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Land use and habitat gradients determine bird community diversity and abundance in suburban, rural and reserve landscapes of Minnesota, USA

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ABSTRACT

Bird species' community responses to land use in the suburbanizing Twin Cities, Minnesota, USA, were contrasted among reserves, rural lands, and suburbs. For each land use type, bird composition, diversity, and abundance were recorded for 2 years in ≈ 99 plots in three sampling units (each ≈ 4500 ha). A habitat gradient defined by canopy structure (grasslands to savannas to forests) was influenced by land use, so ≈ 300 plots were used to characterize simultaneous variation in bird communities along land use and habitat gradients. At broad scales (aggregate of 33 plots covering ≈ 4500 ha) suburbs supported the lowest bird richness and diversity and rural landscapes the most, with reserves slightly below rural. Although reserves were like rural lands in diversity of bird communities, they supported more species of conservation concern, particularly of grasslands and savannas. Differences among land use types varied with habitat structure. Suburbs, rural lands, and reserves had similar forest bird communities, but differed in grassland and savanna bird communities. The extensive rural forests are important for the region's forest birds. Suburban grasslands and savannas had low shrub abundance, low native bird richness and high non-native bird richness and abundance. However, total bird richness and diversity were as high in suburban as in rural and reserve plots because high native richness in suburban forests and high non-native species richness in suburban grasslands and savannas compensated for lower native richness in suburban grasslands and savannas. Bird conservation here and in the Midwest USA should protect rural forests, expand grasslands and savannas in reserves, and improve habitat quality overall.

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1. Introduction

Humans are intensifying their use of land and water as population grows and per-capita resource consumption rises (Vitousek, 1994; Matson et al., 1997). Land-use intensification refers to the incremental increase in human activity on the land for the purpose of satisfying people's material needs

and desires. As land use intensifies, road and population density and cropland or building area increase, while natural vegetation decreases (Lancaster and Rees, 1979; Clergeau et al., 1998). The fastest growing type of land use intensification in the United States is exurban development (Brown et al., 2005). Largely driven by single-family residential development on large lots (>1 ha), exurban development produces a

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dispersed settlement pattern in rural landscapes. This directly affects species populations by modifying or eliminating habitat and changing habitat distribution (Hanson et al., 2005). Because land-use intensification is spatially distributed across regions and can affect large areas, its influence on biodiversity is of great conservation and research interest.

Land-use intensification creates regions that may include a continuum of environmental conditions (Marzluff et al., 2001), from “wildlands” to rural, suburban, and urban lands. It is important to characterize the general effect of land-use intensification on bird community diversity and abundance for regions such as the north-central USA and elsewhere where suburban development is intruding on agriculture lands containing wild lands and small reserves, which together support remnants of the historical vegetation where the species most affected by development are hypothesized to persist.

Land-use intensification influences regional biota in several ways. Initially, the introduction of roads, buildings, pastures, cropland, clear-cuts, etc. into wilderness may increase species richness and diversity by increasing habitat heterogeneity in a landscape (Mellink, 1991; Blair, 1996; Jobin et al., 1996; Blair and Launer, 1997; Cam et al., 2000; Drapeau et al., 2000; Soderstrom and Part, 2000; Glennon and Porter, 2005). The introduction of new elements (e.g. tree or shrub plantings, buildings and lawns) to existing habitats can also increase or maintain species richness (Geis, 1974; Sodhi, 1992; Petit et al., 1999; Crooks et al., 2004). Moreover, land-use intensification often elevates bird abundance (Lancaster and Rees, 1979; Clergeau et al., 1998; Soderstrom and Part, 2000; Crooks et al., 2004), presumably due to higher primary productivity (e.g., fertilization, irrigation) and food introduced purposely or incidentally by humans, through habitat enhancements (e.g., plantings, buildings) that increase opportunities for territory or nesting sites (Sodhi, 1992; Petit et al., 1999), or due to fewer predators (Gering and Blair, 1999). However, as land use continues to intensify, species richness and diversity often fall. For example, suburbanization displaces native vegetation, reducing species richness of native birds (Lancaster and Rees, 1979; Clergeau et al., 1998; Germaine et al., 1998; Rottenborn, 1999; Cam et al., 2000). In urban centers of towns, loss of habitat specialists results in a homogeneous bird community that lacks ground- and scrub-nesting species (Blair, 1996; Clergeau et al., 2006). Intensive agricultural development has similar effects (Balent and Courtiade, 1992).

These patterns suggest that an intermediate level of land-use intensification produces the greatest species richness and diversity in a region. Regional biota respond simultaneously to environmental factors in both habitats (<0.1–10 km²) and landscapes (>100 km²) (Andren, 1994; Allen and O'Connor, 2000; Haire et al., 2000; Jones et al., 2000). Heterogeneity in habitats is provided to a great extent by variety of vegetation structures (e.g., Freemark and Merriam, 1986), while heterogeneity in landscapes in large part is determined by variety of land uses and habitats resulting from land use (Forman and Godron, 1996). In all such cases, an intermediate level of disturbance may create a variety of ecological structures, within and among habitats, which support a greater number of species.

After 1850 agriculture dominated large areas of the US Midwest, and after 1945 suburban and urban land uses increased rapidly (Anderson et al., 1996; Albert, 1995). Today

Midwestern landscapes are composed of combinations of land uses and habitats that vary along a land-use intensification gradient. Given that flora and fauna vary across this continuum, and that land use has influenced the distribution of habitats at different points along the continuum, it is difficult to understand the individual and joint roles of land use and of habitat in relation to local and regional patterns of bird composition and abundance. Advancing understanding of this particular issue is a major goal of our study. In seeking to understand land-use intensification's effect on bird communities in the Twin Cities region, Minnesota, USA, we measured the contribution of reserves, rural lands, and suburbs to current bird community richness, diversity, and abundance. We expected that: (1) Species richness and diversity in habitats would be greatest at intermediate levels of land-use intensity and canopy cover (Connell, 1978; Blair, 1996; Peterson and Reich, 2001). Because of the fine-scale patchiness of vegetation and the greater structural heterogeneity of savannas, at a local level savannas should have greater richness and diversity than forests or grasslands. Suburbs should have lower α - and β -diversity (as defined by MacArthur, 1965) than reserves or rural areas, and rural areas should have higher α - and β -diversity than reserves. (However, the total number of individual birds should peak in suburbs.) (2) Removal and disturbance of native vegetation would reduce landscape heterogeneity and favor non-native species (Mack et al., 2000). Native species, especially those most sensitive to land use (Thompson et al., 1993), would decrease as land-use intensity increases, while non-native species should increase as land-use intensity increases. (3) Bird communities in habitats would vary with land use because the intensity and type of land use affects the characteristics of habitats (Andren, 1994; Donovan et al., 1997; Soderstrom and Part, 2000). In other words, land-use intensity and habitat would be expected to interact.

2. Field methods

2.1. Study region

The study region of 5000 km² is located on the geologically-homogeneous Anoka Sand Plain in the rapidly developing northern Twin Cities metropolitan region. Land cover 150 years ago was 50% savanna, 25% grasslands, 18% forests, and 7% wetlands and lakes (GIS data from MN Department of Natural Resources, St. Paul, MN). A mosaic of large and small habitat patches characterized this area, as elsewhere in the prairie-forest transition (Albert, 1995; Wovcha et al., 1995; Will-Wolf and Montague, 1995). The formerly dominant land cover of savanna is now rare in the entire US Midwest (Nuzzo, 1986).

2.2. Study design

We sampled birds, vegetation, and environmental variables in the 5000 km² study region simultaneously along two gradients: intensifying land use and increasing canopy cover. The land-use intensification gradient in the study region was represented by minimally used reserves (a subset of Marzluff et al.'s (2001) “wildlands”), moderately used rural lands, and

intensively used suburbs. We did not sample the urban segment of the gradient. The reserves, rural lands and suburbs were homogeneous and represented three land-use types. The canopy cover gradient was sampled within each land-use type. For each land-use type we identified three similar circular sampling units of 4000–5500 ha (Fig. 1). Landscape attributes were summarized for the three sampling units in each land-use type (Minnesota Department of Natural Resources, 1999; Minnesota State Demographers Office). Road and population density and developed area were least in the reserve land-use type and greatest in the suburbs (Table 1). The rural land-use type was intermediate in these traits but had the greatest area in cropland, pasture and hay meadows.

The sampling units contained three habitats defined by tree canopy cover (Peterson and Reich, 2001): grassland (0–5% canopy cover), savanna (6–50% canopy cover), and forest (51–100% canopy cover). In this definition, cropland is a grassland and residential developments are usually savannas. A canopy-defined gradient exists in the study region and correlates with significant environmental variables (Reich et al., 2001; Davis et al., 2000). Even though savannas in nature reserves, rural areas, and suburbs experienced different land-use intensities, they all contained areas of 6–50% canopy cover due to land use. Controlling for canopy cover

thus allows other influential environmental variables to be identified. Thus, we separate land use from canopy-defined habitat in contrast to other studies that merged land use and habitat in single classes (Blair, 1996; Petit et al., 1999; Drapeau et al., 2000). This is the “patch-based” approach recommended by Bolger (2001). Patches of forest, savanna and grassland are studied as embedded entities in each of three segments of the urbanizing gradient (wild to rural to suburban) appropriate for the Twin Cities region and Upper Midwest.

Reserve sampling units were entirely within Sherburne National Wildlife Refuge/Sand Dunes State Forest, the Cedar Creek Natural History Area, and Wild River State Park. These reserves contained the historical upland habitats that characterized the region 150 years ago (Albert, 1995; Wovcha et al., 1995). Sampling units in the rural land-use type were located in Stanford, Oxford, and Sunrise Townships, at least 16 km north of the residential developments of the Twin Cities. Remnants of historical habitats were present but embedded in a matrix of fields, pastures, farmsteads, and small housing developments. Sampling units in suburbs (all built after 1945) were located in Blaine, Shoreview, and White Bear Lake. The suburban land-use type contained buildings, roads, yards, and lots, with small areas of historical habitats.

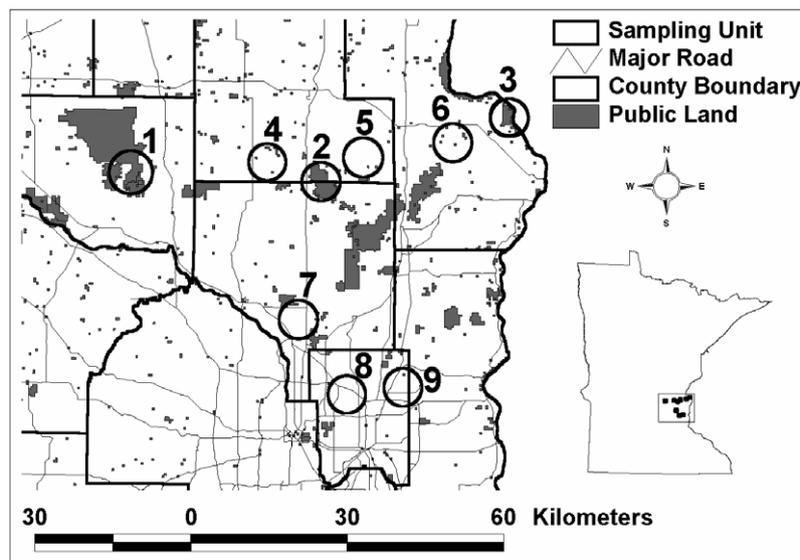


Fig. 1 – Sampling units in the Twin Cities study region, Minnesota, USA. Reserve units were (1) Sherburne/Sand Dunes, (2) Cedar Creek, (3) Wild River; rural units were (4) Stanford Twp., (5) Oxford Twp., (6) Sunrise Twp.; suburban units were (7) Blaine/Coon Rapids, (8) Shoreview, (9) White Bear Lake.

Table 1 – Characteristics of reserve, rural, and suburban land-use types in the Twin Cities region, Minnesota, USA

Land-use type ^a	Roads (km/km ²)	Population (persons/km ²)	Developed uplands ^b (%)	Grassland (%)	Savanna (%)	Forest (%)
Reserve	0.6–0.8	<4	23.1	20.0	6.4	43.9
Rural	0.9–1.1	4–39	44.1	15.9	4.6	29.7
Suburb	>9.0	>39	62.1	4.0	2.6	12.4

a Excludes wetlands and open water.

b Combines built-up land and cropland.

2.3. Sampling

Sampling points were placed at 33 locations in each of the nine sampling units (three replicates of each of the land-use types). Plots were located on a rectilinear grid (points separated by 250 m along transects, and 500 m between transects) overlaid on 1:24,000 USGS topographic maps for each sampling unit using ArcView. The first sampling location within a sampling unit was located randomly, and subsequent grid points were visited along that transect in a predetermined direction. Grid points that fell in a wetland, lake, stream, or highway were not sampled. Instead sampling continued at the next grid point or, if the distance to the next useable grid point was far, sampling was continued in the return direction beginning with the nearest grid point of the adjacent transect. Variables measured at each grid sampling point were (1) vegetation and environmental structure in 15 m-radius plots; (2) land use and bird communities in 100 m-radius plots; and (3) distance to the nearest forest, building, or road.

Environmental variables and woody vegetation were sampled in 1999 (except for four plots sampled in 2000), and birds were sampled in both 1999 and 2000.

In 15 m-radius plots centered on each grid sampling point, vegetation cover by layer was estimated using the Daubenmire cover scale (Mueller-Dombois and Ellenberg, 1974) with an added 0–1% cover class (0–1%, 1–5%, 5–25%, 25–50%, 50–75%, 75–95%, 95–100%). Vegetation layers were defined as canopy (stems \geq 5 cm dbh), tall shrub (1–8 m height), low shrub (<1 m height), tall herb (\geq 0.5 m height), and low herb (<0.5 m height). Pavement, buildings, and vegetation litter in each plot also were given a cover value. Cover values were converted to midpoints for analysis.

For each grid sampling point, the following data were obtained through GIS analyses of USGS 1:24,000 topographic maps corrected with digitized aerial photography (Minnesota Department of Natural Resources, 1999) and field inspection: distance (m) to nearest forest >4 ha, inhabited building, and public road. Distance to lake >4 ha, lake <4 ha, permanent stream, river, or ditch, wetland >0.4 ha, and forest opening >0.1 ha were also measured, found insignificant, and not reported.

At each grid sampling point, birds were recorded one time during the 6-week breeding season in 1999 and a second time in 2000 using a standard point count protocol (Howe et al., 1997; Pomeroy and Dranzoa, 1997; Drapeau et al., 1999). All bird species detected within 100 m-radius of the grid sampling point were recorded during one 10-min period each year on days without rain or significant winds. All but two counts

were begun at 5:30–9:30am Central Daylight Time from May 29 to July 15, 1999 and May 26 to June 29, 2000 by experienced birders (two in 1999; four in 2000). Identifications were cross-checked among observers. Observers moved through plots during the last 5 min of each count to confirm bird identities and flush previously undetected birds. One sampling unit in each land-use type was visited early, one in the middle, and one at the end of the 1999 census period, then sampled in reverse order in 2000 to reduce seasonal variability. We tested for observer difference by modeling total bird abundance and richness in response to observer, land-use type, % canopy cover, and interactions among these factors. Differences among observers explained only a minimal fraction of variance.

In the same 100 m-radius plot used for bird counts, the proportion of land uses was estimated. The land uses were wild/no recent use, tree plantation, pasture, hayed/mowed land, cultivated land, suburban park, and built with structures/pavement. This information was summarized and each plot given a land-use index number for the purposes of ordination (Table 2). Plots were assigned to an index on the basis of the dominant land use (>50%) and other important land uses (20–50% of plot). Vegetation data were also recorded in 100 m plots but are used minimally hereafter.

3. Data analysis

Data analysis focused on (1) understanding general relationships between bird communities and environmental variables along the two gradients in the region (ordination), (2) modeling bird community richness, diversity and abundance relative to land-use type (response to land use), and (3) modeling the inter-related contribution of land-use types and canopy-defined habitats to bird community richness and abundance (land-use and habitat interactions). Bird communities were divided into groups on the basis of whether they were native or non-native to the region, and among native species, whether they were considered sensitive species and likely to require special management in order to persist in the region (Thompson et al., 1993). Native species are defined as those present in native habitats in 1850, and non-native species as those established or introduced to the region after 1850.

3.1. Ordination

The relationship of bird community composition in 1999 and 2000 to land-use types and canopy cover was determined

Table 2 – Land-use index summarizing the land uses observed in 100 m plots

Index	Land uses	Description
1	Wild	No evidence of recent human use (includes tree plantations)
2	Wild with built-up	Wild land with areas of impervious surfaces
3	Agricultural use	Mix of cultivated, pastured, and/or hayed-mowed land
4	Agricultural use with built-up	Cultivated, pastured, and/or hayed-mowed lands with impervious surfaces
5	Built-up with wild or agricultural use	Areas of impervious surface containing areas of agricultural or no human use
6	Built-Up	Impervious surfaces usually with hayed-mowed land (includes parks that are mowed and surrounded by impervious surfaces)

through direct gradient analysis using canonical correspondence analysis (CCA) in PC-ORD Ver. 4.0 (McCune and Mefford, 1999). CCA uses Reciprocal Averaging (RA) derived from principal components analysis (PCA) to make an iterative comparison between species abundance and environmental variables measured in plots. Direct gradient analysis assumes that the most important environmental variables are known. The resulting ordination positions plots with similar species and environmental variables near each other in two or more dimensions. Ordinations were run separately for each year. CCA tests the validity of the association between species and environmental variables by Pearson rank correlation of plots and species against the environmental gradients, followed by a Monte Carlo test of significance of the ordination as a whole (McCune and Mefford, 1999). While CCA is a popular technique, it fails when the important environmental variables are unknown. As a check against this, we performed indirect gradient analysis ordinations using non-metric multidimensional scaling (NMS) and detrended correspondence analysis (DCA). Indirect gradient analysis creates an ordination of plots from species abundance only. Like CCA, DCA uses Principal Components Analysis (PCA), but does not include environmental variables in the analysis. NMS uses a completely different algorithm and approach and provides an independent check against the results of ordinations based on PCA. To relate environmental variables to ordination axes, the ordination axis scores of plots were correlated with environmental variables in JMP Ver. 3.1.6.2 (SAS Institute, 1996) using linear regression for continuous variables and logistic regression for ordinal variables (Chapman, 2001). This approach has been used to correlate bird abundance with environmental data (Davis et al., 2000). Results from the CCA, DCA, and NMS ordinations and the correlations with environmental variables were similar. We present only results from CCA because it displays the relationships between bird communities and environmental variables.

Ordinations were checked for their ability to aggregate plots into distinct groupings with the multi-response permutation procedure (MRPP) available in PCORD. MRPP tests the hypothesis that there are no differences in land-use type/canopy cover groups (e.g., suburban forests versus reserve forests). MRPP demonstrated that the ordination successfully identified distinct bird communities with respect to environmental gradients (for details see Chapman, 2001).

3.2. Response to land use

Maximum and minimum values of richness, diversity (β , H') and abundance in bird communities were modeled with respect to land-use types using regression analysis with an ANOVA test for model significance in JMP Ver. 3.1.6.2. Data were examined at three scales: a regional aggregate of three sampling units in each land-use type; the average for each land-use type (i.e., average of three sampling units containing 33 plots each; $n = 3$); and the average of 33 plots nested in each sampling unit ($n = 99$). Land-use type was treated as a nominal variable.

The Shannon–Weaver measure of α -diversity,

$$H' = -\sum p_i \log_e p_i$$

was calculated at the land-use type and 100 m-plot scales (Shannon and Weaver, 1949; MacArthur and MacArthur, 1961). Whittaker's β -diversity index, a measure of the turnover of species from one habitat to another in a land-use type,

$$\beta = s/\alpha - 1$$

was calculated for the land-use type scale (Whittaker, 1960; Wilson and Shmida, 1984). Following regression analysis, pairwise t-tests were used to determine which pairs of land-use types differed.

3.3. Land use and habitat interactions

Bird community response (richness and abundance) to land-use type (reserve, rural, suburb) and canopy cover (grassland, savanna, forest) was modeled in JMP. Bird richness and abundance in 1999 and 2000 were normally distributed based on a Wilks–Shapiro W -test ($p > 0.1$), or nearly normally distributed based on examination of distributions and normal quantile plots.

The regression model included land-use type, canopy cover (using midpoints of classes), and an interaction term (land-use type \times canopy cover). Land-use type was treated as a nominal, and canopy cover as an ordinal variable.

We investigated several of the environmental variables identified by CCA as significant. One of these, understory woody plant cover, is a significant predictor of bird community composition (Beissinger and Osborne, 1982; Tilghman, 1987; Munyenyembe et al., 1989). The cover of trees and shrubs < 8 m was summed for each plot and averaged over all plots for land-use types and canopy cover combinations (e.g., suburban forest). We modeled in JMP the mean total understory woody plant cover among these land-use types and canopy cover combinations. Model significance was tested with ANOVA.

4. Results

4.1. Land use and habitat determinants of bird community composition

In both 1999 and 2000 the bird communities in the northern Twin Cities region varied with land use but in different ways depending on habitat (Fig. 2). Responses in the 2 years were

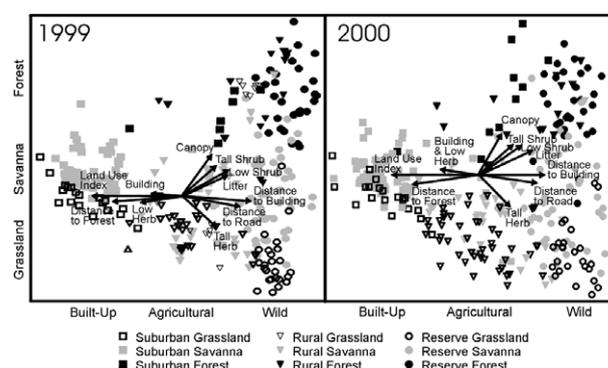


Fig. 2 – Canonical correspondence analysis (CCA) of 1999 and 2000 bird census plots.

similar. The close association of forested plots (filled shapes) in the ordination charts indicated that bird communities were relatively similar in the forests of suburbs, rural lands, and reserves. The divergence of plots (open and shaded shapes) in the lower portion of the ordination charts indicated that bird communities in grasslands and savannas differed markedly among the three land-use types. Land-use, the distance to buildings, forests, and roads, and the cover by low herbaceous vegetation and buildings were strongly associated with Axis 1 but not Axis 2 (Table 3). We interpret Axis 1 to represent the land use gradient. Axis 2 represented a habitat gradient strongly associated with canopy cover, but not other vegetation structural variables. Low shrub cover was more strongly associated with the land use gradient than with the habitat gradient, while litter cover, tall shrub cover, and tall herbaceous vegetation cover were associated with both gradients.

4.2. Richness, diversity, and abundance in relation to land use

In general the rural land-use type ($n = 3$) supported the greatest richness and diversity for all bird species and for native species, and suburbs the least (Table 4), and results for the 2 years were similar. Reserve richness and diversity were measurably below that of rural lands, although statistically reserves and rural lands often did not differ significantly. In aggregate (summing species in all ≈ 99 plots per each land-use type, or for the ≈ 33 plots within each replicate land-use type), suburbs had about 30–40% fewer species and lower beta diversity than rural lands, and richness in reserves was about 5–10% below rural lands. In contrast, at the individual plot scale, diversity (H') and the richness of all species did not vary among land-use types (Table 4). On the other hand, the average plot abundance for all species and for native species was highest in suburbs, though the modeled response was not strongly predictive ($r^2 < 0.279$).

Table 3 – Environmental variables significantly correlated with the axes of CCA ordinations of 1999 and 2000 bird data

	Axis 1		Axis 2	
	1999	2000	1999	2000
Land use index ^a	0.907	0.882	–0.059	–0.009
Distance to forest	0.672	0.646	0.044	0.099
Low herb cover ^b	0.352	0.336	0.019	–0.042
Building cover	0.231	0.260	–0.057	–0.031
Canopy cover	–0.350	–0.289	–0.640	–0.542
Tall herb cover	–0.382	–0.366	0.369	0.405
Tall shrub cover	–0.409	–0.388	–0.446	–0.419
Litter cover	–0.499	–0.492	–0.306	–0.342
Low shrub cover	–0.522	–0.511	–0.385	–0.401
Distance to road	–0.627	–0.647	0.106	0.109
Distance to building	–0.734	–0.740	0.058	0.011

Cover was measured in 100 m plots unless noted. Monte Carlo tests of all correlations were significant at $p = 0.01$.

^a See Table 2.

^b Measured in 15 m plots.

4.3. Non-native, native, and sensitive native bird species

For data averaged for each land-use type ($n = 3$), the modeled response showed that richness of non-natives and natives both peaked in rural lands (Table 4); the model was highly predictive of the data ($r^2 > 0.848$). At the plot level ($n \approx 33$ in each of three land-use type sampling units), the modeled response for non-native species ($r^2 > 0.300$) demonstrated an increase in both richness and abundance from reserves, to rural lands, to suburbs, with a large increase in suburbs. Also at the plot level, native species richness was lowest, and abundance highest, in suburbs, though this was a weak response ($r^2 < 0.102$). Native species richness was about 9 species in suburban plots compared to about 10 species in plots of reserves and rural lands. Native species richness and abundance tended to be higher in reserve plots compared to rural lands, but not significantly so.

The response of those native species that were most sensitive to changes in land use was opposite that of non-native species, increasing in richness and abundance from suburbs, to rural lands, to reserves. Sensitive species richness did not peak in rural lands at the landscape scale, unlike the other species groups. The response in land-use types ($n = 3$) was highly predictive ($r^2 > 0.887$) and in plots ($n \approx 99$) moderately so ($r^2 > 0.353$). The greatest change in sensitive species richness and abundance occurred from rural lands to suburbs, falling by 73–88% at plot and land-use type scales. At the plot level sensitive species richness and abundance fell 48–54% from reserves to rural lands. At the level of land-use type ($n = 3$) sensitive species richness fell 14–24% from reserves to rural lands. Hence, declines in sensitive species were most extreme in suburbs, less so in rural lands at habitat levels, and least severe in rural lands at the level of land-use type where the response was highly predictive.

4.4. Interactions of land use and habitat

Interactions of land-use type and canopy-defined habitat were apparent in the graphed data (Figs. 3 and 4), but regression models demonstrated a strong interaction in non-native species only (Table 5). Non-native species attained their greatest richness and abundance in grasslands and savannas of suburbs, and were slightly elevated in rural grasslands and savannas compared to reserves. They were largely absent from the region's forests. Land use, habitat, and their interaction explained a moderate amount of variation in the model of non-native species richness and abundance for both years ($r^2 = 0.369$ and 0.611). The pattern for sensitive native species likewise was explained reasonable well by the model ($r^2 = 0.456$ and 0.577), but with no interactions between land use and habitat.

The graphed data (Figs. 3 and 4) also showed that the loss of sensitive native species from reserve to suburban forests (1–2 species, 2 individuals) was less than that observed in grasslands and savannas across the same land-use gradient (2.5–3 species, 3–4 individuals). In other words, land-use type had less of an effect on sensitive bird species using forests than on those using grasslands and savannas.

Canopy cover had a generally weak effect on total bird community richness and abundance and native species

Table 4 – Modeled comparisons of richness, diversity and abundance in bird community groups by land-use type (reserve, rural, suburb)

	Year	Reserve	Rural	Suburb	Whole model <i>p</i>	Whole model <i>r</i> ²
Aggregate richness (<i>n</i> ≈ 33)	1999	87	91	63	–	–
	2000	94	95	65	–	–
<i>Average by land-use type (n = 3)</i>						
β-diversity – all species	1999	4.41 (0.27) ^a	4.91 (0.27) ^a	2.63 (0.27) ^b	0.002	0.869
	2000	4.46 (0.21) ^a	5.18 (0.21) ^b	2.88 (0.21) ^c	<0.001	0.911
<i>H'</i> (α-diversity) – all species	1999	3.57 (0.61) ^a	3.67 (0.61) ^a	3.04 (0.61) ^b	<0.001	0.912
	2000	3.55 (0.04) ^a	3.69 (0.04) ^a	3.05 (0.04) ^b	<0.0001	0.965
Richness – all species	1999	57.3 (2.3) ^a	64.0 (2.3) ^a	39.0 (2.3) ^b	<0.001	0.912
	2000	56.3 (1.6) ^a	62.0 (1.6) ^b	41.0 (1.6) ^c	<0.001	0.936
Richness – non-natives	1999	1.0 (0.4) ^a	4.3 (0.4) ^b	3.7 (0.4) ^b	0.004	0.848
	2000	0.3 (0.4) ^a	4.0 (0.4) ^b	3.7 (0.4) ^b	0.002	0.881
Richness – natives	1999	56.3 (2.4) ^a	59.7 (2.4) ^a	35.3 (2.4) ^b	<0.001	0.909
	2000	56.0 (1.7) ^a	58.0 (1.7) ^a	37.3 (1.7) ^b	<0.001	0.937
Richness – sensitive natives	1999	14.0 (0.6) ^a	10.7 (0.6) ^b	1.7 (0.6) ^c	<0.0001	0.971
	2000	14.0 (1.2) ^a	12.0 (1.2) ^a	3.3 (1.2) ^b	0.002	0.887
<i>Average by plot (n ≈ 99)</i>						
<i>H'</i> – all species	1999	2.19 (0.04) ^a	2.16 (0.04) ^a	2.15 (0.04) ^a	0.725	0.023
	2000	2.16 (0.04) ^a	2.13 (0.04) ^a	2.13 (0.04) ^a	0.808	0.038
Richness – all species	1999	10.6 (0.3) ^a	10.9 (0.3) ^a	10.8 (0.3) ^a	0.837	0.031
	2000	10.4 (0.5) ^a	10.1 (0.5) ^a	10.6 (0.5) ^a	0.753	0.090
Richness – non-natives	1999	0.06 (0.07) ^a	0.35 (0.07) ^b	1.4 (0.07) ^c	<0.0001	0.468
	2000	0.06 (0.07) ^a	0.58 (0.07) ^b	1.8 (0.07) ^c	<0.0001	0.518
Richness – natives	1999	10.5 (0.3) ^a	10.5 (0.3) ^a	9.2 (0.3) ^b	0.004	0.071
	2000	10.3 (0.3) ^a	9.5(0.3) ^a	8.8(0.3) ^b	<0.001	0.092
Richness – sensitive natives	1999	2.3 (0.12) ^a	1.2 (0.12) ^b	0.2 (0.12) ^c	<0.0001	0.376
	2000	2.7 (0.11) ^a	1.4 (0.11) ^b	0.2 (0.11) ^c	<0.0001	0.468
Abundance – all species	1999	16.7 (0.7) ^a	16.8 (0.7) ^a	23.4 (0.7) ^b	<0.0001	0.216
	2000	15.9 (0.6) ^a	16.1 (0.6) ^a	23.2 (0.6) ^b	<0.0001	0.279
Abundance – non-natives	1999	0.09 (0.38) ^a	0.76 (0.38) ^b	5.55 (0.38) ^c	<0.0001	0.300
	2000	0.06 (0.32) ^a	1.18 (0.32) ^b	5.54 (0.31) ^c	<0.0001	0.376
Abundance – natives	1999	16.6 (0.6) ^{ab}	16.1 (0.6) ^a	17.8 (0.6) ^b	0.081	0.081
	2000	15.8 (0.6) ^a	14.9 (0.6) ^a	17.6 (0.6) ^b	0.003	0.102
Abundance – sensitive natives	1999	3.2 (0.17) ^a	1.6 (0.17) ^b	0.2 (0.17) ^c	<0.001	0.353
	2000	3.9 (0.17) ^a	1.8 (0.17) ^b	0.4 (0.17) ^c	<0.0001	0.426

Bird community groups consist of all species, native species, non-native species, and sensitive species. Aggregate richness is the cumulative count of species in three sampling units of each land-use type. The averages by plot were modeled as a per-plot average of three sampling units nested in each land-use type. Values with different superscripts are statistically different (*p* < 0.05). Standard errors are in parentheses.

richness and abundance (Table 5, *r*² < 0.156, except for abundance of all species in 2000). However, the graphed data (Figs. 3 and 4) tended to show that richness and abundance of all bird species and of native species was lowest at the extremes of the canopy gradient (<6% and >83% canopy cover) in reserves and rural lands, but not in suburbs. In suburbs the pattern was more complex.

We observed a minor interaction between land use and habitat in 2000 with respect to bird abundance. In 2000 native species abundance was significantly elevated in suburban forests, and sensitive species abundance was significantly depressed in rural forests and equal to sensitive species abundance in suburban forests. A change in richness and abundance of sensitive native species also took place from 1999 to 2000. Between these years, the richness and abundance of sensitive species fell in rural forests, and the richness of sensitive species fell in suburban forests.

The modeled response of understory woody plant cover (low and tall shrub layers) showed the greatest divergence be-

tween land-use types in savannas, although it declined in all habitats along the land-use gradient (*r*² = 0.483, Fig. 5).

5. Discussion

Land use shaped bird communities in the Twin Cities region by changing the composition of landscapes and the qualities of habitats. Responses to land use depended on scale, habitat type, and the component of the bird community in question (see Fig. 6).

5.1. Overall land-use gradient effects

Land uses associated with human settlement were the main drivers of scale- and habitat-dependent change in bird communities along a land-use gradient from wild lands to agricultural lands to suburbs in the Twin Cities region. Although at a plot scale (≈3 ha) suburbs had similar bird species richness as rural or reserve lands, suburban landscapes (≈5000 ha) had

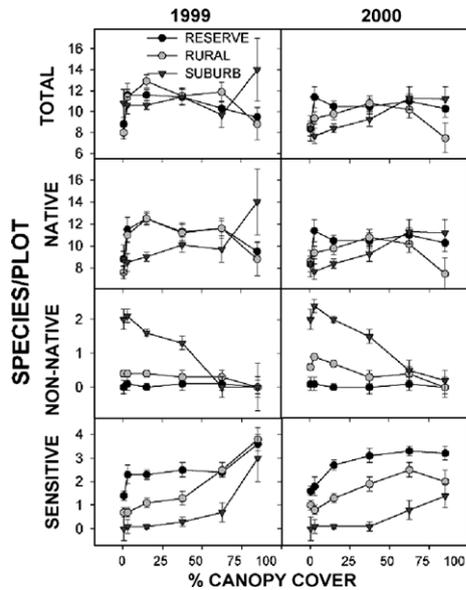


Fig. 3 – Average bird community richness in 100 m plots (1999 and 2000) by canopy cover in land-use types (also see Table 5).

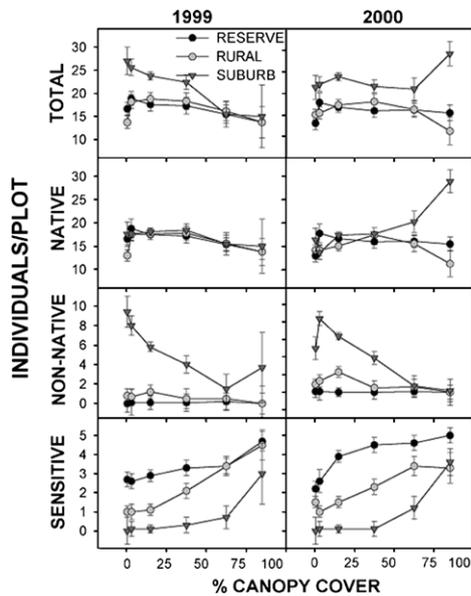


Fig. 4 – Average abundance of individual birds in communities in 100 m plots (1999 and 2000) by canopy cover in land-use types (also see Table 5).

one-third fewer species. Proximity of buildings reliably predicted changes in the bird community and was associated with distance to roads, the amount of short grassland and mowed turf, and the lack of tall shrubs and herbs. The general effect of buildings, roads, and associated displacement of native vegetation on bird communities is well known (Geis, 1974; Walcott, 1974; Emlen, 1974; Tilghman, 1987; Friesen et al., 1995; Mack et al., 2000; Glennon and Porter, 2005).

The environment associated with buildings created conditions in the Twin Cities suburbs that enabled some species to establish larger populations than they achieved in rural and

wild lands (Lancaster and Rees, 1979; Clergeau et al., 1998; Soderstrom and Part, 2000; Crooks et al., 2004). McKinney (2006) noted that non-native and native birds that are urban- and edge-adapted species benefit most from suburban and exurban developed environments, while native species needing large areas of habitat benefit the least. In the Twin Cities and in the United States, residential development may be altering regional species pools due to its scale. Exurban residential development (lot size of 1–16.2 ha or 2.5–40 ac) is the fastest-growing type of land use in the United States and disperses the effects of buildings, roads, and short grasslands across a large landscape (Brown et al., 2005). In the Twin Cities region, rural suburban development (lot size of 0.4–1 ha or 1–2.5 ac) contributes significantly to land-use change as well.

However, in rural areas of the Twin Cities region, where agriculture is interspersed with wild lands, overall bird species richness and diversity were slightly elevated compared to reserves. Rural land uses allowed non-native species to penetrate the wild landscape, but native species benefited also as their richness and diversity were higher in rural lands. This phenomenon of elevated diversity with human use has been attributed to the introduction of new land uses, modification of wild habitat, and increased vegetation structure and variety (Geis, 1974; Sodhi, 1992; Blair, 1996; Petit et al., 1999; Crooks et al., 2004; Glennon and Porter, 2005).

In the Twin Cities region the mechanism behind the elevated rural diversity of native species is best explained by elevated β -diversity at a landscape level. The rural landscape contains a greater variety of habitat patches and represents a different mosaic of habitats than either the reserve landscape or the wild landscape of 1850. The rural landscape still contains wild remnants, including large patches of forests, while also providing new and altered habitats for species that are absent or rare in wild landscapes. Simply put, native habitats mixed with cropland create a landscape with habitat for a wide variety of species (Jobin et al., 1996; Boutin et al., 1999; Soderstrom and Part, 2000; Burke and Nol, 2000). In contrast, β -diversity was dramatically lower in the Twin Cities suburbs, as were landscape scale species richness and diversity. Thus, maintaining high β -diversity, may be essential for maintaining the regional bird species pool in the Twin Cities region and may require minimizing the footprint of residential development in rural landscapes (McKinney, 2006; Glennon and Porter, 2005).

5.2. Land-use gradient effects on habitat

Increased land use intensity altered bird communities more in grasslands and savannas than in forests, with several factors contributing to these patterns. For example, cover of woody and herbaceous plants, and of litter, differed among land use types more in grasslands and savannas than in forests. These changes in the understory and ground layer of a habitat type across the land-use gradient can change the bird community, for instance by reducing the quantity of nesting and feeding locations (Clergeau et al., 2006). Additionally, predation on ground- and shrub/scrub-nesting and feeding bird species may be more severe in habitats where the ground layer and understory are less dense and less able to conceal the birds and their nests. Thus, reserves should have the lowest predation levels, rural lands the next lowest, and suburbs

Table 5 – Modeled bird response (richness and abundance) to land-use types and canopy cover in 100 m plots

Model term		1999			2000		
		Model term p	Whole model r ²	Highest value	Model term p	Whole model r ²	Highest value
Richness							
All species	Whole model	<0.0001	0.165		0.166	0.074	
	Land-use type	0.166		–	0.382		–
	Canopy cover	0.004		6–50% canopy	0.143		–
	Land-use type X canopy cover	0.114			0.574		
Natives	Whole model	<0.0001	0.201		<0.001	0.143	
	Land-use type	0.408		–	0.951		–
	Canopy cover	0.002		6–50% canopy	0.026		6–50% canopy
	Land-use type X canopy cover	0.060			0.132		
Non-natives	Whole model	<0.0001	0.549		<0.0001	0.611	
	Land-use type	<0.0001		Suburb	<0.0001		Suburb
	Canopy cover	<0.0001		0–50% canopy	<0.0001		0–50% canopy
	Land-use type X canopy cover	<0.0001			<0.0001		
Sensitive natives	Whole model	<0.0001	0.523		<0.0001	0.577	
	Land-use type	0.018		Reserve	0.004		Reserve
	Canopy cover	<0.0001		51–100% canopy	<0.0001		51–100% canopy
	Land-use type X canopy cover	0.087			0.229		
Abundance							
All species	Whole model	<0.0001	0.247		<0.0001	0.274	
	Land-use type	<0.001		Suburb	0.037		Suburb
	Canopy cover	0.012		6–50% canopy	0.430		–
	Land-use type X canopy cover	0.325			0.299		
Natives	Whole model	0.131	0.079		<0.0001	0.161	
	Land-use type	0.071		–	0.471		–
	Canopy cover	0.156		–	0.100		–
	Land-use type X canopy cover	0.905			<0.001		
Non-natives	Whole model	<0.0001	0.369		<0.0001	0.479	
	Land-use type	<0.0001		Suburb	0.005		Suburb
	Canopy cover	0.006		6–50% canopy	<0.0001		6–50% canopy
	Land-use type X canopy cover	0.008			0.0001		
Sensitive natives	Whole model	<0.0001	0.456		<0.0001	0.549	
	Land-use type	<0.001		Reserve	0.017		Reserve
	Canopy cover	<0.0001		51–100% canopy	<0.0001		51–100% canopy
	Land-use type X canopy cover	0.378			0.043		

Terms in the whole model were land-use type, canopy cover, and the interaction of land-use type with canopy cover.

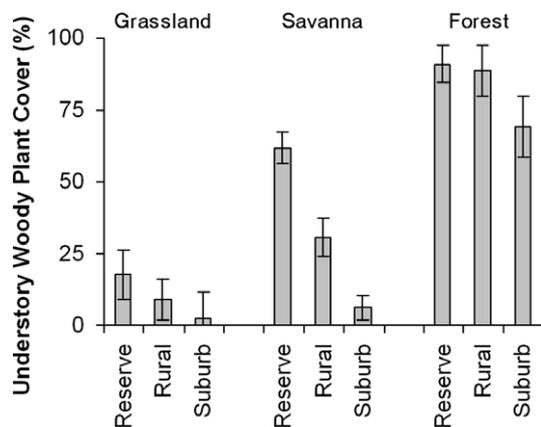


Fig. 5 – Tree and shrub abundance in the understory of land-use types and habitats. Abundance is the average of summed tree and shrub cover in plots. Standard error bar is shown.

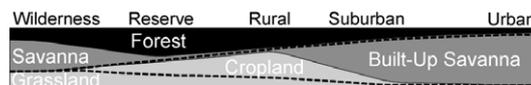


Fig. 6 – Proportions of habitats along the land-use gradient. The thickness of a habitat type is its percentage of total land cover at that point in the land-use gradient. Cropland is a canopy-defined grassland and built-up savanna a canopy-defined savanna. Wilderness percentages are from 1850 General Land Survey data; other percentages are from current land cover data.

the highest levels of predation due to progressively diminishing ground layer and understory vegetation across all habitat types. However, data from artificial nest experiments and other observations reveal conflicting patterns of predation among land use types (Geis, 1974; Hogrefe et al., 1998; Gering and Blair, 1999; Mancke and Gavin, 2000).

5.3. Land-use gradient effects on non-native versus native species

Non-native bird species displayed the strongest response in richness, diversity and abundance to the land-use gradient, especially in suburbs. Suburban grassland and savanna habitat had a disproportionately high abundance of non-native birds. This effect was magnified by the rarity of non-natives in forests, regardless of land use type.

Suburban land use is known to elevate bird abundance, and in the Twin Cities region non-native birds largely created this effect. Some (e.g., [Walcott, 1974](#)) have speculated that non-native bird species displace native species by competing for scarce resources, such as for nest cavities between the introduced House Sparrow and native Eastern Bluebird. However, native bird species abundance was the same regardless of land-use type, though slightly elevated in 2000 in suburban forests. Evidence for a suppressive effect of high non-native abundance on native birds was lacking in our data.

At a plot scale (≈ 3 ha), total species richness and diversity were as high on average in suburbs as in rural lands and reserves. The mechanism behind this was the high richness of native species in suburban forests plus high richness of non-natives in suburban grasslands and savannas which together compensated for low native richness and diversity in suburban grasslands and savannas. Indeed, native species richness in suburban forests was unexpectedly high and consisted of native species whose abundance in the region was greatest in suburban forests: Downy Woodpecker (*Picoides pubescens*), Gray Catbird (*Dumetella carolinensis*), House Wren (*Troglodytes aedon*), Northern Cardinal (*Cardinalis cardinalis*), and Rose-breasted Grosbeak (*Pheucticus ludovicianus*). Optimal conditions may be created for some native species by forests in proximity to habitat elements that are uncommon or absent in rural and reserve landscapes (e.g., shrub patches in short grass, fruit trees, bird feeders, artificial nesting cavities) or reduced competition for those features due to the rarity of other native species ([DeGraaf and Wentworth, 1986](#); [Tzilkowski et al., 1986](#); [Goldstein et al., 1986](#); [Munyenyembe et al., 1989](#); [Germaine et al., 1998](#)).

5.4. Land-use gradient and habitat for sensitive native species

Sensitive native species responded differently to the land-use and habitat gradients than did non-native and native species overall. Others have described a strong response to land use and habitat variables in a subset of an area's avifauna, leading them to conclude that this subset should be the focus of conservation in order to prevent their decline or disappearance at a regional scale (e.g., [Ford et al., 1995](#); [Recher, 1999](#)). Across a gradient of increasing land use intensity we found sensitive species richness and abundance decreased in all habitats, but the effect was most pronounced in grasslands and savannas and least in forests. Land use and canopy were both significant predictors of sensitive species richness and abundance, yet did not interact as was seen for non-native species. Rather, the decrease occurred steadily within habitats across the land-use gradient.

The chief factors responsible for reductions in sensitive native bird species as land use intensified can be summarized as greater competition and predation (discussed above), deteriorating habitat condition (also discussed above), and the multiple factors associated with decreasing β -diversity. Decreasing β -diversity primarily is associated with reductions in the number, size, and connectivity of habitat patches, which should lead the sensitive native species of a region to experience localized extirpations ([Drinnan, 2005](#); [Radford et al., 2005](#)). In rural land-use at the aggregated landscape scale, richness and abundance of sensitive native species were 14–24% lower than in reserves, but in individual plots richness and abundance were only half of that in reserves. In other words, at a landscape level in rural lands there is sufficient habitat to support more than three-quarters of the sensitive native bird species at similar levels of abundance as found in reserves, but only half of those species on average can be found in any one habitat patch. This suggests that at some locations in the rural landscape, the patches of grassland, savanna and forest are large and near enough, and of sufficient quality, that β -diversity there remains nearly as high as in reserves. Elsewhere in the rural landscape, habitat patches are fewer, smaller, farther apart, and in poorer condition for sensitive native species, which causes the average plot level richness and abundance of sensitive native species in rural lands to drop more noticeably at a plot level than a landscape level compared to reserves.

The present number, size, and distribution of the Twin Cities rural forests is more favorable for sensitive native bird species than reserve forests. Rural forest area in the Twin Cities region (31% of the land surface) is greater than that in 1850 and only slightly below the forest cover in reserves. Nineteen of the 25 largest forests (>500 ha) in the region are in the rural landscape. With large forests and substantial forest cover, threshold effects at a landscape level may not exist for sensitive native species using rural forests ([Andren, 1994](#); [Donovan et al., 1997](#); [Burke and Nol, 2000](#); [Bennett et al., 2004](#); [Drinnan, 2005](#)), but they may manifest themselves when forest cover reaches 10–15% of the region's land surface ([Andren, 1994](#); [Radford et al., 2005](#)). It is, however, difficult to judge such issues in a landscape that historically was and remains naturally fragmented in patches of different vegetation types, as is true throughout the Midwestern prairie–forest ecotone (but see [Robinson et al., 1995](#)).

Sensitive native species play a pivotal role in creating patterns of richness, diversity, and abundance in the Twin Cities regional avifauna. Sensitive native species comprised just 5–9% of the native bird species in suburbs, but 25% of native bird species in reserves. This loss of sensitive native species from suburbs, together with a smaller suburban species pool augmented by just five non-native species, decreased richness and diversity in suburban landscapes overall.

5.5. Reserves as refuges for savanna and grassland bird species

All evidence suggests that sensitive native bird species are likely to be extirpated first in the region from grasslands and savannas as land use intensifies. The mechanism for this is the step-wise elimination of sensitive native species from

grassland and savanna habitat patches until a threshold is reached at which a species disappears from the region. It is unlikely that populations of these species will be augmented by immigration from outside the region because this phenomenon of localized extirpations is occurring throughout the Upper Midwest (Warner, 1994; Herkert, 1995). Examining Breeding Bird Survey data (Sauer et al., 2005) for 1966 to 2005 in the prairie–hardwood transition ecoregion (Chicago and Milwaukee to central Minnesota and our study region) show that 13 bird species using grasslands and savannas experienced 1.2–9.5% annual population loss, while just two species using forests experienced declines (1.6–1.7% annually). These grassland and savanna species were Killdeer, Upland Sandpiper, Eastern and Western Meadowlark, Eastern Kingbird, sparrows (Grasshopper, Vesper, Field, Savannah), Dickcissel, Brown Thrasher and woodpeckers (Red-headed, Flicker). Moreover, three once-abundant grassland and savanna birds became exceedingly rare or vanished after 1850 (Upland Sandpiper, *Bartramia longicauda*, Greater Prairie-chicken, *Tympanuchus cupido*, Sharp-tailed Grouse *T. phasianellus*) (Roberts, 1932) most likely because habitat patches became too few and too small and land use practices unfavorable (e.g., Merrill et al., 1999). Hunting may have accelerated the loss of these birds. The only forest bird to have become extinct is the Passenger Pigeon (*Ectopistes migratorius*).

Land use strongly affected savannas of the region by reducing their extent from 50% of the land surface to 5%, with <1% in good condition. This regional loss parallels the continental loss of savanna (Nuzzo, 1986). Today savannas of the region are most extensive and best managed in reserves, where prescribed burning creates varying spatial degrees of canopy and subcanopy closure which, together with the open branching architecture of the dominant oaks, allows sunlight to penetrate to ground level. Savannas contain a high density of shrubs and young trees which are suppressed by fire, but develop into forest in 10–20 years without disturbance every 2–3 years by fire (Faber-Langendoen and Davis, 1995) or continuous light grazing combined with periodic timber cutting (personal observation). Conversely, canopy-defined savannas of rural and suburban landscapes experience too-frequent severe disturbances which remove understory trees and shrubs to a significantly higher degree compared to the understory of savannas in reserves. Hence, maintaining the bird community of savannas requires frequent but moderate levels of disturbance to preserve the understory yet prevent forest succession from occurring.

This type of management is occurring only in reserves. Each reserve is managed by land managing agencies (US Fish and Wildlife Service, University of Minnesota, MN Department of Natural Resources) which employ fire as the principle management tool. On private lands that are still wild in character (i.e., not exurban residences), tree removal and grazing which might sustain grassland and savanna rarely occur together in a way that creates grassland and savanna structure similar to that produced by fire. Moreover, grazing promotes the spread of non-native herbs and shrubs. Lastly, wildfire is rare in the region and aggressively suppressed by local fire departments. As a result, high quality grassland and savanna are rare on private lands and are being maintained largely by professionals in reserves.

All this considered, grassland and savanna birds stand the greatest chance of persistence in the region's reserves where management goals, funding, and expertise can be directed at preserving and creating habitat for these species. Reserves can also serve as springboards to educate and facilitate grassland and savanna bird protection in the surrounding rural landscape. To date, government farm and landowner programs, municipal zoning, and longterm economic changes in the agricultural sector have worked against private success in conserving the region's grassland and savanna bird species.

5.6. Interannual variation

Although results of the 2 years were very similar, some differences were noted. Why did native bird abundance increase in suburban forests from 1999 to 2000, and why did richness and abundance of sensitive native species fall in rural and suburban forests between 1999 and 2000? We suspect that this shift was caused by the effect of drought on sensitive native species in habitats of rural lands and suburbs. In 1998 and 1999 rainfall was near normal across the region while in 2000 it was 5–25 cm below normal (data from Minnesota Climatological Working Group, University of Minnesota, St. Paul). Rainfall at a nearby weather station during the sampling period in May–June 2000 was 9 cm below 1999 rainfall for the same period. It is possible that native birds using all habitats of suburbs in 1999 may have utilized suburban forests to a greater extent in 2000 when the suburban grasslands and savannas became drier than normal. Conversely, sensitive native birds during drought may reduce their use of suburban and rural forests. Indeed, in 1999 Black-and-white Warblers, a sensitive native species at the edge of its range here, were abundant in savannas and forests of the rural landscape, but in 2000 were absent in rural savannas and rare in rural forests. Yet this species remained as common in 2000 in reserve forests as in 1999. Variation in bird abundance due to weather extremes has been detected elsewhere (Mehlman, 1997; Sagarin and Gaines, 2002).

We considered the possibility that the difficulty of detecting birds in forest habitats and differences in observer skill level were responsible for these variations. As noted above, we tested for but did not detect significant variation among the numbers of birds that observers detected in different habitats and land uses.

6. Conservation applications

These findings indicate that preserving the Twin Cities region's avifauna is achieved most effectively by (1) providing reserves for sensitive grassland and savanna birds, (2) protecting rural forests, and (3) managing habitat conditions. This is not to say that rural grasslands and savannas should not also be protected, but given limited expertise and resources for managing private lands, the challenge is greater here than in the region's reserves. Suburban forests also play a significant role in maintaining native species richness and diversity. They however suffer the same problems of limited resources and expertise, and the added challenge of close proximity to buildings and roads.

6.1. Grassland and savanna reserves

Reserves supported higher local abundance of sensitive native species than elsewhere and thus provide the best grassland and savanna habitat in the region for the bird species most affected by land-use intensification. Unfortunately, reserves cover a tiny fraction of the region's land surface. Despite this, reserves offer the best opportunity to prevent further declines of grassland and savanna birds if they contain large, connected patches of grassland and savanna and/or are located near rural lands with grassland and savanna habitats of intermediate quality. If the region's reserves are treated as core habitats and private grasslands and savannas in the rural landscape as components of a larger reserve system, it may be possible to maintain a metapopulation of declining grassland and savanna bird species despite continued erosion of the rest of the region for these species. Achieving this requires reversing forest succession in the region's reserves by using fire, grazing, and tree-cutting. As funding for managing the region's reserves is insufficient already, additional funding for management must be secured from state and federal governments and private granting institutions. Lastly, reserve managers and scientists must become the leaders in identification, protection, and management of the region's best rural grasslands and savannas through collaborations and outreach efforts.

6.2. Rural forests

Since rural forests greatly exceed reserve forests in total area and are nearly as good as reserve forests even for sensitive native species, they likely support more breeding pairs of native bird species and contribute a larger number of offspring to the regional species pool. After land use, distance from buildings is the strongest predictive variable of the patterns of regional bird richness and abundance. Distance from buildings was correlated with distance from roads, cover by short grassland, and other variables associated with suburbanization. Our unpublished data suggest that forest plots which are nearer to buildings have a lower abundance of sensitive native bird species than forest plots farther from buildings.

Establishing conservation districts in zoning, requiring conservation design principles in development plans, and transferring development rights away from forests are three techniques used by some Twin Cities municipalities to protect sensitive natural resources. If all municipalities adopted these standards, rural forests could be protected. Additionally, minimizing the development footprint in rural lands benefits all sensitive bird species regardless of habitat. The development footprint is being minimized in some municipalities by requiring that new development be located next to existing developments and roads, residences be clustered on 0.2 ha (0.5 ac) building lots, and 50–75% of a new development remain in continuous open space.

6.3. Habitat condition

Sensitive native species react more strongly to habitat condition than other native species. Thus, improving habitat condi-

tions in suburban forests and in grasslands and savannas of rural lands will benefit sensitive native species. Forests can be improved by removing the dense understory of non-native shrubs and trees (e.g., common buckthorn, *Rhamnus cathartica*). Because many suburban forests are also municipal parks, there is a chance that management expertise and funding are available to accomplish this. Techniques to improve rural grasslands and savannas are well known, but there are few resources to deliver the technical knowledge and funding for achieving a large scale effect. The best programs available are government-funded private landowner assistance programs, although reserve managers and scientists through their outreach efforts could contribute to this effort.

6.4. Application to other biota

Do the patterns we report for birds hold for other groups of organisms? For instance, are non-native butterflies most abundant in suburban grasslands and savannas and absent from suburban forests? Does native plus non-native butterfly richness peak in rural lands versus reserves and suburbs? Little data exist that relate directly to multiple gradients of habitat and land use. Blair and Launer (1997) observed a steady decrease in butterfly abundance proceeding from a preserve to a business district, which was the opposite pattern seen for bird abundance in our study; but they also reported that butterfly richness peaked in the middle of their disturbance gradient as did total bird richness in our study. We also observed that total woody plant richness was highest in suburbs due to the large number of introduced species, whereas bird richness was higher in rural areas and reserves than in suburbs. Currie (1991) and Pearson and Carroll (1998) examined correlations in richness between different biotic groups at broad scales on different continents and found that there was no predictable association between groups. For instance, the richness of tiger beetle and butterfly species are correlated in North American but not in India where tiger beetle richness is more closely correlated with bird richness (Pearson and Carroll, 1998). By these examples, it seems incomplete to make conservation recommendations using birds alone, although our recommendations, if implemented, would significantly advance conservation in our region and the Midwest USA.

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