Using patch and landscape variables to model bird abundance in a naturally heterogeneous landscape

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Abstract: Regression models were developed to predict relative bird abundance in a naturally heterogeneous landscape using patch and landscape spatial scales. Breeding birds were surveyed with point counts on 140 study sites in 1997 and 1998. Aerial photographs were digitized to obtain habitat patch information, such as area, shape, and edge contrast. Classified remote-sensing data were gathered to provide information on landscape composition and configuration within a 1-km^2 area around the study sites. Stepwise multiple linear regression was used to develop 40 species-specific models within specific habitat types using patch and landscape characteristics. In 38 out of the 40 models, area of the habitat patch was first selected as the most important predictor of relative bird abundance. Variables related to the landscape were retained in 6 of the 40 models. In this naturally heterogeneous region, the landscape surrounding the patch contributed little to explaining relative bird abundance. The models were evaluated by examining how well they predicted relative bird abundance in a test set not included in the original analyses. The results of the test data were reasonable: >79% of the test observations were within the prediction intervals established by the training data.

Résumé : Nous avons élaboré des modèles de régression pour faire des prédictions de l'abondance relative d'oiseaux dans un paysage naturellement hétérogène à l'échelle de la parcelle et à l'échelle du paysage. Les oiseaux reproducteurs ont été inventoriés à 140 sites en 1997 et 1998 par des dénombrements ponctuels. Des photographies aériennes ont été digitalisées, fournissant des informations sur chaque parcelle de terrain, telles que la surface, la forme et le degré de contraste des bordures. Des données obtenues par télédétection ont été colligées pour compléter les informations sur la composition et la configuration du paysage dans un arrondissement de 1 km^2 autour de chaque site. Une régression linéaire multiple pas à pas, basée sur les caractéristiques des parcelles et du paysage, a été utilisée pour mettre au point 40 modèles spécifiques à l'espèce au sein de types d'habitats spécifiques. Dans 38 des 40 modèles, la surface de la parcelle d'habitat est apparue comme le plus important facteur prédictif de l'abondance relative des oiseaux. Les variables reliées au paysage ont été retenues dans 6 des 40 modèles. Dans cette région naturellement hétérogène, les variables reliées au paysage entourant la parcelle de terrain contribuent peu à expliquer l'abondance relative des oiseaux. Les modèles ont été évalués par vérification de leur valeur prédictive de l'abondance relative des oiseaux d'un ensemble de données ne faisant pas partie des analyses d'origine. Les résultats ont été satisfaisants; plus de 79 % des observations du test se situaient dans l'intervalle prévu d'après les modèles.

[Traduit par la Rédaction]

Introduction

Bird abundance and distribution are influenced by many factors operating at different scales. Traditionally, researchers considered the vegetation type and structure of a local area to be the most important predictors of bird species diversity (MacArthur and MacArthur 1961; Karr 1968). However, it has also been recognized that the quality of the habitat patch is just as important as vegetation type and structure (Wiens et al. 1993). Patch quality is reflected in characteristics such as size, shape, and juxtaposition with adjacent habitat patches. Larger patches are correlated with increased bird abundance and species richness (Ambuel and Temple 1983; Askins et al. 1987; Blake and Karr 1987; Bender et al. 1998). Changes in the microclimate around the outer portion of the patch are referred to as edge effects (Saunders et al. 1991) and may lead to higher rates of predation and brood parasitism, thus decreasing patch quality (Askins et al. 1990). The shape of the habitat patch and the type of edge contrast between adjacent habitat patches can influence the edge effects in the patch and have been shown to be important to some bird species (Hawrot and Niemi 1996).

Researchers have realized the shortcomings of focusing only on a local scale when considering ecological processes. The importance of the influence of the landscape context of the patch on the abundance and distribution of bird populations is becoming increasingly recognized (Howe 1984; Wiens et al. 1993; Hanowski et al. 1997; Miller et al. 1997; Mazerolle and Villard 1999; Saab 1999). Patterns in the landscape, such as the total amount of suitable habitat, the spatial arrangement of suitable patches, the diversity of different habitat types, and the level of fragmentation, may affect the suitability of a local habitat patch for different bird

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species. Pearson (1993), Sisk et al. (1997), and Pearson and Niemi (2000) found that the type of habitat surrounding a patch influenced bird abundance within the patch. Saab (1999) determined that landscape characteristics were the primary influence on the distribution of most bird species in riparian forests, while local patch and microhabitat characteristics were of secondary importance. Because of the declines in many bird populations during the past 30 years (Robbins et al. 1989; Askins et al. 1990), it is important to understand how birds are influenced by both local and landscape variables so that effective management policies can be developed. Research focused on these issues is becoming increasingly relevant as natural resources are managed in landscapes that are constantly changing (Sisk et al. 1997). Although the relationship between species distribution and landscape structure has received much attention in recent years, it has primarily been evaluated in agricultural and managed forest landscapes, i.e., landscapes that are fragmented as the result of human activities (Askins and Philbrick 1987; Pearson 1993; Flather and Sauer 1996; Hanowski et al. 1997; Trzcinski et al. 1999, Schmiegelow and Mönkkönen 2002). Few studies have evaluated the effects of landscape structure on breeding birds in naturally heterogeneous landscapes (Edenius and Sjöberg 1997; Mazerolle and Villard 1999).

The development of easily interpretable models that predict the distribution and abundance of wildlife is necessary for managing natural resources (Scott et al. 2002). Traditional models using ground measurements of vegetation structure are labor-intensive and not practical for managers of large, diverse areas. Only recently have researchers examined bird–habitat relationships using habitat cover types (Edenius and Sjöberg 1997; Farina 1997; Sisk et al. 1997; Sallabanks et al. 2000). Creating effective models using relatively easy to obtain and monetarily efficient data is important for land managers. With increased use of remote-sensing imagery and geographical information systems (GIS), models based on habitat cover type and landscape context are relatively easy and less expensive for managers to organize and use.

The main objectives of this study were to (*i*) gather data from a naturally heterogeneous landscape, (*ii*) create species-specific, habitat-specific predictive models, (*iii*) examine the relationship of relative bird abundance with both habitat-patch and landscape variables, and (*iv*) evaluate the resulting models by using a training set / test set approach.

Methods

Study area

The study was conducted on Seney National Wildlife Refuge (hereinafter “Refuge”), which encompasses 38 645 ha, in the Upper Peninsula of Michigan. This region is at the interface between the northern boreal forest and the eastern temperate deciduous forest. The Refuge has a diverse mosaic of relatively undisturbed upland and lowland forests and wetland habitats (Table 1, Fig. 1) and is primarily composed of northern hardwoods (sugar maple, yellow birch, eastern hemlock), upland mixed forests (quaking aspen, white birch, balsam fir), coniferous forests (red pine, white pine, jack pine), wooded wetlands (willow, tag alder, tamarack, *Larix laricina*; black spruce, *Picea mariana*), sedge marshes, and northern bogs (see Table 1 for other scientific names). The Refuge is naturally heterogeneous as the result of glacial activity, postglacial shoreline effects, and natural disturbances. The glacial and postglacial activity has resulted in a naturally fragmented landscape with intricate patterns of sandy ridges and lowland areas (Anderson 1982; Fig. 1). Wooded habitats dominate on the ridges, with marshes and bogs extending fingerlike projections in and around the wooded areas.

Avian-survey methods

One hundred and forty study sites within the Refuge were chosen. To ensure that study sites were located equally in all regions, the Refuge was divided into six sections of equal size. Study sites were chosen in a restricted random fashion within each section until it had a full complement of study sites. Restricted areas excluded from sampling included large bodies of water, areas adjacent to the Refuge headquarters or maintenance buildings, and, for logistic efficiency, areas farther than 1.6 km from roads, trails, or walkable dikes. In each study site, two census points were established with 100-m radii (3.14 ha per census point) a minimum of 200 m apart. Owing to underpacing in the field, it was necessary in some cases to drop one census point of a pair or combine two study sites into one. Of the 140 study sites, 121 had two census points, 10 had one census point, 3 had three census points, and 6 had four census points. Observers (three in total) were trained in distance estimation, and data sheets were examined to ensure that there was no double-counting of individuals between census points. The points were spatially determined using the global positioning system (GPS) Trimble Pathfinder (Trimble Navigation, Ltd. 1995), and locations were imported into the GIS program ArcView (ESRI, Inc. 1996).

We used a 10-min point count (Howe et al. 1997; Chase et al. 2000) to determine the composition of the bird community at each census point in each study site. Each study site was surveyed once in 1997 and once in 1998. Each year, surveying efforts were rotated among the six sections (see above), ensuring that each section was the focus of survey efforts once every 6 sampling days. All surveys were completed 0–4 h after sunrise between 29 May and 10 July. The identity of all individuals seen or heard inside the 100 m radius circle at each census point was recorded. All birds observed within the census point were assigned to a specific habitat patch (location at first detection) during surveys. Individuals that were unidentified, were located outside of the 100 m radius circle, or flew over the habitat were recorded but not used in the analyses. Surveys were not conducted if weather conditions (i.e., wind, rain) did not permit reasonable bird activity.

Local and landscape habitat cover maps

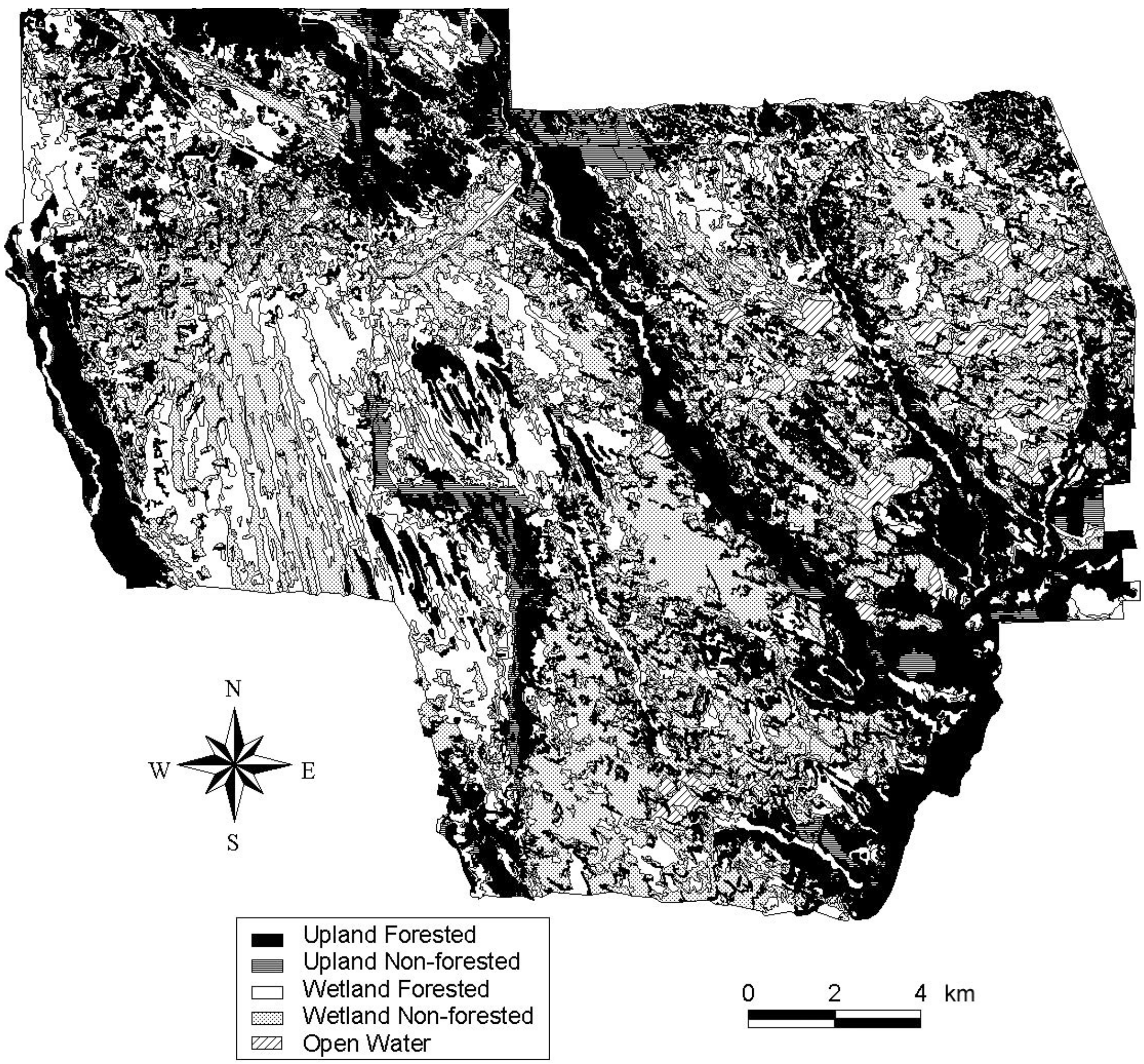
For each study site, a cover map was created by delineating habitat patches within the 100-m radius of each census point, based on the interpretation of 1 : 13 500 infrared photographs taken in August 1996. Each photograph was georeferenced and habitat patches were digitized into ArcView. The minimum mapping unit was approximately 0.01 ha. Habitat patches that extended beyond the boundary of the census point were truncated at the boundary but were incorporated

Table 1. Habitat cover types used to characterize the habitat patches in the 140 study sites, with numbers of sites in the training and test sets and a description of the habitat type.

Habitat type	Training set	Test set	Dominant vegetation
Northern hardwood (NH)	16 (25)	3 (5)	Sugar maple (*Acer saccharum*), beech (*Fagus grandifolia*), yellow birch (*Betula alleghaniensis*), eastern hemlock (*Tsuga canadensis*)
Upland mixed forest (UM)	43 (78)	20 (34)	Quaking aspen (*Populus tremuloides*), white birch (*Betula papyrifera*), balsam fir (*Abies balsamea*), white spruce (*Picea glauca*), red pine (*Pinus resinosa*), white pine (*Pinus strobus*)
Red pine (RP)	24 (49)	11 (19)	Red pine
Jack pine (JP)	28 (66)	10 (22)	Jack pine (*Pinus banksiana*)
Mixed red pine (MR)	23 (43)	12 (24)	Red pine, jack pine, white pine
Lowland shrub marsh (LS)	34 (68)	13 (19)	Tag alder (*Alnus rugosa*), willow (*Salix* spp.), bog birch (*Betula pumila*), sedge (*Carex* spp.), Canada bluejoint grass (*Calamagrostis* spp.)
Sedge marsh (SM)	29 (42)	14 (36)	Sedge, Canada bluejoint grass, cotton grass (*Eriophorum* spp.)
Cattail marsh (CM)	10 (17)	8 (13)	Cattail (*Typha* spp.), sedge

Note: Numbers in parentheses show the number of habitat patches.

Fig. 1. Cover map showing the naturally heterogeneous nature of the Seney National Wildlife Refuge, Michigan, U.S.A.



into the landscape analyses described below. Because the shapes of many of the habitat patches were complex (Fig. 1) and the majority of the study sites did not have point counts directly adjacent to each other, a habitat patch that extended within the boundary of two point counts was considered to be two separate patches. Each habitat patch was classified into 1 of 23 habitat cover type categories. A bird species had to be found on at least 20% of the sites within a particular habitat cover type and a minimum of 10 sites to be modeled to ensure that sample sizes were reasonable for statistical analysis. As a result, eight cover types were used in the analysis, representing 66% of the total area of the study sites (Table 1). Models were not developed for the other 15 habitat types; however, these were incorporated into the landscape analyses. Forested habitat types were characterized with a habitat-modifier variable reflecting the size and density of trees in the habitat patch (Table 2). Habitat patches and cover types were field-verified for each of the 140 study sites.

The landscape habitat cover map was derived from remote-sensing data. Four Landsat Thematic Mapping images (30 × 30 m resolution) were obtained for the Refuge for May 1992, July 1992, August 1993, and October 1992. Four images were used because the change in spectral reflectance of habitat types in different seasons was necessary for accurate classification. Each pixel was classified into 1 of 11 different habitat cover type categories (northern hardwood, upland mixed forest, red pine, jack pine, hayfield/grass, upland shrub, lowland shrub marsh, sedge/cattail marsh, bog, submergent, or open water) with the GIS image-processing program IMAGINE, using an unsupervised classification (ERDAS, Inc. 1997). The accuracy of the classification was examined using 58 predetermined points with known cover types located across the Refuge. The accuracy of the classification was 88%. For the analyses, the landscape surrounding each study site was defined as a 1-km^2 area (100 ha; Drolet et al. 1999) centered on the midpoint between the census points. The landscape-index program FRAGSTATS (McGarigal and Marks 1994) was used to compute landscape metrics on each landscape image. FRAGSTATS was also used to compute patch metrics in each habitat patch on every study site.

Model development: summary of patch and landscape variables

Because FRAGSTATS produces a large number of potential variables, variables were selected a priori to reduce the number of variables considered in the models. Patch and landscape variables generated by FRAGSTATS were selected based on our judgment of their biological significance to the bird community. These variables characterized patch characteristics, edge effects, landscape heterogeneity, and habitat diversity. Paired correlations between variables were examined, and one variable of a correlated pair was eliminated if the correlation was high ($r > |0.60|$). The variable removed was the one we considered to be the least biologically meaningful. As a result of this process, nine variables were retained as independent variables in the regression models, of which four were habitat-patch variables and five were landscape variables (Table 2). The four habitat-patch variables were patch area, patch fractal dimension, a habitat modifier indicating the average size and density of trees in the patch, and a patch edge contrast index indicating the type of edge surrounding the patch. The five landscape variables can be grouped into those that quantify landscape composition (the proportion of habitat in the landscape and patch richness density, which measures the habitat diversity in the landscape) and those that quantify landscape configuration (a landscape edge contrast index, which measures the amount and type of edge in the landscape, patch density in the landscape, and an interspersion/juxtaposition index, which measures landscape heterogeneity).

Statistical analyses

All statistical analyses were conducted using the statistical software program SAS (SAS Institute, Inc. 1996). Stepwise multiple linear regression was used to develop species-specific models to predict relative bird abundance based on the four patch and five landscape variables within eight specific-habitat cover types. The mean number of individuals per habitat patch (i.e., the average from the 1997 and 1998 surveys) was the dependent variable in the models. During the stepwise procedure, an independent variable had to be significant ($P < 0.05$) to be retained in the models. Because previous studies have indicated that species belonging to various migratory groups respond differently to landscape structure (Askins and Philbrick 1987; Flather and Sauer 1996), bird species in our study were characterized as long-distance migrants, short-distance migrants, or permanent residents (Ehrlich et al. 1988).

Residual plots and Cook's distance were examined for normality and outliers, respectively. Because count data typically follow a Poisson distribution (Gutzwiller and Anderson 1986; Rao 1998), a square-root transformation was applied to stabilize the variance. However, when the residual plots of the transformed data were examined, the transformation was only moderately helpful. The residual plots were not significantly changed by the transformation in terms of the distribution and variance of residuals. For ease of interpretation we used untransformed data.

To evaluate the validity of the models, each was tested with an independent test set of study sites (Morrison et al. 1987; Dettmers and Bart 1999). During model building, study sites were organized into groups that had overlapping 1-km^2 landscape images. These groups were randomly chosen to be in the training set or test set until 24% of the study sites were in the test set. Hence, study sites in the test set were not biased by having adjacent sites in the training set, and provided a realistic evaluation of the models. The training and test sets had 106 and 34 sites, respectively. To evaluate each model's performance, the percentage of the observed values in the test set that fell within the 95% prediction intervals established by the training set was calculated. The root mean square error divided by the mean of the dependent variable (i.e., a standardized standard deviation) was used as a coefficient of variation. For example, if this coefficient of variation is 1.43, the standard deviation is 143% of the mean, and these values reflect the width of the prediction interval. A model with a large coefficient of variation will have a large prediction interval, therefore the uncertainty in the prediction is also relatively high. The coefficient of variation is a better indicator of model performance than R^2 in this case because R^2 is scale-dependent and is strongly influenced by the relationship of bird abundance with area.

Results

A total of 6542 individuals representing 113 bird species were recorded on the study sites during surveys in 1997 and 1998. Common Yellowthroat, Swamp Sparrow, Nashville

Table 2. Local patch and landscape variables gathered for each site and entered into the stepwise multiple regression process.

Variable	Description
Local patch variable	
Area (ha)	Area: area of the censused patch
Frac	Fractal dimension: shape complexity of the censused patch; 1 for simple geometric shapes (i.e., circle) and approaching 2 for highly convoluted shapes
Mod	Habitat modifier: 1 of 9 numerical codes indicating the average size and density of trees in the censused patch[a]
Edcon (%)	Patch edge contrast index: percentage of edge involving the censused patch weighted by the degree of structural and floristic contrast between adjacent patches; 100% when all edge is maximum contrast and approaching 0 when all edge is minimum contrast
Landscape variable	
Prop	Proportion: proportion of the landscape composed of the corresponding habitat cover type modeled
PRD (no./100 ha)	Patch richness density: number of different habitat types present in the landscape; a measure of habitat diversity in the landscape
Edge (m/ha)	Landscape edge contrast index: density of edge in the landscape involving all habitat types weighted by the degree of contrast between adjacent patches; larger values result from landscapes with large amounts of hard edge
PD (no./100 ha)	Patch density: density of patches in the landscape
IJ (%)	Interspersion/juxtaposition index: the extent to which habitat types are interspersed in the landscape (landscape heterogeneity); higher values result from landscapes in which habitat types are well interspersed (i.e., equally adjacent to each other)

Note: The table is modified from Saab (1999). For more information on how these indices are computed see McGarigal and McComb (1995).
[a]Seedlings/saplings (1 = regenerating; 2 = poorly stocked; 3 = well stocked), pole timber (4 = poorly stocked; 5 = medium-stocked; 6 = well stocked), and saw timber (7 = poorly stocked; 8 = medium-stocked; 9 = well stocked).

Warbler, Ovenbird, Yellow-rumped Warbler, and Red-eyed Vireo were the most abundant species (see Table A1 for scientific names). The numbers and species of birds recorded were similar in the 2 years. In 1997, 3444 individuals of 100 species were recorded, while in 1998, 3098 individuals of 99 species were recorded. In both years, the six species listed above were the most abundant species on the study sites.

Twenty-two bird species in eight cover types (a total of 40 potential models) had sample sizes that met our criteria for modeling. Thirty-nine statistically significant models were developed. One species selected for modeling, Cedar Waxwing in red pine, did not retain any variables at the 0.05 level, so no model was developed for this species/habitat combination. The models built for each bird species were organized into migratory groups: long-distance migrants (Table 3), short-distance migrants (Table 4), and permanent residents (Table 5). The R^2 values for the models ranged from 0.06 to 0.86, with P values ranging from 0.03 to <0.01. The coefficients of variation ranged from 0.45 to 2.55, with a mean of 1.43. The percentage of the observed values in the test set that fell within the 95% prediction intervals varied from 79 to 100% (Tables 3–5).

The 17 models developed for the long-distance migrants had R^2 values that ranged from 0.18 to 0.86. Twelve models retained patch area as the only independent variable, 3 models included landscape-composition variables, 2 models retained landscape-configuration variables, and 1 model incorporated a local patch variable related to edge effects. The coefficients of variation ranged from 0.45 to 1.90, with a mean of 1.07. The percentages of the test set that fell in the 95% prediction intervals ranged from 79 to 100% (Table 3).

The 18 models developed for the short-distance migrants had R^2 values ranging from 0.10 to 0.77. Eleven models retained patch area as the only independent variable, 3 models retained landscape-configuration variables, 3 models incorporated a local patch variable related to edge effects, and 1 model incorporated a landscape-composition variable. The coefficients of variation ranged from 0.79 to 2.27, with a mean of 1.61. The percentages of the test set that fell in the 95% prediction intervals ranged from 82 to 100% (Table 4).

The models for the permanent resident species were the weakest. The R^2 values for these species ranged from 0.06 to 0.31, with patch area as the only variable retained in all four models. The coefficients of variation ranged from 1.74 to 2.55, with a mean of 2.10. The percentages of the observed values in the test set that fell within the 95% prediction intervals ranged from 91 to 97% (Table 5).

All of the nine independent variables, four habitat-patch and five landscape variables, that were included in the stepwise regression process were retained in at least one model (see Table 6 for summary statistics). Patch area was retained in 38 models. Patch edge contrast index and fractal dimension (both edge-effect variables) were retained in three models and one model, respectively. The habitat modifier, indicating the size and density of trees in the habitat patch, was retained in three models. Proportion of habitat in the landscape of the habitat type modeled and patch richness density (both landscape-composition variables describing the habitat types in the landscape) were retained in three models and one model, respectively. Patch density, landscape edge contrast index, and interspersion/juxtaposition index (all landscape-configuration variables describing the spatial arrangement of patches in the landscape) were retained in two models, one model, and three models, respectively.

In every model developed, patch variables had more influence on bird abundance than landscape variables. In 38 of the 39 models developed, area of the habitat patch was most related to relative bird abundance and accounted for 6–80%

Table 3. Models generated for species characterized as long-distance migrants.

			Partial R^2					
Bird/habitat	Training set (n)	Model[a]	Area	Mod	Edcon	Prop	Edge	IJ
Eastern Wood-Pewee / northern hardwood	25	0.05 + 0.19Area						
Alder Flycatcher / lowland shrub marsh	68	1.07 + 0.38Area – 0.03Edcon	0.56		0.10			
Red-eyed Vireo / northern hardwood	25	–3.30 + 0.71Area + 5.13Prop + 0.02Edge	0.70			0.07	0.05	
Red-eyed Vireo / upland mixed forest	78	0.06 + 0.32Area						
Nashville Warbler / jack pine	66	0.27 + 0.33Area						
Nashville Warbler / lowland shrub marsh	68	0.03 + 0.15Area						
Nashville Warbler / mixed red pine	43	–0.03 + 0.43Area						
Nashville Warbler / red pine	49	0.05 + 0.26Area						
Nashville Warbler / upland mixed forest	78	0.27 + 0.34Area – 2.07Prop	0.30			0.05		
Black-throated Green Warbler / northern hardwood	25	–8.26 + 0.27Area + 0.98Mod	0.43	0.10				
Black-throated Green Warbler / upland mixed forest	78	0.05 + 0.14Area						
Ovenbird / mixed red pine	43	–0.02 + 0.29Area						
Ovenbird / northern hardwood	25	–0.25 + 0.74Area						
Ovenbird / upland mixed forest	78	–0.12 + 0.71Area						
Common Yellowthroat / cattail marsh	17	5.37 + 0.93Area – 6.07Prop – 0.05IJ	0.72			0.08		0.06
Common Yellowthroat / lowland shrub marsh	68	0.36 + 0.89Area						
Common Yellowthroat / sedge marsh	42	0.36 + 0.53Area						

Note: The partial R^2 for each variable in the model and the explained variation (R^2) from patch variables, landscape variables, and the full model are shown.

[a]For descriptions of variables see Table 2.

[b]The number of observations in the test set that fell within the 95% prediction intervals.

of the variation. Only the model of American Robin in upland mixed forest had a variable other than area (fractal dimension), which accounted for most of the variation in abundance. Of the 39 models, 27 only retained patch area at the 0.05 level. Landscape variables were retained in 6 of the 39 models. These landscape variables accounted for 5–14% of the variation in bird abundance. Of these six models, three were bird species characterized as long-distance migrants and three were short-distance migrants. No model for a permanent resident bird species retained landscape variables.

Discussion

The influence of local habitat patch characteristics, particularly patch area, on bird communities is well documented (Askins et al. 1987; Blake and Karr 1987; Hawrot and Niemi 1996; Bender et al. 1998). The structure of the landscape has also been reported to influence bird species richness and abundance in different seasons and different regions (Askins and Philbrick 1987; Pearson 1993; McGarigal and McComb 1995; Flather and Sauer 1996; Hanowski et al. 1997; Sisk et al. 1997; Saab 1999; Trzcinski et al. 1999; Pearson and Niemi 2000). Landscape composition and configuration both have an influence on bird assemblages. Landscape composition reflects the amount of suitable habitat in the landscape that can be used by a bird. The amount of suitable habitat influences metapopulation dynamics and may affect rates of immigration from source to sink populations (Wiens et al. 1993). Landscape configuration refers to the spatial distribution of habitat patches in the landscape. The distribution of patches may influence the movement patterns of individuals because variability in habitat types, distance between suitable habitat types, and variability in patch boundaries may affect the permeability of the landscape (Wiens et al. 1993; McGarigal and Marks 1994). The structure of the landscape may also influence habitat quality within a habitat patch in terms of predation, brood parasitism, competition, and microclimate.

The majority of studies that have examined the relationship between landscape structure and bird communities have done so in landscapes that are fragmented as the result of human disturbance (i.e., agriculture, urban development, managed forests). Landscape structure appears to have a pervasive influence on bird assemblages in human-fragmented landscapes

R^2						
Patch	Landscape	Full model	*P*	Coefficient of variation	Test set (*n*)	Percent correct[b]
0.41	0.00	0.41	<0.001	1.07	5	100
0.66	0.00	0.66	<0.001	1.21	19	95
0.70	0.12	0.82	<0.001	0.49	5	100
0.44	0.00	0.44	<0.001	1.16	34	97
0.18	0.00	0.18	<0.001	1.61	22	100
0.29	0.00	0.29	<0.001	1.90	19	100
0.60	0.00	0.60	<0.001	1.24	24	88
0.63	0.00	0.63	<0.001	1.20	19	79
0.30	0.05	0.35	<0.001	1.46	34	100
0.53	0.00	0.53	<0.001	0.72	5	100
0.24	0.00	0.24	<0.001	1.72	34	100
0.65	0.00	0.65	<0.001	1.14	24	88
0.75	0.00	0.75	<0.001	0.64	5	100
0.71	0.00	0.71	<0.001	0.88	34	100
0.72	0.14	0.86	<0.001	0.45	13	85
0.80	0.00	0.80	<0.001	0.52	19	84
0.50	0.00	0.50	<0.001	0.84	36	100

(Askins and Philbrick 1987; Pearson 1993; Flather and Sauer 1996; Hanowski et al. 1997; Trzcinski et al. 1999), although the effects appear to be less pronounced in managed forests, where habitat loss is not permanent (McGarigal and McComb 1995; Drolet et al. 1999; Mönkkönen and Reunanen 1999). However, the influence of landscape structure in a naturally heterogeneous context is relatively unknown (Edenius and Sjöberg 1997). Edenius and Sjöberg (1997) examined the relationship between landscape composition and bird-species diversity and density in a naturally fragmented boreal biome in Sweden. They found that the composition of the landscape within 1 km of the forest patch had no effect on species richness or density. Instead, they found that patch area had the strongest effect. Woinarski (1993) studied naturally fragmented monsoon rain forest remnants in Australia and found that bird species diversity and abundance were correlated with patch size. The composition of the landscape (the amount of monsoon rain forest within 5 km of the study sites) had a relatively minor impact on birds.

The results of Edenius and Sjöberg (1997) and Woinarski (1993) are consistent with the results of our study, which suggests that landscape structure has a minimal influence on relative species abundance in this naturally heterogeneous landscape after patch area is accounted for. Only a few bird species were influenced by landscape context in this area, and for those models that included landscape information, the explanatory contributions were minimal. Patch area had the primary influence on bird abundance. The correlation of patch area with bird abundance is well documented (Blake and Karr 1987; Wiens 1989; Norment 1991; Woinarski 1993). The range of patch sizes in our analyses (0.01–9.42 ha) was both above and below the territory size of most species studied here. Because birds use the structure of the vegetation to select breeding territories (James 1971; James and Wamer 1982; Niemi and Hanowski 1984), the amount of available habitat as measured by patch area was most important. Hence, patch area had a strong influence in the models. Birds in this landscape likely select areas based on the presence of the appropriate habitat type and the size of the habitat patch (which reflects the number of territories available; see Schmiegelow and Mönkkönen 2002). Landscape variables may not be important in this selection process because the landscape may be of similar quality (i.e., fragmentation, habitat diversity, permeability, edge contrast) across the Refuge.

Table 4. The models generated for species characterized as short-distance migrants.

Bird/habitat	Training set (*n*)	Model[a]	Partial R^2 Area	Frac	Mod	Edcon	PD	IJ	PRD
Yellow-bellied Sapsucker / northern hardwood	25	–0.37 + 0.17Area + 0.01Edcon	0.28			0.14			
Winter Wren / upland mixed forest	78	0.01 + 0.08Area							
Sedge Wren / sedge marsh	42	–0.16 + 0.49Area							
Hermit Thrush / jack pine	66	0.15 + 0.08Area – 0.002Edcon	0.19			0.06			
Hermit Thrush / mixed red pine	43	–0.22 + 0.16Area + 0.003PD	0.45				0.07		
Hermit Thrush / upland mixed forest	78	0.02 + 0.19Area							
American Robin / upland mixed forest	78	1.88 – 1.27Frac							
Yellow-rumped Warbler / jack pine	66	0.04 + 0.39Area							
Yellow-rumped Warbler / mixed red pine	43	–0.02 + 0.46Area							
Yellow-rumped Warbler / upland mixed forest	78	0.12 + 0.18Area							
Savannah Sparrow / sedge marsh	42	–0.10 + 0.20Area							
Song Sparrow / lowland shrub marsh	68	0.11 + 0.11Area							
Song Sparrow / sedge marsh	42	0.04 + 0.14Area							
Chipping Sparrow / mixed red pine	43	1.65 + 0.44Area – 0.03IJ + 0.01PD	0.56				0.04	0.05	
Chipping Sparrow / upland mixed forest	78	0.77 + 0.11Area – 0.10Mod	0.24		0.07				
White-throated Sparrow / upland mixed forest	78	1.05 + 0.08Area – 0.11Mod – 0.06PRD + 0.01IJ	0.12		0.11			0.05	0.06
Swamp Sparrow / lowland shrub marsh	68	–0.13 + 1.26Area							
Swamp Sparrow / sedge marsh	42	0.24 + 0.68Area							

Note: The partial R^2 for each variable in the model and the explained variation (R^2) from patch variables, landscape variables, and the full model are shown.

[a]For descriptions of variables see Table 2.

[b]The number of observations in the test set that fell within the 95% prediction intervals.

Landscape structure may have less of an impact in these naturally fragmented systems because edges between habitat patches are not as hard (i.e., have lower contrast) as those in agricultural or urban areas, and adjacent patches are not as inhospitable. Rather, landscapes that are naturally fragmented are composed of habitat patches which vary in quality and permeability to movement. These landscapes are not static but are composed of patches that shift in space as the result of natural disturbances. Bird species in these natural landscapes have likely evolved strategies for coping with natural fragmentation effects, and their response to landscape structure may be less pronounced (McGarigal and McComb 1995; Kirk et al. 1996).

Previous studies have shown that migratory groups respond to landscape structure in different ways (Askins and Philbrick 1987; Flather and Sauer 1996). In our study, long-distance migrants, short-distance migrants, and permanent residents were seldom influenced by landscape context. The models developed for the long-distance migrants were better overall in terms of the explained variation and lower coefficient of variation than those developed for the other migratory groups, suggesting that long-distance migrants may be most influenced by patch area. The models developed for the permanent-resident species were the weakest of those for the three migratory groups.

In general, the models developed in this study performed well in terms of the amount of variation in abundance they explained for most species. In a validation of the models to see how well they could predict relative bird abundance in a test set, the models performed well, predicting 79–100% of the values in the test sets within the 95% prediction intervals established by the training data. The large coefficients of variation of many of the models may have been due partly to some sample sizes being relatively small and to annual vari-

R^2						
Patch	Landscape	Full model	*P*	Coefficient of variation	Test set (*n*)	Percent correct[b]
0.42	0.00	0.42	<0.01	0.99	5	100
0.19	0.00	0.19	<0.001	2.27	34	100
0.51	0.00	0.51	<0.001	2.15	36	100
0.25	0.00	0.25	<0.001	2.26	22	86
0.45	0.07	0.52	<0.001	1.36	24	92
0.46	0.00	0.46	<0.001	1.21	34	100
0.16	0.00	0.16	<0.001	2.10	34	82
0.54	0.00	0.54	<0.001	1.52	22	91
0.52	0.00	0.52	<0.001	1.45	24	92
0.24	0.00	0.24	<0.001	1.36	34	94
0.46	0.00	0.46	<0.001	1.77	36	100
0.10	0.00	0.10	<0.001	2.25	19	95
0.28	0.00	0.28	<0.001	1.61	36	100
0.56	0.09	0.65	<0.001	1.45	24	100
0.31	0.00	0.31	<0.001	1.67	34	97
0.23	0.11	0.34	<0.001	1.97	34	94
0.77	0.00	0.77	<0.001	0.88	19	100
0.59	0.00	0.59	<0.001	0.79	36	100

ation. The field season of 1997 was wet and cold with a late spring, whereas the 1998 field season was dry and warmer with an early spring. In addition, specific vegetation variables (i.e., canopy height, shrub density, etc.) that are important to birds (James and Wamer 1982; Niemi and Hanowski 1984; Díaz et al. 1998) were not included in the analyses because they are expensive and time-consuming to gather. One of the goals of this study was to examine the effectiveness of models using data that are relatively easy and inexpensive to collect, such as remote-sensing data.

Considering the high variability inherent in ecological data, these models were successful in explaining a large proportion of the variation in relative bird abundance and correctly predicted >79% of the sites reserved in the test set. These models could easily be applied by land managers within the region of study. With remote-sensing and subsequent GIS coverage becoming routinely available, managers can estimate the relative abundance of a species within a selected habitat with appropriate confidence intervals. As the amount of habitat in an area changes as a result of natural or management activities, changes in the bird fauna can be estimated. These types of models can provide managers with a useful tool for making more informed management decisions and predicting future changes in bird populations that would result from alternative management scenarios (Niemi et al. 1998).

The results of the study were influenced by the scale of the investigation. The resolution of the digital habitat cover maps (as set by the minimum patch digitized: 0.01 ha), the resolution of the Landsat imagery (30 × 30 m), and the extent of the landscape analyzed (100 ha) influenced the results. In this area, the 30 × 30 m resolution of the Landsat imagery may be too large to capture all the variation in habitats that may be important to birds. Reanalyzing the data

Table 5. The models generated for species charactzerized as permanent residents.

Bird/habitat	Training set (*n*)	Model[a]	R^2 Patch	R^2 Landscape	R^2 Full model	*P*	Coefficient of variation	Test set (*n*)	Percent correct[b]
Blue Jay / upland mixed forest	78	–0.01 + 0.09Area	0.25	0.00	0.25	<0.001	2.26	34	94
Black-capped Chickadee / upland mixed forest	78	0.07 + 0.05Area	0.06	0.00	0.06	0.03	2.55	34	97
Red-breasted Nuthatch / upland mixed forest	78	–0.01 + 0.10Area	0.31	0.00	0.31	<0.001	1.86	34	91
Cedar Waxwing / mixed red pine	43	0.10 + 0.13Area	0.19	0.00	0.19	<0.01	1.74	24	96
Cedar Waxwing / red pine	49	No variables significant at $P = 0.05$ for entry into the model							

Note: The explained variation (R^2) from patch variables, landscape variables, and the full model are shown.
[a]For descriptions of variables see Table 2.
[b]The number of observations in the test set that fell within the 95% prediction intervals.

Table 6. Summary statistics for patch and landscape variables entered into the stepwise multiple regression models.

Variable[a]	Minimum	Maximum	Mean	SE
Local patch variable				
Area (ha)	0.01	9.42	1.01	0.05
Edcon (%)	0.00	100.00	47.23	0.91
Frac	1.25	1.95	1.43	<0.01
Mod	1	9	7	0.06
Landscape variable				
Prop[b]				
Northern hardwood (%)	0.00	85.12	4.98	1.09
Upland mixed forest (%)	0.00	53.99	7.98	0.79
Red pine (%)	0.00	54.18	13.42	0.92
Jack pine (%)	0.00	46.47	12.80	0.99
Sedge/cattail marsh (%)	0.00	71.72	11.77	1.35
Lowland shrub marsh (%)	0.00	82.83	18.79	1.60
PD (no./100 ha)	10.20	147.94	64.55	2.27
Edge (m/ha)	28.74	187.17	109.50	2.88
PRD (no./100 ha)	4.08	12.24	9.20	0.14
IJ (%)	29.39	88.26	66.94	0.84

[a]For descriptions see Table 2.
[b]Only one of these habitat types was entered into each model: the habitat cover type corresponding to the habitat cover type of the model. Although a percentage is given here, a proportion was used in the models.

using finer and (or) coarser habitat cover maps may yield different results. Habitat selection occurs at multiple scales, and habitat associations often vary among scales of investigation (McGarigal and McComb 1995).

The majority of the landscape variables used in this study were composite measures describing landscape characteristics for all habitat types pooled, with the exception of the proportion of habitat in the landscape of the habitat cover type modeled. Landscape variables that described the configuration of specific habitat cover types may have been important (Miller et al. 1997); however, this would have greatly increased the number of potential explanatory variables. Variables were chosen that were believed to be the most biologically relevant in predicting bird abundance. Because birds use a variety of habitat types throughout the landscape (Kirk et al. 1996), the majority of variables we chose were composite variables.

Conclusions

Birds in naturally fragmented landscapes may respond differently to landscape structure than birds in human-fragmented landscapes. Our results suggest that in this naturally heterogeneous landscape, relative bird abundance was best predicted from the area of suitable habitat patch. Landscape variables contributed little to predicting relative bird abundance after patch area was accounted for. The models developed in this study provided significant statistical relationships, and an evaluation of the models with an independent test set found that they correctly predicted >79% of the test set within 95% prediction intervals. The models could be relatively easily applied to selected species and selected habitat cover types by management in the region of study. With the existing technology of remote-sensing imagery and GIS, the general methodology could be applied to a wide range of land conditions and potential management scenarios where suitable data exist.

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Appendix A

Table A1. Common and scientific names of the bird species used in the analyses.

Common name	Scientific name	Individuals/ha in all habitats combined	Individuals/ha in specific habitats modeled[a]
Alder Flycatcher	*Empidonax alnorum*	0.10	LS 0.54
American Robin	*Turdus migratorius*	0.24	UM 0.23
Black-capped Chickadee	*Parus atricapillus*	0.28	UM 0.19
Black-throated Green Warbler	*Dendroica virens*	0.06	NH 0.53, UM 0.18
Blue Jay	*Cyanocitta cristata*	0.03	UM 0.07
Cedar Waxwing	*Bombycilla cedrorum*	0.56	MR 0.20, RP 5.09
Chipping Sparrow	*Spizella passerina*	0.19	MR 0.39, UM 0.19
Common Yellowthroat	*Geothlypis trichas*	0.84	CM 1.50, LS 1.78, SM 2.95
Eastern Wood-Pewee	*Contopus virens*	0.02	NH 0.19
Hermit Thrush	*Catharus guttatus*	0.15	JP 0.91, MR 0.16, UM 0.20
Nashville Warbler	*Vermivora ruficapilla*	0.54	JP 1.58, LS 0.20, MR 0.35, RP 0.28, UM 0.44
Ovenbird	*Seiurus aurocapillus*	0.15	MR 0.22, NH 0.89, UM 0.48
Red-breasted Nuthatch	*Sitta canadensis*	0.10	UM 0.06
Red-eyed Vireo	*Vireo olivaceus*	0.20	NH 0.92, UM 0.37
Savannah Sparrow	*Passerculus sandwichensis*	0.04	SM 0.04
Sedge Wren	*Cistothorus platensis*	0.09	SM 0.14
Song Sparrow	*Melospiza melodia*	0.15	LS 0.34, SM 0.09
Swamp Sparrow	*Melospiza georgiana*	0.45	LS 1.72, SM 1.48
White-throated Sparrow	*Zonotrichia albicollis*	0.22	UM 0.26
Winter Wren	*Troglodytes troglodytes*	0.05	UM 0.08
Yellow-bellied Sapsucker	*Sphyrapicus varius*	0.02	NH 0.15
Yellow-rumped Warbler	*Dendroica coronata*	0.33	JP 0.89, MR 0.54, UM 0.30

[a]See Table 1 for an explanation of habitat codes.