

LANDSCAPE EFFECTS ON BREEDING SONGBIRD ABUNDANCE IN MANAGED FORESTS

JEREMY W. LICHSTEIN,^{1,3} THEODORE R. SIMONS,^{1,4} AND KATHLEEN E. FRANZREB²

¹*Cooperative Fish and Wildlife Research Unit, Department of Zoology, North Carolina State University, Raleigh, North Carolina 27695 USA*

²*Southern Appalachian Cooperative Ecosystems Studies Unit, Department of Forestry, Wildlife, and Fisheries, University of Tennessee, Knoxville, Tennessee 37901 USA*

Abstract. We examined the relationship between songbird relative abundance and local and landscape-scale habitat variables in two predominately mid- to late-successional managed National Forests in the southern Appalachian Mountains, USA. We used partial-regression analysis to remove correlations between habitat variables measured at different spatial scales (local habitat and square landscape regions with sides of 0.5, 1, and 2 km) and between landscape composition (proportion of different land cover types) and pattern (spatial arrangement of land cover) variables. To account for spatial autocorrelation, we used autoregressive models that incorporated information on bird abundance in the spatial neighborhood surrounding each sample point. Most species, especially Neotropical migrants, were significantly correlated with at least one landscape variable. These correlations included both composition and pattern variables at 0.5–2 km scales. However, landscape effects explained only a small amount of the variation in bird abundance that could not be explained by local habitat. Our results are consistent with other studies of songbird abundance in large managed forests that have found weak or moderate landscape effects. These studies suggest that songbird abundance in forested landscapes will primarily reflect the quantity of different habitats in the landscape rather than the spatial arrangement of those habitats. Although some studies have suggested consolidating clearcuts in large managed forests to reduce edge and landscape heterogeneity, much of the current evidence does not support this management recommendation. An important future challenge in avian conservation is to better understand how the importance of landscape effects varies in relation to (1) the amount of suitable habitat in the landscape, and (2) land use patterns at broader spatial scales.

Key words: forest fragmentation; landscape composition; landscape pattern; managed forests; Neotropical migrants; partial-regression analysis; songbirds; southern Appalachians; spatial autocorrelation; spatial autoregressive models.

INTRODUCTION

Land transformation is the most prominent component of human-induced global change (Vitousek et al. 1997). An important consequence of land use change is habitat fragmentation, which affects fine-scale ecological processes such as pollination (Aizen and Feinsinger 1994), seed dispersal (Aldrich and Hamrick 1998), and animal movement (Haddad 1999), as well as ecosystem processes such as nutrient cycling (Saunders et al. 1991) and disturbance dynamics (Franklin and Forman 1987). Songbirds (Passeriformes) have served as model organisms in a number of studies investigating the individual, population, and community level consequences of forest fragmentation (e.g., Am-

buel and Temple 1983, Blake and Karr 1987, Temple and Cary 1988, Verboom et al. 1991, Villard et al. 1995, Boulinier et al. 1998, Zanette et al. 2000; reviewed by Rolstad [1991]). Coinciding with the proliferation of songbird/fragmentation studies has been a growing awareness that birds, in general, respond to their environment at multiple spatial scales (Wiens and Rotenberry 1981, Orians and Wittenberger 1991, Pearson 1993). However, the relative importance of different scales (e.g., local vs. landscape) may vary according to the proportion of suitable habitat in the landscape and the regional context (McGarigal and McComb 1995, Flather and Sauer 1996, Donovan et al. 1997, Schmiegelow et al. 1997).

Current dogma in the avian conservation literature suggests that sink populations (Pulliam 1988) of forest-breeding Neotropical migrants in fragmented landscapes are maintained by immigration from source populations in large forests (Robinson 1992, Donovan et al. 1995, Robinson et al. 1995, Simons et al. 2000). Many large forests in North America are managed for timber or other wood products, and proper management

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³Current address: Laboratorio de Investigaciones Ecológicas de las Yungas, C.C. 34, Yerba Buena, (4107) Tucumán, Argentina.

⁴Address correspondence to this author.
E-mail: tsimons@ncsu.edu

of these forests is critical to the conservation of Neotropical migrant songbirds and other forest-dependent species. However, there is currently an inadequate knowledge of the landscape-scale effects of management in large forests to offer sound management recommendations, and conclusions based on studies in highly fragmented (e.g., agricultural) landscapes might not be relevant to more continuous forests (McGarigal and McComb 1995, Hagan et al. 1997).

At the scale of individual forest stands (local scale), management will inevitably improve the habitat for some species and degrade it for others (Annand and Thompson 1997, Hagan et al. 1997). It is less clear whether changes within a given stand will affect habitat use in surrounding stands (landscape scale) in large managed forests. If only local effects are important in determining habitat use, the abundance of different species will simply reflect the availability of different habitats, regardless of how these habitats are arranged in space (Andrén 1994). In contrast, if landscape composition or pattern is important, different spatial arrangements of the same habitats will result in different species abundances. Landscape composition and pattern both depend on the spatial arrangement of habitats, but at different levels of resolution. At a coarse scale, the proportion of each habitat within some predefined area determines landscape composition. Given these proportions, habitat configuration at a finer scale (e.g., patch size, shape, and connectivity) determines landscape pattern. In general, the cost and effort of effective management will be least when local effects predominate and the spatial arrangement of habitats can be ignored, will increase when landscape composition is important and the coarse-scale arrangement of patches must be considered, and will be greatest when landscape pattern matters and habitats must be managed at fine spatial scales. Given the limited resources available to managers, it is important to be able to predict when landscape composition and/or pattern are likely to be important.

Recent studies conducted in large managed forests in Europe (Raivio and Haila 1990, Enoksson et al. 1995, Edenius and Elmberg 1996, Jokimäki and Huhta 1996) and North America (Rosenberg and Raphael 1986, McGarigal and McComb 1995, Hagan et al. 1997, Schmiegelow et al. 1997, Penhollow and Stauffer 2000) suggest that songbird distributions are affected by landscape composition and/or pattern even within relatively unfragmented landscapes. Although landscape effects were not strong in most cases, these studies varied considerably in terms of the type and magnitude of species responses to landscape disturbance or heterogeneity. For example, Rosenberg and Raphael (1986) and McGarigal and McComb (1995) found positive effects of landscape heterogeneity on the abundance of most species that responded to the landscape, Hagan et al. (1997) found the opposite trend, and Jokimäki and Huhta (1996) found that response to land-

scape heterogeneity depended on the species' habitat guild. Unfortunately, failure to experimentally or statistically control for correlations between local and landscape scale habitat variables makes it difficult to compare some of these studies. In addition, although a number of studies have investigated songbird response to landscape effects in large managed forests, few studies have been conducted in any one region. Additional studies are needed to understand how the type and strength of response to landscape effects in managed forests depend on (1) the amount of suitable or preferred habitat in the landscape (Andrén 1994), (2) land cover in the surrounding region (McGarigal and McComb 1995, Flather and Sauer 1996, Schmiegelow et al. 1997), and (3) the life histories of the species involved (Hansen and Urban 1992).

We studied the relationship between bird relative abundance and local habitat, landscape composition, and landscape pattern in two National Forests in the southern Appalachian Mountains of the southeastern United States. While much of the early and highly influential work relating forest fragmentation to songbird abundance was conducted in the deciduous forests of the eastern USA (e.g., Robbins 1979, Whitcomb et al. 1981, Askins and Philbrick 1987, Robbins et al. 1989, Askins et al. 1990), we are aware of only one study (Penhollow and Stauffer 2000) examining landscape effects on songbird abundance in a forested landscape in the eastern deciduous forests. The southern Appalachian region is mostly forested, contains the largest network of federal lands in the eastern USA, and is among the most diverse temperate ecosystems in the world (Southern Appalachian Man and the Biosphere [SAMAB] 1996). Thus, the southern Appalachians are likely to play an important role in maintaining future biodiversity in the eastern USA, and there is a need to better understand the landscape-scale impacts of forest management within this region.

In our analysis, we were particularly concerned with two statistical issues that have received inadequate attention in many previous studies relating bird abundance or presence/absence to landscape composition and pattern: (1) correlations between groups of explanatory variables (e.g., local and landscape variables), and (2) positive spatial autocorrelation, which is the tendency for nearby points in space to be more similar to each other than random pairs of points (Legendre and Fortin 1989).

Correlations among explanatory variables often make it difficult to distinguish between local- and landscape-scale habitat effects or between landscape composition (e.g., amount of forest cover) and landscape pattern (e.g., forest fragmentation) effects. Determining the relative importance of these factors is important for conservation and management, and failure to account for their covariances may lead to incorrect interpretations of ecological data. Correlations among explanatory variables may be avoided through careful

study design (see Pearson [1993] for local vs. landscape, McGarigal and McComb [1995] for landscape composition vs. pattern), but this is often logistically difficult in landscape-scale studies. When groups of explanatory variables are correlated, as they are in most observational studies, correlations may be removed by partial-regression analysis (Legendre and Legendre 1998), although this requires the investigator to make subjective decisions about which variables are most important. McGarigal and McComb (1995), Trzcinski et al. (1999), and Villard et al. (1999) used partial-regression analysis to determine bird response to landscape pattern after controlling for landscape composition. Statistically controlling for correlations between local and landscape variables has received relatively less attention, despite the fact that the problem was articulated in an early study investigating bird community response to forest patch size (Ambuel and Temple 1983). Finally, studies that sample entire landscapes without subsampling at local scales, or that pool local subsamples, can not distinguish between local and landscape effects. One cannot know the effect of habitat at a given scale if only that scale is studied (Saab 1999).

Spatial autocorrelation may also be problematic in many field studies. Despite considerable attention in the ecological literature for over a decade (e.g., Legendre and Fortin 1989, Borcard et al. 1992, Legendre 1993), spatial autocorrelation has been essentially ignored in regression models of species response (Augustin et al. [1996] and Klute et al. [*in press*] are rare exceptions). Positive autocorrelation in a response variable may lead to overestimating the effects of autocorrelated explanatory variables in regression models that assume independent errors (Haining 1990:166, Gumpertz et al. 1997). Autocorrelation in species abundance (or any response variable) is not problematic per se, and is expected when the environment is spatially structured (Legendre 1993). The problem arises in classical statistics when species abundance is autocorrelated due to factors not accounted for by the model, resulting in spatially autocorrelated errors. This situation may result from a statistical problem (e.g., a missing explanatory variable that is itself autocorrelated; Haining 1990:332) or contagious processes (Legendre 1993), such as conspecific attraction (Smith and Peacock 1990), that cannot fully be explained by environmental variables. Some studies attempt to avoid spatial autocorrelation by sampling nonoverlapping landscape regions. However, if the landscape is autocorrelated over a broad spatial scale, the physical separation of samples will not ensure their statistical independence. Furthermore, to the extent that such studies are successful at avoiding autocorrelation, they will not be able to recover the fine-scale structure of species distributions, which may be biologically informative (Sokal and Oden 1978b, Rossi et al. 1992, Legendre 1993).

To address these concerns, we used partial-regres-

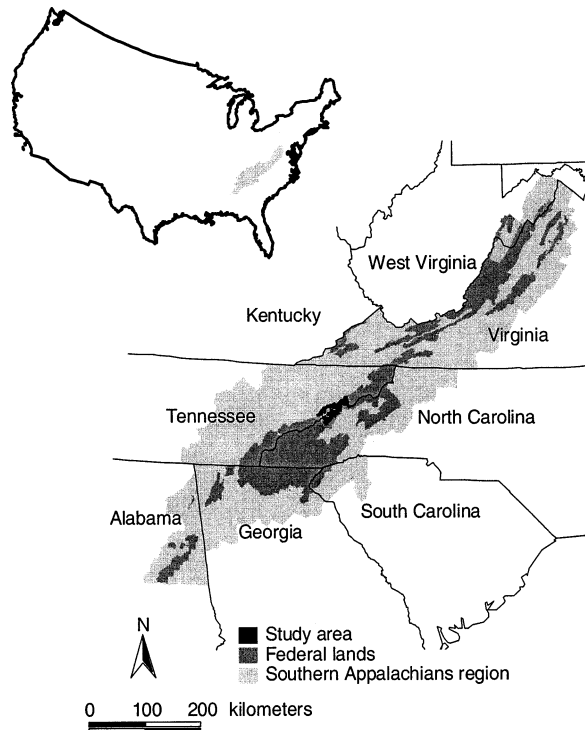


FIG. 1. The southern Appalachians region, defined as the Southern Appalachian Man and the Biosphere (1996) (SAMAB) assessment area. Federal lands constitute 15% of the region. Our study area consists of the French Broad Ranger district of Pisgah National Forest (North Carolina) and the Nolichucky Ranger district of Cherokee National Forest (Tennessee).

sion analysis to remove correlations between local habitat, landscape composition, and landscape pattern variables, and we used spatial autoregressive models (Haining 1990, Cressie 1993) to control for autocorrelation. To determine if results from initial partial regressions (which gave precedence to local habitat effects) were sensitive to the order in which variables were entered in the models, we re-ran the analysis, giving precedence to landscape effects. We believe our modeling approach would be useful for many studies investigating landscape effects on species abundance.

METHODS

Study area

The southern Appalachians region (defined here as the Southern Appalachian Man and the Biosphere [SAMAB] 1996 assessment area) comprises 14.8×10^6 ha from West Virginia and Virginia to northern Alabama and Georgia (Fig. 1). Although regional forest cover, currently 70% (SAMAB 1996), has largely recovered following extensive deforestation in the early 1900s due to industrial logging (Eller 1982, Yarnell 1998), species composition has shifted since preindustrial times as a result of logging, fire suppression (Buckner and Turrill 1999), and introduced species, such as the

chestnut blight (*Endothia parasitica*; SAMAB 1996) and the balsam woolly adelgid (*Adelges piceae*; Rabenold et al. 1998), a homopter pest of high elevation Fraser fir (*Abies fraseri*). Present forest cover is composed primarily of mid- (40–80-yr-old, 50%) and late-successional (>80-yr-old, 20%) forests, with relict stands of old growth (SAMAB 1996). About two thirds of the region's forests are broad-leaved deciduous hardwoods. The 16% of the southern Appalachians in public ownership contains 23% of the region's forests and 63% of the region's late-successional forests (SAMAB 1996). Seventy-five percent of these public lands are under the jurisdiction of the U.S. Forest Service (SAMAB 1996).

Our 60 000-ha study area (35°40'00"–36°07'30" N, 82°37'30"–83°07'30" W) ranged 380–1460 m in elevation and comprised the French Broad Ranger district of Pisgah National Forest (North Carolina, USA) and the Nolichucky Ranger district of Cherokee National Forest (Tennessee, USA) (Fig. 1). Forest cover in the study area, by stand age, is as follows: ≤9 yr, 5%; 10–19 yr, 4%; 20–39 yr, 5%; 40–69 yr, 27%, and ≥70 yr, 59% (Hermann 1996). Most of the younger (<20-yr-old) stands are small (~10 ha) regenerating clearcuts that are scattered throughout the landscape.

The majority of the study area consists of deciduous mesic hardwood forest. Canopy species on mesic sites include (in descending order of importance) *Liriodendron tulipifera*, *Quercus rubra*, *Acer rubrum*, *Betula lenta*, *Tsuga canadensis*, *Magnolia fraseri*, *A. saccharum*, *Fagus grandifolia*, *Aesculus octandra*, *Tilia heterophylla*, and *Betula alleghaniensis*. The understory of mesic forests ranges from woody thickets of *Rhododendron maximum* on acidic soils to a diverse herbaceous assemblage on circumneutral soils (Schafale and Weakley 1990). The remainder of the study area consists of xeric forests, including deciduous hardwoods (*Q. coccinea*, *Q. prinus*, *Q. alba*, and *Oxydendrum arboreum*), evergreen pine (*Pinus rigida*, *P. echinata*, *P. pungens*, and *P. virginiana*), and mixed pine-hardwood forests. *Kalmia latifolia* is the dominant shrub on most xeric sites.

Bird counts

More than 1250 point locations were sampled from mid-May to the end of June in 1997–1999. Prior to analysis, we eliminated points with loud stream noise, heavy cloud cover, or any missing habitat data. This resulted in a data set of 1177 points. Each point was sampled in two of the three years of the study by a total of 22 observers. All observers were trained and field-tested prior to collecting data, and whenever possible (>95% of points) the two counts at each point were conducted by different observers. Observers were regularly rotated to different parts of the study area.

Given the steep topography of our study area, we sampled most points on low-traffic roads (primarily old logging roads) ($n = 570$ points) and hiking trails ($n =$

557 points). We also sampled 50 points along off-road transects (typically three points per transect, 200 m between successive points), so that we could quantify road and trail effects. The location of each point was determined using a global positioning system (GPS) with differential correction (GeoExplorer II, Trimble Navigation, Sunnyvale, California, USA; Trimble Navigation 1996). Nearly every road or trail in the study area longer than one kilometer was sampled, but we avoided sampling parallel roads or trails that were separated by <200 m. On each road or trail, the first point was located by pacing enough 50-m increments to separate the point by 250 m from points on intersecting roads or trails. Additional points were located by pacing 250 m between successive points until the road or trail terminated. If the road or trail was very sinuous, 50 m increments (beyond the initial 250 m) were paced until most or all birds from the previous point were not audible. (Individuals detected at multiple points were recorded only once.) Because the roads we sampled varied in the amount of canopy disturbance, we classified roadside vegetation at each point (see *Methods: Local habitat variables*). In preliminary analyses, we also investigated the importance of road width and the width of the canopy break (if any) above the road as explanatory variables of bird abundance. These variables did not qualitatively affect our results and were omitted from subsequent analyses. Trails were typically <1 m wide without any canopy disturbance caused by the presence of the trail.

Points were sampled for 10 min using the variable circular plot method (Reynolds et al. 1980). Counts were done between sunrise and the hour of 1015 and were not conducted if it was raining. All males seen or heard during the sample period were recorded. Females were recorded only if a conspecific male was not detected at the point, so that only one bird per potential breeding pair was recorded. We recorded if each individual was detected during the first three minutes, next two minutes, and/or last five minutes of the 10-min count. For species with similar male and female vocalizations (e.g., American Crow and Blue Jay; see Table 1 for scientific names), we only recorded every other detection. The horizontal distance from the observer to the initial detection location of each individual was estimated, and subsequent movements were mapped onto data sheets. To improve distance estimates, a circle with 50-m radius was sited by the observer using a laser range-finder (Yardage Pro 400, Bushnell, Overland Park, Kansas, USA) prior to each sample period. Birds flying over the observer were recorded without a distance estimate. Individuals detected at adjacent points were only recorded at the point with the lowest distance estimate.

Local habitat variables

We measured local habitat to (1) control for potentially confounding correlations between local and land-

TABLE 1. Common and scientific names of 25 study species, species codes, habitat guilds, number of individuals observed across two samples at 1177 points, and R^2 values for multiple logistic regression models of singing rates on local and landscape-scale habitat variables.

Common name	Scientific name	Species code	Habitat guild†	Number observed‡	R^2 §
Acadian Flycatcher	<i>Empidonax virescens</i>	ACFL	L	333	...
American Crow	<i>Corvus brachyrhynchos</i>	AMCR	G	836	0.01
Black-and-white Warbler	<i>Mniotilta varia</i>	BAWW	G	677	...
Black-throated Blue Warbler	<i>Dendroica caerulescens</i>	BTBW	L	1313	0.04
Black-throated Green Warbler	<i>Dendroica virens</i>	BTGW	L	1016	0.02
Blue-headed Vireo	<i>Vireo solitarius</i>	BHVI	L	783	0.03
Blue Jay	<i>Cyanocitta cristata</i>	BLJA	G	432	0.04
Canada Warbler	<i>Wilsonia canadensis</i>	CAWA	G	178	0.15
Carolina Chickadee	<i>Poecile carolinensis</i>	CACH	G	429	...
Chestnut-sided Warbler	<i>Dendroica pensylvanica</i>	CSWA	E	677	...
Dark-eyed Junco	<i>Junco hyemalis</i>	DEJU	G	534	0.03
Eastern Towhee	<i>Pipilo erythrophthalmus</i>	ETOW	E	637	...
Eastern Wood-Pewee	<i>Contopus virens</i>	EAWP	G	155	...
Hooded Warbler	<i>Wilsonia citrina</i>	HOWA	G	1176	0.01
Indigo Bunting	<i>Passerina cyanea</i>	INBU	E	859	0.01
Northern Parula	<i>Parula americana</i>	NOPA	L	103	...
Ovenbird	<i>Seiurus aurocapillus</i>	OVEN	L	1903	0.02
Red-eyed Vireo	<i>Vireo olivaceus</i>	REVI	L	2418	...
Rose-breasted Grosbeak	<i>Pheucticus ludovicianus</i>	RBGR	E	160	0.14
Scarlet Tanager	<i>Piranga olivacea</i>	SCTA	L	625	...
Tufted Titmouse	<i>Baeolophus bicolor</i>	TUTM	G	278	...
Veery	<i>Catharus fuscescens</i>	VEER	G	218	...
White-breasted Nuthatch	<i>Sitta carolinensis</i>	WBNU	L	251	...
Wood Thrush	<i>Hylocichla mustelina</i>	WOTH	L	224	0.04
Worm-eating Warbler	<i>Helminthos vermivorus</i>	WEWA	G	288	...

† E, early-successional species; G, generalist; L, late-successional species.

‡ All detections included for American Crow and Blue Jay; detections ≤ 75 m from observer for all other species.§ “Max-rescaled” R^2 in SAS PROC LOGISTIC (Statistical Analysis System 1999) uses the discrete model correction of Nagelkerke (1991), which allows for a maximum R^2 of 1. Empty cells indicate that there were no significant variables in the logistic regression model.

|| Neotropical migrant.

scape variables, and (2) to determine the relative impact of local vs. landscape effects on species abundance. Vegetation at each point was sampled within a circular plot of 10-m radius (Table 2). For points located on roads or trails, the center of the vegetation plot was moved 10 m off the road or trail into the surrounding vegetation. Canopy height, defined as the height of the tallest tree in the plot, was measured with a laser range-finder. Trees were sampled from the center of the plot with a wedge prism (basal area factor 20) (Avery and Burkhart 1983), and each tree counted in the prism (including those outside the 10-m radius plot) was assigned to one of two diameter at breast height (dbh) classes: 0–25 or >25 cm. The percent cover (i.e., percentage of ground surface shaded by foliage) of five vegetation layers (canopy, subcanopy, tall shrub/sapling, low shrub/seedling, and herbaceous) was visually estimated and assigned to one of 10 cover classes (%): <0.1, 0.1–1, 1–2, 2–5, 5–10, 10–25, 25–50, 50–75, 75–95, and >95. For the canopy, subcanopy, and tall-shrub/sapling layers, we calculated the percent cover of all plant species by multiplying each species’ percentage contribution to the layer (visually estimated) by the midpoint of the layer’s cover class. “Importance values” for each species within each plot were then calculated as follows:

Importance value

$$= \Sigma(\text{percent cover in canopy, subcanopy, and tall-shrub layers}) \\ + 10(\text{no. stems counted in wedge prism}).$$

The mean of the summed canopy, subcanopy, and tall-shrub cover class midpoints for all species combined was 130.9% per point, and the mean number of wedge prism stems was 4.7. Thus, our importance values are weighted primarily by foliage cover, and somewhat less so by stems, which sometimes included species poorly represented by the cover data (e.g., large diameter trees whose canopies were outside the plot). Moisture values for each vegetation plot were calculated as a weighted average of importance values, where the weights were moisture values assigned to each plant species (generally following Whittaker [1956]).

To quantify gradients in plant species composition, vegetation plots were ordinated by nonmetric multidimensional scaling (NMDS) using PC-ORD (version 3.18, MjM Software, Gleneden Beach, Oregon, USA; McCune and Mefford 1997). Nonmetric multidimensional scaling uses an iterative algorithm to position plots in a fixed number of dimensions so that the rank order of distances between all pairs of points in the

TABLE 2. Habitat variables used in regression models.

Variable code	Variable definition
Local habitat	
ELEV	Elevation
ELEV ²	(Elevation) ²
MOIST	Site moisture value based on weighted average of plant species moisture values. Low values, xeric; high values, mesic
MOIST ²	(Site moisture value) ²
TOPO (4)	Topographic position (ravine, flat, slope, or ridge)
EDGE (6)	Edge category (sapling/sapling, sapling/pole, sapling/saw, pole/pole, pole/saw, or saw/saw)
RD/TR/OFF (3)	Point located on road, trail, or off-road
RDVEG (3)	Road bordered by <i>Rubus</i> , other shrub species, or no shrubs
CAN	Percent canopy cover
SUBCAN	Percent subcanopy cover
TALLSH	Percent tall shrub/sapling cover
LOWSH	Percent low shrub/seedling cover
HERB	Percent herbaceous cover
DBH>25	Number of >25-cm dbh trees in wedge prism sample
MAXHT	Height of tallest tree
NMDS1	Nonmetric multidimensional scaling (NMDS) axis 1: <i>A. rubra</i> and <i>A. saccharum</i> (negative axis 1 scores) to <i>Q. coccinea</i> (positive scores)
NMDS2	NMDS axis 2: <i>L. tulipifera</i> (negative axis 2 scores)
NMDS3	NMDS axis 3: <i>T. canadensis</i> and <i>R. maximum</i> (negative axis 3 scores) to <i>Q. prinus</i> (positive scores)
Landscape composition	
LCAGE1	≤9-yr-old forest
LCAGE2	10–19-yr-old forest
LCAGE3	20–39-yr-old forest
LCAGE4	40–69-yr-old forest
LCAGE5	≥70-yr-old forest
LCMESIC≥40	≥40-yr-old mesic hardwood forest
LCHARD	Hardwood (mesic and xeric combined)
LCDIV	Shannon diversity index for stand age classes (LCAGE1–5)
Landscape pattern	
LPCORE	Core area: ≥40-yr-old forest, 100-m buffer
LPCWE	Contrast-weighted edge
LPNUMPA	Number of patches
LPMSI	Mean shape index = (patch perimeter)/(√patch area); averaged for all patches

Notes: For categorical variables, the number of categories is given in parentheses. Landscape variables (both cover and pattern measures) were quantified within square regions at three different scales (500-m sides = 25 ha, 1-km sides = 100 ha, and 2-km sides = 400 ha) centered on each sample location.

ordination space corresponds as closely as possible to the rank order of their species compositional differences (Minchin 1987, Legendre and Legendre 1998: 444). We used the Bray-Curtis coefficient (Legendre and Legendre 1998:287), as recommended by Minchin (1987), to calculate compositional differences between plots in terms of plant species importance values. We ran the ordination 10 times to ensure that our results were not sensitive to the initial random configuration of the plots (Legendre and Legendre 1998:446). Studies with simulated plant communities (e.g., Minchin 1987, Wentworth and Ulrey 2000) have shown that NMDS consistently recovers known data structures more effectively than other ordination methods, such as principal component and detrended correspondence analysis, which make unrealistic assumptions about the shape of plant species response curves along environmental gradients (Minchin 1987). Unlike other ordination methods, where the percentage of variation ex-

plained by each axis suggests the number of retained axes, the appropriate number of dimensions for an NMDS ordination is the number beyond which there is a minimal decrease in “stress,” which quantifies the lack of fit between ordination distances and species compositional differences (Legendre and Legendre 1998:448). In our analysis, the stress sequence was 51.2, 27.3, 21.2, 16.7, and 15.5 as the number of dimensions increased from one to five; we selected a three-dimensional solution. Because NMDS axes are arbitrary (Legendre and Legendre 1998:445), a varimax rotation (Johnson and Wichern 1982:426, Legendre and Legendre 1998:478) was used to help interpret the ordination axes. The varimax rotation maximizes the variance of species correlations with the ordination axes, resulting in groups of species with very high and very low axis correlations. Plots with positive scores (positions) along a given axis tend to have high importance values for plant species that are positively

correlated with that axis. The three rotated NMDS axes (Table 2), representing gradients in plant species composition, were used as explanatory variables in subsequent models of bird relative abundance.

In addition to the above vegetation plot variables, several additional local variables were recorded at each sample point (Table 2): (1) Stands were assigned to one of three age classes (sapling \approx 0–10 yr, pole \approx 10–40 yr, or saw timber $>$ 40 yr) for both sides of the road or trail, resulting in six different edge categories (sapling/sapling, sapling/pole, sapling/saw, pole/pole, pole/saw, and saw/saw) that grossly described the habitat within a $>$ 75-m radius of each point. (2) Because shrubby vegetation growing along roadsides, particularly *Rubus* spp., provides quality nesting habitat for some early-successional birds in our study area (J. W. Lichstein, T. R. Simons, and K. E. Franzreb, *unpublished data*), roadside vegetation was designated as *Rubus*, other, or none. (3) The topographic position at each point was designated as ravine, flat, slope, or ridge. (4) Elevation was queried from a digital elevation model (DEM) (Hermann 1996).

Landscape variables

We quantified landscape composition and pattern surrounding each sample location at three spatial scales: 25, 100, and 400 ha, corresponding to squares with sides of 500 m, 1 km, and 2 km, respectively. We quantified variables that described landscape composition in terms of stand age and broad community type (e.g., hardwood vs. pine/mixed), and landscape pattern in terms of the spatial arrangement of different stand ages (e.g., edge length and contrast). Previous studies indicate that these types of variables might be important in explaining bird abundance patterns in large managed forests (e.g., McGarigal and McComb 1995, Penhollow and Stauffer 2000). Landscape variables were calculated from land cover data in the Southern Appalachian Assessment GIS Data Base (Hermann 1996), which includes polygon coverages of forest stands (digitized from 1:24 000 scale aerial photographs) within all National Forests in the Southern Appalachian Assessment area (SAMAB 1996). Although this GIS database was compiled several years prior to our study, there was almost no logging in our study area during or several years prior to our fieldwork. The few sample points that were affected by logging during the study were excluded from our analysis. We reclassified the stands in the GIS database into categories appropriate for our analysis and converted the polygon coverages into the following raster (grid) coverages (cell size = 10×10 m) using ARC/INFO (version 7.2.1; Environmental Systems Research Institute 1998): (1) stand age (five classes; Table 2); (2) hardwood vs. pine/mixed; (3) \geq 40-yr-old mesic hardwood; and (4) core area (\geq 40-yr-old forest located \geq 100 m from younger forest and \geq 100 m from non-National Forest land). Although we did not have land cover data for non-National Forest

TABLE 3. Weights used to calculate the landscape variable "contrast-weighted edge."

Stand age class (yr)	Stand age class (yr)				
	0–10	10–19	20–39	40–69	\geq 70
0–10	0	0.2	0.4	1.0	1.0
10–19		0	0.2	0.7	0.7
20–39			0	0.2	0.3
40–69				0	0
\geq 70					0

Note: Weights define the contrast across an edge between two different stand age classes.

lands, they tended to be more disturbed (e.g., open pasture or early-successional forest) than adjacent National Forest (J. W. Lichstein and T. R. Simons, *personal observations*). We used a large (100-m) buffer when calculating core area to minimize the correlation between core area and other landscape variables that involved \geq 40-yr-old forest. We cut three square regions (sides = 500 m, 1 km, and 2 km), centered on each of the 1177 sample points, from each of the four grids using ARC/INFO. All landscape variables used in our analysis were quantified within these squares using PATCH ANALYST (Elkie et al. 1999), an extension to ARC/VIEW (version 3.2; Environmental Systems Research Institute 1999).

We considered landscape composition variables to be those variables that could be calculated solely from the proportion of different patch types within each square, without any information on how the patches were spatially arranged. We calculated eight composition variables (Table 2): amount of forest in each of five stand age classes, amount of hardwood, amount of \geq 40-yr-old mesic hardwood, and the Shannon Diversity Index (based on the proportions of the five age classes).

We defined landscape pattern variables to be those variables that could only be calculated if the spatial arrangement of patches within each square was known. We calculated four pattern measures (Table 2), with patches defined by stand age class: amount of core area, contrast-weighted edge, number of patches, and mean shape index (a measure of mean patch boundary complexity). Contrast-weighted edge was calculated by weighting the length of each edge segment according to the contrast in stand age across the edge (Table 3).

Detectability

Detectability (the probability that a present bird is detected) (Buckland et al. 1993) may be confounded with habitat, obscuring patterns in bird abundance. We conducted two separate analyses to examine how detectability differed across habitats with respect to (1) distance between individual birds and the observer, and (2) individual singing rates, which may vary with pairing status (Best 1981). In the first analysis, we used program DISTANCE (version 3.5; Thomas et al. 1998)

to estimate effective detection radii for each bird species in six different types of edge habitat and four different topographic positions (see EDGE and TOPO, Table 2). Based on field observations, we believe that these two variables had the greatest impact on detectability with respect to distance. Eliminating all observations with distance estimates >75 m (including flyovers) resulted in similar effective detection radii, within each bird species, across the six edge and four topographic classes, indicating that within-species detectability was roughly equal in these different habitats for birds located ≤ 75 m from the observer. We did not perform this analysis for American Crow and Blue Jay because most detections for these species were flyovers. In all subsequent analyses, we included all detections for American Crow and Blue Jay, and only detections ≤ 75 m from the observer for all other species.

To examine how singing rates varied with respect to habitat, we used data from different time intervals within the 10-min counts to determine if each individual was detected during the first five minutes and/or the last five minutes. (Nearly all detections were aural.) Each individual was classified as being detected in (1) only one of the five-minute intervals (relatively low singing rate), or (2) during both intervals (relatively high singing rate). We used logistic regression (Hosmer and Lemeshow 1989) to model, for each of the 25 species, the probability that individuals were detected during both five-minute intervals as a function of the same local and landscape variables used in bird abundance models. We used stepwise selection in SAS PROC LOGISTIC (version 8; Statistical Analysis System 1999), with significance levels for variables to enter and stay in models set at $\alpha = 0.20$ and 0.01 , respectively.

Bird relative abundance models

Many of the explanatory variables were correlated with each other, and some of the variation in bird abundance could be explained by multiple factors. Therefore, we structured our analysis according to an a priori ranking of parsimony. Because bird species composition in our study area sometimes differs substantially over short distances (<100 m) with changes in local vegetation (J. W. Lichstein and T. R. Simons, *personal observations*), we viewed local habitat to be the most parsimonious explanation for spatial variation in species abundance. After local habitat, we ranked landscape composition as the next-most parsimonious explanation for bird abundance, and landscape pattern the least parsimonious (e.g., Trzcinski et al. 1999). Among the three landscape scales considered, we viewed the smallest scale (500 m) to be the most parsimonious explanation for patterns in bird abundance, and the largest scale (2 km) to be the least parsimonious. Giving precedence to local over landscape variables may seem counterintuitive if one considers habitat selection

by migratory birds to be a hierarchical process (e.g., Hutto 1985), in which individuals select habitats at broad geographical scales and then at increasingly finer scales. Therefore, we reanalyzed our data, giving precedence to landscape variables (see *Results*), to determine if our qualitative conclusions were sensitive to the way we structured the analysis.

We fit models for 25 species, including the 23 species most frequently present at point counts (within 75 m of the observer), as well as two common avian nest predators: American Crow and Blue Jay. Based on field observations and prior to analysis, we classified the 25 species as early-successional, generalist (with respect to stand age), or late-successional (Table 1; see Hamel [1992], Hunter et al. [1993], and Franzreb and Phillips [1996] for habitat preferences of the species in our study area). For each species, the response variable was the square root of the counts summed across the two samples at each of the 1177 point locations. The square-root transformation is a natural transformation for count data, which often have a Poisson distribution (Sokal and Rohlf 1995). In preliminary analyses, our results were not qualitatively affected by different transformations (e.g., logarithmic).

Ordinary least-squares (OLS) models.—We began by fitting ordinary least-squares (OLS) multiple regression models with only local habitat variables. We included quadratic terms for elevation and moisture (Table 2), because we expected some species to have nonlinear responses to these variables. Variables were selected using stepwise selection in SAS PROC REG (Statistical Analysis System 1999). Significance levels for variables to enter and stay in models were $\alpha = 0.20$ and 0.01 , respectively. Categorical variables were coded as zero/one dummy variables and were automatically included in preliminary models. After running the stepwise procedure in PROC REG, we further examined the models in PROC GLM (Statistical Analysis System 1999), which accepts categorical variables, and we removed by hand most variables with $P > 0.001$. We used a conservative α level because our large sample size allowed us to detect habitat effects that explained only a trivial amount of variation in the bird data, and because the sample points were not spatially independent.

Having determined a local habitat model for each species, we then used stepwise selection to add sets of landscape variables in the following order: 500-m composition, 500-m pattern, 1-km composition, 1-km pattern, 2-km composition, and 2-km pattern. At each stage in the analysis, we regressed the next set of variables on all variables previously included in the model for each species, and we used the residuals from these regressions as explanatory variables (e.g., McGarigal and McComb 1995, Trzcinski et al. 1999, Villard et al. 1999) in the stepwise procedure. This partial-regression approach removes correlations between successive sets

of variables, giving precedence to variables previously included in models.

Based on a priori knowledge of habitat use, we restricted the variable selection process to decrease the likelihood of observing spurious correlations. For early-successional species (Table 1), MAXHT, LCAGE3, LCAGE4, LCAGE5, LCMESIC ≥ 40 , and LPCORE were excluded from the selection procedure. RDVEG was included only for early-successional species. For late-successional species (Table 1), LCAGE1, LCAGE2, and LCAGE3 were excluded from the selection procedure. For species that nest and forage primarily in the sapling, subcanopy, and canopy layers (Black-throated Green Warbler, Blue-headed Vireo, Carolina Chickadee, Northern Parula, Red-eyed Vireo, Tufted Titmouse, Scarlet Tanager, and White-breasted Nuthatch), LOWSH and HERB were excluded.

Partial R^2 values were calculated for four groups of habitat variables: (1) elevation and elevation squared, (2) all other local habitat variables combined, (3) all local variables combined (including elevation and elevation squared), and (4) all landscape variables combined. Each partial R^2 was calculated as the difference in R^2 between the full model (which contained all significant variables) and a reduced model (which lacked one of the above groups of variables).

Conditional autoregressive (CAR) models.—To determine if spatial autocorrelation was problematic in our data, we examined Moran's I correlograms (Sokal and Oden 1978a, Legendre and Legendre 1998) of OLS model residuals. Although spatial pattern in residuals does not necessarily reflect the pattern in the true errors (Brownie and Gumpertz 1997), the two patterns should be very similar for large sample sizes (M. L. Gumpertz, *personal communication*; $n = 1177$ in this study).

For species with autocorrelated OLS residuals, we fit conditional autoregressive (CAR) models with Gaussian errors (Haining 1990, Cressie 1993, Lichstein et al. 2002) using the same response (square-root transformed counts) and explanatory variables as in the OLS models. The CAR model assumes that the response at each location i is a function of both the explanatory variables at i (which determine the mean response at i), as well as the values of the response at locations j within the spatial neighborhood of i . An appropriate spatial neighborhood size (radius) is the maximum distance at which OLS residuals are autocorrelated (Cressie 1993). This distance may be estimated by examining a correlogram or semivariogram of the OLS residuals (Cressie 1993). For the CAR model, the conditional expectation (E) of the response at i , given the responses at all other locations j (denoted "[all $Y_{j \neq i}$ " below), is:

$$E[Y_i | \text{all } Y_{j \neq i}] = \mu_i + \rho \sum_{j \neq i} w_{ij}(Y_j - \mu_j)$$

where μ_i is the mean at i (determined by the values of the explanatory variables and their slope coefficients),

ρ is a parameter to be estimated that determines the sign and magnitude of the spatial neighborhood influence, the w_{ij} are predefined weights that determine the relative impact of each location j on i (in our analysis, the w_{ij} are zero if j is not within the neighborhood of i and take on the respective values $(1/\text{distance}_{ij})$ otherwise), and the $Y_j - \mu_j$ are mean-centered responses at j . For positive autocorrelation ($\rho > 0$), if i is surrounded by locations j that have higher (or lower) species abundance than expected from the habitat at j , then i will also tend to have higher (or lower) abundance than expected from the habitat at i .

The significance of each variable in CAR models was assessed with a likelihood ratio test (LR) for nested models (Haining 1990, Hilborn and Mangel 1997):

$$\text{LR} = -2(l_{\text{red}} - l_{\text{full}})$$

where l_{red} and l_{full} are the log-likelihoods of the reduced and full models, respectively, and LR has an approximate χ^2 distribution. R^2 values for CAR models were calculated as follows (Nagelkerke 1991):

$$R^2 = 1 - \exp[-2/n(l_A - l_0)]$$

where n is the sample size, l_A is the log-likelihood of the model of interest (i.e., the alternative hypothesis), and l_0 is the log-likelihood of the null model containing only an intercept (which fits the mean response and ignores autocorrelation). For OLS models, this R^2 yields the identical value as the traditional R^2 . As with the OLS models, partial R^2 values for groups of habitat variables in the CAR models were calculated as the difference in R^2 between the appropriate full and reduced CAR models. We calculated partial R^2 values for ρ (i.e., the improvement in model fit due to including autocorrelation) as the difference between CAR and OLS model R^2 values. Finally, we calculated total R^2 values for ρ (i.e., the proportion of variation in the response that can be explained by autocorrelation alone), where l_A was the log-likelihood of a model containing only an intercept and ρ . All spatial analyses were performed with S-PLUS (Kaluzny et al. 1998, Mathsoft 1999). Detailed instructions for fitting CAR models and computing correlograms in S-PLUS are provided in a supplement to Lichstein et al. (2002: Supplementary Material).

RESULTS

Heterogeneity of sampled landscapes

Despite the high proportion of ≥ 40 -yr-old forest in our study area, our sample points were located in a range of landscape conditions. Younger (< 20 -yr-old) forest comprised $\geq 30\%$ of the landscape in 500×500 m squares surrounding 152 points, and $\geq 40\%$ of the landscape surrounding 73 points (Fig. 2).

Singing rates

Singing rates did not vary with respect to any local or landscape variables for 12 of the 25 species (Table

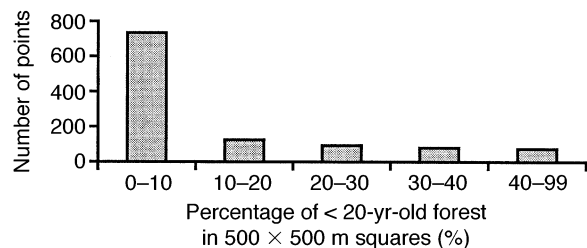


FIG. 2. Heterogeneity of sampled landscapes in terms of the percentage of <20-yr-old forest within 500 × 500 m squares centered on 1177 sample points. Land cover data are from Hermann (1996).

1). Of the remaining species, only two (Rose-breasted Grosbeak and Canada Warbler) had model R^2 values >5%.

Ordinary least-squares models

Ordinary least-squares (OLS) models accounted for 3–47% of the variation in the counts of the 25 species considered (Table 4). After controlling for local habitat variation, 16 species were correlated with at least one landscape variable in OLS models, with $P \leq 0.001$ in most cases (results not shown). Despite this large number of statistically significant correlations, landscape variables explained only a small amount of the variation in the counts after controlling for local habitat effects, with partial R^2 values for the combined effect of landscape composition and pattern ranging 0.5–8% (Fig. 3). Although OLS total model R^2 values were low for many species (Table 4), elevation and other local habitat variables tended to explain much more of the variation in the counts than landscape variables (Fig. 3).

Correlograms

With the exception of Carolina Chickadee, correlograms of OLS residuals showed positive spatial autocorrelation for all 25 species examined, suggesting that the OLS assumption of independent errors was violated. The range (maximum lag distance) of autocorrelation was typically ≤ 500 m (19 species), but was >2 km for Veery (Fig. 4). These distances were used as the neighborhood radii in subsequent conditional autoregressive (CAR) models, except for the Veery CAR model, in which a 900-m neighborhood radius performed better than larger radii in terms of removing positive autocorrelation in the residuals.

For all 24 species (no CAR model was fit for Carolina Chickadee), CAR models removed all, or nearly all, of the positive autocorrelation in the OLS residuals. For seven species, CAR models overcompensated for positive autocorrelation in OLS residuals, resulting in CAR residuals with mild negative autocorrelation (e.g., Eastern Wood-Pewee; Fig. 4), which tends to make significance tests for explanatory variables conservative (Haining 1990). Correlograms demonstrating the

variety of spatial patterns observed in OLS and CAR residuals are shown in Fig. 4.

Conditional autoregressive (CAR) models

The total amount of variation in the species data explained by CAR models ranged 6–52% (CAR total R^2 values; Table 4), representing improvements of 1–11% over OLS models (ρ partial R^2 values; Table 4). These improvements in model fit (due to including the spatial parameter ρ) were significant for all 24 species ($P \leq 0.0001$ for 23 species; $P = 0.0013$ for Worm-eating Warbler). As expected, the parameter estimate for ρ was positive for all 24 species. Conditional autoregressive models without any habitat variables (i.e., models with only two parameters: an intercept and ρ) explained 3–26% of the variation in the counts for the 24 species (ρ total R^2 values; Table 4). Partial R^2 values for ρ were smaller than the corresponding values for ρ total R^2 because the habitat variables explained some of the spatial pattern in the species data; thus there was less autocorrelation to account for when habitat variables were included in the models.

As with OLS models, CAR partial R^2 values for landscape variables tended to be small compared to R^2 values for elevation and other local habitat variables (Fig. 3). The largest partial R^2 value for landscape effects in CAR models was 4.5% (Chestnut-sided Warbler; Fig. 3A). Values of R^2 for all variable types tended to be lower in CAR models than in OLS models (Fig. 3). This reduction in R^2 values is due to the fact that some of the variation explained by the habitat variables in the OLS models was spatially structured on a fine scale (hundreds of meters), and this spatial structure was accounted for by ρ and the associated spatial neighborhood effect in the CAR models.

Fifteen landscape variables that were significant in OLS models ($P \leq 0.001$ in most cases) were not significant ($P > 0.01$) in CAR models (see bold variables in Table 4). After controlling for local habitat, 15 species were significantly ($P \leq 0.01$) correlated with one or more landscape composition variables in CAR models, and, after controlling for local habitat and landscape composition, six species were significantly correlated with one or more landscape pattern variables (Table 4). After controlling for habitat effects at finer scales, 12 species were significantly correlated with one or more 500-m scale landscape variables in CAR models, six species were correlated with one or more 1-km scale landscape variables, and seven species were correlated with one or more 2-km scale landscape variables (Table 4). Among Neotropical migrants, 15 of 18 species were significantly correlated with one or more landscape variables in CAR models, whereas only three of seven residents and short-distance migrants combined were correlated with landscape variables.

Landscape-only models

These CAR models determine landscape effects on bird relative abundance after controlling for local hab-

TABLE 4. Conditional spatial autoregressive (CAR) models for 25 species at 1177 sample points; see Table 1 for species codes and Table 2 for habitat variables.

Species code	$R^2_{\text{total OLS}} \dagger$	Neighbor radius (m) \ddagger	CAR parameter estimates and significance levels	LC§	LP§	500 m§	1 km§	2 km§	$R^2_{\text{partial } \rho }$	$R^2_{\text{total } \rho }$	$R^2_{\text{total CAR}} \# \dagger \ddagger$
CSWA	0.47	750	EDGE*** (0.66 sapling/sapling + 0.26 sapling/pole + 0.47 sapling/saw + 0.08 pole/saw - 0.11 saw/saw), RDVEG*** (0.51 <i>Rubus</i> + 0.07 other), + 0.17 LCAGE1.5h*** + 0.17 ELEV*** + 0.08 LCAGE2.5h*** + 0.06 HERB*** + 0.04 LOWSH* + 0.05 LPCWE_2k	×	...	×	0.05	0.25	0.52
ETOW	0.34	300	EDGE*** (0.66 sapling/sapling + 0.42 sapling/pole + 0.51 sapling/saw - 0.07 pole/saw - 0.09 saw/saw), + 0.13 LCAGE1.5h***, RD/TR/OFF*** (0.32 road + 0.18 trail), + 0.08 ELEV***, RDVEG** (0.20 <i>Rubus</i> + 0.12 other), + 0.07 LCAGE2.5h** - 0.05 SUBCAN* + 0.05 LOWSH* - 0.09 LCAGE1.1k* + 0.06 LCDIV_1k*	×	...	×	×	...	0.01	0.10	0.35
BTGW	0.27	400	-0.23 ELEV*** - 0.11 ELEV2*** + 0.12 MOIST*** + 0.10 MAXHT*** + 0.10 LCMESIC \geq 40.5h*** - 0.12 LCAGE5.2k*** + 0.11 LCME-SIC \geq 40.2k** + 0.06 LCAGE4.5h*	×	...	×	...	×	0.04	0.15	0.31
AMCR	0.07	750	-0.08 ELEV** - 0.08 LPCORE_5h** + 0.06 LCAGE3.5h* + 0.07 LCDIV_1k* - 0.08 LPCORE_1k + 0.07 LPCWE_2k	×	×	×	×	...	0.04	0.08	0.12
RBGR	0.15	500	0.08 ELEV*** + 0.06 LCA-GE2.5h***, RDVEG*** (0.12 <i>Rubus</i> - 0.00 other), + 0.04 LCA-GE1.5h**, EDGE** (-0.05 sapling/sapling - 0.02 sapling/pole + 0.10 sapling/saw + 0.04 pole/saw - 0.05 saw/saw)	×	...	×	0.06	0.12	0.21
HOWA	0.22	300	RD/TR/OFF*** (0.23 road - 0.07 trail), - 0.12 ELEV*** - 0.09 ELEV2***, EDGE*** (0.22 sapling/sapling + 0.13 sapling/pole + 0.30 sapling/saw - 0.10 pole/saw + 0.01 saw/saw), + 0.07 LOWSH** - 0.08 LPCORE_5h** + 0.07 LCME-SIC \geq 40.5h* + 0.06 LCDIV* + 0.05 TALLSH* + 0.06 LCAGE2.2k*	×	×	×	...	×	0.03	0.10	0.24
BTBW	0.36	750	0.35 ELEV*** + 0.18 MAXHT*** - 0.11 ELEV2*** + 0.11 LCME-SIC \geq 40.5h*** - 0.08 NMDS3***, TOPO*** (0.28 ravine + 0.43 flat + 0.09 slope)	×	...	×	0.08	0.26	0.44
EAWP	0.13	500	0.08 ELEV*** + 0.06 MAXHT*** + 0.05 LCAGE2.1k**, RD/TR/OFF* (0.16 road + 0.09 trail), + 0.03 LCAGE3.1k* - 0.04 LCHARD_1k* - 0.03 LPCORE_5h* + 0.03 NMDS3 , TOPO (-0.09 ravine - 0.08 flat - 0.01 slope), EDGE (0.18 sapling/sapling + 0.02 sapling/pole - 0.01 sapling/saw + 0.03 pole/saw + 0.02 saw/saw)	×	×	×	×	...	0.02	0.07	0.15
REVI	0.16	500	-0.13 ELEV2*** + 0.09 MAXHT*** + 0.09 LPCWE_1k*** + 0.12 LPCWE_2k* - 0.06 NMDS1*, RD/TR/OFF* (-0.04 road - 0.19 trail), TOPO (-0.12 ravine - 0.06 flat + 0.02 slope)	...	×	...	×	×	0.05	0.12	0.20

TABLE 4. Continued.

Species code	R^2_{total} OLS†	Neighbor radius (m)‡	CAR parameter estimates and significance levels	LC§	LP§	500 m§	1 km§	2 km§	R^2_{partial} $\rho_{ }$	R^2_{total} $\rho_{ }$	R^2_{total} CAR#††
INBU	0.32	500	EDGE*** (0.59 sapling/sapling + 0.40 sapling/pole + 0.27 sapling/saw – 0.05 pole/saw – 0.16 saw/saw), + 0.09 HERB***, TOPO*** (–0.26 ravine – 0.23 flat – 0.11 slope), RDVEG*** (0.24 <i>Rubus</i> + 0.07 other), + 0.08 LCAGE2.5h*** + 0.08 LCAGE1.5h** – 0.07 NMDS1**, RD/TR/OFF** (0.33 road + 0.20 trail), – 0.05 SUBCAN*	×	...	×	0.05	0.15	0.36
ACFL	0.31	500	TOPO*** (0.31 ravine + 0.41 flat + 0.02 slope), – 0.12 ELEV*** – 0.09 NMDS3*** + 0.06 MAXHT*** + 0.05 LCME-SIC≥40.5h** – 0.04 NMDS2** + 0.05 LCAGE4.5h*	×	...	×	0.04	0.13	0.35
VEER	0.25	900	0.15 ELEV*** + 0.06 ELEV2*** – 0.06 LCAGE2.2k* – 0.03 NMDS3* – 0.04 LCAGE2.1k* + 0.03 LCA-GE1.2k	×	×	×	0.10	0.24	0.35
NOPA	0.06	500	0.04 LCAGE4.5h*** – 0.04 ELEV** – 0.03 NMDS3**, RD/TR/OFF (–0.01 road – 0.06 trail), – 0.02 NMDS2	×	...	×	0.08	0.10	0.15
OVEN	0.14	900	–0.16 ELEV2*** + 0.11 CAN*** – 0.10 LCHARD.2k***, TOPO** (–0.26 ravine – 0.20 flat – 0.06 slope), + 0.07 ELEV*	×	×	0.08	0.13	0.22
BHVI	0.06	500	EDGE*** (–0.13 sapling/sapling – 0.16 sapling/pole – 0.07 sapling/saw + 0.09 pole/saw + 0.17 saw/saw), + 0.09 ELEV*** + 0.05 LPCORE.5h* – 0.06 LPCWE.2k	...	×	×	0.03	0.04	0.09
BLJA	0.03	500	–0.06 LCAGE4.2k** – 0.05 MOIST*, EDGE (0.10 sapling/sapling – 0.00 sapling/pole – 0.11 sapling/saw – 0.15 pole/saw – 0.08 saw/saw)	×	×	0.03	0.03	0.06
BAWW	0.08	300	–0.12 ELEV2***, TOPO* (0.07 ravine – 0.04 flat + 0.15 slope), + 0.06 LPCWE.1k* + 0.05 NMDS2*	...	×	...	×	...	0.02	0.04	0.10
CAWA	0.17	500	0.11 ELEV*** – 0.05 NMDS3*** + 0.05 ELEV2*** + 0.04 NMDS1*** – 0.04 LCAGE2.2k* + 0.03 LOWSH*, TOPO* (0.12 ravine + 0.02 flat + 0.04 slope)	×	×	0.11	0.18	0.27
WOTH	0.03	400	–0.04 NMDS2** – 0.03 ELEV ² – 0.03 MOIST ² + 0.03 LCME-SIC≥40.5h	0.05	0.06	0.08
CACH	0.05	NA	–0.12 ELEV***	NA	NA	NA
DEJU	0.20	300	0.23 ELEV*** + 0.08 ELEV2***, RD/TR/OFF* (0.09 road – 0.03 trail)	0.01	0.07	0.21
SCTA	0.04	300	–0.06 ELEV2**, TOPO* (–0.16 ravine – 0.21 flat – 0.02 slope), RD/TR/OFF (– road – 0.12 trail)	0.03	0.04	0.07
TUTM	0.05	300	–0.06 ELEV***, RD/TR/OFF*** (–0.02 road – 0.13 trail), –0.04 CAN* – 0.03 NMDS2*	0.02	0.03	0.07
WEWA	0.11	300	–0.14 ELEV***, EDGE * (0.06 sapling/sapling + 0.19 sapling/pole + 0.03 sapling/saw + 0.11 pole/saw – 0.00 saw/saw), + 0.03 NMDS2	0.01	0.04	0.12
WBNU	0.04	500	RD/TR/OFF*** (–0.14 road – 0.24 trail), + 0.05 MAXHT**, TOPO* (–0.16 ravine – 0.10 flat – 0.06 slope)	0.03	0.04	0.07

TABLE 4. Continued.

Notes: Species are listed in decreasing order of landscape partial R^2 values in CAR models (Fig. 3A). Variables in CAR models are listed in decreasing order of significance. Equations for CAR parameter estimates and significance levels are characterized as follows: A single significance level is reported for categorical variables (offset by commas); parameter estimates for the levels within categorical variables (offset by parentheses) are relative to "ridge" for TOPO, to "pole/pole" for EDGE, to "off-road" for RD/TR/OFF, and to "no shrubs" for RDVEG. The suffixes "_5h," "_1k," and "_2k" denote landscape scales of 500 m, 1 km, and 2 km, respectively. Landscape variables that were significant in ordinary least-squares (OLS) models ($P \leq 0.001$ in most cases), but not significant in CAR models ($P > 0.01$), appear in bold.

* $P \leq 0.01$, ** $P \leq 0.001$, *** $P \leq 0.0001$.

† " $R^2_{\text{total OLS}}$ " values are overall R^2 values for ordinary least-squares models in which correlations between local habitat, landscape composition, and landscape pattern were successively removed by partial-regression analysis.

‡ "Neighbor radius," as judged from correlograms of OLS residuals, is the distance beyond which locations had no effect on each other in CAR models.

§ The symbol "×" appears in columns LC, LP, 500 m, 1 km, and 2 km for CAR models with at least one significant landscape composition, landscape pattern, 500-m scale landscape (composition or pattern), 1-km landscape, and 2-km landscape variable, respectively. If no respective significant variable exists, ellipses (···) appear.

|| " $R^2_{\text{partial } \rho}$ " (partial R^2 for the spatial parameter ρ) is the improvement in R^2 of CAR models over OLS models.

¶ " $R^2_{\text{total } \rho}$ " values are R^2 values for CAR models containing only an intercept and ρ . $R^2_{\text{total } \rho}$ measures how much variability in species abundance can be explained by autocorrelation alone, without any habitat variables.

" $R^2_{\text{total CAR}}$ " values are R^2 values for CAR models containing both ρ and the habitat variables in the equations.

†† $R^2_{\text{total CAR}} = R^2_{\text{total OLS}} + R^2_{\text{partial } \rho}$; due to rounding errors, numbers in the table do not always fulfill this equality.

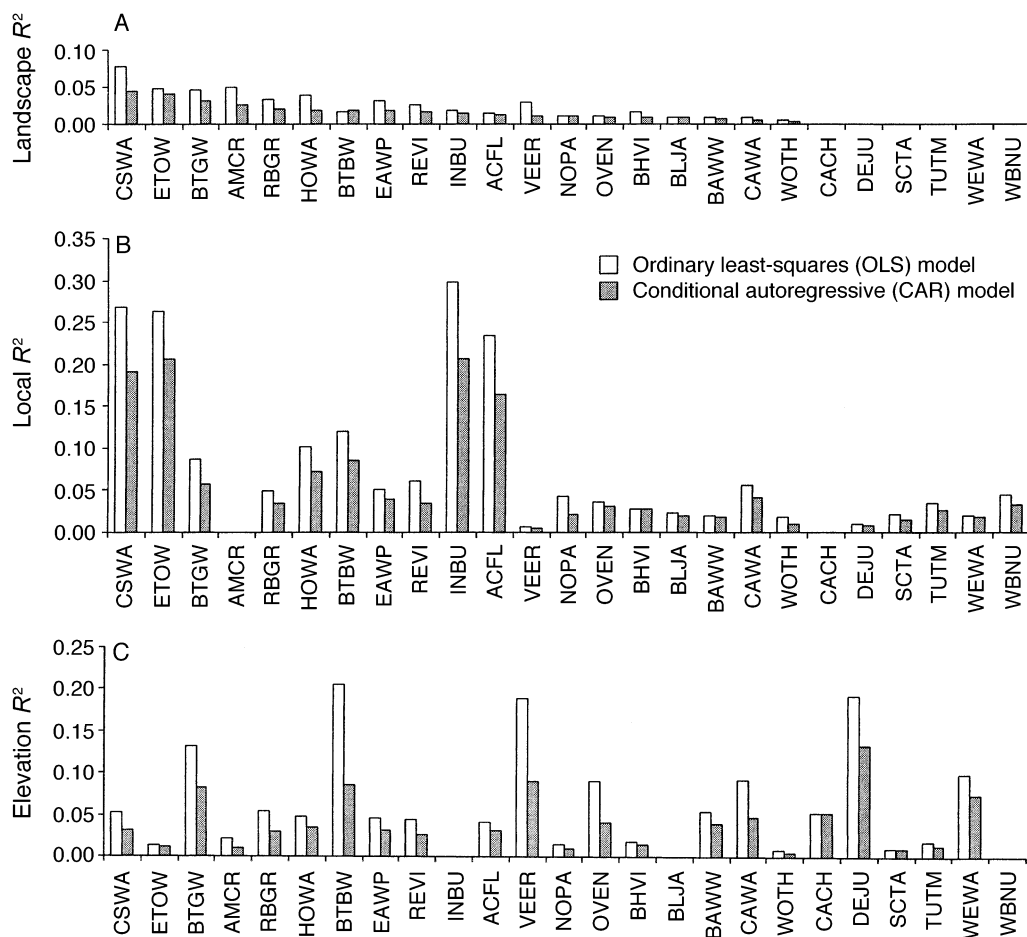


FIG. 3. Partial R^2 values for (A) all landscape composition and pattern variables combined after controlling for local habitat, (B) all local variables excluding elevation (ELEV and ELEV²) after controlling for elevation, and (C) elevation after controlling for other local variables. Landscape variables were regressed on local variables (including elevation) before being added to bird abundance models. Species are listed in order of decreasing landscape sensitivity, defined as the partial R^2 for landscape variables in CAR models. Species codes are as in Table 1.

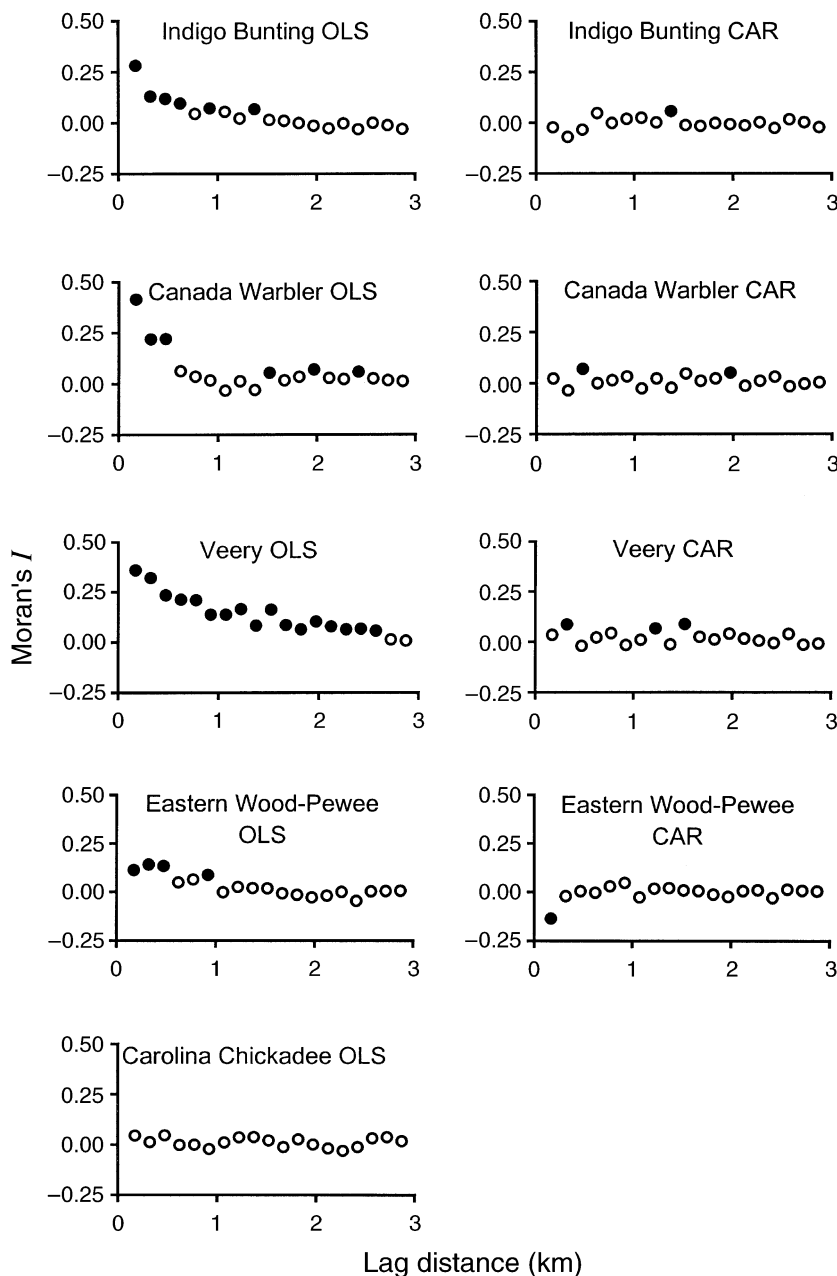


FIG. 4. Moran's I correlograms (Sokal and Oden 1978a, Legendre and Legendre 1998) of residuals from ordinary least-squares (OLS; left) and conditional autoregressive (CAR; right) models for selected species. Moran's I varies from approximately -1 to 1 , with negative and positive values indicating negative and positive autocorrelation, respectively. When there is no spatial pattern in the data, Moran's I is close to zero for large sample sizes ($n = 1177$ here). The lag distance (x -axis) is the midpoint of the distance class within which all possible pairs of points are used to calculate Moran's I . All lag distance classes contained >1000 pairs of points, giving high power to detect values of Moran's I that were significantly different from the value expected under the null hypothesis of no spatial autocorrelation (two-sided randomization test, 1000 permutations). Closed circles indicate that Moran's I is significantly different ($P \leq 0.01$) from null expectation. Open circles indicate that Moran's I is not significantly different from null expectation. Ordinary least-squares residuals for Carolina Chickadee were not autocorrelated, so a CAR model was not fit.

itat and spatial autocorrelation, and are thus conservative with respect to landscape effects. Therefore, we fit OLS models with only landscape variables to determine the maximum amount of variation in the bird

data that could be explained by the landscape. For each species, landscape variables were added in the order described above (*Methods: Bird relative abundance models: Ordinary least-squares (OLS) models*). As be-

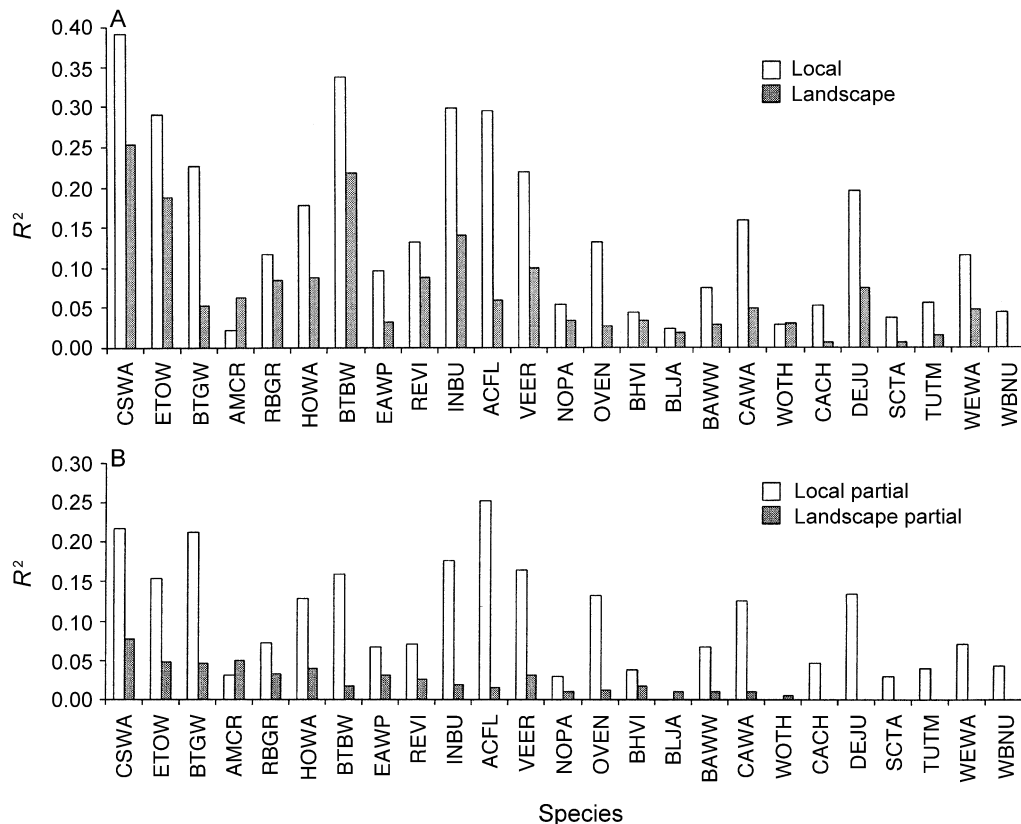


FIG. 5. (A) R^2 values for ordinary least-squares (OLS) models containing only local habitat variables (including ELEV and ELEV²) vs. only landscape variables (landscape composition and pattern combined). (B) R^2 values for OLS models showing the partial effect of local variables (after controlling for landscape variation) vs. the partial effect of landscape variables (after controlling for local variation). Species are listed in order of decreasing landscape effects in conditional autoregressive (CAR) models (Fig. 3A). Species codes are as in Table 1.

fore, each new set of landscape variables was regressed on previously included landscape variables, and the residuals were used as explanatory variables.

Values of R^2 from OLS landscape-only models (Fig. 5A) were higher than landscape partial R^2 values from OLS and CAR models that controlled for local habitat (Fig. 3A). Nevertheless, for most species, R^2 values from OLS landscape-only models were considerably lower than those from OLS models containing only local variables (Fig. 5A). Of the four species with the highest landscape-only R^2 values, three were early-successional species (Chestnut-sided Warbler, Eastern Towhee, and Indigo Bunting) (Fig. 5A).

Partial effect of local variables

Finally, to determine how much of the variation in bird relative abundance could be explained by local habitat after controlling for landscape variation, we added local habitat variables to OLS landscape-only models using stepwise selection as described above (*Methods: Bird relative abundance models: Ordinary least-squares (OLS) models*). For most species, the partial effect of local variables (after controlling for land-

scape variation) was greater than the partial effect of landscape variables (after controlling for local variation; Fig. 5B).

DISCUSSION

Landscape effects

Our results suggest that landscape effects are less important than local factors in determining songbird species abundance in our primarily mid- to late-successional study area. After controlling for local habitat variation, landscape variables explained only a small amount of the variation in the species data (Fig. 5B). In contrast, after controlling for landscape variation, local variables explained a much greater amount of the variation in species abundance (Fig. 5B). When local and landscape variables were considered in isolation of each other, local variables showed stronger effects (Fig. 5A).

Although landscape effects do not appear to be of primary importance in our study area, the abundance of most species was significantly correlated with at least one landscape variable. Our conditional autoregressive (CAR) models were conservative with respect

to landscape effects. These models only considered the partial effect of landscape variables after controlling for local habitat effects and spatial autocorrelation. For some species, CAR models overcompensated for positive autocorrelation in ordinary least-squares (OLS) residuals, resulting in inflated *P* values (Haining 1990). However, negative autocorrelation in CAR residuals was less pronounced than was positive autocorrelation in OLS residuals, and incorporating space into our analysis improved the models overall. Due to the conservative nature of the analysis, it is doubtful that the landscape effects we report in CAR models are spurious. Interestingly, Neotropical migrants, which are thought to be particularly sensitive to forest fragmentation in the eastern United States (Whitcomb et al. 1981), were more frequently correlated with landscape variables in CAR models (15 of 18 species) than were short-distance migrants and resident species (three of seven species). Landscape effects were not limited to composition effects or to the smallest (500-m) landscape scale, but included numerous landscape pattern and larger scale (1- and 2-km) effects. Nevertheless, our results suggest that local habitat is more important than landscape-scale factors in explaining the abundance of most species we considered.

Our results are consistent with other studies in large managed forests that reported only weak landscape effects on songbird abundance (Rosenberg and Raphael 1986, Keller and Anderson 1992, Edenius and Elmberg 1996, Schmiegelow et al. 1997). In contrast, other studies in large forests have reported moderate (McGarigal and McComb 1995, Jokimäki and Huhta 1996, Hagan et al. 1997, Penhollow and Stauffer 2000) or strong (Enoksson et al. 1995) landscape effects. Unfortunately, it is difficult to determine if the importance of landscape effects varied consistently in these studies with respect to forest cover at landscape or regional scales because (1) some of the studies mentioned here did not control for local habitat variation when testing for landscape effects, and (2) some of these studies did not report forest cover data in their study area and/or in the surrounding region. Nevertheless, there is no obvious difference in forest cover at landscape or regional scales between studies that reported weak vs. moderate landscape effects. For example, among studies reporting weak landscape effects, mature forest comprised 50–100% of the sites sampled by Keller and Anderson (1992) and 45% of the study area in Edenius and Elmberg (1996); among studies reporting moderate landscape effects, mature forest comprised 61% of the study area in Jokimäki and Huhta (1996), 50–60% in Hagan et al. (1997), and 66% in Penhollow and Stauffer (2000). Only one study that we are aware of (Enoksson et al. 1995) reported strong landscape effects in a forested landscape. Interestingly, the preferred habitat in that study (deciduous forest) comprised <5% of the sampled landscapes (Enoksson et al. 1995: Table 1).

In addition to this set of studies, two other studies

conducted in large managed forests are relevant to the present investigation. Thompson et al. (1992) compared bird relative abundance between landscapes in which 20% or 0% of the forest had been recently clear-cut. After controlling for the amount of older forest, six species were more abundant in cut landscapes, and one species was more abundant in uncut landscapes. In a similar study, Welsh and Healy (1993) compared landscapes in which 35% and 4% of the forest had been recently cut. Bird diversity and overall abundance were higher in the more disturbed landscapes. After controlling for the area of older forest, no species was more abundant in the less disturbed landscapes. Although these studies did not explicitly test for landscape effects, both suggest that landscape disturbance had little or no negative impact on bird abundance, and that disturbance benefited many species, some of which are considered forest interior breeders (Thompson et al. 1992).

Several studies in large forests that examined landscape effects also found positive effects of disturbance for most species that responded to the landscape (Rosenberg and Raphael 1986, McGarigal and McComb 1995; but see Jokimäki and Huhta [1996]). It is important to point out, however, that it is not necessarily desirable to manage for maximum species diversity or abundance at the landscape scale (Welsh and Healy 1993). The availability of different seral stages in the surrounding region and the habitat requirements of landscape-sensitive species should be considered when making landscape-scale management decisions. In the southern Appalachians region, for example, early-successional forest is more common and late-successional forest is more rare on private compared to public lands (Southern Appalachian Man and the Biosphere 1996). Therefore, species dependent on late-successional forest should be given special consideration when devising management plans for public lands in the southern Appalachians.

In the present study, several late-successional species (Black-throated Blue Warbler, Acadian Flycatcher, Northern Parula, and Blue-headed Vireo) were positively correlated with the amount of older forest in the landscape (Table 4), implying a negative effect of landscape disturbance. Early-successional species (Chestnut-sided Warbler, Eastern Towhee, Rose-breasted Grosbeak, Indigo Bunting) tended to be most strongly correlated with the amount of younger forest in the landscape, implying a positive effect of disturbance. Red-eyed Vireo (a late-successional species) and Black-and-white Warbler (a generalist) were positively correlated with edge density at the landscape scale, suggesting a preference for heterogeneous landscapes containing a mix of stand ages (Table 4). To the extent that landscape effects matter in our study, the species we considered exhibited diverse landscape responses. Any management decision will positively affect some species and adversely affect others (Hagan et al. 1997),

and management aimed at particular species should consider community-wide impacts.

Based on properties of simulated landscapes and a review of studies investigating patch size and isolation effects, Andrén (1994) concluded that landscape effects should arise when the proportion of suitable habitat in the landscape drops below 10–30%. Above that threshold, species abundances should simply reflect the amount of available habitat; i.e., local habitat effects should dominate. However, despite the rarity of early-successional forest in our study area (≤ 9 -yr-old forest occupies 5% of study area), early-successional birds did not respond strongly to the amount of early-successional forest in the landscape after we controlled for local habitat (Fig. 3A). Similarly, Rudnický and Hunter (1993a) also observed little effect of clearcut size on the abundance of early-successional bird species. In contrast to early-successional forest, mid- to late-successional forest comprised $>80\%$ of our study area, and this may explain why late-successional species responded only weakly to the landscape. Nevertheless, several late-successional species in our study were significantly correlated with the amount of older forest in the landscape after we controlled for local habitat. Other studies conducted in landscapes containing $>50\%$ mature forest (e.g., Jokimäki and Huhta 1996, Hagan et al. 1997, Schmiegelow et al. 1997) also reported negative effects of landscape disturbance on late-successional songbirds. The above results suggest that the threshold at which landscape effects arise may differ for early- and late-successional songbirds, and that Andrén's (1994) prediction of a 10–30% threshold does not apply to all species. Early-successional species may be adapted to locate and utilize small patches of isolated habitat. In contrast, late-successional species may be adapted to breeding in continuous forests and may be more sensitive to landscape-scale effects. For both early- and late-successional species, sensitivity to reductions in the amount of their preferred habitat will likely depend on the characteristics of the surrounding landscape matrix (Andrén 1994, Andrén et al. 1997).

In addition to determining the relative importance of local vs. landscape effects, another goal of our analysis was to determine the relative importance of landscape composition vs. pattern. Among studies conducted in forested landscapes, McGarigal and McComb (1995) concluded that landscape composition was more important than landscape pattern, although a number of species were significantly correlated with pattern measures after controlling for the effects of composition. Hagan et al. (1997) and Penhollow and Stauffer (2000) also observed a number of correlations with both landscape composition and pattern measures, but these authors did not control for correlations between the two types of variables. Several studies conducted in fragmented landscapes have attempted to isolate the effects of landscape composition and pattern on songbird dis-

tributions. After controlling for the amount of forest cover in the landscape, Villard et al. (1999) concluded that forest fragmentation adversely affected some species. However, in a similar analysis, Trzcinski et al. (1999) concluded that fragmentation had little effect beyond that explained by forest cover. Based on simulation studies, Fahrig (1997, 1998) concluded that fragmentation, independent of habitat loss, would affect population extinction only under a narrow set of conditions. In the present study, 15 species were significantly correlated with landscape composition variables, but only six species were correlated with pattern measures after controlling for composition. Our results are in accordance with the above studies: landscape composition appears to be more important than landscape pattern in explaining songbird distributions, but some species do respond to the spatial arrangement of patches in the landscape.

Management implications

Our results have important management implications. Some authors have recommended consolidating clearcuts into fewer, larger cuts to decrease edge and heterogeneity in forested landscapes (e.g., King et al. 1996, Hagan et al. 1997). Our results do not support this recommendation. The weak landscape effects reported in our study and others (Rosenberg and Raphael 1986, Keller and Anderson 1992, Edenius and Elmberg 1996, Schmiegelow et al. 1997) suggest that in many managed forests, songbird species abundances will primarily reflect the total availability of different habitats and will only weakly reflect how those habitats are arranged in space. In addition, several studies in forested landscapes (Rosenberg and Raphael 1986, Thompson et al. 1992, Welsh and Healy 1993, McGarigal and McComb 1995) reported many positive and few negative effects of landscape heterogeneity on species abundances. Thus, consolidating clearcuts to reduce landscape heterogeneity may result in more negative than positive effects on songbird abundance. In addition, large clearcuts may be difficult for species with poor dispersal ability, such as some forest herbs (Meier et al. 1995, Pearson et al. 1998), to recolonize following disturbance. In intensively managed landscapes with a low proportion of mature forest, it may be beneficial to consolidate clearcuts to avoid fragmenting what little mature forest remains. However, studies of songbird abundance in more heavily forested landscapes do not support this management strategy. Evidence regarding the landscape-scale effects of management on songbird nesting success in large forests is conflicted (see *Discussion: Limitations*) and currently inadequate to make broad management recommendations. Given the modest landscape effects on songbird abundance observed in most studies conducted in forested landscapes, and the fact that studies in both forested and fragmented landscapes have generally shown landscape composition to be more im-

portant than landscape pattern, we suggest that managers in heavily forested areas would benefit songbird conservation most by managing for habitats that are rare in the surrounding region and acquiring additional land rather than devoting their resources to constructing particular landscape configurations.

Limitations

Our study has two primary limitations. First, bird counts may be poor indicators of habitat quality (Van Horne 1983), particularly in fragmented landscapes where forest birds typically have low nesting success (Braun and Robinson 1996). Several studies reported that clear-cutting does not reduce nesting success in large managed forests (DeGraaf 1995, Hanski et al. 1996), while other studies found negative effects of logging (Yahner and Scott 1988, King et al. 1998) or reported mixed results (Rudnicki and Hunter 1993b). Nest-monitoring data from our study area indicate that nesting success is high enough (40–50% nest survival rate; Mayfield 1975) to sustain viable populations of the three species for which we have sufficient data (Black-throated Blue, Chestnut-sided, and Hooded Warblers; J. W. Lichstein, T. R. Simons, K. C. Weeks, and K. E. Franzreb, *unpublished data*). However, we do not know if nesting success varies across our study area in relation to landscape characteristics.

Second, there was a large amount of unexplained variation in our models, and several factors likely contributed to this. Some breeding pairs were probably undetected, and some of the birds we did detect may have been nonterritorial floaters or unpaired males. However, singing rates were very weakly correlated with local and landscape variables for nearly all species (Table 1), which suggests that pairing success (within species) was similar throughout our study area (Best 1981, Gibbs and Faaborg 1990). Thus, while inaccurate counts of breeding pairs may have introduced noise into our models of bird abundance, there was probably no systematic bias in terms of detecting or failing to detect habitat effects.

Other likely sources of noise in our models concern our habitat data. Many local variables were measured within plots of 10-m radius, which may be too small an area to describe the vegetation in a songbird territory. In addition, some of our points were located along edges between different-aged stands, but vegetation plots were located only in the older stand. To compensate for the lack of vegetation data in the younger stand, we included edge type in our models and assumed that this categorical variable would adequately describe the relatively simple structure of early-successional habitats. While this assumption may not have been valid, the lack of vegetation data from the younger stands did not seem to strongly affect our results: our models were generally more successful for early-successional than for late-successional species. Nevertheless, the limited scale of our local habitat data un-

doubtedly contributed to the unexplained variation in our models. Finally, while we could measure landscape variables over a range of scales, we had no control over the quality of the original land cover data, which was derived from a regional geographic information system (GIS) database (Hermann 1996). Thus, both local and landscape data introduced noise into our analysis, but we do not believe that this noise biased our qualitative conclusion that local habitat is more important than landscape effects in our study area.

Statistical considerations

In our analysis, we sought to address two statistical issues relevant to many studies investigating landscape effects on species response: (1) correlations between local and landscape variables, and between landscape composition and pattern variables; and (2) spatial autocorrelation. Failure to control for local habitat variation, either in the design or analysis stages, makes it difficult to evaluate the magnitude of landscape effects in many published studies. We used partial-regression analysis to separate local and landscape scale effects, and to separate the effects of landscape composition and pattern (e.g., McGarigal and McComb 1995, Trzcinski et al. 1999, Villard et al. 1999). Because results from partial-regression analysis depend on the order in which variables are entered in the model, we compared models where local variables were entered first to models where landscape variables were entered first (Fig. 5). This approach is advisable when a priori reasoning cannot determine which group of variables should be given precedence.

We accounted for spatial autocorrelation in our habitat models to reduce the risk of observing spurious correlations (Haining 1990). Accounting for spatial autocorrelation in large-scale field studies is particularly important, because true replication at the landscape scale is expensive and logistically difficult. In this study, landscape regions centered on adjacent sample locations overlapped considerably, ensuring that landscape variables would be autocorrelated. However, even nonoverlapping landscape regions will be spatially autocorrelated if land cover is autocorrelated over a broad spatial scale. Spatial autocorrelation in explanatory variables is not necessarily problematic in ordinary least-squares (OLS) regression, which assumes independent errors but makes no assumptions about autocorrelation in the response or explanatory variables. It is true that the errors will frequently not be independent if both the response and explanatory variables are autocorrelated (Gumpertz et al. 1997), but this is not necessarily the case. When there is a strong relationship between the response and explanatory variables, all of the spatial pattern in the response may be explained, and the stochastic variation at each sample location may be free to vary independently. In our study, most landscape variables were autocorrelated out to several kilometers (Lichstein 2000), but corre-

lograms of OLS residuals suggest that points need be separated by only 500 m to be considered independent for most species. Thus, there is not a direct relationship between the spatial independence of response and explanatory variables.

Conspecific attraction (Smith and Peacock 1990) may have contributed to autocorrelation in our species data and may also explain what mild landscape effects we did observe. Conspecifics may cluster spatially, for example, to increase opportunities for extra-pair copulations (Ramsay et al. 1999), which are known to be common in north temperate breeding songbirds (Stutchbury and Morton 1995). Conspecific attraction, for whatever reason, is dependent on the spatial distribution of habitats in the landscape; i.e., territorial conspecifics cannot aggregate in space if their habitat is fragmented into isolated patches. Thus, increased abundance in landscapes with a high proportion of preferred habitat may be an indirect result of conspecific attraction. The potential role of conspecific attraction in determining landscape effects on songbird abundance, and in determining spatial patterns in species abundance in general, merits increased attention in future studies.

In addition to improving habitat models and quantifying spatial patterns in species abundance, the available tools for analyzing spatial autocorrelation have implications for the design of field studies. Attempts to avoid autocorrelation by placing sample points far enough apart so as to be independent are unnecessary and probably often unsuccessful. In our study, points separated by <500 m were not independent for most species. In one extreme case, points separated by <2.5 km were not independent (Veery; Fig. 4). If travel time and effort are substantial, the trade-off between sampling intensively (many samples per unit area) and extensively (large aerial coverage) becomes less important. In some studies, it may be possible to increase sample intensity considerably with little loss in extent. Increasing sample intensity offers several advantages: (1) A large number of nonindependent samples, corrected for autocorrelation, probably provides more statistical power than a smaller number of independent samples. Although neighboring samples were not independent in our study, each point provided some new information (i.e., Moran's *I* never approached one, even for adjacent points; Fig. 4). (2) The fine-scale spatial pattern of species distributions can be described quantitatively. These patterns might suggest new hypotheses or aid in designing studies to test existing hypotheses.

CONCLUSIONS

Landscape structure appears to have only weak effects on songbird abundance in the primarily mid- to late-successional National Forests we studied. In contrast to these public forests, private lands in the southern Appalachians are under increasing pressure from a

growing regional human population (Turner et al. 1996, Wear and Bolstad 1998). Our results are probably not applicable to private lands, which tend to be more fragmented and may therefore be more susceptible to landscape-scale impacts.

Although studies in fragmented landscapes have reported strong effects of patch size, patch isolation, or landscape-scale forest cover (e.g., Ambuel and Temple 1983, Robbins et al. 1989, Trzcinski et al. 1999), most studies of songbird abundance in forested landscapes have reported weak or moderate landscape effects. Some authors have recommended consolidating clearcuts in managed forests to decrease edge and landscape heterogeneity (King et al. 1996, Hagan et al. 1997). However, the absence of strong landscape effects in most studies conducted in forested landscapes implies that these recommendations might be inappropriate. Additional studies in landscapes with different amounts of early-, mid-, and late-successional forest and in different regional settings are needed to better understand the landscape-scale effects of forest management on songbird abundance and nesting success.

Important future challenges in conservation include (1) identifying thresholds in the proportion of preferred habitat below which strong landscape effects are likely to occur; (2) determining how these thresholds differ depending on the species involved and the characteristics of the surrounding habitat matrix (Andr  n et al. 1997); and (3) understanding how the effects of forest management and other human disturbances at a given scale interact with land use at broader scales (Flather and Sauer 1996, Donovan et al. 1997).

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