model in the set. K is the number of parameters in a model. Deviance is a measure of the current model's ability to explain the field data, compared to a saturated model that fits the data perfectly by design. Evidence ratio is the degree to which the best model is better than any given model. For example, conifer 12 ha is 1.13 times more likely to be the best model than conifer 3 ha.

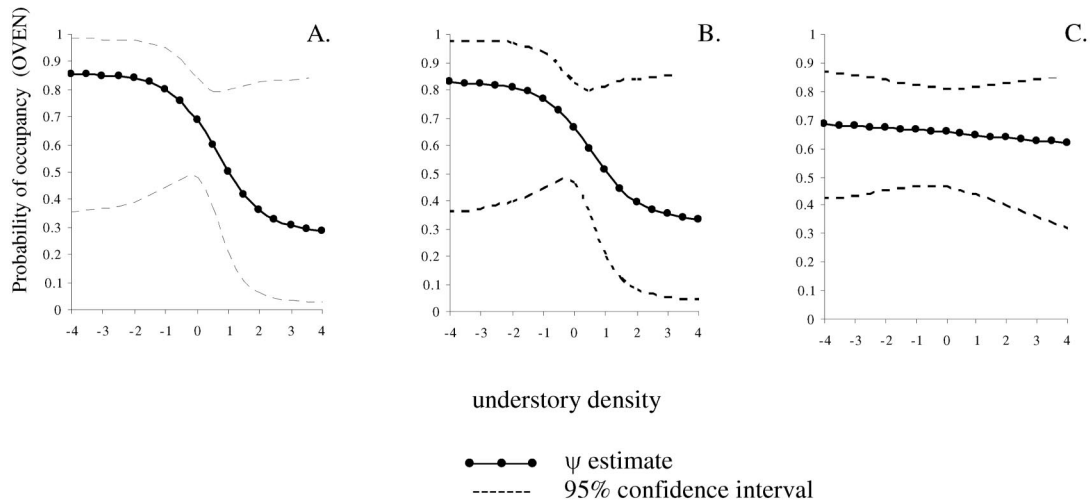


Figure 1. Model averaged prediction plots (and 95% confidence interval) of occupancy models for ovenbirds (*S. auroparillus*) in a mixed northern hardwood-conifer forest in central Vermont, USA, 2003–2004. A–C show the probability of ovenbird occupancy as a function of understory density in 12-, 3-, and 0.2-ha areas surrounding point count stations, respectively. Prediction plots represent the model averaged probability of occupancy from 10 occupancy models based on three 10-minute point counts at each of 20 sites. The effect sizes of all other habitat variables were set to zero.

Table 3. Parameter estimates, including logit link β estimates and SEs, for ovenbird occupancy models based on habitat variables in ($n = 20$) forested study sites in central Vermont, USA

Model	Parameter	β_0 (SE)	β_1 (SE)	β_2 (SE)
Understory 12 ha	$p1 = p2$	1.9849 (0.6290)		
	$p3$	0.1409 (0.5565)		
	ψ	0.8845 (0.5572)	-1.3393 (0.7585)	
Understory 3 ha	$p1 = p2$	1.9817 (0.6299)		
	$p3$	0.1401 (0.5566)		
	ψ	0.7021 (0.5278)	-1.2447 (0.7515)	
Null model	$p1 = p2$	1.9787 (0.6309)		
	$p3$	0.1393 (0.5566)		
	ψ	0.6388 (0.4755)		
Conifer 12 ha	$p1 = p2$	1.9793 (0.6307)		
	$p3$	0.1395 (0.5566)		
	ψ	0.6856 (0.4931)	0.5172 (0.6628)	
Conifer 0.2 ha	$p1 = p2$	1.9787 (0.6310)		
	$p3$	0.1393 (0.5566)		
	ψ	0.6676 (0.4868)	0.2606 (0.4240)	
Understory 12 ha and conifer 12 ha	$p1 = p2$	1.9848 (0.6290)		
	$p3$	0.1409 (0.5565)		
	ψ	0.8855 (0.5581)	-1.3548 (0.8103)	-0.0388 (0.7191)
Conifer 3 ha	$p1 = p2$	1.9784 (0.6310)		
	$p3$	0.1392 (0.5566)		
	ψ	0.6251 (0.4793)	0.2922 (0.5368)	
Understory 0.2 ha	$p1 = p2$	1.9788 (0.6309)		
	$p3$	0.1393 (0.5566)		
	ψ	0.6056 (0.4812)	-0.2175 (0.4177)	
Understory 3 ha and conifer 3 ha	$p1 = p2$	1.9855 (0.6288)		
	$p3$	0.1411 (0.5565)		
	ψ	0.7242 (0.5340)	-1.4155 (0.8436)	-0.2835 (0.6448)
Understory 0.2 ha and conifer 0.2 ha	$p1 = p2$	1.9782 (0.6311)		
	$p3$	0.1392 (0.5566)		
	ψ	0.6362 (0.4922)	-0.1830 (0.4262)	0.2325 (0.4247)

Model parameters are detection probability (p) and probability of occupancy (ψ). Model parameter estimates for are the intercept (β_0) and model effects (β_1 and β_2). Model effects are presented in the order that they appear in the model statement.

warbler occupancy as a function of a habitat attribute at the smallest extent (Table 2). The cumulative weights of models at the 12-, 3-, and 0.2-ha extents were 0.42, 0.47, and 0.08, respectively.

The percent basal area in coniferous trees negatively

affected black-throated blue warbler occupancy (Table 4; Figure 2). The null model ranked seventh, with a weight of 0.02. These results are consistent with previous findings suggesting that this species is more likely to occur in deciduous forests (Holmes 1994). The confidence intervals

Table 4. Parameter estimates, including logit link β estimates and standard errors, for black-throated blue warbler occupancy models based on habitat variables in ($n = 20$) forested study sites in central Vermont, USA

Model	Parameter	β_0 (SE)	β_1 (SE)	β_2 (SE)
Conifer 12 ha	$p1 = p2$	0.6874 (0.5218)		
	$p3$	-0.4886 (0.6485)		
	ψ	-0.0703 (0.6447)	-2.4842 (1.1786)	
Conifer 3 ha	$p1 = p2$	0.6211 (0.5413)		
	$p3$	-0.5250 (0.6522)		
	ψ	0.3097 (0.6958)	-2.0191 (1.0056)	
Conifer 3 ha and understory 3 ha	$p1 = p2$	0.7066 (0.5197)		
	$p3$	-0.4782 (0.6484)		
	ψ	0.3944 (0.6849)	1.2650 (1.1854)	-1.5825 (0.9443)
Understory 3 ha	$p1 = p2$	0.6498 (0.5305)		
	$p3$	-0.5091 (0.6499)		
	ψ	0.2929 (0.6177)	1.8087 (0.9499)	
Conifer 12 ha and understory 12 ha	$p1 = p2$	0.6953 (0.5200)		
	$p3$	-0.4843 (0.6482)		
	ψ	-0.0570 (0.6425)	0.4379 (1.0763)	-2.2784 (1.2326)
Conifer 0.2 ha	$p1 = p2$	0.5553 (0.5645)		
	$p3$	-0.5621 (0.6578)		
	ψ	0.1091 (0.6280)	-0.9919 (0.5898)	
Null model	$p1 = p2$	0.5923 (0.5480)		
	$p3$	-0.5411 (0.6536)		
	ψ	0.1747 (0.5121)		
Understory 0.2 ha	$p1 = p2$	0.5984 (0.5431)		
	$p3$	-0.5376 (0.6524)		
	ψ	0.4255 (0.6621)	0.8817 (0.6244)	
Understory 12 ha	$p1 = p2$	0.6214 (0.5389)		
	$p3$	-0.5248 (0.6516)		
	ψ	0.0853 (0.5472)	1.1308 (0.7931)	
Conifer 0.2 ha and understory 0.2 ha	$p1 = p2$	0.6643 (0.5286)		
	$p3$	-0.5012 (0.6496)		
	ψ	0.2431 (0.6267)	0.7303 (0.5512)	-0.8816 (0.5418)

Model parameters are detection probability (p) and probability of occupancy (ψ). Model parameter estimates for ψ are the intercept (β_0) and model effects (β_1 and β_2). Model effects are presented in the order that they are appear in the model statement.

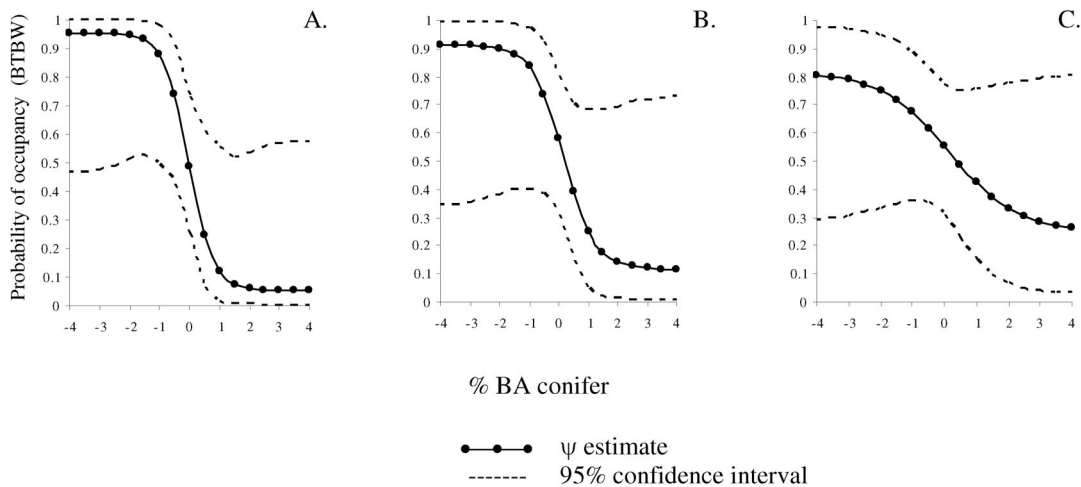


Figure 2. Model averaged prediction plots (and 95% confidence interval) of occupancy models for black-throated blue warblers (*D. caerulescens*) in mixed northern hardwood-conifer forest in central Vermont, USA, 2003–2004. A–C show the probability of black-throated blue warbler occupancy as a function of the percent total basal area in coniferous trees in 12-, 3-, and 0.2-ha areas surrounding point count stations, respectively. Prediction plots represent the model averaged probability of occupancy from 10 occupancy models based on three 10-minute point counts at each of 20 sites. The effect sizes of all other habitat variables were set to zero.

behaved similarly to those in the ovenbird models, where stand-level habitat patterns emerge as the extent in which vegetation is measured increases (Figure 2).

Cumulative Model Weights for Three Extents

Models were strongest overall when a 12-ha area around the point count station was used to characterize habitat

(Tables 1 and 2). Models using the 0.2-ha extent were greatly inferior to those using both larger extents, based on their model weights and ΔAICc values. For both species combined, models that evaluated vegetation at the smallest extent made up 9% of the total model weight. The total weight of 3-ha models was 0.39, and the total weight of 12-ha models was 0.42.

Discussion

Our results demonstrate that stand-level forest structure can be used to predict the occurrence of forest songbirds in northern hardwood-conifer forests. This conclusion, which is consistent with a number of previous studies, such as Brennan and Schnell (2005), Hagan and Meehan (2001), and DeGraaf et al. (1999), is additionally supported by the low ranking of the null model for black-throated blue warbler occupancy. We are less certain about the predictive strength of habitat features for ovenbird occupancy, because the null model for this species ranks among top models. The predictive strength of habitat models for the avian species we evaluated was scale-dependent and improved as local vegetation was measured at larger spatial extents. Models for which habitat covariates described vegetation structure at the smallest extent (0.2 ha, representing the area immediately surrounding a bird point count station) had little or essentially no support. This contrasted with models for which habitat covariates described vegetation structure at 3- and 12-ha extents; these had much greater predictive strength.

The key new finding of this study is that accurate stand-level habitat relationships can only be identified when data are collected at the appropriate extent. We identified an area threshold above which vegetation sampling scope is sufficient to characterize songbird habitat in heterogeneous temperate forest systems. This idea has been discussed conceptually (McGarigal and Marks 1995, Stauffer 2002, Huston 2002, Bisonette 2003) but has not been previously demonstrated with field data.

In studies in which landscape level forest structure was found to be more predictive of bird occurrence than stand-level forest structure (Saab 1999, Mitchell et al. 2001, Grand and Cushman 2003), a mismatch between extent of bird and vegetation sampling may have influenced conclusions. The role of stand-level structure in providing habitat may therefore have been underestimated. This finding has important implications for conservation planning because it means that the structural conditions (e.g., successional or stand development stage) within a forest reserve or land management unit can influence its suitability for different organisms. Regional or landscape scale conservation planning based on assessment of cover type alone, therefore, may be insufficient to capture important habitat relationships occurring at fine scales. Information at both scales, if available, is relevant and desirable based on our results.

Sampling schemes should be appropriate to the scale and pattern of forest patchiness to capture the fullest possible range of forest conditions. Spatial statistics, such as spatial autocorrelation, provide tools for judging the scale of patchiness; these techniques can, in turn, guide sampling regi-

mens for habitat characterization (LeGendre and Fortin 1998). The concept of diminishing returns in model accuracy as sampling extent increases is important for sampling efficiency because stand-level forest structure data at the resolution of individual trees generally needs to be measured on the ground, which is time-consuming and expensive. High-resolution, canopy-penetrating remote sensing technologies, such as light detection and ranging (Hinsley et al. 2002, Goodwin et al. 2006), offer promising, although not widely available, alternatives.

Sampling density did not affect the relative strength of habitat models. The number of plots used to characterize forest structure at the three extents varied from one to nine. At the smallest extent, there was no sampling variance, because only one plot was used, and it represented a 100% census at that extent. Sampling variance was introduced at the two larger extents, as multiple sampling plots were used to characterize the vegetation structure. We used single, unbiased means as independent variables in our models, representing covariate values at each extent for each site. However, given that the number of plots surveyed for local vegetation structure should be greater than one, the optimal number and location of samples remains an interesting question for future work.

Several studies have shown that quantitative habitat descriptions change with the scale of measurement (Gardner et al. 1987, Grand and Mello 2004, Brennan and Schnell 2005). The relative role of differently scaled measures of habitat structure will also depend on the spatial pattern and heterogeneity of a system. Saab (1999) found that the structure of floodplain forests along the Snake River in southeastern Idaho was less important in making predictions about the bird community than the structure of the matrix (or surrounding) habitat. Matrix habitat varied dramatically, ranging from agricultural land use to natural upland vegetation. The dominance of matrix habitat in model selection may be a consequence of structural heterogeneity at that scale. The opposite scenario is plausible depending on study area. For instance, Hagan and Meehan (2002) found that stand-level structure was more important than landscape-level structure in predicting forest songbird occurrence on a managed landscape in Maine. In this case, the landscape was relatively homogeneous (all forest), but stand structure varied considerably between early- and late-successional stands.

Where habitat structure varies at fine scales (i.e., within the stand level), it may be particularly important to measure more than one point sample when one is characterizing habitat for species whose territories are much larger than a typical vegetation plot. The northern hardwood-conifer forests in our study area are characterized by fine-scale heterogeneity as a result of fine-scale variation in soils and topography (Thompson and Sorenson 2000) and disturbance regimens dominated by small-scale events, such as canopy gap formation resulting from the death of one to several trees (Seymour et al. 2002). Territory size ranges from 1 to 4 ha for black-throated blue warblers (Holmes 1994) and from 0.2 to 1.8 ha for ovenbirds (Van Horn and Donovan 1994). That means that an individual of either of these species could be detected in a point count, even when

their territory fails to overlap with the point count station. By increasing the sampling area (extent or “scope”) and density (grain or “intensity”) compared with past studies, we increased the probability of sampling the area that is actually used or selected by detected individuals.

Habitat models developed and applied from coarse-scale, remotely sensed data alone are attractive to scientists and managers because of the availability and relative inexpensiveness of some kinds of remotely sensed information, such as multispectral imagery. Indeed, multiscale models, encompassing scales up to one or several square kilometers, best reflect our understanding of habitat selection as a spatially hierarchical process (Johnson 1980, Robertson et al. 2002, Storch 2003). In accordance with this theoretical framework, our results suggest that the biological basis is weak for excluding stand-level habitat structure from multiscale models. This weakness may be especially true when landscapes are relatively homogeneous at coarse scales but heterogeneous at fine scales. Technology, rather than biology, can drive the trade-off between extent and resolution (Gustafson 1998). Multiscale models that include stand-level structure will offer more accurate alternatives to models based purely on landscape level information whenever fine-grain information is available. GIS-based models provide a coarse filter tool, which should be considered as such and used in conjunction with fine filter tools.

To fine-tune habitat modeling methodologies, more information is needed about the specific scales at which population processes are operational and at which species respond to patterns of habitat structure. Many unanswered questions remain about scale dependencies in habitat selection processes. Specifically, little is known about interactions among spatial extents. There may be a threshold for landscape configuration factors at which coarse-scale habitat structure becomes more important, and nature and strength of stand-level habitat relationships may depend on patterns of habitat structure at higher ordered scales.

Management Implications

Inadequate consideration of stand-level habitat relationships in management planning could have important consequences for biodiversity conservation in northeastern forests. The northern forest region historically was dominated by late-successional and old-growth forests (Lorimer 2001, Lorimer and White 2003). Consequently, it is likely that the fitness of native species adapted to these conditions would increase as the relative abundance of late-successional and old-growth features increases (Aplet and Keeton 1999). Haney and Schaadt’s (1996) findings that territorial density for some neotropical migrants was higher in old-growth (mean territories per 40 ha = 252.2; SE = 38.4) than in younger, managed forest (mean territories per 40 ha = 166.1; SE = 17.8) support this hypothesis.

Because silvicultural practices manipulate stand-structure directly (Franklin et al. 2002), innovative approaches to silviculture could provide opportunities to enhance habitat at local scales (Carey and Curtis 1996, Keeton 2006), when coupled with fine-tuned multiscale habitat models. Because habitat models are among the most widely used tools for

wildlife managers, it is important that they be as accurate as possible. We encourage researchers to include stand-level habitat structure in multiscale models. Furthermore, we recommend considering the biology of study organisms and the scale at which population size, occurrence, and/or relative abundance are estimated when making decisions about the extent and grain of forest sampling for habitat modeling (Stauffer 2002, Huston 2003).

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