

Long-term avian community response to housing development at the boundary of US protected areas: effect size increases with time

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Summary

1. Biodiversity conservation is a primary function of protected areas. However, protected areas also attract people, and therefore, land use has intensified at the boundaries of these lands globally. In the USA, since the 1970s, housing growth at the boundaries (< 1 km) of protected areas has increased at a rate far higher than on more distant private lands. Here, we designed our analyses to address our central hypothesis that increasing housing density in and near protected areas will increasingly alter their avian communities.

2. We quantified the relationship between abundance and richness of protected-area avian species of greatest conservation need, land-cover affiliates (e.g. species associated with natural land cover such as forest breeders) and synanthropes (e.g. species associated with humans) with housing density on the boundary of protected areas and on more distant private lands from 1970 to 2010 in three ecoregions of the USA. We accomplished this using linear mixed-model analyses, data from the US Census Bureau and 90 routes of the North American Breeding Bird Survey.

3. Housing density at the boundary of protected areas tended to be strongly negatively related with the abundance and richness of species of greatest conservation need and land-cover affiliates (upwards of 88% of variance explained) and strongly positively related with synanthropes (upwards of 83% of variance explained). The effect size of these relationships increased in most cases from 1970 to 2010 and was greatest in the densely developed eastern forests. In the more sparsely populated West, we found similar, though weaker, associations.

4. Housing density on private lands more distant from protected areas had similar, but more muted negative effects.

5. *Synthesis and applications.* Our results illustrate that as housing density has increased along the boundary of protected areas, the conservation benefit of these lands has likely diminished. We urge conservation planners to prioritize the purchase of private-land inholdings in order to maximize the extent of unfragmented natural lands within protected areas. Further, we strongly recommend that land-use planners implement boundary management strategies to alter the pattern of human access to protected areas, cluster development to concentrate the footprint of rural housing, and establish conservation agreements through local land trusts to buffer protected areas from the effects of development along protected-area boundaries. To maximize the conservation benefit of protected areas, we suggest that housing development should be restricted within 1 km of their boundaries.

Key-words: avian abundance, avian richness, Breeding Bird Survey, inholding, private land, public land, species of greatest conservation need, synanthrope

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Introduction

Land-use and land-cover change, human population growth, excessive resource use, and climate change are leading drivers of global biodiversity loss (Cincotta, Wisniewski & Engelman 2000; Jetz, Wilcove & Dobson 2007). To stem this loss, laws and regulations have been established to protect biodiversity and critical habitats. One of the most widespread – and arguably the most important – conservation action has been the establishment of protected areas (Gaston *et al.* 2008). Since the founding of Yellowstone National Park in the USA in 1872, protected areas have become the dominant strategy for biodiversity preservation with >12% of the global land surface having some type of protected status (Chape *et al.* 2005). However, protected areas also attract humans, and thus, land-use pressures, such as extraction (Defries *et al.* 2005) and settlement (Wade & Theobald 2009; Radeloff *et al.* 2010), have increased at the boundaries of protected areas throughout the world, often with deleterious effects on protected-area conservation (e.g. Woodroffe & Ginsberg 1998; Brashares, Arcese & Sam 2001).

Globally, land-use pressures at the boundaries of protected areas have greatly intensified since the mid-point of the 20th century (Radeloff *et al.* 2010; Laurance *et al.* 2012). For example, over the past 40 years in the USA, rural housing development in the amenity-rich areas associated with inholdings and protected-area borders has greatly expanded owing to the phenomenon of ‘exurbanization’ (Wade & Theobald 2009; Radeloff *et al.* 2010). A particular concern with housing growth in and near protected areas in the USA is the intensity and frequency of this land-use pressure since the 1970s. For example, development within 1 km of protected areas has outpaced that on more distant private lands by upwards of 13% of the national average and there are predictions for an additional 17 million housing units to be built from the present to 2030 within 50 km of protected areas (Radeloff *et al.* 2010). Housing development can affect biodiversity by causing both habitat loss and fragmentation (Radeloff, Hammer & Stewart 2005; Piekielek & Hansen 2012), which in turn affects ecosystem processes such as animal migrations (Berger 2004), species dispersal (Fagan, Cantrell, & Cosner 1999) and breeding success (Hansen & Rotella 2002). Therefore, increases in housing development at the boundaries of protected areas threaten to erode their conservation benefit (Hansen & DeFries 2007; Brown *et al.* 2014; Wood *et al.* 2014).

In a previous analysis, we determined that protected-area avian communities do indeed covary with housing development: species of greatest conservation need showing negative relationships and synanthropes (i.e. native and non-native species associated with humans) showing positive relationships (Wood *et al.* 2014). However, this work focused on a single year (2000) and provided only a static look at the link between housing density and protected-area avian communities. Despite establishing a

spatial association between housing development and patterns of protected-area avian guild abundance and richness, how this relationship changed over time remained unclear. We investigated how increasing housing density along the boundaries of protected areas and on more distant private lands has affected avian communities in these protected areas. Quantifying this relationship over time is crucial for landscape planning and management purposes because the conservation implications, and their associated costs, will be very different if avian communities have some capacity for adaptation.

Our goal here was to quantify the strength of the relationship of housing density from 1970 to 2010 with protected-area avian guild abundance and richness throughout the conterminous USA. Our central hypothesis was that as housing density in and near protected areas has risen in recent decades, it has increasingly altered the avian communities in these protected areas. Based on the previous efforts (Wood *et al.* 2014), we predicted that if housing density increased from 1970 to 2010, we would detect increasingly negatively relationships for species of greatest conservation need and land-cover affiliates and increasingly positively relationships for synanthropic species. We had two objectives to address this. Specifically, we quantified the following: (i) housing density within, and on immediately adjacent private lands of protected areas (hereafter referred to as housing density at the boundary), and (ii) on private lands more distant from protected-area boundaries (hereafter referred to as housing density outside of protected areas) from 1970 to 2010 vs. the proportional abundance and proportional richness of different avian guilds, including (i) species of greatest conservation need, (ii) land-cover affiliates (i.e. bird species associated with a dominant land-cover type such as forest breeders) and (iii) synanthropes.

Materials and methods

STUDY AREA

Our study area included 12 Bird Conservation Regions (BCRs) spanning the conterminous USA, which we grouped into three broad ecoregions based on similar land-cover composition and avian communities (Fig. 1). BCRs were delineated by the North American Bird Conservation Initiative and have similar climate, vegetation, land use and avian communities (<http://www.nabci-us.org/bcrs.htm>). We analysed three ecoregions (Fig. 1): (i) the Appalachian and Northwoods, which included the Boreal Hardwood Transition (BCR 12), the Atlantic Northern Forest (BCR 14) and the Appalachian Mountains (BCR 28); (ii) the Deserts, which included the Great Basin (BCR 9), Sonoran and Mojave deserts (BCR 33) and the Chihuahuan Desert (BCR 35); and (iii) the Western Mountains and Valleys, which included the Northern Rockies (BCR 10), the Southern Rockies/Colorado Plateau (BCR 16), the Sierra Madre Occidental (BCR 34), the Northern Pacific Rainforest (BCR 5), the Sierra Nevada (BCR 15) and Coastal California (BCR 32).

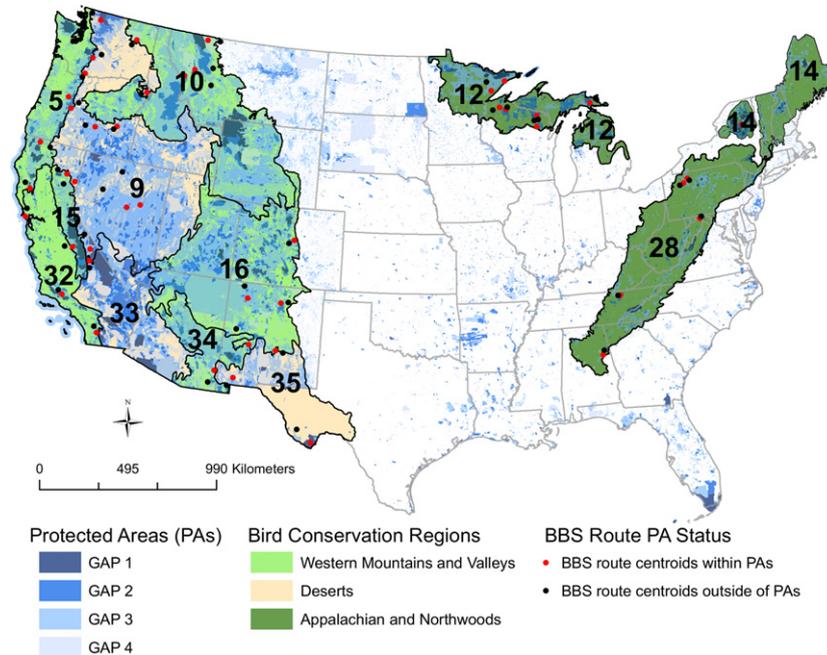


Fig. 1. Distribution of 45 North American Breeding Bird Survey (BBS) route centroids located on the boundary of protected areas (red dots) and their associated outside protected-area 'nearest neighbour' BBS route centroid (black dots). We categorized three ecoregions by a combination of similar Bird Conservation Regions (BCRs). The Appalachian and Northwoods were composed of the Boreal Hardwood Transition (BCR 12), Northern Atlantic Forest (BCR 14) and the Appalachian Mountains (BCR 28). The Deserts were composed of the Great Basin (BCR 9), Sonoran and Mojave deserts (BCR 33) and the Chihuahuan Desert (BCR 35); and the Western Mountains and Valleys were composed of the Northern Rockies (BCR 10), the Southern Rockies/Colorado Plateau (BCR 16), the Sierra Madre Occidental (BCR 34), the Northern Pacific Rainforest (BCR 5), the Sierra Nevada (BCR 15) and Coastal California (BCR 32). BBS routes within protected areas were distributed among four protected-area treatments: Gap Analysis Program (GAP) 1–4. The darker (GAP 1) to lighter (GAP 4) colour gradient represents a higher to lower level of protection.

BREEDING BIRD SURVEY DATA

We gathered breeding bird count data from the North American Breeding Bird Survey [BBS (Sauer, Hines & Fallon 2011)]. We removed BBS route-year data collected by first-year observers and route-year data collected during poor weather. For each BBS route, we used the raw count data (abundance), and estimated species richness using COMDYN (Hines *et al.* 1999) to account for detectability issues common in avian surveys. We averaged both abundance and COMDYN -estimated richness (hereafter richness) within a 5-year window bracketing each of the following five decadal time steps: 1970, 1980, 1990, 2000 and 2010. The 5-year window included the 2 years before and after each time step. We chose the decadal time steps in order to match the US decadal housing density data. At the time of analysis, BBS data were not available for 2012. Thus, for the 2010 time step, we averaged bird abundance and richness data in a 5-year window from 2007 to 2011.

When >50% of a BBS route was within the boundaries of protected areas (see protected areas data), we included it in our sample of protected-area boundary routes. We used this sampling design to quantify housing density on private-land inholdings and on lands immediately adjacent to protected areas. We only included BBS routes that were surveyed in all five decadal time steps so that we could use a repeated-measures sampling design (see Statistical analysis). We identified 45 BBS routes at the boundary of protected areas within the three ecoregions that met these criteria (Fig. 1), of which 13 were in the Appalachian and Northwoods region (average area of BBS route within protected

area, 68%), 14 in the Deserts region (average 80% within protected area) and 18 in the Western Mountains and Valleys (average 70% within protected area).

Further, we were interested in the effect of housing outside protected areas (i.e. protected-area borders or more distant private lands) on protected-area avian communities. To measure this, we matched each protected-area BBS route with the nearest private-land BBS route (i.e. <40% within the boundaries of any protected areas) and calculated the linear distance between pairs using the 'near tool' in ArcGIS 10.1 (ESRI California, USA 2012). We used a <40% threshold in order to capture housing density surrounding BBS routes that were located primarily on private lands neighbouring protected areas, because we hypothesized that the broader modification of the landscape may impact protected-area avian communities. Of the 45 private-land routes in our analysis, 41 intersected the border of a protected area (see Protected areas data), with an average of 23% of BBS route-area located within protected areas. The other four private-land BBS routes (14 186, 69 035, 72 017 and 83 184) were completely outside of protected areas. In order to scale the proximity effect of private-land housing to protected areas, we divided the housing density of the 'nearest neighbour' private-land BBS route by the distance between route centroids. We performed this analysis to guard against overestimating the effects of distant high-density housing areas. In the Appalachian and Northwoods, the average distance between pairs was 30 km. In the Deserts, the average distance was 74 km, whereas in the Western Mountains and Valleys, the average distance was 61 km.

To understand how avian communities may be affected by housing development, and to scale the response variables among regions that vary greatly in avian species diversity, we calculated the proportional abundance and proportional richness of three avian guilds per ecoregion. These included (i) species of greatest conservation need (expected negative association with housing density, see Appendices S1 and S2, Supporting Information), (ii) land-cover affiliates (expected negative association with housing density, Appendices S1 and S2) and (iii) synanthropes (expected positive association with housing density, Appendices S1 and S2). We considered 282 breeding bird species in all, excluding species that do not breed in our study regions, or are difficult to count with BBS methods (waterfowl, shorebirds, waterbirds and raptors, Appendix S2). To calculate proportional abundance and proportional richness of an avian guild, we divided guild abundance or richness of each BBS route by the total abundance or species richness of that route. We checked for correlation between pairs of avian response variables and found that the range of collinearity (absolute value of Spearman's rho) was $|\rho| = 0.1\text{--}0.9$ and was strongest in the Appalachian and Northwoods. Nonetheless, we retained each guild for further analyses to understand the relationships of unique components of regional avian communities with the independent housing density variables.

PROTECTED AREAS DATA

We used the USGS National Gap Analysis Program (GAP) Protected Area Database, version 1.2, released in April 2011, for protected-area boundary information, which demarcated private inholdings within the administrative boundaries of public lands (<http://gapanalysis.usgs.gov/padus/>). We grouped public lands by four protected-area designations. GAP 1 lands have management plans in place to ensure natural processes are allowed or mimicked to maintain a natural state. These lands accounted for 4% of the area (i.e. the combined 400-m linear buffer surrounding BBS routes) of public-land BBS routes included in our study. GAP 2 lands have similar management plans as GAP 1 lands, except that infrequently used management practices, such as fire suppression, may affect the natural community. These lands accounted for 19% of the area of public-land BBS routes considered in our study. GAP 3 lands provide protection for federally endangered and threatened species, but are subject to resource extraction (e.g. mining) or recreation (e.g. off-road vehicle use). These lands accounted for 64% of the area of public-land BBS routes considered in our study. Most public-land private inholdings occur within US Forest Service lands, and the majority of these are categorized as GAP 3. GAP 4 lands are publicly owned and protected from housing development, but have no known mandate for biodiversity protection. These accounted for 13% of the area of public-land BBS routes considered in our study. The majority (87%) of public-land BBS routes under consideration in this study were located primarily (>50% of each BBS route) in GAP 1–3 lands. Three BBS routes in the Northern Rockies (53003, 53015, and 89007) were primarily (>50% of each route) situated on Native American lands, which fall under GAP 4 status. However, we included these routes because they were adjacent to other public lands of our study, dominated by natural land cover (>50% forest or grassland cover, Homer *et al.* 2004), and had the necessary bird data across the time series for our analysis. Housing density, which was our independent variable of interest, is restricted on all of the four public-land categories.

Further, conversion of natural land cover is restricted on all public lands of this analysis, except GAP 4 lands. Thus, we refer to all public lands as protected areas throughout the manuscript. We considered all lands not included within protected-area boundaries as private.

HOUSING DENSITY DATA

We obtained housing density (hereafter referred to as housing) data, which include permanent residences, seasonal housing and vacation units, from the 2000 US Decennial Census. These data were processed at the partial block group level, which is the finest resolution unit for which the US Census Bureau releases data on the year a housing unit was built (Hammer *et al.* 2004). The average size for partial blocks throughout the conterminous USA is 2.45 km², with rural partial block groups being larger, on average, than urban ones. We used housing backcasts calculated from the 2000 census data by Hammer *et al.* (2004) for 1970, 1980 and 1990 housing values. For 2010 housing values, we used a housing projection calculated by Radeloff *et al.* (2010). We used the backcasting method because US Decennial Census data for our earlier time periods are only available at the county level (Hammer *et al.* 2004; Radeloff, Hammer & Stewart 2005). We summarized mean housing at the boundary of 400 m of BBS routes using the tool 'zonal stats' in ArcGIS 10.1. Housing at the boundary and outside protected areas was only moderately correlated from 1970 to 2010 in the Appalachian and Northwoods ($\rho = 0.53\text{--}0.63$), the Deserts ($\rho = 0.33\text{--}0.47$) and the Western Mountains and Valleys ($\rho = 0.53\text{--}0.57$). Because the correlations were not strong in any region, we included both variables in analyses to understand effects of local and regional housing development on protected-area avian community structure.

STATISTICAL ANALYSIS

To quantify the relationship between housing either at the boundary or outside protected areas and the avian community within protected areas, we fitted linear mixed-effects models. We fitted separate models for each guild and region, using either proportional abundance or proportional richness as the response. In each model, we included the fixed effects of either housing at the boundary or housing outside protected areas, time step as a repeated categorical variable, the interaction between housing and time step, and a random effect of BBS route. Our models thus fitted a different slope and intercept to the relationship between the avian community and chosen housing measure for each time step, while additionally allowing for a random shift in intercept due to BBS route. We designed our analysis in this way to address our central hypothesis that increasing housing density in and near protected areas will show increasingly negative relationships on species of greatest conservation need and land-cover affiliates (negative statistical interactions over time) and increasingly positive relationships on synanthropic species (positive statistical interactions over time). The number of observations (i.e. BBS routes within protected areas) was low in all ecoregions, so we fitted a separate model for housing at the boundary or outside protected areas, rather than combining both fixed effects in the same model.

We used a *t*-statistic value of 2.0 to assess variable significance of the fixed-effect parameters, and a *F*-statistic value of 2.5, derived from an ANOVA test, to identify significant interactions

among time steps. We evaluated pairwise comparisons of slopes between time steps using a Markov chain Monte Carlo simulation with a Bonferroni adjustment of the alpha value ($\alpha = 0.05/10 = 0.005$). We fitted linear mixed-effects models using the *lme4* package (Bates, Maechler & Bolker 2012), and the Markov chain Monte Carlo simulation using the *languageR* package (Baayen 2011), in the R statistical software package 2.8.2 (R Core Team 2013).

Results

Housing increased both at the boundary and outside protected areas in all ecoregions from 1970 to 2010 (Fig. 2). Housing at the boundary of protected areas was highest in the Appalachian and Northwoods and lowest in the Deserts and Western Mountains and Valleys (Fig. 2). The pattern was similar for housing outside protected areas, except in the Western Mountains and Valleys, where housing spiked from 1980 to 2010. Ecoregions with the greatest magnitude of relative housing growth at the boundary of protected areas included the Western Mountains and Valleys (129% increase from 1970 to 2010) and the Deserts (83% increase, Fig. 2). Relative housing growth at the boundary of protected areas within the Appalachian and Northwoods was not as strong (43% increase, Fig. 2). Absolute housing growth at the boundary of protected areas (summarized within 400 m of BBS routes) was also highest in the Western Mountains and Valleys (40 units), followed by the Appalachian and Northwoods (22 units) and the Deserts (20 units). The greatest magnitude of relative housing growth outside protected areas occurred again in the Western Mountains and Valleys (265% increase) and the Deserts (142%

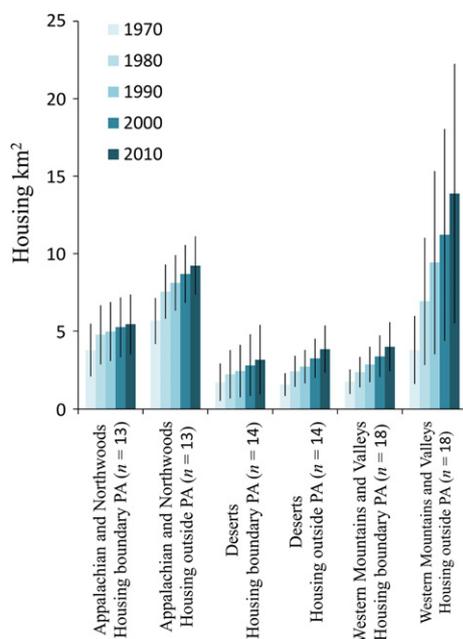


Fig. 2. Mean summary \pm standard error of housing density within and outside protected areas, among three ecoregions of the USA, across five decadal time steps.

increase, Fig. 2). Housing outside protected areas in the Appalachians and Northwoods was high in all time steps, but the magnitude of relative growth was less (62% increase, Fig. 2). Absolute growth outside protected areas was again highest in the Western Mountains and Valleys (69 units), followed by the Appalachian and Northwoods (46 units) and the Deserts (32 units).

The proportional abundance and proportional richness of both species of greatest conservation need and land-cover affiliates were negatively associated with housing at the boundary of protected areas in all ecoregions in all but three time steps (Deserts, proportional richness, species of greatest conservation need, 1980–2000, Fig. 3). These relationships were generally strongest and most consistent in the Appalachian and Northwoods, followed by the Deserts and then by Western Mountains and Valleys. The proportional abundance and proportional richness of species of greatest conservation need and land-cover affiliates were also negatively associated with housing outside protected areas in the Appalachian and Northwoods and the Deserts. We found similar patterns for the proportional abundance of species of greatest conservation need in the Western Mountains and Valleys, but the negative association was further reduced relative to the other ecoregions (Fig. 3). Housing outside protected areas was positively associated with the proportional abundance and richness of land-cover affiliates in the Western Mountains and Valleys, which was in contrast to the other ecoregions. The proportional abundance and proportional richness of synanthropes tended to be positively associated with housing at the boundary of protected areas in all ecoregions (the lone exceptions being proportional richness; 1970 and 1980; in the Deserts), with the strongest relationships again in the Appalachian and Northwoods and the Deserts (Fig. 3). This same guild was positively associated with housing outside protected areas in the Appalachian and Northwoods, with a general trend of an increasingly positive relationship from 1970 to 2010 (Fig. 3).

We found significant negative interactions between the slope of the relationship of species of greatest conservation need (proportional abundance and proportional richness) and land-cover affiliates (proportional richness), and significant positive interactions for synanthropes (proportional abundance) with housing at the boundary of protected areas from 1970 to 2010 in the Appalachians and Northwoods (Fig. 3). We did not find the same significant interactions in other ecoregions, possibly because housing was either comparatively lower or located further away from protected areas, therefore likely muting the effects. Nonetheless, the increasingly significant interactions in the Appalachians and Northwoods reflect the pattern in which the relationship between the proportional abundance of species of greatest conservation need and housing at the boundary of protected areas became progressively, negatively steeper whereas the relationship between the proportional abundance of synanthropes and

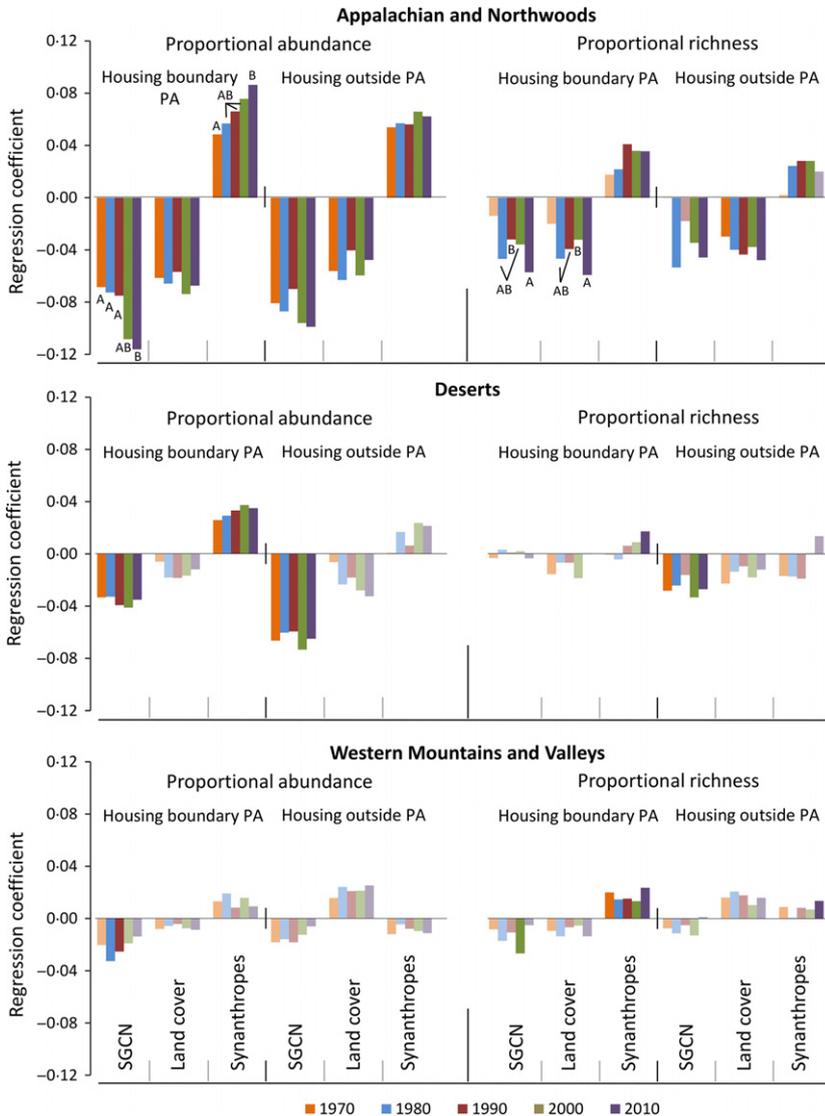


Fig. 3. Coefficient values, calculated from a linear mixed-model analysis, of the relationship among the proportional abundance and proportional richness of three avian guilds, including species of greatest conservation need (SGCN), land-cover affiliates and synanthropes, and the fixed effects of housing at the boundary or outside protected areas (PA) in three ecoregions of the USA. Coefficient values in bolded colour indicate significant slope (t -value ≥ 2.0). Coefficient values with same letter (A–B) indicate slopes between time steps do not significantly differ (F -statistic ≥ 2.5). Pairwise comparisons of slopes between time steps were evaluated using a Markov chain Monte Carlo simulation with a Bonferroni adjustment of the critical alpha value ($\alpha = 0.05/10 = 0.005$).

housing at the boundary of protected areas became progressively, positively steeper from 1970 to 2010 (Fig. 4). An explanation for these trends is that as housing increased in every decade along the boundary of individual protected-area BBS routes from 1970 to 2010, the proportional abundance of species of greatest conservation need declined and synanthropes increased at an increasing rate (Fig. 4). On the other hand, as housing remained low on the boundary of protected-area BBS routes from 1970 to 2010, the proportional abundance of the avian guilds remained similar (Fig. 4).

Discussion

Our central hypothesis was that as housing density in and near protected areas has risen in recent decades, it has increasingly altered the avian communities in these protected areas. Specifically, we predicted that rising housing density from 1970 to 2010 resulted in increasingly negative relationships for species of greatest conservation need and

land-cover affiliates and increasingly positive relationships for synanthropic species. Indeed, we found that from 1970 to 2010, increasing housing density at the boundary of protected areas had strong negative relationships with the abundance and richness of avian species of greatest conservation need and land-cover affiliates, whereas this relationship was positive for synanthropes. We also found that increased housing outside protected areas was negatively related with the abundance and richness of avian species of greatest conservation need in the Appalachian and Northwoods and Desert ecoregions. These relationships were, however, always weaker than the effects of housing at the boundary of protected areas. Although we were only able to look at a small percentage of individual BBS routes for our study (45 total routes), our results provide evidence that the increase in housing density in and near protected areas has had increasingly negative impacts for the biodiversity conservation potential of these lands.

Housing development affects biodiversity across broad spatial–temporal scales (Hansen *et al.* 2005; Suarez-Rubio

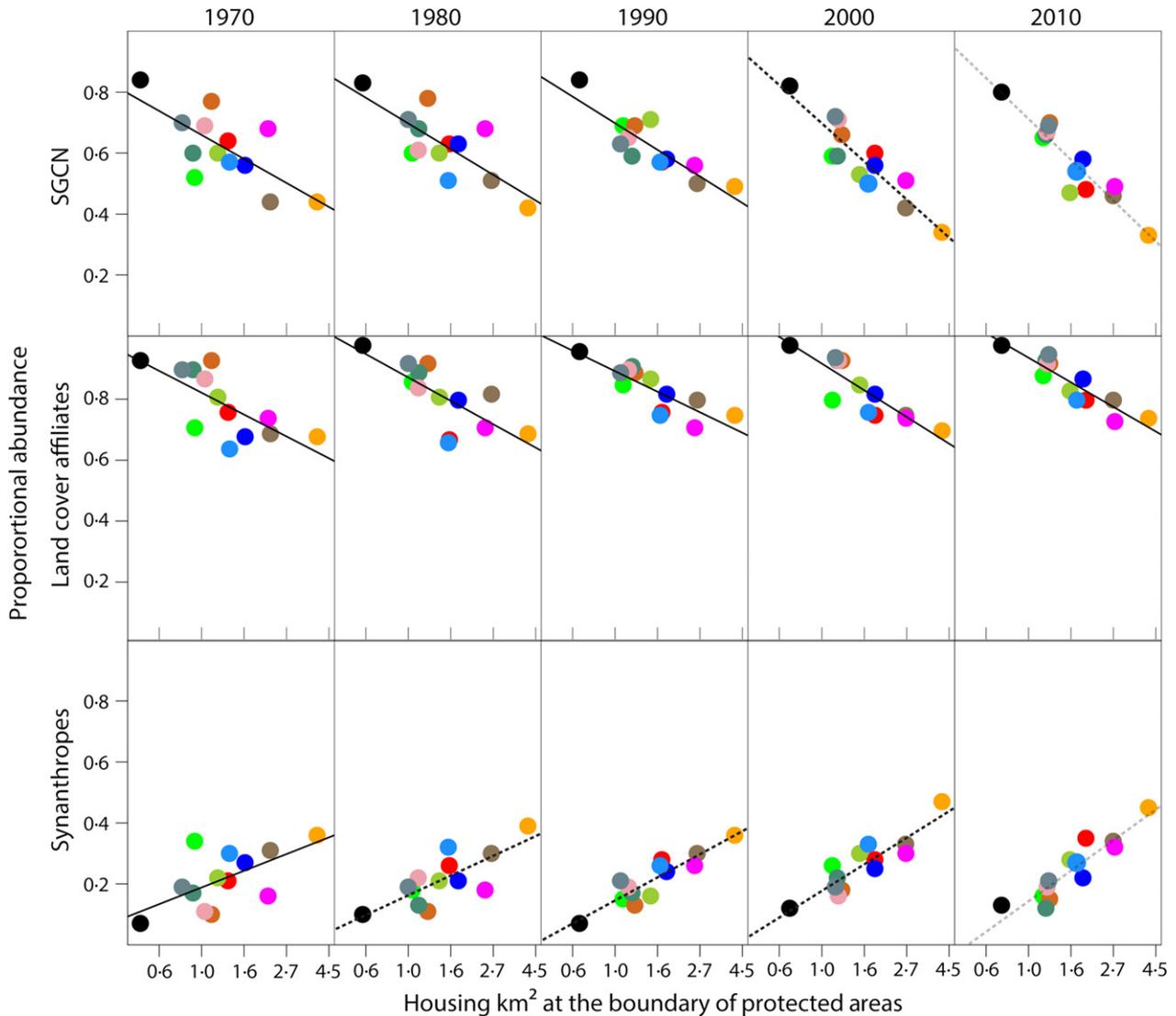


Fig. 4. Scatter plot and associated least-squares fitted line for the proportional abundance of species of greatest conservation need (SGCN), land-cover affiliates and synanthropes with housing density (Housing) at the boundary of protected areas throughout the Appalachian and Northwoods region across five decadal time steps. Housing density was transformed on the natural logarithmic scale for analysis purposes, and the housing density values on the x-axis represent the exponential value (i.e. back-transform) of the transformed data (−0.5, 0, 0.5, 1, 1.5). Individual North American Breeding Bird Survey (BBS) routes are identified by unique colour classification. Lines with different colours (black or grey) or patterns (solid or dashed) indicate a significant interaction of slopes among time steps based on a linear mixed-model analysis.

et al. 2013). Locally, housing development alters avian communities (Marzluff 2001; Bock, Jones & Bock 2008; Suarez-Rubio, Leimgruber & Renner 2010), negatively impacts breeding success (Hansen & Rotella 2002) and introduces non-native predatory pets [e.g. cats (Lepczyk, Mertig & Liu 2004)] and invasive species (Gavier-Pizarro *et al.* 2010). Regionally, housing development is associated with road development (Hawbaker *et al.* 2005), fragmentation and habitat loss (Radeloff, Hammer & Stewart 2005), and the homogenization of landscapes, which in turn negatively affects biological diversity (McKinney 2002, 2006; Pidgeon *et al.* 2007, 2014). We build on the previous studies by illustrating that as housing density has risen from 1970 to 2010 in and near protected areas, this has increasingly

altered avian communities (both abundance and richness) within these lands in many of the ecoregions of the USA. Thus, an increasing effect size has frequently accompanied the rise in rural housing development. More broadly, our findings support the notion that intensifying land use at the boundaries of protected areas likely influences biodiversity within their boundaries (Woodroffe & Ginsberg 1998; Brashares, Arcese & Sam 2001).

A central goal of protected-area management is to ‘protect natural biodiversity along with its underlying ecological structure and supporting environmental process...’ (Dudley 2008). Protected areas in the USA have greater amounts of natural land cover (e.g. forest) than surrounding private lands, have high occurrences of migratory

birds (La Sorte *et al.* 2015) and support higher abundance of breeding species of greatest conservation need and land-cover affiliates (Wood *et al.* 2014). Synanthropes, which include widespread, adaptable species (e.g. American Robin, *Turdus migratorius*), have expanding population sizes (Sauer, Hines & Fallon 2011) and are most likely to thrive near housing developments (Hansen & Rotella 2002). On the other hand, endemic species and habitat specialists are declining [e.g. Kentucky Warbler, *Geothlypis formosa* (Sauer, Hines & Fallon 2011)] and are most at risk due to housing development in and near protected areas. Protected areas in the USA provide habitat heterogeneity across broad spatial extents and largely limit development within their boundaries (Wood *et al.* 2014). Nonetheless, even marginal increases in housing development pose a threat to the amount of natural land cover and, in turn, the structure and diversity of protected-area avian communities (Wood *et al.* 2014). Additionally, even if protected areas have high levels of protection for biodiversity within their boundaries, they are still susceptible to outside land-use pressures that threaten their conservation potential (Piekielek & Hansen 2012), and development can occur on private inholdings within the protected areas (Radeloff *et al.* 2010). We extend the previous findings of Wood *et al.* (2014) by documenting the increasingly negative relationship between past increases in housing development at the boundary of protected areas and avian communities within these protected areas. Here, we show the increasing magnitude of these effects in the densely populated eastern USA, with no evidence that bird assemblages are adapting to housing development trends, and hints at the beginning of a possible degradation of avian communities in protected areas in the West. Understanding the nature and strength of this relationship was not possible with the sampling design employed by Wood *et al.* (2014) because prior work analysed data for a single year only. Further, we found that as housing development has risen on more distant private lands, there were similar, albeit more muted, effects on protected-area avian communities. These findings call to attention the continuing need for the protection of more distant private lands to ensure the ecological integrity of protected areas. Based on our results, we provide further information necessary for the management of housing development within and on surrounding lands of US protected areas.

Stemming the effects of housing development on protected-area biodiversity requires targeted conservation actions. The most important management implication from our study reflects the urgent need to limit housing development on privately owned lands within the boundaries of protected areas (i.e. inholdings) and on lands immediately adjacent to protected areas. We urge conservation planners to prioritize buying and conserving inholdings in order to maximize the extent of unfragmented natural lands within protected areas. Our results suggest that even modest housing growth on inholdings of

protected areas will negatively impact species of greatest conservation need and positively affect synanthropes. Further, our findings imply there is no evidence that bird assemblages are adapting to this land-use intensification, which we suggest indicates possible lag effects of housing development on protected-area avian communities. The increasing strength of these effects was only detectable over the four-decade period of our study, and therefore, our analysis revealed that identifying patterns such as we have done here is likely not possible from shorter-term studies (e.g. Wood *et al.* 2014). While rates of relative housing growth on the boundaries of protected areas are high in the western USA, housing density is still comparatively low there. We recommend protected areas in the West, especially where there are substantial inholdings, or plans for development, should be a priority for conservation efforts. Further, a possible tangential benefit to managing housing growth in the wildland–urban interface throughout the West could be reduced economic impacts tied to fuel-wood management and firefighting costs associated with the protection of structures. There are far fewer protected areas in the eastern USA compared with the West. That is why we suggest that conservation planners focus efforts on purchasing the remaining inholdings in protected areas in the East.

Furthermore, our results suggest that housing development outside protected areas will likely also negatively affect the conservation benefit of these lands. The most critical step to minimize this effect is to constrain and manage the extent of additional housing developments on neighbouring lands of protected areas. Housing growth within 1 km of protected areas has far outpaced the national average (Radeloff *et al.* 2010). While our study was not designed to address the conservation effectiveness of varying buffer-extents of protected areas, we suggest that because housing development has been so strong within 1 km of these lands, development within this buffer should be limited. Our recommendation is precautionary because once homes are built it is not possible to reverse any lasting effects on protected-area biodiversity. A recent review of the effects of residential development on biodiversity revealed inconclusive support for mechanisms (e.g. density, extent) in which patterns of housing development affect natural systems (Pejchar *et al.* 2015). Nonetheless, our work here highlights the urgent need to manage housing developments on private lands adjacent to protected areas in order to maximize conservation of avian communities within protected areas. We recommend that land-use planners consider and implement alternative development strategies such as conservation development (Milder 2007; Pejchar *et al.* 2007; Reed, Hilty & Theobald 2014), clustered development (Odell, Theobald & Knight 2003; Vaughn *et al.* 2014) and conservation easements (Rissman *et al.* 2007) in order to conserve natural and unfragmented habitats on private lands that can supplement protected areas in maintaining ecological processes such as migration (Berger 2004). Further, we suggest that

local planning jurisdictions attempt to anticipate where future development may occur and to use existing, or pass new, ordinances that incentivize development designs that conservation scientists believe will minimize rural development impacts (see Reed, Hilty & Theobald 2014). Only after putting such alternative development strategies into practice will we begin to establish a growing set of examples from which to adaptively confirm or refute these expectations. Also, we strongly recommend that land-use planners implement boundary management strategies to alter the pattern of human access to protected areas. In addition to proactive development planning, we urge protected-area managers to engage the public and private landowners in outreach and education. Such outreach should focus on direct human–wildlife conflicts, indirect conflicts (e.g. pet management), and ways to minimize threats (i.e. invasive plant species) that contribute to the anthropogenic footprint.

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Data accessibility

The following data are available from *Dryad Digital Repository* doi:10.5061/dryad.c2ss6 (Wood *et al.* 2015).

Breeding Bird Survey routes.

Housing density backcast and forecast data summarized in 400-m buffers from associated inside and outside protected-area BBS routes.

National Land Cover Database (2001) proportional land-cover summaries in 400-m buffers of inside protected-area Breeding Birds Survey routes.

Proportional richness and proportional abundance of North American Breeding Bird Survey guilds.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Additional materials and methods.

Appendix S2. BBS code, common and scientific name of 282 bird species from which we created eight bird species groups.