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Research article

House Price Index as an early indicator of development risk to biodiversity

Marlen Acosta Alamo [1,2,*], Lisa L. Manne[1,2], Richard R. Veit[1,2]

[1]College of Staten Island, Biology Department, City University of NY, Staten Island, NY 10314, United States
[2]Graduate Center, Biology Program, City University of NY, New York, NY 10016, United States

*Corresponding author. College of Staten Island, Biology Department, City University of NY, 2800 Victory Blvd, Building 6S, Office 117, Staten Island, NY 10314, United States. E-mail: macostaalamo@gradcenter.cuny.edu

Abstract

Habitat loss due to changes in land cover is one of the main causes of biodiversity decline worldwide. Habitat loss occurs disproportionately in areas of high biodiversity because these same areas are particularly suitable for development. We assessed the effect of development risk on the biodiversity of breeding birds in the United States. We compared the effect of two predictors of habitat loss on the richness, abundance, and rarity of woodland, open-habitat, and urban birds at the local and regional levels. We used the House Price Index—as a measure of development risk—and primary productivity as predictors in simulations of habitat loss. For local scale analysis, we used generalized regression models. For regional-scale habitat loss simulations, we statistically compared the results obtained from each predictor. Locally, development risk and primary productivity interacted in their effect on the richness, abundance, and rarity index of all birds. At the regional level, development risk predicted larger declines in richness and abundance and increases in the rarity of open-habitat birds following habitat loss than primary productivity. For woodland birds, both risk of development- and primary productivity-ordered habitat loss affected richness and rarity levels, while primary productivity had a larger effect on their abundance. The diversity of urban birds was less affected by habitat loss than the other groups of birds. Our study is the first to investigate the usefulness of the House Price Index as a measure of development risk and as a predictor of biodiversity. Proactively recognizing high-development risk areas affords more time for targeted conservation plans in those areas.

Key words: biodiversity loss; bird biodiversity; habitat loss; primary productivity; development risk

Introduction

Habitat loss is one of the leading causes of biodiversity decline worldwide (Newbold et al. 2015, 2016), and by 2100, close to half of the world's ecoregions will be impacted by interactions between habitat loss and climate change (Segan et al. 2016). Habitat loss often impacts regions of high biodiversity or conservation value since these habitats are usually attractive for development or agriculture (Haines-Young 2009, Wintle et al. 2019). The degradation and destruction of natural areas affect species richness, occupancy, and abundance and threaten the population persistence of plants, invertebrates, and vertebrate groups such as amphibians, mammals, and birds (Cushman 2006, De Camargo and Currie 2015, Crooks et al. 2017, Otto et al. 2017, Rossetti et al. 2017). Thus, with the ongoing conversion of natural habitats to urban areas and the threat of urban areas tripling those existing in 2000 in this decade (Seto et al. 2012), there is a need for early indicators of development risk to biodiversity.

Biodiversity assessments combining socioeconomic and environmental factors have demonstrated the importance of both as drivers of biodiversity (Holland et al. 2009, Fidino et al. 2024). For example, increases in economic inequality and higher endemism levels are associated with larger biodiversity loss (Holland et al. 2009); while increasing gentrification and low impervious cover are associated with increases in species richness (Fidino et al. 2024). In this paper, we investigated the usefulness of a socioeconomic variable, the House Price Index (HPI; Federal Housing Finance Agency 2019), as an early indicator of development risk when predicting the effect of non-random habitat loss on biodiversity. In the USA, high HPI values are not always associated with high levels of urbanization or human population size. However, the HPI values can also inform about the lack of supply for increasing housing demands (Deutsch 2015). Thus, HPI is treated here as an indicator that informs about an increase in human interest in an area and the risk of future development to biodiversity in that area. We compared the HPI to the Normalized Difference Vegetation Index (NDVI), used as a measure of primary productivity. Primary productivity is considered one of the major drivers of biodiversity (Gaston 2000), influencing animal distributions and community composition (Pettorelli et al. 2005, 2011).

Theoretical predictions resulting from habitat loss simulations have focused on species richness as a biological index to assess biodiversity change (Rompré et al. 2009, Seabloom et al. 2002). In this paper, we complemented the analysis of changes in species richness following habitat loss with the analysis of changes in two additional biodiversity indices: rarity index and abundance. We used birds as a study group because they have experienced a significant decline in abundance within the last

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five decades in North America and Europe (Rosenberg et al. 2019, Burns et al. 2021) and it is possible that similar trends would be found in less studied areas. We focused on birds of the USA because data sets recording the abundance and occupancy of this taxonomic group are publicly available for this country (Pardieck et al. 2020).

We used random and non-random simulations (i.e. HPI-ordered and NDVI-ordered simulations) to estimate changes in the three aforementioned community indices following habitat loss and then compared results among the different simulation sets. We based our simulations of habitat loss on one of the most robust and general patterns in macroecology, the species-area relationship, which posits that larger areas support higher species richness and abundance (Gaston and Blackburn 2000, Wilson and MacArthur 2016). Large areas experience a heterogeneity of climatic conditions and habitats, making it likely that the geographic distributions of the most common and abundant species overlap with those of the rarest and less abundant species. This overlap increases the communities' overall richness and abundance (Gaston and Blackburn 2000). Therefore, the loss of areas with suitable habitats reduces both the size and the overlap of individual species' geographic distributions, which will be reflected in declines in species richness and increases in species rarity. Abundance may also be affected because, even if the species can disperse to the remaining suitable area, the stability of population size will depend on the quantity and quality of the resources available in the remaining habitat. If resources become limited, this could ultimately lead to declines in population sizes. We can expect these changes in communities' composition regardless of whether the habitat loss is random.

However, when the loss of habitat is not random, and the most suitable areas are lost first, the effects on natural communities are predicted to be stronger than with random loss (Seabloom et al. 2002, Rompré et al. 2009). Thus, we posited that habitat loss ordered by decreasing development risk or vegetation productivity will have an impact higher than random loss on avian community composition, producing steeper losses of species richness and abundance and increases in rarity. Additionally, development risk- and primary productivity-ordered habitat loss will impact woodland, open-habitat, and urban birds differentially. At the local level, we expected that: (i) primary productivity will be positively correlated with the richness, abundance, and rarity of woodland birds and negatively or not correlated to these community indices for open habitat and urban species, and (ii) The development risk of an area will be positively correlated with the local richness, abundance, and rarity of urban and open habitat birds and negatively or not correlated to these community indices for woodland birds. At the regional level, we expect that: (i) the loss of highly productive areas will decrease the richness and abundance and increase the rarity more than what is expected by the loss of areas with high development risk for woodland birds but not for open-habitat and urban birds, and (ii) the loss of areas with high development risk will decrease the richness and abundance and increase the rarity more than what is expected by the loss of high primary productivity areas for urban and open-habitat birds but not for woodland birds.

Methods

Data

Bird survey

We used data on bird occurrence and abundance for the conterminous United States in 2017 from the North American Breeding Bird Survey (i.e. BBS; Pardieck et al. 2020). The BBS is a point count transect survey that has been conducted annually between May and June across the United States since 1966. It has routes measuring 39.2 km. A unique pair of geographic coordinates for each BBS route is assigned at the route start point (Pardieck et al. 2020). Each route is divided into 50 stops placed at ∼800-m intervals. At each stop, a participant conducts a 3-min point count, recording every bird seen or heard within a radius of 400 m. The count begins 30 min before local sunrise and is completed in approximately 5 h. We extracted the county corresponding to each BBS route from the United States County Boundaries map (U.S. Bureau of the Census 2000).

House Price Index (HPI)

As an index of development risk, and thus as a predictor of biodiversity following habitat loss, we used the annual HPI per county for 2017 (Federal Housing Finance Agency 2019). This index is computed using values of the same physical units on repeat transactions, considering only individual single-family residential properties (Calhoun 1996, Bogin et al. 2019). We used the index value for 2017 with a base of 100 in 2000. Thus, changes in house prices since 2000 will be reflected in the 2017 HPI value as percentage increments or reductions from 100. For example, a county with an HPI value of 95 (120) for the year 2017 indicates that house prices have decreased five % (increased 20%) since the year 2000, respectively. Expressing the cumulative change in HPI with the same start year for all areas makes interpreting the changes in the index more straightforward. The 2017 HPI values were very weakly associated with the counties' population size reported in the 2020 census (U.S. Census Bureau 2023) (Pearson's correlation $r = 0.20$, P-value < 0.001). Thus, we interpreted the HPI as an indicator of the risk of development (not as a measure of urbanization). Our rationale was as follows: the more interested people are in living in an area, the more the house price values increase between purchases in that county, and the higher that county's HPI becomes, which can, in turn, inform about the risk of future development for biodiversity.

Selection of BBS routes

For our analysis, we first standardized the county names between the BBS and the HPI data. To each BBS route, we assigned the HPI value of the county containing the route's starting point. While a BBS route might cross from one county into another, we assigned a single HPI value to each route (since adjacent counties tend to have similar HPIs, Fig. 1). Not all USA counties have an HPI value assigned for 2017; thus, we filtered out routes that occurred in counties lacking an HPI value. After applying these filters, we included 2208 routes in our study (Fig. 1).

Species selection and classification

From the total number of species recorded across the 2208 BBS routes, we filtered out unidentified species, hybrids, water birds or seabirds, and species with most of their geographic distribution outside of the USA and Canada. Based on this selection criterion, we included 303 bird species in the study. We then classified each species as a woodland, open-habitat, or urban bird. For the classification of woodland and open-habitat birds, we utilized the species guild list available on the BBS website (https://www.mbr-pwrc.usgs.gov/bbs/guild/guildlst.html) and the species' habitat descriptions provided by the Cornell Ornithology Laboratory (Billerman et al. 2022). Based on these two sources, we considered birds with forests as primary habitat as woodland birds, and birds with grassland, desert, successional

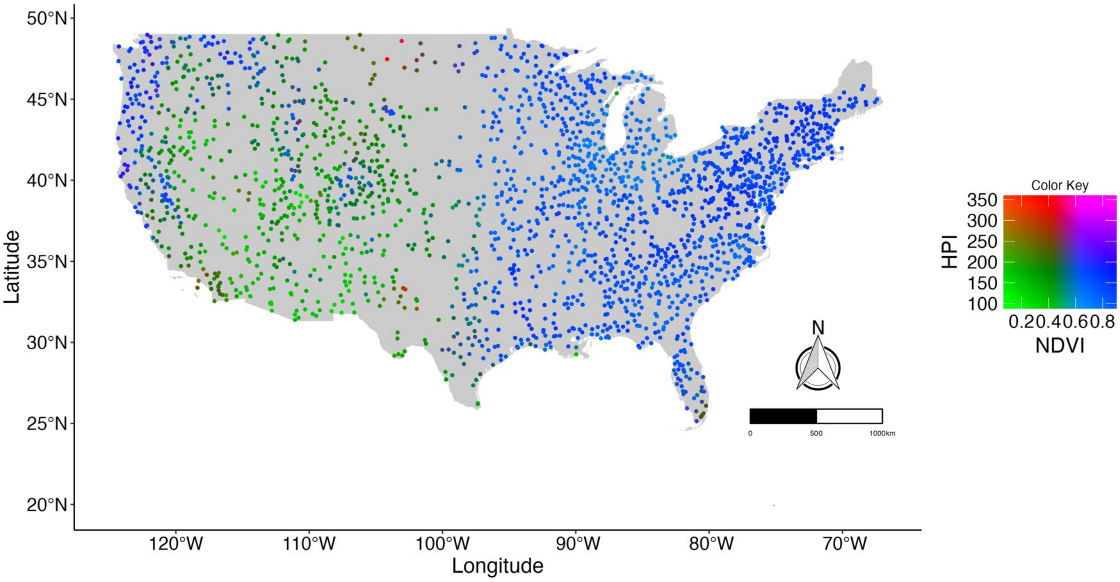

Figure 1. Geographic location of the 2208 Breeding Bird Survey routes in 2017. The color key shows the color of all possible House Price Index and Normalized Difference Vegetation Index (NDVI) combinations. The NDVI values used in this map were extracted using a 25 km radius buffer.

or scrubland, and cliffs as primary habitat were considered as open-habitat species. Birds that reach high abundances and/or nest in urbanized areas were considered urban birds (Blair 1996, Kark et al. 2007), but see Evans et al. (2011) for an alternate framework. Of the 303 species included in the study, 131 were woodland birds, 135 were open-habitat birds, and 37 species were urban. A list of the species names and their classification is shown in Supplementary Table S1. Woodland birds were recorded in 2154 of the BBS routes included in the study, while open-habitat were recorded in 2208 routes, and urban birds were recorded in 2205 routes.

Normalized Difference Vegetation Index (NDVI)

The NDVI is a spectral reflectance measurement that correlates closely with photosynthetic capacity and is commonly used as a proxy for net primary productivity (Kerr and Ostrovsky 2003). We used the NDVI band from the MODIS Terra Vegetation Indices 16-Day Global 1 km dataset v.6 (Didan and Huete 2015) for the months of May to August 2017. We extracted the mean biweekly NDVI value in a 25 km radius buffer around each BBS route coordinate (i.e. the route's starting point). We then estimated the mean NDVI value for each BBS route as the average of the biweekly observations (May–August). The NDVI values reported in the bands were scaled by a factor of 10 000; thus, we rescaled the computed values to the traditional 0–1 scale (Fig. 1). To assess whether the buffer size used to obtain mean NDVI values influenced our results, we additionally extracted NDVI data using buffer radii of 12.5 and 50 km. Results for 12.5 and 50 km buffers did not differ from the 25 km buffer results but are presented in the Supplementary Material.

Distance to the nearest coast and elevation

Non-random habitat loss from coast to inland and from low to high elevation are scenarios previously associated with higher-than-expected species richness loss (Seabloom et al. 2002); thus, we considered them in the analysis. We obtained elevation data from the North America Elevation 1-Kilometer Resolution data set (Commission for Environmental Cooperation (CEC) 2007). However, elevation was strongly correlated to NDVI values ($r \geq 0.6$) and not included in further analyses. We used the Distance to the Nearest Coast Map (1 km resolution) from the National Aeronautics and Space Administration (NASA Ocean Biology Processing Group and Stumpf 2012) to obtain the distance between the starting point of each BBS route and the nearest coast (in km). In this data set, zero represents the coastline, and the distance from the coastline to locations over land is represented with negative numbers. Since all the BBS routes were either inland or on the coast, we multiplied the map by −1 to obtain positive distance values. Distance to the nearest coast was not correlated with other predictors considered in the study ($r < 0.6$); thus, we included it in our models as a control for its impact on biodiversity metrics (see below).

Land cover

We determined the habitat type of each BBS route using the 2015 Land Cover Map of North America at 30 m resolution (Commission for Environmental Cooperation et al. 2020). This map contains 19 land cover categories: six forest types, three grassland types, three shrubland types, two barren land types, wetlands, water, snow and ice, cropland, and urban. We included the proportion of urban and agricultural land cover in areas around each BBS route as control variables in the models (see below). We computed these proportions using buffers with radii of 12.5, 25, and 50 km. We utilized different radius sizes to account for the possible effect of the buffer resolution on the calculation of the proportions. The proportion of BBS routes showing each land cover type as its mode was positively correlated with the proportion of each land cover type in the conterminous USA at 9.6 km resolution (Pearson correlation $r = 0.86$, $P\text{-value} = 0.0002$). Thus, we considered our BBS sample to be representative of the land cover types across the USA.

Community parameter estimates

We characterized local bird assemblages by estimating the per-route richness, abundance, and rarity index for woodland, open-habitat, and urban birds separately. For each of these groups of birds, the species richness per route was estimated as the number of species recorded in the route. The abundance of each bird group per assemblage was estimated by summing the number of individuals of each group recorded at each route. Given the standardized nature of the BBS (Pardieck et al. 2020), we did not correct the abundance estimates to account for the sampling effort. The rarity index per route for each bird group was computed as the sum of the rarity of all species of the group present in the route divided by the group's species richness (i.e. $rarity\ index_k = \frac{\sum_1^{n_k} species\ \ rarity_i}{n_k}$). In the formula, k was the group of species (woodland, open-habitat, or urban) and n_k was the species richness in bird group k. We defined species $rarity_i$ as the reciprocal of the species occupancy, and we estimated it as the reciprocal of the number of routes the species i occupied. Thus, a species found in only one route would have a rarity value of one (maximum possible value), and the less rare the species, the closer to zero its rarity value. We included the species richness of the group (n_k) in the denominator of the rarity index formula to account for possible bias in the rarity index due to differences in the number of species between groups. The value of the rarity index depends on the proportion of rare and unique species in the area, organisms that are frequently more threatened by habitat loss than those common and widespread (Manne and Pimm 2001, Matthews et al. 2014, Pimm et al. 2014).

Local analyses: relationship of biodiversity with HPI and NDVI

We used Generalized Linear regression Models (GLMs) to assess the relationship between local species richness and abundance and HPI and NDVI (both response and predictor variables were not normally distributed). To analyze the influence of group membership (urban/woodland/open-habitat birds), HPI, and NDVI on community metrics, we included an interaction among these variables in the regressions. In addition, we included latitude, distance to the nearest coast, and proportion of urban and crop land cover as control variables in our regressions to account for possible gradients in our community metrics associated with them. We tested for a significant correlation among predictor variables and retained only variables with a correlation coefficient below 0.6. We standardized all numerical predictor variables by subtracting their mean and dividing by their standard deviation. Since the response variables (i.e. richness and abundance) were over-dispersed count data, we used a negative binomial distribution of errors and the log link function to fit the GLMs. We used a significance level of $\alpha = 0.05$ to determine the significance of predictor variables. We performed model diagnostics through visual inspection of residual plots (R package 'DHARMa'). The Q-Q plots of the residuals showed small deviations at the extremes, while the residual versus predicted plots did not show any pattern. The test for outliers was significant for the richness GLM; however, <2.5% of the data points were outliers (outliers: $n = 100$, data points: $n = 6543$). The test for outliers for the abundance GLM was not significant. Given the large number of data points for which the assumptions of the GLMs were met, we chose to continue with them.

We modeled the relationship between this rarity index per route (log-transformed) and the environmental predictors using Generalized Additive Models (GAMs; *gam* function of the 'mgcv' R package). GAMs are used for modeling non-monotonic relationships between variables frequently used in ecology (Wood 2017). GAMs were fitted with a Gaussian distribution of errors and the identity link. All numerical predictor variables were standardized as described above and included in the models as smooth terms. As for the GLMs, we included interactions between HPI, NDVI, and group membership (urban/woodland/open-habitat birds). To determine the significance of predictor variables, we used a significance level of $\alpha = 0.05$. The Q-Q plot of the residuals showed a deviation at the upper extreme, and there was an absence of points for the smaller values in the residual versus predicted plot. The test for outliers was significant; however, <2.5% of the data points were outliers (outliers: $n = 138$, data points: $n = 6543$). To investigate these patterns, we fitted separate GAMs for each bird group. These GAMs included all standardized numerical predictor variables as smooth terms, as well as an interaction term between HPI and NDVI. The patterns in the Q-Q plots and residual versus predicted plots of the GAM containing bird group membership as a variable described above were associated with the open-habitat and urban birds since the GAM for these groups showed the strongest deviations from expectations. These diagnostics indicate that some residual smooth variation is not being captured in the models. Given the large number of data points for which the assumptions of the GAMs were met, we chose to continue with the GAM that included group membership as a variable.

To explore the nature of interaction among HPI, NDVI, and bird group membership in the GLMs and GAM, we utilized three-way interaction plots with HPI as the predictor and NDVI and bird group membership as moderator variables. We divided the NDVI values into three equally sized groups, and the point at the median of each of those groups was chosen for plotting (function *interact_plot* of the 'interactions' R package).

To assess whether the buffer size used to extract mean NDVI values influenced our results, we conducted the regression analyses with NDVI values calculated at different buffer radii (12.5, 25, and 50 km). Only results from the 25 km buffer are presented here; we present results using other buffer sizes in the Supplementary Material.

Regional analyses: habitat loss simulations

At zero percent habitat loss, we estimated the regional richness, abundance, and rarity index of each bird group separately. Thus, these values indicate the regional biodiversity of each bird group before the habitat loss simulations.

Sets of simulations

We ran five sets of simulations for woodland, open-habitat, and urban species separately: (1) random habitat loss, (2) HPI simulation: habitat loss eliminating routes by declining HPI value (i.e. from highest to the lowest development sprawling risk), and (3–5) NDVI simulations: habitat loss eliminating routes by declining NDVI value (i.e. from the most productive to the less productive areas). We performed simulations (3, 4, and 5) using NDVI values extracted with a 25/12.5/50 km buffer, respectively. We ran simulations (4) and (5) to assess the effect that different sizes of the buffer used to obtain mean NDVI values could have on our results.

Sampling of habitat (BBS routes)

We considered as total habitat the number of BBS routes in which each group of birds was present before habitat loss. Thus, we worked with a pool of 2154 routes for woodland birds, 2008 routes for open-habitat, and 2205 routes for urban birds as the initial amount of habitat for each group. For the random simulation set, we simulated habitat loss by randomly selecting (without replacement or ties) a sample size equal to 5% of the total habitat ($n = 108$ routes for woodland birds and $n = 110$ for open-habitat and urban birds). Once a route was selected, it was eliminated from the pool of routes and not included in the subsequent sampling. Thus, at each iteration of the simulation, the size of the pool of routes decreased by five percent of the total habitat (i.e. we conducted habitat loss simulation at 5% increments). We continued this process until 95% of all routes were selected and eliminated from the pool. Note that the sample size for the random selection of routes was always $n = 108$ routes for woodland birds and $n = 110$ for open-habitat and urban birds, independently of the number of routes remaining in the pool at each iteration. We repeated the simulation process 100 times. For the four sets of non-random habitat loss simulations (i.e. one HPI-ordered and three NDVI-ordered simulations), we started with a pool of 2154 routes for woodland birds, 2208 routes for open-habitat, and 2205 routes for urban birds (i.e. the total habitat for each group), and the route selection process consisted of two steps. First, we ordered the routes by the decreasing values of the variable (HPI or NDVI). We selected a pre-sample containing the routes with the highest unique 216 (220) values for woodland (open-habitat and urban birds), including ties (*slice_max* function, R '*dplyr*' package). The sample size of the pre-sample for woodland birds ($n1 = 216$) and for open-habitat and urban birds ($n1 = 220$) corresponds to 10% of the total habitat for each group. Second, from the pre-sample, we simulated habitat loss by randomly selecting (without replacement or ties) a sample size equal to five percent of the total habitat ($n2 = 108$ routes for woodland birds and $n2 = 110$ for open-habitat and urban birds). The routes selected in this second step were eliminated from the pool of routes and not included in the subsequent sampling. The routes not selected in this second step were returned to the initial pool of routes. Thus, at each iteration of the simulation, the size of the pool of routes decreased by five percent of the total habitat and steps one and two were repeated using the updated pool of routes (i.e. we conducted habitat loss simulation at 5% increments). As mentioned above, we conducted the habitat loss simulation until 95% of all routes were selected and eliminated from the pool. The sample sizes for the pre-sample in step one and the random sample in step two were always the same (pre-sample: $n1 = 216$ or 220 and sample: $n2 = 108$ or 110), independently of the number of routes remaining in the pool of routes at each iteration. We iterated this simulation process 100 times for each simulation set.

Simulating local extinction following habitat loss

Independently of the group of birds or simulation set, once a group of routes was selected, we simulated the local extinction of species following habitat loss by eliminating the selected routes from the pool of routes, which is equivalent to setting to zero the occurrence and abundance of the species present in these routes. Then, we re-estimated the regional species richness, abundance, and rarity index across the remaining routes. We re-calculated the abundance and rarity index based on individuals of all species present in the remaining habitat. In this instance, we computed the rarity index by adding the re-calculated rarity value of each species present in the remaining habitat and dividing this sum by the species richness re-calculated for the remaining area.

Statistical analysis

For each group of birds and community metric, we compared the regional estimates resulting from the random, HPI-ordered, and NDVI-ordered simulations at each percentage of habitat lost (i.e. we conducted habitat loss simulation at 5% increments) using an analysis of variance (ANOVA). We considered ANOVA an appropriate choice since the sample sizes were large and equal for the three simulation groups compared ($n = 100$ for random, HPI-ordered, and NDVI-ordered simulations, respectively), which makes the ANOVA test robust to violations of the assumptions of normality and homogeneity of variance among groups. We performed the ANOVA for each NDVI buffer size simulation set. We followed significant ANOVAs with a post hoc Tukey-Kramer analysis.

Results

Relationship between development risk, primary productivity, and local bird biodiversity before the habitat loss simulations

The local richness of woodland birds was predicted to be lower than that of open-habitat birds but higher than that of urban birds; however, these differences were small (Table 1). The local abundance of woodland birds was predicted to be lower than for open-habitat and urban birds; the difference being more marked between woodland and urban birds (Table 1). Increases in both development risk (HPI) and primary productivity (NDVI) were associated with increases in the richness and abundance of local bird assemblages; however, the main effect of development risk on these metrics was smaller than that of primary productivity (Table 1). The main effects of development risk, primary productivity, and the group of birds on local bird richness and abundance were modulated by interactions among these predictors. Areas with high development risk (high HPI values) and intermediate to high primary productivity were associated with high local woodland bird richness and abundance (Table 1, Fig. 2A and D). The local richness and abundance of open-habitat (Fig. 2B and E) and urban species (Fig. 2C and F) per bird assemblage declined with development risk (increases in HPI) at all levels of primary productivity.

The rarity index per bird assemblage was predicted to be higher for woodland birds than for open-habitat and urban birds; the difference being more marked between woodland and urban birds (Table 1). Although the main effects of development risk and primary productivity on the local rarity index were non-significant, these predictors interacted with group membership, affecting the rarity index. For woodland birds, the local rarity index showed a pattern similar to their richness and abundance (Fig. 2G). For open-habitat birds, the local rarity index tended to increase with the risk of development at low and high values of primary productivity (Fig. 2H). Comparatively, the local rarity index did not vary considerably at intermediate values of primary productivity (Fig. 2H). In the case of urban birds, the local rarity index did not vary with increased development risk in high primary productivity areas (Fig. 2I). At intermediate primary productivity levels, the local rarity index of urban birds slightly declined with increases in development risk. In areas with low levels of primary productivity, the local rarity index of urban birds slightly increased at intermediate risk of development (Fig. 2I).

Our models predicted local biodiversity changes associated with the control variables (Table 1). Local species richness increased northward and declined with increases in the proportion of croplands. Local bird abundance increased with increases in the proportion of cropland areas and declined farther from the coasts. The trends that the GAM predicted for the local rarity index were less marked. In general, the rarity index tended to slightly increase with latitude and the proportion of urban land, and slightly decline with the proportion of cropland and distance to the coast.

The effects of the two-way interactions between the bird group, the attractiveness of an area for development, and

Table 1. Standardized coefficients table for models relating environmental predictors and the species richness, abundance, or rarity index of bird assemblages in the USA, for the year 2017.[a]

Predictor	Richness (GLM)	Abundance (GLM)	Rarity index (GAM)^
Open-habitat birds	0.17***	0.63***	−0.14***
Urban birds	−0.11***	0.75***	−0.91***
HPI	0.03***	0.15***	—
NDVI	0.50***	0.58***	—
HPI: NDVI	0.05***	0.12***	***
HPI: Woodland birds	(baseline)	(baseline)	**
HPI: Open-habitat birds	−0.10***	−0.19***	*
HPI: Urban birds	−0.14***	−0.28***	—
NDVI: Woodland birds	(baseline)	(baseline)	***
NDVI: Open-habitat birds	−0.59***	−0.82***	***
NDVI: Urban birds	−0.31***	−0.36***	***
HPI: NDVI: Woodland birds	(baseline)	(baseline)	***
HPI: NDVI: Open-habitat birds	−0.08***	−0.16***	***
HPI: NDVI: Urban birds	−0.07***	−0.14***	***
Latitude	0.02***	—	***
Proportion of urban land	—	—	***
Proportion of cropland	−0.01*	0.07***	***
Distance to coast	—	−0.03**	***
Deviance explained	39.94%	28.23%	65.36%

[a] HPI: House Price Index; NDVI: Normalized Difference Vegetation Index; GLM: Generalized Linear Model, GAM: Generalized Additive Model. For the GLMs and the parametric coefficients of the GAM, open-habitat and urban birds' results are in comparison to the woodland birds (treated as baseline). Significant *P*-values are represented as follows: ***$P < 0.001$, **$P < 0.01$, *$P < 0.05$. Non-significant predictors are denoted with a dash. We also present the proportion of the variability explained by the model (Deviance Explained). NDVI and the proportion of urban and crop land cover were calculated using a 25 km buffer around the BBS route. ^Coefficients for the GAM are shown for the parametric terms when significant. For the smooth terms, only their significance is shown.

primary productivity on local richness, abundance, or rarity index, were included in Supplementary Materials (Supplementary Figs S1 and S2). Sensitivity analyses showed that increasing the resolution of the buffer to extract NDVI, did not drastically change the effect of most predictors on the local community metrics (Supplementary Table S2, Supplementary Fig. S3). For exceptions in this general pattern, see Supplementary Materials.

Development risk predicting the effects of habitat loss on regional breeding birds' biodiversity

Habitat loss from high to low development risk produced shallow species-area relationship (SAR) curves at the regional scale (Fig. 3A–C). On average, more than 50% of the woodland species, 39% of the open-habitat species, and 80% of the urban species were still present in the sample when only 5% of the habitat remained.

For woodland birds, losing the top 25% of the development risk areas produced larger regional richness declines than losing the top 25% of the primary productivity areas or random habitat loss (Fig. 3A, Supplementary Table S6). Lower regional woodland bird richness estimates than those predicted by primary productivity or random habitat loss were also predicted between 55% to 70% of habitat loss by development risk (Fig. 3A, Supplementary Table S6). For open-habitat birds, the development risk consistently predicted larger regional richness declines than primary productivity-ordered or random habitat loss after 15% of habitat loss (Fig. 3B, Supplementary Table S6). For urban birds, development risk predicted regional richness lower than primary productivity or random habitat loss after 35% of habitat loss (Fig. 3C, Supplementary Table S6).

As a predictor of regional abundance following habitat loss, development risk predicted larger declines than primary productivity or random habitat loss only for open-habitat birds (Fig. 3E, Supplementary Table S7). For woodland birds, the loss of high to low primary productivity areas predicted larger regional abundance declines than the loss of high to low development risk areas and random habitat loss (Fig. 3D, Supplementary Table S7). In the case of urban birds, primary productivity better predicted regional abundance declines than development risk, particularly after 25% of habitat loss (Fig. 3F, Supplementary Table S7).

Habitat loss from high to low development risk areas always produced regional rarity indices higher than those predicted by loss of high to low primary productivity areas or random habitat loss for open-habitat and urban birds (Figs 3H and I, Supplementary Table S8). For woodland birds, regional rarity indices higher than those predicted by primary productivity-ordered habitat loss were obtained with the loss of areas with intermediate development risk values (Figs 3G, Supplementary Table S8).

Sensitivity analyses showed that, for all groups of birds, changing the size of the buffer to extract NDVI did not affect the general regional patterns of richness, abundance, and rarity index obtained from the NDVI-ordered simulations of habitat loss (Supplementary Fig. S3, Supplementary Tables S3–S11). Results of the comparisons between random habitat loss and development risk-ordered habitat loss or between random habitat loss and primary productivity-ordered habitat loss are included in Supplementary materials.

Discussion

Sprawling urban development (horizontal, cross-landscape expansion) is more harmful to biodiversity than compact urban development (e.g. vertical expansion or infilling) (Sushinsky et al. 2013), particularly for the species that depend on natural habitat (Geschke et al. 2018). Previous studies have simulated the loss of habitat due to sprawling or compact urban growth and then estimated subsequent biodiversity change (Gagné and Fahrig 2010, Sushinsky et al. 2013, 2017). The simulation approach we used is different in that it illustrates a habitat loss scenario that can include sprawling development and/or placement of compact and dense buildings or infilling. In any case, the selected areas were

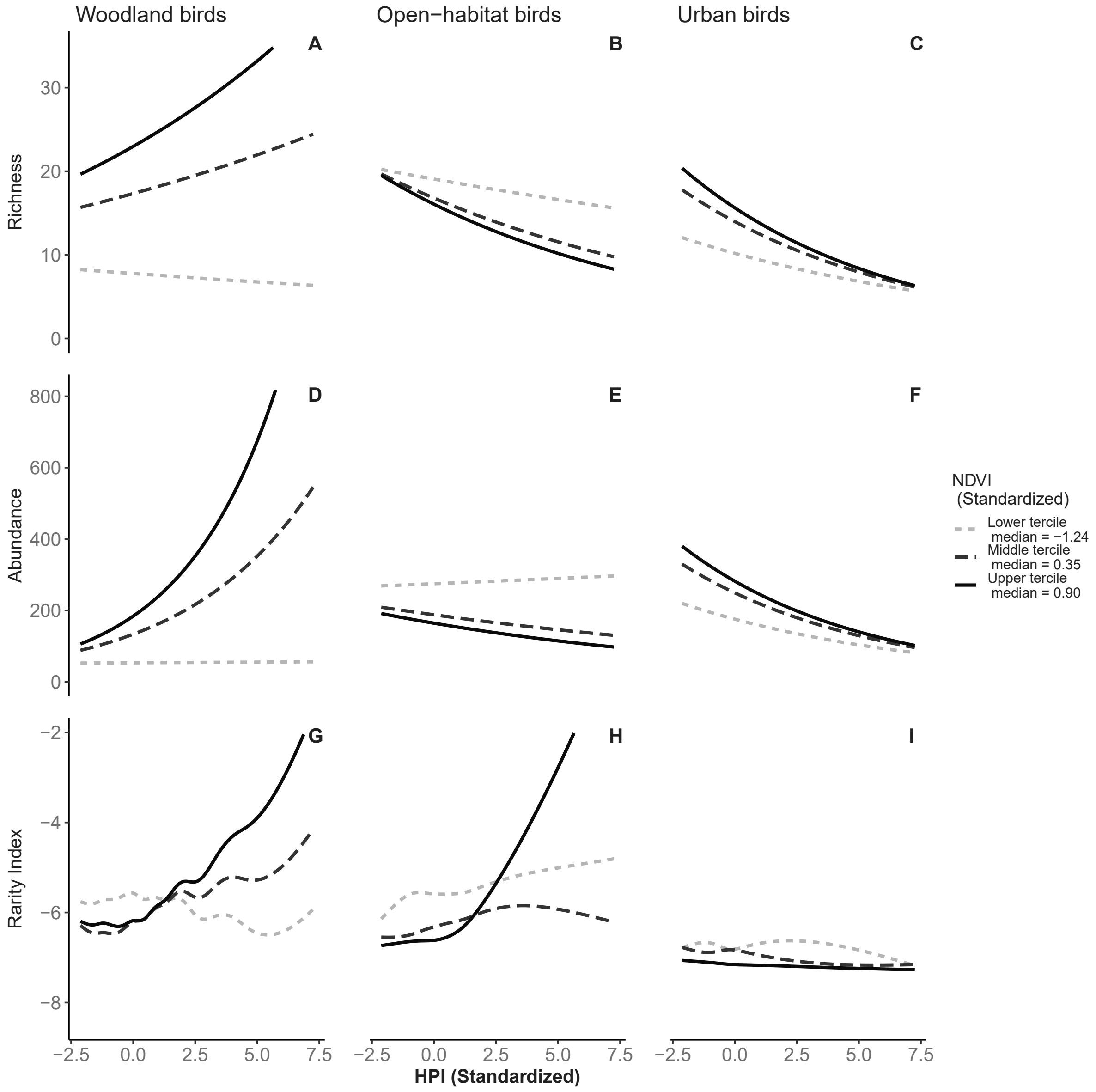

Figure 2. Interaction plots for the relationship between House Price Index (HPI), Normalized Difference Vegetation Index (NDVI), and group membership (i.e., woodland, open-habitat, or urban birds), and the species richness (A–C), abundance (D–F), or rarity index -log-transformed- (G–I) of bird assemblages in the USA, for the year 2017. NDVI was extracted with a buffer of a 25 km radius around the initial point of the BBS routes.

assumed to be completely modified into a human-made landscape and thus totally unsuitable for the bird species once found there.

The HPI was not a direct measure of urbanization, and not all high-HPI values were in cities or suburbs. Further, we did not correct the HPI by state or region. Thus, areas that had high growth in HPI values were not necessarily areas with high absolute dollar values or human population values (see Table 2, most of the top 15 HPI values in our analysis are in areas with lower human populations). However, high HPI areas could be areas with high value for species, as demonstrated by our results. Conserving these areas could incur minimal costs yet yield a high biodiversity value. High HPI values can be associated with exurban growth and risk of development and, thus, a risk of not acting for conservation (because human interest in the areas is increasing).

Development risk interacts with primary productivity in predicting local bird biodiversity

Because of interactions between primary productivity and development risk, there were different responses of local richness and abundance to these two predictors among the three bird groups. Woodland bird richness, abundance, and rarity index increased with higher development risk for high and intermediate primary productivity values. This makes sense because urban areas with large green spaces provide heterogeneous environmental conditions that support higher levels of avian richness than cities with small or no green spaces (Callaghan et al. 2018, Leveau 2021). A similar effect of primary productivity could explain the higher estimates of the richness, abundance, and rarity index of woodland birds in high-development risk areas. However, the sites with the highest risk of development were areas that were not in

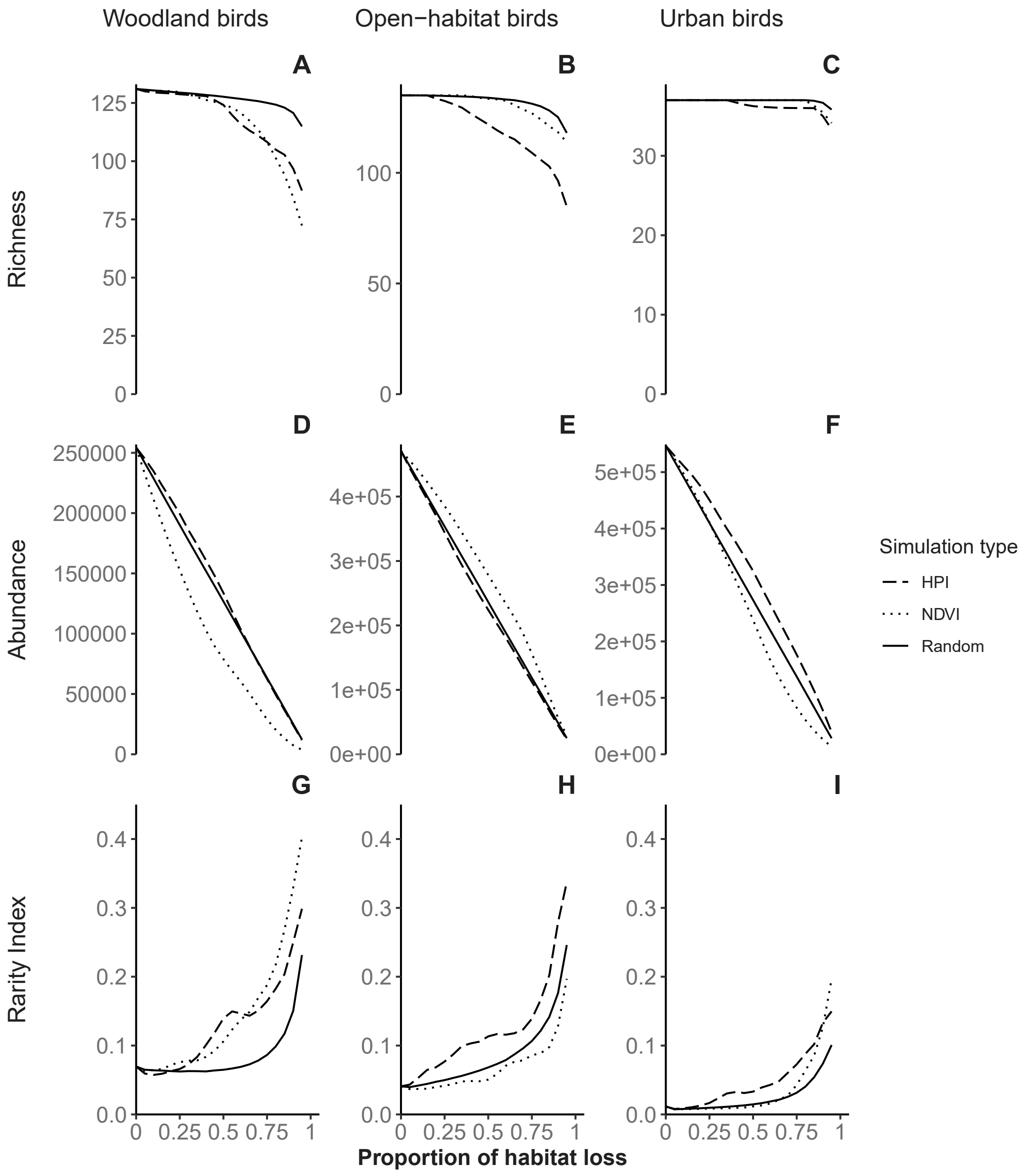

Figure 3. Effect of habitat loss on regional biodiversity. (A–C) Species Richness, (D–F) Abundance, and (G–I) Rarity Index of three groups of birds: woodland (left), open-habitat (center), and urban birds (right) during 2017. Habitat loss was simulated at 5% increments. Solid lines indicate the mean value of the biodiversity indices across 100 random simulations. Dashed lines indicate the mean value of the biodiversity indices across 100 HPI-ordered simulations (HPI: House Price Index). Dotted lines indicate the mean value of the biodiversity indices across 100 NDVI-ordered simulations (NDVI: Normalized Difference Vegetation Index).

Table 2. The top 15 2017 House Price Index values included in the analyses and the county population density as of 2020.

State	County	HPI	Population density per mile^2
Montana	Richland	353.53	5.51
North Dakota	Williams	347.80	19.71
Texas	Yoakum	281.28	9.62
Texas	Midland	272.46	188.80
North Dakota	Stark	266.62	25.20
North Dakota	Mercer	263.38	8.01
Nevada	White Pine	246.96	1.02
California	Los Angeles	245.10	2466.95
Montana	Valley	237.99	1.54
Wyoming	Teton	236.2	5.84
Texas	Andrews	235.89	12.40
Oregon	Hood River	234.93	45.93
North Dakota	McLean	228.63	4.63
Montana	Custer	228.56	3.14
North Dakota	Ward	228.15	34.73

cities (see Table 2). Therefore, we cannot directly compare these results to the literature because we did not assess the impact of urbanization directly. The use of indices of potential future development as predictors of biodiversity is an area that requires more study.

For open-habitat birds, local richness and abundance declined with higher development risk across all primary productivity values. However, at the lowest levels of primary productivity, the richness and abundance values were the highest, and their decline with the increase in development risk was less marked than for intermediate/high primary productivity areas. Open-habitat birds were less dependent on primary productivity at the level of the sampling unit, which was expected since open-habitat ecosystems like grasslands and shrublands are among the less productive ecosystems of temperate terrestrial biomes (Melillo et al. 1993, Rafique et al. 2016). The rarity index of these birds increased with the risk of development at both high and low productivity values. At the highest levels of risk of development, we would expect to find the rarest open-habitat species at locations of low primary productivity but not of high primary productivity. A potential explanation for this unexpected result is that if areas of high risk for development with high primary productivity values contain a heterogeneous landscape with sufficient open spaces, the rarest open-habitat species may be also found there. Nevertheless, there was some uncaptured variability in the model for the rarity index. Thus, there are almost certainly unmeasured variables affecting the relationship between risk for development and the rarity index at locations with high primary productivity.

In the case of urban birds, local richness and abundance also declined with higher development risk across all primary productivity values, although less markedly at low primary productivity locations. This pattern is possible because the risk of development is not necessarily linked with existing urban centers, where this group may be present in higher numbers. Urban birds tended to be slightly more common in high-development risk areas with intermediate primary productivity and rarer in intermediate-development risk areas with low primary productivity, presumably due to this group's tolerance of human activities (Samia et al. 2015). Further, the rarity regression models for the urban birds showed a larger amount of uncaptured variation than those for the woodland and open habitat birds. Clearly, in the locations that we studied, urban birds demonstrated a large amount of variability, not behaving as a unified group (Marzluff 2017).

Development risk as a predictor of regional biodiversity of breeding birds

At the regional level, losing the areas with the highest development risk values (i.e. the top 25% of values) did not drastically affect the richness and rarity index of breeding birds. This pattern was also observed when areas with higher primary productivity were lost, even though high development risk was not correlated with high primary productivity. Thus, the same species present in areas of the highest development risk or primary productivity could be found in areas of lower development risk or primary productivity, with a relatively high percentage of species remaining even in the last 5% of the habitat. This pattern arises when assemblages include many common, widespread species (Rybicki and Hanski 2013) since these species are generally less sensitive to habitat loss than more specialized species (Matthews et al. 2014). Furthermore, USA biomes have experienced land use changes mostly since the European settlement (Steyaert and Knox 2008, Whitlock et al. 2018, Li et al. 2023), but the speed of these changes has declined or stabilized in the last century, particularly the land conversion to cropland or pastures (Haines-Young 2009, Franco-Solís and Montanía 2021, Li et al. 2023). Thus, it may be that regional bird assemblages in the USA are more robust to reduced habitat areas, perhaps being more vulnerable to other human disturbances such as introduced/invasive species that compete for resources (Murphy and Romanuk 2014). The results from this study align with those reported by Desrochers et al. (2011) and De Camargo and Currie (2015) in northern temperate forests, where the authors estimate that almost 50% of the natural area can be turned into a human-modified landscape before there are adverse effects on total bird richness (i.e. 44% in Desrochers et al. 2011 and 47% in De Camargo and Currie 2015).

After the loss of areas with the highest values of primary productivity or development risk, further habitat loss differentially impacted the biodiversity of the three groups of birds. We treat each group separately below.

Woodland birds

At intermediate levels of habitat loss, the richness of woodland species declined, and their irreplaceability increased. The differences in these indices between development risk and primary productivity simulations were significant but relatively small. Thus, areas of intermediate values (either development risk or primary productivity) became important for preventing regional richness loss (Marzluff 2017) and increases in the rarity index of woodland birds. It is possible that there was an interaction between development risk and primary productivity for this group, similar to what we found at the local level. Interrelations between environmental factors (such as low amounts of impervious surfaces) and socioeconomic factors (such as increases in high-income residents) have also been associated with increased species richness (of mammals) across the USA (Fidino et al. 2024). However, with a low quantity of habitat remaining (75% of habitat loss), areas of low development risk could support higher richness and lower rarity index values than areas of low primary productivity. In the case of woodland bird abundance, the rate of decline was always greatest when the loss was ordered by primary productivity, having the steepest declines of the three groups. Thus, the more productive areas supported higher numbers of individuals. Although areas of high to intermediate risk for development are important to maintain high richness levels and low rarity index of these birds, primary productivity appears to be more important for maintaining bird abundance. This result underscores the importance of understanding the link between development risk and primary productivity and how they relate to woodland bird biodiversity.

Open-habitat birds

The biodiversity of open-habitat birds was the most affected by the loss of areas with intermediate development risk. The declines in abundance and increases in the irreplaceability of species were always larger in development risk simulations than in primary productivity simulations. Once 15% of habitat had been lost; richness declined more rapidly when areas with higher development risk were lost, compared to loss of higher productivity areas. Thus, species found in areas with high to intermediate development risk were not as reliably found within areas of lower development risk, and areas of high development risk were important to maintaining the abundance of open-habitat birds. Because open habitat birds are mostly associated with low primary productivity areas (Fetcher et al. 2023), it is not surprising that losing high productivity areas caused little effect on the richness and rarity index of these birds. Most of the top 15 development risk values in the study were from Great Plains states (i.e. Montana, North Dakota, Wyoming, Texas), where grasslands predominate. Future development in these areas could contribute to the degradation of an ecosystem already threatened globally by agricultural land conversion (Douglas et al. 2023). These results underscore the importance of areas of intermediate to high development risk for the conservation of open-habitat species at a regional level, particularly grassland birds.

Urban birds

Urban birds had the lowest rarity indices of the three bird groups, and roughly 80% of the species were still present after 95% of the habitat was lost. Thus, high values of regional richness and low values of rarity index for urban birds could be maintained in areas of all values of development risk and primary productivity levels, as could be expected of generalist or phenotypically plastic species (Evans et al. 2011, Marzluff 2017). Further, abundance equal to or higher than the expected with random habitat loss could be supported in areas with intermediate to low primary productivity and across all levels of development risk. With continuous habitat loss due to urban expansion, bird assemblages might experience a transition from woodland-dominated to open-habitat-dominated to urban-dominated assemblages and, ultimately, biotic homogenization since this last group of generalist species has a higher tolerance to human-altered environments than more specialized groups (Callaghan et al. 2020).

General considerations

The land cover map utilized in the analysis only included croplands and urban land cover as a representation of human-modified land covers. Thus, the additional effect that other human-modified habitats (for example, mining areas or tree-logging zones) may have in the diversity of groups like woodlands and open-habitat birds (Desrochers et al. 2011) could not be reflected in the regression models.

The habitat loss simulations were snapshots of potential biodiversity impacts under habitat loss ordered by development risk or primary productivity, and the number of species/individuals lost may have been underestimated. Even when species richness was predicted to be high at 95% of habitat loss, processes such as extinction debt (Tilman et al. 1994, Vellend et al. 2006, Savage and Vellend 2015) can exacerbate the results presented here. In the long term, the number of species supported by five percent of suitable habitat would be affected by competition (Buchmann et al. 2013) for extremely limited resources (see Askins et al. 2007 for an analysis of habitat loss in grassland birds), which could lead to lower total richness values than the ones the simulations in this study have predicted. Other sources of underestimation of richness loss may be that the simulations in this study addressed macroecological patterns that did not include the effects of habitat fragmentation (Rybicki and Hanski 2013) or complex environmental processes such as climate change, species characteristics, or biological interactions present in real ecosystems (Manne et al. 2007, Swift and Hannon 2010, Buchmann et al. 2013, Pimm et al. 2014). Likewise, the abundance values predicted here may be overestimated and should not be extrapolated to viable populations. A reduced natural habitat will probably be insufficient to maintain the viability of populations of a large number of species (Desrochers et al. 2011, Rybicki and Hanski 2013) in the long term, because the abundance that a small amount of habitat can support will be limited (Bender et al. 1998, Tilman et al. 1994, Swift and Hannon 2010, Halley and Iwasa 2011, He and Hubbell 2011). However, our simulation approach was based on setting the occurrence and abundance of all species in the areas lost to zero. This was an extreme scenario, and as stated above, biodiversity declines may happen more slowly with gradual habitat loss (Devictor et al. 2008).

Another methodological consideration is that the HPI was not necessarily correlated to current levels of development. Thus, two counties with different levels of development and net house prices may have experienced similar proportional increases in the value of the houses since 2000 (i.e. have similar HPI values). For example, on the 99th percentile of HPI values in the sample, there were four BBS routes in North Dakota in counties containing only 0.26% urban area, compared to four BBS routes in California, in a county containing 35.06% urban area (United States Census Bureau 2010). A high HPI value reflects local conditions and rapid growth relative to places nearby. For example, in the past two decades, North Dakota has experienced a rapid population increase resulting from the growth of the oil and natural gas industries and the associated increase in the job market (Archbold et al. 2014). Although the HPI cannot be interpreted as a direct measure of current development risk,—because it does not contain information about increases in commercial buildings or multi-family residences—it does inform about areas becoming increasingly attractive for humans. These areas will more likely undergo substantial anthropogenic disturbances in the future if the increases in house prices lead to new housing developments and the urban growth that usually comes with it. Further, we have compared the performance of HPI as a predictor of biodiversity following habitat loss with an environmental predictor. A future step would be to compare the performance of HPI to other socioeconomic indices.

Conclusion

Conservation efforts in areas of high development risk may be an economically viable option to maintain regional bird biodiversity. Areas of intermediate to high development risk supported high regional richness and abundance and low rarity index of open-habitat birds. These areas may be particularly important for the conservation of specialized species like grassland birds, which are globally threatened. Increasing the primary productivity of high development risk areas by retaining or including green spaces of heterogeneous vegetation in development plans could contribute to the high richness and low rarity index of woodland species at the regional level. Our study is the first to investigate the usefulness of HPI as a measure of development risk, and as a predictor of indices of biodiversity. Our results support including socioeconomic and ecological variables in conservation assessments of the impact of anthropogenic change on local and regional diversity. Last, proactively recognizing high development risk areas affords more time for conservation practitioners and land managers to formulate targeted conservation plans for those areas.

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Author contributions

Marlen Acosta Alamo (Conceptualization [supporting], Data curation [lead], Formal analysis [lead], Methodology [equal], Visualization [lead], Writing—original draft [lead], Writing—review & editing [equal]), Lisa L. Manne (Conceptualization [lead], Formal analysis [supporting], Funding acquisition [lead], Methodology [equal], Project administration [lead], Supervision [lead], Writing—review & editing [equal]), and Richard R. Veit (Data curation [supporting], Writing—review & editing [supporting])

Supplementary data

Supplementary data is available at *JUECOL* online.

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Data availability

The data that support the results of this study are openly available from the North American Breeding Bird Survey [https://www.pwrc.usgs.gov/BBS/RawData/], the U.S. Bureau of the Census [https://www.sciencebase.gov/catalog/item/4f4e4a2ee4b07f02db615738], the Commission for Environmental Cooperation [http://www.cec.org/north-american-environmental-atlas/land-cover-30m-2015-landsat-and-rapideye/], the Federal Housing Finance Agency [https://www.fhfa.gov/DataTools/Downloads/Pages/House-Price-Index-Datasets.aspx#atvol], the U.S. Geological Survey [https://lpdaac.usgs.gov/products/mod13a2v006/], the NASA [https://oceancolor.gsfc.nasa.gov/docs/distfromcoast/]

References

Archbold CA, Dahle T, Jordan R. Policing "The Patch": police response to rapid population growth in oil boomtowns in western North Dakota. *Police Q* 2014;**17**:386–413. https://doi.org/10.1177/1098611114549629

Askins RA, Chávez-Ramírez F, Dale BC *et al.* Conservation of grassland birds in North America: Understanding ecological processes in different regions. *Ornithol Monogr* 2007;**64**:1–46. http://dx.doi.org/10.1525/0078-6594(2007)64[1:COGBIN]2.0.CO;2

Bender DJ, Contreras TA, Fahrig L. Habitat loss and population decline: a meta-analysis of the patch size effect. *Ecology* 1998;**79**:517–33. https://doi.org/10.1890/0012-9658

Billerman SM, Keeney BK, Rodewald PG, Schulenberg TS (eds). *Birds of the World*. Cornell Laboratory of Ornithology, 2022. https://birdsoftheworld.org/bow/home

Blair RB. Land use and avian species diversity along an urban gradient. *Ecol App* 1996;**6**:506–19. https://doi.org/10.2307/2269387

Bogin A, Doerner W, Larson W. Local house price dynamics: new indices and stylized facts. *Real Estate Econ* 2019;**47**:365–98. https://doi.org/10.1111/1540-6229.12233

Buchmann CM, Schurr FM, Nathan R *et al.* Habitat loss and fragmentation affecting mammal and bird communities—the role of interspecific competition and individual space use. *Ecol Inf* 2013;**14**:90–8. https://doi.org/10.1016/j.ecoinf.2012.11.015

Burns F, Eaton MA, Burfield IJ *et al.* Abundance decline in the avifauna of the European Union reveals cross-continental similarities in biodiversity change. *Ecol Evol* 2021;**11**:16647–60. https://doi.org/10.1002/ece3.8282

Calhoun CA. *OFHEO House Price Indexes: HPI Technical Description*. Office of Federal Housing Enterprise Oversight, 1996. https://www.fhfa.gov/PolicyProgramsResearch/Research/PaperDocuments/1996-03_HPI_TechDescription_N508.pdf

Callaghan CT, Benedetti Y, Wilshire JH *et al.* Avian trait specialization is negatively associated with urban tolerance. *Oikos* 2020;**129**:1541–51. https://doi.org/10.1111/oik.07356

Callaghan CT, Major RE, Lyons MB *et al.* The effects of local and landscape habitat attributes on bird diversity in urban greenspaces. *Ecosphere* 2018;**9**:e02347. https://doi.org/10.1002/ecs2.2347

Commission for Environmental Cooperation (CEC). *North America Elevation 1-Kilometer Resolution*, 3rd edn. Natural Resources Canada (NRCan), Instituto Nacional de Estadística y Geografía (INEGI), U.S. Geological Survey (USGS), 2007. http://www.cec.org/north-american-environmental-atlas/shaded-relief-2007/

Commission for Environmental Cooperation (CEC), Canada Centre for Remote Sensing (CCRS), Earth Sciences Sector et al. *2015 Land Cover of North America at 30 meters v.2*. [Map], 2020. http://www.cec.org/north-american-environmental-atlas/land-cover-30m-2015-landsat-and-rapideye/

Crooks KR, Burdett CL, Theobald DM *et al.* Quantification of habitat fragmentation reveals extinction risk in terrestrial mammals. *Proc Natl Acad Sci U S A* 2017;**114**:7635–40. https://doi.org/10.1073/pnas.1705769114

Cushman SA. Effects of habitat loss and fragmentation on amphibians: a review and prospectus. *Biol Conserv* 2006;**128**:231–40. https://doi.org/10.1016/j.biocon.2005.09.031

De Camargo RX, Currie DJ. An empirical investigation of why species–area relationships overestimate species losses. *Ecology* 2015;**96**:1253–63. https://doi.org/10.1890/13-2362.1

Desrochers RE, Kerr JT, Currie DJ. How, and how much, natural cover loss increases species richness. *Glob Ecol Biogeogr* 2011;**20**:857–67. https://doi.org/10.1111/j.1466-8238.2011.00658.x

Deutsch T. Planning and monitoring of urban development: the role of the housing price index. *Econ Bus Rev* 2015;**17**:165–84. https://doi.org/10.15458/85451.3

Devictor V, Julliard R, Couvet D *et al.* Birds are tracking climate warming, but not fast enough. *Proc R Soc B* 2008;**275**:2743–8. https://doi.org/10.1098/rspb.2008.0878

Didan D, Huete A. *MOD13A2 MODIS/Terra Vegetation Indices 16-Day L3 Global 1km SIN Grid*. NASA LP DAAC, 2015. http://doi.org/10.5067/MODIS/MOD13A2.006

Douglas DJT, Waldinger J, Buckmire Z *et al.* A global review identifies agriculture as the main threat to declining grassland birds. *Ibis* 2023;**165**:1107–28. https://doi.org/10.1111/ibi.13223

Evans KL, Chamberlain DE, Hatchwell BJ *et al.* What makes an urban bird?: what makes an urban bird? *Glob Chang Biol* 2011;**17**:32–44. https://doi.org/10.1111/j.1365-2486.2010.02247.x

Federal Housing Finance Agency. *Annual House Price Indexes Counties (Developmental Index; Not Seasonally Adjusted)*. 2019. https://www.fhfa.gov/DataTools/Downloads/Pages/House-Price-Index-Datasets.aspx#atvol

Fetcher N, Stratford JA, Steele MA *et al.* Species diversity, primary productivity, and photosynthetic pathway in grasslands of eastern Pennsylvania. *Ecosphere* 2023;**14**:e4532. https://doi.org/10.1002/ecs2.4532

Fidino M, Sander HA, Lewis JS *et al.* Gentrification drives patterns of alpha and beta diversity in cities. *Proc Natl Acad Sci U S A* 2024;**121**:e2318596121. https://doi.org/10.1073/pnas.2318596121

Franco-Solís A, Montanía CV. Dynamics of deforestation worldwide: a structural decomposition analysis of agricultural land use in South America. *Land Use Policy* 2021;**109**:105619. https://doi.org/10.1016/j.landusepol.2021.105619

Gagné SA, Fahrig L. The trade-off between housing density and sprawl area: minimising impacts to forest breeding birds. *Basic Appl Ecol* 2010;**11**:723–33. https://doi.org/10.1016/j.baae.2010.09.001

Gaston KJ. Global patterns in biodiversity. *Nature* 2000;**405**:220–7. https://doi.org/10.1038/35012228

Gaston KJ, Blackburn TM. *Pattern and Process in Macroecology*. Blackwell Science Ltd, 2000.

Geschke A, James S, Bennett AF *et al.* Compact cities or sprawling suburbs? Optimising the distribution of people in cities to maximise species diversity. *J Appl Ecol* 2018;**55**:2320–31. https://doi.org/10.1111/1365-2664.13183

Haines-Young R. Land use and biodiversity relationships. *Land Use Policy* 2009;**26**:S178–S186. https://doi.org/10.1016/j.landusepol.2009.08.009

Halley JM, Iwasa Y. Neutral theory as a predictor of avifaunal extinctions after habitat loss. *Proc Natl Acad Sci U S A* 2011;**108**:2316–21. https://doi.org/10.1073/pnas.1011217108

He F, Hubbell SP. Species–area relationships always overestimate extinction rates from habitat loss. *Nature* 2011;**473**:368–71. https://doi.org/10.1038/nature09985

Holland TG, Peterson GD, Gonzalez A. A cross-national analysis of how economic inequality predicts biodiversity loss. *Conserv Biol* 2009;**23**:1304–13. https://doi.org/10.1111/j.1523-1739.2009.01207.x

Kark S, Iwaniuk A, Schalimtzek A *et al.* Living in the city: can anyone become an 'urban exploiter'? *J Biogeogr* 2007;**34**:638–51. https://doi.org/10.1111/j.1365-2699.2006.01638.x

Kerr JT, Ostrovsky M. From space to species: ecological applications for remote sensing. *Trend Ecol Evol* 2003;**18**:299–305. https://doi.org/10.1016/S0169-5347(03)00071-5

Leveau LM. Big cities with small green areas hold a lower species richness and proportion of migrant birds: a global analysis. *Urban For Urban Green* 2021;**57**:126953. https://doi.org/10.1016/j.ufug.2020.126953

Li X, Tian H, Pan S *et al.* Four-century history of land transformation by humans in the United States: 1630–2020. *Earth Syst Sci Data* 2023;**15**:1005–35. https://doi.org/10.5194/essd-2022-135

Manne LL, Pimm SL. Beyond eight forms of rarity: which species are threatened and which will be next? *Anim Conserv* 2001;**4**:221–9. https://doi.org/10.1017/S1367943001001263

Manne LL, Williams PH, Midgley GF *et al.* Spatial and temporal variation in species-area relationships in the Fynbos biological hotspot. *Ecography* 2007;**30**:852–61. https://doi.org/10.1111/j.2007.0906-7590.05121.x

Marzluff JM. A decadal review of urban ornithology and a prospectus for the future. *Ibis* 2017;**159**:1–13. https://doi.org/10.1111/ibi.12430

Matthews TJ, Cottee-Jones HE, Whittaker RJ. Habitat fragmentation and the species-area relationship: a focus on total species richness obscures the impact of habitat loss on habitat specialists. *Divers Distrib* 2014;**20**:1136–46. https://doi.org/10.1111/ddi.12227

Melillo JM, McGuire AD, Kicklighter DW *et al.* Global climate change and terrestrial net primary production. *Nature* 1993;**363**:234–40. https://doi.org/10.1038/363234a0

Murphy GEP, Romanuk TN. A meta-analysis of declines in local species richness from human disturbances. *Ecol Evol* 2014;**4**:91–103. https://doi.org/10.1002/ece3.909

NASA Ocean Biology Processing Group (OBPG), & Stumpf RP. *Distance to Nearest Coastline: 0.01-Degree Grid*, 2012. https://oceancolor.gsfc.nasa.gov/docs/distfromcoast/

Newbold T, Hudson LN, Arnell AP *et al.* Has land use pushed terrestrial biodiversity beyond the planetary boundary? A global assessment. *Science* 2016;**353**:288–91. https://doi.org/10.1126/science.aaf2201

Newbold T, Hudson LN, Hill SLL *et al.* Global effects of land use on local terrestrial biodiversity. *Nature* 2015;**520**:45–50. https://doi.org/10.1038/nature14324

Otto R, Garzón-Machado V, del Arco M *et al.* Unpaid extinction debts for endemic plants and invertebrates as a legacy of habitat loss on oceanic islands. *Diversity and Distributions* 2017;**23**:1031–41. https://doi.org/doi:10.1111/ddi.12590

Pardieck KL, Ziolkowski Jr. DJ, Lutmerding, M *et al. North American Breeding Bird Survey Dataset 1966—2019: U.S. Geological Survey Data Release.* U.S. Geological Survey, Patuxent Wildlife Research Center, 2020. https://doi.org/10.5066/P9J6QUF6

Pettorelli N, Ryan S, Mueller T *et al.* The Normalized Difference Vegetation Index (NDVI): unforeseen successes in animal ecology. *Clim Res* 2011;**46**:15–27. https://doi.org/10.3354/cr00936

Pettorelli N, Vik JO, Mysterud A *et al.* Using the satellite-derived NDVI to assess ecological responses to environmental change. *Trends Ecol Evol* 2005;**20**:503–10. https://doi.org/10.1016/j.tree.2005.05.011

Pimm SL, Jenkins CN, Abell R *et al.* The biodiversity of species and their rates of extinction, distribution, and protection. *Science* 2014;**344**:1246752–https://doi.org/10.1126/science.1246752

Rafique R, Fang Z, de Jong R *et al.* Global and regional variability and change in terrestrial ecosystems net primary production and NDVI: A model-data comparison. *Remote Sens* 2016;**8**:177. https://ezproxy.gc.cuny.edu/login?url=https://search.ebscohost.com/login.aspx?direct=true&db=a9h&AN=114038245&site=ehost-live

Rompré G, Robinson WD, Desrochers A *et al.* Predicting declines in avian species richness under nonrandom patterns of habitat loss in a Neotropical landscape. *Ecol Appl* 2009;**19**:1614–27. https://doi.org/10.1890/08-1207.1

Rosenberg KV, Dokter AM, Blancher PJ *et al.* Decline of the North American avifauna. *Science* 2019;**366**:120–4. https://doi.org/10.1126/science.aaw1313

Rossetti MR, Tscharntke T, Aguilar R *et al.* Responses of insect herbivores and herbivory to habitat fragmentation: a hierarchical meta-analysis. *Ecol Lett* 2017;**20**:264–72. https://doi.org/doi:10.1111/ele.12723

Rybicki J, Hanski I. Species-area relationships and extinctions caused by habitat loss and fragmentation. *Ecol Lett* 2013;**16 Suppl 1**:27–38. https://doi.org/10.1111/ele.12065

Samia DSM, Nakagawa S, Nomura F *et al.* Increased tolerance to humans among disturbed wildlife. *Nat Commun* 2015;**6**:8877. https://doi.org/10.1038/ncomms9877

Savage J, Vellend M. Elevational shifts, biotic homogenization and time lags in vegetation change during 40 years of climate warming. *Ecography* 2015;**38**:546–55. https://doi.org/10.1111/ecog.01131

Seabloom EW, Dobson AP, Stoms DM. Extinction rates under nonrandom patterns of habitat loss. *Proc Natl Acad Sci USA* 2002;**99**:11229–34. https://doi.org/10.1073/pnas.162064899

Segan DB, Murray KA, Watson JEM. A global assessment of current and future biodiversity vulnerability to habitat loss–climate change interactions. *Glob Ecol Conserv* 2016;**5**:12–21. https://doi.org/10.1016/j.gecco.2015.11.002

Seto KC, Güneralp B, Hutyra LR. Global forecasts of urban expansion to 2030 and direct impacts on biodiversity and carbon pools. *Proc Natl Acad Sci U S A* 2012;**109**:16083–8. https://doi.org/10.1073/pnas.1211658109

Steyaert LT, Knox RG. Reconstructed historical land cover and biophysical parameters for studies of land-atmosphere interactions within the eastern United States. *J Geophys Res* 2008;**113**:2006JD008277. https://doi.org/10.1029/2006JD008277

Sushinsky JR, Rhodes JR, Possingham HP *et al.* How should we grow cities to minimize their biodiversity impacts? *Glob Chang Biol* 2013;**19**:401–10. https://doi.org/10.1111/gcb.12055

Sushinsky JR, Rhodes JR, Shanahan DF *et al.* Maintaining experiences of nature as a city grows. *E&S* 2017;**22**:22. https://doi.org/10.5751/ES-09454-220322

Swift TL, Hannon SJ. Critical thresholds associated with habitat loss: a review of the concepts, evidence, and applications. *Biological Reviews* 2010;**85**:35–53. https://doi.org/10.1111/j.1469-185X.2009.00093.x

Tilman D, May RM, Lehman CL *et al.* Habitat destruction and the extinction debt. *Nature* 1994;**371**:65–6.

United States Census Bureau. *Percent Urban and Rural In 2010 by State and County*. 2010. https://www.census.gov/programs-surveys/geography/guidance/geo-areas/urban-rural/2010-urban-rural.html

U.S. Bureau of the Census. *U.S. County Boundaries [Vector Digital Data]*. U.S. Bureau of the Census, 2000. https://www.sciencebase.gov/catalog/item/4f4e4a2ee4b07f02db615738

U.S. Census Bureau. County-level 2020 Census Urban and Rural Information for the U.S., Puerto Rico, and Island Areas sorted by state and county FIPS codes [Dataset]. 2023. https://www2.census.gov/geo/docs/reference/ua/2020_UA_COUNTY.xlsx

Vellend M, Verheyen K, Jacquemyn H *et al.* Extinction debt of forest plants persists for more than a century following habitat fragmentation. *Ecology* 2006;**87**:542–8. https://doi.org/10.1890/05-1182

Whitlock C, Colombaroli D, Conedera M *et al.* Land-use history as a guide for forest conservation and management. *Conserv Biol* 2018; **32**:84–97. https://doi.org/10.1111/cobi.12960

Wilson EO, MacArthur RH. *The Theory of Island Biogeography*. Princeton University Press, 2016.

Wintle BA, Kujala H, Whitehead A *et al.* Global synthesis of conservation studies reveals the importance of small habitat patches for biodiversity. *Proc Natl Acad Sci U S A* 2019;**116**:909–14. https://doi.org/10.1073/pnas.1813051115

Wood SN. *Generalized Additive Models: An Introduction with R*, 2nd edn. Chapman and Hall/CRC, 2017. https://doi.org/10.1201/9781315370279

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