

# Anthropogenic drivers of avian community turnover from local to regional scales

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## Abstract

Anthropogenic change has altered the composition and function of ecological communities across the globe. As a result, there is a need for studies examining observed community compositional change and determining whether and how anthropogenic change drivers may be influencing that turnover. In particular, it is also important to determine to what extent community turnover is idiosyncratic or if turnover can be explained by predictable responses across species based on traits or niche characteristics. Here, we measured turnover in avian communities across North America from 1990 to 2016 in the Breeding Bird Survey using an ordination method, and modeled turnover as a function of land use and climate change drivers from local to regional scales. We also examined how turnover may be attributed to species groups, including foraging guilds, trophic groups, migratory distance, and breeding biomes. We found that at local scales, land use change explained a greater proportion of variance in turnover than climate change variables, while as scale increased, trends in temperature explained a greater proportion of variance in turnover. We also found across the study region, turnover could be attributed to one of a handful of species undergoing strong expansions or strong declines over the study time period. We did not observe consistent patterns in compositional change in any trait groups we examined except for those that included previously identified highly influential species. Our results have two important implications: First, the relative importance of different anthropogenic change drivers may vary with scale, which should be considered in studies' modeling impacts of global change on biodiversity. Second, in North American avian communities, individual species undergoing large shifts in population may drive signals in compositional change, and composite community turnover metrics should be carefully selected as a result.

## KEYWORDS

birds, climate change, land use, spatial scaling, traits, turnover

## 1 | INTRODUCTION

Anthropogenic change has altered the composition and function of ecological communities across the globe (Kampichler et al., 2012; Magurran et al., 2010). While local biodiversity has not necessarily declined everywhere in response to such changes, species turnover

is often higher than predicted by null models (Dornelas et al., 2014; Stegen et al., 2013; Vellend et al., 2017). Turnover in bird communities has been attributed to both climate and land cover change. Climate change in North America and Europe has led to both positive and negative impacts on bird populations as climate suitability changes throughout species ranges (Mason et al., 2019; Stephens

et al., 2016), and some species may be in the process of shifting their distributions to maintain suitable climate conditions (Tingley et al., 2009). For many species, habitat loss and land cover change may be even more direct drivers of population change across North America (Rittenhouse et al., 2012; Scholtz et al., 2017).

Although climate change and land cover change are both expected to impact bird communities, the two factors may differ in the spatial scales over which they are expected to act. Unfortunately, evidence describing the relative importance of different anthropogenic change drivers across spatial scales in explaining turnover in local and regional avian communities has been inconsistent and requires further investigation (Barnagaud et al., 2017; Jarzyna et al., 2015), although evidence from work on determinants of species occurrences may provide initial predictions. For example, at local scales where a species occurs within their range may be more dependent on habitat availability (Hurlbert & White, 2007; Lawton & Woodroffe, 1991). At broader scales, species ranges may be best determined by climatic envelopes (Araújo et al., 2013; Stephenson, 1990), leading to an increase in importance of climate change in driving regional species turnover. The scale at which land use and climate vary may also play a role in determining the scale at which changes are most influential, as variables that are autocorrelated at short distances may be less likely to influence processes at larger scales.

At the community scale, environmental change is expected to result in community turnover as the environment becomes more suitable for some species and less suitable for others. Turnover is often characterized by compositional change that results from local colonizations and extinctions (Koleff et al., 2003). However, changes in species abundances alone may reflect substantial shifts in community organization, even in the absence of colonizations and extinctions. As such, metrics of turnover that incorporate shifts in species abundances over time may be more sensitive for capturing community responses and attributing variation in community turnover to environmental change. Changes in species abundances—but not community composition or richness—have been demonstrated as responses to environmental change in systems such as freshwater fish (Shimadzu et al., 2015), fire-disturbed grassland and shrubland ecosystems (Jones et al., 2017), and desert rodents (Thibault et al., 2004).

Bird communities have exhibited both compositional change and shifts in relative abundance over the past five decades, and the degree of community change has been found to vary by ecosystem type and level of human influence (Kampichler et al., 2014; Schipper et al., 2016). North American avian communities are undergoing compositional shifts in species occurrences, such as range expansions driven by biotic homogenization in response to anthropogenic change (La Sorte & McKinney, 2007). Additionally, many species have experienced notable widespread, long-term changes in abundance (Rosenberg et al., 2019). The breadth and severity of observed breeding bird declines in particular increases the urgency for understanding the drivers of avian community turnover and how anthropogenic change may play a role in driving compositional shifts.

Community compositional change may result from systematic changes driven by changes in the climate or habitat suitability of

sites leading to selection for certain niche properties or traits of species suited to the new environment (Vellend, 2016). Alternatively, community turnover may be driven primarily by drift or idiosyncratic changes in the abundances of individual species (Siqueira et al., 2020; Vellend, 2016), such as an expanding invasive species or a decline due to disease, that are not necessarily indicative of reshuffling of the community in response to a set of environmental pressures. In North American avian communities over the past several decades, evidence of both dynamics has been observed, including broad declines in groups such as forest and grassland breeding species (Rosenberg et al., 2019), foliage-gleaning insectivores (Jones et al., 2003) and long-distance migrants (Zurell et al., 2018), as well as more species-specific changes such as the expansion of Eurasian Collared-dove (*Streptopelia decaocto*; Hengeveld, 1993; Scheidt & Hurlbert, 2014). Modeling compositional change in response to measured changes in climate and land use may help distinguish selective shifts in communities from less predictable, individual species responses.

Using a long-term observational dataset of North American breeding bird communities, the Breeding Bird Survey (BBS; Pardieck et al., 2018), we assess how community turnover has changed over time, the relative contribution of climate change and land use changes in driving compositional turnover in breeding bird communities from local to regional scales, and we examine whether community change is being driven by individual species effects or foraging guild, trophic group, migratory status, and breeding biome. We predict that at smaller scales, land use change drivers will have stronger explanatory power in a model of species compositional turnover, while at larger scales, climatic changes will be more important.

## 2 | MATERIALS AND METHODS

### 2.1 | Data sources

Abundance data for breeding bird communities across the United States and Canada came from the North American Breeding Bird Survey (BBS; Pardieck et al., 2018). BBS routes are surveyed on a single morning during the breeding season (typically June), and consist of 50 evenly spaced point count stops arrayed along a 40-km roadside route. We included BBS routes in our analysis for which GIS route paths were available (US routes: [https://www.mbr-pwrc.usgs.gov/bbs/geographic\\_information/GIS\\_shape\\_files\\_2012.html](https://www.mbr-pwrc.usgs.gov/bbs/geographic_information/GIS_shape_files_2012.html), Canadian routes: Hudson et al., 2014), and for which path length was between 38 km and 42 km. We omit the small number of routes that depart substantially from 40 km because of increased uncertainty in how well the route path reflects the exact point count locations. Routes had to be sampled at least three times in every 4-year window from 1990 to 2010 in Canada and from 1992 to 2016 in the United States. These slightly different temporal windows were necessary to align with the differential availability of land cover data in the two countries (see below). We grouped BBS routes for the scale analysis by Bird

Conservation Region (BCR; Bird Studies Canada & NACBI, 2014), which represent ecologically distinct regions in North America with similar bird communities, habitats, and resource management challenges. We excluded BBS routes in small or poorly sampled BCRs that contained fewer than 25 routes, because those BCRs could not be included in analyses at the largest regional scale (see below). This resulted in a sample size of 749 total routes with comparable temporal sampling over 4-year windows within our study period.

At a 5-km buffer around each BBS route path, we obtained three variables representing climate and land use change: annual breeding season minimum and maximum temperature, and the change in proportion cover for each land cover class over the study period. We calculated the average annual breeding season (May, June and July) temperature over time from 1990 to 2010 in Canada and 1992 to 2016 in the United States, with daily minimum and maximum temperature data obtained at a 1-km scale from Daymet (Thornton et al., 2018). We obtained land cover data at 30-m resolution for US BBS routes from the National Land Cover Database (NLCD; Yang et al., 2018) and for Canadian BBS routes from Agriculture and Agri-food Canada (AAFC; Agriculture & Agri-food Canada, 2015), and calculated the change in proportion land cover for each class from 1992 to 2016 in the United States and 1990 to 2010 in Canada. In order to compare changes in class between the two datasets, we collapsed more detailed classes between the two datasets to a common scale, which included the following classes: water, forest, urban, agricultural, grasslands, and wetlands (see Table S1).

For each focal route at each scale, we measured three environmental change variables. Land cover change was measured as the change in proportion cover from the beginning of the study period to the end of the study period (1990–2010 at Canadian routes, 1992–2016 at US routes) for the land cover class that exhibited the greatest absolute change in proportion cover during this time window. Temperature change based on both minimum and maximum temperature was estimated as the slope of a simple linear model of annual average temperature over time during the study period. Minimum and maximum temperature changes were examined as opposed to changes in mean temperature as minimum and maximum temperatures may not shift at the same

rate (Zhang et al., 2011), and may impact breeding birds through different mechanisms.

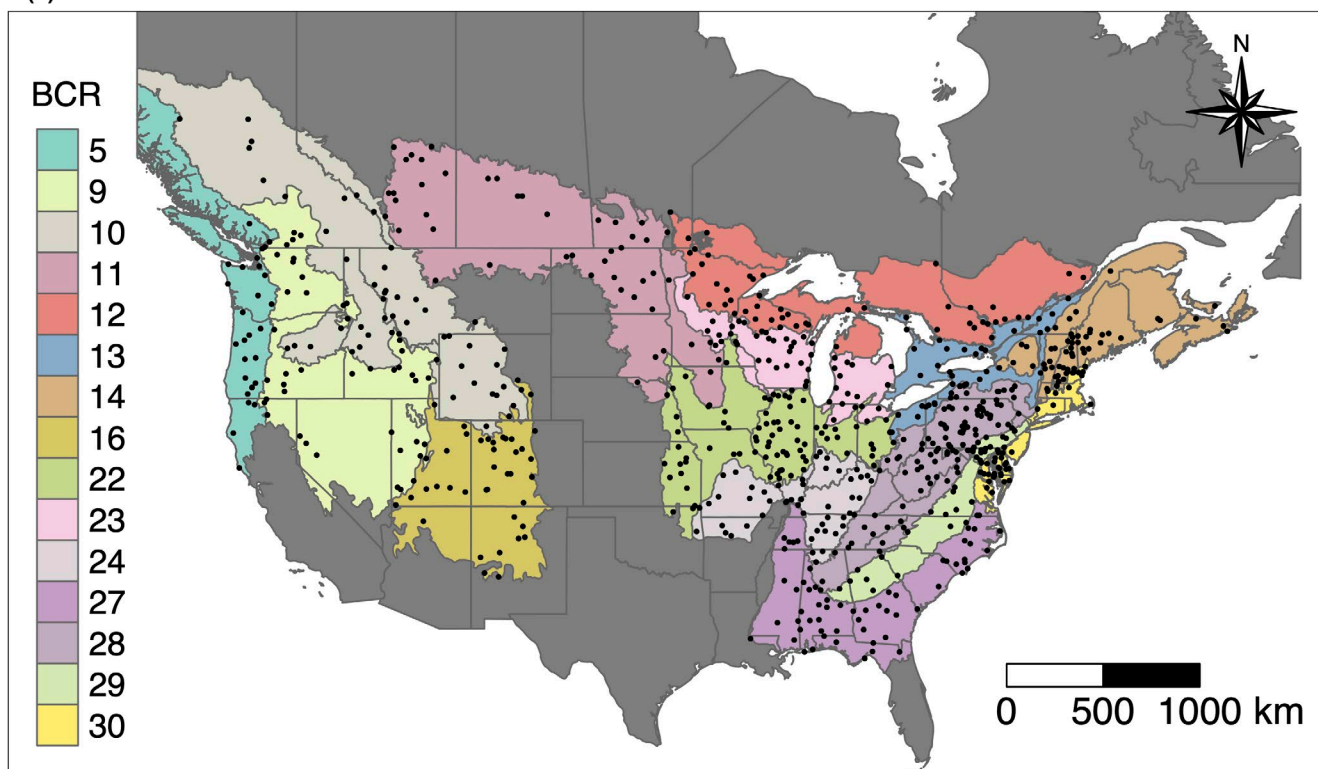
We averaged annual species counts across 4-year time windows at BBS survey routes. We omitted any nocturnal species, water birds, or birds of prey, as these species are not well sampled by the BBS protocol (Butcher et al., 1987). We also omitted transient occurrences of species from our analysis, defined as observations of a species at a survey route where they only occurred in 1 year out of four, as infrequently occurring “transient” species do not show strong predictable responses to the local habitat or climatic conditions (Snell Taylor et al., 2018). As a result, at some survey locations, time series will capture the transition of species from transient to non-transient (or “core” species, *sensu* Snell Taylor et al., 2018) across different 4-year time windows. Because transient occurrences of species are not tied to the local environment, this outcome reflects our goal to capture community shifts in response to environmental change, rather than community shifts that are a result of transient dynamics.

## 2.2 | Measuring turnover

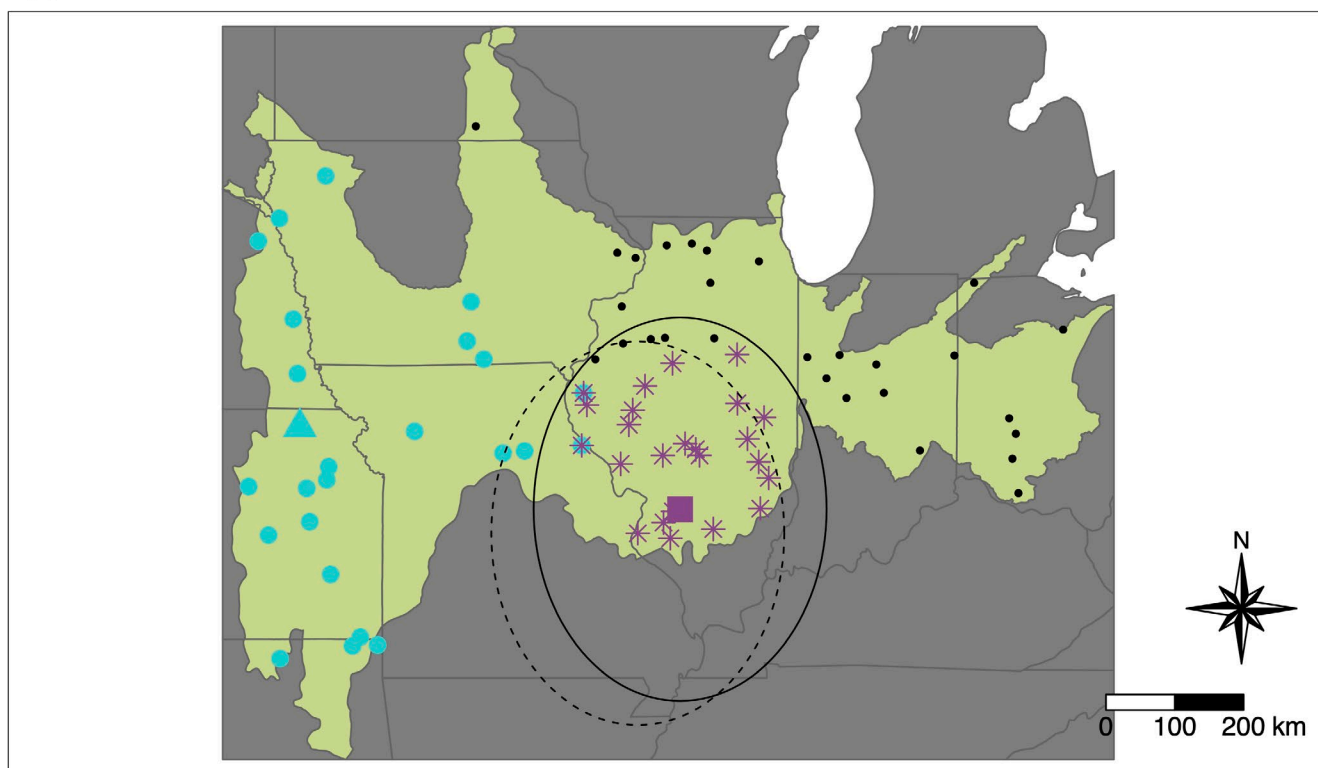
We examined shifts in community composition across a range of spatial scales. To do this, we aggregated BBS routes by nearest neighbor (averaging species counts across aggregated routes), considering communities at the scale of one BBS route, and aggregates of up to 25 total routes (Figure 1b). The average distance between BBS routes at the 25-route scale ranged from 141 to 461 km across the BCRs examined in this study (Figure S1a), with a lower density of routes within BCRs in western North America. One consequence of this is that aggregated BBS routes with higher average distances may consist of more spatially heterogeneous communities than aggregates from closer routes. Despite this geographic variation in the sampling extent covered, we deemed it most important to keep the actual surveyed area constant, which is why we define scale based on the number of BBS routes. At coarser scales, two adjacent focal routes would overlap substantially in the sets of aggregated nearest neighbor routes, leading to non-independence in metrics of compositional change at routes within

**FIGURE 1** (a) Map showing Breeding Bird Survey (BBS) routes included in the study (black dots) and Bird Conservation Regions (BCRs; shaded polygons). BBS routes were included in the analysis if they were surveyed at least three times in each 4-year window from 1992 to 2016 at US routes and 1990–2010 at Canadian routes. BCRs were retained if they contained at least 25 BBS routes. BCRs included in our analysis: Northern Pacific Rainforest (5), Great Basin (9), Northern Rockies (10), Prairie Potholes (11), Boreal Hardwood Transition (12), Lower Great Lakes/St. Lawrence Plain (13), Atlantic Northern Forests (14), Southern Rockies Colorado Plateau (16), Eastern Tallgrass Prairie (22), Prairie Hardwood Transition (23), Central Hardwoods (24), Southeastern Coastal Plain (27), Appalachian Mountains (28), Piedmont (29), New England/Mid-Atlantic Coasts (30). (b) BBS routes in BCR 22. Blue triangle and purple square indicate two focal routes, while blue dots and purple stars show nearest 24 neighboring BBS routes to the two focal routes, respectively, showing aggregations of BBS routes for measuring turnover at regional scales. These two focal routes are from the low-overlapping subset of routes selected to reduce non-independence (see Section 2)—in the low-overlapping subset of focal routes, at the largest, regional scale, these two focal routes overlap only at two locations, denoted by purple stars on top of blue circles. The solid black circle shows approximate neighborhood area of routes at the 25-route scale for the purple square focal route, while the dotted circle shows approximate area of 25-route scale for a neighboring focal route in the full set of BBS routes, demonstrating the higher overlap between focal routes as scale increases in the full dataset of BBS routes. Black dots are other BBS routes in this BCR that are included in the analysis but are part of different 25-route aggregations [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

(a)



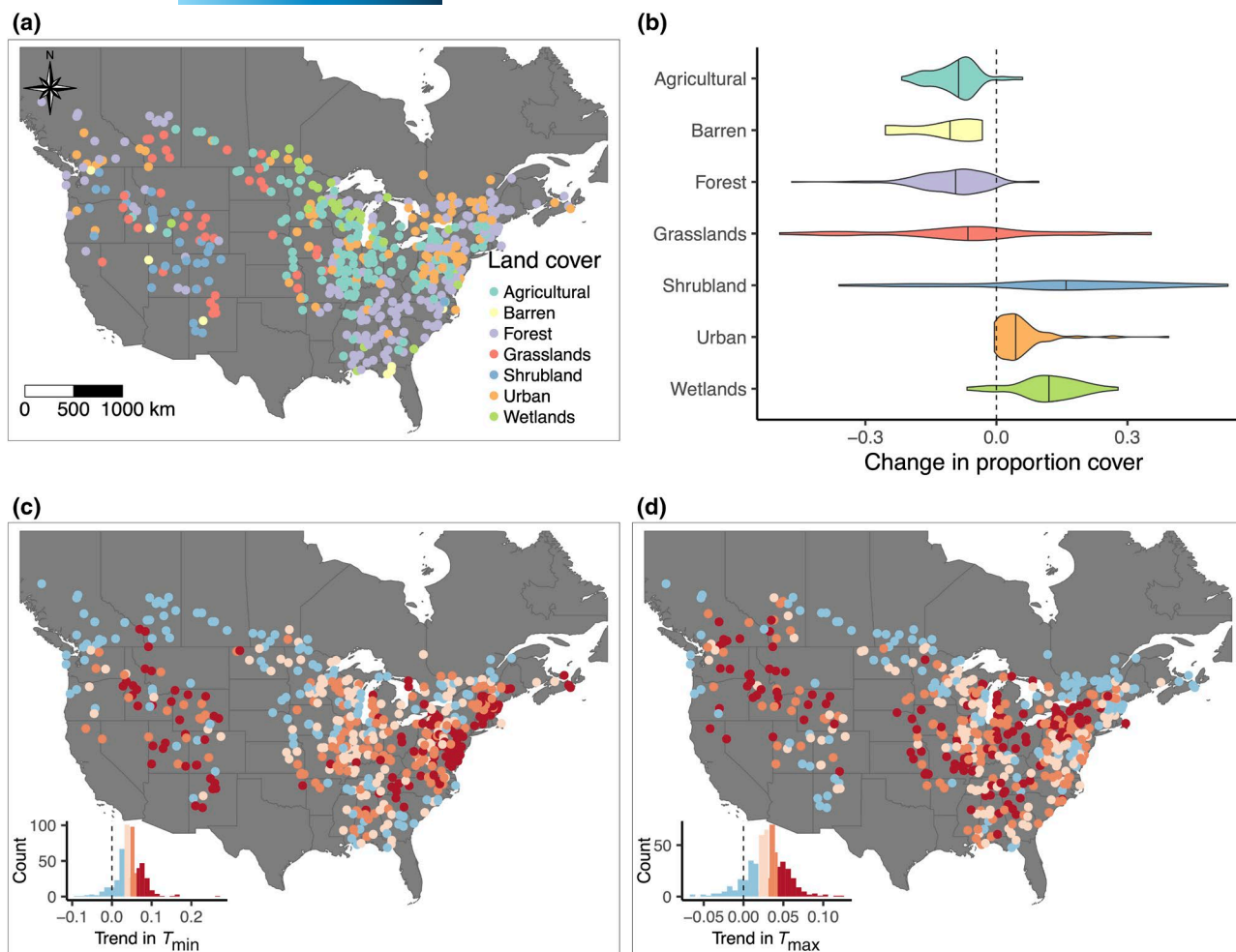
(b)



a BCR (Figure S1b). To examine how robust our results were to this degree of overlap, we also analyzed a low-overlapping subset of 33 focal routes, in which at the largest 25-route scale, no more than 10 routes overlapped between different focal route aggregates

(mean overlap at 25-route scale was only four routes for this low-overlapping subset).

We measured compositional shifts in BBS communities at each scale by conducting an ordination of log-transformed species



**FIGURE 2** Changes in land cover and climate variables at Breeding Bird Survey sites from 1992 to 2016 at US routes and 1990–2010 at Canadian routes. (a) Category of land cover that changed the most at each BBS route during the time period. (b) Number of BBS routes in each land cover class where the maximum proportion cover increased or decreased. (c) Linear trend in minimum temperature during the breeding season (May, June, and July). Colors indicate quartiles. (d) Linear trend in maximum temperature during the breeding season (May, June, and July). Colors indicate quartiles [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

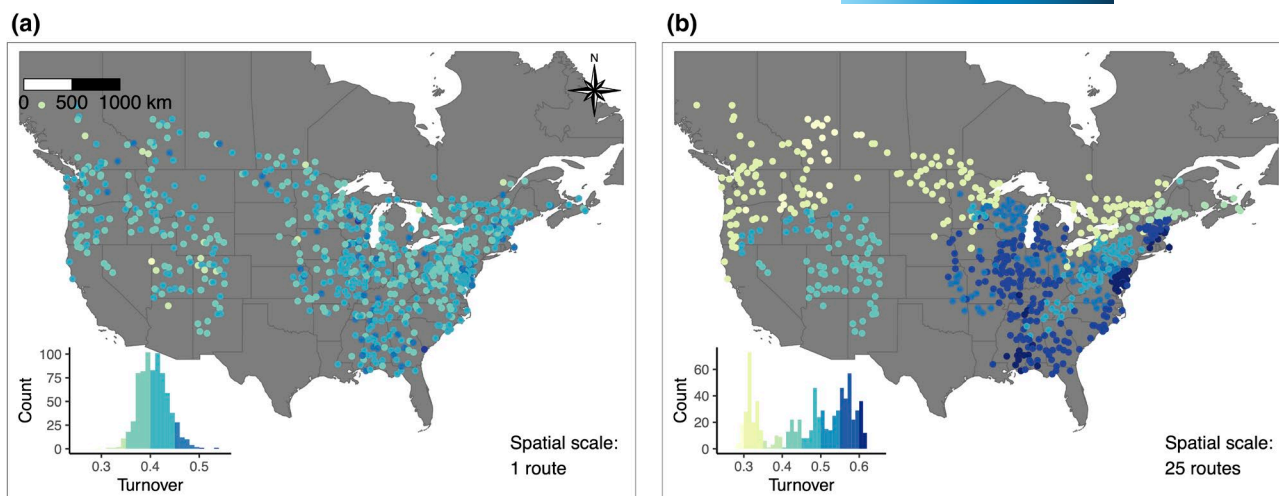
abundances averaged across 4-year time windows, using the functions provided in the “vegclust” package in R (De Cáceres et al., 2019; R Core Team, 2019). To do so, we first calculated a dissimilarity matrix with Euclidean distances across the 4-year time bins for each focal route at each spatial scale. The dissimilarity matrices were then used in a principal components analysis (PCA). We characterized community turnover by calculating trajectory directionality of the focal route community over 20 (in Canada) or 24 (in the United States) years measured at 4-year resolution, using the movement of the five or six time points in ordination space. Trajectory directionality describes the degree to which a community follows a consistent path in one direction in multidimensional ordination space. Trajectory directionality scores range from 0 to 1, with values close to 0 indicating little compositional change (e.g., as expected from independent random walks in species abundances) and values of 1 (corresponding to a perfectly straight trajectory through ordination space) indicating compositional shifts that are directional, as in primary or secondary succession. An important benefit of this metric

is the ability to incorporate changes in communities over a time series containing multiple time steps, to examine consistent trends in ordination space through time. Directionality has been used to examine community dynamics spatially and temporally, including as a response to environmental gradients in disturbances and anthropogenic change in forest communities (Fernandes Neto et al., 2019; Zald et al., 2020), stream fish (Mota-Ferreira et al., 2021), and harmful algal blooms (Li et al., 2021).

### 2.3 | Variance partitioning

At each scale from one route up to 25 aggregated routes, we modeled directionality (henceforth, “community turnover,” or simply “turnover”) as a function of land cover change and temperature change at that scale using ordinary least squares linear regression. We then did a variance partitioning analysis to determine how much variance was uniquely explained by land cover change and the two





**FIGURE 3** Community turnover based on trajectory directionality (see text) over 4-year time windows at Breeding Bird Survey routes between 1990 and 2016. Turnover scores ranged from 0 to 1, with 0 indicating little directional turnover, while values of 1 indicate a strongly directional trajectory over the study period. (a) Local turnover at individual BBS routes. (b) Regional turnover of focal routes aggregated with the 25 nearest neighbor routes within each focal route's Bird Conservation Region [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

climate change variables and how much variance was shared between the two sets of predictors (Legendre & Legendre, 1998). We repeated this analysis for the full set of focal routes as well as the low-overlapping subset of routes.

We chose OLS linear regression because our goal was to partition the variance explained in turnover uniquely by our predictor variables as well as the shared variance across all predictor variables, which is possible with  $R^2$  values from linear regression. However, as our turnover metric is bounded between 0 and 1, we examined the impact of using OLS linear regression as opposed to a regression method designed for response variables bounded from 0 to 1, beta regression, as implemented in the “betareg” package (Zeileis et al., 2021). We found that OLS parameter estimates were more conservative than estimates from beta regression, but that pseudo- $R^2$  estimates from the beta regression were almost exactly equal to  $R^2$  estimates at all scales (Figures S2 and S3). As a result, we present the variance partitioning results using  $R^2$  estimates from OLS linear regressions.

## 2.4 | Decomposing turnover by species and traits

Turnover at BBS routes may be the result of a strong population trend in an individual species or due to trends in groups of species that share similar traits (Jarzyna & Jetz, 2017). We attempted to distinguish between those two cases by first estimating the contribution of individual species to turnover at local and regional scales (three BBS routes and 25 BBS routes, scales at which land cover and climate change variables were most explanatory of turnover, respectively). For each species occurring at each BBS location, we recalculated turnover while omitting that species, and the difference between turnover with and without each species was a measure of

that species' impact on the turnover metric. For each BBS survey location, we then identified which species had the greatest impact on turnover at each scale.

We conducted a similar analysis with species foraging guilds, trophic groups, migratory guilds, and breeding biomes, determining the difference between turnover with or without the species in each group or guild at both local and regional scales. Foraging guilds, trophic groups, and migratory guild data for species were obtained from Hurlbert and White (2007) and breeding biomes were obtained from Rosenberg et al. (2019), with the exception of two species missing from the dataset: Bicknell's Thrush *Catharus bicknelli* and Gunnison's Sage-Grouse (*Centrocercus minimus*), which we grouped into breeding biome categories based on the species' breeding range. We did not include any guild with fewer than five species in these analyses. For simplicity, we combined Forest Generalist, Eastern Forest, Western Forest, and Boreal Forest groups into a single “Forest” group and did not present results from Introduced and Wetland groups in the main text. Breeding biome grouping results for the complete set of groups can be found in Figure S5. A list of species and their foraging, trophic, migratory, and breeding biome guild assignments can be found in Table S2.

## 3 | RESULTS

Across BBS routes, we found regional variation in the most common form of land cover change. BBS routes in eastern North America, especially the US Southeast, were most likely to show the greatest change in forest cover over the study period, with a median decrease in forest cover at these sites around 10% (Figure 2a,b). BBS routes in central North America most often showed decreases in agricultural area, while western and mountainous BBS routes were most likely

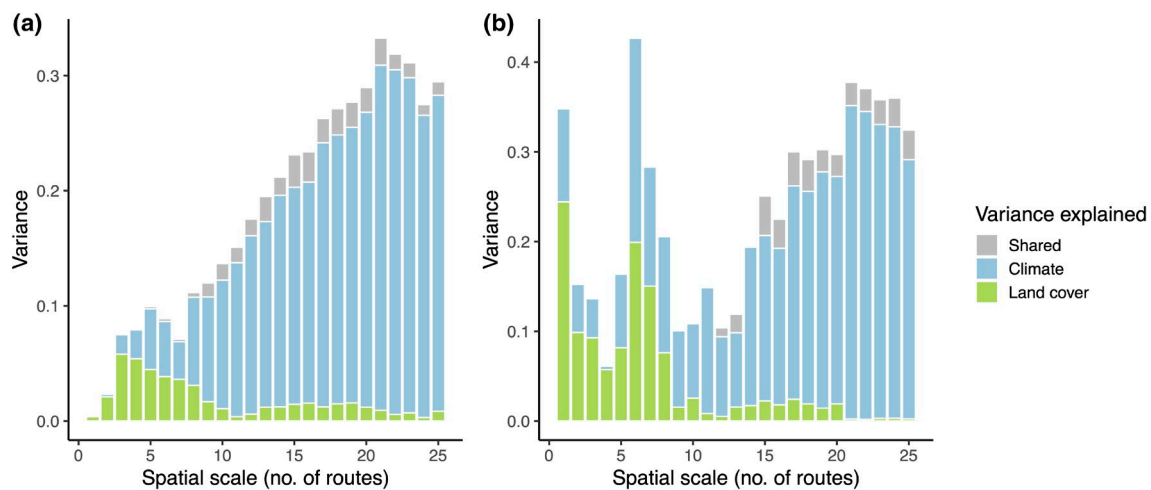
to show increases in shrubland or decreases in grassland cover. An increase in urban cover was most commonly the largest class of land cover change in eastern and northern BBS routes, at a few sites by increases of over 30%. Most BBS routes experienced warming trends in temperature, especially in areas of the Rocky Mountains and eastern United States, with stronger increases overall in minimum rather than maximum temperature over the study period (Figure 2c,d).

At the scale of a single BBS route, most routes showed low turnover in community composition and abundance with only weak geographic signal (Figure 3a). When BBS routes were aggregated to sets of 25 nearest neighboring routes to examine regional trends in community composition, we found that the central, southeastern, and coastal Atlantic regions showed stronger turnover, while the Pacific Northwest, northern Great Plains, and southeastern Canada showed lower turnover in community compositional shifts (Figure 3b). At regional scales, turnover tended to be more extreme (lower across the northernmost routes, and higher at routes in the Southeast) than at local scales.

When considering all focal BBS routes, including those that might overlap geographically at the largest scales, the amount of explained variance in community turnover increased with spatial scale, from <10% at the smallest scales to 30% at the largest scales. At the smallest scales, between one to five BBS survey routes aggregated, land cover change accounted for the majority of explained variation, while as scale increased, a greater proportion of variation was explained by changes in temperature (Figure 4a,b). Shared variance

between land cover change and climate change predictors was low across scales, but increased as scale increased. These patterns were qualitatively consistent when examining only the focal BBS routes within the low-overlapping subset of BBS routes, although the maximum variance explained for land cover at small scales was much higher (Figure 4a,b).

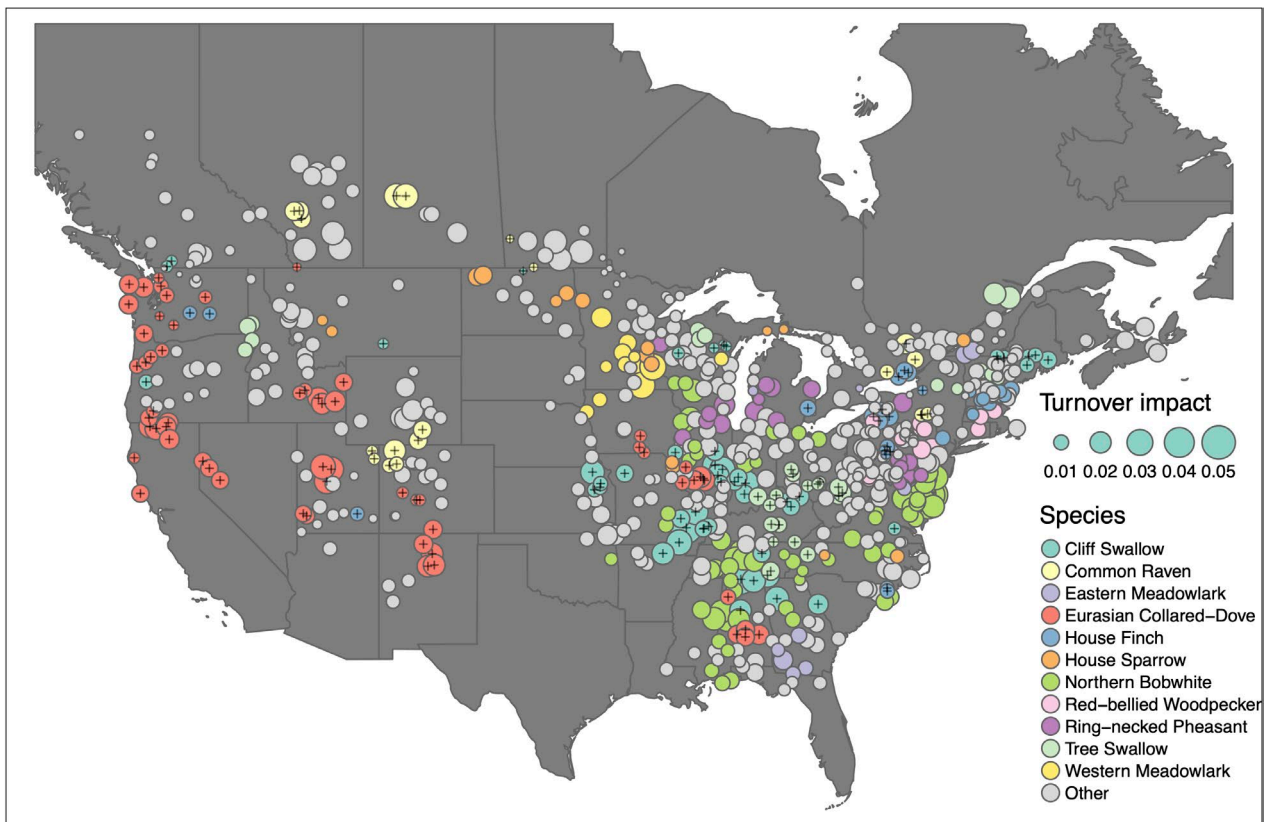
Across BBS survey routes, the species with the largest impact on community turnover at local and regional scales was often one of a short list of high-impact species, and high-impact species typically showed regional influence across many nearby BBS routes (Figure 5a,b). For example, Northern Bobwhite (*Colinus virginianus*) declines were the most important species driving community turnover across the southeast and eastern United States. Increases in Eurasian Collared-dove were particularly important in driving turnover across the western United States and in parts of the US Midwest. Tree Swallow (*Tachycineta bicolor*) population increases were especially influential along the Appalachians and Cliff Swallow (*Petrochelidon pyrrhonota*) increases had a high impact on turnover across the US Midwest and Ozarks regions (Figure 5). Other high-impact species with more limited regional influence included Red-bellied Woodpecker (*Melanerpes carolinus*), Western Meadowlark (*Sturnella neglecta*), and Ring-necked Pheasant (*Phasianus colchicus*; all declining), and House Finch (*Haemorhous mexicanus*; increasing in some areas, decreasing in others). Of those high-impact species, impact on turnover showed greater geographic variation at regional scales than local (Figure S4).



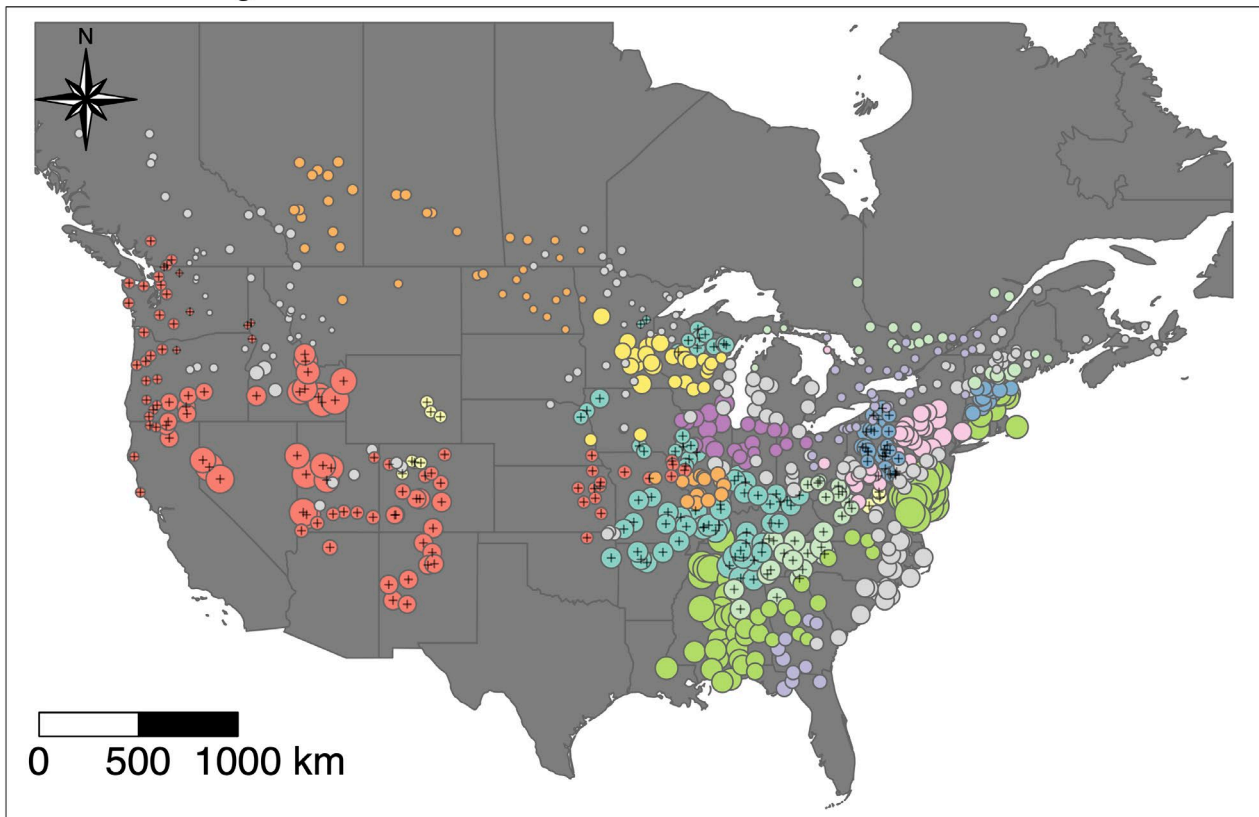
**FIGURE 4** Variance in turnover explained uniquely by land cover change (green) and climate change (trend in minimum and maximum temperature during the breeding season; blue), as well as the shared variance (gray) from local (individual Breeding Bird Survey routes) to regional scales (focal routes aggregated up to 25 nearest neighbor routes within each Bird Conservation Region). Variance partitioning was conducted with the (a) full set of routes and (b) a subset of 33 focal routes chosen to minimize overlap of route aggregates at the broadest scales to below 40% within each Bird Conservation Region [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

**FIGURE 5** Impact on turnover determined by subtracting the directionality excluding the focal species from the overall directionality. At (a) regional and (b) local scales (three Breeding Bird Survey routes and 25 survey routes, respectively), the species with the greatest positive difference was identified, indicating that turnover increased most with the inclusion of that species. Size of dots indicates magnitude of turnover impact, color shows species, and BBS routes with + signs are survey locations where the focal species is increasing in population while empty circles indicate decreasing populations based on BBS trend estimates at each site [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

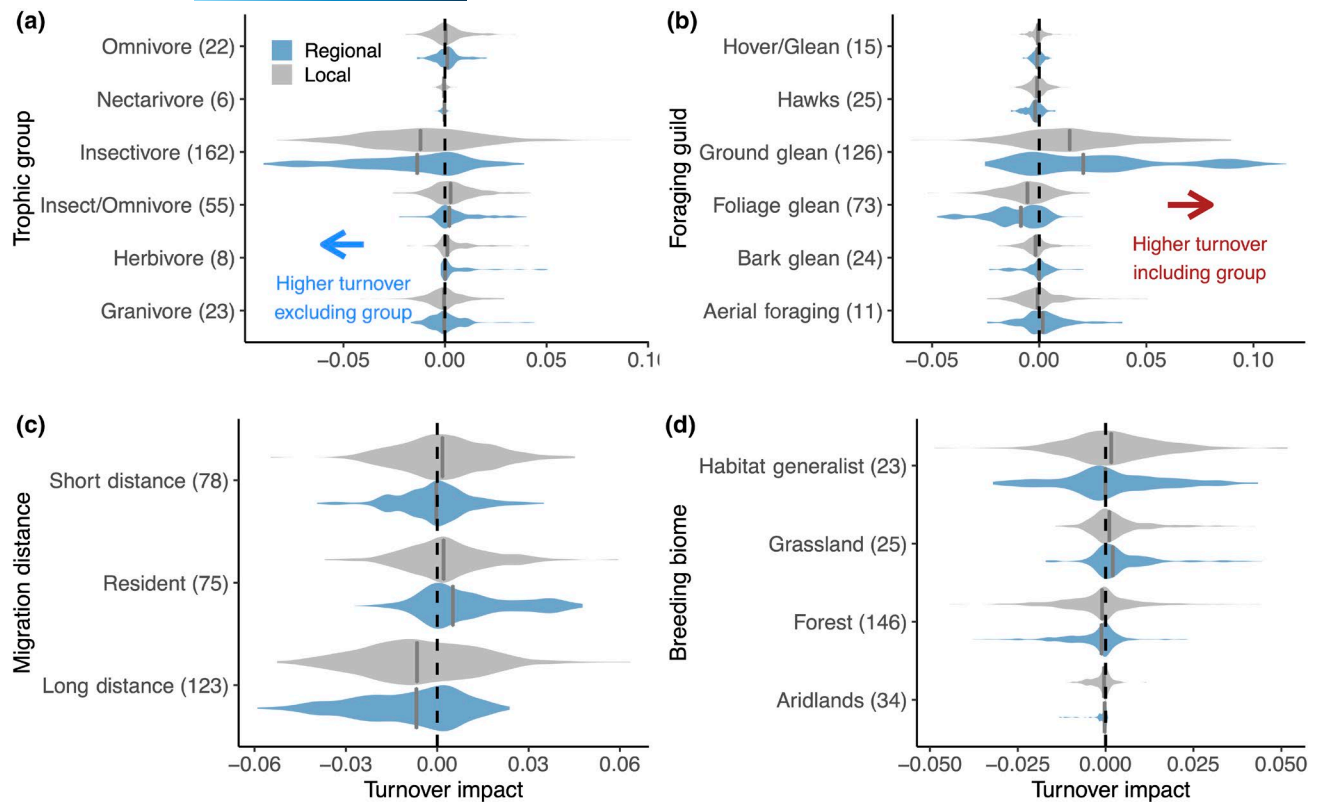
## (a) Scale: local



## (b) Scale: regional







**FIGURE 6** The impact of (a) trophic group, (b) foraging guild (here, “hawks” refers to airhawkers, a group that includes swallows), (c) migratory guild, and (d) breeding biome on community turnover measures at local (3 BBS routes; gray) and regional (25 BBS routes; blue) scales. Guild impact on turnover was determined by subtracting the turnover calculated when excluding the focal group of species from the overall turnover value when all species were included. Positive values indicate that turnover increased most with the inclusion of that group and negative values indicating that the community excluding that species group showed greater turnover. Violin plots show the distribution of turnover impact for each group across Breeding Bird Survey routes in the analysis, with black lines showing median values across all survey routes. The number of species in each group is indicated in parentheses for each y-axis label [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

We also examined the impact of individual foraging guilds, trophic groups, and migratory guilds on turnover at the local and regional scales. The impact of different groups was similar across both scales. We found that across foraging guilds, ground gleaners had the highest positive impacts on turnover (i.e., turnover in a community was highest with ground gleaners included), while turnover at a BBS survey route tended to be higher when foliage gleaning species were excluded (Figure 6a). We found that the impacts on turnover for most trophic groups were centered on zero. One exception was insectivores, which when excluded from sites resulted in higher turnover values for the remaining community (Figure 6b). Resident species had the highest impact across BBS survey routes on community turnover (Figure 6c). We did not find substantial impacts on turnover by excluding or including species by their breeding biome (Figure 6d).

## 4 | DISCUSSION

We found evidence for weakly directional shifts in avian communities across the United States and Canada, with stronger turnover at regional scales than local scales. At local scales, land use change

explained more variation in community turnover than climate change variables, while temperature trends were more explanatory at broader scales. Regional turnover and to a weaker extent local turnover were often heavily influenced by one of a handful of species undergoing broad regional increases or decreases. We did not find evidence of strong guild or group-level impacts on turnover at either scale, except in groups which included one or more of previously identified high-impact individual species.

Our results finding greater importance of land use change at local scales and of climate change at broader regional scales in explaining turnover are in alignment with the expected role of habitat and climate in determining species occurrences across scales (Lawton & Woodroffe, 1991). Locally, species occupancy of particular patches or landscapes may be driven by the availability of suitable habitat or biotic interactions with competitors or predator species (Snell Taylor et al., 2020). At regional and broader scales, species occurrences are driven by suitability of climatic conditions. Trends in temperature explained more total variation in community turnover as scale increased, perhaps emphasizing the importance of climate in driving species occurrences at the broadest, regional scales and potentially providing support for efforts to predict future species distributions

based predominantly on climate (Langham et al., 2015; Pearson & Dawson, 2003). Changing suitability of climate conditions has been shown to explain widespread impacts to breeding bird communities in other continental regions as well, such as Europe (Gregory et al., 2009). At the smallest scales, unexplained variance was highest, which may be due to processes that influence populations that we did not incorporate into our model such as variation in resource availability or fine-scale habitat attributes. There may also be unaccounted for uncertainty in our analysis because potential uncertainty in turnover could not be incorporated into models predicting turnover. As synergistic or interactive effects of land use and climate changes on biodiversity are documented and greater focus is placed on how those changes impact organisms mechanistically (Schulte to Bühne et al., 2020), it will be important to consider the appropriate scale at which drivers operate in understanding biodiversity change.

At local and regional scales across the United States and Canada, we found that community turnover was strongly influenced by just a handful of species, often for idiosyncratic and species-specific reasons. In particular, the westward expansion of the invasive Eurasian Collared-dove was a strong driving force of community compositional shifts, consistent with work demonstrating the dominance of human-associated and non-native species at BBS routes more broadly (Sofaer et al., 2020). We also found that increases in Cliff Swallow and Tree Swallow populations were drivers of turnover especially across the Midwest and southern Appalachian regions. Cliff Swallow and Tree Swallow breeding ranges have expanded southward in recent decades, potentially as a result of anthropogenic creation of nesting sites in the case of Tree Swallows (Wright et al., 2019) and expansion by Cliff Swallows into suitable but unoccupied nesting sites underneath bridges in the Southeast (McNair, 2013). Declines in ground gleaning species, including Ring-necked Pheasant and Northern Bobwhite, were also highly influential, which may be in response to changing agricultural and land management practices (Hernandez et al., 2013; Taylor et al., 2018). Across scales, the importance of individual species life histories is highly relevant in describing turnover over the past two and a half decades. The importance of land use change in providing context for strong species-specific responses across regional scales points to a limitation of our analysis in representing the complexities of species-habitat mismatches and land cover change processes at the community level. Our results also highlight a challenge in using community turnover metrics that incorporate abundance—patterns in turnover can easily be driven by individual species with very strong abundance trends. While metrics that include species abundances can describe compositional shifts in more detail than metrics based solely on colonization and extinction, examining the extent to which community-level patterns are driven by one or a few species using an approach like the one we have used here (see also Shimadzu et al., 2015) may provide additional insights into ecological processes driving turnover.

We did not find strong, consistent guild-level impacts on community turnover at local or regional scales, except for those groups which include many previously identified high-impact species, such as ground gleaners and residents. Community turnover across scales

tended to be higher when neotropical migrants, foliage gleaners, and insectivores were excluded. This may indicate inconsistent changes in abundance of species in those groups, with some species in these groups experiencing declines and others experiencing increases in the study region. Analysis of population trends by family has found declines in groups such as Parulidae and Tyrannidae while increases have been observed in Polioptidae and Vireonidae (Rosenberg et al., 2019). Recent work has suggested that the trait dependence of responses to climate changes differs geographically (Mason et al., 2019), complicating efforts to understand changes in community composition by predicting species responses using niche characteristics. Examining how components of overall turnover can be attributed to functional groupings of species may provide useful insights into processes driving community turnover, especially in identifying whether particular groups of species show similar or diverging trends. While we focused on categorical groupings of species, temporal shifts in continuous functional traits have also been observed in avian communities over the past several decades (Jarzyna & Jetz, 2017), and understanding how those trends relate to anthropogenic change across scales is an important and complementary approach to the analysis presented here.

The results of this study suggest that of the turnover in breeding bird communities observed from 1990 to 2016, local scale shifts in abundance distributions tended to be more explained by land use change than climate change variables, but with a substantial amount of unexplained variation. That unexplained variation may be attributed to species-specific, idiosyncratic responses such as range expansions or disease dynamics, rather than predictable changes at the level of foraging guilds, trophic groups, or migratory distances. At regional scales, greater shifts in community composition were observed and a greater proportion of variation in those shifts was explained by changes in temperature during the breeding season, although a majority of variation in community turnover remained unexplained. Future work investigating biodiversity change in response to anthropogenic drivers should incorporate information about the most relevant scales at which those processes operate.

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## CONFLICT OF INTEREST

The authors report no conflict of interest.

## DATA AVAILABILITY STATEMENT

All underlying data for these analyses are publicly available. Code to replicate analyses and figures is available on GitHub (<https://github.com/gdicecco/community-turnover>) and archived on Zenodo (<https://doi.org/10.5281/zenodo.5620167>).

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