Contributed Paper

Systematic Temporal Patterns in the Relationship Between Housing Development and Forest Bird Biodiversity

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Abstract: *As people encroach increasingly on natural areas, one question is how this affects avian biodiversity. The answer to this is partly scale-dependent. At broad scales, human populations and biodiversity concentrate in the same areas and are positively associated, but at local scales people and biodiversity are negatively associated with biodiversity. We investigated whether there is also a systematic temporal trend in the relationship between bird biodiversity and housing development. We used linear regression to examine associations between forest bird species richness and housing growth in the conterminous United States over 30 years. Our data sources were the North American Breeding Bird Survey and the 2000 decennial U.S. Census. In the 9 largest forested ecoregions, housing density increased continually over time. Across the conterminous United States, the association between bird species richness and housing density was positive for virtually all guilds except ground nesting birds. We found a systematic trajectory of declining bird species richness as housing increased through time. In more recently developed ecoregions, where housing density was still low, the association with bird species richness was neutral or positive. In ecoregions that were developed earlier and where housing density was highest, the association of housing density with bird species richness for most guilds was negative and grew stronger with advancing decades. We propose that in general the relationship between human settlement and biodiversity over time unfolds as a 2-phase process. The first phase is apparently innocuous; associations are positive due to coincidence of low-density housing with high biodiversity. The second phase is highly detrimental to biodiversity, and increases in housing density are associated with biodiversity losses. The long-term effect on biodiversity depends on the final housing density. This general pattern can help unify our understanding of the relationship of human encroachment and biodiversity response.*

Keywords: animals, birds, forest, functional groups, housing, North America, temporal pattern, woodland

Patrones Sistemáticos Temporales en la Relación entre Desarrollos Urbanos y la Biodiversidad de Aves de Bosque

Resumen: *Mientras la gente invade cada vez más las áreas naturales, una pregunta que surge es cómo afecta esto a la biodiversidad de aves. La respuesta depende parcialmente de escalas. Con escalas amplias, las poblaciones humanas y la biodiversidad se concentran en las mismas áreas y se asocian positivamente, pero en escalas locales la gente y la biodiversidad se asocian negativamente. Investigamos si también existe una tendencia sistemática temporal en la relación entre la biodiversidad de aves y el desarrollo urbano. Usamos una regresión lineal para examinar las asociaciones entre la riqueza de especies de aves de bosque*

y el crecimiento urbano en los Estados Unidos (exceptuando a Alaska y Hawái) a lo largo de 30 años. Nuestras fuentes de datos fueron el Censo Norteamericano de Aves Reproductoras y el censo estadunidense del año 2000. A lo largo de la parte de Estados Unidos que estudiamos, la asociación entre la riqueza de especies de aves y la densidad urbana fue positiva para virtualmente todos los gremios con excepción de las aves que anidan en el suelo. Encontramos una trayectoria sistemática de la declinación de la riqueza de especies de aves conforme aumentaba la urbanización con el tiempo. En las eco-regiones con desarrollo más reciente, donde la densidad urbana era aún baja, la asociación con la riqueza de especies de aves fue neutral o positiva. En las eco-regiones que se desarrollaron con anterioridad y donde la densidad urbana fue la más alta, la asociación de la densidad urbana con la riqueza de especies fue negativa con la mayoría de los gremios y se volvía más fuerte en las siguientes décadas. Proponemos que en general, la relación entre los asentamientos humanos y la biodiversidad ocurre a lo largo del tiempo como un proceso de 2 fases. La primera es aparentemente inocua: las asociaciones son positivas debido a la coincidencia entre la baja densidad urbana y la alta biodiversidad. La segunda fase es altamente dañina para la biodiversidad, y los incrementos en la densidad urbana están asociados con pérdidas en la biodiversidad. El efecto a largo plazo sobre la biodiversidad depende de la densidad urbana final. Este patrón general puede ayudar a unificar nuestro entendimiento de la relación entre la invasión humana y la respuesta de la biodiversidad.

Palabras Clave: animales, aves, bosque, grupos funcionales, vivienda, América del Norte, patrón temporal

Introduction

Species around the globe are threatened by expanding human populations (Gaston et al. 2003; Seto et al. 2012). Worldwide, human populations are growing at higher rates in biodiversity hotspots (Cincotta et al. 2000), and human development threatens biodiversity (e.g., Cincotta et al. 2000; Cardillo et al. 2006; Pidgeon et al. 2007). The relationships between people and biodiversity, however, can be either positive or negative, partly because of scale dependency (Pautasso 2007). At continental scales, human population density is positively correlated with many taxa (e.g., mammals, Ceballos & Ehrlich 2002; birds, Gaston & Evans 2004; snakes & amphibians, Balmford et al. 2001). The underlying pattern is correlation rather than causation though. People tend to settle where biodiversity is highest, and these positive relationships indicate a conservation conflict (Balmford et al. 2001). At local scales, there is generally a negative relationship between human populations and biodiversity. For example, arthropod diversity declines as urbanization increases (McKinney 2008), and Neotropical migrant bird species richness is lower where housing development is common (Kluza et al. 2000; Burhans & Thompson 2006; Pidgeon et al. 2007).

We hypothesize, however, that in addition to the scale dependency there is also a systematic temporal pattern in the relationship between development and biodiversity. At first, the association is positive as people settle in areas that are particularly productive and hence species rich. In addition, new resources may be introduced (e.g., seeds at feeders, openings with brush piles, small pastures, water), which may increase the number of niches available and attract additional species. However, as the number of houses increases over time, the association between development and biodiversity becomes negative as development asserts its direct effects on land cover and species. In Fig. 1, we express this hypothesis in a conceptual model of the association between species richness and human settlement over time.

The conterminous United States is an ideal study area to test this hypothesis because of its highly variable development patterns (Radeloff et al. 2010). Recently the number of houses in rural areas has grown, in particular in places rich in natural amenities such as forests (Radeloff et al. 2005), lake shores (Gonzales-Abraham et al. 2007), mountain valleys (Francis et al. 2012), and riparian areas (Bark et al. 2009) (i.e., the very places that are especially valuable for biodiversity). Housing development in forests is particularly troublesome because the ecological effect size of each house tends to be much larger than its direct footprint due to noise, pets, introduction of exotic species (McKinney & Lockwood 1999; Gavier-Pizarro et al. 2010), forest fragmentation (Zhou et al. 2011; Glennon & Kretser 2013), and the extirpation of understory species (Vellend et al. 2006). Furthermore, while temporary disturbances, like timber harvest, may maintain or increase species richness if their frequency and intensity are intermediate relative to a given forest's time to reach maturity (Rittenhouse et al. 2010), permanent disturbances like residential development typically diminish native species richness (McKinney 2002). However, if our hypothesis is true that preferential settlement of people in biodiversity rich areas results in early positive relationships that subsequently become negative as housing density increases, then there may be 2 reasons for concern. First, initial positive associations may mask later problems and delay conservation responses and, second, if development is concentrated in biodiversity-rich areas, then it will ultimately have the worst possible impact.

We examined whether there is a consistent temporal pattern in the relationship between forest bird species richness and housing development over time. We hypothesized that as time advances, there are predictable trajectories of response to development: initially relationships are positive, but they become increasingly negative
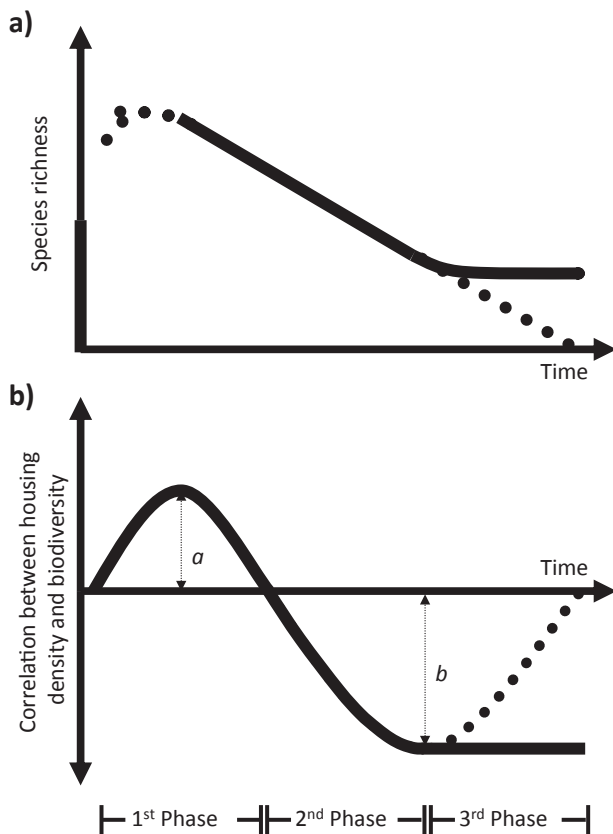
Figure 1. Proposed conceptual model of the effect of housing density on biodiversity through time and the corresponding trajectory of species richness: (a) species richness trajectory of a given site over time and (b) the nature of the relationship between housing density and biodiversity over time (a, maximum positive association between housing density and biodiversity; b, maximum negative effect of housing density on biodiversity). In the first phase, houses are located initially in fertile, highly productive areas that are also biodiversity hotspots, and settlement exerts a neutral or slightly positive effect on avian diversity primarily because the correlation of both housing density and biodiversity with productivity dominates the relationship. Over time, development increases and the nature of the relationship changes so that during the second phase negative effects associated with houses dominate the relationship. In the third phase, the effect depends on the final settlement density. If all areas are completely developed, then the correlation will approach zero.

over time. To test our hypothesis and investigate our conceptual model empirically (Fig. 1), we analyzed breeding bird data collected from 1970 to 2000 across the conterminous United States, organized in different functional guilds and with a focus on forested ecoregions.

We used a natural experiment of different settlement histories in different forested regions of the United States. Euroamerican settlement occurred earliest in the East, then proceeded westward through the Midwestern states to the West Coast and occurred latest in interior and western mountainous regions, where rugged topography impeded transportation and made farming difficult (Beck & Haase 1989). Today, housing density and the extent of settled area are much higher in the East than in the interior and western mountainous region. Thus, comparing relationships in different ecoregions allowed us to characterize potentially different phases of response to the Euroamerican settlement process.

Methods

We used Bailey's ecoregions at the province level (Bailey 1995) to select predominantly forested ecoregions (Pidgeon et al. 2007) based on forest area estimates from the National Land Cover Data set (Vogelmann et al. 2001). These 20 predominantly forested ecoregions range in size from 9,600 km^2 (Black Hills Coniferous Forest Province) to 699,300 km^2 (Eastern Broadleaf Forest [Continental] Province).

We obtained bird data from the North American Breeding Bird Survey (BBS) (Sauer & Fallon 2012). The BBS is coordinated by the U.S. Geological Survey, Patuxent Wildlife Research Center, and Environment Canada, National Wildlife Research Centre. No routes are in urban areas, and the survey focuses on rural parts of the United States. Each 39.4 km route is surveyed annually during the breeding season by a competent volunteer who conducts fifty 3-min point counts spaced at 0.8 km intervals, during which she or he records all birds detected (Bystrak 1981).

We limited the species for our analysis to those that use forest, forest edge, and woodland during the breeding season and that have been observed on ≥30 routes (Supporting Information). We analyzed this group as a whole and in 7 functional guilds based on their migratory habit (Neotropical migrants, short distance migrants, permanent resident species), nest locations (species that nest in cavities, on or within 1 m of the ground, or in the forest interior), and affinity with humans (full synanthropes; Johnston 2001). These functional guilds were not mutually exclusive (e.g., many cavity nesters were also included in the permanent residents' guild). We followed standard methods to minimize surveyor bias (Bystrak 1981; Sauer & Peterjohn 1994) and accounted for detection bias by using the program COMDYN to estimate route-level richness for each guild and year (Hines et al. 1999).

To relate bird data with the decadal housing data (see below), we selected bird data collected in years near the end of each decade. We averaged the species richness estimator for the 5 years bracketing each U.S. Census year

in the analysis (1970, 1980, 1990, 2000). For example, the richness estimate for a given BBS route in 1990 was the average from 1988 to 1992, or, because not all routes were surveyed in all years, the subset of available years in the 5-year span in which that route was surveyed. There was a slight, but statistically significant, increase in species richness as the number of available years for a route increased (average 60 species when only 1 year was available, versus 67 when 5 years were available). However, because data availability was better in later decades, but our general trend was a decrease in species richness (see Results), we suggest this artifact of BBS data availability did not cause the patterns we report. The number of routes included our analyses was 1573 in 1970, 1974 in 1980, 2411 in 1990, and 2788 in 2000.

Housing density estimates were derived from the 2000 decennial U.S. Census. We analyzed housing density at the partial block group level and used backcasts of housing density for each decade back to 1970 (Radeloff et al. 2010). Backcasting is necessary because the U.S. Decennial Census does not provide housing density data below the county scale prior to 1990 (Radeloff et al. 2001; Hammer et al. 2004). Therefore, earlier housing density can only be estimated, not measured, at the necessary resolution. However, our estimates for prior decades match available county housing totals, thereby representing housing densities that are both accurate and of high resolution (Hammer et al. 2004, 2009; Radeloff et al. 2005, 2010; Lepczyk et al. 2007). Housing density was averaged within 19.7 km of the centroid of each BBS route (1200 km^2), a common approach when comparing BBS bird data with variables characterizing the surrounding environment (Flather & Sauer 1996; Pidgeon et al. 2007; Lepczyk et al. 2008; Albright et al. 2011). In some of our analyses, we focused regional analyses on the 9 largest ecoregions (Fig. 2) and calculated the mean and coefficient of variation (cv) of housing density for the 1200 km^2 areas surrounding BBS routes in each of these ecoregion for each decade.

Statistical Analyses

We conducted linear regression analysis of bird species richness as a function of housing density for each decadal point, 1970, 1980, 1990, and 2000. To meet the assumptions of normality and linearity, we transformed housing density to log$_{10}$ after adding 1 to each density estimate. Residuals versus fitted values plots were used to evaluate homoscedasticity. Each analysis was performed on all 20 ecoregions combined and for the 9 largest ecoregions individually to test for unique associations of avian guilds and distinct patterns across the United States. Regression models were fit in SAS. To assess significance, we used Bonferroni correction. Specifically, we analyzed 10 spatial units (i.e., 9 ecoregions and the entire U.S. forested area) and 8 bird guilds for a total of 80 regressions, re-

sulting in an adjusted p value of 0.1/80 = 0.00125 as a guide to determining the significance of associations between avian guilds and housing density. We tested for spatial autocorrelation with semivariograms of the model residuals. Where spatial autocorrelation was present, we parameterized additional general linear models with a spatial exponential covariance structure and reestimated model coefficients. Model significance, as presented in the results, is from models that accounted for spatial covariance, when necessary. We expected to find differences in the magnitude of slopes due to differences in the size of the species pool in each guild (Supporting Information).

Because both habitat loss and fragmentation affect bird species occupancy patterns, we tested for the influence of these factors to ensure our results were not spurious. First, we computed Spearman's rank correlations among housing density, the area of agriculture (a proxy for habitat loss), forest area, and area of core forest (a measure of fragmentation) to determine the degree to which these variables may be confounded in their relationship to bird richness. Second, we modeled the species richness of each guild as a function of housing density, agricultural area, and core forest area in multiple linear regression models. For each regression model, we applied hierarchical partitioning to determine the independent contribution of each factor to species richness when the others were held constant (Chevan & Sutherland 1991; Supporting Information).

Results

Our analysis captured a wide range of housing densities, spanning 1 house/km^2 in landscapes surrounding BBS routes in the Southern Rocky Mountain Mixed Forest in 1970 to 61 houses/km^2 in the Eastern Broadleaf Forest (Oceanic) ecoregion in 2000. From 1970 to 2000, housing density increased continually in our study landscapes in all 9 ecoregions (Fig. 3), but the pattern of housing contrasted markedly between the lowest density ecoregions, where the coefficient of variation of housing density either stayed the same or increased over decades, and the 4 most densely settled ecoregions, where it decreased over time (from 2.77 and 1.51 to 2.15 and 1.22 in the Eastern Broadleaf Forests and the Continental and Oceanic ecoregions, respectively; Supporting Information). Differences in housing density among ecoregions were far larger than the differences among decades in any given ecoregion. For example, the density of housing in the Eastern Broadleaf Forest (Oceanic) in 1970 exceeded that of any other forested ecoregion in 2000.

Across the forested conterminous United States (a linear extent of approximately 4500 km), associations between housing density and bird species richness were mostly positive or neutral and stayed so over the 30 years
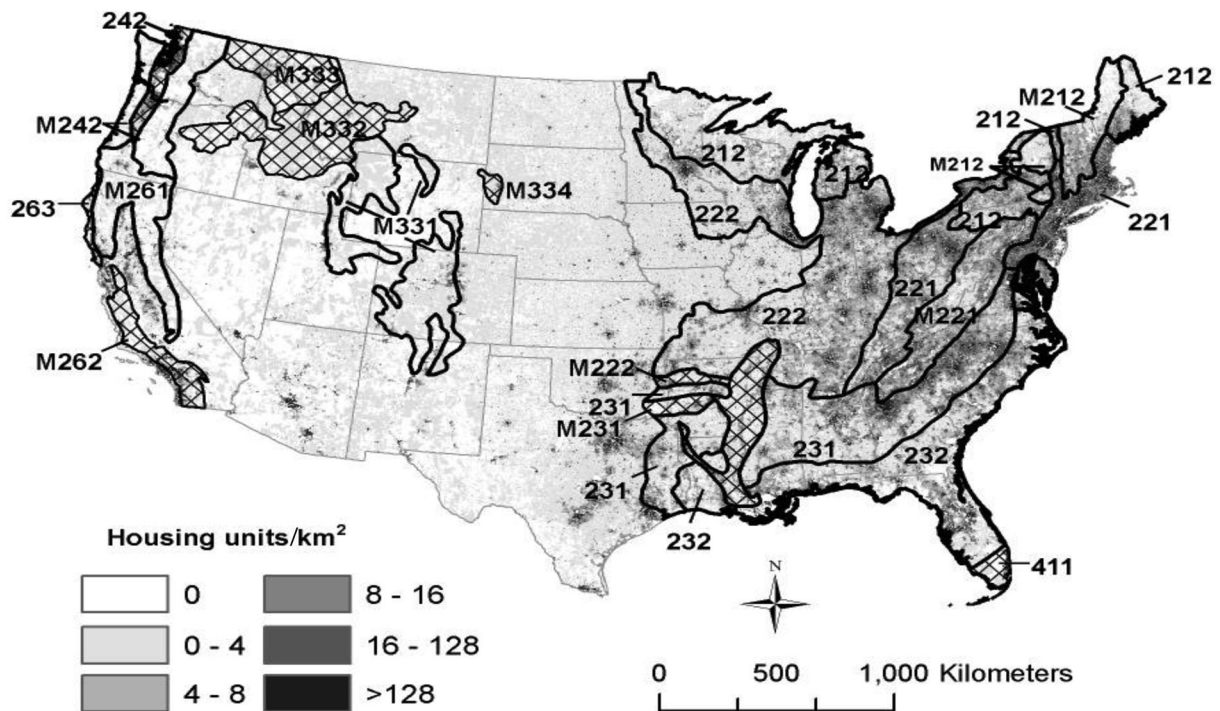
Figure 2. Forested ecoregions and housing density in the conterminous United States in 2000. The 9 largest forested ecoregions are outlined in black, others are cross-hatched. Ecoregions names are as follows, from lowest to highest housing density: M331, Southern Rocky Mountain Mixed Forest; M261, Sierra Mixed Forest–Steppe; M212, Adirondack-New England Mixed Forest; 212-Laurentian Mixed Forest; M221, Central Appalachian Mixed Forest; 232, Outer Coastal Plain Mixed Forest; 231, Southeast Mixed Forest; 222, Eastern Broadleaf Forest (Continental); 221, Eastern Broadleaf Forest (Oceanic).

(Fig. 4). Ground nesting species were the notable exception, exhibiting an increasingly negative association with housing over time.

However, among ecoregions, we found markedly different response patterns. First, we observed that associations between bird species richness and housing density were generally positive in the ecoregions that were settled most recently and where housing density was lowest, but associations between bird species richness and housing density were negative in ecoregions with higher housing density that were settled earlier. Second, within a given ecoregion, once the relationships were negative they tended to become more strongly negative with advancing decades.

There were also differences in response patterns among guilds (Figs. 5a–h). The guilds that followed our proposed trajectory of association between housing density and avian biodiversity most closely were Neotropical migrants, cavity nesting species, and permanent residents. In all these guilds, associations between bird species richness and housing density in the Southern Rocky Mountains and Sierran Mixed ecoregions (the 2 ecoregions with the lowest housing density) were positive, but these associations in the Outer Coastal Plain Mixed, Southeastern Mixed

forest, and the 2 Eastern Broadleaf ecoregions (the 4 ecoregions with the highest housing density) were negative.

In the Adirondack–New England and the Laurentian Mixed forest ecoregions (the ecoregions with intermediate housing densities), associations between bird species richness and housing density differed by guild. For most guilds the association was more strongly negative in the Laurentian Mixed forest than in the Adirondack-New England forest. In these ecoregions, ground nesting species, Neotropical migrants, and forest interior species already crossed the threshold from positive to negative association at intermediate housing densities by 1980. However, permanent residents and cavity nesting species exhibited mostly positive associations at the intermediate housing density levels in these 2 ecoregions, but they exhibited negative associations in ecoregions with higher housing densities.

Both ground nesting and forest interior guilds had essentially no positive associations with housing density in any ecoregions, and their main trend was more negative associations in ecoregions with higher housing density. Synanthropes, on the other hand, exhibited essentially only positive associations, which were weakest at the highest and lowest housing densities. Short-distance
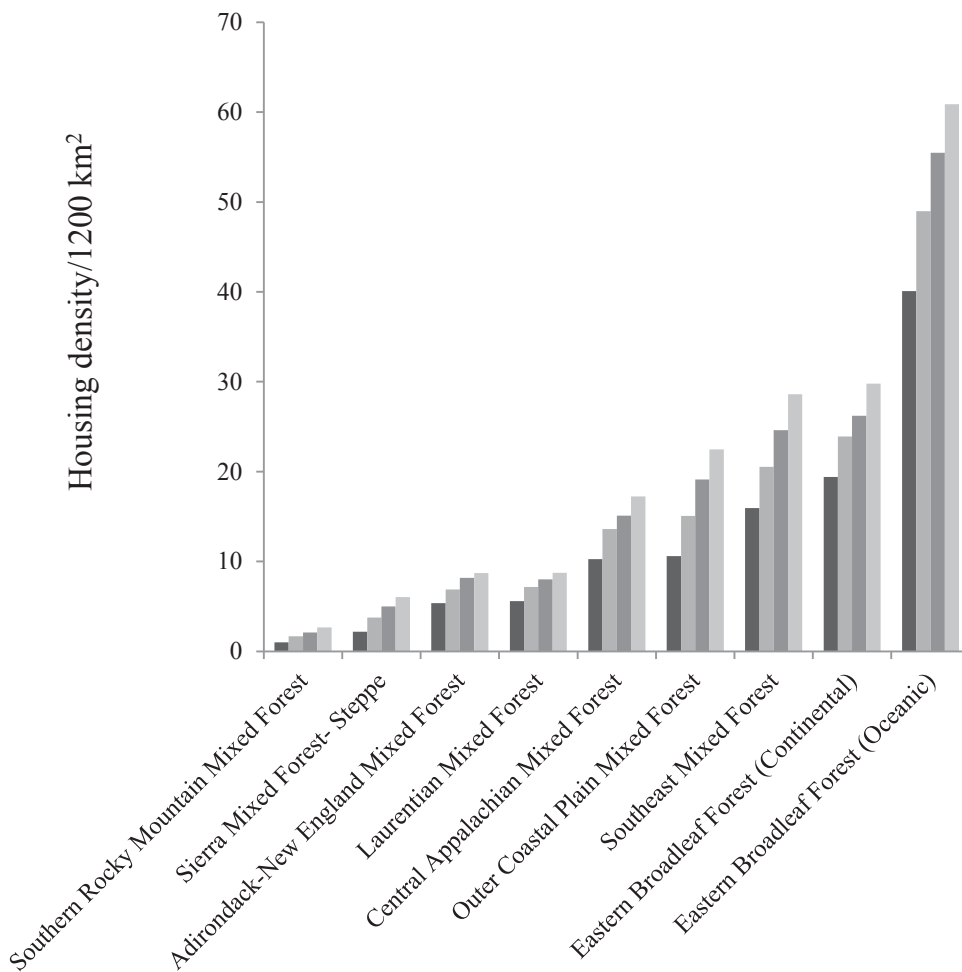
Figure 3. Average housing density in the 19.4-km radius (1200 km²) circular landscapes around North American Breeding Bird Survey routes in the 9 largest forested ecoregions of the coterminous United States from 1970 to 2000 (by decade from left in each set of bars).
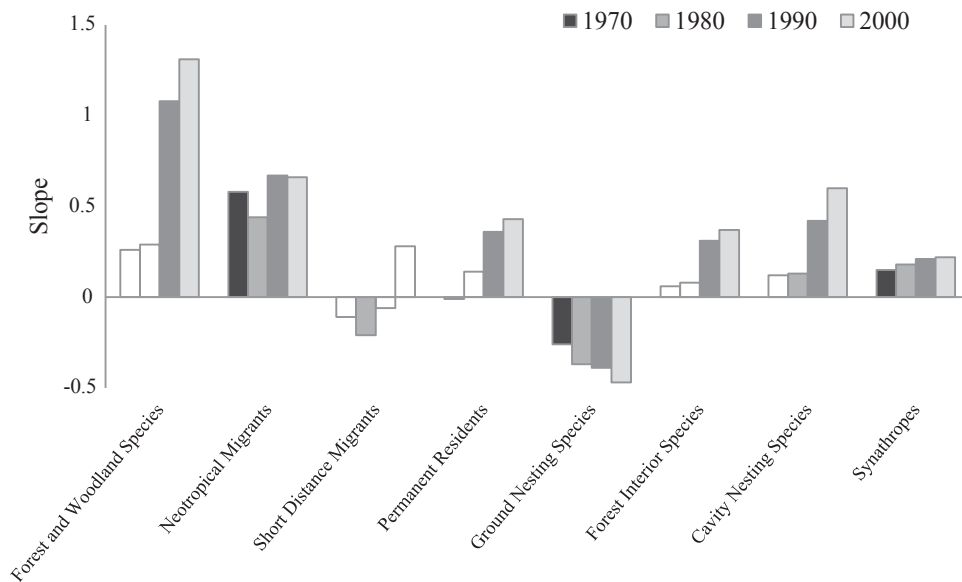

Figure 4. The association between housing density and bird species richness, as indicated by the slope from linear regression, of 8 functional guilds of forest and woodland species across the 20 forested ecoregions of the conterminous United States by decade. Unfilled bars indicate nonsignificant associations.

migrants showed no clear pattern of associations among ecoregions.

Correlations of housing density with forest area, agricultural area, and forest fragmentation were generally weak, suggesting that housing is not often strongly asso-ciated with other factors that may be related to bird abundance. Furthermore, our multivariate models showed that housing density had in most cases a high independent contribution, even when other factors were included (Supporting Information). For example, in the
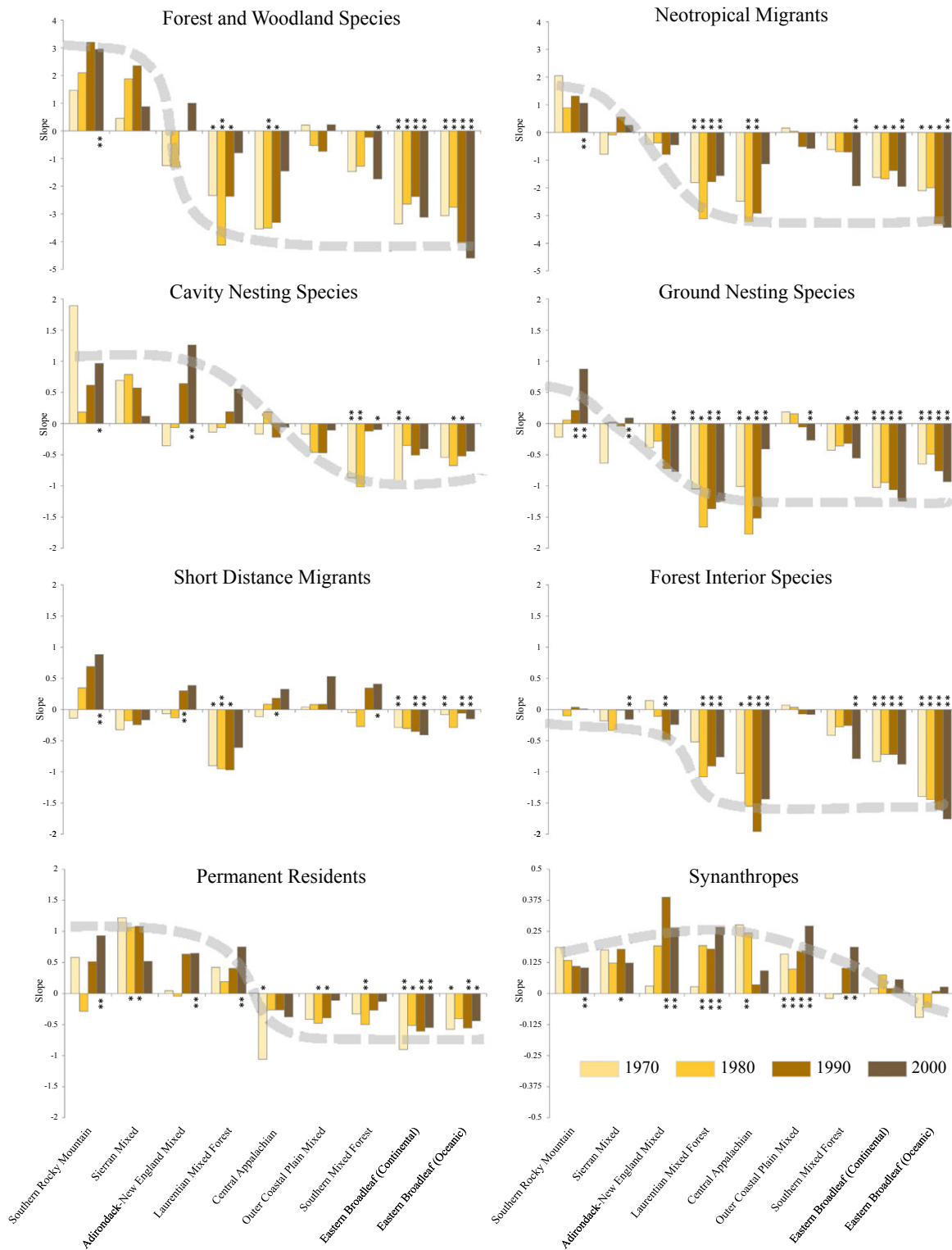
*Figure 5. The association between bird species richness, as indicated by the slope from linear regression, of 8 functional guilds and housing density in the 9 largest forested ecoregions of the conterminous United States. Ecoregions are arranged on x-axis from lowest housing density on left to highest housing density on the right. Along this density gradient, the association between housing and bird species richness shifts from positive or neutral to increasingly negative. The dashed line illustrates how the associations of different guilds cross this threshold at different housing density levels. Asterisks indicate statistical significance: * p < 0.01, ** p < 0.00125.*

Adirondack–New England ecoregion, where housing and agriculture were moderately correlated, the independent contribution of housing in models of species richness was generally high, suggesting that housing was strongly associated with bird species richness even when other variables were included. Only in the Central Appalachian and Eastern Deciduous (Oceanic) ecoregions did the other factors exhibit higher independent contributions than housing density. For detailed results of this assessment of other factors, see Supporting Information.

Discussion

We found strong evidence for a temporal trajectory in the associations of bird species richness and housing density. Associations between housing and bird species richness were positive in the ecoregions that were settled last and had low housing densities and were negative in the ecoregions that have been settled the longest and had the highest housing densities (Fig. 5). These patterns were particularly pronounced in 4 guilds: forest and woodland species, Neotropical migrants, cavity nesters, and permanent residents. Two guilds showed almost exclusively negative relationships (ground nesters and forest interior species), and these were stronger in the ecoregions that have been settled the longest.

Our comparisons among ecoregions implicitly captured different histories of the settlement process. Within each ecoregion, we also examined changes over 3 decades. Housing density in the forested rural landscapes of the conterminous United States has relentlessly increased over time, especially in rural areas that are rich in natural amenities (Radeloff et al. 2005; Lepczyk et al. 2007; Mockrin et al. 2013). We found increasingly strong and largely negative relationships between housing density and bird species richness within virtually all ecoregions, and the forested United States as a whole, over the 30 years we studied. These patterns are consistent with our conceptual model (Fig. 1). Only synanthropes had generally positive relationships, but these were weakest in ecoregions that have been settled the longest, likely because the high overall housing density facilitates uniform synanthrope occupancy.

Our results suggest that the response of bird biodiversity to development through time follows a systematic temporal trajectory, and there are ecological explanations to support this notion. In the first phase of development, when there are only a few houses, we suggest that avian species richness remains either stable, if the effect of houses is truly benign, or increases slightly (Fig. 1a) due to modifications that create habitat or food resources for new species. In this phase, human impact is so limited that no species are excluded, but new species may be attracted, resulting in a potential positive relationship between housing density and biodiversity (Fig. 1b).

Ultimately though, our results suggest that the positive nature of the relationship between housing and bird diversity is transient. The duration of the first phase depends on the productivity of a region, the degree of habitat modification, and the rate and extent of settlement. The association between housing density and biodiversity will be most strongly positive (*a* in Fig. 1b) where the differential in biological productivity between settled and nonsettled areas is high and when settlement occurs preferentially in these high-productivity places. This is likely the case in the Southern Rocky Mountains and the Sierran Mixed Forest ecoregions, where water limits productivity, and river valleys are rich in biodiversity and the only places where settlement on a large scale is feasible. Indeed, these 2 ecoregions were settled most recently (Beck & Haase 1989) and were the only ecoregions where associations of housing with birds were generally positive. But positive associations between birds and housing represent a major conservation concern if they are caused by preferential development in those places that are most important for biodiversity due to their resource concentration, a pattern termed the conservation conflict (Balmford et al. 2001).

A common trajectory is that initial settlement leads to growing infrastructure (e.g., roads, power lines), facilitating contagious development (Hawbaker et al. 2006). Continued expansion of settlement inevitably leads to a second phase of the association of housing and bird species richness, characterized by species losses. This second settlement phase is exemplified by the 2 Eastern Broadleaf Forest ecoregions, which have been settled the longest. By 1970, average housing density there was already high (Fig. 3), and as the variance in housing density diminished, the strength of the association between bird species richness and housing became increasingly negative. The relationship between biodiversity and human settlement in this second phase is generally negative as habitat quality declines due to processes that accompany high housing density, including the replacement of forest with nonhabitat, fragmentation and isolation of forest patches (Ferraz et al. 2007), diminished invertebrate prey availability within the remaining forest (Burke & Nol 1998), and human subsidies to predators (Lepczyk et al. 2004).

In the second phase of settlement, the maximum negative effect size (*b* in Fig. 1b) depends on how many species can persist in highly modified habitats and on the magnitude of development. Regions with low productivity are particularly sensitive to disturbances, and populations of animals in these regions are less resilient to changes that accompany human settlement than are populations in regions of naturally high productivity (Huston 2005). Whether the relationship between bird diversity and human settlement will ultimately remain strongly negative or trend toward zero depends on the settlement patterns in the final landscape. If an entire area were to

become densely settled (an impossibility if there are protected reserves devoid of houses), then the correlation would become zero as the housing gradient vanishes.

We also found some interesting exceptions to these general patterns. In the Laurentian Mixed Forest, strong negative associations in the 1980s were followed by weaker associations thereafter, especially for forest and woodland species, Neotropical migrants, and forest interior species. This ecoregion harbors some of the most species-rich forest breeding bird communities in the entire United States (Pidgeon et al. 2007), and housing was relatively sparse until the 1970s (Radeloff et al. 2005). During the 1970s, however, housing density increased rapidly, a pattern termed the rural rebound because of the explosive housing growth in areas with high natural amenities (Johnson & Beale 1998). We suggest that weakening associations after the 1970s may reflect an accommodation of species richness to the slower pace of housing density growth in subsequent decades. The other exceptions to the general rule of increasingly negative associations over time were the 2 southeastern U.S. ecoregions, which exhibited relatively weak negative associations of housing with birds despite their relatively high housing density. We speculate that in these ecoregions the great increase in timber harvest, which more than doubled from 1960 to 2000 (Wear & Greis 2012) and the associated lack of forest structural and species diversity may be implicated. Our hierarchical partitioning results highlighted the contribution of core forest for bird species richness in the southeastern ecoregions, lending support for the role of forest disturbance in shaping avian communities.

The exceptions to the general rule of increasing strength in the relationship between housing and bird species richness highlight the fact that among the forested ecoregions of the United States many differences exist other than housing. The variation in broad trends among functional groups in different ecoregions (gray dashed lines in Fig. 5) highlights the variation in approximate thresholds at which the response of species richness to housing density changed from positive to negative. Each guild–ecoregion combination is a product of a different set of environmental and biotic factors that interact with housing density and the avian community, resulting in unique manifestations of the intermediate disturbance hypothesis (Connell 1978). The western forests are mostly dominated by conifers, generally dryer, and naturally patchy, while the eastern forests are often dominated by deciduous tree species, are more humid, and existed historically as contiguous patches of very broad extent. Differences in patterns of avian species richness are related to these variables, and we are not suggesting that housing density is the sole factor driving species richness patterns. However, we focused on housing density because it has strongly increased in many rural areas in recent decades (Radeloff et al. 2010). The

relationships between housing density and bird species richness showed consistent patterns both among and within ecoregions (Fig. 5), suggesting that despite environmental differences, the effect of housing on birds followed a predictable temporal pattern.

Across the United States, the association between birds and housing density was generally positive. These relationships represent an amalgam encompassing all forested areas, ranging from the magnolia and bald cypress forests of the Southeast, to the mixed deciduous–coniferous forest of the Great Lakes region, and to the mixed conifer forests of the western mountains. At this broad spatial scale, we observed a positive association between bird species richness and housing density for 6 of 8 functional guilds (Fig. 3). This association likely reflected naturally higher bird species richness in the more productive ecoregions of the eastern forests (Pidgeon et al. 2007), which also have higher densities of human settlement. The exceptions were ground nesting species, which were increasingly negatively associated with housing density as time advanced, and short distance migrants, which exhibited little pattern. Ground nesting species are particularly vulnerable to predators associated with houses (Odell & Knight 2001) and thus are especially sensitive to increasing housing density.

The predominantly positive association between bird diversity and houses at the national scale concurs with previous findings (Evans & Gaston 2005; Tratalos et al. 2007). Ultimately, however, there is reason for concern. Many areas of high natural amenity (i.e., river corridors, lakeshores, wetland complexes, forests), are high in species diversity. The trends apparent in our results suggest that bird species richness is increasingly influenced by human settlement. Although these correlations do not prove causation, the strengthening associations through time suggest that housing density, or factors closely correlated with housing density, are gaining importance in shaping the patterns of bird species richness. The increasing strength of the relationships also is an indication that our opportunities to affect positive measures for biodiversity are becoming limited because the variation in housing density in rural landscapes has decreased in most ecoregions with advancing decades. Thus, the negative associations between birds and human settlement evident in Eastern Broadleaf Forest should serve to warn conservation practitioners of trends to come in western ecoregions where settlement began later and, ultimately, of trends we can anticipate across the forests of the United States.

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Supporting Information

Classification of forest and woodland species into guilds (Appendix S1), expanded methods and results (Appendix S2), coefficents of variation of housing density (Appendix S3), scatter plots of potential factors associated with bird species richness (Appendix S4), table of Spearman rank correlations between potential factors associated with bird species richness (Appendix S5), table of coefficients of factors resulting from multiple linear regression models (Appendix S6), and results of hierarchical partitioning showing percent independent contribution of factors in models of avian guild species richness in 1990 and 2000 (Appendix S7) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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