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RESPONSE OF AVIAN COMMUNITIES IN LARGE-RIVER FLOODPLAINS TO ENVIRONMENTAL VARIATION AT MULTIPLE SCALES

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Abstract. Large-river floodplains have been subjected to profound human-caused alteration, but subsequent effects on landbirds in these habitats are largely unknown. To assess the extent to which landscape measures might serve as ecological indicators in these systems, we examined patterns of habitat use by forest birds along a 380-km stretch of the Wisconsin River, USA. We surveyed forest bird communities during the breeding season in 1999 and 2000 at 48 sites divided among six reaches of the 100-year floodplain. Several tree and bird species thought to be characteristic of floodplain forests in Wisconsin, based on earlier surveys, appear to have declined in abundance or were absent altogether, even in reaches located in a 150-km undammed stretch of the river. Bird species richness was similar among reaches, but overall abundance was notably lower at the two northernmost reaches. The most widespread and abundant birds were those that are typically associated with forest edge habitats, but several species associated with forest interior conditions were also relatively abundant. A canonical correspondence analysis based on a model derived from the entire pool of environmental variables indicated that most of the variation in avian community structure was accounted for by geographic variables describing latitudinal changes and distance from potential source habitats along the Mississippi River. Partial ordinations and univariate variance partitioning, however, showed confounding among environmental variable sets and revealed that local-habitat measures tended to explain somewhat more variation than geographic variables. Metrics describing landscape pattern and composition accounted for the least amount of independent variation among the three variables sets. Our results indicate that landscape measures are necessary, but not sufficient to describe patterns of habitat use by forest birds in the Wisconsin River floodplain. Moreover, our data suggest that, while maintaining habitat for forest birds is still possible in these areas, it may be more difficult to conserve species with an affinity for conditions that characterize floodplains. This study further demonstrates that, for some species, designations such as ''forest interior'' or ''edge'' are not always portable from one region to another or even over relatively short distances within a region.

Key words: forest bird community; habitat fragmentation; historic land cover; landscape metrics; large-river floodplain; multivariate analyses; spatial scale; Upper Midwest, USA; variance partitioning; Wisconsin River.

INTRODUCTION

Large-river floodplains play an important role in maintaining biodiversity by providing an extraordinary array of habitats (Gregory et al. 1991, Naiman and Décamps 1997). These areas are also among the first to be altered by expanding human populations and economic growth, and as a result are counted among the world's most endangered ecosystems (Nilsson and Dynesius 1994). Direct effects stem from changes in land use, especially agriculture, logging, and urbanization. Bottomland hardwood forests in the United States, for example, have declined at a rate that is five times greater than for other hardwood forest types (Abernethy and Turner 1987). Indirect effects are the consequence of changes in the rivers that floodplains border; the hydrology of nearly 98% of rivers in the United States has been altered by dams, levees, and diversions (Abramovitz 1996).

The widespread loss and degradation of floodplain habitats are pressing concerns in the conservation of avian diversity (Brawn et al. 2001). Of the four terrestrial bird species that have gone extinct in North America since European settlement, three were dependent on floodplain forests (Askins 2000). Yet, riverine habitats have continued to support some of the richest avifaunas on the continent (Knopf et al. 1988, Ohmart 1994). In the Midwestern United States, some of the largest remaining blocks of habitat for forest birds are found in the floodplains of large rivers (Emlen et al. 1986, Grettenberger 1991). Comparative studies in this region have shown that bird species richness in riverine

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woodlands exceeds that of upland sites on the upper Mississippi River by a factor of two to one (Knutson et al. 1995). Nonetheless, there are few published studies of bird–habitat relationships in large-river floodplains to guide management and conservation efforts (Knutson et al. 1995).

Because large-river systems connect entire regions and are associated with a variety of aquatic/riparian/upland interactions (Naiman and Décamps 1997), calls for integrated management over broad spatial scales appear to be well founded (Sparks 1995). The difficulties inherent in monitoring many species over large areas, however, have created an urgent need for reliable biodiversity indicators: measurable variables that reflect the status of native species in a given location. It has been suggested that descriptors of landscape structure and composition may be suitable for this task (O'Neill et al. 1997), and the widespread availability of relatively inexpensive remote-sensing imagery that is often used to describe landscape patterns make this an attractive option for managers. For many bird species, studies conducted in non-riverine settings have demonstrated that such an approach may indeed be effective (Freemark 1995, McGarigal and McComb 1995, Villard et al. 1999, Howell et al. 2000).

Here, we investigated the relationship between environmental measures at multiple scales and habitat use by birds in floodplain forests of the Wisconsin River, USA. We emphasized avian communities and functional groups throughout to gain a broad perspective; single-species relationships will be examined separately (J. R. Miller, M. D. Dixon, and M. G. Turner, *unpublished manuscript*). To assess the effectiveness of landscape measures in explaining variation in bird distributions, we first document patterns of avian habitat use at forested sites that vary in both landscape and geographic context. We then examine the degree to which variation in the structure and composition of bird communities can be explained by landscape patterns, geographic context, and local habitat features.

STUDY AREA AND METHODS

The Wisconsin River bisects the state of Wisconsin, USA, from northeast to southwest, draining an area of 31, 800 km^2. The river is island braided (Schumm 1985) with a wide and shallow channel, vegetated mid-channel islands, large sandbars, and a drop in elevation of $\sim$0.5 m/km over its 692 km length. The hydrology of the Wisconsin River has a long history of human alteration, beginning in the 1830s with dams for gristmills and sawmills, followed by impoundments for log storage and subsequent transport downriver. Today, there are 26 mainstem dams, all constructed between 1890 and 1950, to provide stable flows or flow storage for hydroelectric power generation and flood control (Durbin 1997). Downstream effects of dams typically include reduced peak flows, enhanced low flows, reduced sediment loads, and channel narrowing (Williams and Wolman 1984). In addition, channel incision below dams may result in lower rates of groundwater recharge and, in time, a contraction of the active floodplain (Ligon et al. 1995). The first 150 km of the river upstream from the confluence with the Mississippi are undammed.

Study sites

In 1999, we delineated six study reaches of the 100-year floodplain on the lower half of the Wisconsin River (Fig. 1), avoiding urban areas and flowages, or reservoirs. The reaches collectively spanned three geographic provinces: the Western Upland, the Central Plain, and the Northern Highland (Martin 1965). The Western Upland is in the Driftless Area, the unglaciated portion of Wisconsin, and is characterized by deeply dissected terrain and soils rich in nutrients and organic matter. In contrast, the Central Plain and Northern Highland are relatively flat and associated with sandy soils (Martin 1965). Human population density in the counties bordering the river has increased since the 1930s in all three provinces, but especially north of Sauk City (Freeman et al. 2003), which is where the larger cities occur. South of Sauk City, the uplands along the Wisconsin have generally not experienced the degree of clearing that occurred in the northern part of the state as the result of timber harvest or due to intensive agriculture farther south. The southernmost dam on the river occurs just above Sauk City.

The six reaches ranged from 12 km to 21 km in length (Table 1). Vegetation types within the floodplain included row crops, hay meadows, sand prairie, savanna, sedge meadows, open wetlands, and forest. Curtis (1959) noted that the extent of lowland forests in southern Wisconsin had decreased by less than half since settlement, although Mossman (1988) observed that the loss of high-quality bottomland forested habitat has been much greater. Since the 1930s, there has been an overall increase in forest cover along the river, much of which has been due to reforestation after farm abandonment, particularly in the Central Plain (Bürgi and Turner 2002, Freeman et al. 2003).

Although some conifers occurred in our research areas, particularly in the two northernmost reaches, our study focused on forests mainly comprised of hardwoods. Curtis (1959) described the lowland forests of southern Wisconsin as belonging to one of two broad categories. The more open-canopied ''southern wet forest'' was dominated by the most flood-tolerant tree species, such as silver maple (*Acer saccharinum*), black willow (*Salix nigra*), river birch (*Betula nigra*), eastern cottonwood (*Populus deltoides*), and swamp white oak (*Quercus bicolor*). In these forests, the understory was relatively open because frequent flooding prevented many tree seedlings and shrubs from becoming established. Drier or more stable sites were dominated by the more close-canopied ''southern wet-mesic forest'' which had a better-developed and more diverse under-

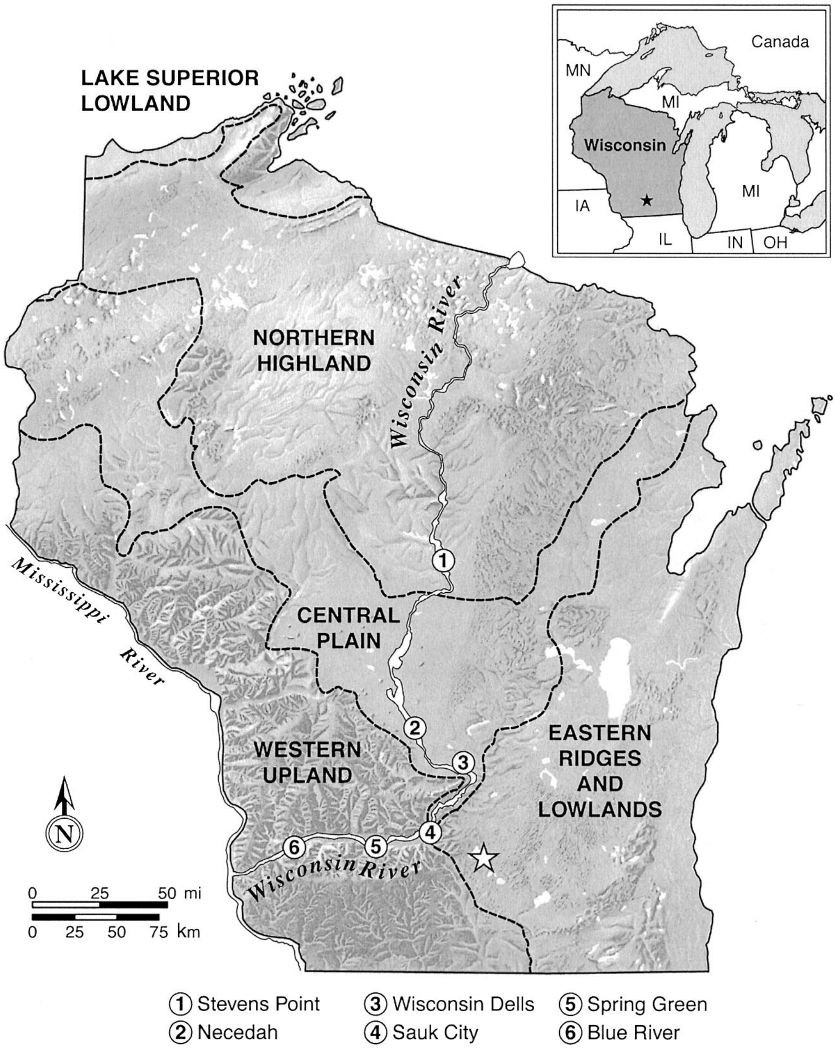

FIG. 1. Map of Wisconsin showing geographic provinces (Martin 1965) and the locations of study reaches along the Wisconsin River where birds were surveyed in 1999 and 2000. The Wisconsin state capitol, Madison, is also indicated by a star.

story; dominant trees included silver maple, green ash (*Fraxinus pennsylvanica*), American elm (*Ulmus americana*), and basswood (*Tilia americana*). Southern wet-mesic forest succeeds wet forest with a long-term drop in the water table or reductions in the severity of flooding (Mossman 1988).

Avian surveys

In each of the six reaches, we established eight transects at least 400 m apart in floodplain forests. Transects were roughly perpendicular to the river and positioned relative to a random starting point that was at least 60 m from a forest edge. On each transect, we established five census points at intervals ≥125 m. We surveyed the avifauna at each point twice annually in 1999 and in 2000: once between the third week of May and the second week of June, and again between the third week of June and second week of July. All transects in a given reach were surveyed on a single day, and successive surveys were at least three weeks apart. Birds were surveyed between sunrise and ~10:00 (Central Standard Time [CST]) using fixed-radius point counts (Ralph et al. 1993, 1995), during which we recorded the species and number of all birds seen and

TABLE 1. Characteristics of six study reaches of a 100-year floodplain on the Wisconsin River, Wisconsin, USA.

Reach	Length (km)	Area (km^2)	Forest (%)	Agriculture (%)
Stevens Point	12	17.4	46.7	14.1
Necedah	20	32.6	52.8	19.1
Wisconsin Dells	21	106.0	42.4	31.9
Sauk City	17	53.2	44.0	25.2
Spring Green	18	32.0	49.4	10.5
Blue River	16	27.6	56.9	1.3

TABLE 2. Variables used to describe avian survey locations in Wisconsin River floodplain forests.

Abbreviation	Description
Geographic variables	
DISTMISS	Distance (km) along the Wisconsin River from a transect to the confluence with the Mississippi River.
NORTHING	Average *y* coordinate (UTM) for plots on a transect.
Landscape variables	
DISTEDGE	Average distance (m) from points on a transect to the patch edge.
DISTRIV	Average distance (m) from points on a transect to the Wisconsin River.
AREA	Area (ha) of forest patch in which a transect was located.
SHAPE	Perimeter-to-area ratio of a forest patch relative to that of a circle.
LC30, LC60	Percentage of plots on a transect that were forested in 1930 and forested in 1960, respectively.
F100, F1500	Percentage of forested area within 100 m and within 1500 m of a transect, respectively.
AG1500	Percentage of agricultural land within 1500 m of transect.
ED100, ED1500	Density of patch edges (m/ha) within 100 m and within 1500 m of a transect, respectively.
AI100, AI1500	Aggregation of forest within 100 m and within 1500 m of a transect, respectively. AI equals 0 when there are no like adjacencies among forested map cells and increases to 1 when forested map cells are aggregated into a single patch.
CNT100, CNT1500	Contagion of cell types within 100 m and within 1500 m of a transect, respectively. This index equals 0 when every cell is a different patch type and increases to 1 when the landscape consists of a single patch.
IJI1500	Interspersion and juxtaposition of patch types within 1500 m of a transect. IJI approaches 0 as the distribution of adjacencies among patch types becomes increasingly uneven and increases to 1 when all patch types are equally adjacent to all other patch types.
CORE	Total amount of core area (ha) of forest ($>$200 m from a non-forest edge) within 1500 m of a transect.
NCORE	Number of individual core areas of forest within 1500 m of a transect.
WIDTH	For each transect, forest width (km) perpendicular to the river (transect side).
Local habitat variables	
RELEV	Average elevation (m) for plots on a transect minus the 100-year flood elevation.
CAN	Percent of canopy (T1 + T2) cover (see *Study Area and Methods; Fine-scale habitat measures* for details).
SUBCAN	Percent subcanopy (T3) cover, (see *Study Area and Methods; Fine-scale habitat measures* for details).
SHRUB	Percent shrub (S1 + S2) cover, (see *Study Area and Methods; Fine-scale habitat measures* for details).
ZANTHO	Number of subplots on a transect on which *Zanthozylum americanum* was present.
WETCAN	Average wetland score (T1 + T2) for dominant trees on a transect. Scores for an individual tree range from 1 (obligate wetland species) to 5 (upland species); see *Study Area and Methods; Data analyses* for details.
WETSUB	Average wetland score (T3) for dominant trees on a transect. Scores for an individual tree range from 1 (obligate wetland species) to 5 (upland species); see *Study Area and Methods; Data analyses* for details.
BREAKS	Number of breaks in the tree canopy on a transect.
OAKS	Average number of oaks in the canopy for plots on a transect.
SNAGS	Average number of standing dead trees $>$10 cm dbh for plots on a transect.
LGTREES	Average number of live trees $>$50 cm dbh for plots on a transect.

heard within 50 m during an 8-min sampling period. Surveys were not conducted if it was raining, nor if estimated wind speed exceeded 32 km/h. Four observers rotated visits to individual transects in each breeding season, and two observers participated in the study during both years.

Broad-scale habitat measures

We used a number of broad-scale measures to describe the spatial context of each transect (Table 2). Geographic variables included the distance along the Wisconsin River between each transect and the Mississippi River confluence. We included this variable because extensive bottomland forests exist along the Upper Mississippi that may serve as source habitats and the Mississippi is known as a prime flyway in North America for migratory birds. To isolate the effects of proximity to the Mississippi River from those associated with increasing latitude, we derived the northing from GPS data and calculated an average for points on a transect.

Land-cover data for the 1990s were derived for each of the six reaches from digital orthophotos (Freeman et al. 2003). These data were used to quantify a suite of variables (Table 2) that described landscape structure and composition in the area surrounding a given transect. Land-cover data outside the 100-year floodplain were compiled using the Wisconsin Initiative for Statewide Cooperation on Landscape Analysis and Data (WISCLAND) database (*available online*).[4] WISC-

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[4] ⟨http://www.dnr.state.wi.us/org/at/et/geo/data/wlc.htm⟩

LAND includes land-cover maps derived from Landsat TM imagery by the University of Wisconsin's Environmental Remote Sensing Center (Lillesand et al. 1998).

We measured the area of the patch in which a transect occurred, as well as the percentage of forest cover and agricultural land within concentric buffers with radii of 100 m and 1500 m. We also measured several variables describing landscape structure within these buffers using FRAGSTATS software (McGarigal and Marks 1995). Given a minimum distance of 400 m between transects, there was overlap in these buffers in some cases, possibly raising concerns regarding pseudoreplication. Our inference space, however, was already restricted to the lower half of the Wisconsin River because transects were not placed randomly, but rather were located wherever conditions were suitable (i.e., avoiding deep sloughs and oxbows, limited to forested habitats). Still, we noted transects where there was an overlap in buffers and flagged these for closer examination in the event that we detected strong landscape effects attributable to buffer-derived variables.

Because the width of riparian forest is often used as an analog for patch area in avian studies (Groom and Grubb 2002), we measured overall floodplain forest width on the transect side of the river along an axis that included the transect (i.e., perpendicular to the river). We also determined the location of each transect relative to the river and to forest patch edges, including those created by primary and secondary roads, which typically created canopy gaps of 30 m or more. Because vegetation structure and composition are, in part, a function of past land use, we used coverages derived from historic aerial photos (Freeman et al. 2003) to determine the percentage of points on a given transect that were forested in the 1930s and in the 1960s.

Fine-scale habitat measures

We quantified local habitat features (Table 2) within 50 m of each census point by establishing nine circular subplots, each with a 5-m radius; one subplot was centered on the census point itself and two were located at 20-m intervals on a transect in each cardinal direction. We identified the dominant tree species and estimated overall canopy cover over each subplot for each of three layers based on tree height (T1, >20 m; T2, 10–20 m; and T3, 5–10 m). Shrub cover was estimated for each of two height classes (S1, 2–5 m and S2, <2 m), and one particular shrub, prickly ash (*Zanthoxylum americanum*), was noted if present. Prickly ash is a native species in Wisconsin that has increased greatly in the understory of floodplain forests, forming dense thickets, as the result of flood control on wetter sites and fire suppression on drier sites (Liegel 1988). All cover estimates were expressed as discrete categories (5, >75%; 4, 50–75%; 3, 25–50%; 2, 5–25%; and 1, <5%). For each of the four orthogonal transects and at the center plot, we measured the dbh of the largest tree and scored all standing dead trees within 10 m as large (>30 cm dbh) or small (10–30 cm dbh). We also noted the number of canopy gaps over the entire plot and categorized these breaks by their understory as meadow, shrub, or open water.

Data analyses

Transects were treated as the units of analysis in this study. We averaged all local habitat measures across the points on a transect to provide a site-level estimate. Dominant tree species at each census point were assigned a wetland score with lower scores assigned to more flood-tolerant trees (Table 2; Reed 1988); these scores were summed for trees in each canopy layer at a survey plot. The values for several measures were summed to create single variables (Table 2): T1+T2 (CAN), S1+S2 (SHRUB), WET1+WET2 (WETCAN), and LC30+LC60 (HIST). Because oaks (*Quercus* spp.) are an important source of food and nesting sites to numerous bird species, but have declined in abundance as the result of fire exclusion (Robbins 1991), we created a variable to reflect the relative abundance of this group of trees in the canopy of each plot (Table 2).

We used MANOVA to compare differences in environmental conditions among reaches. We were particularly interested in north–south trends in landscape or local habitat variables because our study spanned several geographic provinces and the lower third of our overall study area was undammed. Two analyses were conducted, one for each set of variables, and when overall tests were significant, individual measures were evaluated for differences among reaches.

To minimize the effect of rare bird species, we excluded those with fewer than five occurrences from all data analyses. We also excluded flyovers, nocturnal, and crepuscular birds, aerial insectivores, raptors, shorebirds, and waterfowl because our methods were not appropriate for censusing them. The maximum number of individuals recorded on a single survey during each year was used to estimate the annual abundance of each species at each site. We used the maximum number of individuals rather than the average because averaging values across a breeding season would produce a misleading estimate for species that were not present or not singing during one or more surveys. We used repeated-measures analysis of variance to test for annual differences in overall bird abundance, with reach as the main effect and year as the repeated measure. There was no evidence of strong interannual effects on avian abundance (time, $P = 0.230$), or year-by-reach interactions ($P = 0.160$). Given these results, and because annual differences were not the focus of this study, we averaged species relative abundance across years.

We used correspondence analysis (CA; ter Braak and Smilauer 1998), an indirect ordination technique, to examine variation in avian composition and abundance among transects. In indirect ordination analyses, primary gradients in community structure are derived from the species data independently of measured environmental variables. Using reciprocal averaging of species scores and site scores, CA constructs a theoretical variable (represented by the x axis) that best explains variation in the species data. A second variable (represented by the y axis) is then constructed by the same process to explain residual variation, with the constraint that it is orthogonal to the first axis (ter Braak 1995). Species abundances were log-transformed to counteract skewness (ter Braak 1986) and downweighted to de-emphasize rarer species, according to the procedure of Hill (1979).

To examine the relationship between bird community structure and measured environmental variables, we used canonical correspondence analysis (CCA; ter Braak and Smilauer 1998). CCA is an extension of CA, but is a direct ordination technique in that the axes are constrained to be linear combinations of designated environmental variables. The resulting diagram depicts the relationship between the abundance of individual species, study sites, and measured environmental gradients; the location of site scores relative to vectors indicates the environmental characteristics of the sites (ter Braak 1986, ter Braak and Prentice 1988). Congruent configurations between CCA and CA indicate the extent to which patterns in the species data can be explained by the environmental variables that have been measured (Økland 1996). Biplot scaling and interspecies distances were used in both ordinations.

In the first CCA, a forward selection procedure was used to identify the minimal subset of measures from the geographic, landscape, and local habitat variable sets that best explained variation in the species data (ter Braak and Smilauer 1998). Variables were retained in calculation of site scores when their addition significantly improved the fit of the CCA model ($P \leq 0.05$). The decision to add each variable was determined by independent tests between model F values and the distribution of 500 Monte Carlo F values generated from the preceding CCA model, without the variable (ter Braak and Smilauer 1998). The relative contribution of selected variables to the explanatory power of the CCA axes was determined by their intraset correlations (ter Braak and Smilauer 1998).

We used partial constrained ordination to quantify the independent explanatory power of the three environmental variable sets as well as potential confounding among them (Borcard et al. 1992, Anderson and Gribble 1998, Cushman and McGarigal 2002). For each variable set, we first conducted a CCA using the forward selection procedure described above to identify the minimal subset of variables that best explained variation in the bird data. We then conducted three additional constrained ordinations with each of these subsets: two using one of the other subsets as covariables and the third combining both of the other subsets as covariables. When covariables are included in the analysis, the effect of these variables is partialed out (ter Braak 1988). This technique allowed us to partition the variance in the species data into eight components: (1) that explained solely by geographical variables, (2) that explained solely by landscape variables, (3) that explained by solely by local habitat variables, (4) that shared by geographical and landscape variables, (5) that shared by geographical and local habitat variables, (6) that shared by landscape and local habitat variables, (7) that shared among all three variable sets, and (8) unexplained variance.

For each CCA, the proportion of the total amount of variance in the species data explained by the environmental variables (after removing the effect of any covariables, if included) was determined by the ratio of the sum of canonical eigenvalues and the sum of unconstrained eigenvalues (Borcard et al. 1992). For all constrained ordinations, we used Monte Carlo tests with 199 permutations under the null model to determine the significance of the relationship between the species and constraining environmental variables, given the covariables if present (ter Braak and Smilauer 1998).

In addition to multivariate analyses, we quantified the relationship between the three sets of environmental variables and several univariate response groups. Here, we focused on species richness, avian abundance, and three functional groups that we considered especially likely to respond to landscape patterns. These groups included forest interior species (species that nest only within the interior of forests and rarely occur near edges), forest edge species (species that typically use forest edges, adjacent fields and large clearings), and Neotropical migratory birds. This last group was included because habitat fragmentation has often been implicated in the decline of numerous migratory bird populations (Askins et al. 1990, Faaborg et al. 1995).

Species were assigned a priori to functional groups based on a review of the literature (Ambuel and Temple 1983, American Ornithologists' Union 1983, Freemark and Collins 1992, Robbins et al. 1989; Table 3). For each functional group as well as species richness and bird abundance, we examined all possible regression models within each of the three sets of environmental variables and identified the ''best'' model from each set on the basis of biological relevance, R^2, and a second-order variant of Akaike's Information Criterion (AIC; Akaike 1973) that corrects for small-sample bias (AIC$_c$; Hurvich and Tsai 1991, Burnham and Anderson 1998). AIC is an extension of likelihood theory that provides a robust and objective means for model selection. Although models with the minimum AIC$_c$ value were designated ''best,'' we also reported all models with $\Delta\text{AIC}_c \leq 2$ of the minimum because these are also considered to be viable alternatives (Burnham and Anderson 1998). Only models with three variables or fewer were retained for further consideration.

''Best'' models were subjected to a univariate analogue of the multivariate variance partitioning method (Legendre and Legendre 1998). The univariate approach is conceptually similar to the multivariate technique, but rather than removing the effect of variable sets by treating them as covariables, we used partial regressions on residuals. Also, the explained variation that is shared by environmental components is not as precise as that derived in a multivariate context because in univariate partitioning it is derived by subtraction and not by the estimation of a specific parameter (Legendre and Legendre 1998).

RESULTS

Environmental variables

Overall, silver maple dominated the two tree canopy layers at our study sites; out of 2160 subplots, it was dominant on 362 (T1) and 649 (T2) of them. Other abundant T1 trees included green ash ($n = 149$ subplots) and swamp white oak ($n = 104$). Since Curtis' work, the Dutch elm fungus (*Ceratocystis ulmi*) has virtually eliminated American elm as a dominant canopy species, although it was the second most abundant T2 tree ($n = 242$) and the most numerous T3 tree ($n = 397$). Subdominant species for these layers again included swamp white oak, green ash, and river birch. Other species that were moderately abundant in most reaches were Hill's oak (*Quercus ellipsoidalis*), black oak (*Quercus velutina*), northern hackberry (*Celtus occidentalis*), bitternut hickory (*Carya cordiformis*), and basswood (*Tilia americana*). At our northernmost site, silver maple was still dominant in the canopy, but subdominants included trees typical of northern hardwood forests, such as trembling aspen (*Populus tremuloides*), red maple (*Acer rubrum*), and red oak (*Quercus rubrum*).

There were significant differences among reaches in landscape measures (Wilks' lambda = 0.0273; $F = 2.56$; df = 65, 145.7; $P < 0.0001$) and in local habitat variables (Wilks' lambda = 0.0582; $F = 2.66$; df = 50, 153.9; $P < 0.0001$). The area of forest patch in which a site occurred was substantially larger at our southernmost reach, Blue River. Standing dead trees were, on average, slightly larger at both Blue River and Spring Green. There was a tendency toward larger trees in the southern reaches, and the number of flood-tolerant trees in the canopy decreased for reaches upriver. Still, there were no statistically significant geographic trends among variables in either set (Tables 3 and 4).

Bird community

We observed 9919 individual birds representing 92 species during the two-year study. Fifty-two species met our conditions for inclusion in data analyses (Table 5). Of these, the number of species detected per reach showed little variability, ranging from 41 at Stevens Point to 46 at Blue River. The average relative abundance of individual birds was remarkably similar for the Blue River, Wisconsin Dells, and Sauk City reaches (between 1300 and 1325 individuals per reach), and somewhat less at Spring Green (1221 individuals). Relative abundance in the Necedah and Stevens Point reaches was substantially lower (893 and 886, respectively).

There was a strong correlation between a species' relative abundance and the number of transects on which it occurred ($R^2 = 0.894$). Ten species occurred on >90% of the transects (Table 5). Most of these species tend to reach their greatest abundance in edge habitats, and all are widespread forest generalists that are common in upland and lowland habitats. At the other end of the spectrum, nine species had a relative abundance <20 and occurred on fewer than 25% of the transects (Table 5). One of these, the Mourning Warbler, is a boreal species that is fairly common in northern Wisconsin, but uncommon in the southern part of the state (Robbins 1991, Pitocchelli 1993). The Tufted Titmouse, on the other hand, is a southern species (Grubb and Pravosudov 1994) that colonized Wisconsin during the 20th century but still has a rather patchy distribution (Robbins 1991). Other species that were rare in this study, such as the Eastern Bluebird and the Field Sparrow, are more frequently found in open habitats, such as shrubby pastures or old fields, than in forests (Robbins 1991). Similar to our findings, DeJong (1976) also found the Least Flycatcher to be rare in Wisconsin River floodplain forests, but described them as abundant in upland habitats. Two species thought to be indicative of high-quality floodplain forest in southern Wisconsin (Mossman 1988, 1991) were notable for their absence: neither the Kentucky Warbler (*Oporornis formosus*), nor the Cerulean Warbler (*Dendroica cerulea*), were recorded on surveys during the course of the study.

In the CA, the sum of all unconstrained eigenvalues was 0.665, a measure of the total variation in the species data. The dispersion of CA site scores in multivariate space roughly mirrored their geographic configuration (Fig. 2). Sites at Blue River, the reach nearest the Mississippi confluence, are grouped to the right side of the primary axis, which accounted for 17.8% of the variation in species composition; next are the sites in the Spring Green reach. The sites at Wisconsin Dells, Necedah, and Stevens Point occur on the left side of the primary axis and tend to segregate in that order on the secondary axis, which accounted for 8.9% of bird community variation. The Sauk City sites were dispersed among the point cloud that comprises transects at the two Central Plain reaches.

The first CCA, which included a subset of environmental measures selected from all three variable sets, accounted for 42.3% of the variance in the community data and the relationship between the species and environmental variables was highly significantly ($F = 2.71$, $P = 0.005$). The configuration of site scores (Fig.

TABLE 3. Scientific names, common names, and functional group assignments for bird species included in analyses (following American Ornithologists' Union 1983).

Scientific name	Common name	Migratory class†	Habitat use‡
Coccyzus americanus	Yellow-billed Cuckoo	NTM	I/E
Zenaida macroura	Mourning Dove	SDM	E
Archilochus colubris	Ruby-throated Hummingbird	NTM	E
Ceryle alcyon	Belted Kingfisher	NTM	
Melanerpes erythrocephalus	Red-headed Woodpecker	SDM	E
Melanerpes carolinus	Red-bellied Woodpecker	RES	I/E
Sphyrapicus varius	Yellow-bellied Sapsucker	SDM	I/E
Picoides pubescens	Downy Woodpecker	RES	I/E
Picoides villosus	Hairy Woodpecker	RES	I
Colaptes auratus	Northern Flicker	SDM	I/E
Dryocopus pileatus	Pileated Woodpecker	RES	I
Contopus virens	Eastern Wood-Pewee	NTM	I/E
Empidonax minimus	Least Flycatcher	NTM	I/E
Sayornis phoebe	Eastern Phoebe	SDM	I/E
Myiarchus crinitus	Great Crested Flycatcher	NTM	I/E
Vireo flavifrons	Yellow-throated Vireo	NTM	I/E
Vireo gilvus	Warbling Vireo	NTM	E
Vireo olivaceus	Red-eyed Vireo	NTM	I/E
Corvus brachyrhynchos	American Crow	SDM	E
Cyanocitta cristata	Blue Jay	SDM	I/E
Poecile atricapilla	Black-capped Chickadee	RES	I/E
Baeolophus bicolor	Tufted Titmouse	RES	I
Sitta carolinensis	White-breasted Nuthatch	RES	I/E
Certhia americana	Brown Creeper	SDM	I
Troglodytes troglodytes	House Wren	SDM	E
Polioptila caerula	Blue-gray Gnatcatcher	NTM	I/E
Sialia sialis	Eastern Bluebird	SDM	E
Catharus fuscescens	Veery	NTM	I
Hylochichla mustelina	Wood Thrush	NTM	I/E
Turdus migratorius	American Robin	SDM	E
Dumetella carolinensis	Gray Catbird	NTM	I/E
Bombycilla cedrorum	Cedar Waxwing	NTM	E
Vermivora pinus	Blue-winged Warbler	NTM	E
Dendroica petechia	Yellow Warbler	NTM	E
Setophaga ruticilla	American Redstart	NTM	I
Protonotaria citrea	Prothonotary Warbler	NTM	I/E
Seiurus aurocapillus	Ovenbird	NTM	I
Oporornis philadelphia	Mourning Warbler	NTM	I/E
Geothlypis trichas	Common Yellowthroat	NTM	I/E
Piranga olivacea	Scarlet Tanager	NTM	I
Pipilo erythrophthalmus	Eastern Towhee	SDM	I/E
Spizella passerina	Chipping Sparrow	NTM	E
Spizella pusilla	Field Sparrow	SDM	E
Melospiza melodia	Song Sparrow	SDM	E
Cardinalis cardinalis	Northern Cardinal	RES	I/E
Pheuticus ludovicianus	Rose-breasted Grosbeak	NTM	I/E
Passerina cyanea	Indigo Bunting	NTM	E
Agelaius phoeniceus	Red-winged Blackbird	SDM	E
Quiscalus quiscula	Common Grackle	SDM	E
Molothrus ater	Brown-headed Cowbird	SDM	E
Icterus galbula	Baltimore Oriole	NTM	E
Carduelis tristis	American Goldfinch	SDM	E

† Based on American Ornithologists' Union (1983), Robbins (1991). Abbreviations: NTM, Neotropical migrant; SDM, short-distance migrant; RES, year-round resident.

‡ Based on Ambuel and Temple (1983), Freemark and Collins (1992), Robbins et al. (1989). Abbreviations: E, forest edge; I, forest interior; I/E, forest interior or edge.

3) was quite similar to the pattern resulting from the CA (Fig. 2), although there was much greater interspersion of site scores among and within reaches in the CCA, especially along the secondary axis. Forward selection produced a model that consisted of both geographic variables, five landscape measures, and three local habitat variables (Figs. 3 and 4). The landscape variables described configuration at relatively small scales (ED100 and CNT100) and composition at somewhat broader scales (F1500 and AG1500). The two geographic variables made the greatest contribution to the explanatory power of both axes (Appendix A). The variable SHRUB contributed strongly to the primary axis (intraset correlation = -0.607), and WETCAN made a substantial contribution to both axes (intraset correlations both >0.40). This latter relationship reflected the pattern of more flood-tolerant trees in the southern reaches that was noted in the reach-level data (Table 4).

TABLE 4. Values (mean ± 1 SE) for landscape and local habitat variables measured at transects ($n = 8$) in each study reach (see *Study Area and Methods*). The order of reaches from left to right corresponds to a south-to-north progression (see Fig. 1).

Variable	Blue River	Spring Green	Sauk City
Landscape variables			
DISTEDGE	$91.4^{ab} \pm 10.6$	$97.0^{ab} \pm 28.1$	$92.9^{ab} \pm 13.2$
DISTRIV	$353.1^{a} \pm 118.2$	$120.6^{bc} \pm 37.1$	$178.4^{ab} \pm 24.0$
AREA	$412.2^{a} \pm 97.9$	$122.3^{bc} \pm 32.5$	$207.6^{ac} \pm 25.6$
SHAPE	$0.09^{b} \pm 0.03$	$0.34^{a} \pm 0.12$	$0.02^{b} \pm 0.01$
LC60	$0.90^{ab} \pm 0.07$	$0.95^{ab} \pm 0.03$	$1.00^{a} \pm 0.00$
LC30	0.70 ± 0.12	0.80 ± 0.80	0.88 ± 0.08
F100	$87.5^{ac} \pm 2.4$	$96.2^{b} \pm 1.3$	$88.4^{a} \pm 4.3$
F1500	$57.9^{ac} \pm 4.0$	$61.0^{a} \pm 2.9$	$48.1^{b} \pm 4.3$
AG1500	$13.0^{a} \pm 2.5$	$11.8^{a} \pm 2.6$	$14.8^{ab} \pm 2.5$
ED100	$53.0^{ab} \pm 8.6$	$25.6^{a} \pm 7.6$	$48.7^{ab} \pm 13.4$
ED1500	88.9 ± 10.4	72.7 ± 5.0	85.5 ± 6.0
CORE	30.3 ± 7.3	59.5 ± 21.0	60.1 ± 25.0
NCORE	$6.8^{a} \pm 1.1$	$5.4^{a} \pm 0.6$	$3.4^{b} \pm 0.8$
WIDTH	993.8 ± 212.3	595.8 ± 98.5	888.6 ± 127.1
Local habitat variables			
RELEV	$12.6^{ab} \pm 0.7$	$16.6^{ac} \pm 0.9$	$17.0^{ac} \pm 0.7$
CAN	$36.4^{ab} \pm 1.8$	$40.1^{a} \pm 1.3$	$37.7^{ab} \pm 1.4$
SUBCAN	$19.4^{ab} \pm 1.0$	$17.8^{b} \pm 1.1$	$21.2^{a} \pm 0.7$
SHRUB	$27.0^{a} \pm 1.5$	$25.2^{a} \pm 5.8$	$39.2^{b} \pm 1.7$
ZANTHO	$2.8^{a} \pm 0.8$	$3.5^{a} \pm 1.3$	$7.4^{b} \pm 1.5$
WETCAN	$4.3^{a} \pm 0.1$	$4.8^{ac} \pm 0.3$	$4.7^{ac} \pm 0.2$
WETSUB	$2.36^{a} \pm 0.06$	$2.46^{ac} \pm 0.13$	$2.84^{b} \pm 0.14$
BREAKS	$0.75^{a} \pm 0.08$	$0.78^{a} \pm 0.15$	$0.98^{ab} \pm 0.14$
SNAGS	$12.55^{a} \pm 2.19$	$11.28^{ac} \pm 1.46$	$5.4^{b} \pm 0.80$
LGTREES	$2.60^{ab} \pm 0.46$	$3.17^{b} \pm 0.23$	$2.78^{a} \pm 0.35$
OAKS	$3.00^{ab} \pm 0.41$	$2.73^{ab} \pm 0.86$	$2.20^{ab} \pm 0.62$

Notes: Superscript letters within rows indicate that a variable differed significantly among reaches (ANOVA, $P < 0.05$); values with different letters are significantly different at $P < 0.05$ (LSD). See Table 2 for variable descriptions.

Variance partitioning

Similar to results of the initial CCA, the partial CCA explained over 40% of the total variation in the species data (Table 6). The relative contributions of the three environmental data sets were markedly different, however, with local habitat variables (BREAKS, ZANTHO, WETCAN, WETSUB, and OAKS) accounting for 21.7% of the total variance, the two geographic variables explaining 18.5%, and the landscape variables (DISTRIV, CNT1500, and CORE) explaining 12% (Table 6). Approximately one quarter of the explained variation, however, was confounded among variable sets. Notably, nearly 70% of the variation explained by the geographic variables was jointly explained by local habitat measures, but <7% the variance accounted for by landscape variables was shared with the local habitat set. The geographic, landscape, and local habitat ordinations all explained significant amounts of the total community variation ($P = 0.005$).

As with the partial ordinations, the univariate variance partitioning revealed substantially different patterns than that which emerged from the initial CCA. Geographic models included only one variable and explained the greatest amount of variation for only one of the five response groups, total bird abundance (41.6%; Table 7), and nearly 70% of this explained variation was shared with other landscape and local habitat measures. However, this pattern still held when the effects of landscape and local habitat variables were removed and may reflect the lower abundance of birds at the two northernmost reaches. Geographic models explained virtually none of the total variance associated with the distribution of Neotropical migrants or forest interior species.

Models describing landscape composition and configuration explained the most variation for one group, forest interior species (33%); over 60% of this was shared with local habitat variables (Table 8). When covariables were included in the analyses, landscape variables explained <6% of the variance in patterns of habitat use by Neotropical migrants and <5% of the variance in the distribution of forest edge species. Past land cover emerged as an important explanatory variable in half of the ''best'' and alternative candidate landscape models (Table 7, Appendix B).

Whether considering total explained variation or that explained independently, models comprising local habitat characteristics accounted for the greatest amount of variation in patterns of species richness, Neotropical migrant species, and forest edge species (Table 7). Over half of the total variation explained by these models was confounded with either geographic variables, landscape variables, or both (Table 7). The variables that appeared most often in ''best'' and alternative candidate local habitat models included LGTREES, SNAGS, and WETCAN (Table 7, Appendix B).

TABLE 4. Extended.

Wisconsin Dells	Necedah	Stevens Point
127.3^{a} ± 22.6	112.6^{a} ± 17.0	66.4^{b} ± 13.4
295.0^{a} ± 55.1	185.5^{ab} ± 38.0	82.4^{c} ± 23.3
197.1^{bc} ± 30.4	249.8^{a} ± 48.3	95.2^{b} ± 25.1
0.05^{b} ± 0.02	0.07^{b} ± 0.01	0.07^{b} ± 0.03
0.95^{ab} ± 0.03	0.85^{a} ± 0.07	0.80^{b} ± 0.10
0.80 ± 0.09	0.68 ± 0.14	0.90 ± 0.05
89.5^{a} ± 2.2	79.3^{c} ± 4.5	93.5^{ab} ± 2.0
55.3^{ab} ± 2.6	50.7^{bc} ± 3.1	56.1^{ab} ± 2.2
8.3^{a} ± 2.4	25.6^{b} ± 3.8	9.3^{a} ± 1.7
45.0^{ab} ± 10.2	78.3^{b} ± 14.6	28.9^{a} ± 8.7
89.15 ± 3.4	84.7 ± 3.2	96.4 ± 2.1
30.8 ± 7.0	22.7 ± 9.3	22.9 ± 2.8
5.8^{a} ± 0.7	4.0^{a} ± 0.6	4.6^{a} ± 0.4
1019.1 ± 200.9	893.8 ± 134.7	690.1 ± 143.5
16.6^{ac} ± 0.7	11.0^{b} ± 1.1	18.2^{c} ± 1.8
36.0^{ab} ± 1.6	36.0^{b} ± 1.8	35.2^{b} ± 1.6
17.1^{b} ± 1.5	19.4^{ab} ± 1.4	17.8^{b} ± 0.7
40.0^{b} ± 2.8	29.3^{a} ± 3.7	34.8^{ab} ± 2.9
9.0^{b} ± 2.0	7.4^{ab} ± 1.8	6.0^{ab} ± 1.2
5.8^{b} ± 0.4	5.0^{c} ± 0.2	5.8^{b} ± 0.3
2.84^{b} ± 0.18	2.37^{a} ± 0.08	2.79^{bc} ± 0.11
0.90^{a} ± 0.15	1.38^{b} ± 0.13	0.88^{a} ± 0.13
7.57^{bc} ± 1.55	10.37^{ac} ± 1.36	7.80^{ab} ± 1.15
2.50^{ab} ± 0.26	1.68^{b} ± 0.34	2.38^{ab} ± 0.39
3.80^{a} ± 0.71	2.11^{b} ± 0.60	2.03^{b} ± 0.41

DISCUSSION

Floodplain forests along the Wisconsin River support a rich and diverse assemblage of birds. On our surveys we recorded seven of the eight woodpecker species that occur in Wisconsin, as well as many long- and short-distance migrant species. Forest generalists and edge species were ubiquitous and numerically dominant, but we also recorded eight species that typically nest in forest interiors (Ambuel and Temple 1983, Robbins et al. 1989, Freemark and Collins 1992). Of the species that occurred at our sites, the Prothontary Warbler is considered dependent on extensive floodplain forests throughout its range and is thought to be an indicator for the quality of these habitats (Petit 1999). Other species (e.g., Pileated Woodpecker, Veery), although not restricted to floodplains in their breeding ranges, tend to reach their greatest abundance there (DeJong 1976, Emlen et al. 1986, Mossman 1989, Poole and Gill 1996); some members of this group (Warbling Vireo, Yellow Warbler) were indeed absent from upland forests during previous surveys along the Wisconsin River (DeJong 1976). On the other hand, we recorded several species (e.g., Least Flycatcher, Scarlet Tanager) that tend to reach their greatest abundance in upland habitats and are uncommon or rare in riverine woodlands. The Ovenbird, a forest interior specialist (Van Horn and Donovan 1994), was quite rare in floodplains of the upper Mississippi River (Knutson et al. 1995) and was described by DeJong (1976) as being far more common in upland (vs. bottomland) forests along the Wisconsin River, yet this species occurred on more than half of the transects and was relatively abundant. Collectively, the composition of the avian assemblages reflects a diverse mosaic of habitats in the Wisconsin River floodplain.

An assortment of measures that are often used to describe landscape mosaics in avian research did explain a portion of the variation in bird community structure and composition in our study reaches. However, landscape metrics that have typically accounted for substantial variation in avian habitat use in other studies explained very little in forested reaches of the Wisconsin River. The relationship between patch area and species richness, for example, has been well documented (Wiens 1989), yet this term was not selected in our ordinations or in the ''best'' univariate models and was included in only one alternative candidate model (for Neotropical migrants, Appendix B). Sallabanks et al. (2000) also noted that patch size had only a small effect in their examination of a forest bird community in the Roanoke River floodplain.

Overall forest width has sometimes been used as an analogue for patch size in riverine habitat studies, including work focused on large-river floodplains in the Midwest, where it accounted for substantial variation in habitat use by birds (Knutson et al. 1995). The width of floodplain forest was not included in any models in our study. In some upland studies, the total amount of

TABLE 5. Number of transects ($n = 48$) on which a species was detected, and the total number of detections for bird species included in analyses for 1999 and 2000.

Common name	Abbreviation†	No. transects	No. detections‡
Yellow-billed Cuckoo	YBCU	34	93
Mourning Dove	MODO	15	23
Ruby-throated Hummingbird	RTHU	5	6
Belted Kingfisher	BEKI	9	11
Red-headed Woodpecker	RHWO	10	15
Red-bellied Woodpecker	RBWO	39	104
Yellow-bellied Sapsucker	YBSA	21	100
Downy Woodpecker	DOWO	47	213
Hairy Woodpecker	HAWO	30	70
Northern Flicker	NOFL	13	16
Pileated Woodpecker	PIWO	16	23
Eastern Wood-Pewee	EAWP	48	375
Least Flycatcher	LEFL	2	10
Eastern Phoebe	EAPH	7	8
Great Crested Flycatcher	GCFL	47	348
Yellow-throated Vireo	YTVI	26	47
Warbling Vireo	WAVI	16	29
Red-eyed Vireo	REVI	47	379
American Crow	AMCR	36	111
Blue Jay	BLJA	45	214
Black-capped Chickadee	BCCH	48	504
Tufted Titmouse	TUTI	9	9
White-breasted Nuthatch	WBNU	47	340
Brown Creeper	BRCR	12	14
House Wren	HOWR	32	242
Blue-gray Gnatcatcher	BGGN	38	106
Eastern Bluebird	EABL	5	7
Veery	VEER	14	42
Wood Thrush	WOTH	26	109
American Robin	AMRO	41	209
Gray Catbird	GRCA	40	304
Cedar Waxwing	CEDW	28	87
Blue-winged Warbler	BWWA	10	20
Yellow Warbler	YWAR	18	37
American Redstart	AMRE	34	132
Prothonotary Warbler	PROW	12	23
Ovenbird	OVEN	33	329
Mourning Warbler	MOWA	5	7
Common Yellowthroat	COYE	40	167
Scarlet Tanager	SCTA	34	96
Eastern Towhee	EATO	23	107
Chipping Sparrow	CHSP	6	8
Field Sparrow	FISP	6	19
Song Sparrow	SOSP	48	653
Northern Cardinal	NOCA	46	279
Rose-breasted Grosbeak	RBGR	42	190
Indigo Bunting	INBU	27	83
Red-winged Blackbird	RWBL	25	92
Common Grackle	COGR	15	55
Brown-headed Cowbird	BHCO	46	277
Baltimore Oriole	BAOR	33	103
American Goldfinch	AMGO	32	81

Note: See Table 3 for scientific names.
† Used in subsequent tables and figures.
‡ Detections within 50 m of census points, not including flyovers.

forest in the surrounding landscape has been found to exert a more powerful influence on birds in a wooded patch than patch area per se (e.g., Robinson et al. 1995). In this regard, our findings were similar to those of Knutson et al. (1995), who reported that bird abundance did not vary with the amount of forest within 800 m, even for species considered to be area sensitive. Although the amount of forest within 1500 m of a transect did exert a moderately strong influence in our first CCA, it was included in only three univariate models and never accounted for $>5\%$ of the variation in the response variable.

Proximity to edge habitats has been found to play a key role in structuring bird communities (e.g., Flaspohler et al. 2001, Baker et al. 2002). Distance-to-edge and variables reflecting edge density did enter into some of our analyses, but explained relatively small amounts of variation. Even for species generally con-

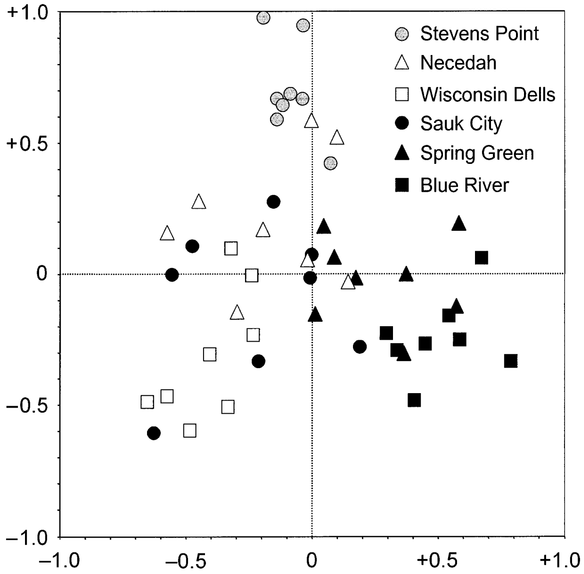

FIG. 2. Locations of site scores in the space defined by a correspondence analysis (CA) of bird community composition from early to mid-summer, 1999–2000.

sidered to have an affinity for forest edges, the ''best'' model accounted for <20% of the variation in habitat use. Again, Sallabanks et al. (2000) also found edge effects on floodplain forest birds to be negligible.

Patterns of past land cover are not usually considered in avian studies (but see Knick and Rotenberry 2000) and yet such a term was included in models for all of the functional groups that we examined except edge species. This may be related to natal philopatry or site tenacity, as suggested by Knick and Rotenberry (2000), but such a descriptor is also likely to integrate information on forest structure that may give it more explanatory power than individual variables describing present conditions (e.g., canopy cover, shrub cover, basal area, etc.).

Overall, the variation explained by landscape measures in this study tended to be somewhat less than that attributed to geographic or local habitat variables, and much of the variance that was explained by landscape measures was confounded with these other two sets of environmental variables. This is not to say that landscape factors were not important, but rather that the amount of variation that can be attributed to these factors independent of variables measured at other scales suggests that landscape metrics alone will not suffice as indicators of bird communities in the Wisconsin River floodplain. Perhaps the importance attributed to landscape factors in other studies has been exaggerated through confounding with factors operating at other spatial scales. It is also possible that forest fragmentation along the Wisconsin has not yet progressed to the point that landscape pattern exerts a strong influence on bird species distributions. Many of our transects occurred in relatively large patches (i.e., hundreds of hectares) and the proportion of forested habitat in our study reaches ranged from 40% to 60%. Spatially explicit population models have indicated that landscape structure becomes a dominant factor only when the amount of suitable habitat is reduced to 10–50% of the landscape (Fahrig 1998, Flather and Bevers 2002). In his review of fragmentation effects on birds and mammals, Andrén (1994) documented a threshold at the midpoint of this range (30% suitable habitat remaining), below which landscape measures correlated strongly with species distributions.

Species in large-river floodplains may also exhibit behavioral responses to landscape structure that are fundamentally different from those observed in the upland habitats that form the basis for much of our understanding of fragmentation effects. As we have noted, bottomlands along the Wisconsin River are comprised of a mosaic of cover types resulting from differences in elevation, soil, and hydrology, in addition to human land use. Others have suggested that species in habitats that are naturally patchy may be less responsive to edge or area effects (Finch 1991, Freemark 1995, Tewksbury et al. 1998). Even if this were true for only some of the species in our study, it is possible

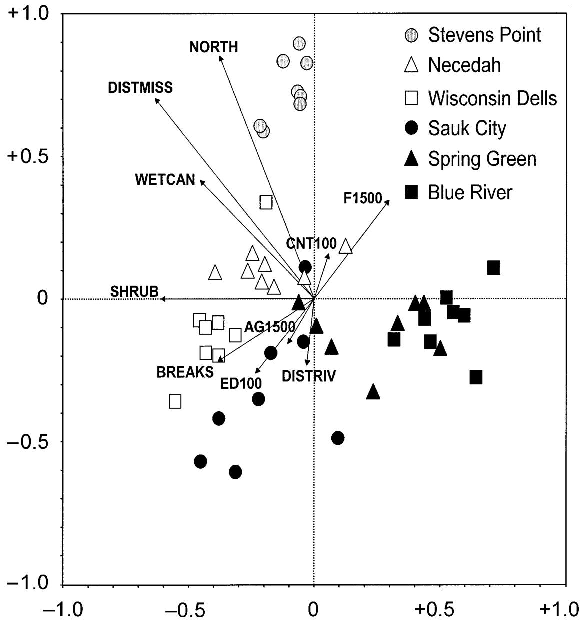

FIG. 3. Locations of site scores in the space defined by a canonical correspondence analysis (CCA) of bird community composition from early to mid-summer, 1999–2000, using geographic, landscape, and local habitat variables. The lengths of the vectors indicate the relative importance of each environmental variable in the model, and the angle between vectors indicates the correlation between variables. The origin (0,0) is the mean of each environmental variable, and vectors apply equally in the negative direction. The rank of a site with respect to a given environmental variable is approximated by projecting the site point in the diagram perpendicularly onto the environmental vector. See Table 2 for variable codes.

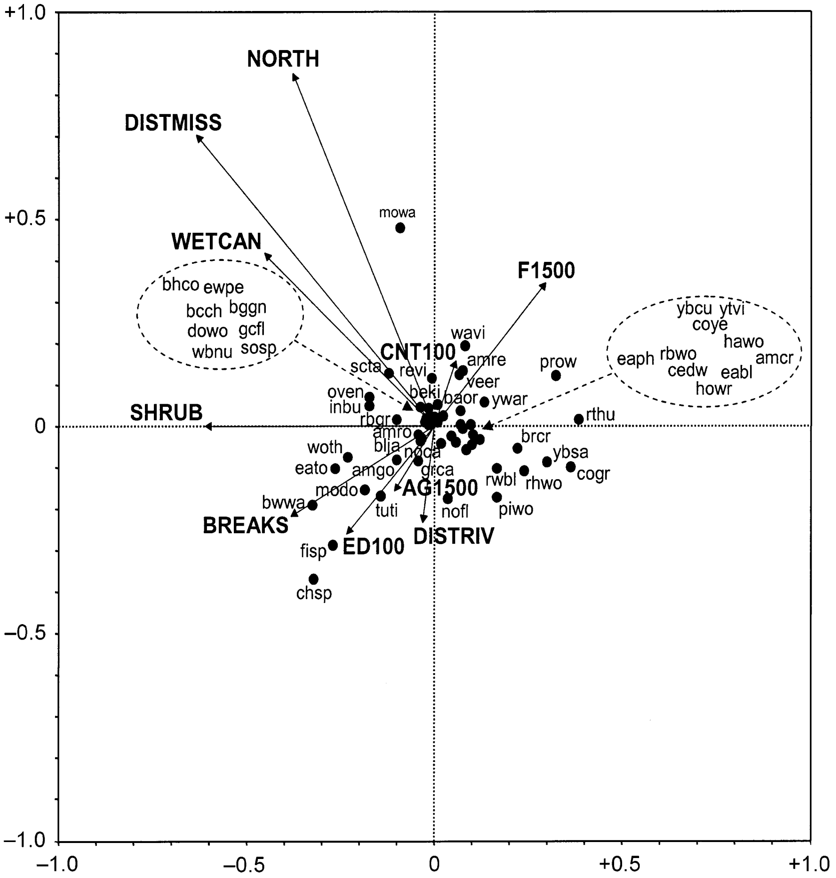

FIG. 4. Locations of species scores in the space defined by a CCA of bird community composition from early to mid-summer, 1999–2000, using geographic, landscape, and local habitat variables. Species scores near the origin in each quadrant are enclosed in dashed circles and in their relative positions. See Table 2 for variable codes and Table 5 for species codes.

that their patterns of habitat use may mask effects of landscape structure on more sensitive species in community- or guild-level analyses.

Villard (1998) observed that interpretations of habitat-use patterns based on metrics such as patch area or distance-to-edge focus our attention on proximate conditions, whereas processes that underlie such patterns may operate at broader scales than are considered in many studies (also see Ricklefs and Schluter 1993). Our sites were located in three distinct geographic provinces, encompassing a rather broad range of biophysical conditions when one considers that the entire length of river that we studied was >400 km. Physiographic transitions of this magnitude would not be found, for example, along a similar length of the nearby upper Mississippi River (Mossman 1988). The two geographic variables that we examined did explain a greater share of independent variation than did landscape measures in most analyses. At least part of this explanatory power likely stems from unmeasured characteristics of the surrounding uplands related to topography, land cover, or land use in the surrounding uplands, especially when considering the number of upland bird species that we observed in the floodplain. This may not be the case in a regional context that is more homogeneous.

Although landscape measures were relatively poor indicators of avian community structure and composition along the Wisconsin River, this may not necessarily be the case for all floodplain habitats or for individual species in riverine areas. Generally, landscape

TABLE 6. Results of variance partitioning based on canonical correspondence analyses.

Component	Explained variation (%)
Geographic only	9.3
Landscape only	7.8
Local habitat only	11.6
Geographic–landscape	0.6
Geographic–local	6.5
Landscape–local	1.5
Geographic–landscape–local	2.1
Total	40.6

Note: The percentage of explained variation was calculated as a proportion of the total trace of the species data = 0.665.

TABLE 7. Results of multiple linear regression analyses indicating ''best'' models, based on AIC_c.

	First variable		Second variable		Third variable		
Response	Variable	Partial R^2	Variable	Partial R^2	Variable	Partial R^2	Model R^2
Geographic models							
Species richness	−NORTHING	0.270					0.270
Bird abundance†	−NORTHING	0.416					0.416
Neotropical migrant species richness	NORTHING	0.001					0.001
Forest interior species richness	−NORTHING	0.002					0.002
Forest edge species richness	−NORTHING	0.238					0.238
Landscape models							
Species richness	LC30‡	0.054	SHAPE	0.058	IJI1500	0.112	0.224
Bird abundance†	LC60‡	0.102	−DISTEDGE	0.009	AI1500	0.053	0.166
Neotropical migrant species richness	−ED100	0.105	−F1500	0.046	NCORE	0.029	0.180
Forest interior species richness	−ED100	0.098	IJI1500	0.151	F100	0.083	0.330
Forest edge species richness	SHAPE	0.052	−DISTEDGE	0.058	IJI1500	0.080	0.190
Local habitat models							
Species richness	LGTREES	0.179	SNAGS	0.093	BREAKS	0.065	0.337
Bird abundance†	SNAGS	0.079	LGTREES	0.103			0.182
Neotropical migrant species richness	RELEV	0.199	−WETSUB	0.045	−WETCAN	0.107	0.350
Forest interior species richness	LGTREES	0.143	SHRUB	0.103			0.246
Forest edge species richness	−WETCAN	0.230	LGTREES	0.068	BREAKS	0.045	0.343

Note: See Table 2 for variable codes and Appendix B for other candidate models.
† Square-root transformed.
‡ Arcsine transformed.

indices are likely to have greater explanatory power when there are strong differences among landscape elements that affect habitat quality (Wiens et al. 1987). Much evidence also shows that when levels of habitat loss are high, the size and configuration of remnants assume a critical role in determining species distributions (Saunders et al. 1991, Andrén 1994). Loss of habitat need not be great, however, to affect patterns of use by birds (Small and Hunter 1988, Rich et al. 1994, Miller et al. 1998, Develey and Stouffer 2001), again depending on the extent to which a given system is naturally fragmented (Wiens 1989). This latter point emphasizes that knowledge of the biotic and abiotic processes that define a given system is fundamental to understanding the effects of land cover change on biodiversity (Schmiegelow and Monkkonen 2002).

Conservation implications

By preserving extensive wooded patches in large-river floodplains, it is possible to provide habitat for forest birds generally, including species that historically were more closely associated with uplands, but no longer find woodlands that are sufficiently large to sustain them. Maintaining large forest blocks along the Wisconsin River is likely to be easier than accommodating the full set of species that now occur there,

TABLE 8. Percentage of variation explained by variance partitioning based on multiple linear regression.

			Species richness		
Component	Species richness	Bird abundance	Migrant	Interior	Edge
Geographic only	12.9	13.2	0.1	0.2	7.6
Landscape only	2.0	0.3	5.7	13.0	4.3
Local habitat only	18.1	8.2	8.4	2.4	13.7
Geographic–landscape	6.7	18.4	0.0	0.0	1.1
Geographic–local	3.7	5.9	0.0	0.0	7.2
Landscape–local	11.3	3.2	12.3	20.0	9.1
Geographic–landscape–local	3.8	4.1	0.0	0.0	7.9
Total	58.6	53.4	26.5	35.6	50.8

Note: See Table 7 for regression models.

especially those that have an affinity for conditions that characterize bottomlands, such as the Cerulean Warbler and the Kentucky Warbler. To accomplish this greater task, it will first be necessary to implement a disturbance regime that more closely mimics the timing and magnitude of historic flows (Richter et al. 1996). The character of the Wisconsin River floodplain is much changed, even if one compares present conditions to those described just a half century ago (Curtis 1959). It seems reasonable to expect that the 150-km stretch below the last dam at Sauk City would more closely reflect historic patterns of disturbance, but recent evidence suggests this is not the case. Upstream dams have caused a lowering of the water table (Pfeiffer 2001), probably through channel incision, and effectively raised the elevation of the floodplain. Tree species that depend on periodic floods appear to be declining in number; for example, the large patches of cottonwoods that Curtis (1959) documented were not in evidence at the sites we surveyed. Emulating historic flows would be a step in the right direction toward restoring or preserving some of the defining features of floodplains, but the goal of achieving pre-settlement habitat conditions is probably unrealistic (Shafroth et al. 2002).

There are inherent dangers in the extrapolation of habitat affinities for a given species, as such affinities may be specific to a particular region or set of landscapes. In Wisconsin, for example, the Yellow-bellied Sapsucker is associated with bottomlands south of the Tension Zone, but with uplands north of there; the Veery is most common in lacustrine ash swamps in the north and floodplains in the south (Mossman 1988). Many of the species that we included in the ‘‘forest interior’’ functional group received this designation based, at least in part, on work done in upland forest patches of southern Wisconsin that were near our own study sites (Bond 1957, Ambuel and Temple 1983); yet, the same sensitivities to patch edge and area were not evident in our results.

It must be remembered that richness or abundance may not reflect the full effect of changes in land use or land cover, even for ‘‘area-sensitive’’ or ‘‘edge-sensitive’’ species. Populations in sink habitats may be maintained through dispersal even though they are experiencing high rates of predation or parasitism, as has been described for forested areas elsewhere in the Midwest (Robinson et al. 1995). Research on nest success and mortality is obviously necessary before this determination can be made. This study of habitat relationships at the community and guild levels is one component in a hierarchical approach that also includes single-species analyses, and ultimately an examination of potential mechanisms underlying patterns of habitat use.

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APPENDIX A

Summary statistics for the first two axes in CCA and intraset correlations for variables that were used to constrain the ordination are available in ESA's Electronic Data Archive: *Ecological Archives* A014-028-A1.

APPENDIX B

Alternate candidate models ($\Delta AIC_c \leq 2$ of the minimum AIC_c) for multiple linear regressions are available in ESA's Electronic Data Archive: *Ecological Archives* A014-028-A2.