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USING LANDSCAPE ECOLOGY TO TEST HYPOTHESES ABOUT LARGE-SCALE ABUNDANCE PATTERNS IN MIGRATORY BIRDS[1]

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Abstract. The hypothesis that Neotropical migrant birds may be undergoing widespread declines due to land use activities on the breeding grounds has been examined primarily by synthesizing results from local studies. Growing concern for the cumulative influence of land use activities on ecological systems has heightened the need for large-scale studies to complement what has been observed at local scales. We investigated possible landscape effects on Neotropical migrant bird populations for the eastern United States by linking two large-scale inventories designed to monitor breeding-bird abundances and land use patterns. The null hypothesis of no relation between landscape structure and Neotropical migrant abundance was tested by correlating measures of landscape structure with bird abundance, while controlling for the geographic distance among samples.

Neotropical migrants as a group were more "sensitive" to landscape structure than either temperate migrants or permanent residents. Neotropical migrants tended to be more abundant in landscapes with a greater proportion of forest and wetland habitats, fewer edge habitats, larger forest patches, and with forest habitats well dispersed throughout the scene. Permanent residents showed few correlations with landscape structure and temperate migrants were associated with habitat diversity and edge attributes rather than with the amount, size, and dispersion of forest habitats. The association between Neotropical migrant abundance and forest fragmentation differed among physiographic strata, suggesting that landscape context affects observed relations between bird abundance and landscape structure. Finally, associations between landscape structure and temporal trends in Neotropical migrant abundance were counter to those observed in space. Trends in Neotropical migrant abundance were negatively correlated with forest habitats. These results suggest that extrapolation of patterns observed in some landscapes is not likely to hold regionally, and that conservation policies must consider the variation in landscape structure associations observed among different types of bird species and in physiographic strata with varying land use histories.

Key words: eastern USA forests; forest fragmentation; land-use impacts; landscape ecology; landscape structure; Neotropical migrant birds; regional analysis; spatial and temporal correlations.

INTRODUCTION

Much of the evidence linking population declines of Neotropical migrant birds to habitat changes is based on long-term monitoring studies of a particular woodlot or reserve, or studies comparing species abundance patterns among forest fragments within a relatively confined geography (see Askins et al. 1990 for a review). The patterns of population decline documented in this literature appear to be consistent from place to place. However, general regional patterns are difficult to infer when results across independent studies are combined, unless the studies can be shown to be a representative sample (Brown and Maurer 1989). This problem, coupled with the observation that variability of local populations can manifest as population stability over broader geographic areas (Fahrig and Merriam 1994), calls for regional approaches to complement what has been learned from local investigations (Lubchenco et al. 1991).

Although the North American Breeding Bird Survey (BBS) has contributed to continental and regional investigation of Neotropical bird population dynamics (Robbins et al. 1989*b*, Sauer and Droege 1992), analyses of survey trends have typically failed to consider accompanying habitat patterns. How the spatial configurations of habitats affect the distribution and abundance of organisms is a question increasingly associated with landscape ecology (Naveh and Leiberman

[1] For reprints of this Special Feature, see footnote 1, p. 1.

1984, Forman and Godron 1986, Turner 1989). A landscape perspective extends the traditional study of homogeneous patches to consideration of the overall land type mosaic (Hobbs 1993, Wiens et al. 1993). To investigate possible landscape effects in a regional study of spatial and temporal patterns of Neotropical migrant bird abundance, we merged two independent large-scale monitoring efforts: the BBS and digital land use and land cover data from the U.S. Geological Survey (USDI, Geological Survey 1987). By linking these data spatially, we were able to couple information on bird relative abundances with land use and habitat patterns immediately surrounding each BBS survey route.

We tested the general null hypothesis that Neotropical migrant bird abundances were unrelated to landscape structure by examining three questions: (1) Do Neotropical migrant birds, as a group, correlate with landscape structure uniquely when compared to birds with other migratory habits? (2) Does the pattern of correlation between Neotropical migrants and landscape structure vary among regions with different land use histories? (3) Is the pattern of correlation between landscape structure and temporal trends of Neotropical migrants consistent with that observed spatially? We focused our investigation on the forested region of the eastern United States.

Methods

Geographic information on bird relative abundance and population change

The BBS provides information on relative abundance of bird species at a landscape scale. The survey consists of >3000 roadside routes located on secondary roads throughout the United States and southern Canada. Each route is 39.4 km long and is surveyed once each year in June. A competent observer conducts 50 3-min point-counts at 0.8-km intervals on the roadside, recording all birds heard and seen during the counts. This avian species pool was then partitioned into categories (i.e., Neotropical migrants, temperate migrants, and permanent residents) according to Peterjohn and Sauer (1993).

All analyses of BBS data are complicated by limitations of the survey method, in that counts are a biased index to the population (Barker and Sauer 1992, Barker et al. 1993). The proportion of individuals counted along a survey route may be quite low (<0.5), and differs according to various factors, including the observer's ability to perceive, identify, and record birds (Sauer et al. 1994). In addition, there is evidence of a start-up effect among observers, who tend to have lower counts the first year they survey a route (Erskine 1978). Observer effects can thus bias estimates of population change and relative abundance on BBS routes. Furthermore, estimates of mean relative abundance on a route are complicated by population change, which causes abundance to be year-specific.

For comparison with landscape attributes along BBS routes, we estimated population change and mean relative abundance over the survey period (1966–1993) on each route for individual bird species that were observed. Population change was modeled on individual routes as a regression of the natural logarithm of counts plus 0.5 (to avoid domain errors) against year. In the analyses, we mitigated the observer effects by including indicator variables for observers and omitting the first survey year for each observer on the route. We used a marginal mean count (Searle et al. 1980) from the regression to estimate the relative abundance in the middle year of the survey for the mean observer. Although still containing route-specific biases, these marginal mean estimates of relative abundance do control for biases associated with observer changes and trend.

Linking landscape structure with bird abundance

Digital land use and land cover data from the U.S. Geological Survey were used to quantify landscape structure within a circular scene of radius 19.7 km centered on each BBS route (area ≈1200 km^2). A radius of half the length of a BBS route was chosen to guarantee that each landscape scene would contain the whole route. High-altitude aerial photographs, usually at scales smaller than 1:60 000, were used to digitize and transfer land use and land cover data to 1:250 000 base maps in grid format (USDI, Geological Survey 1987). Each grid cell (200 × 200 m) was classified into one of nine broad land types, including urban or built-up land, agricultural land, rangeland, forest land, water, wetland, barren land, tundra, and perennial snow or ice, based on criteria specified in Anderson et al. (1976).

Landscape structure measures were of four general types: composition, diversity/edge, patch characteristics, and patch configuration (Table 1). Many of the same landscape structure measures, albeit over areas less extensive than those we used in our study, have been shown to be associated with the distribution and abundance of birds (Whitcomb et al. 1981, Ambuel and Temple 1983, Lynch and Whigham 1984, Freemark and Merriam 1986, Blake and Karr 1987, van Dorp and Opdam 1987, Lescourret and Genard 1994).

The simplest measure of landscape structure is land type composition, or the proportion of four major land uses within each scene (Table 1). Habitat area alone, however, has been an insufficient predictor of regional changes in bird abundance (Väisänen et al. 1986), indicating a need for explicit measures of spatial heterogeneity. Diversity and edge variables represent com-

TABLE 1. Landscape structure attributes based on U.S. Geological Survey Land Use and Land Cover Digital Data.

Landscape attribute	Description
Composition	Proportion of the landscape scene in:
F	Forest land
W	Wetland
A	Agriculture (cropland and pasture)
U	Urban land
Diversity/edge	
H'	Shannon diversity index: $H' = \sum_{i=1}^{n} P_i \ln P_i$, where P_i is the proportion of land type i, and n is the number of land types in the landscape scene.
D	Measures land type dominance, the tendency for one or a few land types to comprise a majority of the landscape. Calculated as: $D = \ln n + \sum_{i=1}^{n} P_i \ln P_i$, dominance is scaled to vary over 0–1, where $D \rightarrow 1$ reflects landscapes dominated by one or a few land types.
C	Measure of land type contagion, the extent to which land types are aggregated in contiguous patches. $C = n \ln n + \sum_{i=1}^{n} \sum_{j=1}^{n} P_{ij} \ln P_{ij}$, where P_{ij} is the probability that land type i is adjacent to land type j. Contagion is scaled to vary over 0–1, where $C \rightarrow 1$ indicates a clumped pattern (see O'Neill et al. 1988).
E_T	Total edge among all land types.
$E_{F/A}$	Edge between forest and agricultural land.
$E_{F/U}$	Edge between forest and urban land.
Patch characteristics	
F_S	Average size of forest patches.
$F_\#$	Number of forest patches.
A_S	Average size of agriculture patches.
$A_\#$	Number of agriculture patches.
U_S	Average size of urban patches.
$U_\#$	Number of urban patches.
Patch configuration	
$D_{P/A}$	Fractal dimension based on the perimeter–area method (see Krummel et al. 1987). Measures the complexity of forest patch shape.
D_G	Fractal dimension based on the grid method (see Milne 1991). Measures the dispersion of forest patches.

posite measures of landscape structure, summarizing information about all (or several) of the land types comprising the mosaic. We included them as potential attributes affecting Neotropical migrant bird abundance, based on their noted influence on organism dispersal and biotic interactions (Wiens et al. 1985). Patch characteristics and configuration are land type-specific measures of landscape structure, included to capture fragmentation effects. In addition to patch attributes of natural (forest) habitats, we also examined patch characteristics associated with disturbed habitats (agriculture and urban land uses).

The statistics of geographic association

We used Mantel's test (Mantel 1967, Manly 1991) to examine the association between bird data and landscape structure attributes. Mantel's test evaluates the association between differences in attributes on different routes. Although the data were not collected according to an experimental design, the samples are random and therefore allow the use of Mantel's test (Manly 1991:115). Because it is clear that spatial patterns do exist in relative abundances and trends of Neotropical migrant birds (e.g., Sauer and Droege 1992), we also included geographic distance as an independent variable in the analysis. Consequently, the model we fit to each bird species is:

$$a_{ij} = \tau_0 + \tau_{AB.C} b_{ij} + \tau_{AC.B} c_{ij} + \epsilon_{ij},$$

where a_{ij} is the difference in bird relative abundance between routes i and j; b_{ij} is the difference in the landscape variable between routes i and j; c_{ij} is the distance between the starting points of routes i and j; $\tau_{AB.C}$ is the relationship between a_{ij} and b_{ij} when c_{ij} is fixed; $\tau_{AC.B}$ is the relationship between a_{ij} and c_{ij} when b_{ij} is fixed; τ_0 is the intercept; and ϵ_{ij} is the error term. Hypotheses were tested using $\tau_{AB.C}$, which quantifies the association between bird data and landscape structure attributes that is independent of distance effects. For all analyses, species were treated as replicates; for each bird species, a separate model was fit using each landscape structure attribute. From these analyses, we extracted the slope of the relation between bird species data and landscape attribute (estimated regression coefficients $\hat{\tau}_{AB.C}$) and the sample size (i.e., number of survey routes where a species was observed) used in each species analysis.

RESULTS AND DISCUSSION

Migratory habit and landscape structure

To address our first question of whether or not Neotropical migrant abundances are, as a class, associated with landscape structure, a mean $\hat{\tau}_{AB.C}$ among all Neotropical migrants $\bar{\tau}_{AB.C}$ was estimated. If bird relative abundance from route to route is not related to landscape structure, then $\bar{\tau}_{AB.C}$ among Neotropical migrants would not be expected to deviate from 0. Bird species had to be observed on ≥30 routes to be included in the analysis. We found that Neotropical migrant abundance was related to landscape structure. H_0: $\bar{\tau}_{AB.C} = 0$ was rejected ($P < 0.05$) in 17 of 18 landscape structure attributes (Table 2). In addition, the actual pattern of association between Neotropical migrant abundances and landscape structure was biologically sen-

TABLE 2. Mean slopes ($\bar{\tau}_{AB.C}$) and probabilities of $\bar{\tau}_{AB.C} = 0$ for the relations between landscape structure and relative abundance of birds in the eastern United States. One-way ANOVA tests for differences among migratory categories in their association with landscape attributes. The number of species contributing to the estimate of the mean ranges from 70 to 73 for Neotropical migrants, from 32 to 34 for temperate migrants, and from 21 to 22 for permanent residents.

Landscape attribute	Neotropical		Temperate		Resident		ANOVA	
	$\bar{\tau}_{AB.C}$	$P(\bar{\tau} = 0)$	$\bar{\tau}_{AB.C}$	$P(\bar{\tau} = 0)$	$\bar{\tau}_{AB.C}$	$P(\bar{\tau} = 0)$	F	$P(\bar{\tau}_N = \bar{\tau}_T = \bar{\tau}_R)$*
Composition								
F	0.18	<0.01	0.07	0.19	0.09	0.08	19.3	<0.01
W	0.06	<0.01	0.05	0.11	0.05	0.19		
A	−0.20	<0.01	−0.11	0.07	−0.12	0.04	7.4	<0.01
U	−0.13	<0.01	−0.16	<0.01	−0.04	0.07	4.0	0.02
Diversity/edge								
H'	−0.06	0.01	−0.12	<0.01	0.03	0.34	5.9	<0.01
D	0.06	0.01	0.12	<0.01	−0.03	0.34	6.0	<0.01
C	0.07	<0.01	0.11	<0.01	0.01	0.46		
E_T	−0.05	0.04	−0.14	<0.01	0.03	0.40	4.9	0.01
$E_{F/A}$	−0.07	0.01	−0.13	<0.01	<0.01	>0.99		
$E_{F/U}$	−0.08	<0.01	−0.15	<0.01	<0.01	0.95	7.5	<0.01
Patch characteristics								
F_S	0.09	<0.01	0.05	0.16	0.04	0.33	6.6	<0.01
$F_\#$	−0.13	<0.01	−0.12	<0.01	−0.02	0.54	4.2	0.02
A_S	−0.11	<0.01	−0.06	0.04	−0.10	0.01	6.9	<0.01
$A_\#$	0.01	0.61	−0.13	<0.01	0.02	0.61	9.9	<0.01
U_S	−0.05	<0.01	−0.05	<0.01	−0.02	0.31	3.6	0.03
$U_\#$	−0.12	<0.01	−0.15	<0.01	−0.04	0.09		
Patch configuration								
$D_{P/A}$	−0.07	<0.01	−0.05	0.03	−0.03	0.41		
D_G	−0.15	<0.01	−0.04	0.33	−0.12	0.12	10.7	<0.01

* Subscripts on $\bar{\tau}$ are N, Neotropical; T, Temperate; and R, Resident. Only significant ($P < 0.05$) results are presented.

sible. For instance, landscape scenes that were characterized by greater retention of natural habitats (i.e., forest and wetlands) supported greater relative abundances of Neotropical migrants than did landscapes with high proportions of human-dominated land uses (i.e., agriculture and urban land). The relative abundance of Neotropical migrants was lower in landscape scenes where diversity and edge were higher and forest edges were more complex ($D_{P/A}$); average forest patch size was small and the number of forest patches was high; and the distance among forest land tended to be high (D_G). In contrast, permanent residents were conspicuous by their "insensitivity" to variation in landscape structure, with only three of 18 landscape attributes yielding an average significant deviation from the null hypothesis of $\bar{\tau}_{AB.C} = 0$ (Table 2). Finally, temperate migrant abundances were associated with a moderate number of landscape structure attributes. The distinguishing pattern among these short-distance migrants was their strong correlation with diversity and edge attributes and the absence of association with attributes related to the amount, size of patch, and dispersion of forest habitats.

These results suggest that Neotropical migrants are related to landscape structure in a way that is unique when compared to species with other migratory habits. Differences among migratory strategies in landscape structure associations were tested using a one-way ANOVA (Proc GLM, SAS Institute 1985). Slope estimates ($\hat{\tau}_{AB.C}$) from Mantel's test were the dependent variables proportionately weighted by sample size (number of routes), and each landscape attribute was tested separately. ANOVA results confirmed that landscape structure associations differed ($P < 0.05$) among migratory habit categories in 13 of 18 landscape attributes (Table 2). Past studies have noted differences among migratory habitat categories with respect to population trends (Robbins et al. 1989*b*, Johnston and Hagan 1992). Explanations for these differences include: differential susceptibility of Neotropical migrants to forest fragmentation (Whitcomb et al. 1981, Robbins et al. 1989*a*); differential susceptibility of permanent residents, and, to a lesser degree, temperate migrants, to severe weather (Robbins et al. 1989*b*); and the broader environmental tolerances expected in permanent residents and temperate migrants relative to Neotropical migrants (Stevens 1989, O'Connor 1992). The patterns of association between relative abundance and landscape structure we report in Table 2 are consistent with these explanations.

TABLE 3. Mean slopes ($\bar{\tau}_{AB.C}$) and probabilities of $\bar{\tau}_{AB.C} = 0$ for the relations between landscape structure and trend of Neotropical migrants from 1966 to 1993 in the eastern United States. The number of species contributing to the estimate of the mean for Neotropical migrants ranges from 70 to 73.

Landscape attribute	Neotropical migrants		Landscape attribute	Neotropical migrants	
	$\bar{\tau}_{AB.C}$	$P(\bar{\tau} = 0)$		$\bar{\tau}_{AB.C}$	$P(\bar{\tau} = 0)$
Composition			Patch characteristics		
F	−0.02	0.12	F_S	−0.03	<0.01
W	0.01	0.62	$F_\#$	0.02	0.07
A	0.20	0.16	A_S	0.00	0.70
U	−0.01	0.29	$A_\#$	0.00	0.89
			U_S	0.00	0.79
Diversity/edge			$U_\#$	−0.01	0.36
H′	0.01	0.16			
D	−0.01	0.26	Patch configuration		
C	0.00	0.84	$D_{P/A}$	0.02	0.36
E_T	0.02	0.04	D_G	0.01	0.13
$E_{F/A}$	0.02	0.11			
$E_{F/U}$	−0.02	0.03			

Landscape associations in strata with varying land use histories

Because landscape structure varies regionally, habitat features and species composition are expected to vary geographically, as well. Habitat selection should thus reflect differing landscape conditions, habitat features, and species pools (Hansen et al. 1993), suggesting that a comprehensive understanding of species–habitat relations requires study in different areas throughout their geographic range (Martin 1992, Maurer and Heywood 1993). To ask whether or not landscape structure associations vary geographically, we focused on Neotropical migrants and a landscape structure measure reflective of forest fragmentation (D_G). We examined the association between Neotropical migrant relative abundance and forest fragmentation within physiographic strata as defined by Robbins et al. (1986). Bird species had to be observed on ≥10 routes in each stratum to be included in this analysis. Spearman rank correlation between mean $\tau_{AB.C}$ and mean D_G was used to test whether or not fragmentation effects on Neotropical migrant relative abundance were similar among strata (H_0: $r_s = 0$). Rank correlation among physiographic strata ($r_s = -0.67$, $P = 0.0006$) showed that slopes ($\bar{\tau}_{AB.C}$) differed among strata, indicating that Neotropical migrant associations with forest fragmentation varied in different portions of the eastern United States. This pattern could not be attributed simply to a general retention of forest habitats, because a comparable stratum-level analysis with the average proportion of forest habitats revealed no relation ($P = 0.19$). Whether variation in landscape structure associations among strata can be attributed to differences in land use history, or to variation in species composition (i.e., differences in the species comprising the Neotropical migrant group among strata), or to an interaction between these factors is difficult to address with our current data sets. Information on land use changes over time and a more detailed examination within strata of the species comprising the broad group called Neotropical migrants will be required to more fully address this issue.

Temporal trends and landscape structure

In addressing the relation between landscape structure and temporal trends in Neotropical migrants, we were limited by the cross-sectional nature of the land use data. Consequently, we were unable to directly examine the change in bird populations with change in landscape attributes over time. Despite this limitation, we were interested in whether or not landscape structure associations with temporal trends in Neotropical migrants were consistent with those observed in our previous analysis of spatial variation in relative abundance. To do this, we estimated route-specific trends for each Neotropical migrant from the BBS for the period 1966–1993. Again, bird species had to be observed on ≥30 routes to be included in the analysis. Mantel's test was used to quantify the association with landscape attributes as before, except that composite trend estimates were used as the dependent variable in the models.

Two results are notable. First, we found few associations between Neotropical migrant trends and landscape structure (Table 3); in particular, only three of 18 landscape attributes (total edge, edge among forest and urban land uses, and mean size of forest patches) were related to temporal trends in Neotropical migrants (H_0: $\bar{\tau}_{AB.C} = 0$, $P < 0.05$). Second, we found counterintuitive results with mean size of forest patches and total edge. Trends in Neotropical abundance were lower in those landscapes with larger forest patches and higher in those landscapes characterized by greater amounts of edge environments. The possibility exists that these

results are spurious, due simply to random chance, particularly in light of the small number of associations observed. However, the pattern is consistent among other landscape structure attributes with marginal ($0.05 < P < 0.20$) significance (Table 3). The proportion of the scene in forest and agriculture, Shannon diversity, forest/agriculture edge, and the number and dispersion of forest patches all indicate that Neotropical migrant trends tend to be lower in those landscape scenes that apparently have been subjected to lesser degrees of anthropogenic disturbance. Similar results have been observed by others; James et al. (1996) observed an average species decline among wood warblers in several upland and highland physiographic strata, and Sauer and Droege (1992) observed a preponderance of declining trends among Neotropical migrants along the Appalachian Mountains, regions characterized by a greater retention of forest habitats. These results suggest that factors other than fragmentation of forest habitats on the breeding ground should receive greater consideration in explaining temporal trends in Neotropical migrants. However, in the absence of land use time series, interpretation is difficult since the rate of land use change may be high in these relatively undisturbed areas.

Conclusions and Implications

Human actions associated with land use and natural resource management are having what many believe to be unprecedented effects on natural habitats and ecosystems. Understanding the influence of landscape structure on spatial and temporal patterns of species abundance is an important component of developing prescriptive management recommendations to conserve biological resources. We are far from that capability. Much of what has been reported in the literature is of a descriptive nature (Wiens 1992*b*), documenting patterns of association such as we have reported here. We acknowledge the danger of inferring causation from correlations, a pervasive problem associated with this scale of investigation. However, this should not preclude macroecological study. Careful interpretation and analysis of extant data sources serves an important heuristic function (Carpenter 1990), can lead to insights into the factors affecting patterns in the distribution and abundance of species (Brown 1984), and can provide a regional context for interpreting and guiding future local studies (Askins et al. 1990, Wiens 1992*a*). By coupling data on landscape structure to the BBS, and therefore to its sample design, statistical concerns about combining independent local studies to infer regional patterns can be ameliorated.

In this paper, we have demonstrated that Neotropical migrant birds as a group are broadly associated with landscape features and have patterns of association that differ from those of temperate migrants and nonmigratory species. To our knowledge, this is the first demonstration of these associations at a regional scale. However, the generality of our results is limited by two consequences of the association analysis. First, while migration habits define a grouping of management and ecological interest, birds in each migration group have a variety of breeding habitats and responses to fragmentation. Our results simply suggest that a preponderance of species in the group show an association, but we do not imply that any group is homogeneous in response to the landscape variables. Second, the landscape variables were chosen to explore whether or not associations between bird abundances and attributes of habitat composition, diversity, and fragmentation could be detected regionally, not to indicate which attribute among a related set of landscape features is most important in discriminating the groups.

Although the results we observed across the eastern United States were, on the whole, consistent with the findings from local studies, our analyses also highlight the risks associated with broad application of conservation strategies (Kareiva 1987, Martin 1992). Species with varying migratory habits responded differently to spatial variation in landscape structure, and Neotropical migrant species showed different patterns of association with forest fragmentation in different physiographic strata. Similarly, temporal patterns of Neotropical migrant abundance were associated with landscape structure in a way that was counter to those suggested by a spatial analysis of bird abundance. These results indicate that extrapolation of patterns observed in local studies may not hold regionally. Policy makers and managers should consider landscape context in defining and implementing conservation policy.

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