ASSOCIATIONS OF FOREST BIRD SPECIES RICHNESS WITH HOUSING AND LANDSCAPE PATTERNS ACROSS THE USA

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Abstract. In the United States, housing density has substantially increased in and adjacent to forests. Our goal in this study was to identify how housing density and human populations are associated with avian diversity. We compared these associations to those between landscape pattern and avian diversity, and we examined how these associations vary across the conterminous forested United States. Using data from the North American Breeding Bird Survey, the U.S. Census, and the National Land Cover Database, we focused on forest and woodland bird communities and conducted our analysis at multiple levels of model specificity, first using a coarse-thematic resolution (basic models), then using a larger number of fine-thematic resolution variables (refined models). We found that housing development was associated with forest bird species richness in all forested ecoregions of the conterminous United States. However, there were important differences among ecoregions. In the basic models, housing density accounted for <5% of variance in avian species richness. In refined models, 85% of models included housing density and/or residential land cover as significant variables. The strongest guild response was demonstrated in the Adirondack–New England ecoregion, where 29% of variation in richness of the permanent resident guild was associated with housing density. Model improvements due to regional stratification were most pronounced for cavity nesters and short-distance migrants, suggesting that these guilds may be especially sensitive to regional processes. The varying patterns of association between avian richness and attributes associated with landscape structure suggested that landscape context was an important mediating factor affecting how biodiversity responds to landscape changes. Our analysis suggested that simple, broadly applicable, land use recommendations cannot be derived from our results. Rather, anticipating future avian response to land use intensification (or reversion to native vegetation) has to be conditioned on the current landscape context and the species group of interest. Our results show that housing density and residential land cover were significant predictors of forest bird species richness, and their prediction strengths are likely to increase as development continues.

Key words: Breeding Bird Survey (BBS); biodiversity; birds; estimated richness; forest; guilds; housing; human population; landscape; National Land Cover Data (NLCD); U.S. Census; woodland.

INTRODUCTION

In the United States, housing density and human populations have substantially increased in and near forests, both on the fringes of cities and in rural areas that offer highly sought natural amenities (Johnson and Beale 1994, Radeloff et al. 2005*a, b*, Lepczyk et al. 2007). In the 1990s alone, U.S. housing units increased by >13 million units (U.S. Census Bureau 2001). Between 1982 and 1997, developed land increased by 34%, primarily at the expense of forest and cropland (Alig et al. 2004). A substantial amount of new housing occurs at low and medium density (Maestas et al. 2001,

Gillham 2002), a pattern that maximizes the disturbance zone, i.e., the area within which the value of wildlife habitat is degraded (Theobald et al. 1997). These trends are likely to continue in the future, and this raises the question of how biodiversity is affected by housing and human population growth.

The majority of prior research suggests that increases in housing density and associated development such as roads (Hawbaker and Radeloff 2004), power lines, and support services are accompanied by habitat loss and degradation for native species (see Plate 1; Hansen et al. 2005). The effects of development on biodiversity are especially well documented for birds (Engels and Sexton 1994, Theobald et al. 1997, Maestas et al. 2003, Stein et al. 2005, Smith and Wachob 2006, Soh et al. 2006). Housing development changes ecosystem processes (Marzluff et al. 2001), and is associated with altered nesting vegetation structure (Borgmann and Rodewald

2004), changing mammalian and avian predator communities (Crooks and Soule 1999, Kluza et al. 2000), lower invertebrate prey for bird species (Burke and Nol 1998), higher rates of nest predation and parasitism (Phillips et al. 2005, Tewksbury et al. 2006), and increasing disease exposure (Marzluff 1997). As a result, avian communities appear to be quite sensitive to housing development as the densities of some avian species have been observed to decline with exurban development as low as 0.095 house/ha (Odell and Knight 2001).

Negative correlations between bird populations and human presence are not surprising, but they are not the only relationship between human presence and bird biodiversity that has been reported. In Europe and Africa, areas with high bird species richness correspond with locations that have high human populations, a pattern that is most likely caused by collinearity rather than any causal relationships (Balmford et al. 2001, Chown et al. 2003, Gaston and Evans 2004, Norris and Harper 2004). On the other hand, in North America, studies along rural-to-urban gradients have found an intermediate disturbance pattern in which bird species richness peaked in suburban settings that occur midway between the rural and the urban endpoints (Blair 1996).

It is clear that birds covary with landscape composition, pattern, and human population density in a variety of ways; however the geographic extent of past studies has generally been narrow, approaches have not been uniform, and the influence of these factors in different geographic areas remains ambiguous. Moreover in forested ecosystems the main focus of human impact studies has been on assessing landscapes where the primary land use change was the conversion of forest vegetation either to an earlier successional stage (e.g., clear-cutting) or to agriculture. While valuable, such approaches do not fully capture the effects of housing density (S. G. Miller et al. 2001, J. R. Miller et al. 2003), particularly when the presence of homes may be difficult to detect with remotely sensed imagery. Furthermore, avian response is also affected by the life histories shared by groups, or guilds, of species. Houses have been found to be negatively correlated with territorial species, Neotropical migrants, forest interior species, and insectivorous ground/shrub nesting species in the arid Southwest (Mills et al. 1989, Green and Baker 2003), and in temperate upland and lacustrine forests of eastern North America (Friesen et al. 1995, Kluza et al. 2000, Lindsay et al. 2002). On the other hand, permanent residents with omnivorous food habits and exotic species have been found to respond positively to housing development (Allen and O'Connor 2000; C. A. Lepczyk, C. H. Flather, V. C. Radeloff, A. M. Pidgeon, R. B. Hammer, and J. Liu, *unpublished manuscript*). For these reasons, the relative importance of housing density, land cover, and landscape pattern and their interactions in shaping avian biodiversity pattern over broad geographic areas is unclear.

Our objectives in this study were threefold. First, we sought to characterize the dominant patterns of association between housing and avian biodiversity in forested ecosystems. To accomplish this, we evaluated the importance of housing variables relative to broader measures of landscape composition and structure to explaining variation in avian richness. We focused on forest bird communities, and conducted our analysis at multiple levels of model specificity. In the basic model (coarse thematic resolution), we examined the response of forest birds to the amount of land within broad land cover classes and total housing density. In the refined model (fine thematic resolution), we examined if more specifically defined land cover classes, landscape indices, and housing density classes resulted in important gains in explaining variation in bird species richness. Second, we wanted to quantify the degree to which these observed patterns of association varied geographically. Initially, the spatial extent of our analysis was the entire forested region of the conterminous United States. This defined a broad-extent baseline against which we compared individual models for nine ecoregions where forests dominated. Finally, we wanted to quantify the degree to which housing effects varied among different guilds of forest birds. This final objective was accomplished by repeating the analyses outlined for the first and second objectives and using the richness of eight guilds of forest birds as separate response variables, which we anticipated a priori to have varying responses to human-caused landscape change.

Because our focus was forest birds, we assumed that the proportion of forests in the landscape would have a strong positive effect on species richness patterns; that the proportion of intensively developed land would have negative effects on richness of all guilds except those adapted to human settlement (hereafter, synanthropes); and that higher housing density would correspond with lower species richness in all but the synanthrope guild. We predicted several inverse associations between guild richness and anthropogenic impacts on forests as follows:

1) Richness of species that nest close to the ground in the forest (hereafter, ground-nesting guild) would be inversely correlated with housing density and human populations because of their high sensitivity to predation by domestic and mesopredators, both of which are often more abundant in the vicinity of humans (Coleman et al. 1997, Crooks and Soule 1999, Lepczyk et al. 2004).

2) Richness of both forest interior species and cavity nesters would be inversely correlated with housing density due to loss of nesting and foraging sites in the vicinity of settlements (Fraterrigo and Wiens 2005) and positively correlated with forest amount (area).

3) Neotropical migrant richness would be sensitive to landscape patterns and permanent resident richness would be relatively insensitive to housing density based on the findings of Flather and Sauer (1996).

4) Richness of full synanthropes would be higher in forested areas with high residential development and higher edge densities between forest and residential land cover, due to the extensive availability of human subsidies (Lepczyk et al. 2004).

METHODS

Forest and woodland breeding bird data

We used the North American Breeding Bird Survey (BBS; Sauer et al. 2003) as our source of data on native forest bird distribution and abundance. The BBS is an annual monitoring system, which censuses permanent monitoring sites administered by the U.S. Fish and Wildlife Service, and provides data on the relative abundance of birds across the 48 conterminous United States and southern Canada from as far back as 1966 in some areas. The survey includes >4000 routes located on secondary roads, each 39.4 km long. The geographic allocation of samples is semi-systematic with route starting locations randomly located within degree blocks of latitude and longitude (Sauer et al. 2003). The number of routes within a degree block varies across the conterminous United States with higher densities in the East (4–8 routes/degree block) than the West (1 route/degree block), the difference in sampling intensity being originally determined by the availability of qualified observers (Bystrak 1981). Each route is surveyed once each year during the breeding season by a competent volunteer who conducts 50 three-minute point counts spaced at 0.8-km intervals along the roadside, recording all birds detected. The first year an observer conducts a survey, counts tend to be lower (Erskine 1978); therefore the first year data for a new observer on a route were not included in our analysis. Similarly data collected during poor weather conditions, outside of the peak breeding season window specified for a particular location (usually in June), or outside the start and finish time standards specified by the survey design (see Bystrak 1981, Robbins et al. 1986) were not included in our analysis. Species were limited to those that use forest, including forest edge, and woodland during the breeding season, and that had been observed on ≥30 routes (Appendix A).

In cases where conspecifics, unidentified to species, were sympatric, we used the following approach. If the total number of individuals labeled as unidentified was <4% of the total individuals counted in a state, we deleted from analysis those individuals that were not identified to species. However if unidentified individuals made up ≥4% of the total in a state, we counted all individuals to genus only. For example, in seven states, both Eastern and Spotted Towhees were recorded, and in all but one of these, unidentified towhees made up <3% of total towhees, so these were omitted from analysis. In Nebraska, however, unidentified towhees made up 11% of recorded towhees, so in that state we reclassified all Spotted and Eastern Towhees as Towhee.

Birds were grouped into eight functional guilds (Table 1) based on shared habitat preferences or behavioral characteristics (Appendix A). Our most inclusive group comprised all species using forest or woodland. Within this assemblage, species were grouped according to (1) migratory status (i.e., resident, temperate, or tropical migrant), (2) nest placement (i.e., on or within 1 m of ground, cavity, or forest interior; species could be included in ≥1 of these groups), or (3) full synanthropes (see Johnston 2001; Table 1).

Because raw BBS counts of species are known to be downwardly biased (not all birds present on a route are detected), we used the program COMDYN (Hines et al. 1999) to estimate route-level species richness, by year and guild, from the raw counts of individuals for each species. The COMDYN estimate is based on the Nichols et al. (1998) extension of capture–recapture theory to species richness estimation and is based on a closed population model that accounts for heterogeneity in species detection as in Boulinier et al. (1998). We averaged the species richness estimator for the five years bracketing the year 2000. A variable number of years, ranging from one to five, were used in this calculation of the decadal average, depending on how many of the years 1998–2002 contained data that met observer and weather standards (Table 1). The decision to use this averaging method was made based on the desire to include as many routes in the analysis as possible. We tested for, and found, no interaction between either geographic location and number of routes included in the decadal average, or between the decadal average and the number of routes used to calculate the average value. Of 3420 BBS routes examined, 2787 included forest or woodland birds in one or more of the years 1998–2002; of these, 284 routes included only one year of data from this period.

Land cover, housing, and human population data

The center of the minimum bounding rectangle that encompassed the digitized BBS route was used to locate a 19.7 km radius buffer (one-half the length of a BBS route) to define ~1200-km^2 landscapes (sensu Flather and Sauer 1996, Donovan and Flather 2002) within which we evaluated the landscape context of each BBS route in terms of landscape composition, landscape structure, and human presence (Fig. 1). This broadscale approach eliminates spurious results related to edge effects, and ensures that each route is centrally located within the 19.7-km buffer despite variation in the BBS route paths.

To characterize the effects of people, we incorporated block level data from the 1990 and the 2000 U.S. Decennial Census (U.S. Census Bureau 2001). The Decennial Census represents a complete enumeration of people, and is available as GIS data. The smallest spatial unit for which housing and population data is reported is the census block. The size of the census block varies, depending on the presence of roads, rivers, and

TABLE 1. Forest guild summary information for bird species in eight forest guilds in the conterminous United States.

Guild	No. routes (% ≥3 yr/≤2 yr)	Definition	Source
Forest species	2787 (80/20)	species that regularly breed in or on the edge of forest or woodland	Ehrlich et al. (1988), Poole (2005)
Neotropical migrant	2773 (77/23)	any western hemisphere species that breeds in forest or woodland, all or part of whose populations breed north of the U.S.–Mexico border and winter south of that line	Finch and Stangel (1993), Poole (2005)
Forest short-distance migrant	2784 (79/21)	any species that breeds in forest or woodland, and for which substantial populations winter north of the U.S.–Mexico border	
Forest permanent resident	2751 (76/24)	any species in which substantial populations reside in the same ecoregion in winter and summer	
Forest interior species	2022 (68/32)	either (1) species has higher density in interior forest conditions, or (2) habitat fragmentation is listed as a management concern	Whitcomb et al. (1981), Boulinier et al. (1998), Poole (2005), Danz et al. (2007)
Forest ground- or low-nesting species	2770 (78/22)	mean height of nest ≤1 m	
Forest cavity-nesting species	2769 (78/22)	species that nest in cavities	
Full synanthropes	2505 (71/29)	species that use forest edge or woodland, in which most populations have major dependence on variables influenced by humans	Johnston (2001)

Notes: The number of routes from the North American Breeding Bird Survey (BBS) in the conterminous United States for which an estimate of guild richness for the five-year period 1998–2002 was available, is shown, followed in parentheses by the percentage of routes for which the richness estimator was derived from ≥3 years of data and from ≤2 years of data. Guild definitions and published sources used to establish guild membership are also shown. Membership in guilds is not mutually exclusive.

other features that allow delineation. Generally, census blocks are smallest in areas with high housing and population density, and can be as small as a city block; the average area of a census block in the conterminous United States is ~100 ha. However, housing density is not uniformly distributed within a census block, and this may have potentially introduced errors when large blocks were subdivided by our buffers around the route centroids, because we had to assume uniform distribution as the most parsimonious assumption in the absence of other data on housing unit patterns and locations. These errors are in all likelihood small though, because the vast majority of the census blocks were fully contained in our buffers, and size errors of omission and commission due to nonuniformly distributed housing units are likely to cancel each other out. Based on the 1990 and 2000 census block data, we calculated housing density, household density (i.e., occupied housing units as opposed to vacant or seasonally occupied units), seasonal housing density, and population density within each 1200-km^2 landscape. Densities were based on the terrestrial area in each fixed buffer distance (i.e., each 1200-km^2 landscape) to account for smaller terrestrial area in buffers that included oceans or large water bodies.

Data on landscape composition were derived from National Land Cover Data (NLCD). The NLCD is a classification of 1992 and 1993 Landsat Thematic Mapper satellite imagery (Vogelmann et al. 2001), includes 21 cover classes, and is available for the entire conterminous United States. We analyzed land cover composition at two levels. For our basic models, we calculated the proportions of forest, seminatural, and intensive uses (Table 2) within each landscape. Because our analysis was limited to ecoregions dominated by forest, we viewed the land cover category "forest" as a land use. Where the proportion of forest is low in our sample areas, we assert it is generally due to human activities.

Within each 1200-km^2 landscape we also calculated landscape pattern metrics of two general types: land cover-specific patch characteristics and landscape-level edge density. For each land cover type we included the proportion of landscape covered, number of patches, edge density, mean patch size, and mean core area index. The selection of these measures was based on their association with avian patterns (Donovan et al. 1995, Flather and Sauer 1996, Donovan and Flather 2002). Landscape composition and pattern measures were calculated using FragstatsVersion3 (K. McGarigal, S. A. Cushman, M. C. Neel, and E. Ene, *unpublished software*).

Statistical analysis

We sought to quantify the association of forest guild species richness with landscape composition, landscape pattern, and human presence across the United States. We used Bailey's ecoregions at the province level (hereafter termed ecoregions) to select predominantly forested ecoregions, of which there are 20 within the
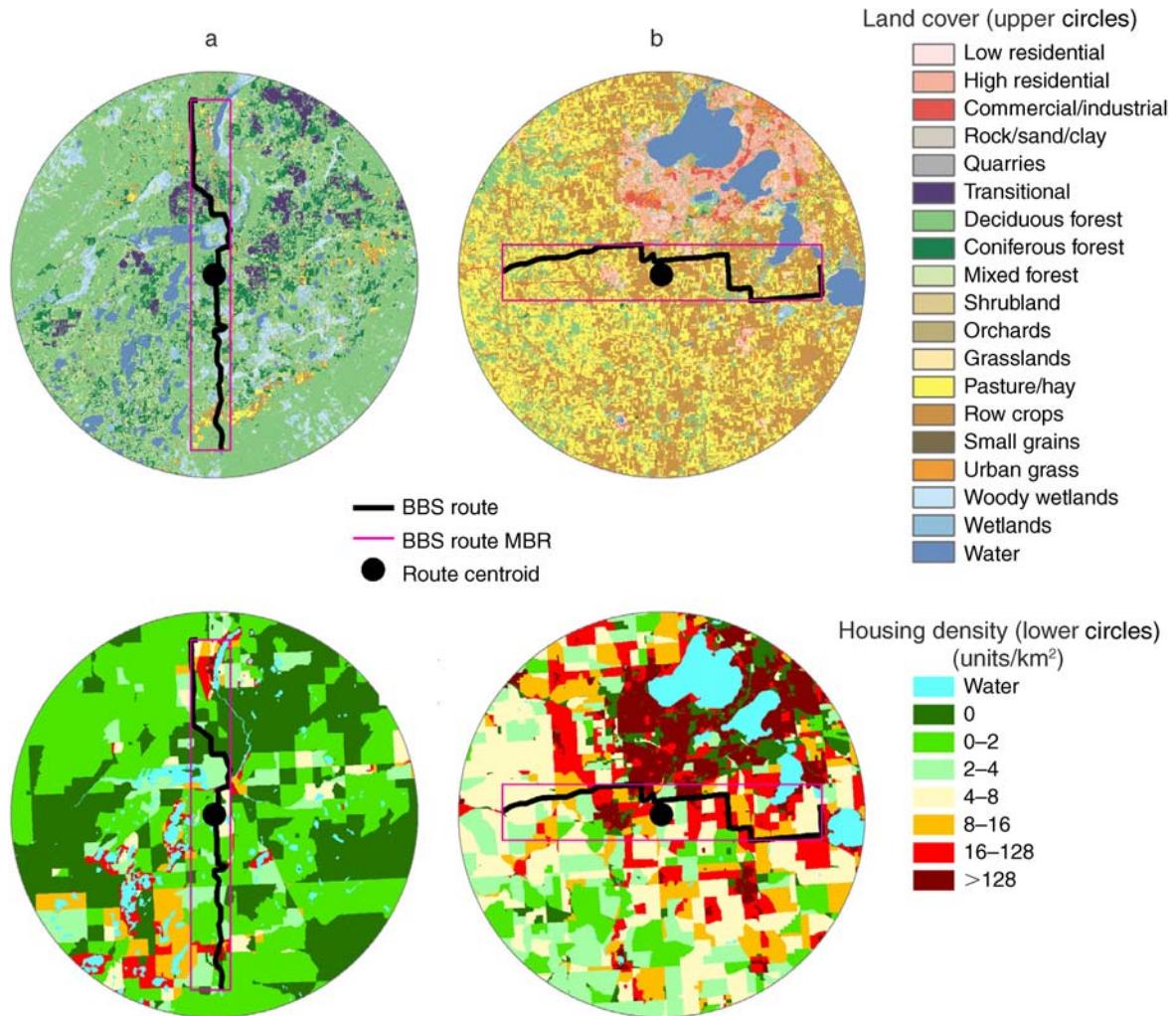
Fig. 1. Example of land cover (top row) and housing density (lower row) within a 19.7 km radius buffer centered on the centroid of the minimum bounding rectangle (MBR) encompassing two Breeding Bird Survey (BBS) routes located (a) in northwestern Wisconsin (left-hand circles) and (b) south of Madison, Wisconsin, USA (right-hand circles).

conterminous United States (Bailey 1995; Fig. 2). We conducted the analysis first using four predictive variables, one measure of housing density, and three broad land cover composition classes (hereafter termed basic models). Then, seeking to improve on the explanatory power of the basic models, we conducted a second analysis, using a greater number of more narrowly defined predictive variables; we partitioned housing and human density into component parameters (Table 2), and included not only land cover composition, but also landscape pattern (hereafter termed refined models; Table 2). We conducted each of these analyses on all 20 ecoregions combined, and also stratified by ecoregion, to test for unique associations of avian guilds and distinct patterns across the United States. The number of BBS routes varies among ecoregions. We felt that the loss of information that would result from limiting the number of routes

included per ecoregion, or from limiting which forested ecoregions were analyzed, would be deleterious to our goals. Thus we opted to include all available information from forested areas, examine the results for trends due to an imbalanced design, and to acknowledge the imbalance in number of routes per ecoregion in interpretation of results.

In the basic models, we investigated species richness of all forest birds, and each of the eight guilds vs. the predictor variables of housing density in 2000, the abundance of forest, seminatural, and intensive use land cover. We conducted the analysis across all ecoregions, and for each of the 20 forested ecoregions individually. Multiple regression models were derived for each guild in turn, with the significance threshold set at $P \leq 0.05$ (Proc REG, SAS 8.0). Following each set of regressions, we checked residual plots to ensure that the distribution of unexplained variance was random. This analysis of

TABLE 2. Candidate independent variables used to predict avian bird species richness.

Basic human and landscape variables	Refined human and landscape variables	Description	Source
Housing and human population			
2000 housing density	2000 housing density	no. housing units in census blocks	2000 Census
	2000 seasonal housing density	no. seasonally occupied housing units in census blocks	2000 Census
	2000 household density	no. permanently occupied housing units in census blocks	2000 Census
NA†	1990 housing density	no. housing units in census blocks	1990 Census
	1990 seasonal housing density	no. seasonally occupied housing units in census blocks	1990 Census
	1990 household density	no. permanently occupied housing units in census blocks	1990 Census
NA†	2000 population density	no. people residing in census blocks	2000 Census
NA†	1990 population density	no. people residing in census blocks	1990 Census
Landscape composition			
Forestland	forestland	tree canopy accounts for 25–100% of the cover; includes areas where the soil or substrate is periodically saturated with or covered by water as defined by Cowardin et al. (1979) and forest or shrubland vegetation accounts for 25–100% of the cover	summation of NLCD classes 41, 42, 43, and 91
Intensive land uses	low intensity residential	vegetation comprises 20–70% of cover, most commonly includes single-family housing units	NLCD class 21
	high intensity residential	vegetation comprises <20% of cover, while constructed materials make up ≥80% of cover	NLCD class 22
	commercial/industrial/transportation	includes infrastructure (e.g., roads and railroads) and all highly developed areas not in class 22	NLCD class 23
	quarries/mines/gravel pits	areas of extractive mining	NLCD class 32
	orchards/vineyards/other	areas maintained for the production of fruits, nuts, berries, or ornamentals	NLCD class 61
	row crops	crops (e.g., corn, cotton, and vegetables)	NLCD class 82
	small grains	graminoid crops (e.g., wheat and rice)	NLCD class 83
	fallow	cropland without visible vegetation	NLCD class 84
	urban/recreational grasses	grasses planted in developed settings (e.g., parks, golf courses, airport grass)	NLCD class 85
Seminatural land	bare rock/sand/clay	perennially barren earthen material	NLCD class 31
	transitional	areas of sparse cover that are dynamically changing (includes forest clear-cuts)	NLCD class 33
	shrubland	shrub canopy is 25–100% of cover	NLCD class 51
	grasslands/herbaceous	natural or seminatural herbaceous vegetation makes up ≥75% of cover	NLCD class 71
	emergent herbaceous wetlands	75–100% perennial herbaceous vegetation cover; periodically saturated with or covered with water	NLCD class 92
Landscape pattern			
NA	no. patches	estimated for each land cover class (19)	NLCD
	mean patch size	estimated for each land cover class (19)	NLCD
	mean core area index	estimated for each land cover class (19)	NLCD
	edge density	estimated for each land cover class (19)	NLCD
	total edge density	landscape-wide across all land cover classes (1)	NLCD

Notes: Housing density attributes are based on the U.S. Decennial Census (U.S. Census Bureau 2001). Land cover classes are from the National Land Cover Database (NLCD; Vogelmann et al. 2001). Landscape structure was calculated on land cover classes. Independent variables were calculated for each 19.7 km radius (1200 km^2) landscape surrounding a BBS route. Housing and population density were calculated by dividing numbers by the terrestrial area within each landscape.

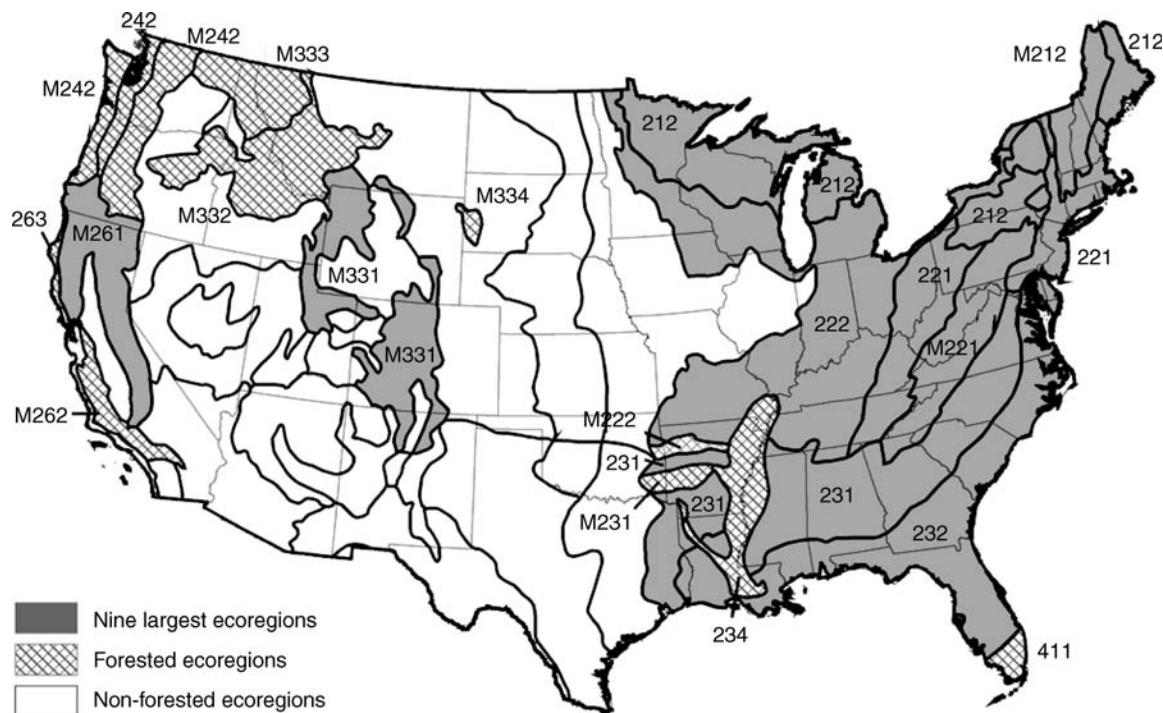† NA, not applicable; variables were not used in the basic model analysis.

Fig. 2. Forested ecoregions in the conterminous United States (after Bailey [1995]). Basic models were developed for all 20 labeled ecoregions while refined models were developed for the nine largest ecoregions. Key to ecoregions: 212, Laurentian Mixed Forest; M212, Adirondack–New England; 221, Eastern Broadleaf Forest (Oceanic); M221, Central Appalachian; 222, Eastern Broadleaf Forest (Continental); M222, Ozark; 231, Southeastern Mixed Forest; M231, Ouachita; 232, Outer Coastal Plain Mixed Forest; 234, Lower Mississippi Riverine Forest; 242, Pacific Lowland Mixed Forest; M242, Cascade; M261, Sierran; M262, California Coastal Range; 263, California Coastal Steppe/Mixed forest/Redwood Forest; M331, Southern Rocky Mountain; M332, Middle Rocky Mountain; M333, Northern Rocky Mountain; M334, Black Hills; 411, Everglades.

individual ecoregions and guilds resulted in 158 of 160 possible models (20 ecoregions × eight guilds). In two cases, there were too few routes containing members of a given guild to conduct regression analysis (i.e., in ecoregion M334, Black Hills, only four of the seven BBS routes contained synanthropes, and in ecoregion M262, California Coastal Range, too few routes included forest interior species for analysis).

In the refined model analysis we again investigated species richness of all forest birds, and each of the eight guilds in a multiple regression framework with backward selection procedure (Proc REG, SAS 8.0). Multiple regression analysis with backward selection was conducted for each guild in turn with a set of narrowly defined variables (Table 2), with the threshold for retention set at $P \leq 0.01$. The set of candidate predictive variables included 1990 and 2000 U.S. Census data (because we anticipated a possible time lag in response to changes in habitat and human presence; Wiens 1985, Desmond et al. 2000) for housing density, seasonal housing density, and household density, the abundance of 19 NLCD land cover classes, and their landscape pattern. Following each set of regressions, residual plots revealed that the distribution of unexplained variance was random.

Nine ecoregions contained a sufficient number of BBS routes to allow ecoregion-level model building in the refined model analysis due to the large number of independent variables included. The ecoregions retained for this analysis were 212 (Laurentian Mixed Forest), M212 (Adirondack–New England), 221 (Eastern Broadleaf Forest [Oceanic]), 222 (Eastern Broadleaf Forest [Continental]), M221 (Central Appalachian), 231 (Southeastern Mixed Forest), 232 (Outer Coastal Plain Mixed Forest), M261 (Sierran), and M331 (Southern Rocky Mountain, Fig. 2). Of the 72 potential models (nine forest ecoregions × eight guilds), two could not be estimated because there were too few routes with synanthropes in ecoregions M261 and M331. Differences in the ability of our independent variables to explain variability in richness across all nine ecoregions were tested using an ANOVA (Proc GLM, SAS 8.0), using model adjusted R^2 values as the response variable.

In order to quantify the association of housing density and residential land cover with guild richness, we identified the model with the highest adjusted R^2 value that included these variables, and for which the overall model was still statistically significant ($P < 0.05$). Based on this model, we calculated the value of Δadjusted R^2 (i.e., change in adjusted R^2) after removing housing and residential land cover variables from these models. This

was equivalent to assessing the partial R^2 of the housing and residential land cover variables, considered as a unit. Finally, we examined the difference in predictive power of the two analyses, i.e., a limited number of broadly encompassing variables and a large number of relatively specific variables.

We conducted extensive tests to address potential spatial autocorrelation. All models were initially parameterized without taking spatial covariance into account. Spatial autocorrelation was then examined with semivariograms calculated on the model residuals for a selection of models. We selected models where we suspected that spatial autocorrelation may have been present (i.e., where P values were high), and ensured adequate representation of both basic and refined models at the two scales of analysis: across ecoregions and individual ecoregions. The models selected for semivariogram analyses included (1) all eight basic models for each guild calculated across all 20 ecoregions, (2) 11 of the 160 basic models calculated for individual ecoregions, (3) four of the eight refined models calculated across all 20 ecoregions, and (4) eight of the 70 refined models calculated for individual ecoregions. In cases where spatial autocorrelation was present in the residuals, we parameterized additional general linear models with a spatial exponential covariance structure, reestimated model coefficients, and presented both types of models.

We decided against using general linear models with a spatial covariance structure for all our models, because spatial autocorrelation was largely absent, and because general linear models with a spatial covariance structure do not allow for calculating and reporting an R^2 value. R^2 values were generally low in our models and we felt this was important information, which we did not want to omit.

Results

Forest bird diversity pattern

The average estimated species richness of forest and woodland species across the 20 forested ecoregions was 58.2 species per BBS route (minimum 6.1, maximum 103.3). Richness patterns varied by guild (Fig. 3). Among the nine largest forested ecoregions, average species richness varied moderately, ranging from 48.6 species/route in ecoregion M331, Southern Rocky Mountain, to 68.7 species/route in ecoregion M212, Adirondack–New England (Fig. 3). Among the guilds, Neotropical migrants were the most species rich in all ecoregions except in the western U.S. ecoregions M261, Sierran, and M331, Southern Rocky Mountain, where the number of short-distance migrant species was highest.

Among the three nesting guilds, estimated richness of cavity nesters was consistently higher than richness of either the interior-nesting guild or ground-nesting guild. Ecoregion M212, Adirondack–New England, exhibited the highest species richness for interior nesters, ground

nesters, Neotropical migrants, and short-distance migrants. Cavity nester richness was highest in ecoregion 231, Southeast Mixed Forest, and permanent resident richness was highest in ecoregion M261, Sierran. Richness of full synanthropes was consistently lowest and did not exceed 3.8 species/route.

Land cover and housing patterns

The predictor variables for the basic models exhibited strong spatial pattern, and a large range of values. For example, the mean proportion of forest ranged from <20% with high coefficients of variation (CV) in two ecoregions (M262, the California Costal Range and 411, Everglades), to >85% forest cover with little variation (CVs <8) in the Ouachita (M231) and Adirondack–New England ecoregions (M212, Fig. 4). Intense land uses covered, on average, <2% of landscapes in five ecoregions, and ranged to almost 50% in the Lower Mississippi Riverine Forest (ecoregion 234). Mean housing density varied by two orders of magnitude among the 20 ecoregions.

Spatial autocorrelation

The semivariogram analysis showed a clear pattern. Spatial autocorrelation was present in the coarsest models, i.e., the basic models run across all 20 ecoregions. We did not find significant spatial autocorrelation in basic models for individual ecoregions and refined models both across all ecoregions and for individual ecoregions (Appendix C). Essentially, models conducted at the ecoregion scale, and with the extended variable set of the refined models, captured the spatial variation and removed spatial autocorrelation from the residuals.

For the basic models run across all 20 ecoregions, we derived models both with and without a spatial covariance structure. Model coefficients varied slightly (Table 3), but the main conclusions from our models remain. As outlined in the *Methods*, we presented both types of models to provide R^2 values, which can not be calculated for models that incorporate a spatial covariance structure.

Results from the basic models

Our basic models used only four independent variables (proportion of forest, seminatural and intense land use, and housing density) to model bird species richness. When we grouped the 20 ecoregions, the basic model captured 22% of the variance in overall forest bird species richness, and 30–36% of the observed variance of forest interior species, ground-nesting species, and Neotropical migrants. The basic models for the entire United States explained very little variance (1–6%) in richness of cavity nesters, short-distance migrants, or permanent residents (Table 4).

Analyzing individual ecoregions resulted, in some cases, in markedly stronger models. For example, basic models for species richness of all forest birds resulted in
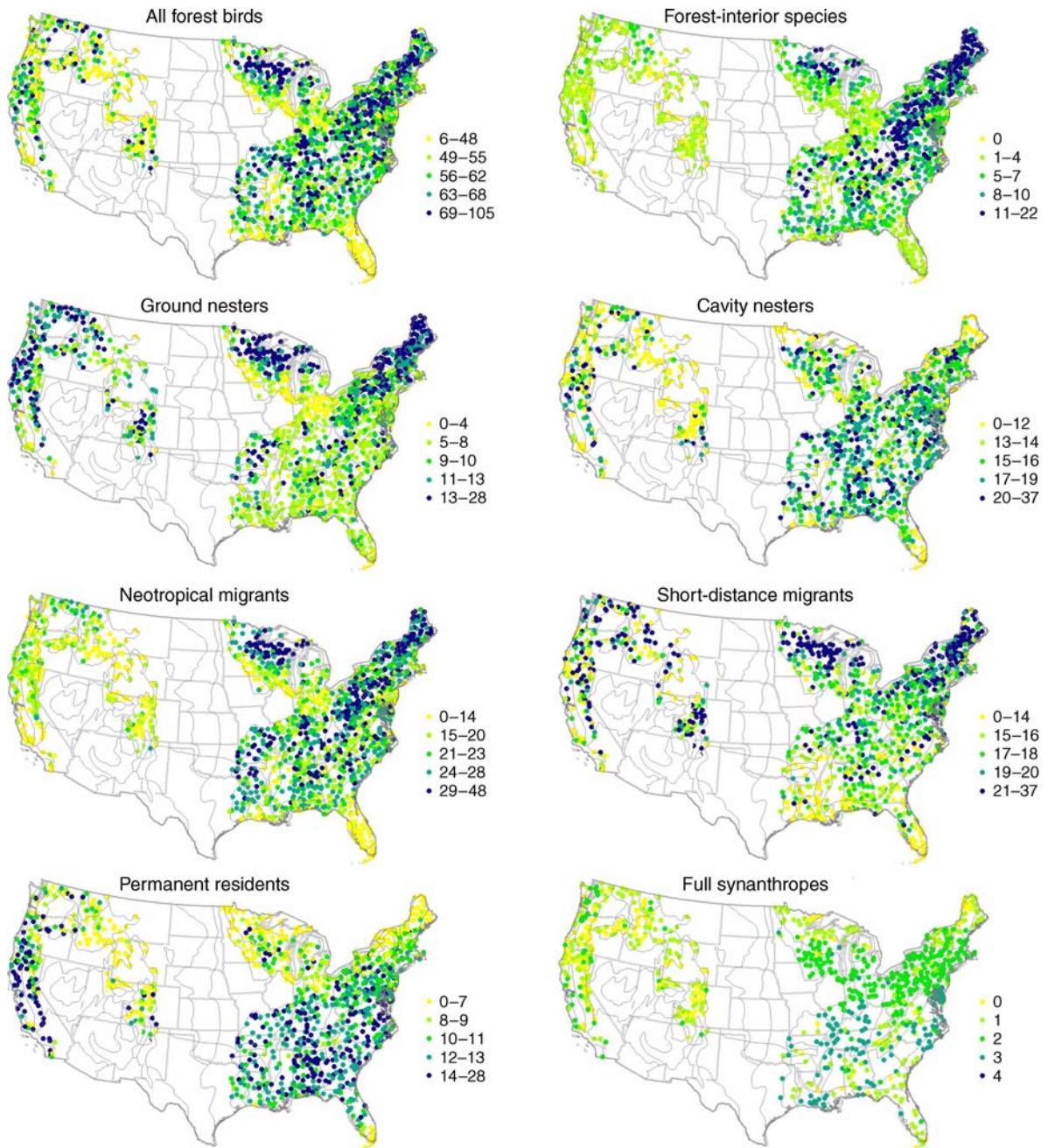
FIG. 3. Species richness patterns of the eight forest bird guilds. Size of the points does not reflect actual size of the landscapes; points were enlarged to better show differences in richness. For guilds that had zero representatives on ≤10 BBS routes, the zero class is not depicted as a separate category.

an adjusted R^2 of 0.39 in Eastern Broadleaf Forest (ecoregion 222); an adjusted R^2 of 0.92 in Everglades (ecoregion 411); and an adjusted R^2 of 0.65 in the California Coastal Range (M262). However, these last two ecoregions are relatively small, with ≤21 BBS routes, which may contribute to the strong coefficients of determination of these models. The basic models were not significant in almost half of the 20 ecoregions (45%).

We found no systematic pattern in our comparison of basic model results at the national scale and ecoregion scales, leading us to conclude that larger ecoregions did not disproportionately influence the national scale analysis. Spatial structure, analyzed in semivariograms, was absent in most cases; an exception was Neotropical migrants in ecoregion 232 (Outer Coastal Plain Mixed Forest). However when the spatial covariance structure
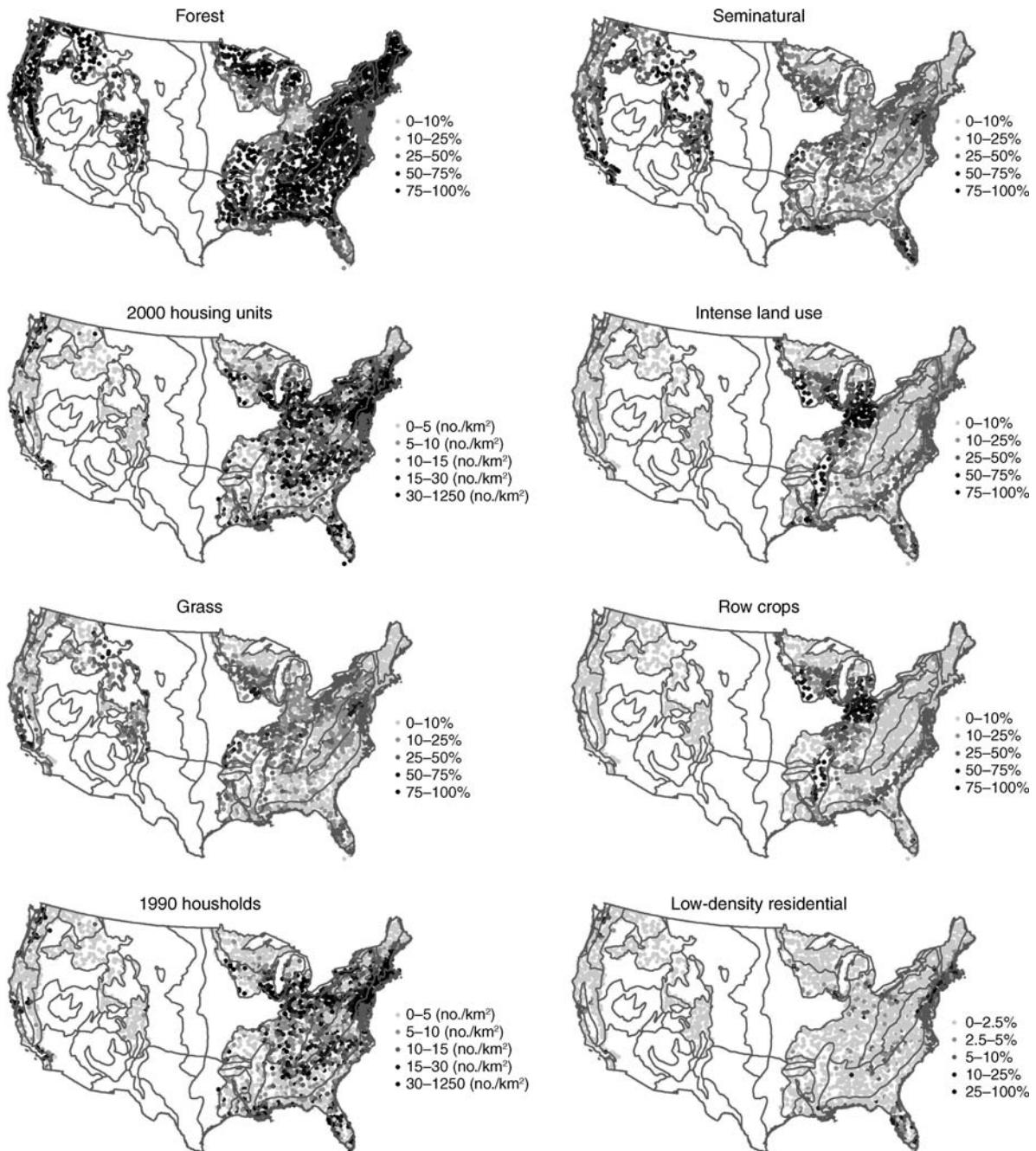
FIG. 4. Pattern of some predictive variables used in models. The top four variables were included in basic models, and the bottom four were frequently included in refined models.

was incorporated in the regression model, the resulting model coefficients remained essentially unchanged (results not shown).

Basic models of species richness for specific guilds within ecoregions were significant in a majority of cases (81 of 138, or 59%). Four ecoregions, each including six to 10 BBS routes, accounted for the bulk of the nonsignificant models (M222, Ozark Broadleaf Forest–Meadow; M231, Ouachita Mixed Forest–Meadow; 263,

Californian Coastal Steppe and Mixed Forest; and M334, the Black Hills Coniferous Forest). In the larger ecoregions, guilds for which a large number of significant models were found included interior-nesting species, ground-nesting species, and synanthropes. Explanatory power of the models was highly variable, reaching a maximum R^2 of 0.94 for Neotropical migrants in ecoregion 411, the Everglades. Models in the Everglades ecoregion were generally very strong, as

TABLE 3. Basic models of the association between avian guilds and four independent variables, for which spatial autocorrelation was in evidence.

Guild and variable	Uncorrected		Corrected for autocorrelation	
	Coefficient	P	Coefficient	P
Forest species				
Intensive land uses	0.07299	**0.0295**	−0.02931	**0.4158**
Forestland	0.2351	<0.0001	0.1987	<0.0001
Seminatural land	−0.05068	0.1215	−0.00759	0.8265
2000 housing density	−0.01797	0.0009	−0.01809	0.0008
Interior-nesting guild				
Intensive land uses	−0.01438	**0.1736**	−0.03591	**0.0003**
Forestland	0.05684	<0.0001	0.05785	<0.0001
Seminatural land	−0.06956	<0.0001	−0.02944	0.0022
2000 housing density	−0.00002	**0.9915**	−0.00328	**0.0216**
Ground-nesting guild				
Intensive land uses	−0.05349	<0.0001	−0.0338	0.0006
Forestland	0.05231	<0.0001	0.06659	<0.0001
Seminatural land	−0.02064	**0.0251**	−0.00636	**0.5000**
2000 housing density	−0.0052	0.0007	−0.00481	0.0018
Cavity-nesting guild				
Intensive land uses	0.05024	<0.0001	0.03492	0.0044
Forestland	0.04684	<0.0001	0.0413	0.0002
Seminatural land	0.0122	0.278	0.007271	0.5391
2000 housing density	−0.00352	0.0589	−0.00342	0.0850
Neoptropical migrants				
Intensive land uses	0.03838	**0.0358**	−0.02561	**0.1686**
Forestland	0.1424	<0.0001	0.1269	<0.0001
Seminatural land	−0.06083	**0.0007**	0.0109	**0.5445**
2000 housing density	−0.01138	0.0001	−0.00963	0.0004
Intensive land uses	−0.0017	0.8752	−0.00053	0.9623
Short-distance migrants				
Forestland	0.02816	0.0055	0.03355	0.001
Seminatural land	−0.00922	0.3835	−0.00527	0.6268
2000 housing density	−0.00497	0.0046	−0.00556	0.0018
Permanent residents				
Intensive land uses	0.01762	**0.0772**	0	**0.9999**
Forestland	0.02644	0.0046	0.01778	0.0434
Seminatural land	0.00857	0.3784	−0.00204	0.8294
2000 housing density	−0.00102	0.5267	−0.00103	0.5025
Synanthropes				
Intensive land uses	0.006816	0.0042	0.004403	0.0804
Forestland	−0.00693	0.002	−0.00744	0.0008
Seminatural land	−0.00602	**0.0103**	0.002846	**0.2546**
2000 housing density	0.000434	0.2373	0.000313	0.3725

Note: Coefficients and significance for the uncorrected and correctly specified model are shown, with changes in significance highlighted in bold.

were models in ecoregion M262, Californian Coastal Range. However, while 14 models explained more than half the variance (Fig. 5), in most instances less than half of the variance was explained, and in 19 models, the R^2 was <0.1.

Understanding the associations between housing growth and forest bird biodiversity was a major goal of our study. We thus examined how much explanatory power was lost from the models when we removed housing density. Removing housing density reduced the adjusted R^2 in almost all cases, and in three cases housing density accounted for a relatively large proportion of the explanatory power of the model (i.e., for

forest interior species in M333, Northern Rocky Mountain ecoregion, and for both cavity nesters and permanent residents in 411, Everglades; Table 4). However, in most basic models, the adjusted R^2 decreased by <5% when removing housing density, even though that was in many cases a substantial portion of the overall explanatory power.

We also examined the partial P values for the four independent variables in the basic models, to assess their relative importance in predicting bird biodiversity. Forestland cover and housing density tied in the number of models in which they were included (23 of 158 models with a P value <0.05, Table 5). As expected, the

TABLE 4. Adjusted (Adj.) R^2 values (with ΔAdj. R^2 and sample size) of basic models explaining variance due to housing density and percent cover of forest, intense land use, and seminatural land use, in 20 forested ecoregions of the United States for eight avian guilds.

Ecoregion (province level)	Model attributes	Forest species	Nesting guild			Migratory habit
			Interior	Ground	Cavity	Neotropical
All forested	Adj. R^2	0.22***	0.34***	0.36***	0.03***	0.30***
	ΔAdj. R^2	−0.02	†	−0.01	−0.01	−0.01
	No. routes	1803	1708	1803	1802	1801
212	Adj. R^2	0.06	0.39	0.29	†	0.16
	ΔAdj. R^2	†	−0.01	−0.02	†	−0.03
	No. routes	203	203	203	203	203
M212	Adj. R^2	†	†	0.09	0.22	†
	ΔAdj. R^2	†	†	−0.02	−0.01	†
	No. routes	79	79	79	79	79
221	Adj. R^2	0.31	0.39	0.32	0.11	0.38
	ΔAdj. R^2	†	†	−0.03	†	†
	No. routes	192	190	192	192	192
M221	Adj. R^2	†	0.21	0.04‡	0.12	†
	ΔAdj. R^2	†	−0.01	†	†	†
	No. routes	112	112	112	112	112
222	Adj. R^2	0.39	0.53	0.55	0.10	0.45
	ΔAdj. R^2	−0.02	†	−0.01	−0.01	†
	No. routes	318	311	318	318	318
M222	Adj. R^2	†	†	†	†	†
	No. routes	6	6	6	6	6
231	Adj. R^2	0.16	0.24	0.15	†	0.16
	ΔAdj. R^2	−0.01	†	−0.02	†	−0.02
	No. routes	195	190	195	195	195
M231	Adj. R^2	†	†	†	†	†
	No. routes	7	7	7	7	7
232	Adj. R^2	0.26***	0.24***	0.05***	0.10***	0.29***
	ΔAdj. R^2	−0.03	†	†	†	†
	No. routes	248	239	248	248	248
234	Adj. R^2	0.27	0.45	0.40	0.16	0.39
	ΔAdj. R^2	†	+0.01	−0.09	†	†
	No. routes	34	33	34	34	34
242	Adj. R^2	0.43	0.09‡	†	†	0.55
	No. routes	18	15	18	18	18
M242	Adj. R^2	†	0.09	†	†	†
	ΔAdj. R^2	†	+0.01	†	†	†
	No. routes	58	56	58	58	58
M261	Adj. R^2	†	0.41	0.21	0.10	0.33
	ΔAdj. R^2	†	+0.01	+0.01	+0.01	−0.02
	No. routes	95	82	95	95	95
M262	Adj. R^2	0.65	§	0.66	0.55	0.77
	ΔAdj. R^2	+0.01	†	+0.01	−0.03	†
	No. routes	21	11	21	21	20
263	Adj. R^2	†	†	†	†	†
	No. routes	10	9	10	10	10
M331	Adj. R^2	0.12	0.07‡	0.21	†	0.20
	ΔAdj. R^2	−0.01	†	−0.04	†	−0.02
	No. routes	102	76	102	102	102
M332	Adj. R^2	0.22	0.15	0.18	†	0.20
	ΔAdj. R^2	†	+0.02	+0.01	†	−0.01
	No. routes	55	45	55	55	54
M333	Adj. R^2	†	0.32	†	†	†
	ΔAdj. R^2	†	−0.10	†	†	†
	No. routes	31	28	31	31	31
M334	Adj. R^2	†	†	0.80‡	†	†
	No. routes	8	8	8	8	8
411	Adj. R^2	0.92	†	†	0.79	0.94
	ΔAdj. R^2	−0.06	†	†	−0.08	−0.05
	No. routes	11	8	11	11	11

Notes: ΔAdj. R^2 is the change in variance explained after removing housing variables from models. $P \leq 0.05$ unless otherwise noted. Following the convention of Bailey (1995), an "M" in the ecoregion name indicates a mountain ecoregion.

*** $P \leq 0.001$; † $P > 0.1$; ‡ $0.05 < P \leq 0.1$.

§ Models could not be constructed because there were too few BBS routes with sufficient bird guild data (i.e., ecoregion M222 and three other guild–ecoregion cases).

Table 4. Extended.

	Migratory habit	
Short-distance	Permanent resident	Full synanthropes
0.06***	0.01***	0.12***
−0.01	†	†
1802	1794	1646
0.08	0.03	0.19
−0.03	†	−0.01
203	201	191
†	0.23	0.31
†	−0.05	−0.06
79	77	70
0.06	†	0.06
−0.04	†	+0.01
192	192	192
0.07	0.11	0.09
−0.01	−0.01	+0.01
112	112	110
0.07	0.27	0.04
−0.03	0	0
318	316	315
†	†	†
6	6	6
†	0.05	0.07
†	−0.02	†
195	195	193
†	†	†
7	7	6
0.06***	0.05***	0.18***
†	†	†
248	248	245
†	0.21	†
†	+0.03	†
34	34	33
0.41	†	†
18	18	18
†	†	0.18
†	†	0.04
58	58	37
†	†	0.13
†	†	−0.02
95	95	62
†	0.58	0.50
†	+0.02	+0.02
20	21	19
0.71	†	†
10	10	9
0.13	0.10	0.01
†	†	†
102	102	71
0.23	0.10	0.31
−0.02	†	+0.02
55	52	35
†	†	0.55
†	†	+0.03
31	31	21
†	†	§
8	8	4
0.78	0.68	†
−0.03	−0.10	†
11	11	5

majority of the relationships between bird species richness and proportion of forest were positive, whereas the relationships between bird species richness and housing density were negative in most cases. What was surprising was the lack of a clear signal in the association of bird species richness with the proportion of the landscape under intensive use and the fact that it was most often positively correlated with bird species richness.

Results from the refined models

The regression models based on the more detailed land cover classes, housing variables, and landscape pattern metrics were significant models for all ecoregions and all guilds (Table 6). These refined models explained more variance than the basic models across all 20 forested ecoregions, and in the nine largest ecoregions individually. Across all 20 ecoregions, models explained 10–20% more variance in six of eight cases. In five cases, the refined model captured >25% more variance in richness than the basic model (ground-nesting and cavity-nesting species in ecoregion M262, the Sierran ecoregion; short-distance migrants, interior forest nesting species, and all forest birds in ecoregion 232, the Outer Coastal Plain Mixed Forest; Table 6).

When analyzing the 20 forested ecoregions as a unit, the refined models for forest bird richness explained 35% of the variance (Table 6). Models for specific guilds outperformed the model for all forest nesters in three cases. Explanatory power reached 56% for the interior-nesting guild, 48% for Neotropical migrants, and 42% for the ground-nesting guild. Three of the nine ecoregions exhibited models for all forest species that outperformed the 20 ecoregion-wide model. These three ecoregions were all in the eastern United States, and included the Outer Coastal Plain Mixed Forests in the Southeast (ecoregion 232; adjusted R^2 value of 0.57) and both the oceanic and the continental Eastern Broadleaf Forest (ecoregions 221 and 222; adjusted R^2 values of 0.41 and 0.46, respectively).

In models for specific guilds in individual ecoregions, 19 of the 78 models captured about half of the variance, and only seven models captured ≤10% of the variance, with the remainder capturing between 11% and 40% (Fig. 5). Strength of associations of individual guilds with explanatory factors varied widely among ecoregions. For example in ecoregion M221, 17% of variation in richness of forest ground-nesting species was associated with landscape composition, pattern, and housing, while in ecoregions 222 and M261 these variables explained >56% of variation in richness of ground-nesting species.

Guilds that were particularly well modeled in the different ecoregions included interior species where 40% or more of the variability in richness was explained in five ecoregions, and forest Neotropical migrants and forest ground-nesting species, both for which explanatory power exceeded 40% in three ecoregions. On the
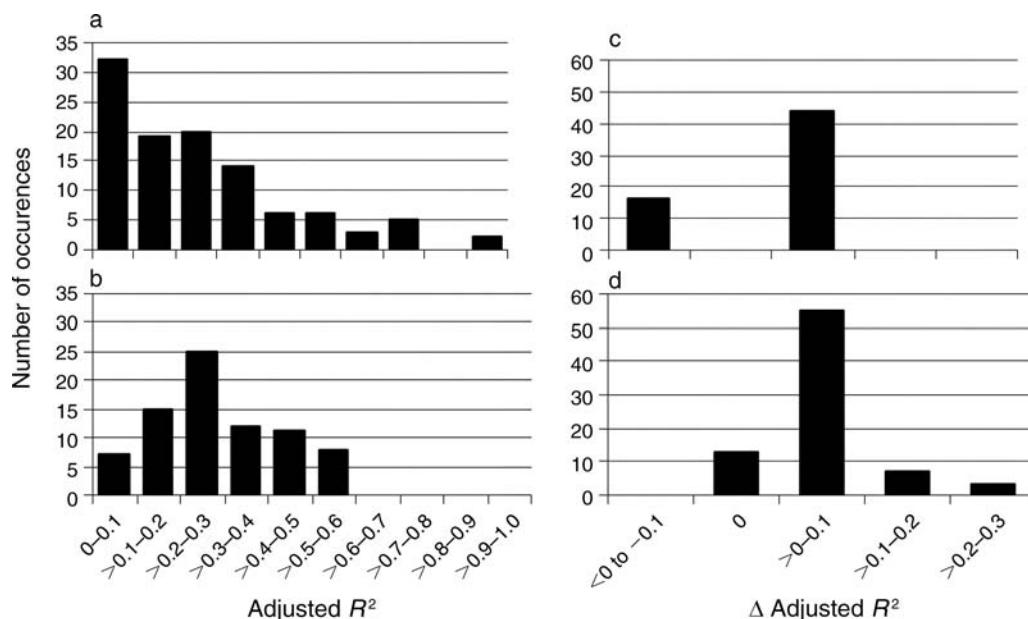
FIG. 5. Adjusted R^2 values by class, and change in adjusted R^2, by class, resulting from (a) 138 basic models encompassing 20 forested ecoregions, and (b) 61 refined models encompassing the nine largest forested ecoregions, within the conterminous United States. The figure also shows change in adjusted R^2 in (c) basic models, and (d) refined models after housing variables were removed from models. Data represent model results for forest and woodland species in seven guilds: interior-, ground-, and cavity-nesting species, Neotropical and short-distance migrants, permanent residents, and full synanthropes.

other hand, model performance for permanent residents was poorer, with four of the six models having an adjusted R^2 value of <10%.

Each ecoregion had at least one guild with a modeled adjusted R^2 value of >30%, and in four ecoregions (221, 222, 232, and M261) richness of four guilds was modeled with an adjusted $R^2 \geq 40\%$ (or nearly so in M261 where the value was 0.39). The ecoregion where species richness was most consistently associated with land cover and housing variables was 222, the Eastern Broadleaf (Continental) ecoregion, where models for five guilds had adjusted $R^2 \geq 40\%$. The best model also occurred in this ecoregion where 59% of the variance in richness of the ground-nesting guild was captured. However, three mountain ecoregions (M212 in the Adirondacks, M221 in the Appalachians, and M331 in the southern Rockies) exhibited generally less powerful models.

Land cover variables in the refined models

Consistent with our findings for the basic models, abundance of forestland cover was the most important variable in the refined models, and was retained in 45 of the 78 stepwise regression models (Appendix B). For all guilds, percent cover of forest was included in the refined models across the 20 forested ecoregions. Landscapes with higher proportions of forest were associated with higher richness of all forest birds and forest interior, ground-nesting, and Neotropical migrant guilds. Cavity-nesting species, short-distance migrants, and permanent residents were positively associated with proportion of

forest in four ecoregions, while full synanthropes were positively associated with proportion of forest in one ecoregion.

Because our focus was forest birds, it is not surprising that the independent variable most frequently included in models was proportion of forest, but the availability of forest in the ecoregions affected this variable's contribution to explaining patterns of variability in richness. In ecoregion 222 (Eastern Broadleaf Forest [Continental]), which contained the lowest average proportion of forest in landscapes surrounding BBS routes, forest was associated with richness variability in all eight guilds. In contrast, in the most forested ecoregion (M212, Adirondack–New England) models for only two guilds included forest.

For all guilds except permanent residents, models included percent cover of grassland/herbaceous, row crops, and open water (Fig. 4, Appendix B). These variables were retained in 32, 29, and 27 of the refined models. Another important land cover variable was the percent cover in the low density residential class, which is discussed in conjunction with the housing density variables (see *Results: Housing and residential...*).

Landscape pattern of nonresidential land cover was associated with variability of richness in ground-nesting species, short-distance migrants, and synanthropes in all nine ecoregions, and in >75% of ecoregions for most other guilds. The exception was the permanent resident guild, in which nonresidential landscape pattern was associated with richness in only five of nine models. Species richness across all guilds in ecoregions 222 and

TABLE 5. Relationship (direction of response) of eight avian guilds for the 20 forested ecoregions to proportion of the landscape in three land cover categories, and housing density, tallied by significance of response, as indicated by the partial P associated with the four predictive variables with spatial autocorrelation accounted for as necessary.

Direction of response, by guild	Intensive land uses			Forest			Semi natural land cover			Housing density in 2000		
	$P \leq$ 0.05	$0.05 <$ $P \leq 0.1$	$P >$ 0.1	$P \leq$ 0.05	$0.05 <$ $P \leq 0.1$	$P >$ 0.1	$P \leq$ 0.05	$0.05 <$ $P \leq 0.1$	$P >$ 0.1	$P \leq$ 0.05	$0.05 <$ $P \leq 0.1$	$P >$ 0.1
Forest and woodland nesters												
+	0	0	8	3	2	10	2	1	7	0	0	10
−	0	1	11	0	0	5	1	1	8	3	0	7
Neotropical migrant												
+	0	0	5	5	1	7	2	2	7	2	2	5
−	1	1	13	0	0	7	0	0	9	2	2	7
Short-distance migrant												
+	3	0	5	2	1	5	1	0	7	0	0	9
−	0	2	10	1	1	10	2	1	9	4	0	7
Permanent migrant												
+	1	1	9	2	1	13	2	0	13	3	1	7
−	0	0	9	0	0	4	0	0	5	1	2	6
Forest-interior-nesting species												
+	1	0	6	3	2	10	0	0	10	0	1	8
−	1	1	10	0	0	4	2	0	7	1	1	8
Ground-nesting species												
+	0	3	3	3	2	9	0	1	7	2	0	6
−	0	0	14	0	0	6	0	0	12	4	1	7
Cavity-nesting species												
+	3	0	9	2	2	11	3	1	8	0	0	9
−	0	0	8	0	0	5	1	0	7	0	1	10
Full synanthrope												
+	3	0	11	1	0	9	1	2	9	1	2	8
−	0	0	5	1	0	8	1	0	6	0	0	8
Tally of all guilds												
+	11	6	56	21	11	74	11	7	68	8	6	62
−	1	6	80	2	1	49	8	2	62	15	7	60

212 was associated with a significantly greater proportion of landscape pattern variables than in ecoregion M331 (mean proportion = 0.50, 0.43, and 0.19, respectively, $P < 0.05$).

The landscape pattern variable most frequently retained was edge density of transitional cover, which remained in 13 of the 70 models. Transitional cover includes, but is not limited to, regenerating forest. The occurrence of early successional forest whether anthropogenic or natural in origin, contributed to bird species richness in several guilds.

Housing and residential land cover variables in the refined models

Residential development also proved to be a strong associate of richness patterns in the refined models. Of the 78 models, 69 included housing density and/or residential land cover as significant variables (Table 6). Taking a closer look at these models, 44% included one variable, while the rest included two, three, or in two cases four housing or residential land cover variables. Of

the 60 models of individual ecoregions, housing density was included 52 times, proportion of residential land cover 30 times, and landscape pattern of residential areas was included 42 times in models explaining avian richness patterns. Housing density variables for 1990 and 2000 were both selected in 21 of the ecoregion level models, and in six of the nine ecoregion level models variables from both decades were included (Appendix B). Thus there was no strong evidence for a time lag in avian response to housing.

Two ecoregions stood out where guild richness exhibited strong responses to housing density: M212, Adirondack–New England and M331, Southern Rocky Mountains. In M212 between 30% and 100% of the explained variability of four guilds was due to housing density, while in M331 between 27% and 64% of the explained variability in four guilds was due to housing density. On the other hand, in five ecoregions, the average reduction in the adjusted R^2 value when housing was removed from models was <0.05, despite individual

TABLE 6. Adjusted (Adj.) R^2 values (with ΔAdj. R^2 and sample size) resulting from refined models explaining variance due to housing density and land cover variables in forested ecoregions of the United States for eight avian guilds.

| Ecoregion (province level) | Model attributes | Forest species | Nesting guild | | | Migratory habit |
			Interior	Ground	Cavity	Neotropical
All forested	Adj. R^2	0.35***	0.56***	0.42***	0.18***	0.48***
	ΔAdj. R^2	−0.02***	−0.01***	−0.02***	0	−0.01***
	No. routes	1802	1707	1796	1801	1787
212	Adj. R^2	0.22	0.48	0.34	0.17	0.30
	ΔAdj. R^2	−0.02	−0.03	−0.03	−0.02	−0.02
	No. routes	202	202	199	196	202
M212	Adj. R^2	0.11	0.05	0.30	0.37	0.27
	ΔAdj. R^2	−0.07	−0.01	−0.14	−0.03	−0.04
	No. routes	78	78	75	77	78
221	Adj. R^2	0.41	0.51	0.42	0.23	0.56
	ΔAdj. R^2	−0.05	−0.01	−0.01	−0.15	−0.02
	No. routes	191	189	184	187	191
M221	Adj. R^2	0.15	0.28	0.17	0.30	0.07
	ΔAdj. R^2	−0.03	−0.05	−0.02	−0.01	−0.01
	No. routes	111	189	109	107	111
222	Adj. R^2	0.46	0.57	0.59	0.22	0.50
	ΔAdj. R^2	0	−0.04	−0.01	0	−0.02
	No. routes	317	310	314	314	315
231	Adj. R^2	0.27	0.26	0.26	0.11	0.35
	ΔAdj. R^2	−0.02	−0.01	0	−0.01	0
	No. routes	194	189	191	191	194
232	Adj. R^2	0.57	0.50	0.19	0.25	0.55
	ΔAdj. R^2	−0.04	−0.10	−0.11	0	−0.06
	No. routes	247	238	231	234	247
M261	Adj. R^2	0.28	0.42	0.57	0.41	0.39
	ΔAdj. R^2	−0.05	−0.02	−0.01	0	−0.06
	No. routes	94	81	90	92	94
M331	Adj. R^2	0.21	0.32	0.30	0.10	0.26
	ΔAdj. R^2	−0.08	−0.01	−0.12	−0.04	−0.07
	No. routes	101	75	98	101	101

Notes: ΔAdj. R^2 is the change in value after removing housing variables from models. $P \leq 0.05$ unless otherwise noted. Following the convention of Bailey (1995), an "M" in the ecoregion name indicates a mountain ecoregion.

*** $P \leq 0.001$.

† Models could not be constructed for these two ecoregions using the backward selection regression procedure due to low species richness.

cases showing a relatively strong association (e.g., cavity nesters in ecoregion 221, Δadjusted $R^2 = 0.15$).

The strongest guild response to housing density was shown by permanent residents in M212, the Adirondack–New England ecoregion, where the model consisted solely of an intercept plus two measures of housing density in the year 2000. In fact, the permanent resident guild was most consistently associated with housing or residential land cover in five other ecoregions; one-third to one-half of the explained variability in this guild was due to these factors (Table 6, Appendix B). Richness of ground-nesting species was also associated with housing; in three ecoregions, one-third to one-half of the explained variability was due to housing. Similarly, housing made a strong contribution to models of short-distance migrants in ecoregion M331, cavity nesters in ecoregion 221, and full synanthropes in ecoregion 222, where its removal from models resulted in a percentage reduction in adjusted R^2 values of 36%, 35%, and 65%, relative to the model that included housing variables, respectively.

DISCUSSION

Housing development in the United States has significant effects on forest bird diversity. The majority of our models of forest bird species richness improved when a measure of housing development was added to the models. The most important variable determining forest bird species richness was the amount of forest cover, which was not surprising. However we were surprised that measures of housing density were as important as measures of forest fragmentation in most models of avian diversity. Forest fragmentation effects on bird diversity have been well documented (e.g., Robinson et al. 1995, Donovan et al. 1997, Hobson and Bayne 2000). In contrast, we know much less about the underlying processes that cause the relationships between housing development and bird diversity, and our findings suggest that more research is needed to reveal these mechanisms.

Our results highlight that housing development affects forest bird species richness in all forested ecoregions of the conterminous United States. However, there were important differences among ecoregions. These regional

TABLE 6. Extended.

	Migratory habit	
Short-distance	Permanent resident	Full synanthropy
0.16***	0.19***	0.32***
−0.01***	0	−0.01***
1801	1783	1631
0.25	0.09	0.29
−0.01	−0.05	−0.04
202	200	190
0.19	0.29	0.50
−0.11	−0.29	−0.25
78	76	69
0.22	0.04	0.12
−0.02	−0.02	−0.05
191	191	191
0.38	0.28	0.24
−0.01	−0.14	0
111	109	109
0.12	0.46	0.23
−0.01	−0.17	−0.08
314	315	314
0.12	0.06	0.17
−0.01	−0.03	−0.09
194	194	192
0.40	0.17	0.24
−0.03	0	−0.04
247	247	244
0.25	0.33	†
−0.03	0	
91	94	61
0.33	0.08	†
−0.21	−0.02	
100	101	70

differences were the reason why the local models for individual ecoregions generally outperformed the global models across all forested ecoregions. Model improvements due to ecoregion stratification were most pronounced for cavity-nesting and short-distance migrant guilds, suggesting that these avian groups may be especially sensitive to regionally specific processes. We also observed varying patterns of association between avian richness response variables and landscape structure, suggesting that landscape context is an important mediating factor in understanding how biodiversity may respond to landscape changes.

The two ecoregions with the best performing models were the Everglades and California Coastal Range. We attribute the high explanatory power in these ecoregions largely to the amount of and spatial arrangement of forest in each. Only ~20% of the Everglades ecoregion is composed of forest and in the California Coastal Range, sclerophyll forests occupy north-facing wetter sites, and alternate with shrub-dominated chaparral (Bailey 1995). Thus, forest birds in these ecoregions are spatially clustered in the forest patches while the surrounding matrix primarily is non-habitat, and that means that the abundance of forest cover can predict forest bird species richness especially well.

When comparing model results for specific guilds with those for all forest nesting birds, we found that models generally performed better when birds were partitioned into guilds, and were particularly strong for ground-nesting, interior-nesting, and Neotropical migrant guilds. However, partitioning the avian community by guild did not always improve model performance. Notable exceptions were the models for permanent residents, which often captured less variability than the corresponding models for all forest bird nesters in the same ecoregions. This was surprising since permanent residents may be expected to track changes in local landscape conditions more closely than migratory species, as their occupancy is not seasonal, and suggests that richness of residents may be affected by global climate effects that are unrelated to landscape condition (Nott et al. 2002).

When comparing our results for the basic and the refined models, the general finding was that refined models resulted in higher R^2 values. Species richness of forest birds can be modeled better with detailed land cover classes, more specific housing density variables, and landscape indices in addition to measures of land cover class abundance (Fig. 5). This is not just a function of larger models generally outperforming models with fewer variables. The final models after the backward selection procedure often included a similar number of variables as the basic models, and we compared adjusted R^2 values thus taking the number of variables into account. The better performance of the refined models can also not be attributed to a few specific explanatory classes exhibiting higher explanatory power than the general classes used in the basic models. Our results show that a large number of different variables were retained in the refined models for different forest ecoregions and different avian guilds. This suggests that different mechanisms may be important in different ecoregions and for different guilds, and the higher performance of the refined models is caused by their ability to capture some of these differences. This highlights, again, our speculation that landscape context will affect associations of bird species richness with housing and landscape pattern. Our finding that housing was included in 71 of the 78 refined models, with the number of narrowly defined variables available in the backward selection procedure, suggests that housing, or factors associated with housing, is an important factor in shaping habitat quality for forest birds.

Support for our initial predictions was generally positive, but associations were more complex than expected. Most of the guilds that we expected to be associated with housing development were indeed best modeled when housing variables were included. However, our findings were less clear with regard to the directions of the effects. This is partially a limitation of our approach. We used backward-selected regression and we needed to parse the large number of predictor variables in our refined models. The limitation of this

PLATE 1. In forested ecoregions the density of houses, such as this one, is associated with variation in bird species richness in 85% of models. Photo credit: Adrian Lesak.

approach is that the signs of individual variables in the refined models cannot be reliably interpreted because they are context specific (Chatterjee and Price 1991). Variable signs can only be interpreted for the basic models, which generally did not perform as well.

We had assumed that forest amount would have a strong positive effect on forest bird species richness as a whole, and on all guilds with the exception of synanthropes. This assumption was somewhat trivial, but testing it was necessary to ensure that our data and analysis approach confirmed this most basic expectation. As expected, forest amount was the most important variable. In the basic models, a positive association with species richness was observed 21 and 11 times for $P < 0.05$ and $P < 0.1$, respectively, compared with only three negative relationships, including one with synanthropes. In the refined models, forest cover was the most important variable, and was included in 55 of the 78 models. In the most heavily forested ecoregion, M212 (Adirondack–New England, 86% forested land cover), 1990 housing and minimum patch size of orchards provided the most, albeit minimal, explanatory power for variation in forest species richness (Appendix B), suggesting that factors other than land cover and housing influence bird distribution in this ecoregion. In M331, the southern Rocky Mountain ecoregion, where 48% of the land cover is forest and housing density is <3 units/km^2, two-thirds of the explained variation in richness of forest nesters was due to the proportion of

forest, and one-third reflected the association with housing density and the number of patches of low intensity residential. The same combination of housing variables was significant in explaining the variability of forest nesters in M261, the Sierran ecoregion, which has 64% forest cover and 6 houses/km^2 in the 1200-km^2 landscapes surrounding BBS routes.

Our first specific prediction had been that richness of ground-nesting species would be strongly and negatively associated with housing variables, due to higher density of domestic and wild mesopredators in the vicinity of houses. Indeed housing variables were included in eight of the 10 refined models for the ground-nesting guild, suggesting a strong association with this guild. However, the importance of housing variables in modeling richness of ground-nesting species varied widely. In three ecoregions one-third to one-half of the explained variability was associated with housing variables, whereas in the other ecoregions, housing variables corresponded to very little of the explained variability. In the basic models, housing variables also were associated with very little of the explained variability.

Our second prediction was that richness of both forest interior species and cavity-nesting species would be lower in areas with more housing due to loss of nesting and foraging sites. For both of these guilds, housing variables were rarely included in the models, and were associated with only a small fraction of the variability when they were selected. Most variability of forest

interior species richness was associated with the proportion of forest, grassland/herbaceous, and row crops, and with edge density of urban grasses.

In response to our third prediction, that Neotropical migrants and permanent residents would have different levels of sensitivity to landscape pattern, we found equivocal results. Edge density of residential land cover was included in the refined models of Neotropical migrant species richness for the forested United States and three individual ecoregions, as well as in three ecoregion level models of permanent resident richness.

Finally, we had predicted that synanthropes would be positively associated with intensive land uses, edge density, and housing density. Six of the seven refined models for synanthropes included housing density or residential land cover. The model for the remaining ecoregion, 232, with 248 routes, was composed of open water and row crops, and only three of the refined models for synanthopes included edge density variables.

Prior studies have conflicting reports of the relationships between the intensity of human land use, populations, and density vs. avian biodiversity (e.g., Friesen et al. 1995, Nilon et al. 1995, Kluza et al. 2000, Gaston and Evans 2004, Evans and Gaston 2005, Phillips et al. 2005). The associations generally vary with scale of the analysis (C. A. Lepczyk, C. H. Flather, V. C. Radeloff, A. M. Pidgeon, R. B. Hammer, and J. Liu, *unpublished manuscript*); at broad scales, birds and humans often exhibit positive associations while at finer scales negative associations are observed. We did find positive associations between housing variables and bird biodiversity in 14 of our basic models ($P < 0.1$). Eight of the 14 cases of positive correlations with housing variables occurred in the case of permanent residents, and Neotropical migrants (four cases each). This may suggest that these guilds are particularly prone to exhibit overlap of high species richness areas with areas where human settlements are common. We also observed 15 cases where intensive land use was positively correlated with bird species richness. These model results may represent situations where areas of high net primary productivity attract both high densities of humans and high biodiversity. The three cases of positive association between full synanthropes and housing may simply reflect habitat modifications in settlements that benefit synanthropic species.

Interpreting the positive correlations needs to be done carefully though. For example in the heavily forested Adirondack–New England ecoregion M212, forest interior species were positively associated with the proportion of low intensity residential land cover, which occupied on average 1% of the landscape. In this ecoregion, low intensity housing may provide small forest openings while maintaining high canopy cover, perhaps simulating forest gaps caused naturally by, for example, tree fall disturbance. Thus it is possible that low intensity housing creates conditions suitable for both gap-associated species like Canada Warbler

(*Wilsonia canadensis*) while leaving surrounding forest intact so that conditions are suitable for other forest interior associates. On the other hand, the positive association between forest interior species and low intensity residential land cover may simply be attributable to the road-based survey design of the BBS, and the association of houses with roads.

Last but not least, we found many instances of negative correlation of housing density with bird species richness, which concurs with findings of Lepczyk et al. (C. A. Lepczyk, C. H. Flather, V. C. Radeloff, A. M. Pidgeon, R. B. Hammer, and J. Liu, *unpublished manuscript*). Negative relationships were found in the majority of the basic models for forest and woodland species, short-distance migrants, ground-nesting, and cavity-nesting species, and we suggest that future housing growth will likely increase the number of cases where negative relationships occur.

Although different taxa have different habitat requirements and respond differently to anthropogenic perturbations, bird species are good indicators of the response of forest biodiversity to forest disturbance (Martin and Finch 1995). Our analysis was conducted primarily in the largest ecoregions, but the impact of housing development on biodiversity is not limited to these areas. Forested areas everywhere are affected by housing development, and land use planners and regulators need to incorporate planning and design criteria that promote landscape patterns over time that serve to conserve species diversity in the landscape. Unfortunately, our results suggest that simple, generally applicable, land use recommendations may be difficult to obtain. Rather, anticipating future avian response to land use intensification or retrogression (reversion) to native vegetation will depend on the current landscape context and the species group of conservation interest.

Methodological considerations

Averaging the bird richness metric over up to five years of data, and including only those species for which the BBS data included ≥30 detections provided a robust estimator with which to evaluate associations with housing, and landscape composition and structure. Unfortunately, the relatively great topographic relief typical of forests of the western United States means that individual forested ecoregions are smaller than in the eastern United States thus encompassing fewer BBS routes. Our analysis depended on sufficient sample size (>90 routes) and thus excluded small ecoregions (those containing approximately <90 BBS routes) from individual analysis with our refined models.

Another limitation of the BBS data is due to the fact of where they are located. Because of the location of BBS routes on secondary roads, the universe of housing density and residential land cover in our study is truncated relative to the ecoregions in which the BBS routes exist. The routes, and thus the landscapes we analyzed, avoid both the most highly urbanized and

developed areas of the United States, as well as wilderness areas. This means that our findings can not be generalized beyond the range of housing density and land cover proportions included in this study.

Responses of bird species to the combination of niche-defining elements in each ecoregion was unique. This in turn affected the nature of guild associations with landscape elements, a point that is illustrated by comparing associations in M331, the Southern Rocky Mountain ecoregion, with 221, the Eastern Broadleaf (Oceanic) ecoregion. In M331 housing density in 2000 averaged 3 units/km^2 and composed at least one-third of model explanatory power for four of seven guilds. A mechanism that may explain this pattern is that at very low densities houses are accompanied by habitat resources that enhance habitat quality for member species in several guilds. In contrast, in ecoregion 221, housing density in 2000 averaged 64 units/km^2 and made a negligible contribution to model explanatory power for all guilds with the exception of cavity nesters. Housing density this high may be above a response threshold for most guilds. In other words, the density of housing may be so high that it is above a level at which changes in bird species richness are associated with changes in housing density. Finally, it is important to remember that the role of site-specific habitat variables, which can contribute substantially to explaining patterns of avian distribution (e.g., Bolger et al. 1997), was not analyzed in this study.

Management implications

Rural, forested areas throughout the United States have experienced strong housing growth since the 1970s (Radeloff et al. 2005a, Lepczyk et al. 2007), and housing growth is likely to remain strong in areas with many natural amenities (e.g., forests, lakes; Hammer et al. 2004). Furthermore, the trend is toward more dispersed development (Radeloff et al. 2005a). Our results show that housing density and residential land cover are already significant predictors of forest bird species richness, and effects are likely to increase as development continues. Human land use and settlement patterns are becoming increasingly important factors that shape biodiversity pattern in the United States. This calls for a proactive approach.

The majority of the nation's forests are in private ownership. We now have a chance and a responsibility to shape development patterns. National conservation plans need to incorporate housing in their formulations. By examining patterns at the broadest possible scales, this study provides context for interpreting and guiding future regional studies. As avian conservation efforts become increasingly integrated at the national scale and even international scale (e.g., North American Bird Conservation Initiative [*available online*],[6] Partners In Flight [Rich et al. 2004], U.S. Shorebird Conservation Plan [*available online*]),[7] nationwide studies such as this one, that examine the association of avian patterns with landscape structure and housing density become ever more useful and relevant. The recent development of several conservation plans at the national and international scale demonstrates the general buy-in of the conservation community to this idea.

LITERATURE CITED

Alig, R. J., J. D. Kline, and M. Lichtenstein. 2004. Urbanization on the US landscape: looking ahead in the 21st century. Landscape and Urban Planning 69:219–234.

Allen, A. P., and R. J. O'Connor. 2000. Hierarchical correlates of bird assemblage structure on northeastern USA lakes. Environmental Monitoring and Assessment 62:15–35.

Bailey, R. G. 1995. Description of the ecoregions of the United States. Second edition revised and expanded. Miscellaneous Publication Number 1391 (revised). USDA Forest Service, Washington, D.C., USA.

Balmford, A., J. L. Moore, T. Brooks, N. Burgess, L. A. Hansen, P. Williams, and C. Rahbek. 2001. Conservation conflicts across Africa. Science 291:2616–2619.

Blair, R. B. 1996. Land use and avian species diversity along an urban gradient. Ecological Applications 6:506–519.

Bolger, D. T., T. A. Scott, and J. T. Rotenberry. 1997. Breeding bird abundance in an urbanizing landscape in coastal California. Conservation Biology 11:406–421.

Borgmann, K. L., and A. D. Rodewald. 2004. Nest predation in an urbanizing landscape: the role of exotic shrubs. Ecological Applications 14:1757–1765.

Boulinier, T., J. D. Nichols, J. E. Hines, J. R. Sauer, C. H. Flather, and K. H. Pollock. 1998. Higher temporal variability of forest breeding bird communities in fragmented landscapes. Proceedings of the National Academy of Sciences (USA) 95:7497–7501.

Burke, D. M., and E. Nol. 1998. Influence of food abundance, nest-site habitat, and forest fragmentation on breeding Ovenbirds. Auk 115:96–104.

Bystrak, D. 1981. The North American breeding bird survey. Studies in Avian Biology 6:34–41.

Chatterjee, S., and B. B. Price. 1991. Regression analysis by example. Second edition. Wiley, New York, New York, USA.

Chown, S. L., B. J. Van Rensburg, K. J. Gaston, A. S. L. Rodrigues, and A. S. Van Jaarsveld. 2003. Energy, species richness, and human population size: conservation implications at a national scale. Ecological Applications 13:1233–1241.

Coleman, J. S., S. A. Temple, and S. R. Craven. 1997. Cats and wildlife: a conservation dilemma. Cooperative Extension Publications, University of Wisconsin-Extension, Madison, Wisconsin, USA.

Cowardin, L. M., V. Carter, F. C. Golet, and E. T. LaRoe. 1979. Classification of wetlands and deepwater habitats of the United States. U.S. Department of the Interior, Fish and Wildlife Service, Washington, D.C., USA.

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[6] ⟨http://www.bsc-eoc.org/nabci.html⟩
[7] ⟨http://www.fws.gov/shorebirdplan/USShorebird.htm⟩

Crooks, K. R., and M. E. Soule. 1999. Mesopredator release and avifaunal extinctions in a fragmented system. Nature 400:563–566.

Danz, N. P., G. J. Niemi, J. Lind, and J. M. Hanowski. 2007. Birds of western Great Lakes forests. University of Minnesota, Duluth, Minnesota, USA. ⟨www.nrri.umn.edu/mnbirds⟩

Desmond, M. J., J. A. Savidge, and K. M. Eskridge. 2000. Correlations between burrowing owl and black-tailed prairie dog declines: a 7 year analysis. Journal of Wildlife Management 64:1067–1075.

Donovan, T. M., and C. H. Flather. 2002. Relationships among North American songbird trends, habitat fragmentation, and landscape occupancy. Ecological Applications 12:364–374.

Donovan, T. M., P. W. Jones, E. M. Annand, and F. R. Thompson III. 1997. Variation in local-scale edge effects: mechanisms and landscape context. Ecology 78:2064–2075.

Donovan, T. M., F. R. Thompson III, J. Faaborg, and J. R. Probst. 1995. Reproductive success of migratory birds in habitat sources and sinks. Conservation Biology 9:1380–1395.

Ehrlich, P. R., D. S. Dobkin, and D. Wheye. 1988. The birder's handbook: a field guide to the natural history of North American birds. Simon and Schuster, New York, New York, USA.

Engels, T., and C. Sexton. 1994. Negative correlation of blue jays and golden-cheeked warblers near an urbanizing area. Conservation Biology 8:286–290.

Erskine, A. J. 1978. The first ten years of the cooperative breeding bird survey in Canada. Canadian Wildlife Service Report Series 42:1–61.

Evans, K. L., and K. J. Gaston. 2005. People, energy and avian species richness. Global Ecology and Biogeography 14:187–196.

Finch, D. M., and P. Stangel, editors. 1993. Status and management of Neotropical migratory birds. USDA Forest Service General Technical Report RM-229.

Flather, C. H., and J. R. Sauer. 1996. Using landscape ecology to test hypotheses about large-scale abundance patterns in migratory birds. Ecology 77:28–35.

Fraterrigo, J. M., and J. A. Wiens. 2005. Bird communities of the Colorado Rocky Mountains along a gradient of exurban development. Landscape and Urban Planning 71:263–275.

Friesen, P. F., J. Eagles, and R. J. Mackay. 1995. Effects of residential development on forest dwelling Neotropical migrant songbirds. Conservation Biology 9:1408–1414.

Gaston, K. J., and K. L. Evans. 2004. Birds and people in Europe. Proceedings of the Royal Society B 271:1649–1655.

Gillham, O. 2002. The limitless city: a primer on the urban sprawl debate. Island Press, Washington, D.C., USA.

Green, D. A., and M. G. Baker. 2003. Urbanization impacts on habitat and bird communities in a Sonoran Desert ecosystem. Landscape and Urban Planning 63:225–239.

Hammer, R. B., S. I. Stewart, R. L. Winkler, V. C. Radeloff, and P. R. Voss. 2004. Characterizing dynamic spatial and temporal residential density patterns from 1940–1990 across the North Central United States. Landscape and Urban Planning 69:183–199.

Hansen, A. J., R. L. Knight, J. M. Marzluff, S. Powell, K. Brown, P. H. Gude, and A. Jones. 2005. Effects of exurban development on biodiversity: patterns, mechanisms, and research needs. Ecological Applications 15:1893–1905.

Hawbaker, T. J., and V. C. Radeloff. 2004. Roads and landscape pattern in northern Wisconsin based on a comparison of four road data sources. Conservation Biology 18:1233–1244.

Hines, J. E., T. Boulinier, J. D. Nichols, J. R. Sauer, and K. H. Pollock. 1999. COMDYN: software to study the dynamics of animal communities using a capture–recapture approach. Bird Study (Supplement) 46:S209–S217.

Hobson, K. A., and E. Bayne. 2000. Effects of forest fragmentation by agriculture on avian communities in the southern boreal mixed woods of western Canada. Wilson Bulletin 112:373–387.

Johnson, K. M., and C. L. Beale. 1994. The recent revival of widespread population growth in nonmetropolitan areas of the United States. Rural Sociology 59:655–667.

Johnston, R. F. 2001. Synanthropic birds of North America. Pages 49–68 in J. M. Marzluff, R. Bowman, and R. Donnelly, editors. Avian ecology and conservation in an urbanizing world. Kluwer Academic, Boston, Massachusetts, USA.

Kluza, D. A., C. R. Griffin, and R. M. Degraaf. 2000. Housing developments in rural New England: effects on forest birds. Animal Conservation 3:15–26.

Lepczyk, C. A., R. B. Hammer, V. C. Radeloff, and S. I. Stewart. 2007. Spatiotemporal dynamics of housing growth hotspots in the North Central U.S. from 1940–2000. Landscape Ecology, in press.

Lepczyk, C. A., A. G. Mertig, and J. G. Liu. 2004. Assessing landowner activities related to birds across rural-to-urban landscapes. Environmental Management 33:110–125.

Lindsay, A. R., S. S. Gillum, and M. W. Meyer. 2002. Influence of lakeshore development on breeding bird communities in a mixed northern forest. Biological Conservation 107:1–11.

Maestas, J. D., R. L. Knight, and W. C. Gilgert. 2001. Biodiversity and land-use change in the American Mountain West. Geographical Review 91:509–524.

Maestas, J. D., R. L. Knight, and W. C. Gilgert. 2003. Biodiversity across a rural land-use gradient. Conservation Biology 17:1425–1434.

Martin, T. E., and D. M. Finch, editors. 1995. Ecology and management of neotropical migratory birds: a synthesis and review of critical issues. Oxford University Press, New York, New York, USA.

Marzluff, J. M. 1997. Effects of urbanization and recreation on songbirds. Pages 89–102 in W. M. Block and D. M. Finch, editors. Songbird ecology in southwestern forests: a literature review. USDA Forest Service, Fort Collins, Colorado, USA.

Marzluff, J. M., R. Bowman, and R. Donnelly, editors. 2001. Avian ecology and conservation in an urbanizing world. Kluwer Academic, Boston, Massachusetts, USA.

Miller, J. R., J. A. Wiens, N. T. Hobbs, and D. M. Theobald. 2003. Effects of human settlement on bird communities in lowland riparian areas of Colorado (USA). Ecological Applications 13:1041–1059.

Miller, S. G., R. L. Knight, and C. K. Miller. 2001. Wildlife responses to pedestrians and dogs. Wildlife Society Bulletin 29:124–132.

Mills, G. S., J. B. Dunning, and J. M. Bates. 1989. Effects of urbanization on breeding bird community structure in southwestern desert habitats. Condor 91:416–428.

Nichols, J. D., T. Boulinier, J. E. Hines, K. H. Pollock, and J. R. Sauer. 1998. Inference methods for spatial variation in species richness and community composition when not all species are detected. Conservation Biology 12:1390–1398.

Nilon, C. H., C. N. Long, and W. C. Zipperer. 1995. Effects of wildland development on forest bird communities. Landscape and Urban Planning 32:81–92.

Norris, K., and N. Harper. 2004. Extinction processes in hot spots of avian biodiversity and the targeting of pre-emptive conservation action. Proceedings of the Royal Society B 271:123–130.

Nott, M. P., D. F. DeSante, R. B. Siegel, and P. Pyle. 2002. Influences of the El Nino/Southern Oscillation and the North Atlantic Oscillation on avian productivity in forests of the Pacific Northwest of North America. Global Ecology and Biogeography 11:332–342.

Odell, E. A., and R. L. Knight. 2001. Songbird and medium-sized mammal communities associated with exurban devel-

opment in Pitkin County, Colorado. Conservation Biology 15:1143–1150.

Phillips, J., E. Nol, D. Burke, and W. Dunford. 2005. Impacts of housing developments on Wood Thrush nesting success in hardwood forest fragments. Condor 107:97–106.

Poole, A., editor. 2005. The birds of North America. Cornell Laboratory of Ornithology, Ithaca, New York, USA. ⟨http://bna.birds.cornell.edu/BNA/⟩

Radeloff, V. C., R. B. Hammer, and S. I. Stewart. 2005a. Rural and suburban sprawl in the U.S. Midwest from 1940 to 2000 and its relation to forest fragmentation. Conservation Biology 9:793–805.

Radeloff, V. C., R. B. Hammer, S. I. Stewart, J. S. Fried, S. S. Holcomb, and J. F. McKeefry. 2005b. The wildland–urban interface in the United States. Ecological Applications 15: 799–805.

Rich, T. D., et al. 2004. Partners in flight North American landbird conservation plan. Cornell Laboratory of Ornithology, Ithaca, New York, USA.

Robbins, C. S., D. Bystrak, and P. H. Geissler. 1986. The breeding bird survey: its first fifteen years, 1965–1979. Resource Publication 157. U.S. Department of the Interior, Fish and Wildlife Service, Washington, D.C., USA.

Robinson, S. K., F. R. Thompson III, T. M. Donovan, D. R. Whitehead, and J. Faaborg. 1995. Regional forest fragmentation and the nesting success of migratory birds. Science 267: 1987–1990.

Sauer, J. R., J. E. Fallon, and R. Johnson. 2003. Use of North American Breeding Bird Survey data to estimate population change for bird conservation regions. Journal of Wildlife Management 67:372–389.

Smith, C. M., and D. G. Wachob. 2006. Trends associated with residential development in riparian breeding bird habitat along the Snake River in Jackson Hole, WY, USA: implications for conservation planning. Biological Conservation 128:431–446.

Soh, M. C. K., N. S. Sodhi, and S. L. H. Lim. 2006. High sensitivity of montane bird communities to habitat disturbance in peninsular Malaysia. Biological Conservation 129: 149–166.

Stein, S. M., R. E. McRoberts, R. J. Alig, M. D. Nelson, D. M. Theobold, M. Eley, M. Dechter, and M. Carr. 2005. Forests on the edge: housing development on America's private forests. USDA Forest Service, Pacific Northwest Research Station, Portland, Oregon, USA.

Tewksbury, J. J., L. Garner, S. Garner, J. D. Lloyd, V. Saab, and T. E. Martin. 2006. Tests of landscape influence: nest predation and brood parasitism in fragmented ecosystems. Ecology 87:759–768.

Theobald, D. M., J. R. Miller, and N. T. Hobbs. 1997. Estimating the cumulative effects of development on wildlife habitat. Landscape and Urban Planning 39:25–36.

U.S. Census Bureau. 2001. Census 2000 summary file 1. U.S. Census Bureau, Washington, D.C., USA.

Vogelmann, J. E., S. M. Howard, L. Yang, C. R. Larson, B. K. Wylie, and N. van Driel. 2001. Completion of the 1990s National Land Cover Data Set for the conterminous United States from Landsat Thematic Mapper data and ancillary data sources. Photogrammetric Engineering and Remote Sensing 67:650–662.

Whitcomb, R. F., C. S. Robbins, J. F. Lynch, B. L. Whitcomb, M. K. Klimkiewicz, and D. Bystrak. 1981. Effects of forest fragmentation on avifauna of the eastern deciduous forest. Pages 125–206 in R. L. Burgess and D. M. Sharpe, editors. Forest island dynamics in man-dominated landscapes. Springer-Verlag, New York, New York, USA.

Wiens, J. A. 1985. Habitat selection in variable environments: Shrub-steppe birds. Pages 227–250 in M. L. Cody, editor. Habitat selection in birds. Academic Press, New York, New York, USA.

APPENDIX A

Classification of forest species by guild (*Ecological Archives* A017-079-A1).

APPENDIX B

Regression model coefficients for forest and woodland species, classed by migratory, nesting, and syanthrope guild, for the forested United States and the nine large forested ecoregions (*Ecological Archives* A017-079-A2).

APPENDIX C

Variograms showing spatial autocorrelation in model residuals (*Ecological Archives* A017-079-A3).