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# Housing development erodes avian community structure in U.S. protected areas

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*Abstract.* Protected areas are a cornerstone for biodiversity conservation, but they also provide amenities that attract housing development on inholdings and adjacent private lands. We explored how this development affects biodiversity within and near protected areas among six ecological regions throughout the United States. We quantified the effect of housing density within, at the boundary, and outside protected areas, and natural land cover within protected areas, on the proportional abundance and proportional richness of three avian guilds within protected areas. We developed three guilds from the North American Breeding Bird Survey, which included Species of Greatest Conservation Need, land cover affiliates (e.g., forest breeders), and synanthropic species associated with urban environments. We gathered housing density data for the year 2000 from the U.S. Census Bureau, and centered the bird data on this year. We obtained land cover data from the 2001 National Land Cover Database, and we used single- and multiple-variable analyses to address our research question. In all regions, housing density within protected areas was positively associated with the proportional abundance or proportional richness of synanthropes, and negatively associated with the proportional abundance or proportional richness of Species of Greatest Conservation Need. These relationships were strongest in the eastern forested regions and the central grasslands, where more than 70% and 45%, respectively, of the variation in the proportional abundance of synanthropes and Species of Greatest Conservation Need were explained by housing within protected areas. Furthermore, in most regions, housing density outside protected areas was positively associated with the proportional abundance or proportional richness of synanthropes and negatively associated with the proportional abundance of land cover affiliates and Species of Greatest Conservation Need within protected areas. However, these effects were weaker than housing within protected areas. Natural land cover was high with little variability within protected areas, and consequently, was less influential than housing density within or outside protected areas explaining the proportional abundance or proportional richness of the avian guilds. Our results indicate that housing development within, at the boundary, and outside protected areas impacts avian community structure within protected areas throughout the United States.

Key words: *avian abundance; avian richness; biodiversity; housing density; inholding; land cover; private land; public land.*

## Introduction

Expanding human populations and attendant land use changes are the primary factors driving changes in biological diversity (Vitousek et al. 1997, Cincotta et al. 2000, Liu et al. 2003, Foley et al. 2005). Much of the burden of global biodiversity conservation is placed on publicly owned protected areas (Bruner et al. 2001, Naughton-Treves et al. 2005, Gaston et al. 2008, Joppa et al. 2008, Robles et al. 2008, Flather et al. 2009). Protected areas account for approximately one-eighth of

the global land surface (Chape et al. 2005) and, in addition to biodiversity conservation, are important for cultural preservation (Stevens 1997), economic viability (Dixon and Sherman 1991), and poverty alleviation (Naughton-Treves et al. 2005, Andam et al. 2010). Especially over the last three decades, the total global protected areas network has increased rapidly to conserve in situ biodiversity (Naughton-Treves et al. 2005). Nonetheless, numerous globally important habitats (e.g., Mediterranean scrub) remain below targets for land area conservation (Brooks et al. 2004). Furthermore, protected areas are often situated in high-elevation areas that are far from population centers (Hansen and Rotella 2002, Joppa and Pfaff 2009). Yet, protected areas that are located on suitable lands for

human habitation are potentially affected by stresses from outside the protected area boundaries.

Throughout the world, development has been particularly strong adjacent to protected areas and on private inholdings (Gude et al. 2006, Wade and Theobald 2009, Radeloff et al. 2010, Gimmi et al. 2011, Laurance et al. 2012), which potentially diminishes the conservation benefit of these lands. For example, in the United States, much of the forest and grassland habitats on private lands are intensively used by humans (Mitchell 2000, Haynes 2003), with nearly two million hectares of forest and grassland converted to cropland (e.g., for the manufacture of ethanol) or developed land (e.g., urbanization, transportation, or small built-up areas) from 2002 to 2007 (USDA 2009). Concomitant with this land use intensification, open lands in the wildland–urban interface are increasingly converted to roads (Hawbaker et al. 2005, Watts et al. 2007) and housing developments (Radeloff et al. 2005*b*) due to amenity-driven rural and exurban development (Fuguitt 1985, Gustafson et al. 2005, Hammer et al. 2009). These changes in land use are having a significant impact on biological conservation (McKinney 2002, Hansen et al. 2005). The key question is how private land use intensification both within and in the vicinity of protected areas affects their ability to maintain biodiversity (Brashares et al. 2001, Rivard et al. 2001, Parks and Harcourt 2002, Walsh et al. 2003, DeFries et al. 2005, Mcdonald et al. 2008, Wittemyer et al. 2008). In light of the role of protected areas in maintaining habitat and biodiversity, and the increasing anthropogenic activity within and near these lands, our goal was to determine whether land use intensification on inholdings and on adjacent private lands of protected areas has had a detectable effect on avian biodiversity within protected areas of six ecologically unique regions of the United States.

Our objective was to quantify the effect of housing density within (i.e., private land inholdings), at the boundary, and outside protected areas, and natural land cover within protected areas, on the proportional abundance and proportional richness of three avian guilds within protected areas. The avian response guilds were (1) native and nonnative species associated with human habitation (synanthropes); (2) species associated with the dominant natural land cover type of a region, including forest, grassland, and shrubland breeders (hereafter "land cover affiliates"); and (3) Species of Greatest Conservation Need (SGCN) as identified by individual State Wildlife Action Plans (Association of Fish and Wildlife Agencies 2011). We predicted that: (1) synanthropes would be positively associated with housing density within and outside protected areas and negatively associated with natural land cover within protected areas, because of their positive associations with anthropogenically modified environments (Johnston 2001); and (2) land cover affiliates and SGCN would be positively associated with natural land cover

within protected areas and negatively associated with housing density within and outside protected areas, because of their negative associations with human modified environments (Poole 2005, Pidgeon et al. 2007).

## MATERIALS AND METHODS

### Study area

The spatial extent of our study was the conterminous United States (Fig. 1). Within this area, we selected six regional study areas based on combinations of Bird Conservation Region categorizations (Table 1, Fig. 1). Bird Conservation Regions (BCR) are ecologically unique regions with similar climate, vegetation, land use, and avian communities, and were developed by the North American Bird Conservation Initiative (more information *available online*).[5] We included a total of 14 Bird Conservation Regions that spanned a range of vegetation structure and habitat types from grassland prairies to shrubland deserts to western and eastern forests, and we grouped similar regions (e.g., Sonoran and Mojave Desert, and Chihuahuan Desert) to obtain higher sample sizes of bird surveys (Table 1). We excluded Bird Conservation Regions with few protected areas (e.g., Southeastern Coastal Plain and Central Mixed Grass Prairie) because of a lack of bird survey locations within protected area boundaries (<10). Habitats and avian communities change rapidly based on elevation gradients. Therefore, we assessed differences in elevation within each Bird Conservation Region and excluded those with major differences within and outside protected-area boundaries (e.g., Coastal California and the Northern Pacific Rainforest).

### Breeding Bird Survey data

We analyzed breeding bird counts collected by the North American Breeding Bird Survey (BBS; Sauer et al. 2008). The BBS is an annual roadside survey that has been conducted since 1966 along >4000 routes throughout the United States and Canada. Each BBS route is 39.4 km long, and all birds seen or heard at 50 point counts, surveyed for 3 min, spaced at 0.8-km intervals along the route, are recorded (Sauer et al. 2008). We considered 360 bird species that commonly breed throughout our study regions, and are readily detectable using BBS survey methods (Supplement). We did not include birds that are challenging to quantify with BBS methods such as waterfowl, waterbirds, and raptors (Supplement). We averaged the raw abundance of individuals organized for a five-year window centered on the year 2000. Furthermore, to account for biases in species detectability inherent when performing wildlife surveys, we estimated richness of the avian community on each BBS route using COMDYN (Hines et al. 1999). Similar to the raw abundance, we averaged the
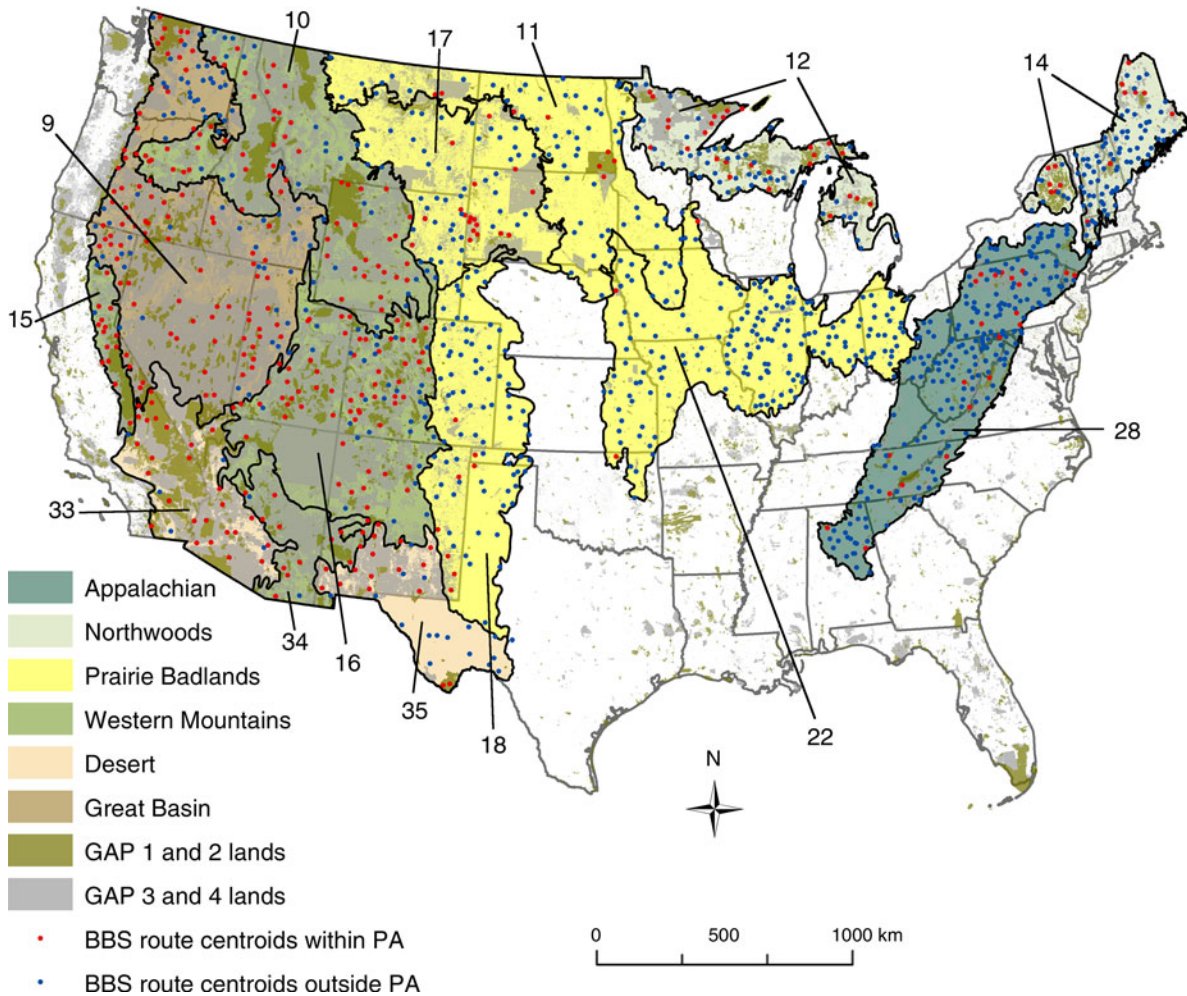
Fig. 1. Distribution of 1225 North American Breeding Bird Survey (BBS) centroids, within and outside protected areas (PA), throughout six regions of the United States. Regions were categorized by either a unique Bird Conservation Region (Appalachian [Bird Conservation Region 28] and Great Basin [9]) or combinations of similar Bird Conservation Regions. The Northwoods category is composed of the United States portions of Boreal Hardwood Transition (12) and the Atlantic Northern Forest (14). The Prairie Badlands is composed of the Prairie Potholes (11), Badlands and Prairies (17), Shortgrass Prairie (18), and Eastern Tallgrass Prairie (22) regions. The Western Mountains is composed of the Northern Rockies (10), Sierra Nevada (15), Southern Rockies/ Colorado Plateau (16), Sierra Madre Occidental (34), and the Desert category is composed of the Sonoran and Mojave Deserts (33) and the Chihuahuan Desert (35). GAP 1 lands are areas of permanent protection from conversion of natural land cover. GAP 2 lands are similar to GAP 1 except for the use of management practices that affect the quality of the natural community. GAP 3 lands have permanent protection from conversion of natural land cover, but are subject to resource extraction, and GAP 4 lands have no known mandate for protection.

TABLE 1. Bird Conservation Region (BCR) composite name, BCR region combinations (see Fig. 1), and sample size for breeding bird survey routes within protected areas (PA), boundary of PA, and outside PA.

| BCR composite name | BCR combination | Sample size | | |
|---|---|---|---|---|
| | | Within PA | Boundary of PA | Outside PA |
| Appalachian | 28 | 24 | 119 | 88 |
| Northwoods | 12, 14 | 41 | 100 | 31 |
| Prairie Badlands | 11, 17, 18, 22 | 37 | 146 | 220 |
| Western Mountains | 10, 15, 16, 34 | 143 | 65 | |
| Desert | 33, 35 | 43 | 8 | 12 |
| Great Basin | 9 | 88 | 60 | |

*Note:* In the Western Mountains and Great Basin Bird Conservation regions, only two treatments were possible, within and on the boundary of protected areas.

COMDYN-estimated richness organized for a five-year window centered on the year 2000. We removed routes that were only surveyed in one year during the five-year window. We choose the year 2000 in order to match the most recent available decadal housing census for which two years of bird data both before and after the census were available. We removed BBS route–year data from first-year observers, and BBS route–year data collected during poor weather. Prior to analyzing data, it was necessary to explore patterns of spatial autocorrelation among BBS routes within regions. We fit semivariograms of the residuals of the total abundance and the COMDYN-estimated richness of bird species per BBS route (Legendre and Fortin 1989). We detected no apparent patterns of spatial autocorrelation in any of our six regions for abundance (Appendix A). There was slight autocorrelation for the COMDYN-estimated richness of BBS routes within the Prairie Badlands regions, but not for the other five regions (Appendix B). Not all routes were surveyed in each year over the five-year window. Thus, we checked for differences in abundance and COMDYN-estimated richness for all routes using a Kruskal-Wallis test, with number of years a route was counted as the treatment. When Kruskal-Wallis tests were significant, we employed a nonparametric multiple-comparisons procedure, based on relative contrast effects, using nparcomp (Konietschke 2011), in the R statistical software package (R Development Core Team 2012). We used a Bonferroni adjustment to the critical alpha value of $0.05/6 = 0.008$ to assess significance. We removed routes that were counted in years where abundance and COMDYN-estimated richness were significantly different. In all regions, except for the Western Mountains, we were able to include all routes that were surveyed at least two years throughout the five-year window. We were only able to retain routes counted in four and five years in the Western Mountains.

For each route, we calculated the proportional abundance and the proportional COMDYN-estimated richness (hereafter proportional richness) of several avian guilds as our response variables. These included synanthropes, land cover affiliates, and SGCN (Supplement). We define synanthropes as native and nonnative species that are associated with human modified environments during the breeding season (Johnston 2001), and we included 30 species that were identified as urban habitat affiliates (Supplement; Johnston 2001). We added an additional six species that are associated with urban and suburban environments, including Northern Flicker (*Colaptes auratus*), Northwestern Crow (*Corvus caurinus*), Brown-headed Cowbird (*Molothrus ater*), Bronzed Cowbird (*Molothrus aeneus*), Great-tailed Grackle (*Quiscalus mexicanus*), and Northern Rough-winged Swallow (*Stelgidopteryx serripennis*; Supplement). We identified land cover affiliates as species that are associated with the dominant natural land cover type of a BBS route, which included forest

and woodland, grassland, or shrublands breeders. Synanthropes were not mutually exclusive from the land cover affiliates guild. For example, we also included Brown-headed Cowbird in the grassland land cover affiliates guild (Supplement). We used the Birds of North America database to identify synanthrope species that were not identified by Johnston (2001) as being associated with urban environments, and land cover affiliate habitat affinities (Poole 2005). To create the SGCN guilds, we joined species from individual State Wildlife Action Plans that were either totally or partially within the boundaries of a Bird Conservation Region for a Bird Conservation Region-specific SGCN guild. Similar to our estimation of species richness of the entire avian community within each study region, we used COMDYN to estimate richness of the avian guilds within each region. To calculate proportional abundance and proportional richness of an avian guild, we divided the abundance, or COMDYN-estimated richness, of an avian guild at a given BBS route by the total number of birds detected at that route, or the total COMDYN-estimated richness, out of a possible 360 species (Supplement). We checked for correlation between pairs of avian response variables within each Bird Conservation Region and found the range of correlation was weak to strong (absolute value Spearman's correlation coefficient, $|\rho| = 0.1$–$0.9$). Thus, we included each guild for further analyses to understand the relationships of distinct components of the regional avian community with the independent housing and land cover variables among treatments within each Bird Conservation Region.

### Housing density and land cover data

We obtained housing density (hereafter referred to as housing) data for the year 2000 from the U.S. decennial census and processed at the partial block group level (Hammer et al. 2004). Partial blocks are the finest resolution spatial unit for which the U.S. Census Bureau releases data on the year a housing unit was built (Hammer et al. 2004). The U.S. Census Bureau does not provide boundaries for partial blocks, and because of this, we generated boundaries by aggregating smaller census blocks, for which data on the year a house was built is not released (Hammer et al. 2004). The average size for partial blocks throughout the conterminous United States is 2.45 km$^2$, and rural partial block groups are, on average, larger than urban partial block groups. We obtained land cover data from the 2001 National Land Cover Data (NLCD; Homer et al. 2004). We centered the BBS data on the year 2000, rather than 2001, because among the independent variables, we prioritized housing over land cover. We also assumed natural land cover did not drastically change within protected areas between years. For each of our Breeding Bird Surveys routes, we summarized housing per square kilometer and the proportion of land cover classes within 400 m of a route using the "zonal statistics" tool

in ArcGIS 9.3 (ESRI 2008). We selected a buffer width of 400 m to conform to BBS survey protocol of recording birds detected within this distance. Housing was positively correlated with the proportion of intensively managed land (i.e., developed and row crop agriculture from the 2001 NLCD data) within each Bird Conservation Region ($\rho = 0.20$–$0.76$). Thus, we elected to remove intensively managed land from further analysis and use housing as the dominant anthropogenic independent variable.

We were interested in the potential differences of natural land cover (e.g., forest) within, at the boundary, and outside protected areas and how this may influence avian communities. We used the dominant natural land cover type of a BBS route as the independent variable for analyses. In the Appalachians, the typical cover was the total of deciduous, mixed, and evergreen forest (i.e., forest land cover composite), which characterized forest land cover (98%). Grassland accounted for the other 2% of land cover. Forest land cover composite was also the dominant natural land cover for all BBS routes in the Northwoods. In the Western Mountains, forest land cover composite was typically the dominant land cover (64%). However, shrubland and grassland was also present and accounted for 36% and 5% of cover on routes, respectively. In the Prairie Badlands, grassland was the dominant land cover type (92%), with the forest land cover composite (4%), and shrubland (4%) accounting for the other land cover types. In the desert region, shrubland was the dominant land cover type (94%) along with grassland (3%) and the forest land cover composite (3%), and these were also the dominant natural land cover types in the Great Basin (70%, 22%, and 9%, respectively). We used the dominant natural land cover type of a BBS route to determine which avian response guilds were included for regional analyses. We included synanthropes and the regional specific SGCN for analysis within each Bird Conservation Region. For land cover affiliates, we analyzed bird species breeding in forest and woodland, grassland, or shrubland depending on the dominant natural land cover of a BBS route.

### Protected-areas data

We obtained protected area boundary information from the USGS National Gap Analysis Program (GAP) Protected Area Database version 1.2 released in April 2011, which delineates actual land holdings, thus capturing private inholdings within the administrative boundaries of public lands (data *available online*).[6] We grouped public lands by four GAP analysis protected area designations. GAP 1 lands accounted for 5% of the area of BBS routes within public lands, and are areas of permanent protection from conversion of natural land cover. These lands are managed to maintain a natural

[6] http://gapanalysis.usgs.gov/padus/

state where disturbance events are allowed or mimicked. GAP 2 lands accounted for 12% of the area of BBS routes within public lands, and are similar to GAP 1 lands, except for the use of management practices (e.g., fire suppression) that affect the quality of the natural community. GAP 3 lands accounted for 72% of the area of BBS routes within public lands, and have permanent protection from conversion of natural land cover, but are subject to resource extraction. GAP 3 lands include most National Forest lands, where many private inholdings are located. GAP 4 lands have no known mandate for protection and accounted for 10% of the area of BBS routes within public lands. Nonetheless, the majority of GAP 4 lands included in our analysis was Native American land in the Prairie Badlands that have individual wildlife management plans. We explored grouping BBS routes along a gradient of protected-area status (i.e., GAP 1, GAP 2, GAP 3, or GAP 4). However, there were not enough BBS routes located within the boundaries of each category, or in similar categories (e.g., GAP 1 and GAP 2), for analysis purposes. Therefore, we grouped all public land types for our analysis.

The independent data sources of our analysis were housing density, both within and outside protected areas, and natural land cover within protected areas. Housing development and conversion of natural land cover are restricted on all public lands, except conversion of natural land cover on GAP 4 lands. Thus, we refer to all public lands as protected throughout the manuscript. However, we note that other types of land use, such as forest harvest, are permitted on some of the public lands that we studied. We considered all lands not included within protected area boundaries as private.

Bird survey locations occurred either within the boundaries ("within," >50% of Breeding Bird Survey route), at the boundary ("boundary," 0.1–49.5%), or on private lands ("outside," 0%) of protected areas, and these three categories were used as treatments for analyses. We used these cutoff points rather than a continuous measure of protected-area status (i.e., proportion of BBS route within protected areas) because we were interested in broad-scale differences of housing, land cover, and the avian community among the three treatments. The Western Mountains and Great Basin were comprised of only within and boundary treatments. In these regions, there is a high amount of public land area, and low number of BBS routes, compared with the central and eastern regions of our study (Fig. 1). Thus, it was difficult to find private land BBS routes within these regions. The Appalachian, Northwoods, Prairie Badlands, and Desert were comprised of within, boundary, and outside treatments. In all, we included 1225 Breeding Bird Survey routes for analysis with 376 occurring within, 498 at the boundary, and 351 outside of protected areas (Table 1, Fig. 1).

## Statistical analysis

In a first exploratory analysis, we investigated the degree of avian community dissimilarity among treatments within each of the six Bird Conservation Regions. We conducted a one-way analysis of similarities test (ANOSIM; Carr 1997), using the Bray-Curtis dissimilarity of the square-root-transformed average abundance of the 360 bird species in consideration of our study (i.e., not the avian response guilds), grouped by BBS route. The ANOSIM statistic is defined as:

$$R = (r_{\mathrm{b}} - r_{\mathrm{w}}) / \left( \frac{n(n-1)}{2} \right)$$

where $r_{\mathrm{b}}$ and $r_{\mathrm{w}}$ are the mean ranked dissimilarity between and within treatments, respectively, and $n$ is the total number of samples (Clarke 1993). We used 999 Monte Carlo permutations to generate the random test statistic, $R$, which typically ranges from 0 to 1. Larger $R$ values indicate larger dissimilarity of the avian community among treatments within a Bird Conservation Region. We evaluated pairwise comparisons among treatments using a Bonferroni-adjusted alpha value ($0.05/3 = 0.017$). We performed the ANOSIM analysis in the Primer v6 software package (Clarke and Gorley 2006).

To explore differences in housing, natural land cover, and the proportional abundance and richness of the avian guilds among treatments, within a Bird Conservation Region, we used a Kruskal-Wallis test, with protected-area status as the treatment. When Kruskal-Wallis tests were significant, we employed a nonparametric multiple comparisons procedure, based on relative contrast effects, using nparcomp (Konietschke 2011). We used a Bonferroni adjustment to the critical alpha value of $0.05/3 = 0.017$ to assess significance. We used a Wilcoxon rank sum test for the Western Mountains and Great Basin because housing, land cover, and avian abundance and richness metrics were categorized by only two treatments. We used a significance threshold of $P \leq 0.05$.

To address our main goal, we quantified the effect of housing density within, at the boundary, and outside protected areas, and natural land cover within protected areas, on the proportional abundance and richness of synanthropes, land cover affiliates, and SGCN within protected areas. We used the BBS-route housing per square kilometer extracted from the 400-m route buffer for all "within" BBS routes as the within (i.e., inholdings and immediately adjacent private lands) independent variable. To gather data on private land housing outside of protected-area boundaries, we paired each BBS-route centroid located within protected areas, with the nearest BBS-route centroid either at the boundary or outside protected-area boundaries using the "near" tool in ArcGIS 9.3. We divided housing of the outside BBS-route centroid by the distance between paired BBS-route centroids to account for proximity effects of housing

density outside protected areas. This procedure was designed to avoid overestimating the effects of high housing areas that were far from protected areas. We grouped Bird Conservation Regions within similar areas, which were defined as regionally sharing a majority of natural land cover type to increase the sample size necessary for the following analyses. We combined the Appalachian and Northwoods (eastern forests group) and the Desert and Great Basin (desert shrubland group). For the new regions, we recalculated SGCN guild proportional abundance and proportional richness based on the inclusion of additional SGCN species from the combined state wildlife action plans (Supplement). We explored if land cover outside protected area boundaries affected avian communities within, in a similar analysis, and did not find support for this. Thus, we did not include land cover data from outside protected areas for this analysis.

We used simple- and multiple-linear regression to quantify the strength of association of housing and land cover within and housing outside protected area boundaries with the avian guilds within protected-area boundaries. We parameterized each model in a stepwise approach, first fitting the univariate combination of either the housing and natural land cover within or housing outside protected areas. Second, we fit more complex models composed of combinations of the independent variables. We calculated the second-order Akaike information criterion ($AIC_c$) for each model, and subsequently calculated the $\Delta AIC_c$ and $AIC_c$ weights ($w_i$) for each model within a set, which we used to rank models. We assessed model assumptions, and if necessary, we applied transformations. In all cases, we log-transformed housing within and outside protected areas. No other transformations were necessary. In order to explore possible interactions of the independent variables, we fit models including the three predictors, plus all two-factor interactions between predictors. We used an $F$ statistic, derived from an ANOVA test, to assess significance. We determined the significance value of the $F$ statistic by calculating the 97.5% quantile of the $F$ distribution, in a two-way design because we had no a priori expectation of relationships among the three independent variables. The $F$ statistic threshold ranged from 1.98 to 2.04 among regions, and we used these values to indicate significant interactions.

Additionally, in a follow-up analysis for visualization purposes, we quantified the effects of housing outside protected areas on the proportional abundance and proportional richness of avian guilds estimated from routes occurring within protected areas. We calculated the difference in housing between BBS-route centroid pairs selected by the near analysis (i.e., BBS-route housing outside – BBS-route housing within), and we divided this difference by the distance between BBS-route centroid pairs to account for proximity effects of high- or low-intensity housing. We created a "housing intensity" variable based on the wildland–urban inter-

face definition of 6.17 houses/km$^2$, or 1 house/40 acres (Radeloff et al. 2005b), to distinguish between high ($>$6.17 houses/km$^2$) and low-intensity ($<$6.17 houses/ km$^2$) housing outside protected areas. In a few cases, housing intensity within protected areas was above the wildland–urban interface threshold and greater than housing intensity outside protected areas. We categorized these cases as high housing intensity. We used the housing intensity variable as the treatment in a Wilcoxon rank sum test with the avian guilds as response variables. We used a Wilcoxon rank sum test because we expected that the proportional abundance of synanthropes would be higher in protected areas adjacent to high-intensity private land housing, whereas, land cover affiliates and SGCN would be higher in protected areas adjacent to low-intensity private land housing. We used a significance threshold of $P \leq 0.05$.

## RESULTS

We found that avian communities varied considerably among treatments in all Bird Conservation Regions ($R = 0.12$–$0.31$, $P < 0.01$), except for the Desert ($R = 0.17$, $P = 0.06$) and Western Mountains ($R = 0.01$, $P = 0.31$), where they were similar (Table 2). The avian communities within protected-area boundaries were largely different from private lands ($R = 0.19 - 0.59$, $P < 0.01$), and to a lesser extent, from those along the protected area boundaries ($R = 0.12 - 0.34$, $P < 0.01$), with the exception being the Desert ($R = 0.13$, $P = 0.11$), where the difference was not as pronounced (Table 2).

Generally, housing was lowest within protected areas and highest along the boundary of protected areas (Fig. 2). Where comparable, housing outside protected areas was highest in one of four regions (Prairie Badlands; Fig. 2). The opposite pattern occurred for dominant natural land cover, which was greatest within protected areas, medium along the boundary, and lowest on private lands (Fig. 2). The only exceptions to this pattern was the Northwoods, where dominant natural land cover was similar within protected areas and at their boundaries, and the Desert, where dominant natural land cover was similar within protected areas and on private lands (Fig. 2).

The proportional abundance and proportional richness of synanthropes was significantly higher outside or at protected area boundaries than within (Fig. 3). The only exception to this pattern was the Desert, where both the proportional abundance and proportional richness of synanthropes were similar among treatments (Fig. 3). Although the differences were visually apparent, sample sizes were small for the Desert region, thus affecting the significance level outputs of the Kruskal-Wallis analysis. Similar to the differences in natural land cover among treatments, the proportional abundance and proportional richness of land cover affiliates and SGCN were significantly higher in protected areas than either the boundaries or outside of protected areas (Fig. 3). This pattern was true, except in four of six regions,

TABLE 2. Analysis of similarities (ANOSIM) matrices of avian communities among three protected area status treatments: within, on the boundary, and outside protected areas (PA), within six BCRs of the United States.

| Region and treatment | Within PA | Boundary of PA | Outside PA |
|---|---|---|---|
| **Appalachian** | | | |
| Within PA | | <0.01 | <0.01 |
| Boundary of PA | 0.27 | | 0.14 |
| Outside PA | 0.42 | 0.05 | |
| **Northwoods** | | | |
| Within PA | | <0.01 | <0.01 |
| Boundary of PA | 0.34 | | 0.17 |
| Outside PA | 0.24 | 0.05 | |
| **Prairie Badlands** | | | |
| Within PA | | <0.01 | <0.01 |
| Boundary of PA | 0.20 | | <0.01 |
| Outside PA | 0.59 | 0.25 | |
| **Western Mountains** | | | |
| Within PA | | 0.31 | ⋯ |
| Boundary of PA | 0.01 | | ⋯ |
| Outside PA | ⋯ | ⋯ | |
| **Desert** | | | |
| Within PA | | 0.11 | <0.01 |
| Boundary of PA | 0.13 | | <0.01 |
| Outside PA | 0.19 | 0.43 | |
| **Great Basin** | | | |
| Within PA | | <0.01 | ⋯ |
| Boundary of PA | 0.12 | | ⋯ |
| Outside PA | ⋯ | ⋯ | |

*Notes:* Numbers below the diagonals are ANOSIM $R$ values. Numbers above the diagonals are $P$ values. ANOSIM $R$ values generally range from zero to one. A value of zero indicates identical avian communities, whereas a value of one indicates completely separate avian communities among treatments. Pairwise comparisons among habitats were evaluated with a Bonferroni-adjusted $P$ value: $0.05/3 = 0.02$. In the Western Mountains and Great Basin Bird Conservation regions, only two treatments were possible, within and on the boundary of protected areas (excluded comparisons shown with ellipses).

where the proportional richness of SGCN was similar within protected areas and at the boundary (Fig. 3).

We found that the proportional abundance of synanthropes was positively related to housing within protected areas in all regions ($R^2 = 0.04$ to $0.71$, $P \leq 0.03$), with the strongest effects in the Appalachian and Northwoods (Table 3). On the other hand, the proportional abundance of land cover affiliates were negatively related to housing within protected areas in the Appalachian and Northwoods ($R^2 = 0.51$, $P < 0.01$; Table 3), and the proportional abundance of SGCN was negatively related to housing within protected areas in all regions ($R^2 = 0.08$ to $0.65$, $P < 0.01$), particularly in the Appalachian and Northwoods (Table 3). Similar to the relationship for housing within protected areas, housing on outside private lands was positively related with synanthropes in all regions except the Western Mountains, but the effect was often less than that of housing within protected areas (Table 3). Housing outside protected areas was negatively associated with the proportional abundance of land cover affiliates in
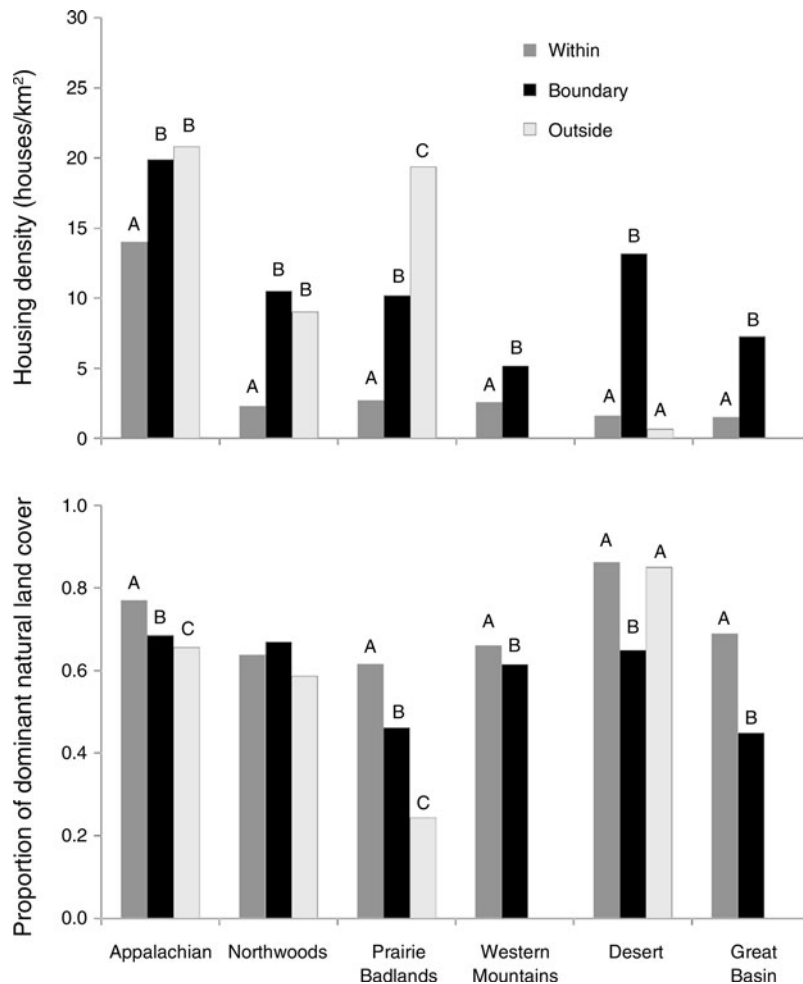
Fig. 2. Mean summary of housing density and proportion of the dominant natural land cover (e.g., grassland in the Prairie Badlands) of a Breeding Bird Survey route. The three treatment types represented protected area status: within protected areas (PA), on the boundary of PA, and outside PA. Bars with same letter above them do not differ significantly among habitats (Wilcoxon rank sum test, or Kruskal-Wallis test with nonparametric multiple comparisons procedure based on relative contrasts effects, type Tukey, with Bonferroni-adjusted $P$ value: $0.05/3 = 0.02$).

the Appalachian and Northwoods ($R^2 = 0.27$, $P < 0.01$), and unexpectedly, positively related in the Western Mountains ($R^2 = 0.04$, $P = 0.02$), and the Desert and Great Basin ($R^2 = 0.03$, $P = 0.04$; Table 3). Yet, in all regions, housing outside protected areas was negatively associated with the proportional abundance of SGCN within protected areas ($R^2 = 0.07$ to $0.24$, $P < 0.01$), with the strongest effects again in the Appalachian and Northwoods (Table 3). The dominant natural land cover within protected areas was not significantly associated with avian guilds, except for with land cover affiliates in the Prairie Badlands ($R^2 = 0.37$, $P < 0.01$) and the Western Mountains ($R^2 = 0.06$, $P < 0.01$; Table 3), and SGCN in the Desert and Great Basin ($R^2 = 0.13$, $P < 0.01$; Table 3).

We found similar relationships for the proportional richness of avian guilds with housing and land cover as with proportional abundance, though the effects were

weaker (Table 4). The proportional richness of synanthropes was positively related to housing within protected areas in all regions except the Prairie Badlands ($R^2 = 0.06$ to $0.39$, $P < 0.01$), with the strongest relationships again occurring in the Appalachian and Northwoods (Table 4). The proportional richness of land cover affiliates and SGCN within protected areas was negatively related with housing within protected areas, but only in the Appalachian and Northwoods and the Western Mountains (SGCN; Table 4). In the Appalachian and Northwoods, housing outside protected areas was positively related with the proportional richness of synanthropes ($R^2 = 0.25$, $P < 0.01$), yet negatively related with SGCN and land cover affiliates in the Appalachian and Northwoods ($R^2 = 0.12$ and $0.16$, respectively; $P < 0.01$; Table 4). Unexpectedly, the proportional richness of land cover affiliates within protected areas was positively related with housing
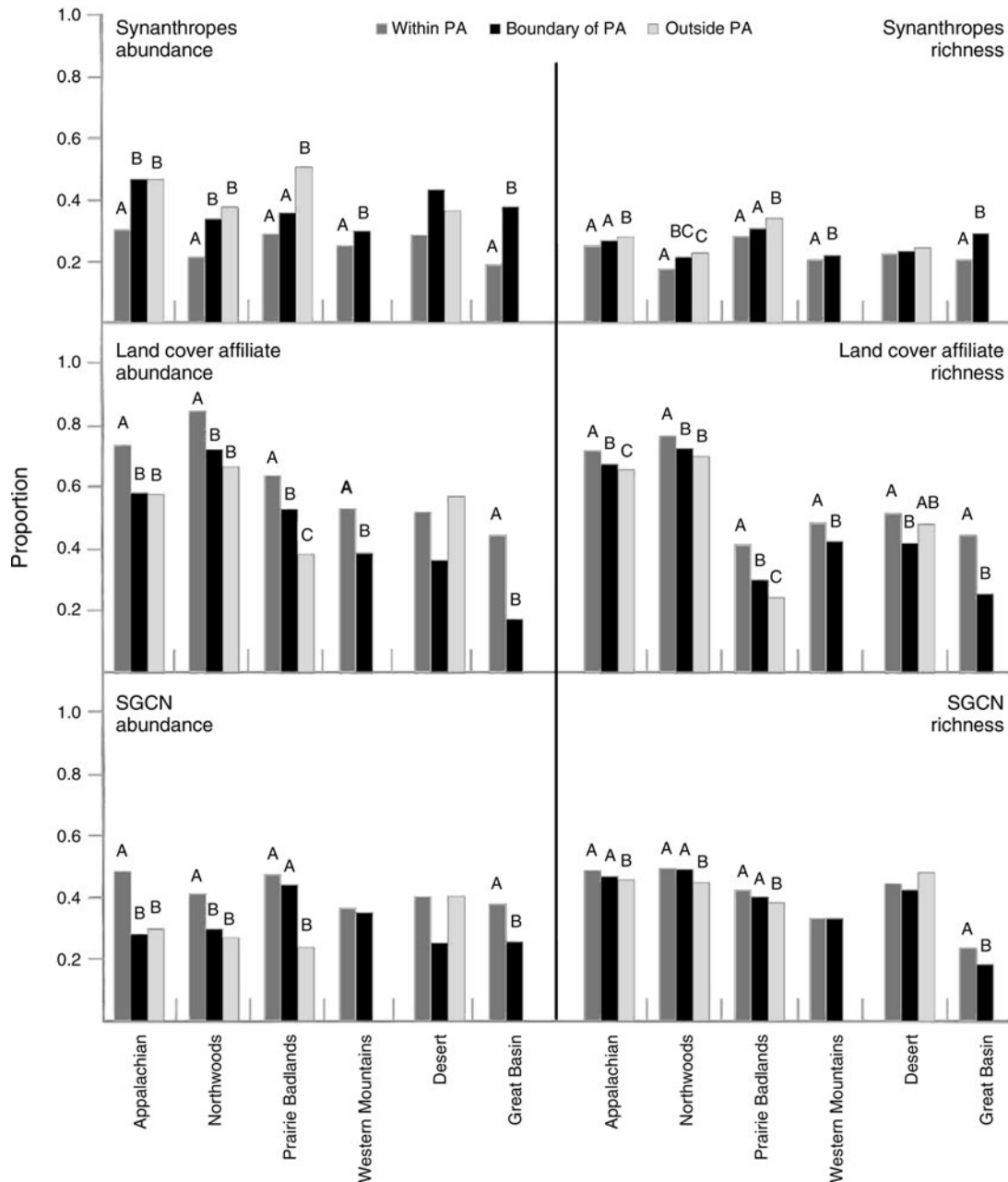
Fɪɢ. 3. Mean summary of the proportional abundance of synanthropes; land cover affiliates, i.e., forest associated breeders (Appalachian, Northwoods, and Western Mountains), grassland associated breeders (Prairie Badlands), and shrubland-associated breeders (Desert and Great Basin); and Species of Greatest Conservation Need (SGCN). The three treatment types are (1) within protected areas (PA), (2) on the boundary of PA, and (3) outside PA. Bars with same letter above them indicate the proportional abundance of an avian guild does not differ significantly among treatments (Wilcoxon rank sum test, or Kruskal-Wallis test with nonparametric multiple comparisons procedure based on relative contrasts effects, type Tukey, with Bonferroni-adjusted $P$ value: $0.05/3 = 0.02$).

outside protected areas in three regions, with the strongest effects in the Prairie Badlands ($R^2 = 0.20$, $P < 0.01$; Table 4). The relationship between the dominant natural land cover within protected areas and proportional richness of avian guilds within protected areas was less clear (Table 4). We found positive relationships

between the dominant natural land cover and synanthropes in the Appalachian and Northwoods ($R^2 = 0.10$, $P = 0.03$), with land cover affiliates in the Western Mountains ($R^2 = 0.04$, $P = 0.03$) and Prairie Badlands ($R^2 = 0.20$, $P = 0.01$), and with SGCN in the Desert and Great Basin ($R^2 = 0.16$, $P < 0.01$; Table 4).

TABLE 3. Adjusted $R^2$, $AIC_c$, $\Delta AIC_c$, and $AIC_c$ model weight ($w_i$) results of univariate and multiple regression model selection analysis investigating the relationships of the proportional abundance of synanthropes, land cover affiliates, and Species of Greatest Conservation Need (SGCN) with housing density within protected areas (PA), outside of PA, and the dominant land cover of a North American Breeding Bird Survey (BBS) route within PA, among four regions.

| Region and model | Synanthropes | | | | Land cover affiliates | | | | SGCN | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | $R^2$ | $AIC_c$ | $\Delta AIC_c$ | $w_i$ | $R^2$ | $AIC_c$ | $\Delta AIC_c$ | $w_i$ | $R^2$ | $AIC_c$ | $\Delta AIC_c$ | $w_i$ |
| **Appalachian and Northwoods** | | | | | | | | | | | | |
| 1) Housing within PA† | **0.71**⁺ | −139.18 | 0 | 0.55 | **0.51**⁻ | −113.70 | 0 | 0.54 | **0.65**⁻ | −119.63 | 0 | 0.57 |
| 2) Housing outside PA† | **0.28**⁺ | −99.34 | 39.84 | 0 | **0.27**⁻ | −95.97 | 17.74 | 0 | **0.24**⁻ | −85.24 | 34.40 | 0 |
| 3) Land cover within PA | 0.02 | −85.87 | 53.31 | 0 | 0.03 | −83.47 | 30.23 | 0 | 0 | −73.56 | 46.07 | 0 |
| 1 and 2 | **0.70** | −137.24 | 1.93 | 0.21 | **0.50** | −111.50 | 2.20 | 0.18 | **0.63** | −115.82 | 3.82 | 0.08 |
| 1 and 3 | **0.69** | −135.79 | 3.39 | 0.10 | **0.48** | −110.34 | 3.36 | 0.10 | **0.64** | −117.69 | 1.95 | 0.21 |
| 2 and 3 | **0.25** | −96.77 | 42.40 | 0 | **0.21** | −91.95 | 21.76 | 0 | **0.20** | −82.16 | 37.48 | 0 |
| 1, 2, and 3 $^{(1\times2)}$ | **0.69** | −135.09 | 4.09 | 0.07 | **0.49** | −109.55 | 4.16 | 0.07 | **0.62** | −113.67 | 5.96 | 0.03 |
| 1, 2, and 3 $^{(1\times3)}$ | **0.68** | −133.92 | 5.26 | 0.04 | **0.48** | −109.27 | 4.43 | 0.06 | **0.64** | −115.76 | 3.88 | 0.08 |
| 1, 2, and 3 $^{(2\times3)}$ | **0.68** | −133.70 | 5.47 | 0.04 | **0.48** | −109.33 | 4.37 | 0.06 | **0.62** | −113.47 | 6.16 | 0.03 |
| **Prairie Badlands** | | | | | | | | | | | | |
| 1) Housing within PA† | **0.43**⁺ | −61.95 | 5.46 | 0.05 | 0.01 | −17.82 | 14.09 | 0 | **0.46**⁻ | −27.17 | 3.18 | 0.09 |
| 2) Housing outside PA† | **0.17**⁺ | −50.71 | 16.69 | 0 | 0 | −17.73 | 14.18 | 0 | **0.25**⁻ | −17.23 | 13.11 | 0 |
| 3) Land cover within PA | 0.07 | −46.97 | 20.43 | 0 | **0.37**⁺ | −31.91 | 0 | 0.32 | 0.03 | −9.16 | 21.19 | 0 |
| 1 and 2 | **0.53**ˣ | −67.41 | 0 | 0.69 | 0 | −15.85 | 16.06 | 0 | **0.51** | −29.25 | 1.10 | 0.25 |
| 1 and 3 | **0.38** | −58.79 | 8.61 | 0.01 | **0.37** | −31.02 | 0.89 | 0.20 | **0.44** | −25.37 | 4.97 | 0.04 |
| 2 and 3 | 0.15 | −48.93 | 18.48 | 0 | **0.38** | −31.56 | 0.35 | 0.27 | **0.34**ˣ | −20.19 | 10.15 | 0 |
| 1, 2, and 3 $^{(1\times2)}$ | **0.51**ˣ | −65.23 | 2.17 | 0.23 | **0.30** | −26.95 | 4.96 | 0.03 | **0.49** | −27.04 | 3.30 | 0.08 |
| 1, 2, and 3 $^{(1\times3)}$ | **0.40** | −58.91 | 8.50 | 0.01 | **0.35** | −29.25 | 2.66 | 0.08 | **0.50** | −27.56 | 2.79 | 0.11 |
| 1, 2, and 3 $^{(2\times3)}$ | **0.40** | −58.92 | 8.48 | 0.01 | **0.36** | −29.59 | 2.31 | 0.10 | **0.54** | −30.34 | 0 | 0.43 |
| **Western Mountains** | | | | | | | | | | | | |
| 1) Housing within PA† | **0.04**⁺ | −264.63 | 0.04 | 0.22 | 0 | −14.94 | 14.34 | 0 | **0.08**⁻ | −87.87 | 19.38 | 0 |
| 2) Housing outside PA† | 0.01 | −261.60 | 3.07 | 0.10 | **0.04**⁺ | −21.23 | 8.06 | 0.01 | **0.15**⁻ | −98.30 | 8.95 | 0.01 |
| 3) Land cover within PA | 0.03 | −263.06 | 1.61 | 0.10 | **0.05**⁺ | −23.25 | 6.03 | 0.02 | 0.03 | −80.01 | 27.24 | 0 |
| 1 and 2 | 0.03 | −262.13 | 2.54 | 0.06 | 0.03 | −17.29 | 11.99 | 0 | **0.15** | −97.92 | 9.32 | 0.01 |
| 1 and 3 | **0.04** | −264.67 | 0 | 0.22 | **0.08**ˣ | −25.46 | 3.83 | 0.07 | **0.15** | −96.86 | 10.38 | 0 |
| 2 and 3 | 0.02 | −261.11 | 3.56 | 0.04 | **0.10** | −28.52 | 0.76 | 0.30 | **0.18** | −102.01 | 5.24 | 0.06 |
| 1, 2, and 3 $^{(1\times2)}$ | **0.05** | −263.74 | 0.93 | 0.14 | **0.08** | −24.25 | 5.04 | 0.04 | **0.18** | −100.65 | 6.60 | 0.03 |
| 1, 2, and 3 $^{(1\times3)}$ | **0.04** | −262.76 | 1.91 | 0.09 | **0.12**ˣ | −29.28 | 0 | 0.44 | **0.22** | −107.25 | 0 | 0.77 |
| 1, 2, and 3 $^{(2\times3)}$ | **0.04** | −262.78 | 1.90 | 0.09 | **0.10** | −26.71 | 2.57 | 0.12 | **0.20** | −103.71 | 3.54 | 0.13 |
| **Desert and Great Basin** | | | | | | | | | | | | |
| 1) Housing within PA† | **0.34**⁺ | −179.87 | 0 | 0.43 | 0 | 13.90 | 5.96 | 0.02 | **0.18**⁻ | −14.78 | 20.48 | 0 |
| 2) Housing outside PA† | **0.03**⁺ | −132.93 | 46.93 | 0 | **0.03**⁺ | 9.90 | 1.96 | 0.18 | **0.07**⁻ | −0.20 | 35.06 | 0 |
| 3) Land cover within PA | 0.01 | −131.51 | 48.35 | 0 | 0 | 14.21 | 6.27 | 0.02 | **0.13**⁺ | −7.68 | 27.58 | 0 |
| 1 and 2 | **0.32** | −175.75 | 4.12 | 0.05 | **0.06**ˣ | 7.94 | 0 | 0.48 | **0.20**ˣ | −18.00 | 17.26 | 0 |
| 1 and 3 | **0.34** | −179.17 | 0.69 | 0.30 | 0 | 15.60 | 7.67 | 0.01 | **0.27** | −28.60 | 6.66 | 0.03 |
| 2 and 3 | 0.03 | −131.12 | 48.74 | 0 | 0.01 | 13.63 | 5.69 | 0.03 | **0.18** | −14.54 | 20.72 | 0 |
| 1, 2, and 3 $^{(1\times2)}$ | **0.33** | −175.82 | 4.05 | 0.06 | **0.05**ˣ | 10.13 | 2.19 | 0.16 | **0.32**ˣ | −35.26 | 0 | 0.85 |
| 1, 2, and 3 $^{(1\times3)}$ | **0.34** | −176.99 | 2.88 | 0.10 | 0.04 | 11.83 | 3.90 | 0.07 | **0.28** | −29.28 | 5.97 | 0.04 |
| 1, 2, and 3 $^{(2\times3)}$ | **0.33** | −175.89 | 3.98 | 0.06 | 0.02 | 14.28 | 6.34 | 0.02 | **0.29** | −30.30 | 4.96 | 0.07 |

*Notes:* $R^2$ values in boldface type are significant. Univariate independent variables are labeled with a number (1–3), which correspond to the numbered variables included in the multiple regression analyses. Signs following significant univariate model $R^2$ values are coefficient directions. We fit one, two-way interaction for all multiple-variable models. Superscript numbers in parentheses following full multiple-variable models indicate the two-way interaction for a given model. An x superscript following adjusted $R^2$ values of multiple variable models indicates a significant two-way interaction. We used an $F$ statistic threshold, derived from an ANOVA test, of 1.98 to 2.04 to indicate significant interactions. We used AIC, $\Delta AIC_c$, and $AIC_c$ model weights to rank models, whereas we provide the $R^2$ values as a measure of fit of each model.

† Housing density natural log-transformed for all models.

Out of 144 multiple-variable models, we detected 13 significant interactions, which had considerable model support (i.e., $\Delta AIC_c < 2$; Tables 3 and 4). Of note, we uncovered significant interactions between housing within and outside protected areas explaining the proportional abundance of synanthropes occurring on routes within protected areas in the Prairie Badlands, and of land cover affiliates and SGCN in the Desert and Great Basin (Table 3). We found significant interactions for similar models explaining proportional richness of synanthropes and SGCN in the Prairie Badlands, and land cover affiliates in the Appalachian and Northwoods (Table 4). These interactions highlighted the combined effect of housing within and housing outside protected areas explaining the structure of these protected area avian guilds.

We detected broad patterns of the importance of each variable explaining avian guild abundance and richness among regions. In most cases, housing within protected areas was present in the best supported models (i.e.,

TABLE 4. Adjusted $R^2$, $AIC_c$, $\Delta AIC_c$, and $AIC_c$ model weight ($w_i$) results of univariate and multiple regression model selection analysis investigating the relationships of the proportional richness of synanthropes, land cover affiliates, and SGCN with housing density within protected areas (PA), outside of PA, and the dominant land cover of a BBS route within PA, among four regions.

| | Synanthropes | | | | Land cover affiliates | | | | SGCN | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Region and model | $R^2$ | $AIC_c$ | $\Delta AIC_c$ | $w_i$ | $R^2$ | $AIC_c$ | $\Delta AIC_c$ | $w_i$ | $R^2$ | $AIC_c$ | $\Delta AIC_c$ | $w_i$ |
| **Appalachian and Northwoods** | | | | | | | | | | | | |
| 1) Housing within PA† | **0.39**⁺ | −150.75 | 1.90 | 0.14 | **0.33**⁻ | −118.45 | 1.57 | 0.20 | **0.28**⁻ | −133.01 | 0 | 0.43 |
| 2) Housing outside PA† | **0.25**⁺ | −141.69 | 10.97 | 0 | **0.16**⁻ | −108.55 | 11.47 | 0 | **0.12**⁻ | −124.30 | 8.71 | 0.01 |
| 3) Land cover within PA | **0.10**⁺ | −133.76 | 18.90 | 0 | 0 | −100.73 | 19.28 | 0 | 0.04 | −120.03 | 12.97 | 0 |
| 1 and 2 | **0.38** | −148.92 | 3.74 | 0.06 | **0.37**ˣ | −120.02 | 0 | 0.43 | **0.23** | −129.10 | 3.91 | 0.06 |
| 1 and 3 | **0.43** | −152.66 | 0 | 0.37 | **0.31** | −116.03 | 3.99 | 0.06 | **0.28** | −132.22 | 0.79 | 0.29 |
| 2 and 3 | **0.23** | −139.43 | 13.22 | 0 | **0.18** | −108.25 | 11.77 | 0 | 0.07 | −120.90 | 12.11 | 0 |
| 1, 2, and 3 (1×2) | **0.41** | −150.39 | 2.27 | 0.12 | **0.37**ˣ | −118.85 | 1.17 | 0.24 | **0.23** | −127.85 | 5.16 | 0.03 |
| 1, 2, and 3 (1×3) | **0.43** | −151.34 | 1.32 | 0.19 | **0.31** | −115.18 | 4.84 | 0.04 | **0.27** | −130.00 | 3.01 | 0.10 |
| 1, 2, and 3 (2×3) | **0.41** | −150.41 | 2.24 | 0.12 | **0.31** | −115.05 | 4.96 | 0.04 | **0.26** | −129.50 | 3.51 | 0.08 |
| **Prairie Badlands** | | | | | | | | | | | | |
| 1) Housing within PA† | 0.02 | −78.03 | 2.55 | 0.06 | 0.01 | −12.55 | 23.86 | 0 | 0.10 | −76.47 | 0 | 0.45 |
| 2) Housing outside PA† | 0.10 | −80.58 | 0 | 0.21 | **0.20**⁺ | −19.20 | 17.21 | 0 | 0.05 | −74.79 | 1.68 | 0.19 |
| 3) Land cover within PA | 0.04 | −78.61 | 1.97 | 0.08 | **0.20**⁺ | −18.91 | 17.50 | 0 | 0.01 | −73.34 | 3.13 | 0.09 |
| 1 and 2 | 0.11 | −80.02 | 0.56 | 0.16 | 0.14 | −15.95 | 20.46 | 0 | 0.03 | −73.25 | 3.22 | 0.09 |
| 1 and 3 | 0.01 | −76.80 | 3.78 | 0.03 | **0.27**ˣ | −21.02 | 15.39 | 0 | 0 | −72.39 | 4.09 | 0.06 |
| 2 and 3 | 0.09 | −79.21 | 1.37 | 0.10 | **0.56**ˣ | −36.41 | 0 | 0.72 | 0 | −71.24 | 5.23 | 0.03 |
| 1, 2, and 3 (1×2) | 0.11 | −78.95 | 1.63 | 0.09 | **0.38** | −25.11 | 11.29 | 0 | 0 | −71.06 | 5.41 | 0.03 |
| 1, 2, and 3 (1×3) | 0.12 | −79.30 | 1.28 | 0.11 | **0.44** | −28.15 | 8.26 | 0.01 | 0 | −70.68 | 5.79 | 0.02 |
| 1, 2, and 3 (2×3) | 0.15 | −80.13 | 0.45 | 0.17 | **0.54**ˣ | −34.42 | 1.99 | 0.27 | 0 | −70.79 | 5.68 | 0.03 |
| **Western Mountains** | | | | | | | | | | | | |
| 1) Housing within PA† | **0.06**⁺ | −429.29 | 3.18 | 0.11 | 0 | −61.12 | 15.96 | 0 | **0.07**⁻ | −319.89 | 7.92 | 0 |
| 2) Housing outside PA† | 0 | −421.77 | 10.70 | 0 | **0.07**⁺ | −70.21 | 6.87 | 0.02 | **0.12**⁻ | −327.80 | 0 | 0.21 |
| 3) Land cover within PA | 0 | −421.60 | 10.87 | 0 | **0.04**⁺ | −65.66 | 11.42 | 0 | 0.02 | −313.01 | 14.79 | 0.00 |
| 1 and 2 | **0.05** | −426.32 | 6.15 | 0.02 | 0.05 | −66.39 | 10.69 | 0 | **0.12** | −326.56 | 1.24 | 0.11 |
| 1 and 3 | **0.09**ˣ | −432.47 | 0 | 0.53 | **0.08**ˣ | −70.74 | 6.34 | 0.02 | **0.07** | −319.71 | 8.09 | 0 |
| 2 and 3 | **0.02** | −423.43 | 9.04 | 0.01 | **0.11**ˣ | −75.73 | 1.34 | 0.28 | **0.12** | −326.83 | 0.97 | 0.13 |
| 1, 2, and 3 (1×2) | **0.04** | −424.80 | 7.67 | 0.01 | **0.08** | −69.79 | 7.29 | 0.01 | **0.13** | −327.34 | 0.47 | 0.17 |
| 1, 2, and 3 (1×3) | **0.08**ˣ | −430.27 | 2.20 | 0.18 | **0.13** | −77.08 | 0 | 0.55 | **0.13** | −327.59 | 0.21 | 0.19 |
| 1, 2, and 3 (2×3) | **0.08**ˣ | −429.65 | 2.82 | 0.13 | **0.11** | −73.99 | 3.09 | 0.12 | **0.13** | −327.57 | 0.24 | 0.19 |
| **Desert and Great Basin** | | | | | | | | | | | | |
| 1) Housing within PA† | **0.13**⁺ | −325.90 | 8.07 | 0.01 | 0 | −44.85 | 9.97 | 0 | 0.03 | −178.06 | 20.92 | 0 |
| 2) Housing outside PA† | 0.01 | −309.78 | 24.19 | 0 | **0.07**⁺ | −53.19 | 1.64 | 0.16 | 0.01 | −175.79 | 23.19 | 0 |
| 3) Land cover within PA | 0.03 | −311.92 | 22.05 | 0 | 0.01 | −45.48 | 9.35 | 0 | **0.17**⁺ | −196.18 | 2.80 | 0.10 |
| 1 and 2 | **0.18** | −330.83 | 3.13 | 0.07 | **0.09**ˣ | −54.82 | 0 | 0.37 | 0.01 | −174.36 | 24.62 | 0 |
| 1 and 3 | **0.15** | −327.38 | 6.58 | 0.01 | 0.02 | −46.70 | 8.12 | 0.01 | **0.17** | −195.79 | 3.19 | 0.08 |
| 2 and 3 | **0.02** | −309.21 | 24.76 | 0 | 0.05 | −50.45 | 4.37 | 0.04 | **0.19**ˣ | −198.98 | 0 | 0.41 |
| 1, 2, and 3 (1×2) | **0.20** | −333.96 | 0 | 0.34 | **0.08**ˣ | −53.38 | 1.44 | 0.18 | **0.16** | −193.62 | 5.36 | 0.03 |
| 1, 2, and 3 (1×3) | **0.20** | −333.25 | 0.71 | 0.24 | **0.09**ˣ | −53.77 | 1.05 | 0.22 | **0.17** | −193.73 | 5.25 | 0.03 |
| 1, 2, and 3 (2×3) | **0.20** | −333.86 | 0.10 | 0.33 | 0.05 | −48.57 | 6.25 | 0.02 | **0.20**ˣ | −198.63 | 0.35 | 0.35 |

*Notes:* $R^2$ values in boldface type are significant. Univariate independent variables are labeled with a number (1–3), which correspond to the numbered variables included in the multiple regression analyses. Plus or minus signs following significant univariate model $R^2$ values are coefficient directions. We fit one, two-way interaction for all multiple-variable models. Superscript numbers in parentheses following full multiple-variable models indicate the two-way interaction for a given model. A superscript x following adjusted $R^2$ values of multiple variable models indicates a significant two-way interaction. We used an $F$ statistic threshold, derived from an ANOVA test, of 1.98 to 2.04 to indicate significant interactions. We used AIC, $\Delta AIC_c$, and $AIC_c$ model weights to rank models, whereas we provide the $R^2$ values as a measure of fit of each model.

† Housing density natural log-transformed for all models.

highest relative $AIC_c$ importance value) explaining the proportional abundance and richness of synanthrope species (Tables 3 and 4, Fig. 4). Housing outside protected areas was not as influential as housing within protected areas, explaining protected area avian guild abundance and richness (Fig. 4). Yet, this variable was present in the best supported models for the proportional abundance of SGCN in the Western Mountains and land cover affiliates in the Desert and Great Basin (Fig. 4). Furthermore, housing outside protected areas

was included in the best supported models for the proportional richness of synanthropes and land cover affiliates in the Prairie Badlands, SGCN in the Western Mountains, and land cover affiliates in the Desert and Great Basin (Fig. 4). Land cover within protected areas was less important than housing within, and similar to housing outside protected areas, explaining protected area avian guild abundance and richness (Fig. 4). However, these results do not downplay the significance of natural land cover to avian communities within
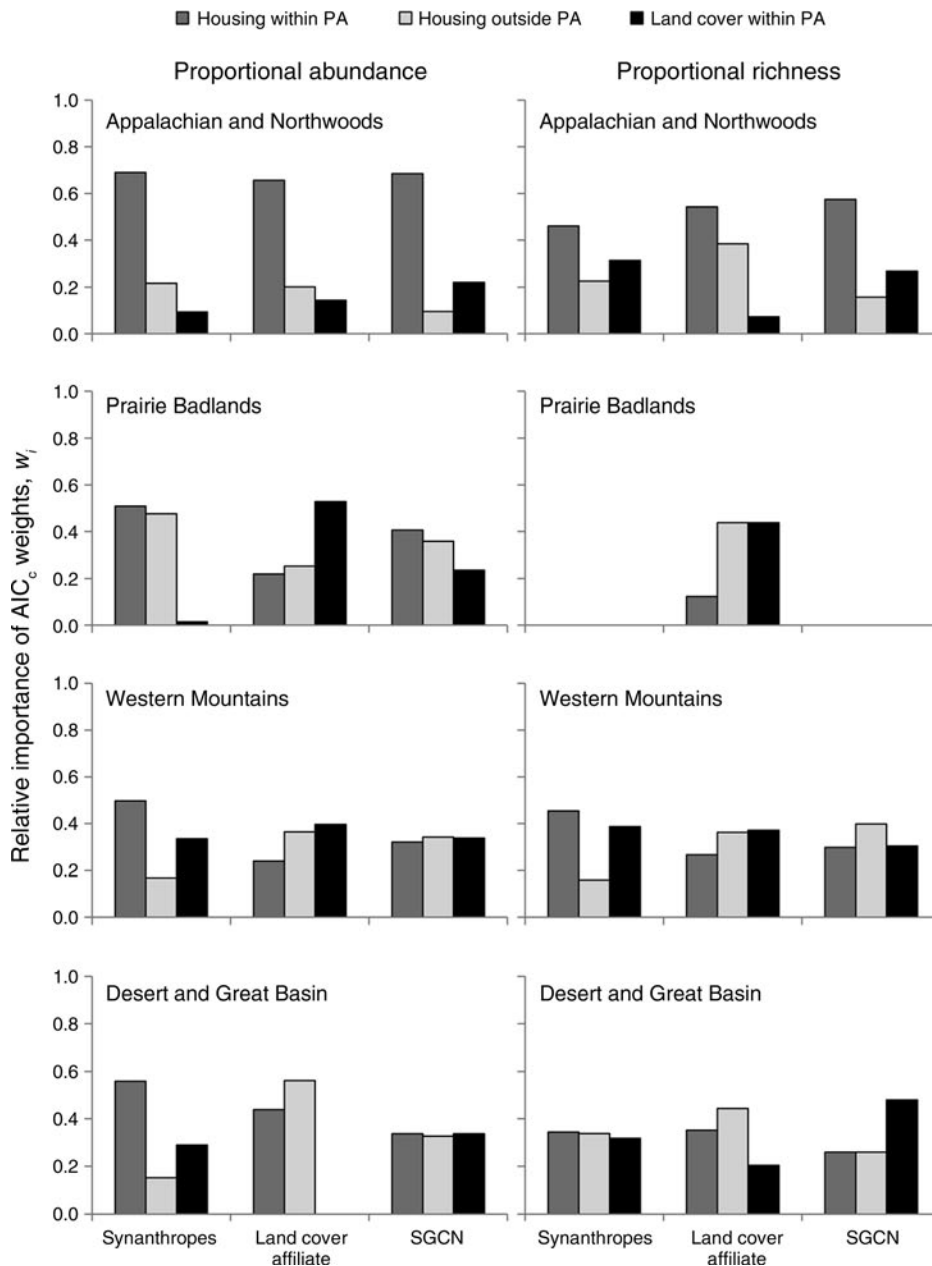
FIG. 4. Relative importance of AIC$_c$ model weights ($w_i$) for three independent variables (housing density within, and outside protected areas [PA], and the dominant land cover of a BBS route within PA), explaining the proportional abundance and richness of three avian guilds (synanthropes, land cover affiliates, and Species of Greatest Conservation Need [SGCN]) among four regions. We calculated relative importance values of a region as the sum of $w_i$ for a given significant independent variable of a model set (nine possible models for a given avian guild within a region), divided by the total sum of the $w_i$ for a given significant independent variable among the three avian guilds. Relative importance $w_i$ values range from 1, indicating high variable importance, to 0.

protected areas. An example is the lower natural land cover and the lower proportional abundance and proportional richness of SGCN species outside protected areas (Fig. 3). The lack of support for high variable importance of natural land cover in our regression analysis most likely reflects the high proportion and low variability of this covariate within protected areas among regions, which likely influenced the fit of models

(Fig. 2). Nonetheless, this variable was included in the best supported models for the proportional abundance of land cover affiliates in the Prairie Badlands and the Western Mountains, and the proportional richness of SGCN in the Desert and Great Basin (Fig. 4).

Although housing within protected areas was generally the best supported variable influencing protected area avian guilds, in all regions, high-intensity housing
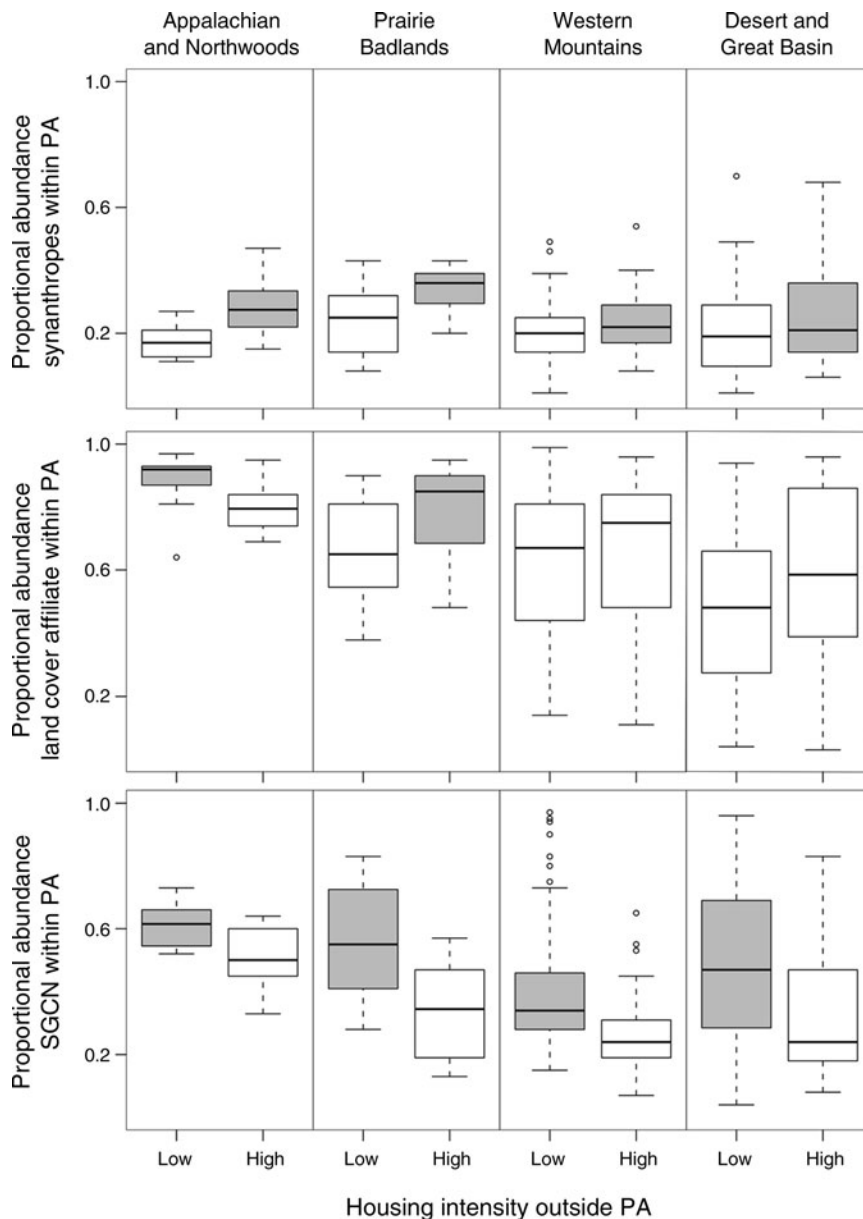
FIG. 5. Boxplot summaries of the proportional abundance of synanthropes, land cover affiliates, and Species of Greatest Conservation Need (SGCN) within protected areas of four regions. Housing intensity outside of protected areas was categorized as low (<6.17 houses/km$^2$ or 1 house/40 acres) or high (>6.17 houses/km$^2$ or 1 house/40 acres), based on the definition of wildland–urban interface (WUI). Boxes shaded in gray indicate the proportional abundance of a protected-area bird guild was significantly different between housing intensity levels, within a region, based on a Wilcoxon rank sum test at $P$ value $\leq 0.05$. The bold lateral bars represent the median proportional abundance values, the boxes represent the first and third quantiles, and the whiskers depict the range of the data.

outside protected areas was associated with higher proportional abundance of synanthropes within protected areas (Fig. 5). These relationships were significant in all regions: the Appalachian and Northwoods, $W_{44} = 65$, $P < 0.01$; Prairie Badlands, $W_{31} = 47$, $P < 0.01$; the Desert and Great Basin, $W_{124} = 1025$, $P = 0.02$; and the Western Mountains, $W_{44} = 1413$, $P = 0.01$ (Fig. 5). In contrast, high-intensity housing outside protected areas resulted in lower proportional abundance of SGCN

within protected areas (Fig. 5). These relationships were significant in each region: Appalachian and Northwoods, $W_{44} = 365$, $P < 0.01$; Prairie Badlands, $W_{31} = 149$, $P < 0.01$; the Western Mountains, $W_{140} = 1619$, $P < 0.01$; and the Desert and Great Basin, $W_{124} = 1832$, $P < 0.01$. We uncovered a similar relationships for land cover affiliates in the Appalachian and Northwoods, $W_{44} = 373$, $P < 0.01$ (Fig. 5). However, unexpectedly, in the Prairie Badlands land cover affiliates within protect-

ed areas were proportionally more abundant when housing intensity was high on outside private lands ($W_{49} = 49$, $P < 0.01$; Fig. 5).

We detected similar patterns for the association between the proportional richness of avian guilds within protected areas and high-intensity housing outside. However, the differences were weaker than proportional abundance. Proportional richness of synanthropes within protected areas was associated with high-intensity housing outside protected areas in the Appalachian and Northwoods ($W_{44} = 73$, $P < 0.01$) and the Western Mountains ($W_{31} = 1470$, $P < 0.01$). In the Desert and Great Basin, high-intensity housing resulted in lower proportional richness of SGCN ($W_{44} = 1653$, $P < 0.01$), and we found a similar relationship for land cover affiliates in the Appalachian and Northwoods ($W_{44} = 365$, $P < 0.01$), Prairie Badlands ($W_{31} = 46$, $P = 0.01$), and the Desert and Great Basin ($W_{124} = 1001$, $P = 0.02$).

## DISCUSSION

Our results suggest that housing development both within and adjacent to protected areas has a negative impact on avian community structure within protected area. Throughout the United States, we found housing was inversely related with natural land cover. Furthermore, we found housing on inholdings or outside protected area boundaries was often positively associated with the proportional abundance and proportional richness of synanthropic species and negatively associated with the proportional abundance and proportional richness of land cover affiliates and SGCN within protected areas. These findings are in line with what would be expected according to the species–area relationship (MacArthur and Wilson 1967), where housing reduces the area of natural land cover, resulting in lower abundance and richness of avian communities.

According to our results, protected areas of the United States generally provide a safe haven for native avian communities, presumably because of more abundant natural land cover combined with lower anthropogenic stresses within protected area boundaries. Our findings are similar to studies in other areas that also found natural land cover and biodiversity to be greater in protected areas than surrounding lands. For example, in tropical countries, land cover clearing and subsistence hunting and agriculture were reduced in protected areas compared with adjacent lands (Bruner et al. 2001). Similarly, within North American protected areas, there were no noticeable differences of land cover loss before and after protected area establishment (Nagendra 2008). In South Africa, native arthropods and reptiles were more diverse and abundant in protected areas compared to surrounding rangeland (Fabricius et al. 2003). On the other hand, the distribution of many global species of conservation concern falls outside the boundaries of protected areas (Rodrigues et al. 2004). Nevertheless, our results suggest that the protected areas of the United States are successful at limiting housing development,

maintaining natural land cover, and harboring avian communities of conservation attention compared with surrounding private lands. Thus, protected areas of the United States may serve as sources for regional avian metapopulations (Robinson et al. 1995).

Of particular note, our results also support findings that housing development near protected areas has created strains on protected areas themselves (Hansen et al. 2005, Gude et al. 2006). Among all regions, we found private lands adjacent to protected areas had significantly higher housing, corroborating evidence of increases in housing on private inholdings and at protected area boundaries over the past half-century (Radeloff et al. 2010). Development pressure has been particularly strong in the western portions of North America, in part, because the high proportion of protected land provides amenities attractive for human habitation (Hansen et al. 2005). Although land trusts and nongovernmental agencies work to conserve private lands (Merenlender et al. 2004), increases in housing within or adjacent to protected areas destroy habitat and threaten biodiversity (e.g., reduction of wildlife corridors and/or fragmentation; Hansen and DeFries 2007, DeFries et al. 2010, Piekielek and Hansen 2012).

Indeed, this housing development on private lands affects landscape composition and biodiversity. For example, in the western United States, private lands surrounding protected areas are fragmented due to exurban development (Piekielek and Hansen 2012). Exurban development creates fragmented conditions, which, in turn, affect biodiversity (Fahrig 2003, Radeloff et al. 2005a). Forest breeding birds throughout the majority of the United States are generally negatively associated with housing (Kluza et al. 2000, Pidgeon et al. 2007). Additionally, exurban housing developments are associated with the reduction of native bird distributions in California (Jongsomjit et al. 2012) and are positively associated with synanthropic species in North Carolina (Suarez-Rubio et al. 2010). In some instances, low-density housing development creates conditions resulting in high avian species richness (e.g., intermediate disturbance hypothesis), but at higher densities, the relationship is negative (i.e., ecosystem stress hypothesis; Lepczyk et al. 2008).

Housing developments also create novel habitats, which benefit some bird species (Bock et al. 2008, Robb et al. 2008, Lerman and Warren 2011). For example, in Phoenix, Arizona, native desert bird abundance was higher in wealthy urban neighborhoods with native plant landscaping, adjacent to large desert tracts (Lerman and Warren 2011). Similarly, in rural southeastern Arizona, exurban development of ranchland positively affects native bird species richness by providing "ecological oases" (sensu Bock et al. 2008) in an otherwise harsh environment. Furthermore, resource supplementation is generally associated with housing developments, particularly given the popularity of bird feeding among homeowners (Robb et al. 2008). However, the

bird group likely to benefit most from housing developments and supplemental feeding are synanthropes, while bird species of conservation concern are often negatively impacted (Evans et al. 2009). Our findings of the positive association between richness of land cover affiliates within protected areas and housing outside protected areas in the central prairies and western mountains of the United States lend support, at a landscape scale, to the findings in the desert southwest. However the relationship between birds and housing in the desert southwest appears to follow a quadratic curve as it becomes negative with increasing housing density (Bock et al. 2008). Thus, at higher housing densities, with their accompanying habitat loss and fragmentation, it appears a threshold is reached, beyond which avian community structure and abundance suffers (Fahrig 2001, Zuckerberg and Porter 2010, Suarez-Rubio et al. 2013).

Additional threats to biodiversity often accompany housing developments and fragmentation in rural areas. Free-ranging cats are responsible for bird (Lepczyk et al. 2004) and other wildlife depredations (Crooks and Soulé 1999), and fragmented landscapes support higher densities of avian nest predators and brood parasites (Robinson et al. 1995, Donovan and Flather 2002). Furthermore, in addition to threats to wildlife, rural housing is associated with invasive plants. In New England forests, invasive exotic plants are more strongly related to housing density than other anthropogenic stresses such as roads (Gavier-Pizarro et al. 2010a). In southwestern Wisconsin, housing developments in high conservation value forests facilitates the spread of nonnative plants via landscaping and conditions amiable to plant invasion (e.g., trails; Gavier-Pizarro et al. 2010b). In addition to fragmentation and habitat loss, such threats most likely occur following housing development on inholdings of public forest lands or adjacent to protected-area boundaries. The combination of these processes likely contributes to the degradation of protected area native avian communities.

A novel finding from our study was that, in addition to the pressure of private land development on biodiversity outside protected area boundaries, we found that this same development pressure threatens biodiversity within. Our results support findings of other studies investigating similar patterns. For example, in Ghana, Africa, human population size surrounding protected area reserves was significantly related to the extinction rate of carnivores and ungulates within reserves (Brashares et al. 2001). While in western equatorial Africa, during the latter part of the 20th century, common chimpanzee (*Pan troglodytes*) and western gorilla (*Gorilla gorilla*) within protected areas experienced dramatic population declines attributed to hunting and disease pressures associated with road networks and dense human populations in cities outside protected area boundaries (Walsh et al. 2003). Although exurban development throughout the United States differs in intensity and patterns from high-density human settlement in tropical countries, our results show that this development pressures adjacent to protected areas threatens biodiversity within.

Anthropogenic pressures on private lands in North America adjacent to protected areas also influence ecological processes and biodiversity within. In Canadian national parks, terrestrial mammal species, especially those with large home ranges, are negatively associated with human-dominated landscapes outside protected areas (Rivard et al. 2001). Similarly, in national parks of the western United States, extirpation rates of large mammals are often negatively associated with high human density outside park boundaries (Parks and Harcourt 2002). Thus, if development pressure is high around small reserves, mammal species that require large areas will likely be extirpated as a result of direct conversion of suitable habitat. Our results extend these findings to also highlight the negative impacts on avian communities. Across broad geographic regions of the United States, we found high housing density outside protected areas substantially altered the avian community within. Although housing growth has recently slowed compared with the 1970s (Radeloff et al. 2010), our findings suggest even marginal increases of housing growth on the boundary of protected areas could degrade protected area avian communities. Invasive species (exotics in our case) are associated with an increase in species diversity in some systems (e.g., McKinney 2006, 2008), and the synanthropes guild of our study, which includes exotics, is strongly positively associated with housing, both within and outside of protected areas. However, we show that throughout protected areas of the United States, the abundance and richness of native Species of Greatest Conservation Need and land cover affiliates are negatively related with housing on inholdings or adjacent lands. Thus, without effective measures to curtail the rates and locations of exurban development, the conservation benefit of protected areas will likely diminish.

In order to maintain protected areas as refugia for biodiversity, prioritizing conservation actions on private lands is necessary. In locations where private land housing is dense (e.g., Appalachians), land use planning is most important. In locations where private land housing is low, land use planning is a lower priority. Alternative strategies for preserving land near protected areas (e.g., conservation easements [Merenlender et al. 2004, Rissman et al. 2007] and cluster housing [Theobald et al. 1997, Gagné and Fahrig 2010]) should be pursued with the intent to maximize unfragmented natural land cover while minimizing development. We recommend focusing on conserving natural vegetation cover on private inholdings, since even modest housing gains on these lands are likely to greatly degrade protected area biodiversity. Furthermore, it is critical to maintain ecologically sensitive private lands adjacent to protected areas that serve as necessary habitats for

ecosystem processes such as migration (Berger 2004) and reproduction (Donovan et al. 1995, Hansen and Rotella 2002).

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## SUPPLEMENTAL MATERIAL

### Appendix A

Semivariograms of the residuals of the total abundance of bird species per Breeding Bird Survey route within six regions (*Ecological Archives* A024-085-A1).

### Appendix B

Semivariograms of the residuals of the total COMDYN-estimated avian species richness per Breeding Bird Survey route within six regions (*Ecological Archives* A024-085-A2).

### Supplement

Breeding Bird Survey (BBS) code, and common and scientific names of 360 bird species from which we created 12 bird species groups (*Ecological Archives* A024-085-S1).