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SPATIAL AUTOCORRELATION AND AUTOREGRESSIVE MODELS IN ECOLOGY

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Abstract. Recognition and analysis of spatial autocorrelation has defined a new paradigm in ecology. Attention to spatial pattern can lead to insights that would have been otherwise overlooked, while ignoring space may lead to false conclusions about ecological relationships. We used Gaussian spatial autoregressive models, fit with widely available software, to examine breeding habitat relationships for three common Neotropical migrant songbirds in the southern Appalachian Mountains of North Carolina and Tennessee, USA.

In preliminary models that ignored space, the abundance of all three species was correlated with both local- and landscape-scale habitat variables. These models were then modified to account for broadscale spatial trend (via trend surface analysis) and fine-scale autocorrelation (via an autoregressive spatial covariance matrix). Residuals from ordinary least squares regression models were autocorrelated, indicating that the assumption of independent errors was violated. In contrast, residuals from autoregressive models showed little spatial pattern, suggesting that these models were appropriate.

The magnitude of habitat effects tended to decrease, and the relative importance of different habitat variables shifted when we incorporated broadscale and then fine-scale space into the analysis. The degree to which habitat effects changed when space was added to the models was roughly correlated with the amount of spatial structure in the habitat variables.

Spatial pattern in the residuals from ordinary least squares models may result from failure to include or adequately measure autocorrelated habitat variables. In addition, contagious processes, such as conspecific attraction, may generate spatial patterns in species abundance that cannot be explained by habitat models. For our study species, spatial patterns in the ordinary least squares residuals suggest that a scale of 500–1000 m would be appropriate for investigating possible contagious processes.

Key words: CAR model; habitat model; landscape effects; Moran's I; Neotropical migrant songbirds; spatial autocorrelation; spatial autoregressive model; trend surface analysis.

INTRODUCTION

Spatial autocorrelation is frequently encountered in ecological data, and many ecological theories and models implicitly assume an underlying spatial pattern in the distributions of organisms and their environment (Legendre and Fortin 1989). Typically, species abundances are positively autocorrelated, such that nearby points in space tend to have more similar values than would be expected by random chance. This pattern is often driven by multiple causes that may be exogenous (e.g., autocorrelated environment, disturbance) and/or endogenous (e.g., conspecific attraction, dispersal limitation, demography) (Sokal and Oden 1978*b*, Legendre 1993). In addition to its ecological significance, spatial autocorrelation is problematic for classical statistical tests, such as ANOVA and ordinary least squares (OLS) regression, that assume independently distributed errors (Haining 1990:161–166; Legendre 1993). When the response (e.g., species abundance) is autocorrelated, the assumption of independence is often invalid, and the effects of covariates (e.g., environmental variables) that are themselves autocorrelated tend to be exaggerated (Gumpertz et al. 1997).

Legendre (1993) suggested two general frameworks for incorporating space into ecological analysis. In the "raw data approach," species–environment relationships are modeled by partial regression analysis (univariate case for individual species) or constrained ordination (multivariate case for community analysis; Borcard et al. 1992, Legendre and Legendre 1998); in both cases, the effect of space is partitioned out by site variables or trend surface analysis. In the "matrix approach," species and environment data are represented by matrices of ecological distances between sample locations, and spatial data are contained in a matrix of

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geographic distances. The correlation between species and environment, while controlling for space, is calculated by a partial Mantel test (Manly 1986, Legendre and Legendre 1998). The above methods have important limitations. For example, the raw data approach accounts for broadscale spatial trend but not for the fine-scale autocorrelation that induces nonindependent errors. Improvements to the methods of Legendre (1993) have been suggested by Legendre and Borcard (1994), Legendre and Legendre (1998), and Borcard and Legendre (2002), but few ecological studies to date have incorporated fine-scale autocorrelation into species–environment analysis.

One approach to analyzing species–environment relationships in the presence of fine-scale autocorrelation is the class of spatial autoregressive models (Haining 1990, Cressie 1993). These models can be thought of as two-dimensional extensions of one-dimensional autoregressive models popular in time-series analysis (Cressie 1993). Spatial autoregressive models have been known for decades in the statistical literature (Besag 1974), but have been used by ecologists in only a few studies (Pickup and Chewings 1986, Augustin et al. 1996; Klute et al., *in press*). Theoretically, autoregressive models can be fit to a variety of response distributions, including normal (auto-Gaussian), binary (autologistic), and Poisson (auto-Poisson). However, the auto-Poisson model can only have negatively autocorrelated errors (Besag 1974, Cressie 1993:553–555) and is therefore of limited practical use. The autologistic model has been used in several ecological applications (Augustin et al. 1996; Klute et al., *in press*). ''Pseudolikelihood'' parameter estimates for the autologistic model can be obtained with standard logistic regression software, but the standard errors tend to underestimate the true sampling variability (Gumpertz et al. 1997). Parameter estimates for the auto-Gaussian model cannot be obtained with ordinary regression software, because the estimated mean function and spatial covariance matrix interact so that an iterative fitting procedure is necessary (Haining 1990: 128). Recent development of software for fitting auto-Gaussian models (Kaluzny et al. 1998) significantly expands the tools available to ecologists for analyzing autocorrelated data.

In this paper, we use auto-Gaussian models to extend the single species raw data approach of Legendre (1993) to account for fine-scale spatial autocorrelation. We develop models of species abundance as a function of local- and landscape-scale habitat variables using data from a 3-yr breeding bird study in managed forests in the southern Appalachian Mountains, USA. This region supports a diverse assemblage of Neotropical migratory songbirds (Passeriformes), many of which are thought to be experiencing long-term population declines (Robbins et al. 1989*b*, Askins et al. 1990). While degradation of wintering (Robbins et al. 1989*b*, Sherry and Holmes 1996) and migratory (Moore et al. 1995) habitats are likely important, habitat change on the breeding grounds remains a prominent hypothesis in explaining population declines of Neotropical migrants (Brittingham and Temple 1983, Wilcove 1985, Temple and Cary 1988, Robinson et al. 1995). Numerous breeding studies have documented reduced abundance (e.g., Ambuel and Temple 1983, Robbins et al. 1989*a*), pairing success (e.g., Gibbs and Faaborg 1990, Villard et al. 1993), or nesting success (e.g., Donovan et al. 1995, Robinson et al. 1995) in highly fragmented forests, and the conservation of Neotropical migrant songbird populations is thought to depend, in part, on the preservation of large forest tracts in North America (Wilcove 1985, Donovan et al. 1995, Robinson et al. 1995). Despite this widely held belief, little is known about nesting success or habitat use by breeding Neotropical migrants in large forests (Simons et al. 2000). Recent studies in both Europe and North America suggest that landscape structure may affect breeding songbird habitat use even in large forested areas (e.g., McGarigal and McComb 1995, Edenius and Elmberg 1996, Jokimäki and Huhta 1996, Hagan et al. 1997, Schmiegelow et al. 1997).

The present analysis seeks an understanding of how southern Appalachian songbirds respond to their breeding habitat at local and landscape scales. Our results are relevant to Neotropical migratory bird conservation (Hagan and Johnston 1992, Martin and Finch 1995), as well as to the more general ecological question of how organisms respond to environmental variation at different spatial scales (Wiens 1989). We hope that our discussion of statistical methods will be valuable to the many ecologists who are currently analyzing spatially autocorrelated data.

METHODS

Study area

The southern Appalachians, USA, region is 70% forested (SAMAB 1996), including remnant old-growth stands and extensive tracts of second-growth forest that have regrown following industrial logging from the late 1800s through the 1930s (Eller 1982, Yarnell 1998). The U.S. Forest Service manages most of the public lands in the southern Appalachians. Our study area (35°40′00″–36°07′30″ N, 82°37′30″–83°07′30″ W) encompassed 60 000 ha of previously logged forest from 380 to 1460 m elevation in the French Broad Ranger District of Pisgah National Forest (North Carolina) and the Nolichucky Ranger District of Cherokee National Forest (Tennessee). Current forest cover in the study area, by stand age, is: ≤9 yr, 5%; 10–19 yr, 4%; 20–39 yr, 5%; 40–69 yr, 27%; and ≥70 yr, 59% (Hermann 1996). Most younger stands (<20 yr old) were created by small (~10 ha) clearcuts, which are scattered throughout the landscape. The majority of the study area consists of deciduous mesic hardwood forests. Xe-

TABLE 1. Habitat variables used in regression models.

Variable	Description
Local habitat variables	
ELEV	elevation
ELEV^2	(elevation)^2
TOPO (4)	topographic position (ravine, flat, slope, or ridge)
EDGE (6)	edge category (early-early, early-mid, early-late, mid-mid, mid-late, or late-late)
RD/TR/OFF (3)	point located on road, trail, or off-road
RDVEG (3)	road bordered by *Rubus*, other shrub species, or no shrubs
CAN	percentage of canopy cover
SUBCAN	percentage of subcanopy cover
TALLSH	percentage of tall shrub/sapling cover
LOWSH	percentage of low shrub/seedling cover
HERB	percentage of herbaceous cover
DBH25–50	number of 25–50 cm dbh trees in wedge prism sample
DBH>50	number of >50 cm dbh trees in wedge prism sample
MAXHT	height of tallest tree
NMDS1	NMDS axis 1: *Quercus rubra* and *Acer saccharum* (negative axis 1 scores) to *Q. coccinea* (positive scores)
NMDS2	NMDS axis 2: *Liriodendron tulipifera* (negative axis 2 scores)
NMDS3	NMDS axis 3: *Tsuga canadensis* and *Rhododendron maximum* (negative axis 3 scores) to *Q. prinus* (positive scores)
Landscape variables	
LS≤9	proportion of ≤9-yr-old forest
LS≤9^2	(proportion of ≤9-yr-old forest)^2
LSMESIC40–69	proportion of 40–69 yr-old mesic hardwood forest
LSMESIC≥70	proportion of ≥70-yr-old mesic hardwood forest
LSCORE	proportion of core area (≥40-yr-old forest that is >100 m from edge with younger forest and >100 m from non-National Forest land)
LSDIV	Simpson's diversity index ($1/\Sigma p_i^2$), where p_i refers to the proportion of six landcover categories (stands ≤9, 10–19, 20–39, 40–69, and ≥70 years old, and non-National Forest land)

Notes: For categorical variables, the number of categories is given in parentheses. All landscape variables were measured within 250 m radius circles, centered on each sample location. Abbreviations: dbh, diameter at breast height, 1.4 m above the ground surface; NMDS, nonmetric multidimensional scaling.

ric hardwoods and pine (*Pinus* spp.) occupy dry slopes and ridges.

Bird counts

Our database consisted of 1177 point locations sampled from mid-May to the end of June in 1997–1999. Each point was sampled in two different years of the study under favorable weather conditions. Points were spaced ~200 m apart along low-traffic roads ($n = 570$), hiking trails ($n = 557$), and off-road transects ($n = 50$). The location of each point was recorded with a differentially corrected global positioning system (GPS; GeoExplorer II; Trimble Navigation, Sunnyvale, California, USA). At each point, we recorded the number and identity of breeding pairs, along with a horizontal distance estimate from the observer, during a 10-min period using the variable circular plot method (Reynolds et al. 1980). Counts were conducted between sunrise and 10:15 h. In our analysis, we only included detections with distance estimates ≤75 m from the observer. Using this distance cut-off, detectability (the probability that a present bird is detected), which was estimated with the computer program DISTANCE (Thomas et al. 1998), was roughly equal across the different habitats sampled. Additional details concerning bird counts can be found in Lichstein et al. (2002).

Local scale habitat

Vegetation data were recorded within 10 m radius plots at each sample location (Table 1). Nonmetric multidimensional scaling (NMDS), a robust nonparametric ordination method (Minchin 1987), was used to generate axes representing gradients in floristic composition. Stand age was assigned to one of three successional stages (early, mid, or late) for both sides of the road or trail, yielding six edge categories: early-early, early-mid, early-late, mid-mid, mid-late, and late-late. Additional details on local habitat data can be found in Lichstein et al. (2002).

Landscape scale habitat

Landcover maps of the southern Appalachians region are available from the Southern Appalachian Assessment GIS Data Base (Hermann 1996). This database includes forest stand coverages (digitized from 1:24 000 scale aerial photographs) for all National Forests in the SAMAB (1996) assessment area. We used ARC/INFO (ESRI 1998) to quantify landscape composition within a 250 m radius circle centered on each sample point (Table 1). Because adjacent points were separated by ~200 m, landscape circles overlapped considerably, ensuring some spatial autocorrelation in landscape variables. The present analysis is restricted to simple landscape composition variables measured at a single scale. A more thorough landscape analysis does not qualitatively change our results (Lichstein et al. 2002).

Statistical analysis

Our general goal was to evaluate how the apparent importance of different habitat variables changed depending on the scale(s) of spatial dependence accounted for by the regression models. We began by fitting models that ignored both broadscale spatial trend and fine-scale autocorrelation. We then examined how these models changed after accounting for broadscale trend, and we partitioned the explained variation in species abundance to nonspatially structured environment, spatially structured environment, and broadscale trend following Legendre (1993). Finally, we examined models that also accounted for fine-scale autocorrelation. All analyses were performed with S-PLUS (Kaluzny et al. 1998, MathSoft 1999). S-PLUS codes and detailed instructions for performing all analyses in this paper may be found as a supplement available in ESA's Electronic Data Archive.

Study species and preliminary analysis.—We analyzed point count data for three species of Neotropical migrant warblers (Parulidae) that are common in our study area: the Chestnut-sided Warbler (*Dendroica pensylvanica*), the Hooded Warbler (*Wilsonia citrina*), and the Black-throated Blue Warbler (*Dendroica caerulescens*). These species were selected because they represent a range of habitat preferences: the Chestnut-sided Warbler is an edge/early successional specialist, the Hooded Warbler is an edge/mature forest generalist, and the Black-throated Blue Warbler is a mature forest specialist. In addition, these species were the focus of a concurrent nesting success study. Although patterns in bird abundance do not necessarily reflect habitat quality (Van Horne 1983), all three species reproduce successfully in our study area (~50% nest success rate; Weeks 2001; J. W. Lichstein, T. R. Simons, and K. E. Franzreb, *unpublished data*); therefore, patterns in their abundance are likely to have some adaptive significance.

In all regression models discussed below, the response variable was the square-root-transformed count (Sokal and Rohlf 1995) for each species, summed across the two samples at each of the 1177 point locations. Quantitative explanatory variables were standardized to mean zero and unit variance, and categorical variables were coded as zero/one dummy variables. Plots of ordinary least squares (OLS) partial residuals against each explanatory variable (Rawlings et al. 1998:350) indicated constant variances for all three species. These plots suggested nonlinear responses to ELEV (Hooded and Black-throated Blue Warbler) and LS≤9 (Chestnut-sided Warbler), and the appropriate quadratic terms were added to these models. Frequency histograms of residuals and normal probability plots (Rawlings et al. 1998:357) indicated normality for the Black-throated Blue Warbler, while residuals for the Chestnut-sided and the Hooded Warbler were not normal (although both distributions were roughly symmetric). To investigate how nonnormality would affect our results, we compared OLS models, for which classical parametric tests assume normality (Rawlings et al. 1998:325), to Poisson and negative-binomial models for count data using generalized linear models (McCullagh and Nelder 1989). Results from OLS, Poisson, and negative-binomial models were qualitatively similar (Lichstein 2000), and we therefore proceeded with the normal errors model due to its greater flexibility in fitting spatial autoregressive models (Cressie 1993; see Introduction).

Habitat (''OLS environment'') models.—For each species, we fit OLS multiple regression models to habitat variables (hereafter, ''OLS environment models''), ignoring both broadscale spatial trend and fine-scale autocorrelation. For each species, we began with a model that included all of the habitat variables listed in Table 1 and sequentially eliminated by hand variables with $P > 0.01$.

Habitat + trend (''OLS trend/environment'') models.—We used trend surface analysis to model broadscale spatial pattern in the species data. This analysis has two primary aims (Legendre 1993, Legendre and Legendre 1998): (1) to guard against false correlations between species and environment, as may arise when an unmeasured environmental factor causes a common spatial structure in the species and in the measured environmental variables; and (2) to determine if there is a substantial amount of broadscale spatially structured variation in the species data that is unexplained by the measured environmental variables.

We fit a trend surface to bird abundance by regressing the species data on all third-degree polynomial terms of the spatial coordinates of the sample locations:

$$z = b_0 + b_1x + b_2y + b_3x^2 + b_4xy + b_5y^2 + b_6x^3 + b_7x^2y + b_8xy^2 + b_9y^3$$

where z is the response variable (square-root-transformed species counts), b_0–b_9 are parameters, and x and y are the spatial coordinates of the sample locations. Prior to analysis, x and y were centered on their respective means to reduce collinearity with higher order terms (Legendre and Legendre 1998:527) and standardized to unit variance. Nonsignificant trend surface terms were removed by stepwise selection.

Following Legendre (1993), the proportion of variation in the species data explained by nonspatially structured environment, spatially structured environment, and spatial trend (independent of environment) was partitioned using partial regression analysis (Legendre and Legendre 1998). The total variation in the species data explained by trend and environment combined was obtained from ''OLS trend/environment models,'' which included both the trend surface terms and the habitat variables from the OLS environment models.

Habitat + trend + autocorrelation (''CAR trend/environment'') models.—Because trend surface analysis only accounts for broadscale spatial pattern (Legendre and Borcard 1994), we next examined how OLS trend/environment models changed when we accounted for fine-scale autocorrelation using auto-Gaussian models. Spatial auto-Gaussian models take on one of two common forms (conditional and simultaneous), depending on how the spatially correlated error structure is specified (Haining 1990, Cressie 1993). Cressie (1993:408) recommends the conditional autoregressive (CAR) model over the simultaneous model. We fit both models, and the results were nearly identical. We report results for the CAR model only. The ''CAR trend/environment model'' accounts for both broadscale trend (via inclusion of trend surface terms) and fine-scale autocorrelation (via the correlated error structure; see below).

The difference between OLS and CAR models can be understood by considering the expected value and distribution of **Y**, the vector of observed responses. For both models, **Y** is assumed to have a multivariate normal (MVN) distribution:

$$\mathbf{Y} \sim \mathrm{MVN}[\mu, \mathbf{V}]$$

where μ, the vector of means, is equal to $\mathbf{X\beta}$ ($\mathbf{X}$ is a matrix of independent variables, and $\boldsymbol{\beta}$ is a vector containing their slopes), and $\mathbf{V}$ is an $n \times n$ covariance matrix (n is the number of observations). In the OLS model, the expected value of an observation Y at a location i is simply μ_i, and the covariance matrix is

$$\mathbf{V} = \mathbf{I}\sigma^2$$

where $\mathbf{I}$ is the identity matrix (ones on the diagonal and zeros elsewhere) and σ^2 is a constant. Thus, every Y_i has the same variance (σ^2), and the covariance between Y_i and Y_j is zero for all locations $i \neq j$ (Rawlings et al. 1998:87).

In the CAR model, the conditional expectation of Y_i, given the response at all other locations, is μ_i plus a weighted sum of the mean-centered counts at locations j:

$$\mathrm{E}(Y_i \mid \text{all } Y_{j\neq i}) = \mu_i + \rho\Sigma_{j\neq i}w_{ij}(Y_j - \mu_j)$$

where ρ is a parameter to be estimated that determines the direction (positive or negative) and magnitude of the spatial neighborhood effect, w_{ij} are weights that determine the relative influence of location j on location i, and $Y_j - \mu_j$ are the mean-centered counts at locations j (Haining 1990:88, Cressie 1993:407). Thus, CAR models, and autoregressive models in general, assume that the response is a function of both the explanatory variables (μ in the equation above) and the values of the response at neighboring locations (the summation in the equation above). In the context of species-environment analysis, and assuming positive autocorrelation ($\rho > 0$), the CAR model has the following interpretation: if location i is surrounded by locations j, which, based on the habitat at j, have higher (or lower) species abundance than expected, then i will also tend to have higher (or lower) species abundance than expected from the habitat at i. This framework is well-suited for modeling the abundance of species whose distributions are controlled by a combination of exogenous (e.g., habitat) and endogenous (e.g., clonal growth, conspecific attraction) factors. In most cases, it is reasonable to assume that distant locations will affect each other less than nearby locations; therefore, the weights (w_{ij}) in the CAR model are typically defined to decrease with increasing distance between i and j (e.g., $w_{ij} = 1/\text{distance}_{ij}$) and are zero if i and j are not within each other's spatial neighborhood (zone of influence). An appropriate neighborhood size is the maximum distance at which the residuals from an OLS model are autocorrelated. This distance may be judged from a semivariogram or correlogram of the OLS residuals (Cressie 1993:557). See Haining (1990), Cressie (1993), and Gumpertz et al. (1997) for further discussion of weight definitions.

The above expression for the expected value of Y_i in the CAR model implies the following covariance matrix:

$$\mathbf{V} = (\mathbf{I} - \rho\mathbf{W})^{-1}\mathbf{M}$$

where $\mathbf{W}$ is an $n \times n$ matrix with zeros on the diagonal and the neighbor weights (w_{ij}) in the off-diagonal positions, and $\mathbf{M}$ is an $n \times n$ matrix with the conditional variances ($\sigma_1^2, \ldots, \sigma_n^2$) of $\mathbf{Y}$ (i.e., the variances of $\mathbf{Y}$ given the realized values of the spatial neighbors) on the diagonal and zeros in the off-diagonal positions (Haining 1990:88, Cressie 1993:433). In contrast to the OLS model, covariances in the CAR model (off-diagonal elements of $\mathbf{V}$) are nonzero and increase the closer locations i and j are to each other. In the present analysis, we assumed that the conditional variances of $\mathbf{Y}$ were constant (i.e., $\mathbf{M} = \mathbf{I}\sigma^2$), which is a special case of the general model described above. (See Haining [1990:129] for a discussion of nonconstant variances in auto-Gaussian models.) The unconditional variances in the CAR model (diagonal elements of $\mathbf{V}$) are generally not constant and depend on ρ and the locations of the spatial neighbors (see Haining 1990: Fig. 3.8), but not on the realized values of the neighbors.

Prior to fitting CAR models, we examined directional correlograms (±180° azimuths = 0°, 45°, 90°, and 135°; angular tolerance = ±22.5°) of OLS trend/environment residuals to determine if autocorrelation was isotropic (the same in all geographic directions; Haining 1990: 66, Legendre and Legendre 1998:721). Anisotropy was not detected for any of the three species. Based on correlograms of OLS trend/environment residuals and empirical trials, we selected a 750 m radius spatial neighborhood for all three species. We fit CAR models with three different neighbor weight definitions: $w_{ij} = 1$, 1/distance$_{ij}$, and (1/distance$_{ij}$)^2. We selected an appropriate weight function based on model fit (maximized likelihood) and by how well the model accounted for autocorrelation in the residuals. We selected $w_{ij} =$ (1/distance$_{ij}$)^2 for the Chestnut-sided Warbler and $w_{ij} =$ 1/distance$_{ij}$ for the Hooded and Black-throated Blue Warblers.

We calculated R^2 for the CAR models using the following formula (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, 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 formula yields the identical value as the traditional R^2 (the proportion of the mean-centered response sum of squares that is explained by the independent variables).

Habitat effects.—To provide a common ground for assessing the importance of habitat variables in OLS and CAR models, we evaluated the contribution of each variable to model fit with a likelihood ratio test for nested models (Haining 1990:142), with the reduced model containing a subset of the variables in the full model:

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

where LR is the likelihood ratio test statistic, and l_{red} and l_{full} are the log-likelihoods of the reduced and full models, respectively. Under the null hypothesis that the reduced and full models fit the data equally well, LR has an approximate χ^2 distribution with degrees of freedom equal to the number of additional parameters in the full model.

Finally, we wished to gain some insight into how spatial pattern in the habitat variables would affect their apparent importance in the three types of regression models. We assumed that the probability of observing ‘‘false correlations’’ (Legendre and Legendre 1998: 769) between the species and habitat data would increase when the two were spatially structured at similar scales. For a given habitat variable, we predicted that the change in its apparent importance when trend and autocorrelation were incorporated into the models would be related to the degree to which the habitat variable was structured at broad and fine spatial scales, respectively. For example, if a habitat variable showed little broadscale trend but strong fine-scale autocorrelation, the importance of the variable should be similar in OLS environment and OLS trend/environment models, but might decrease in CAR trend/environment models.

For each habitat variable, we calculated the change in its effect due to incorporating broadscale trend in the model as:

$$\Delta\mathrm{LR}_{\mathrm{trend}} = \mathrm{LR(OLS\ environment)} - \mathrm{LR(OLS\ trend/environment)}$$

where LR(OLS environment) and LR(OLS trend/environment) are LR statistics for a given habitat variable in OLS environment and OLS trend/environment models, respectively. We predicted that $\Delta\mathrm{LR}_{\mathrm{trend}}$ would be positively correlated with the degree to which each habitat variable was spatially structured on a broad scale. To describe the broadscale structure of the habitat variables, we performed OLS trend surface regressions (separate regression for each habitat variable) on all third-degree polynomial terms of the spatial coordinates of the sample locations. Nonsignificant trend surface terms were removed by stepwise selection. We used the R^2 from these trend surface models (’’R^2_{trend}’’) as an index of broadscale structure in each habitat variable.

We calculated the change in the effect of each habitat variable when fine-scale autocorrelation was added to the model as

$$\Delta\mathrm{LR}_{\mathrm{autocor}} = \mathrm{LR(OLS\ trend/environment)} - \mathrm{LR(CAR\ trend/environment)}$$

where LR(OLS trend/environment) and LR(CAR trend/environment) are LR statistics for a given habitat variable in OLS trend/environment and CAR trend/environment models, respectively. We predicted that $\Delta\mathrm{LR}_{\mathrm{autocor}}$ would be positively correlated with the degree to which the habitat variables were autocorrelated on a fine scale. To describe this fine-scale autocorrelation, we used the residuals from the trend surface analysis of each habitat variable to compute Moran’s I correlograms (see Spatial autocorrelation below). Trend surface analysis removes broadscale structure, so any spatial pattern remaining in the residuals is due to fine-scale autocorrelation. For each habitat variable, we calculated ’’I_{mean},’’ the average value of Moran’s I_{std} (standardized version of I; see Appendix) out to a lag distance of 775 m (the approximate size of the spatial neighborhood in the CAR models), as an index of fine-scale autocorrelation.

In order to calculate R^2_{trend} and I_{mean}, categorical habitat variables were transformed into pseudo-quantitative variables (see below).

Spatial autocorrelation.—We used Moran’s I correlograms (Sokal and Oden 1978*a*, Legendre and Legendre 1998) to evaluate spatial pattern in the (square-root-transformed) bird counts, in the residuals from the three types of species–environment regression models, and in the residuals from the trend surface models of the habitat variables. Under the null hypothesis of no spatial autocorrelation, I has an expected value near zero for large n, with positive and negative values indicating positive and negative autocorrelation, respectively. Because I does not vary strictly between -1 and $+1$, we standardized I by dividing by its maximum

TABLE 2. Ordinary least squares (OLS) and conditional autoregressive (CAR) models of bird abundance.

	R^2						Neighborhood effect	
Species	OLS env	trend	OLS trend/env	autocor	CAR trend/env	$\hat{\rho}$	200 m†	400 m‡
Chestnut-sided Warbler	0.48	0.26	0.53	0.17	0.55	3361.6	0.25	0.06
Hooded Warbler	0.20	0.08	0.22	0.12	0.25	17.3	0.26	0.13
Black-throated Blue Warbler	0.36	0.22	0.39	0.26	0.46	19.0	0.29	0.14

Notes: R^2 values are given for the following models: ''OLS env'' = habitat only; ''trend'' = broadscale spatial trend surface; ''OLS trend/env'' = habitat + trend; ''autocor'' = fine-scale autocorrelation (conditional autoregressive [CAR] model with only intercept and ρ); ''CAR trend/env'' = habitat + trend + autocorrelation. In CAR models, neighborhood effects are modeled by the estimated spatial parameter, $\hat{\rho}$, along with the neighbor weights: $w_{ij} = (1/\text{distance}_{ij})^2$ for the Chestnut-sided Warbler and $1/\text{distance}_{ij}$ for the Hooded and the Black-throated Blue Warblers. ''Neighborhood effect'' is the expected increase in the response (square-root-transformed count) at location i where the sum of the mean-centered responses at locations j in i's spatial neighborhood is $+3$. Neighborhood effect was calculated as $\hat{\rho}\Sigma_{j\neq i} w_{ij}(Y_i - \mu_j)$, which is the autoregressive component of the conditional expectation of Y_i in the CAR model. As an arbitrary but realistic example, we assumed that $\Sigma(Y_i - \mu_j) = 3$ for locations j in i's spatial neighborhood.

† Neighborhood effect was calculated assuming all j in i's spatial neighborhood are 200 m away from i.

‡ Neighborhood effect was calculated assuming all j in i's spatial neighborhood are 400 m away from i.

attainable value to yield I_{std} (Haining 1990:234–235; see Appendix). Significance tests of I for raw data (i.e., bird counts), OLS residuals, and CAR residuals are distinct and are explained in detail in the Appendix. The first lag distance interval in the correlograms included all pairs of points separated by $\leq$250 m, and subsequent intervals (out to a maximum distance of 3100 m) were 150 m wide. All intervals contained at least 1000 pairs of points, providing high power to detect spatial pattern.

For each lag distance, we used a randomization test with 999 permutations (see Appendix) to determine the probability, under the null hypothesis of no spatial autocorrelation, of observing a value of I as large as the observed value (one-tailed test for positive autocorrelation; Haining 1990:231, Legendre and Legendre 1998:720). For each correlogram, we tested for global significance (i.e., the correlogram contains at least one positively autocorrelated value) using a Bonferroni corrected α^* of $0.05/20 = 0.0025$ (nominal α of 0.05; 20 lags; Legendre and Legendre 1998:721). Within each correlogram, the significance of I for each lag distance was assessed using the progressive Bonferroni correction suggested by Legendre and Legendre (1998:671 and 721–723), in which the ith lag is tested at $\alpha^* = \alpha/i$, with $\alpha = 0.05$. This procedure is appropriate when autocorrelation is expected at the shortest lags and one wishes to know the range (maximum lag distance) of autocorrelation (Legendre and Legendre 1998:721).

In order to calculate I, categorical habitat variables (TOPO, EDGE, RD/TR/OFF, and RDVEG; Table 1) were transformed into pseudo-quantitative variables by assigning integer values to classes ranked along ecological gradients: the four TOPO classes were ranked from driest to wettest (ridge = 0, slope = 1, flat = 2, ravine = 3); the six EDGE classes were ranked in increasing order of disturbance due to recent logging (late-late = 0, mid-late = 1, mid-mid = 2, early-late = 2, early-mid = 3, early-early = 4); the three RD/TR/OFF classes were ranked in order of increasing vegetation disturbance (off-road = 0, trail = 1, road = 2); the three RDVEG classes were ranked in increasing order of use by early successional birds as nesting habitat in our study area (J. W. Lichstein, T. R. Simons, and K. E. Franzreb, *unpublished data*; none = 0, shrubs other than *Rubus* = 1, *Rubus* = 2).

Significance tests for the presence of spatial autocorrelation require the condition of second-order stationarity (Legendre and Legendre 1998:718). Broadscale trend in the unmodeled bird counts violated stationarity assumptions; significance tests of I for the raw bird counts should therefore be interpreted as testing for the presence of spatial pattern that may reflect trend rather than fine-scale autocorrelation.

RESULTS

OLS environment models

OLS environment models explained 48, 20, and 36% of the variation in the counts for the Chestnut-sided, Hooded, and Black-throated Blue Warbler, respectively (Table 2). All models included both local- and landscape-scale habitat variables (Fig. 1, Table 3). OLS environment models explained much of the broadscale spatial pattern in the counts for all three species, as seen in the overall shift in the correlograms towards zero (Fig. 2: compare correlograms for counts to those for OLS environment residuals). The OLS environment model for the Chestnut-sided Warbler also explained some of the fine-scale spatial pattern in the counts, as seen in the more rapid decline in Moran's I for the OLS environment residuals compared to the counts (Fig. 2). In contrast, OLS environment models explained little of the fine-scale autocorrelation in the counts for the Hooded and the Black-throated Blue Warblers: the shape of the correlograms for the counts and OLS en-

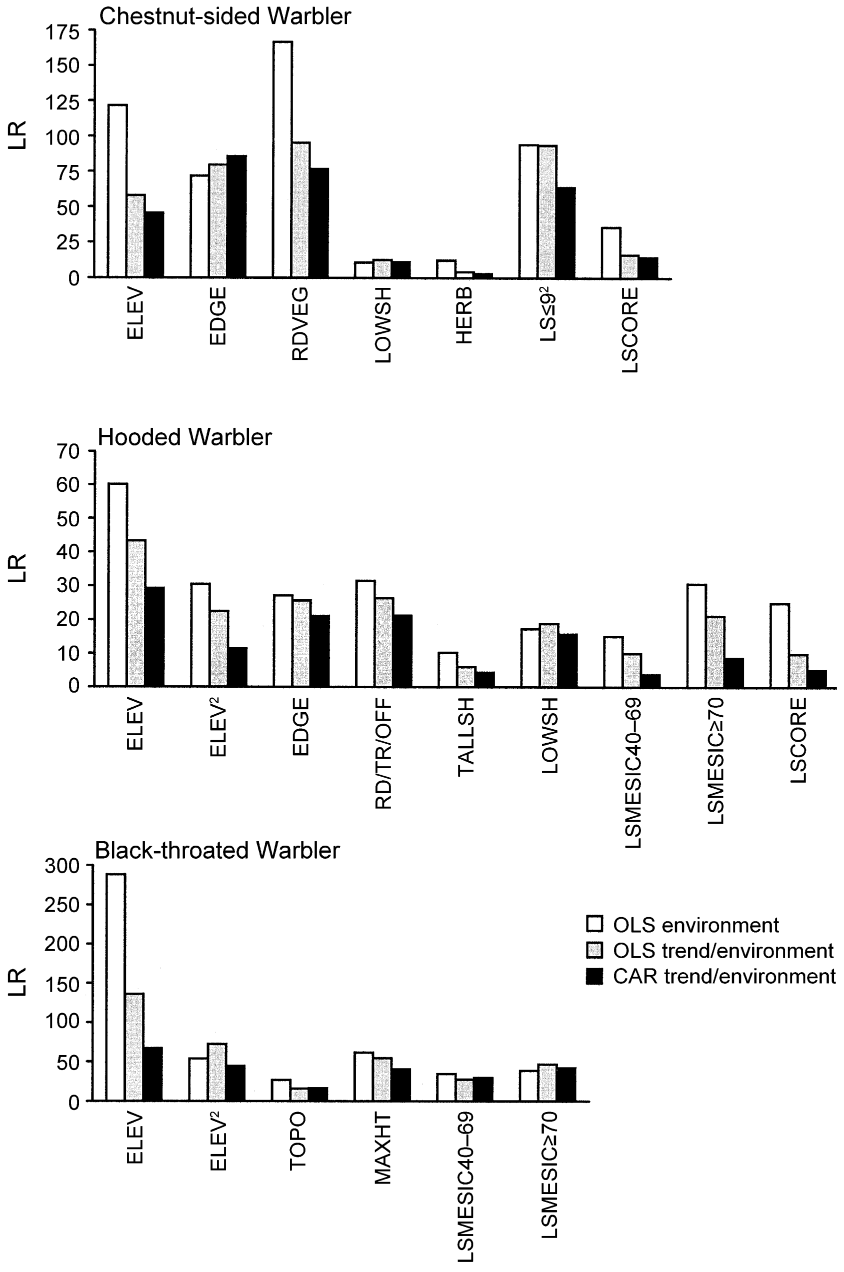

FIG. 1. Likelihood ratio (LR) statistics for habitat variables in ordinary least squares (OLS) environment, OLS trend/environment, and conditional autoregressive (CAR) trend/environment models. Larger LR values indicate a greater contribution to model fit. *P* values and parameter estimates are given in Table 3. See Table 1 for descriptions of habitat variables.

vironment residuals were similar for these two species (Fig. 2). For all three species, OLS environment residuals were positively autocorrelated (global Bonferroni test for correlograms significant at $\alpha^* = 0.0025$), indicating that the assumption of independent errors was violated.

OLS trend/environment models

Trend surface analysis explained 26, 8, and 22% of the variation in the counts for the Chestnut-sided, Hooded, and Black-throated Blue Warbler, respectively (Table 2). OLS trend/environment models, which included both the trend surface terms and the habitat variables, explained only slightly more variation than OLS environment models: 53, 22, and 39% for the Chestnut-sided, Hooded, and Black-throated Blue Warbler, respectively (Table 2). The reason for this marginal improvement is clear from the partitioning of explained variation due to trend, spatially structured environment (‘‘trend/environment’’), and nonspatially

TABLE 3. Parameter estimates for habitat variables in regression models.

Habitat variable	OLS environment model	OLS trend/environment model	CAR trend/environment model
Chestnut-sided Warbler			
ELEV	0.18****	0.13****	0.13****
EDGE	****	****	****
Early-early	0.39	0.40	0.44
Early-mid	0.28	0.28	0.24
Early-late	0.34	0.33	0.34
Mid-late	0.11	0.10	0.10
Late-late	−0.05	−0.06	−0.07
RDVEG	****	****	****
Rubus	0.52	0.39	0.37
Other shrubs	0.09	0.04	0.05
LOWSH	0.05**	0.05***	0.05***
HERB	0.05***	0.03$^{\mathrm{NS}}$	0.03$^{\mathrm{NS}}$
LS$\leq 9^2$	0.05****	0.05****	0.04****
LSCORE	−0.10****	−0.06****	−0.07***
Hooded Warbler			
ELEV	−0.15****	−0.15****	−0.15****
ELEV^2	−0.09****	−0.09****	−0.08***
EDGE	****	***	***
Early-early	0.19	0.21	0.16
Early-mid	0.05	0.05	0.05
Early-late	0.28	0.25	0.23
Mid-late	−0.13	−0.15	−0.13
Late-late	−0.04	−0.04	−0.03
RD/TR/OFF	****	****	****
Road	0.19	0.22	0.23
Trail	−0.05	−0.02	0.00
TALLSH	0.06**	0.05$^{\mathrm{NS}}$	0.04$^{\mathrm{NS}}$
LOWSH	0.08****	0.08****	0.08****
LSMESIC40–69	0.09***	0.08**	0.06$^{\mathrm{NS}}$
LSMESIC≥70	0.13****	0.12****	0.09**
LSCORE	−0.11****	−0.08**	−0.06$^{\mathrm{NS}}$
Black-throated Blue Warbler			
ELEV	0.34****	0.28****	0.23****
ELEV^2	−0.12****	−0.15****	−0.14****
TOPO	****	**	***
Flat	0.42	0.30	0.28
Ravine	0.31	0.23	0.21
Slope	0.09	0.07	0.03
MAXHT	0.16****	0.15****	0.13****
LSMESIC40–69	0.13****	0.13****	0.15****
LSMESIC≥70	0.14****	0.16****	0.16****

Notes: A single significance level is reported for categorical variables. Parameter estimates for the levels of TOPO are relative to ''ridge,'' those for EDGE are relative to ''mid-mid,'' those for RD/TR/OFF are relative to ''off-road,'' and those for RDVEG are relative to ''no shrubs.'' Quantitative variables, except for quadratic terms (ELEV^2 and LS$\leq 9^2$), were standardized to mean zero and unit variance prior to analysis, so their parameter estimates are referenced to a common scale. OLS = ordinary least squares; CAR = conditional autoregressive.

$^{**}P \leq 0.01$; $^{***}P \leq 0.001$; $^{****}P \leq 0.0001$; NS = not significant ($\alpha = 0.01$).

structured environment (Fig. 3): after controlling for environmental (habitat) effects, broadscale trend explains only a small amount of additional variation in the species data. While much of the variation explained by the habitat variables was correlated with spatial trend (trend/environment fraction in Fig. 3), there were substantial nonspatially structured habitat effects for all three species (environment fraction in Fig. 3).

Incorporating broadscale trend into OLS models had little effect on the fine-scale spatial pattern in the residuals: the overall shapes of the OLS environment and OLS trend/environment correlograms were nearly identical within each species (Fig. 2). This is to be expected: a third-degree polynomial trend surface cannot explain spatial variation on the scale of hundreds of meters in a study area that spans tens of kilometers. As with OLS environment models, correlograms for OLS trend/environment models showed that the OLS assumption of independent errors was violated (global Bonferroni test significant at $\alpha^* = 0.0025$ for all three species). OLS trend/environment residuals were significantly autocorrelated out to 625 m for the Chestnut-sided Warbler, 325 m for the Hooded Warbler, and $\sim$1500 m for the Black-throated Blue Warbler. While incorporating trend did not account for fine-scale autocorrelation, there was an overall shift in Moran's *I* toward zero in the OLS trend/environment compared to OLS environment correlograms (Fig. 2). The amount by which each correlogram shifted toward zero reflects the amount of additional broadscale variation in the species data explained by OLS trend/environment over OLS environment models (trend fraction in Fig. 3): the addition of trend surface terms improved OLS models more for the Chestnut-sided and the Black-throated Blue Warbler than for the Hooded Warbler (Fig. 3); accordingly, the shift in the correlograms towards zero was more noticeable for the Chestnut-sided and the Black-throated Blue Warbler (Fig. 2).

As expected, LR statistics for many habitat variables were reduced in OLS trend/environment models compared to OLS environment models, although in the case of the Black-throated Blue Warbler, the reduction in LR was large only for ELEV (Fig. 1). The reduction in LRs indicates that the habitat variables had less impact on model fit after controlling for broadscale spatial trend. In most cases, parameter estimates (Table 3) reflected LRs (Fig. 1), tending to be lower in magnitude in OLS trend/environment than in OLS environment models for variables with reduced LRs in OLS trend/environment models.

CAR trend/environment models

CAR trend/environment models explained 55, 25, and 46% of the variation in the species data for the Chestnut-sided, Hooded, and Black-throated Blue Warbler, respectively (Table 2). These R^2 values represent a modest but significant improvement in CAR over OLS trend/environment models. Likelihood ratio tests for the spatial parameter (ρ) were significant for Chestnut-sided ($\hat{\rho} = 3361.6$, LR = 57.6, $P < 0.0001$), Hooded ($\hat{\rho} = 17.3$, LR = 41.7, $P < 0.0001$), and Black-throated Blue Warbler ($\hat{\rho} = 19.0$, LR = 131.5, $P < 0.0001$), indicating that, after controlling for habitat effects and broadscale trend, species abundance at sam-

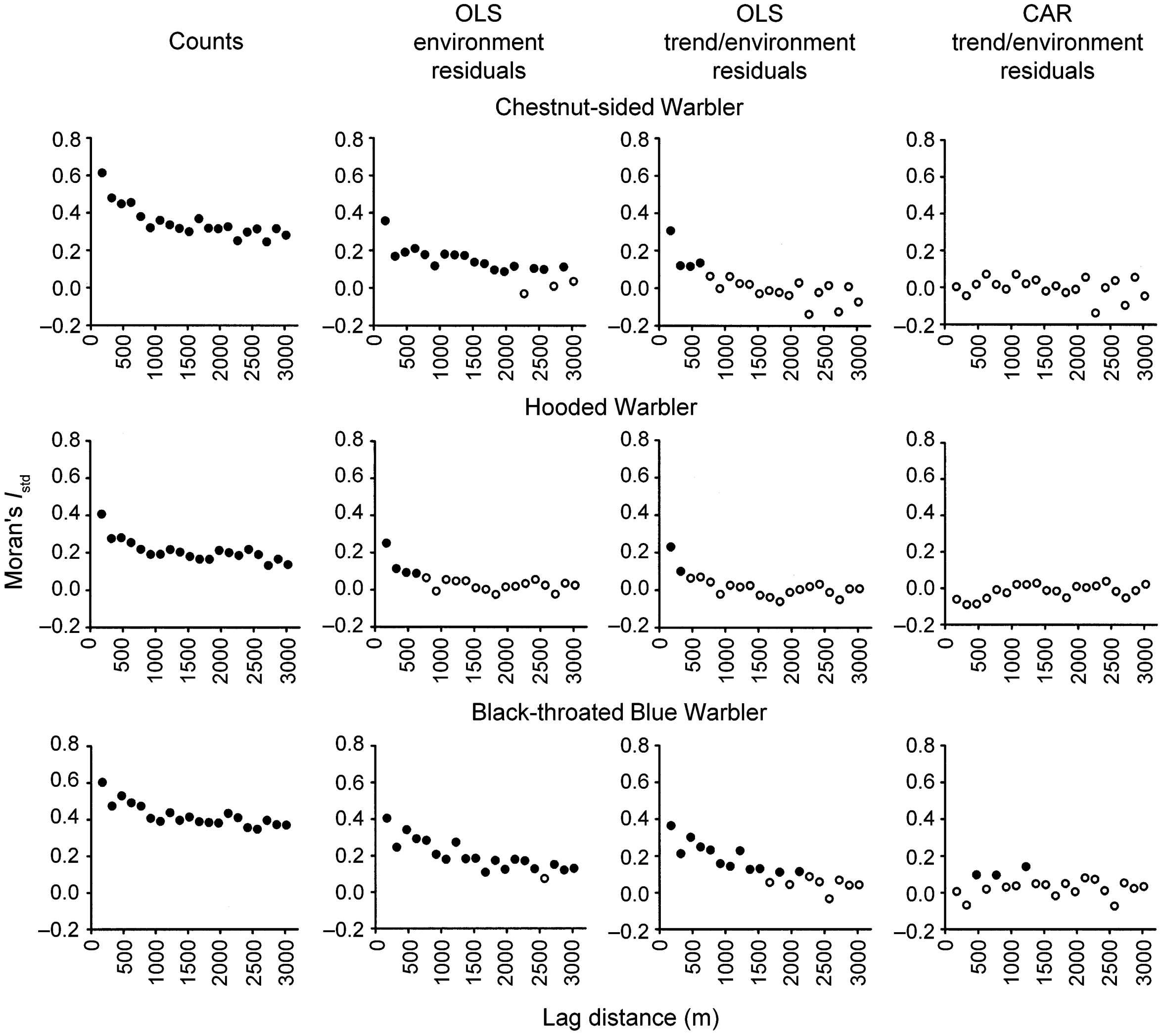

FIG. 2. Moran's I_{std} correlograms of (square-root transformed) bird counts, residuals from ordinary least squares (OLS) environment models, residuals from OLS trend/environment models, and residuals from conditional autoregressive (CAR) trend/environment models. I_{std} (I standardized to vary between $+1$ and -1; see Appendix) has an expected value near zero for no spatial autocorrelation, with negative and positive values indicating negative and positive autocorrelation, respectively. Each point represents the value of I_{std} calculated from all possible pairs of sample locations that are separated by the lag distance (150 m wide intervals) on the x-axis. Closed circles indicate values of I_{std} that are significantly larger than the value expected under the null hypothesis of no positive autocorrelation (one-tailed test with $\alpha = 0.05$ adjusted using progressive Bonferroni correction of Legendre and Legendre [1998:721]; see *Methods: Statistical analysis: Spatial autocorrelation*); open circles are not significantly larger than the null expectation.

ple points was significantly positively correlated with abundance at nearby points. The relatively high $\hat{\rho}$ for the Chestnut-sided Warbler results from defining the neighbor weights (w_{ij}) as $(1/\text{distance}_{ij})^2$, as opposed to $1/\text{distance}_{ij}$ for Hooded and Black-throated Blue Warblers. When $\hat{\rho}$ is adjusted for w_{ij}, the spatial neighborhood effect is similar for all three species (Table 2).

To determine how much of the variation in the species data could be explained by autocorrelation alone, we fit CAR models containing only an intercept (overall mean response) and ρ, where the w_{ij} were the same as in the CAR trend/environment models. These pure autocorrelation CAR models explained 17, 12, and 26% of the variation in the species data for the Chestnut-sided, Hooded, and Black-throated Blue Warbler, respectively (Table 2).

In contrast to OLS models, residuals from CAR trend/environment models showed little spatial pattern (Fig. 2), suggesting that the CAR models were appropriate (Pickup and Chewings 1986). Of the three species, the global Bonferroni test for correlograms of CAR residuals was significant ($\alpha^* = 0.0025$) only for the Black-throated Blue Warbler. Residuals from the CAR model for this species were positively autocor-

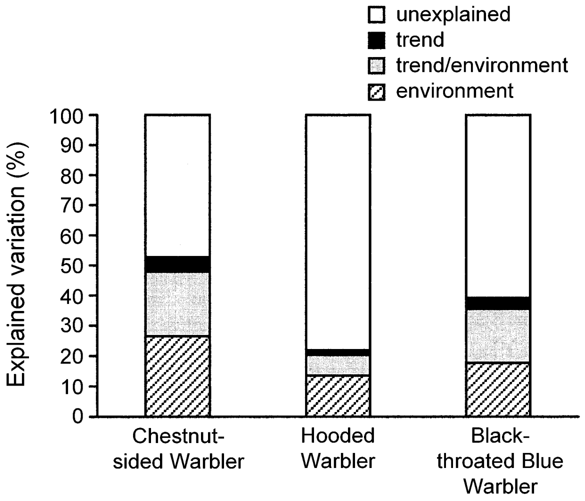

FIG. 3. Percentage of variation in species data in ordinary least squares (OLS) trend/environment models explained by nonspatially structured environment, spatially structured environment (''trend/environment''), and trend (independent of environment). Broadscale space was modeled by trend surface analysis, and the explained variation was partitioned using partial regression analysis following Legendre (1993). The ''trend'' fraction is equal to the improvement in R^2 values from OLS trend/environment models over OLS environment models (Table 2). The ''trend'' and ''trend/environment'' fractions combined are equal to the R^2 values from the trend surface models of species counts. The ''trend/environment'' and ''environment'' fractions combined are equal to the R^2 values from OLS environment models. OLS trend/environment models account for broadscale trend but not for fine-scale autocorrelation.

related at several lag distances, but the degree of autocorrelation was greatly reduced compared to the OLS trend/environment model (Fig. 2). Because the permutation procedure we used to test for autocorrelation in CAR residuals is not strictly valid (see Appendix), significance tests for CAR residuals should be interpreted with caution. Regardless, it is clear from the small values of I that there is little spatial pattern in the CAR residuals (Fig. 2).

Comparison of LRs from CAR trend/environment models to those from OLS trend/environment models showed the same general trend as comparison of LRs from OLS trend/environment to OLS environment models: for Chestnut-sided and Hooded Warblers, the effect of several habitat variables were reduced when autocorrelation was accounted for, while for the Black-throated Blue Warbler, only the effect of ELEV changed substantially (Fig. 1). As with the comparison of habitat parameter estimates between the two OLS models, the magnitude of parameter estimates in CAR trend/environment vs. OLS trend/environment models (Table 3) tended to reflect differences in LRs between the two models (Fig. 1).

Habitat effects

For all three species, the relative importance of habitat variables shifted across the three types of models (Fig. 1). For example, EDGE was the fourth most important variable in the Chestnut-sided Warbler OLS environment model, but was the most important variable in the CAR model. For the Black-throated Blue Warbler, ELEV was the single dominant variable in the OLS environment model, but was one of several important variables in the CAR model. In addition to shifts in relative importance, the overall magnitude of habitat effects tended to decrease in spatially more complex models, especially for the Hooded Warbler (Fig. 1). For this species, landscape variables (LSMESIC40–69, LSMESIC≥70, and LSCORE) were highly significant in the OLS environment model but were marginally significant or nonsignificant in the CAR model (Table 3).

Residuals from trend surface models of habitat variables showed positive autocorrelation for all variables included in regression models of bird abundance (Fig. 4; global Bonferroni test significant at $\alpha^* = 0.0025$ for all habitat correlograms). A few local habitat variables (ELEV, ELEV^2, RD/TR/OFF, and RDVEG; Fig. 4A) and all four landscape variables (Fig. 4B) exhibited extreme spatial patterns, with Moran's I_{std} approaching one (perfect positive autocorrelation) at the shortest lags.

Scatter-plots of $\Delta\mathrm{LR}_{\mathrm{trend}}$ vs. the broadscale trend in habitat variables (R^2_{trend}) showed positive relationships for Chestnut-sided and Hooded Warblers (Fig. 5). The relationship was weak for the Black-throated Blue Warbler and depended on a single outlier (ELEV). Scatter-plots of $\Delta\mathrm{LR}_{\mathrm{autocor}}$ vs. the fine-scale autocorrelation in habitat variables (I_{mean}) showed similar patterns, with a strong positive relationship for the Hooded Warbler and noisy positive relationships for the Chestnut-sided and Black-throated Blue Warblers (Fig. 5).

DISCUSSION

It is well known that ignoring spatial autocorrelation can lead to overestimating environmental effects on species abundance (Haining 1990:166, Legendre 1993), yet there are few examples in the ecological literature that address this issue in the regression context (see Klute et al., *in press*). We have demonstrated how autocorrelation can be incorporated into species–environment analysis via autoregressive models fit with widely available software. In ordinary least squares (OLS) regression, the assumption of independent errors can be checked by examining a correlogram of the residuals (although raw data test procedures for Moran's I are not valid in this case; see Appendix). In contrast to OLS models, autoregressive models assume correlated errors, and a correlogram of the residuals provides a check on the appropriateness of the spatial structure of the model: if the model is appropriate, then

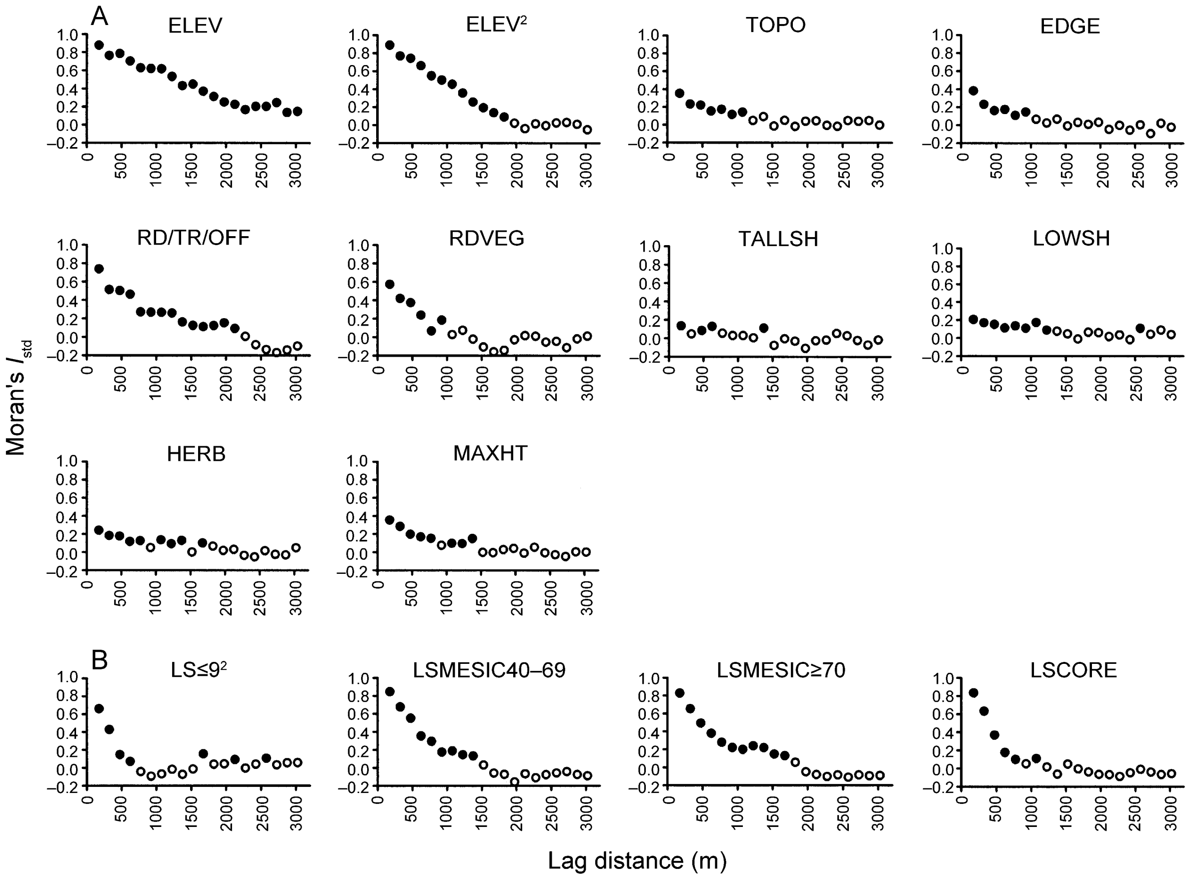

FIG. 4. Moran's I_{std} correlograms for (A) local and (B) landscape-scale habitat variables included in regression models. Broadscale pattern was removed from habitat variables via trend surface analysis, and the residuals from the trend surface models were used to calculate I_{std}. Closed and open circles, respectively, indicate values of I_{std} that are significantly different and not different from the null expectation (one-tailed test for positive autocorrelation with progressive Bonferroni correction; see Fig. 2 legend for details). See Table 1 for descriptions of habitat variables.

the residuals should have little or no spatial pattern (Cliff and Ord 1981:197, Pickup and Chewings 1986). In this study, residuals from OLS habitat models were autocorrelated, and incorporating spatial trend did little to correct this statistical problem. Residuals from autoregressive (CAR) models showed little or no autocorrelation, suggesting that these models were appropriate and provided a reasonable picture of habitat effects on bird abundance. Moreover, autoregressive models fit the data better than OLS models: after controlling for the effects of habitat variables and broadscale trend, the spatial parameter (ρ) in the CAR models was highly significant due to the positive correlation between species counts at sample points located within each other's spatial neighborhood (zone of influence).

For all three species considered, the magnitude of habitat effects, as well as the relative importance of different habitat variables, shifted as we incorporated different spatial scales into the analysis. Models that ignored both broadscale trend and fine-scale autocorrelation showed stronger habitat effects than models that accounted for trend, and these in turn showed stronger habitat effects than autoregressive models that accounted for both trend and autocorrelation (Fig. 1). Habitat effects were stronger in spatially deficient models because space and habitat were confounded (Gumpertz et al. 1997). For example, trend surface models explained 8–26% of the species data, but OLS trend/environment R^2 values were only 2–5% higher than OLS environment R^2 values (Table 2) because the trend surfaces were largely redundant with the habitat data. Similarly, pure autocorrelation models explained 12–26% of the species data, but CAR trend/environment R^2 values were only 2–7% higher than OLS trend/environment R^2 values (Table 2) because much of the variation explained by the pure autocorrelation models was redundant with the variation explained by the OLS trend/environment models. If habitat, trend, and autocorrelation explained independent components of variation in the species data, then R^2 values for habitat, trend, and autocorrelation models would be additive.

The extent to which habitat effects changed as space was added to the models was related to the degree of spatial structure in the habitat variables (Fig. 5). How-

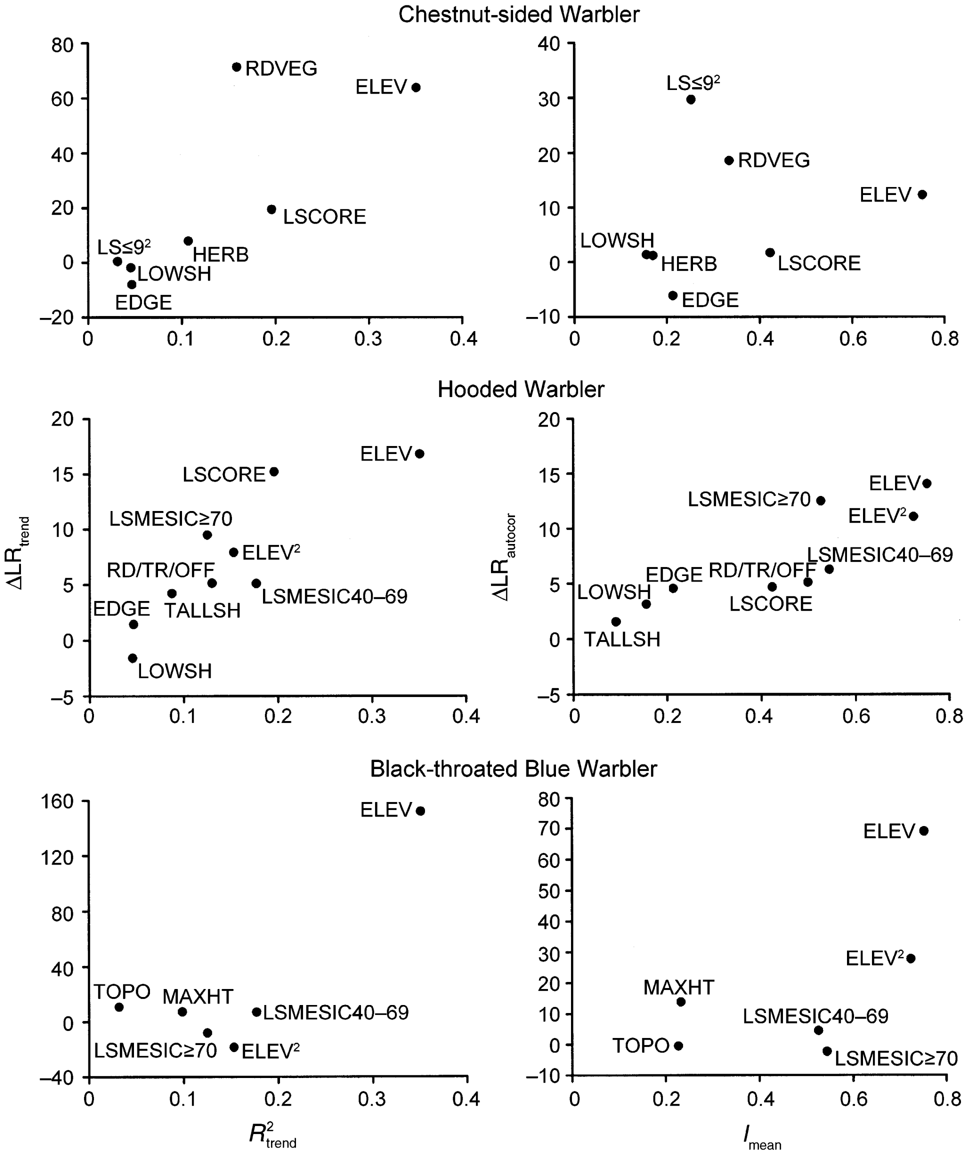

FIG. 5. Change in habitat effects in models of increasing spatial complexity plotted against spatial structure indices for habitat variables. ΔLR_{trend} is the change in the importance of a given habitat variable when broadscale spatial trend was added to regression models of bird abundance; i.e., the decrease in likelihood ratio (LR) from ordinary least squares (OLS) environment to OLS trend/environment models (see Fig. 1). R^2_{trend} (R^2 from regression of each habitat variable on third-degree polynomial trend surface) estimates the degree to which habitat variables were spatially structured at a broad scale. $\Delta LR_{autocor}$ is the change in the importance of a given habitat variable when fine-scale autocorrelation was added to regression models of bird abundance; i.e., the decrease in LR from OLS trend/environment to CAR trend/environment models (see Fig. 1). I_{mean} (mean of Moran's I_{std} out to a lag of 775 m; see Fig. 4) estimates the degree to which habitat variables were spatially structured on a fine scale. See Table 1 for descriptions of habitat variables.

ever, these relationships were noisy for two of the three species. When space (broad or fine scale) is incorporated into a regression model, the importance of a spatially structured habitat variable will be strongly affected only if (1) the spatial patterns in the species and habitat data overlap considerably and (2) this common spatial pattern can alternatively be explained by the new spatial terms in the model. The positive relationships in Fig. 5 show that the above two conditions are more likely to hold for habitat variables with strong spatial structures. On the other hand, the scatter in Fig. 5 indicates that the degree of spatial structure in a habitat variable is, by itself, a poor predictor for how much the variable's importance will decrease when space is incorporated into the model.

Throughout this paper, we have treated trend as a potential source of false correlations between species and environment (Legendre and Legendre 1998:769);

e.g., when an unmeasured environmental factor causes similar spatial patterns in species abundance and in an unimportant habitat variable that happened to be measured. In this context, only the nonspatially structured component of the species–environment correlation is assumed to reflect a meaningful relationship. Two issues complicate this interpretation. First, the spatially structured component of environmental variation may in fact be important to the species: spatial structure in the species–environment relationship does not guarantee the presence of a false correlation, only the possibility of one. Second, what is perceived as spatially vs. nonspatially structured environmental variation is sensitive to the degree of the polynomial trend surface. A third-degree polynomial model is often used (e.g., Borcard et al. 1992, Legendre 1993), and Legendre and Legendre (1998:741) offer some additional guidance. However, the decision is somewhat subjective, and it would be worthwhile to consider if one's results are qualitatively affected by fitting a more or less complex surface (Brownie and Gumpertz 1997). These two issues reflect the general problem in ecology of interpreting correlations when, as is almost always the case, the true model is unknown. In species–environment regression models, purely statistical criteria will seldom inform us if a trend surface model is needed and, if so, the appropriate level of complexity. Rather, the researcher must make subjective decisions based on the goals of the analysis and prior knowledge of the system (Legendre and Legendre 1998:769–770).

Following Legendre (1993), we have referred to broadscale spatial dependence as trend and fine-scale dependence as autocorrelation. Conceptually, Legendre and Legendre (1998:11) define autocorrelation as arising from interactions between responses at sites within each other's ''zone of spatial influence,'' as would result from ''contagious biotic processes such as growth, mortality, migration, and so on (Legendre 1993).'' In contrast, trend is defined as a spatial pattern arising from the influence of spatially structured explanatory variables (Legendre and Legendre 1998:11). Other definitions may be found in the geostatistical literature, where trend (or ''drift'') is considered a deterministic shift in the mean and autocorrelation the result of stochastic processes (e.g., Journel and Rossi 1989). When the processes generating the spatial pattern are not known, as is often the case in observational field studies, trend and autocorrelation are difficult to distinguish on conceptual grounds (Legendre and Legendre 1998: 724–725). Nevertheless, trend and autocorrelation may be distinguished in the regression context by the following practical definitions: autocorrelation refers to spatial pattern in OLS residuals that may be modeled with a correlated error structure (e.g., CAR model in this paper); trend refers to broadscale patterns that may be modeled with environmental variables or trend surface terms. With these practical definitions in mind, what is perceived as trend vs. autocorrelation in regression will depend on the size of the study area and the proximity of sample locations. For example, in a regional-scale bird study in which sample locations are separated by several kilometers, the trend in our data that was not explained by habitat (trend fraction in Fig. 3) would appear as autocorrelation (spatially structured OLS residuals), and the autocorrelation in our data would appear as nonspatially structured noise, because the sample locations would be spaced too far apart to detect the fine-scale spatial patterns we observed (Fig. 2).

Our results have implications for designing field studies. Correlograms of OLS residuals suggest that in our study, sample locations separated by 750 m were statistically independent for Chestnut-sided and Hooded Warblers and nearly so for the Black-throated Blue Warbler (Fig. 2). However, spacing our points this far apart would have resulted in a considerably smaller sample size due to increased travel time. While each closely spaced point did not represent an independent sample, there was at least some new information provided by each point; i.e., Moran's I_{std} did not approach one even at the shortest lag distance in correlograms of OLS residuals. A large sample size, corrected for autocorrelation, likely provided more statistical power to detect habitat effects than the smaller number of independent samples we could have collected with the same resources. This scenario is probably common in landscape-scale field studies.

In addition to a larger sample size, our study design allowed us to detect spatial patterns in species distributions that would have been overlooked by more widely spaced sample locations. Classical regression models explained, on average, only about a third of the variation in the species data. However, some of the unexplained variation, rather than appearing as random noise, was spatially structured on a fine scale. Several factors may account for this. Mis-specifying the form of a model (e.g., assuming a linear model when the true relationship is nonlinear) may lead to autocorrelated residuals, as can failing to include (or poorly measuring) an important explanatory variable that is itself autocorrelated (Cliff and Ord 1981:197, 211; Haining 1990:332–334). In our study, we do not think that misspecification was a problem, because we checked the relationship between the response and all explanatory variables using partial residual plots (Rawlings et al. 1998). We cannot rule out measurement error or missing habitat variables as explanations for autocorrelation in the residuals. However, we suggest that the spatial pattern was due, at least in part, to the behavior of the birds. Conspecific attraction results in some high-density areas, while other areas of equally suitable habitat may be underutilized (Cody 1981). This aggregation would result in autocorrelated residuals from habitat models, because habitat would not fully explain the species' spatial distribution (Augustin et al. 1996). Aggregation may give individuals more opportunities to seek extrapair copulations (EPCs; Ramsay et al. 1999), which are known to be common in north temperate breeding passerines (Stutchbury and Morton 1995). EPCs have been documented for Hooded (Stutchbury et al. 1994) and Black-throated Blue Warblers (Chuang et al. 1999). In addition to seeking EPCs, aggregation may be due to dispersing animals cueing on the presence of conspecifics as an indicator of habitat quality (Smith and Peacock 1990).

While the presence of conspecifics may sometimes reflect a superior habitat, bird habitat selection is in part a stochastic process (Haila et al. 1993, 1996). Dispersing individuals settling randomly in one of several suitable sites may later attract conspecifics, resulting in spatial aggregations that cannot be explained by habitat alone. Site fidelity in a temporally variable environment (Wiens 1985, Wiens et al. 1986), combined with conspecific attraction, could also generate spatial patterns in animal abundance that are poorly explained by habitat. However, as there was little disturbance (e.g., logging) in our study area during or several years prior to the study, this is an unlikely explanation for the spatial patterns we observed. Numerous other spatially contagious processes could explain autocorrelated species data, with predation and natal dispersal being among the most obvious. However, limited data from nest monitoring suggests that adult mortality during the breeding season is rare in our study area (J. W. Lichstein, T. R. Simons, and K. E. Franzreb, *unpublished data*), and natal dispersal in birds in general (Greenwood and Harvey 1982), and in Hooded (Evans Ogden and Stutchbury 1994) and Black-throated Blue Warblers (Holmes et al. 1992) in particular, is thought to be too spatially extensive to explain the fine-scale autocorrelation we observed. While our data cannot resolve which, if any, of the above processes generated autocorrelation in the species data, conspecific attraction, for whatever reason, seems the most likely candidate. Our results suggest 500–1000 m (i.e., the scale of autocorrelation in the OLS regression residuals) would be an appropriate scale for future studies of possible social interactions or other contagious processes in these species.

The models presented here are in accordance with our understanding of the species' breeding ecology. In our study area, the Chestnut-sided Warbler is found primarily at high elevations in regenerating stands or other recently disturbed sites. The strong correlation with the presence of *Rubus* along roadsides is likely due to the species' frequent use of this vegetation as a nesting substrate (J. W. Lichstein, T. R. Simons, and K. E. Franzreb, *unpublished data*). There was also a strong correlation with the proportion of regenerating forest in the landscape, probably due to the rarity of this habitat type in our study area (Andrén 1994, Andrén et al. 1997). At the local scale, Hooded Warbler abundance was correlated with disturbed sites and sites with heavy shrub cover. In our study area, Hooded Warblers nest in thick woody undergrowth in a variety of habitats, including roadsides, tree-fall gaps in mature forest, and *Rhododendron* thickets (Weeks 2001). At the landscape scale, Hooded Warbler abundance was positively correlated with older forest and negatively correlated with the amount of core area. While this suggests a preference for heterogeneous landscapes, the correlations were weak after controlling for autocorrelation. Thus, results from the CAR model imply that the Hooded Warbler responds primarily to local rather than landscape-scale habitat features in our study area. Finally, the Black-throated Blue Warbler had a strong nonlinear relationship with elevation. This species is absent at the lowest elevations in our study area. Its abundance increases up to ~1000 m and levels off at higher altitudes. After correcting for autocorrelation, the relative effect of other variables (e.g., canopy height and landscape composition) increased. The importance of landscape scale variables was expected, as the Black-throated Blue Warbler is considered area sensitive, preferring large forest patches in fragmented landscapes (Robbins et al. 1989*a*). The fact that this species responded to landscape composition in our study area (a large forest within a mostly forested region) emphasizes the sensitivity of some forest-interior Neotropical migrants to landscape-scale effects (Faaborg et al. 1995, Freemark et al. 1995).

CONCLUSIONS

A prominent feature of the OLS models in this study is the large amount of unexplained variation (Fig. 3). This variation likely consists of four components: (1) broadscale spatial structure (including that due to unmeasured habitat variables or missing interaction terms), which could be explained by a more complex trend surface model; (2) fine-scale spatial structure, as seen in the autocorrelated OLS residuals (Fig. 2); (3) stochasticity in bird habitat selection (Haila et al. 1993, 1996); and (4) measurement error in the response and explanatory variables.

Our results are consistent with previous studies that found both local and landscape-scale effects on songbird habitat use in large managed forests (e.g., McGarigal and McComb 1995, Jokimäki and Huhta 1996, Hagan et al. 1997) and in other settings (e.g., Pearson 1993, Bolger et al. 1997, Saab 1999). After controlling for spatial autocorrelation, the abundance of Chestnut-sided and Black-throated Blue Warblers remained strongly correlated with landscape composition, while the abundance of the Hooded Warbler was only weakly correlated with the landscape.

Habitat variables that were highly spatially structured (e.g., elevation and landscape variables) showed weaker effects in models that accounted for broadscale trend and/or fine-scale autocorrelation. The decision to include trend surface terms in a species–environment model is not clear-cut, nor is determining the complexity of the trend surface. In contrast, spatially autocorrelated errors should always be accounted for in a regression model (Haining 1990:161–166), via an autoregressive framework or some other correlated error structure (see Upton and Fingleton 1985:372, Haining 1990:90, Brownie and Gumpertz 1997).

In OLS regression, the assumption of spatial independence can be checked by plotting a correlogram of the residuals. We also recommend examining correlograms of environmental variables as a useful step in exploratory data analysis. In this study, the overlap in GIS-derived landscape circles at adjacent sample points contributed to autocorrelation in landscape variables; however, these variables would have been autocorrelated even if the circles were nonoverlapping, due to the broad range of autocorrelation in landscape composition (Fig. 4B). Thus, geographic separation of sampled landscapes does not guarantee statistical independence.

Ensuring that samples are spatially independent is logistically difficult and is a misguided goal for many field studies, as much can be learned from the spatial pattern in the data (Sokal and Oden 1978*b*, Legendre and Fortin 1989, Rossi et al. 1992). Nevertheless, it is often the case that a researcher wishes to know the strength of species–environment relationships after controlling for autocorrelation. This paper builds on the approach of Legendre (1993) by controlling for fine-scale autocorrelation in single-species regression analysis using auto-Gaussian models. Autoregressive models have seldom been used by ecologists, due, in part, to the difficulty of fitting or evaluating the models without appropriate software. Recently developed software makes the auto-Gaussian model accessible to a broad group of practitioners. Future software packages that calculate standard errors for the autologistic model would provide another important tool for ecologists.

Autoregressive models are intuitively appealing in situations, such as the present study, in which individuals are thought to interact with neighboring conspecifics. Numerous other spatial models could be formulated to test alternative hypotheses. For example, models with spatially lagged explanatory variables (Haining 1990:339, 354–357) could be specified if autocorrelation was suspected to result from spillover effects of neighboring habitat. It is important to appreciate, however, that conceptually distinct models with fundamentally different interpretations (e.g., autoregressive errors vs. lagged explanatory variables) may be impossible to distinguish on statistical grounds alone (Haining 1990:341). As software for fitting complex spatial models becomes more readily available, we caution that the analytical process must be guided by a detailed knowledge of the species' natural history.

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APPENDIX

MORAN'S *I* TESTS FOR AUTOCORRELATION IN RAW DATA AND REGRESSION RESIDUALS

Moran's I for raw data is

$$I_{\text{raw}} = (n/S_{\text{o}})\left[\sum_i \sum_j w_{ij}(Y_i - Y_{\text{mean}})(Y_j - Y_{\text{mean}})\right] \div \sum_i (Y_i - Y_{\text{mean}})^2$$

where n is the number of locations, S_{o} is the sum of the weights (w_{ij}) that define the proximity (or interaction strength) between locations i and j, and Y_i is the value of the variable of interest at location i (Sokal and Oden 1978*a*, Upton and Fingleton 1985:170, Legendre and Legendre 1998:715). To produce a correlogram, I is calculated for a number of lag distance intervals, with w_{ij} typically defined as one for site pairs separated by a distance contained in the lag interval and zero otherwise; in this case S_{o} is twice the number of site pairs in the lag interval, because the weights include both w_{ij} and w_{ji}.

Moran's I for OLS residuals is

$$I_{\text{res}} = \mathbf{e}'\mathbf{W}\mathbf{e}/\mathbf{e}'\mathbf{e}$$

where $\mathbf{e}$ is the vector of observed residuals and $\mathbf{W}$ is an $n \times n$ matrix containing the w_{ij} (Upton and Fingleton 1985:337, Haining 1990:146). I_{res} yields the same value for residuals as I_{raw}, except for the multiplier n/S_{o} (Upton and Fingleton 1985: 337).

I_{raw} attains a maximum of (Haining 1990:234)

$$|I_{\max}| = (n/S_{\text{o}})\left\{\sum_i \left[\sum_j w_{ij}(Y_j - Y_{\text{mean}})\right]^2 \div \sum_i (Y_i - Y_{\text{mean}})^2\right\}^{1/2}.$$

I_{res} attains the same maximum, without the multiplier n/S_{o}. After dividing by its maximum, I varies between $+1$ and -1 and can be interpreted as a spatial autocorrelation index (Haining 1990:235). Note that the multiplier n/S_{o} cancels out if I_{raw} is divided by its maximum, so standardized values of I_{raw} and I_{res} are comparable.

Tests for significant departures of I_{raw} and I_{res} from their null expectations may be accomplished by converting to standard normal deviates (see Upton and Fingleton 1985:171–173 for I_{raw}; Upton and Fingleton 1985:338 for I_{res}). Alternatively, the significance of I_{raw} and I_{res} may be assessed by permutation. We adopted the latter approach, which is appropriate for small samples (Cliff and Ord 1981:205) and does not assume a normal sampling distribution of I (Upton and Fingleton 1985:171, 339). Tests were based on a distribution of 1000 values, which included 999 random permutations and the reference value (the observed value for which the test is desired; Legendre and Legendre 1998:22–25).

A permutation test for I_{raw} is (Upton and Fingleton 1985: 174): (A) Randomly reassign the observed values $\mathbf{Y}$ to the n sample locations. (B) Calculate I_{raw} from the randomized data.

(C) Repeat steps A and B 999 times; add to these the reference value to generate a null distribution for I_{raw}.

Unlike raw data, OLS residuals cannot simply be randomly permuted in space to test for autocorrelation, because the residuals, by definition, are correlated (e.g., they sum to zero), even if the true, unknown errors are independent (Cliff and Ord 1981:200, Upton and Fingleton 1985:331). Therefore, the appropriate null hypothesis for OLS residuals is not spatial randomness, but the spatial pattern expected in the residuals from the model of interest if it truly had independent errors. A permutation test for I_{res} is (Upton and Fingleton 1985:340): (A) Generate n independent values ε from a normal distribution with mean zero and unit variance and assign them to the n locations of the actual data. (B) Regress ε on $\mathbf{X}$, where $\mathbf{X}$ is the design matrix (intercept plus explanatory variables) for the OLS model of interest. (C) Calculate I_{res} using the residuals from step B. Note that I_{res} is scale independent, so any variance in step A would yield the identical results (Cliff and Ord 1981:206, Upton and Fingleton 1985:340). (D) Repeat steps (A)–(C) 999 times; add to these the reference value to generate a null distribution for I_{res}.

Testing for autocorrelation in residuals from spatial autoregressive (e.g., CAR) models is problematic, and we are aware of no formal test (Cliff and Ord 1981:240; B. Fingleton, *personal communication*). In theory, one could use a permutation test similar to that described above for OLS residuals by modifying step A to generate spatially autocorrelated ε according to the assumed spatial model (see Kaluzny et al. 1998:144–145) and fitting the spatial model in step B. However, unlike OLS models in which the error structure is defined, the error structure in autoregressive models is unknown (i.e., the spatial parameter, ρ, must be estimated from the data). Thus, it is not clear what spatial error structure should be simulated in step A of the procedure. In place of a formal test, we used the raw data procedure for I (see above) to test for autocorrelation in CAR residuals (Upton and Fingleton 1985:347). This procedure should yield reasonable results for large n, where the model imposes minimal restrictions on the residuals (Upton and Fingleton 1985:337).

Programs to perform permutation tests for I_{raw} and I_{res} are included in the supplementary material.

SUPPLEMENTARY MATERIAL

S-PLUS code and detailed instructions for performing all analyses in this paper are available at ESA's Electronic Data Archive: *Ecological Archives* M072-007-S1.