

# Bird community change only partially matches landscape habitat change across five decades in North America

## Authors

Martha Paola Barajas Barbosa<sup>†\*1,2,3</sup>, Kimberly L. Thompson<sup>†\*1,3</sup>, Nicolas Bianco<sup>4</sup>, Nadja Klein<sup>4</sup>, and Jonathan M. Chase<sup>1,3</sup>

<sup>†</sup> shared first authorship

## Affiliations

<sup>1</sup>German Centre for Integrative Biodiversity Research (iDiv), Halle-Leipzig-Jena, Leipzig, Germany

<sup>2</sup>UFZ - Helmholtz Centre for Environmental Research, Department of Community Ecology, Halle (Saale), Germany

<sup>3</sup>Department of Computer Science, Martin Luther University Halle-Wittenberg, Halle (Saale), Germany

<sup>4</sup>Scientific Computing Center, Karlsruhe Institute of Technology, Karlsruhe, Germany

Corresponding author emails: [kimberly.thompson@idiv.de](mailto:kimberly.thompson@idiv.de), [paolabarajas@gmail.com](mailto:paolabarajas@gmail.com)

## Abstract

A common expectation is that as habitats in a landscape change, so do communities within them. However, this niche-based expectation assumes species persist in their favored habitats regardless of how much habitat remains; geometric constraints can counter this when heterogeneous landscapes supply too little of each habitat type for specialists to persist, allowing generalists to dominate. Using North American Breeding Bird Survey data and land-cover reconstructions spanning nearly 50 years, we show environmental heterogeneity decreased slightly, while bird composition became slightly more heterogeneous. Species presence supported niche-based explanations, whereas weighting dominant species revealed patterns consistent with geometric constraints; in both cases, bird community changes were small relative to land-cover shifts. Gains were concentrated among species of intermediate habitat breadth that exploit habitat edges and mosaics, while the broadest generalists declined. Assessing biodiversity responses to land-cover change therefore requires tracking both which species persist and which come to dominate.

## INTRODUCTION

It is commonly thought that human activities are homogenizing the planet and the species therein; no matter whether in temperate or tropical regions, across continents, there are certain species that can be encountered almost everywhere people are (1, 2). This biotic homogenization is attributed to several factors, including habitats becoming more similar across the landscape (i.e., via agricultural expansion or urbanization, 3, 4), the loss of rare species, and the expansion of widespread dominant species (5). If pervasive, biotic homogenization can lead to declines in overall biodiversity in a landscape even when declines at smaller scales may be undetectable (6, 7). However, while biotic homogenization is often considered to be the primary biodiversity pattern that emerges from human activities (8, 9), it is equally plausible that local communities can become more different from one another through time, either as a result of increased heterogeneity of habitats in the landscape and/or heterogeneous gains and losses of species in the landscape; a process often referred to as biotic differentiation (5, 10). Together, both biotic homogenization and differentiation represent changes in  $\beta$ -diversity, or the composition of species in a community. Regardless of the change in direction of  $\beta$ -diversity, the consequence for landscape-level biodiversity depends on the balance between gains of species in some communities or losses from others (5).

Both biotic homogenization and differentiation emerge because of changes to the habitat conditions in the landscape and how species respond to those habitats (7). For example, when landscapes become dominated by similar kinds of habitats, such as agricultural or urban landscapes, species that are more well suited to those habitats become widespread and the overall composition of species across those landscapes is therefore homogeneous, reflecting the homogenization of habitats in the landscape. Alternatively, when habitats in a landscape become more heterogeneous through time, for example, when widespread forested landscapes are used for

different purposes, the landscape can become a mosaic of vegetation in different states, ranging from open meadows to early and late successional habitats, as well as human-dominated landscapes. This in turn creates a more heterogeneous landscape dominated by different species and higher levels of  $\beta$ -diversity (11, 12).

While changes in habitat heterogeneity are usually thought to drive changes in species composition, and thus the homogenization or differentiation of  $\beta$ -diversity across landscapes, this perspective assumes that species distributions are primarily influenced by the availability of habitat types. However, this is a strongly 'niche-based' perspective that need not be the only, or even primary, way by which communities assemble. Although habitat differences can generate compositional differences in species through a simple sorting mechanism (13), this will often not be realized in dynamic metacommunities where dispersal limitation, stochastic drift (i.e., the basis of the equilibrium theory of island biogeography, 14), and neutral theory (15) can interact with, or counteract, the influence of habitat heterogeneity and niche filtering on community structure (16, 17). For example, in a finite landscape, changes in the heterogeneity of habitats interact with the total amount of a given habitat type in that landscape. When the total area available of a given habitat type is too small, viable populations of many specialist species will not be able to persist due to demographic stochasticity and/or Allee effects, leading to metapopulation extinction (18, 19). Thus, despite the presence of that species' preferred habitat type in the landscape, habitat generalists may be favored (20, 21). Such trade-offs between the area of available habitat types in the landscape and the number of different types of habitat (i.e., its heterogeneity) can decouple changes in the degree of habitat heterogeneity from changes in the  $\beta$ -diversity in that landscape; a mechanism known as the area-heterogeneity trade-off (19, 22, 23). While habitat heterogeneity is often found to be a predominant driver of patterns of diversity in landscapes (24, 25), these patterns

can be tempered when diversity is measured on smaller spatial scales (26, 27). As a consequence, there is mixed support for the area-heterogeneity trade-off with varying levels of coupling between heterogeneity and diversity when habitat area is finite (22, 23, 28-31).

As both the habitat heterogeneity and total area available of distinct habitat types change through time as a consequence of anthropogenic activities, there are multiple possible outcomes of how  $\beta$ -diversity would be expected to change with changing habitat heterogeneity. We illustrate the two ends of the continuum of alternatives with a simple landscape that becomes more heterogeneous in habitat types through time, although this can be reversed by reading right to left instead of left to right (Fig. 1). Under the niche hypothesis, increasing habitat heterogeneity through time would increase the diversity of types of specialist species that can persist in the landscape, leading to an increase in  $\beta$ -diversity or differentiation through time (and vice versa for decreases in heterogeneity, Fig. 1). Alternatively, if species are not as strongly limited by habitat type compared to other metacommunity processes, such as dispersal limitation or stochasticity (17), increasing the heterogeneity of habitat types can reduce the area required by habitat specialists below a threshold, and generalists that use multiple habitats would be expected to dominate (Fig. 1).

In order to examine these alternative perspectives on how changing habitat heterogeneity in landscapes leads to changes in the compositional differentiation of communities, we combined the North American Breeding Bird Survey with harmonized land-cover reconstructions spanning 1973 to 2020. We aggregated 577 bird-survey routes containing a total of 481 species into 74 metacommunities of comparable extent (10,000 to 20,000 km<sup>2</sup>, mean 15,039 km<sup>2</sup>), each containing 3 to 20 routes that were rarefied to standardize sampling effort (Figure S1), and summarized bird abundances and land-cover composition in twelve consecutive 4-year intervals. For every pair of

routes within a metacommunity and every interval we estimated environmental heterogeneity (EH), which here we use synonymously with habitat heterogeneity, as the spatial turnover in land-cover composition. We estimated bird  $\beta$ -diversity as the ratio of  $\gamma$ - to  $\alpha$ -diversity using Hill numbers that differentially weight species by relative abundance (32). A Bayesian hierarchical model estimated temporal trends in both habitat heterogeneity and  $\beta$ -diversity within each metacommunity and the relationship between those trends across metacommunities in a single step, propagating uncertainty in the trends through to the estimated relationship.

We asked three questions. First, has environmental heterogeneity within these metacommunities increased or decreased over five decades, and have their communities differentiated or homogenized? Second, do rates of change in environmental heterogeneity and rates of change in  $\beta$ -diversity covary positively, and does the answer depend on whether  $\beta$ -diversity is evaluated with weighting more strongly towards the rare end of the abundance distribution (i.e., species richness) or the more dominant end of the abundance distribution? Third, if rates of change in environmental heterogeneity and rates of change in  $\beta$ -diversity do not covary positively, are the species that gain in relative abundance the broad habitat generalists expected under an area-limited alternative, and do shifts in the composition of communities correspond to the magnitude of land-cover reorganization they experienced?

## RESULTS

After harmonizing the Annual National Land Cover Database (NLCD, 33) with a modeled historical land-cover reconstruction (34) and assessing the agreement between the two products, we found that aggregating the original thirteen classes into eight resolved the most frequent confusions and raised mean metacommunity-level accuracy to 72% (mean Cohen's kappa=0.49), which we judged sufficient for the analyses that follow (Supplementary Materials and Methods, Figures S2-S9).

## Trends in environmental heterogeneity and $\beta$ -diversity

Across the contiguous United States, metacommunities experienced a small mean decline in environmental heterogeneity (EH), corresponding to an average increase in homogeneity of 0.25% per 4-year interval (posterior mean slope,  $\hat{\beta}_{EH} = -0.25\%$ , 95% credible interval (CI) [-2.12%, 1.82%]). If this mean rate were sustained across the 1973-2020 study period, it would correspond to a 3% increase in environmental homogenization. However, change in EH varied considerably among metacommunities: 19 of 74 became more heterogeneous, and 12 of these had 95% credible intervals that excluded zero (Figure S10). Thus, although the mean estimated trend was toward environmental homogenization, a subset of metacommunities experienced increases in environmental heterogeneity.

In contrast, mean rates of change in  $\beta$ -diversity were positive, indicating an average tendency of communities within metacommunities to become more compositionally differentiated. We measured  $\beta$ -diversity as the ratio of  $\gamma$ - to  $\alpha$ -diversity using Hill numbers of order  $q=0$ ,  $q=1$ , and  $q=2$  that differentially weight diversity based on relative abundances. The increasing  $\beta$ -diversity was evident at  $q=0$ , where  $\beta$ -diversity is based on species richness with all species weighted equally regardless of abundance ( $\hat{\beta}_{q=0} = 0.32\%$ , 95% CI [-0.93%, 1.98%]), at  $q=1$ , when species were weighted based on the effective number of common species ( $\hat{\beta}_{q=1} = 0.52\%$ , 95% CI [-1.73%, 2.92%]), and at  $q=2$ , where  $\beta$ -diversity is based on the effective number of dominant species ( $\hat{\beta}_{q=2} = 0.58\%$ , 95% CI [-3.27%, 4.23%], Fig. S10). However, uncertainty and variation among metacommunities increased with diversity order, as reflected by progressively wider credible intervals from  $q=0$  to  $q=2$ .

Although the mean  $\beta$ -diversity trends were positive, not all metacommunities became more differentiated. At  $q=0$ , 20 of 74 metacommunities had negative posterior mean slopes, indicating

that localities in metacommunities became more similar to one another; however, only one of these had a 95% credible interval excluding zero (Fig. S10). The same number of metacommunities (20 of 74) had negative posterior mean slopes at  $q=1$ , with three 95% credible intervals excluding zero (Fig. S10). At  $q=2$ , 24 of 74 metacommunities had negative posterior mean slopes, seven of which had 95% credible intervals excluding zero (Fig. S10). Thus, evidence for within-metacommunity biotic homogenization was uncommon at  $q=0$  and  $q=1$ , but was more frequent at  $q=2$  when  $\beta$ -diversity values emphasized dominant species.

## Environmental heterogeneity differentially affects rare and dominant species

Rates of change in environmental heterogeneity (EH) were positively associated with rates of change in  $\beta$ -diversity when all species were weighted equally ( $q=0$ ;  $\hat{\beta}_{\Delta\beta \sim \Delta EH} = 0.10$ , 95% CI [-0.14, 0.35],  $P(\hat{\beta}_{\Delta\beta \sim \Delta EH} > 0 | data) = 0.79$ ; Fig. 2, Table S1). Here,  $\beta$ -diversity incorporates every pairwise comparison among localities within a metacommunity and is particularly sensitive to rare species when  $q=0$ . Additionally, a posterior mean ( $\hat{\beta}_{\Delta\beta \sim \Delta EH}$ ) value of 0 would indicate no association between the rate of change in EH and the rate of change in  $\beta$ -diversity, while values of 1 and -1 would indicate 1:1 positive and negative relationships, respectively. The posterior distribution describing the relationship between the rate of change in EH and the rate of change in  $\beta$ -diversity when  $q=0$  therefore provides moderate support that the rate of change in  $\beta$ -diversity increased as the rate of EH change increased, albeit with substantial uncertainty.

This pattern reversed when species were weighted by their relative abundances. When  $\beta$ -diversity emphasized the effective number of common species ( $q=1$ ), the rate of change in  $\beta$ -diversity was negatively associated with the rate of change in EH ( $\hat{\beta}_{\Delta\beta \sim \Delta EH} = -0.10$ , 95% CI [-0.47, 0.27],  $P(\hat{\beta}_{\Delta\beta \sim \Delta EH} > 0 | data) = 0.30$ ; Fig. 2, Table S1). This relationship became more strongly

negative when  $\beta$ -diversity emphasized dominant species ( $\hat{\beta}_{\Delta\beta \sim \Delta EH} = -0.48$ , 95% CI [-1.03, 0.08],  $P(\hat{\beta}_{\Delta\beta \sim \Delta EH} > 0 | data) = 0.05$ ; Fig. 2, Table S1). Thus, 95% of posterior draws supported a negative association between the rate of change in EH and the rate of change in  $\beta$ -diversity among dominant species. Taken together, the sign of the relationship between changing EH and changing  $\beta$ -diversity depended on how strongly species were weighted by abundance, shifting from positive when rare species contributed equally to negative when dominant species carried most of the weight.

We performed several sensitivity analyses to examine the robustness of the opposing result between  $\beta$ -diversity emphasizing rare species ( $q=0$ ) and dominant species ( $q=2$ ). First, we excluded two influential metacommunities and found the same opposing positive and negative relationships at  $q=0$  and  $q=2$ , albeit with a slightly weaker negative association at  $q=2$  (Fig. S11, S12, S13, Table S1). Similarly, when we estimated  $\beta$ -diversity from four routes randomly sampled within each metacommunity, we found qualitatively consistent results with those from all pairwise community comparisons (Fig. S14, S16, Table S1). When we repeated the four-route subsampling analysis after excluding the same two influential metacommunities (Fig. S15), the  $q=0$  and  $q=1$  results remained qualitatively similar to the primary analysis, but the relationship between the rate of change in EH and the rate of change in  $q=2$   $\beta$ -diversity was near zero (Fig. S14, S16, Table S2).

## Subtle shifts in bird habitat-association composition are decoupled from land-cover change

Because  $q=0$  counts every species equally while  $q=2$  is set almost entirely by the few dominant ones, their opposing relationship suggests that increasing EH was associated with localities becoming less similar in their rare species but more similar in their dominant species. One explanation for this could be that the habitats contributing to EH are too small to sustain most

specialist populations, so that generalist species able to use many habitat types become abundant wherever habitat composition changes.

We scored each of 481 species included into our analyses by habitat breadth, which we defined as the number of land-cover categories each species is associated with from IUCN Red List habitat classifications (35), reclassified to match our land-cover classes (Materials and Methods). After doing so, we found gains were small and confined to the middle of the breadth range, with species associated with four habitat categories increasing in relative abundance between 1973-1976 and 2017-2020 ( $\hat{\beta}=0.1\%$ , 95% CI [0.0%, 0.2%],  $P(\hat{\beta} > 0|data)=0.99$ ; Fig. 3; Table S2), and those associated with five habitats showing a similar but far more uncertain increase ( $\hat{\beta}=0.0\%$ , 95% CI [0.0%, 0.2%],  $P(\hat{\beta} > 0|data)=0.66$ ; Fig. 3, Table S2). However, the broadest generalists associated with six habitat categories declined ( $\hat{\beta}=-0.3\%$ , 95% CI [-0.6%, -0.1%],  $P(\hat{\beta} > 0|data)=0.01$ ; Fig. 3, Table S2). Of the set of 481 species, there were only seven of these broad generalists, and the estimated decline was driven largely by the house sparrow (*Passer domesticus*; Fig. S17), whose populations have fallen in developed areas in North America in recent decades (36). When we excluded *P. domesticus*, the decline among the extreme generalist species (e.g., Brewer's blackbird, Swainson's thrush) was still present (Fig. S18, Fig. S19, Table S2). The increase in abundance was therefore focused on species with intermediate-to-broad habitat use, rather than to the most generalist species, but the magnitude of these shifts was small.

We next asked whether these group-level abundance changes translated into reorganization of species composition in the metacommunity. Habitat specialists tended to dominate, such that all 74 metacommunities occupied a narrow region of the compositional space (Fig. 4A, 4B). Within that region, species of intermediate habitat breadth proportionally increased to make up a slightly larger share of individuals between the earlier (1973-1976) and later (2017-2020) part of

the time series (Fig. 4C). Over the five-decade time series, most metacommunities shifted towards higher relative abundance of intermediate-breadth species, such as Northern cardinal and turkey vulture, while a minority shifted toward single-habitat specialists, such as the pine warbler (Fig. 4D, Fig. S19, Fig. S20). The shift toward intermediate-breadth species was concentrated in the southeast and lower Midwest of the USA, whereas communities in the mountain west and northern plains changed little in their habitat associations in either direction (Fig. S20).

We found that habitat structures in the metacommunities sorted mainly along a gradient from forest-dominated to agriculture-dominated landscapes (Fig. 4A, 4E). There was little temporal change along this gradient between the early (1973-1976) and late (2017-2020) time periods, but where it did occur, agriculture and urban cover increased at the expense of forest and shrub- and grassland (Fig. 4F, Fig. S21). The largest land-cover shifts occurred in the southeast, but otherwise the magnitude of land-cover change showed no clear geographic structure (Fig. S21).

Importantly, we found little association between observed land-cover shifts and the compositional shifts in bird communities. Specifically, metacommunities with the largest land-cover shifts did not experience the largest changes in the habitat breadth of their birds (Fig. 5A). Some were substantially reorganized in land cover while corresponding bird communities changed little in the composition of habitat breadth, and others showed bird compositional change despite little land-cover change. While the majority of metacommunities experienced greater shifts in land-cover composition, the metacommunities with higher magnitude shifts in habitat-breadth compositions were centered in the midwestern US (Fig. 5B), where many were simultaneously moving towards more urban compositions (Fig. S21). Notably, conversion of forest to agriculture did not reliably yield communities with fewer forest specialists and more habitat generalists. The reversal between rare and dominant species therefore reflects modest, spatially variable shifts in

which species are abundant, rather than a continental replacement of specialists by generalists.

## DISCUSSION

After five decades of change across the contiguous United States, landscapes changed relatively little in their broad land-cover composition, and where they did change, agriculture and urban land typically expanded while forest, shrubland, and grassland declined. On average, this made landscapes slightly more homogeneous through time, despite wide variation among landscapes. Bird metacommunities tracked these changes differently depending on which part of the community was emphasized. When all species were weighted equally ( $q=0$ ), communities became more differentiated where landscapes became more heterogeneous and less differentiated where landscapes homogenized. This is consistent with classic species sorting, in which changes in habitat composition alter which species occur across localities. In contrast, when dominant species were weighted more heavily ( $q=2$ ), communities tended to homogenize even where landscapes became more heterogeneous. This pattern is more consistent with the area-heterogeneity trade-off, in which increasing habitat heterogeneity within a fixed landscape reduces the area of each habitat type and favors species able to persist across habitat mosaics.

Whether localities within a metacommunity homogenize or differentiate depends on how  $\alpha$ - and  $\gamma$ -diversity change together, because  $\beta$ -diversity is the relationship between diversity at these two scales rather than an independent component of diversity. Localities become more similar ( $\beta$ -diversity decreases) either when widespread species become more widespread, so  $\alpha$  increases while  $\gamma$  remains largely unchanged, or when narrowly distributed species disappear, so  $\gamma$  decreases while  $\alpha$  remains largely unchanged. Conversely, localities become more different ( $\beta$  increases) either when widespread species disappear from some localities, so  $\alpha$  decreases while  $\gamma$  remains largely unchanged, or when narrowly distributed species are gained, so  $\gamma$  increases while

$\alpha$  remains largely unchanged (5). Thus, a change in  $\beta$ -diversity alone does not reveal the process producing it; that requires examining the accompanying changes in both  $\alpha$  and  $\gamma$ .

Our slight mean trend toward differentiation at  $q=0$ , which strengthened where environmental heterogeneity increased, most likely reflects the loss of formerly widespread species from some localities while regional species richness changed relatively little. Increasing heterogeneity often produces smaller and more fragmented patches of each habitat type, which could make these local losses more frequent and uneven across localities. At the same time, occurrence-based change contains a large stochastic component. In an agricultural landscape in southwestern France, local bird assemblages changed largely independently of land-cover change and in ways consistent with random colonization and local extinction (37). Such idiosyncratic gains and losses of rare species can add considerable noise to occurrence-based  $\beta$ -diversity and may help explain why the relationship with environmental heterogeneity was relatively weak.

When we considered patterns of diversity response when common species were emphasized in the metrics at  $q=2$ , our observed trends toward homogenization most likely reflect the same few species increasing in relative abundance across many localities, so that communities once dominated by different species increasingly share the same dominant ones. Much recent change in North American bird communities has been driven by a small number of species with large shifts in abundance (38). Across BBS routes, common species have also responded more positively to changes in human land cover, whereas declines in pasture have been associated with losses of less common and rare species (39). In our metacommunities, several widespread species, including northern cardinal and turkey vulture, increased their share of individuals. Where heterogeneity increased, the growing interspersed mosaic of farmland, developed areas, and remnant forest may provide favorable habitat mosaics for these species while reducing the amount of any

one habitat available to specialists. This also helps explain why previous studies have found stronger temporal homogenization when relative abundances are considered than when communities are described by occurrence alone (40, 41).

These two results suggest that niche sorting and the area-heterogeneity trade-off act on different parts of community change rather than providing competing explanations. The area-heterogeneity trade-off predicts that specialists eventually disappear when the area of suitable habitat falls below that needed to sustain populations (19, 22). Yet species can persist at low abundance well before local extinction occurs. In the Northern Great Plains, species specialized on grasslands tend to have more negative population trends (42), and continent-wide, grassland birds have lost both more individuals and a larger share of their populations than birds associated with other biomes (43). Likewise, area-sensitive forest-interior birds can persist at low densities in small woodlots despite high nest predation and brood parasitism, in part because immigration from larger forest tracts can maintain local populations (44, 45). Changes in which species remain present therefore may continue to follow niche-sorting expectations even while changes in relative abundance already reflect the loss of habitat area. If these abundance declines eventually translate into delayed local extinctions, the positive relationship between heterogeneity and occurrence-based  $\beta$ -diversity should weaken through time.

The species that gained in our metacommunities were generally not the broadest habitat generalists, but species with intermediate habitat breadth that often exploit transitions between habitats. Northern cardinals (*Cardinalis cardinalis*) nest in shrubby edges and forage on open ground, while turkey vultures (*Cathartes aura*) roost in forest and forage over open land and roadsides. Increasing interspersion of forest, farmland and development can therefore increase the amount of edge habitat even where no single land-cover class changes strongly. At the same time,

the broadest generalists declined, driven in part by the house sparrow (*Passer domesticus*), whose populations have fallen in developed areas (36). Introduced species more generally have lost a substantial share of their North American populations (43), and expanding development has been associated with lower bird counts across common and rare species alike (39). The homogenization of dominant species therefore reflects a relatively modest reweighting toward a few edge- and mosaic-tolerant species rather than a wholesale replacement of specialists by generalists. Habitat breadth based on IUCN classifications is also coarse because it combines habitats used across the annual cycle, and local abundance, geographic range size and habitat breadth represent distinct dimensions of commonness that are only partly correlated (46).

Bird communities also changed less in habitat-breadth composition than their landscapes changed in broad land-cover composition, and the few metacommunities in which birds changed more strongly were concentrated in the Midwest. Part of this mismatch likely reflects the coarse resolution of land-cover classes. In the southeast, for example, conversion of hardwood or mixed forest to pine plantation remains classified as forest even though it can strongly alter bird communities and favor species such as the pine warbler (*Setophaga pinus*). Similarly, replacement of hay and pasture by row crops, or changes in mowing frequency, can leave land classified as agriculture while sharply reducing nesting habitat for grassland birds. Bird communities also respond to drivers beyond land cover, including climate-driven shifts in breeding ranges and continent-wide declines in abundance (43). Strong breeding-site fidelity can further delay community responses because adults may continue to return to degraded territories for several years. Historical classification errors in land cover will weaken these relationships further. Because our analyses are observational, they describe how changes in environmental heterogeneity and  $\beta$ -

diversity covary among landscapes rather than establishing that land-cover change caused the observed community changes.

Taken together, these results show that the ecological consequences of landscape change depend strongly on which part of biodiversity is being measured. Changes in habitat heterogeneity can increase differences among localities in species occurrence while simultaneously making those same localities more similar in the species that dominate them. The apparent contradiction disappears once the underlying changes in  $\alpha$  and  $\gamma$ , and the distinction between persistence and abundance, are considered together. Species sorting determines where species continue to occur across a changing landscape, whereas reductions in habitat area can alter their abundance well before they disappear. Thus, the same landscape can become more heterogeneous in land cover, more differentiated in the identities of its rarer species, and more homogeneous in its dominant species. More broadly, this means that landscape change cannot be understood from a single biodiversity metric, or from land-cover change alone. The processes that reorganize communities operate differently across scales and across common and rare species, and may become visible at different stages of decline. Understanding biodiversity change therefore requires linking changes in  $\alpha$ -,  $\beta$ -, and  $\gamma$ - diversity and relative abundance to disentangle how land-use change alters both the composition and spatial heterogeneity of landscapes

## **MATERIALS AND METHODS**

### **Data and Preprocessing**

#### **North American Breeding Bird Survey Data**

We used data from the North American Breeding Bird Survey (47, 48), a monitoring program that has been conducting annual surveys across the United States and Canada since the

late 1960s and has provided data for many important insights into bird population and community level changes over time in response to changing habitats (49, 50). Bird surveys take place during the height of the breeding season, primarily in May or June, with expert observers traveling along 39.2 km-long roadside routes and stopping every 800 meters to record every individual seen or heard within 400 meters. We filtered bird survey data and spatial coordinates for the period of 1966-2023 to ensure that routes met quality control standards and occurred within the contiguous United States to enable pairing the surveys with long-term land-cover data (see below). To identify a set of BBS routes that provided adequate temporal coverage, we quantified how many routes had been sampled at regular intervals during 1966-2023. Specifically, we evaluated whether routes had been surveyed at least once within 3-, 4-, or 5-year intervals. We examined multiple interval lengths and starting years because while shorter intervals provide finer temporal resolution, they also reduce the number of eligible routes; whereas longer time intervals allow inclusion of more routes. Our aim was to balance this tradeoff by identifying a subset of routes with a consistent sampling history extending back to the 1970s. Consequently, we opted to move forward with a subset of routes that had been sampled at least once within 4-year intervals during the period of 1973-2020, which yielded a sample size of 786 routes (Figure S1). We constructed route-by-species abundance matrices for each 4-year interval within the period of 1973-2020 by calculating the mean abundance of each species detected in each route from the surveys available within that interval. For routes sampled fewer than four times in a given interval, we averaged abundances over the available surveys without inserting zeroes for unsampled years, so each abundance value represents the interval-specific average for a given species-route combination.

To facilitate estimation of beta diversity (see Calculating  $\beta$ -diversity and environmental heterogeneity below), we aggregated the routes into spatial polygons (i.e., metacommunities),

ensuring that each polygon had relatively similar areas (10,000-20,000 km<sup>2</sup>) and contained at least three routes. First, we overlaid the routes on a 200×200 km grid (40,000 km<sup>2</sup> cell size) and assigned each route to its corresponding grid cell. We then built convex hull polygons with a minimum of three routes using the corresponding grid cell area. Second, to retain additional routes not captured in the initial step, we performed hierarchical clustering on the geographic coordinates of routes in small polygons (<10,000 km<sup>2</sup>), isolated routes, or pairs. Clusters were retained as polygons if their convex hull area was within the target range (10,000-20,000 km<sup>2</sup>) and contained at least 3 routes. This procedure was repeated iteratively until no additional eligible clusters could be formed. Third, for polygons larger than 20,000 km<sup>2</sup>, we implemented a trimming procedure by iteratively removing the most distant route (relative to the polygon centroid) and recalculating convex hull areas until polygons fell within the target size range. These efforts resulted in a sample size of 74 spatial polygons that contained a total of 577 routes, with polygons containing between 3 and 20 routes (average = 7.8 routes per polygon) and extents ranging from 10,000–20,000 km<sup>2</sup> (average = 15,039 km<sup>2</sup>) (Figure S1).

#### Land-cover Data

To obtain complete land-cover data from 1973-2020, we harmonized two products from the United States Geological Survey: The Annual National Land Cover Database (NLCD, 33) and a historical land-use and land-cover scenarios product (34). The NLCD provides annual, 30-meter resolution maps of sixteen cover classes for the contiguous United States from 1985-2023 (Table S3), which were generated with an ensemble of machine-learning algorithms that reconstruct land cover through time. The historical land-cover scenarios provide annual maps of fourteen classes at 250-meter resolution for the contiguous United States from 1938-1992 (Table S3), modeled from the 1992 NLCD baseline and incorporating historical data on agriculture, elevation, soils, climate, hydrography, and transportation networks (34).

Because the two land-cover products used similar classification schemes, only minor adjustments were required to harmonize them. We first resampled the NLCD maps to a 250-meter resolution using the nearest-neighbor method to match the spatial resolution of the historical land-cover data. We then reclassified the NLCD land-cover codes to align with the historical scheme (Table S3). This process involved directly matching equivalent classes between the two products, aggregating the four NLCD “developed” classes into a single “urban” class, and omitting the “mining” class that was unique to the historical data. This reclassification yielded 13 land-cover classes: barren, cultivated cropland, grassland, hay/pasture, shrubland, deciduous forest, evergreen forest, mixed forest, herbaceous wetland, woody wetland, urban/developed, perennial ice/snow, and open water.

Due to the eight-year overlap between the two products (1985-1992), we evaluated their agreement during this period to better understand the uncertainty in the historical land-cover data. We used a stratified random sampling approach, which is well suited for map accuracy assessment (51). We drew 1000 random points per land-cover class and compared the historical land-cover classes to those from the resampled NLCD at the same locations. We also repeated this procedure within each spatial polygon by drawing 1000 points per polygon to assess local agreement. For both the national and polygon-level comparisons, we calculated overall accuracy (proportion of correctly classified points) and Cohen’s Kappa statistic, which accounts for agreement expected by chance. In addition, we calculated class-specific statistics at the national level, including sensitivity (true positive rate), specificity (true negative rate), and balanced accuracy (the mean of sensitivity and specificity).

Preliminary evaluation of classification agreement for the period of overlap indicated systematic confusion among several cover classes, leading us to aggregate them into broader

categories to improve consistency across products. Specifically, we combined cultivated cropland and hay/pasture into an “Agriculture” class, deciduous, evergreen, and mixed forest into a “Forest” class, shrubland and grassland into a “Shrub/Grassland” class, and herbaceous and woody wetlands into a “Wetland” class, while retaining the remaining classes. This resulted in eight land-cover classes: agriculture, shrub/grassland, forest, barren, urban/developed, wetland, perennial ice/snow, and open water. We then repeated the accuracy assessment using this aggregated classification scheme.

#### Relating land-cover to bird communities

We quantified the annual proportional cover of the eight land-cover classes from our harmonized dataset for each BBS route. To define the spatial extent for land-cover extraction, we buffered each route by 400 meters, reflecting the distance within which observers record bird abundances. For each year from 1973 to 2020, we calculated the proportional cover within the buffered area of each of the thirteen land-cover classes that resulted from the initial harmonization of the NLCD and historical scenarios (i.e., prior to further aggregation to improve accuracy). Since many land-cover pixels did not completely overlap with the BBS area, we weighted pixels by the amount of overlap with the BBS area. We then averaged these annual estimates across each 4-year interval (1973-1976, 1977-1980, etc.) to match the temporal resolution of the BBS data. We then constructed route-by-land-cover matrices for each 4-year interval, where matrix cells contained the proportional coverage of the land cover classes. Finally, to match the eight land-cover classes that resulted from the final aggregation of land-cover classes, we summed proportional covers for the classes we aggregated. None of the routes contained the cover class perennial ice/snow, so we were then left with seven total land-cover classes.

## Habitat Associations

For bird species detected in either the first or last time interval (1973-1976 and 2017-2020, respectively) in any spatial polygon, we compiled their habitat associations from the IUCN red list (35). We extracted broad categorizations of the habitats in which each species could be found (e.g., Forest, Wetlands), as well as more detailed categorizations (e.g., subtropical/tropical moist lowland forest, shrub-dominated wetlands). Habitat information could not be retrieved automatically from the IUCN Red List, so we extracted habitat associations for each species manually. This required manual taxonomic harmonization between the scientific names used in the BBS data and those used by the IUCN Red List. For species listed as hybrids in the BBS, if each species forming the hybrid shared the same habitat associations according to the IUCN red list, we also recorded those habitats for the hybrid. However, if there were any differences in the list of habitats associated with either of the parent species of the hybrid, we excluded the hybrid species. We also excluded birds identified only to genus level. For all subspecies, we used the habitat associations listed for the parent species because these matched. Finally, if we were unable to find a match between the scientific name in the BBS data and scientific name in the IUCN red list, which can occur if a species has been renamed but not yet updated in the BBS data, we matched species by their common names. Out of 504 species detected in either the first- or last-time interval, we successfully extracted information on the habitat associations for 481 of them; the remaining species 23 were excluded. We then reclassified the detailed habitat associations for these 481 species to match the seven land-cover classes from our harmonized land-cover data (Table S4).

## Calculating $\beta$ -diversity and environmental heterogeneity

### Bird communities

For each 4-year interval, we examined pairs of routes within each spatial polygon and quantified three  $\beta$ -diversity metrics, each capturing different facets of spatial variation in bird community composition. Employing coverage-based and sample-size-based standardization (sensu 32) at 95% sample coverage, we calculated  $\beta$ -diversity as the ratio between  $\gamma$ -diversity (summed species richness across a pair of routes) and  $\alpha$ -diversity (mean species richness between the pair of routes) using Hill numbers of order  $q = 0, 1$ , and  $2$ . For  $q = 0$ ,  $\beta$ -diversity reflects differences in species richness, with all species weighted equally regardless of abundance ( $\beta_{q=0}$ ). For  $q = 1$ ,  $\beta$ -diversity is based on the effective number of common species, weighting species in proportion to their relative abundance ( $\beta_{q=1}$ , equivalent to the exponential of Shannon entropy). For  $q = 2$ ,  $\beta$ -diversity emphasizes the effective number of dominant species ( $\beta_{q=2}$ , equivalent to the inverse Simpson diversity and isolating changes in dominance structure).

We calculated each of these  $\beta$ -diversity metrics for all possible pairs of routes within each spatial polygon and for each 4-year interval. To derive a single  $\beta$ -diversity value per metric for each polygon and time interval, we averaged the pairwise values computed within each polygon/time-interval combination.

### Environmental heterogeneity

We estimated environmental heterogeneity (EH) as the spatial turnover of land-cover composition, for pairs of routes within each spatial polygon and for each 4-year interval. For each pair of routes, we quantified environmental heterogeneity as the ratio between  $\gamma$ -diversity (pooled count of the land-cover classes across both routes) and  $\alpha$ -diversity (mean count of the land-cover classes between routes) using the Shannon Diversity Index. The Shannon Diversity Index

measures the evenness of different land-cover classes within a route, by accounting for similarity in both the identity and proportion of land-cover classes. To derive a single environmental heterogeneity value for each polygon and time interval, we averaged the pairwise values computed within that polygon.

## Trends in $\beta$ -diversity and environmental heterogeneity

To estimate the relationship between temporal trends of  $\beta$ -diversity and environmental heterogeneity, we implemented a Bayesian hierarchical model (52). In the first level of the hierarchy, we modeled linear temporal trends for each log-transformed  $\beta$ -diversity metric (i.e.,  $\beta_{q=0}$ ,  $\beta_{q=1}$ , and  $\beta_{q=2}$ ) and log-transformed environmental heterogeneity (EH) within each spatial polygon as

$$\log(\beta\text{-diversity})(s,t) = \alpha_0(s) + \alpha(s)t + e(s,t) \quad (1)$$

$$\log(\text{EH})(s,t) = \eta_0(s) + \eta(s)t + u(s,t) \quad (2)$$

where  $s$  indexes spatial polygons and  $t$  represents the 4-year interval. Furthermore,  $\alpha(s)$  and  $\eta(s)$  represent the slopes of the temporal trends for the  $\beta$ -diversity of bird communities and environmental heterogeneity, respectively, while  $\alpha_0(s)$  and  $\eta_0(s)$  are their intercepts. The residual terms  $e(s,t) \sim N(0, \sigma_e^2(s))$  and  $u(s,t) \sim N(0, \sigma_u^2(s))$  denote independent Gaussian errors that are identically distributed over time but exhibit location-specific variances.

In the second level of the hierarchy, we modeled the relationship between the temporal trends of each  $\beta$ -diversity metric and the environmental heterogeneity trend across spatial polygons using a linear regression model of the form:

$$\alpha(s) = \phi_0 + \phi \eta(s) + v(s) \quad (3)$$

where  $v(s) \sim N(0, \sigma_v^2)$ . Here,  $\phi_0$  represents the global intercept,  $\phi$  quantifies how changes in environmental heterogeneity influence temporal trends in bird  $\beta$ -diversity, and  $v(s)$  is

independently and identically distributed noise capturing polygon-specific deviations from the overall relationship. Unlike a two-step approach that first estimates  $\alpha(s)$  and  $\eta(s)$  and then uses those values in a separate regression to estimate  $\phi$ , the hierarchical Bayesian approach jointly estimates all parameters by treating  $\alpha(s)$ ,  $\eta(s)$  as unobserved random variables. In this way uncertainty is propagated through to  $\phi$ , and yielding more reliable credible intervals (Figure S22).

To complete the Bayesian model specification, we made the following prior choices. The priors for the intercept terms  $\alpha_0(s)$ ,  $\eta_0(s)$ ,  $\phi_0$  are weakly informative Gaussian priors, and the variance parameters  $\sigma_e^2(s)$ ,  $\sigma_u^2(s)$ ,  $\sigma_v^2$  follow weakly informative Inverse-Gamma priors. These prior choices are widely used in hierarchical Bayesian models and support efficient posterior sampling through Gibbs algorithms (53). We ran 4 chains of 10,000 samples each, discarded the first 5,000 as burn-in, and obtained a total of 20,000 posterior draws. Convergence was assessed using standard diagnostic criteria.

## Relative abundance and habitat breadth

To understand whether shifts in bird communities were driven by changes in the representation of common/dominant species, we examined the relationship between relative abundance and the habitat breadth of each species. We used relative abundance rather than absolute abundance because the trend of absolute abundance is well established, with losses in the billions when comparing bird abundances between the 1970s and present day from the same dataset (43). Additionally, understanding whether communities are homogenizing or differentiating requires understanding changes in the proportional representation of common and dominant species, rather than their absolute numbers.

For the first- and last-time interval (1973-1976 and 2017-2020, respectively), we calculated the relative abundance of the 481 species for which we were able to extract habitat associations, within each spatial polygon (i.e., metacommunity), as well as the habitat breadth of each species, measured as the total number of habitat associations. The number of habitat associations ranged from one to seven, but there was only one species (*Tyto alba*, Western barn owl) with seven associations, so we moved this species into the 6-habitat-associations group.

We implemented a Bayesian beta regression with logit link function and random effects to link relative abundance (RA) to species' habitat breadth while accounting for variation among species and metacommunities:

$$RA_{cit} \sim \text{Beta}(\mu_{cit} \varphi, (1 - \mu_{cit}) \varphi) \quad (4)$$

where  $\mu_{cit}$  is the expected relative abundance of species  $i$  in metacommunity  $c$  at time  $t$  and  $\varphi > 0$  is a precision parameter. The expected relative abundance is then modeled on the logit scale as a function of covariates and random effects as:

$$\text{logit}(\mu_{cit}) = \beta_0 + \beta_T I_t + \beta_B \text{Breadth}_i + \beta_{TB} (I_t \times \text{Breadth}_i) + b_{0i} + b_{Ti} I_t + u_{0c} + b_{Tc} I_t \quad (5)$$

where  $I_t$  is the time factor ( $I_t = 0$  if baseline 1973-1976, and  $I_t = 1$  if 2017-2020);  $\text{Breadth}_i$  is the number of habitat associations for species  $i$ ;  $\beta_0$ ,  $\beta_T$ ,  $\beta_B$ , and  $\beta_{TB}$  represent the global intercept, the main effects of time and habitat breadth, and their interaction, respectively. Including the interaction between time and habitat breadth allows us to account for temporal changes in relative abundance to depend on species' habitat specialization. The terms  $b_{0i}$  and  $b_{Ti}$  are species-specific random intercepts and time slopes, while  $u_{0c}$  and  $u_{Tc}$  are metacommunity-specific random intercepts and time slopes, respectively. We specified the random effects as normally distributed with zero mean, and separate variance components for each intercept and slope term. Moreover, we assumed prior independence between intercepts and slopes within each grouping factor. In

practice, this corresponds to specifying independent random intercepts and slopes for both species and metacommunities, rather than estimating full correlation matrices. However, it is worth noting that these assumptions are made for the priors thus still allowing for dependencies in their posterior distributions.

We used weakly informative Gaussian priors on the fixed effects, and exponential priors on the group-level standard deviations and the Beta precision parameter. We ran 4 chains of 4,000 samples each, discarded the first 1,000 as burn-in, and obtained a total of 12,000 posterior draws which yielded satisfactory convergence results.

## Visualizing compositional change

To illustrate changes in the composition of habitat breadth and land cover between 1973–1976 and 2017–2020, we plotted each of the 74 metacommunities in multivariate spaces defined by six habitat-association categories and seven land-cover categories, respectively. These plots show the distribution of metacommunities in each space and their shifts between time periods. Because the habitat-breadth and land-cover plots represent different category sets and are therefore dimension-specific projections, we used total variation distance (TVD) to directly compare the magnitude of temporal change across the two compositions. For each metacommunity  $i$ , we calculated TVD as

$$TVD_i = \frac{1}{2} \sum_{k=1}^K |p_{ik,t2} - p_{ik,t1}| \quad (6)$$

where  $p_{ik,t}$  is the proportion of bird relative abundance in habitat-breadth category  $k$ , or the proportion of land cover in category  $k$ , at time  $t$ , and  $K$  is the number of categories in the composition (six habitat-breadth categories or seven land-cover categories). TVD ranges from 0 to 1, where 0 indicates no change in composition between time periods and 1 indicates no overlap in composition.

## Model diagnostics and sensitivity analyses

We evaluated convergence of all models using standard diagnostic criteria, including R-hat values and effective sample size (54). To confirm that the model was appropriate to address our questions, we assessed whether the spatial extent of polygons, which ranged from 10,000 to 20,000 km<sup>2</sup> and defined our metacommunities, was related to the predicted trends in environmental heterogeneity and in  $\beta_{q=0}$ ,  $\beta_{q=1}$ ,  $\beta_{q=2}$ . Specifically, we examined whether polygons with larger extents tended to exhibit greater changes in these trends and found no clear patterns (Fig. S23-S26).

For the  $\beta$ -diversity models, we also tested the influence of each data point using the Pareto k-statistic, which highlights potential outliers (Pareto k-statistic > 1.00). While we detected several possible outliers in each  $\beta$ -diversity model, we found that two spatial polygons had high consistently high Pareto k-statistics (values  $\geq 1.5$  in at least two out of the three models). Therefore, we fit these models again without these two polygons.

To test whether our results were sensitive to the number of routes used in the  $\beta$ -diversity calculations, we repeated the workflow described in ‘Calculating  $\beta$ -diversity and environmental heterogeneity’ for both bird communities and the environment using four randomly sampled routes within each spatial polygon. Within each spatial polygon and for each time interval, we drew 99 random sets of four routes without replacement, and calculated  $\beta_{q=0}$ ,  $\beta_{q=1}$ ,  $\beta_{q=2}$ , and EH as the mean across these 99 estimates. We then fit Bayesian hierarchical models to these data with the same structure described above, evaluated model convergence, and quantified the influence of each data point. In these models, as well, we found two spatial polygons with high Pareto k-statistics (values  $\geq 1.5$  in at least two out of the three models) and therefore we refit models without these two polygons.

Finally, for the habitat association model, we also refit the model without the house sparrow (*Passer domesticus*), which was potentially influential in driving the negative change in relative abundance for the group of species with six habitat associations.

All analyses were conducted in R version 4.5.1.

## REFERENCES

1. J. D. Olden, L. Comte, X. Giam, The Homogocene: A research prospectus for the study of biotic homogenisation. *NeoBiota* **37**, 23-36 (2018).
2. B. H. Daru, T. J. Davies, C. G. Willis, E. K. Meineke, A. Ronk, M. Zobel, M. Pärtel, A. Antonelli, C. C. Davis, Widespread homogenization of plant communities in the Anthropocene. *Nature communications* **12**, 6983 (2021).
3. Q. Liu, A. Buyantuev, J. Wu, J. Niu, D. Yu, Q. Zhang, Intensive land-use drives regional-scale homogenization of plant communities. *Science of the Total Environment* **644**, 806-814 (2018).
4. Z. Peng, X. Qian, Y. Liu, X. Li, H. Gao, Y. An, J. Qi, L. Jiang, Y. Zhang, S. Chen, Land conversion to agriculture induces taxonomic homogenization of soil microbial communities globally. *Nature Communications* **15**, 3624 (2024).
5. S. A. Blowes, B. McGill, V. Brambilla, C. F. Chow, T. Engel, A. Fontrodona-Eslava, I. S. Martins, D. McGlinn, F. Moyes, A. Sagouis, Synthesis reveals approximately balanced biotic differentiation and homogenization. *Science Advances* **10**, eadj9395 (2024).
6. B. J. Cardinale, A. Gonzalez, G. R. Allington, M. Loreau, Is local biodiversity declining or not? A summary of the debate over analysis of species richness time trends. *Biological Conservation* **219**, 175-183 (2018).
7. R. J. Rolls, D. C. Deane, S. E. Johnson, J. Heino, M. J. Anderson, K. E. Ellingsen, Biotic homogenisation and differentiation as directional change in beta diversity: synthesising driver–response relationships to develop conceptual models across ecosystems. *Biological Reviews* **98**, 1388-1423 (2023).
8. M. L. McKinney, J. L. Lockwood, Biotic homogenization: a few winners replacing many losers in the next mass extinction. *Trends in Ecology & Evolution* **14**, 450-453 (1999).
9. A. J. Nowakowski, L. O. Frishkoff, M. E. Thompson, T. M. Smith, B. D. Todd, Phylogenetic homogenization of amphibian assemblages in human-altered habitats across the globe. *Proceedings of the National Academy of Sciences* **115**, E3454-E3462 (2018).
10. J. B. Socolar, S. C. Mills, J. J. Gilroy, D. E. Martínez-Revelo, C. A. Medina-Urbe, E. Parra-Sanchez, M. Ramirez-Gutierrez, J. Sand Sæbø, H. S. Meneses, G. Pérez, Tropical biodiversity loss from land-use change is severely underestimated by local-scale assessments. *Nature Ecology & Evolution* **9**, 1643-1655 (2025).
11. M. Redon, L. Berges, T. Cordonnier, S. Luque, Effects of increasing landscape heterogeneity on local plant species richness: how much is enough? *Landscape Ecology* **29**, 773-787 (2014).

12. P. Padmanabha, G. Nicoletti, D. Bernardi, S. Suweis, S. Azaele, A. Rinaldo, A. Maritan, Landscape and environmental heterogeneity support coexistence in competitive metacommunities. *Proceedings of the National Academy of Sciences* **121**, e2410932121 (2024).
13. J. M. Chase, M. A. Leibold, *Ecological niches: linking classical and contemporary approaches*. (University of Chicago Press, 2003).
14. R. H. MacArthur, E. O. Wilson, *The theory of island biogeography*. (Princeton University Press, Princeton, New Jersey, USA, 1967).
15. S. P. Hubbell, *The unified neutral theory of biodiversity and biogeography*., Princeton Monographs in Population Biology (Princeton University Press, Princeton, New Jersey, USA, 2001).
16. M. A. Leibold, M. Holyoak, N. Mouquet, P. Amarasekare, J. M. Chase, M. F. Hoopes, R. D. Holt, J. B. Shurin, R. Law, D. Tilman, The metacommunity concept: a framework for multi-scale community ecology. *Ecology letters* **7**, 601-613 (2004).
17. M. A. Leibold, J. M. Chase, *Metacommunity Ecology*. (Princeton University Press, Princeton, New Jersey, USA, 2008).
18. C. E. Brassil, Mean time to extinction of a metapopulation with an Allee effect. *Ecological Modelling* **143**, 9-16 (2001).
19. R. Kadmon, O. Allouche, Integrating the effects of area, isolation, and habitat heterogeneity on species diversity: a unification of island biogeography and niche theory. *The American Naturalist* **170**, 443-454 (2007).
20. M. Marvier, P. Kareiva, M. G. Neubert, Habitat destruction, fragmentation, and disturbance promote invasion by habitat generalists in a multispecies metapopulation. *Risk Analysis: An International Journal* **24**, 869-878 (2004).
21. I. Hanski, O. Ovaskainen, The metapopulation capacity of a fragmented landscape. *Nature* **404**, 755-758 (2000).
22. O. Allouche, M. Kalyuzhny, G. Moreno-Rueda, M. Pizarro, R. Kadmon, Area–heterogeneity tradeoff and the diversity of ecological communities. *Proceedings of the National Academy of Sciences* **109**, 17495-17500 (2012).
23. L. Heidrich, S. Bae, S. Levick, S. Seibold, W. Weisser, P. Krzystek, P. Magdon, T. Nauss, P. Schall, A. Serebryanyk, Heterogeneity–diversity relationships differ between and within trophic levels in temperate forests. *Nature ecology & evolution* **4**, 1204-1212 (2020).
24. A. Stein, K. Gerstner, H. Kreft, Environmental heterogeneity as a universal driver of species richness across taxa, biomes and spatial scales. *Ecology Letters* **17**, 866-880 (2014).
25. J. Hortal, K. A. Triantis, S. Meiri, E. Thébault, S. Sfenthourakis, Island species richness increases with habitat diversity. *The American Naturalist* **174**, E205-E217 (2009).
26. R. Tamme, I. Hiiesalu, L. Laanisto, R. Szava-Kovats, M. Pärtel, Environmental heterogeneity, species diversity and co-existence at different spatial scales. *Journal of Vegetation Science* **21**, 796-801 (2010).
27. I. Seiferling, R. Proulx, C. Wirth, Disentangling the environmental-heterogeneity–species-diversity relationship along a gradient of human footprint. *Ecology* **95**, 2084-2095 (2014).

28. M. P. Barajas-Barbosa, P. Weigelt, M. K. Borregaard, G. Keppel, H. Kreft, Environmental heterogeneity dynamics drive plant diversity on oceanic islands. *Journal of Biogeography* **47**, 2248-2260 (2020).
29. J. Hortal, L. M. Carrascal, K. A. Triantis, E. Thébault, S. Meiri, S. Sfenthourakis, Species richness can decrease with altitude but not with habitat diversity. *Proceedings of the National Academy of Sciences* **110**, E2149-E2150 (2013).
30. R. Chocron, C. H. Flather, R. Kadmon, Bird diversity and environmental heterogeneity in North America: a test of the area–heterogeneity trade-off. *Global Ecology and Biogeography* **24**, 1225-1235 (2015).
31. S. Khan, L. Fahrig, A. E. Martin, Support for an area–heterogeneity tradeoff for biodiversity in croplands. *Ecol. Appl.* **33**, e2820 (2023).
32. A. Chao, N. J. Gotelli, T. Hsieh, E. L. Sander, K. Ma, R. K. Colwell, A. M. Ellison, Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies. *Ecological monographs* **84**, 45-67 (2014).
33. U.S. Geological Survey (USGS). (2024).
34. T. Sohl, R. Reker, M. Bouchard, K. Sayler, J. Dornbierer, S. Wika, R. Quenzer, A. Friesz, Modeled historical land use and land cover for the conterminous United States. *Journal of Land Use Science* **11**, 476-499 (2016).
35. IUCN. (2026), vol. 2026.
36. L. A. Berigan, E. I. Greig, D. N. Bonter, Urban house sparrow (*Passer domesticus*) populations decline in North America. *The Wilson Journal of Ornithology* **132**, 248-258 (2020).
37. A. Baselga, S. Bonthoux, G. Balent, Temporal beta diversity of bird assemblages in agricultural landscapes: land cover change vs. stochastic processes. *PLoS One* **10**, e0127913 (2015).
38. H.-X. Zou, C. Hsieh, P. L. Zarnetske, K. Zhu, B. C. Weeks, Abundance redistribution increases predator-prey interaction potentials among North American birds. *bioRxiv*, 2025.2012. 2019.695589 (2025).
39. K. P. Davis, H. R. Sofaer, L. Pejchar, Land cover differentially affects abundance of common and rare birds. *Global Change Biology* **29**, 2999-3009 (2023).
40. M. L. McKinney, F. A. La Sorte, Invasiveness and homogenization: synergism of wide dispersal and high local abundance. *Global Ecology and Biogeography* **16**, 394-400 (2007).
41. J. P. Wayman, J. P. Sadler, T. E. Martin, L. J. Graham, H. J. White, J. A. Tobias, T. J. Matthews, Unravelling the complexities of biotic homogenization and heterogenization in the British avifauna. *Journal of Animal Ecology* **93**, 1288-1302 (2024).
42. M. D. Correll, E. H. Strasser, A. W. Green, A. O. Panjabi, Quantifying specialist avifaunal decline in grassland birds of the Northern Great Plains. *Ecosphere* **10**, e02523 (2019).
43. K. V. Rosenberg, A. M. Dokter, P. J. Blancher, J. R. Sauer, A. C. Smith, P. A. Smith, J. C. Stanton, A. Panjabi, L. Helft, M. Parr, P. P. Marra, Decline of the North American avifauna. *Science* **366**, 120-124 (2019).
44. C. S. Robbins, D. K. Dawson, B. A. Dowell, Habitat area requirements of breeding forest birds of the middle Atlantic states. *Wildlife monographs*, 3-34 (1989).

45. B. G. Peterjohn, J. R. Sauer, C. S. Robbins, in *Ecology and management of Neotropical migratory birds: a synthesis and review of critical issues*, T. E. Martin, D. M. Finch, Eds. (Oxford University Press, Oxford, 1995), pp. 3-39.
46. L. Godet, P. Gaüzere, F. Jiguet, V. Devictor, Dissociating several forms of commonness in birds sheds new light on biotic homogenization. *Global Ecology and Biogeography* **24**, 416-426 (2015).
47. D. J. Ziolkowski, M. Lutmerding, W. B. English, V. I. Aponte, M. A. R. Hudson, U. S. G. Survey, Ed. (2023).
48. U.S. Geological Survey (USGS), U. S. G. S. (USGS), Ed. (Patuxent Wildlife Research Center, 2004).
49. G. J. Di Cecco, A. H. Hurlbert, Anthropogenic drivers of avian community turnover from local to regional scales. *Global Change Biology* **28**, 770-781 (2022).
50. M. L. Hobi, L. S. Farwell, M. Dubinin, D. Kolesov, A. M. Pidgeon, N. C. Coops, V. C. Radeloff, Patterns of bird species richness explained by annual variation in remotely sensed Dynamic Habitat Indices. *Ecological Indicators* **127**, 107774 (2021).
51. A. M.-C. Wadoux, G. B. Heuvelink, S. De Bruin, D. J. Brus, Spatial cross-validation is not the right way to evaluate map accuracy. *Ecological Modelling* **457**, 109692 (2021).
52. C. K. Wikle, Hierarchical Bayesian models for predicting the spread of ecological processes. *Ecology* **84**, 1382-1394 (2003).
53. G. Casella, E. I. George, Explaining the Gibbs sampler. *The American Statistician* **46**, 167-174 (1992).
54. A. Gelman, J. B. Carlin, H. S. Stern, D. B. Rubin, *Bayesian data analysis*. (Chapman and Hall/CRC, 2013).

## Acknowledgments

We thank the ‘Biodiversity Synthesis’ group at iDiv, as well as S. Blowes, who provided advice on the analyses, D. Jian Xiong Tan, who provided advice on their presentation, and A. Cord, who co-hosted an interdisciplinary workshop with NK at which this collaboration was initiated. We also extend our thanks to the citizen scientists who support the North American Breeding Bird Survey.

**Funding:** MPBB, KLT, and JMC were supported by the German Center for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig (DFG FZT 118-202548816). KLT and JMC were also supported by an ERC Advanced Grant (MetaChange) funded by the European Union (101098020). NB and NK were supported by the Deutsche Forschungsgemeinschaft (DFG, German Research Foundation) through the Emmy Noether grant KL3037/1-1 and the TRR391

within the project A07, grant number 520388526. All authors gratefully acknowledge the support of the Junge Akademie, which funded the workshop at which this collaboration was initiated.

**Author contributions:**

Conceptualization: J.M.C. (lead), M.P.B.B. (supporting), K.L.T. (supporting)

Data Curation: K.L.T. (lead), M.P.B.B. (supporting)

Methodology: K.L.T. (lead), M.P.B.B. (supporting), J.M.C. (supporting), N.B. (supporting), N.K. (supporting)

Formal analysis: M.P.B.B. (equal), K.L.T. (equal), N.B. (equal)

Funding acquisition: J.M.C. (lead), NK (supporting)

Project administration: M.P.B.B. (equal), K.L.T. (equal)

Supervision: J.M.C. (lead), N.K. (supporting)

Visualization: M.P.B.B. (equal), K.L.T. (equal), N.B. (equal)

Writing—original draft: M.P.B.B. (equal), K.L.T. (equal), J.M.C. (equal), N.B. (equal)

Writing—review & editing: M.P.B.B. (equal), K.L.T. (equal), J.M.C. (equal), N.B. (equal), N.K. (supporting)

**Competing interests:**

The authors have no competing interests to declare.

**Data Availability**

Data associated with this work are publicly available. The North American Breeding Bird Survey data that support the findings of this study were derived from resources available in the public domain and are available at <https://doi.org/10.5066/P9GS9K64>; spatial data are available at <https://databasin.org/datasets/02fe0ebbb1b04111b0ba1579b89b7420/>. Data from the Annual National Land-cover Database were derived from resources available in the public domain and are available at <https://doi.org/10.5066/P94UXNTS>. Historical land-cover data were derived from resources available in the public domain and are available at <https://www.sciencebase.gov/catalog/item/59d3c73de4b05fe04cc3d1d1>. The habitat-association data are openly available from The IUCN Red List of Threatened Species. Version 2026-1 at [www.iucnredlist.org/en](http://www.iucnredlist.org/en). Code to reproduce analyses, as well as output data such as model objects, are provided via the following link, which will be converted to a permanent identifier upon publication: <https://github.com/chase-lab/betabirds.git>.

## Figures

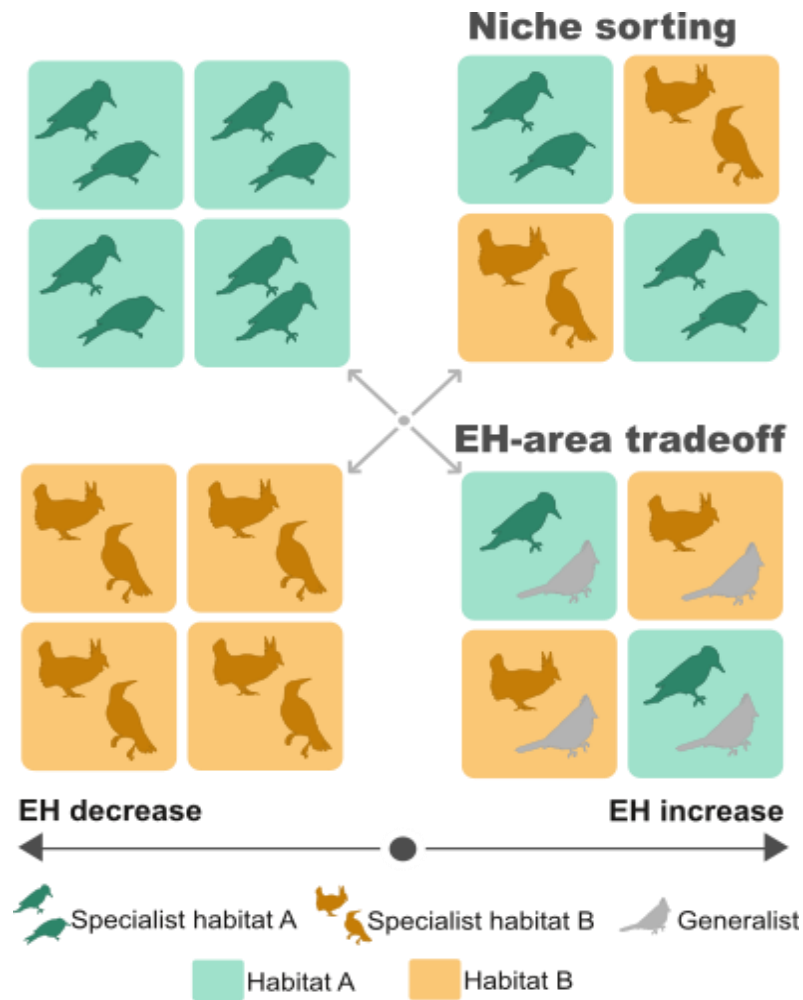


**Fig. 1. Competing predictions for how bird  $\beta$ -diversity responds to increasing environmental heterogeneity.** Starting with two metacommunities each with homogeneous land-cover and supporting two different specialist species in each of its communities (left column), the niche hypothesis predicts that as environmental heterogeneity increases, all four specialist species will persist and sort by habitat, so communities differ more in composition than before and  $\beta$ -diversity increases (top right). Alternatively, the area-heterogeneity tradeoff predicts that when environmental heterogeneity increases, specialists may not have sufficient area to persist and thus would be replaced by generalist species that are able to thrive in habitat mosaics (bottom right). In this case communities also differ more in composition than before and  $\beta$ -diversity increases, but as a result of the extirpation of a specialist and colonization by a generalist. We can also predict that as environmental heterogeneity decreases (i.e., reading the graph from right to left),  $\beta$ -diversity should decrease.

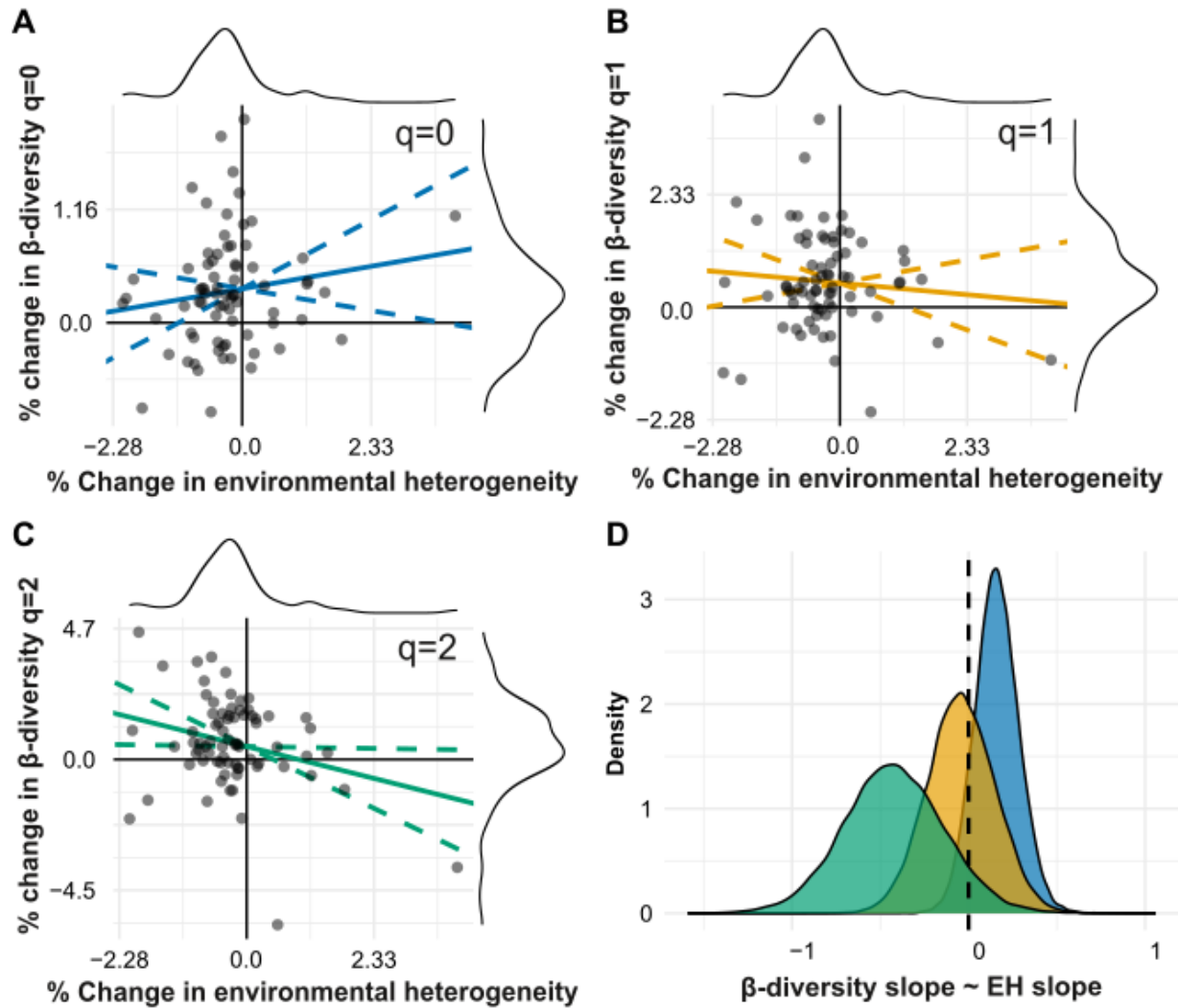


**Figure 2: Association between the rate of change in environmental heterogeneity (EH) and the rate of change in bird  $\beta$ -diversity (i.e., spatial turnover) per 4-year intervals from 1973-2020 for Hill numbers ( $q=0, 1, 2$ ) that emphasize different regions of the abundance distribution.**  $q = 0$  (i.e., species richness) weights all species equally regardless of abundance (A),  $q = 1$  weights the effective number of common species more heavily (B), and  $q = 2$  weights the effective number of dominant species more heavily (C). The overall trend and 95% credible intervals are shown in solid and dashed lines, respectively, while the posterior mean of each metacommunity is displayed as grey points. When  $q=0$ , the rate of change in  $\beta$ -diversity increases as the rate of change in EH increases, supporting the niche hypothesis (A). This relationship shifts as relative abundance is given more weight, moving from a slightly negative relationship between the rate of change in EH and the rate of change in  $\beta$ -diversity when  $q=1$  (B), to a strongly negative relationship when  $q=2$  (C), which supports the area-heterogeneity tradeoff. Posterior distributions of the regression slopes for each Hill number further illustrate the opposing relationship between  $q=0$  and  $q=2$  (D).

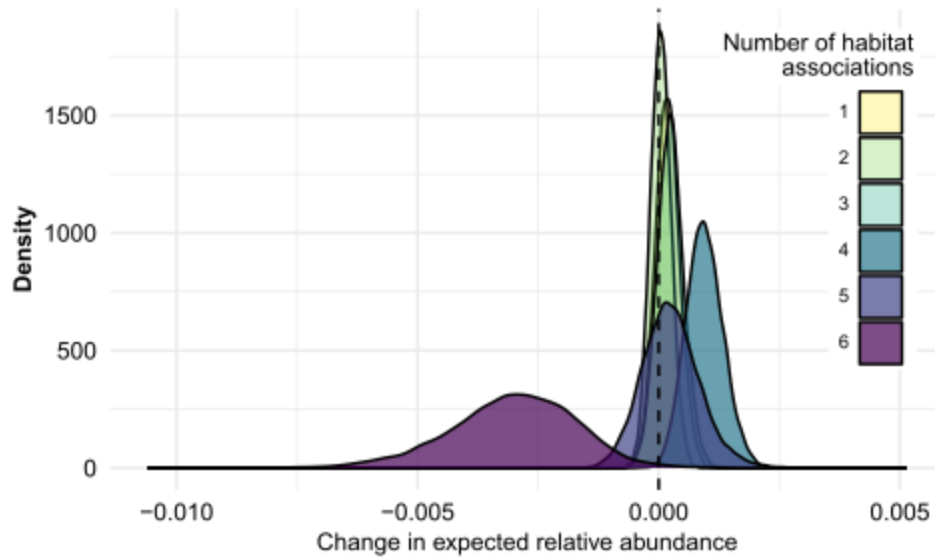


**Figure 3: Changes in bird relative abundance through time (from 1973–1976 to 2017–2020) along a gradient of habitat specialization.** Posterior distributions showing the expected change in relative abundance between 1973–1976 and 2017–2020 for 481 bird species with one (specialists) to six (generalists) habitat associations. Positive values indicate higher (expected) relative abundance in 2017–2020 than in 1973–1976, whereas negative values indicate that (expected) relative abundance was higher in 1973–1976. Model predictions show that species with 6 habitat associations declined in their relative abundance in 2017–2020, relative to 1973–1976. Alternatively, the model predicts that species with 4 habitat associations increased in relative abundance in 2017–2020, relative to 1973–1976.

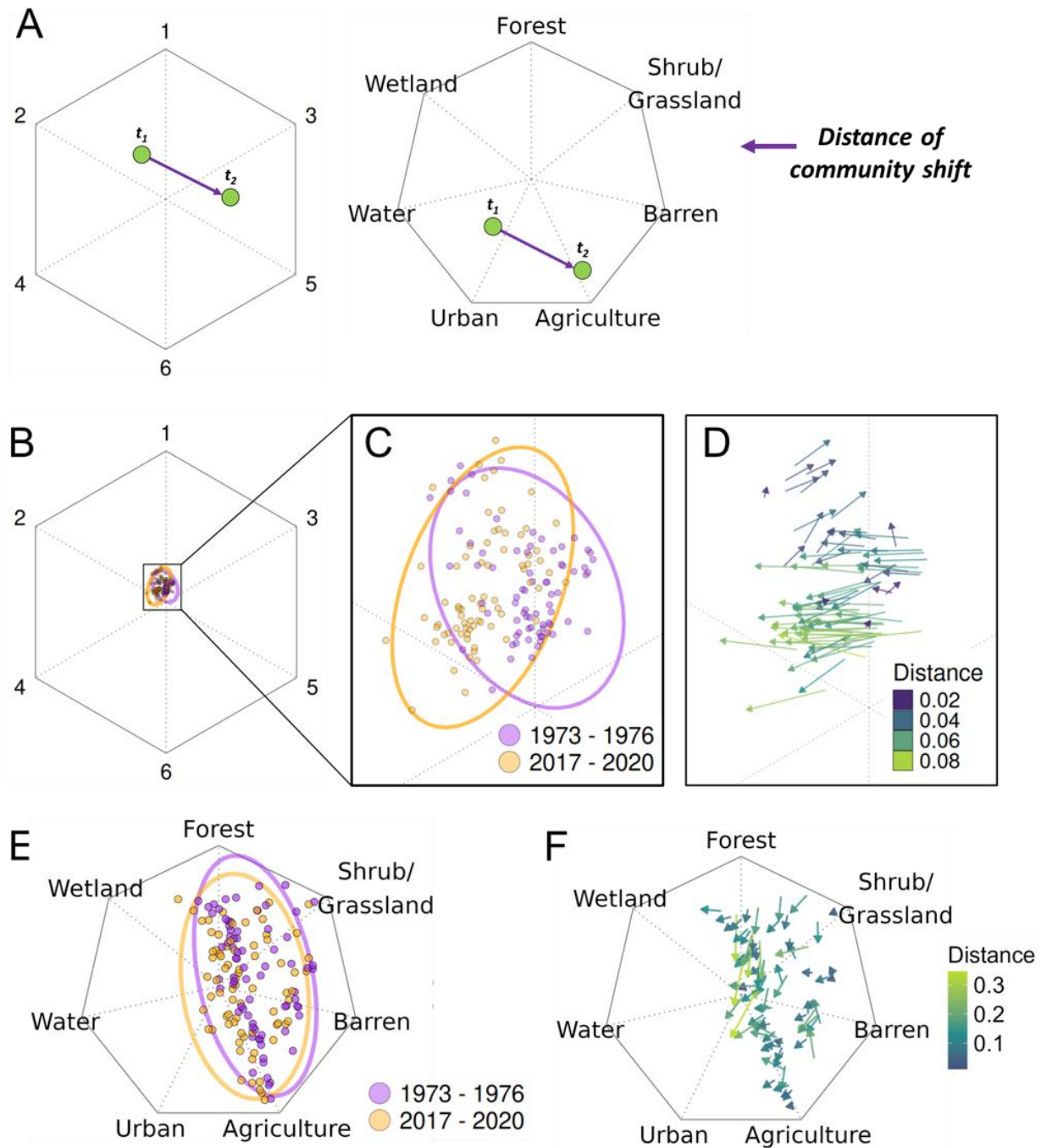


**Figure 4: Direction of compositional change in bird metacommunities and the environment.** In the multivariate space created by a hypothetical metacommunity composed of individuals with 1 (i.e., specialist) to 6 (i.e., extreme generalist) habitat associations and composed of seven land-cover categories, the distance from time 1 ( $t_1$ ) to time 2 ( $t_2$ ) represents the compositional shift of the metacommunity (A). Plotting the relative abundance of bird species with different habitat breadths for each of the 74 metacommunities reveals strong clustering close to but above the center (where the center indicates a perfect balance among

habitat associations) (**B**). Magnifying the area highlighted in the rectangle in B, metacommunities in 1973-1976 were composed primarily of species with 1-3 habitat associations, but in 2017-2020, this shifted towards compositions with 1, 2, and 4 habitat associations (**C**). The distance of each metacommunity shift shows that the majority of metacommunities moved toward 2 and 4 habitat associations, although several metacommunities moved in the opposite direction toward the vertex representing 1 habitat association (**D**). The land-cover composition of the 74 metacommunities reveals that many metacommunities were distributed along an axis spanning from forest to agriculture (where the center indicates a perfect balance among land-cover categories) (**E**). The distance of each metacommunity shift in land-cover composition shows that the majority of metacommunities shifted minimally, with many moving towards stronger agriculture and urban representation (**F**).

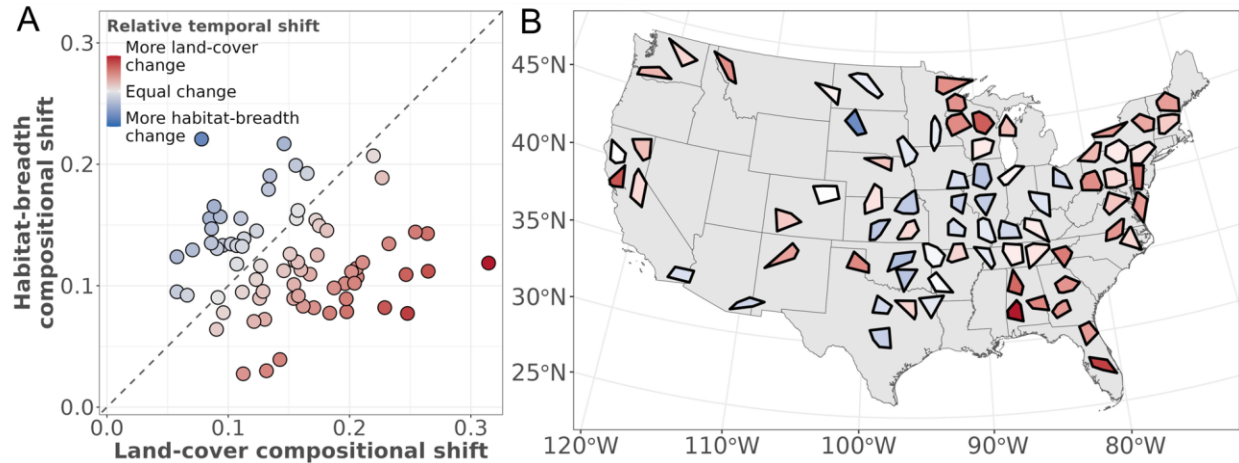


**Figure 5: Comparison of compositional shifts in bird metacommunities and the environment between 1973-1976 and 2017-2020.** The majority of metacommunities experienced more change in their land-cover composition than in the composition of specialist and generalist species, where values of 0 indicate no compositional change and values of 1 indicate complete compositional change (A). If bird metacommunities perfectly track changes in the environment, values would fall along the dotted line. The small number of metacommunities that did exhibit more change in the habitat-breadth composition of birds than in land-cover change were located in the midwestern USA, while the metacommunities with the highest magnitude imbalance in land-cover change relative to bird habitat-breadth change were more spread, though predominantly in the north and southeast (B).

# Supplementary Materials

## This PDF file includes:

Supplementary Text  
Figs. S1 to S26  
Tables S1 to S4

\*Corresponding authors. Email: [paolabarajas@gmail.com](mailto:paolabarajas@gmail.com), [kimberly.thompson@idiv.de](mailto:kimberly.thompson@idiv.de)

## This PDF file includes:

Supplementary Text  
Figs. S1 to S26  
Tables S1 to S4

## Supplementary Text

### Land-cover accuracy assessment

During the years in which the NLCD and historical land-cover scenario maps overlapped (1985-1992), agreement between the two products was moderate at the national scale, with a mean Cohen's kappa of 0.49 (range: 0.48-0.50) and an average pixel-level match rate of 53% (range: 52%-54%) (Figure S2). Within spatial polygons, overall accuracy was similar (mean: 55%, range: 13%-83%), but agreement as measured by Cohen's kappa was lower (mean: 0.37, range: 0.09-0.60) (Figure S3). At the national level, sensitivity was consistently low across most land-cover classes (Figure S4), with frequent misclassifications observed between cultivated cropland and hay/pasture, among forest types (deciduous, evergreen, and mixed), between shrubland and grassland, and between herbaceous and woody wetlands (Figure S5). Based on these patterns, we aggregated these categories into 'Agriculture', 'Forest', 'Shrub/Grassland', and 'Wetland' classes, and repeated the accuracy assessment.

Following class aggregation, both national and polygon-level agreement improved. At the national level, mean Cohen's kappa increased to 0.55 (range: 0.54-0.56) with overall pixel-level accuracy of 61% (range: 60%-62%) (Figure S6). Agreement within polygons also increased (mean Cohen's kappa: 0.49, range: 0.12-0.70), and mean accuracy reached 72% (range: 17%-93%) (Figure S7). Sensitivity (true positive rate) exceeded 0.80 for all aggregated classes except Wetland, which improved to 0.48 (Figure S8). Persistent misclassification remained, with Barren land often confused with Shrub/Grassland, Wetland with Forest, Urban/Developed with Agriculture, Forest, and Shrub/Grassland, and Perennial Ice/Snow with Barren (Figure S9). However, the improved overall and class-level accuracy, particularly at the polygon level, demonstrates that aggregation substantially enhanced comparability between products and supports the utility of the harmonized land-cover dataset for the further analyses in this study.

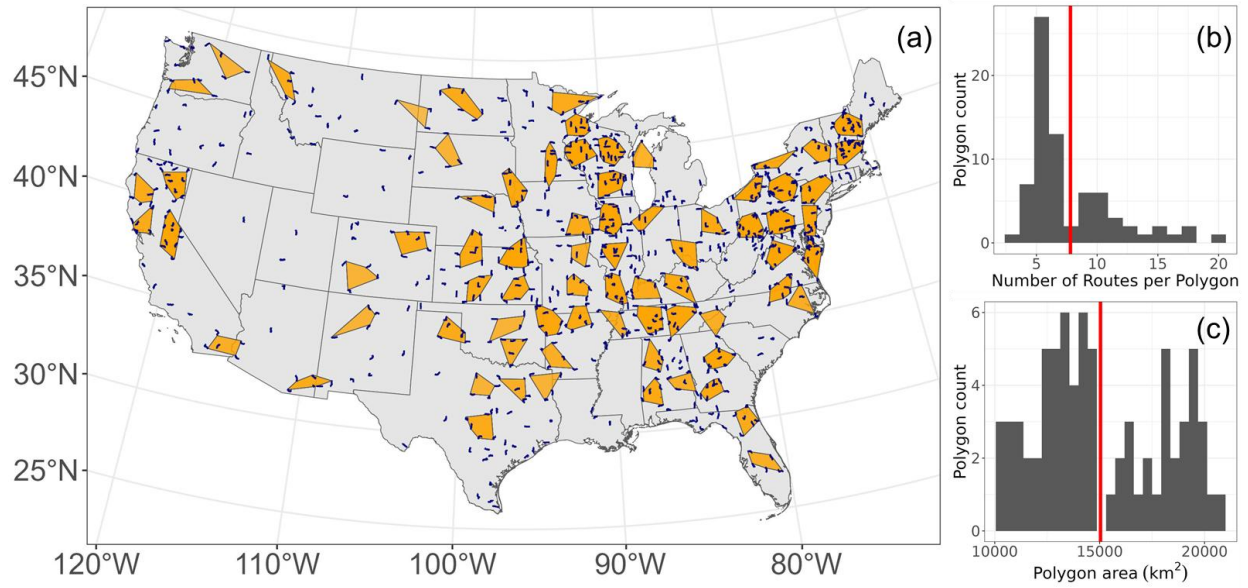


**Figure S1.**

(a) Map of the 74 spatial polygons, i.e. metacommunities (orange), that contain 594 North American Breeding Bird Survey routes (dark blue), each sampled at least once in every 4-year interval from 1973–2020. Routes not within or at the vertex of a spatial polygon were too isolated to be assigned to existing spatial polygons or to form new spatial polygons. Distribution of the number of routes per polygon which ranged from 3 to 20 routes with a mean of 7.8 (solid red line) (b), and polygon area which ranged from 10,272 to 20,781 km<sup>2</sup> with a mean of 15,040 km<sup>2</sup> (solid red line) (c).

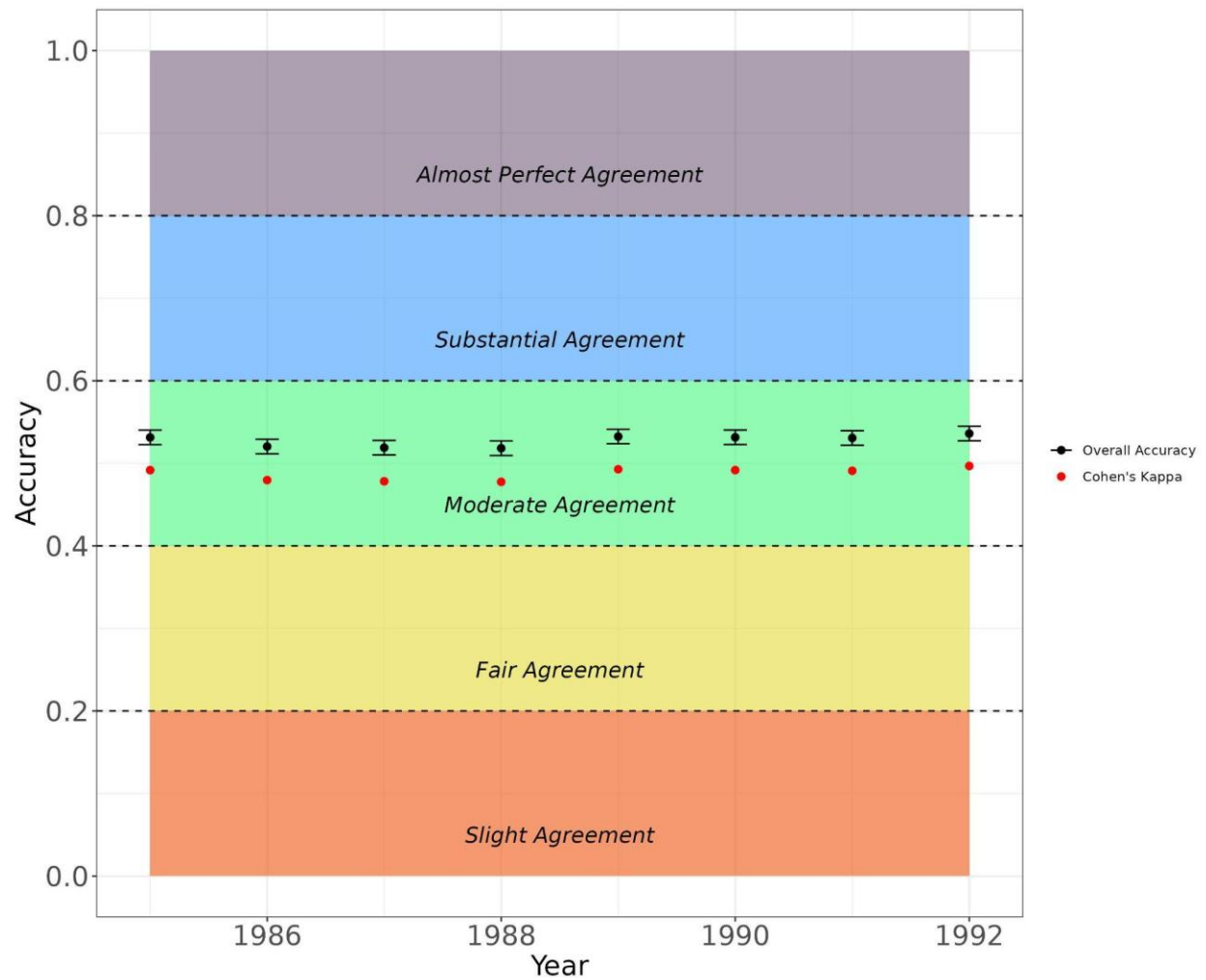


**Figure S2.**

Overall accuracy and Cohen's Kappa statistic for each year of overlap between National Land Cover Database maps and historical land-cover scenario maps revealed only moderate agreement across 13 land-cover classes when comparing 1000 random points for the contiguous United States.

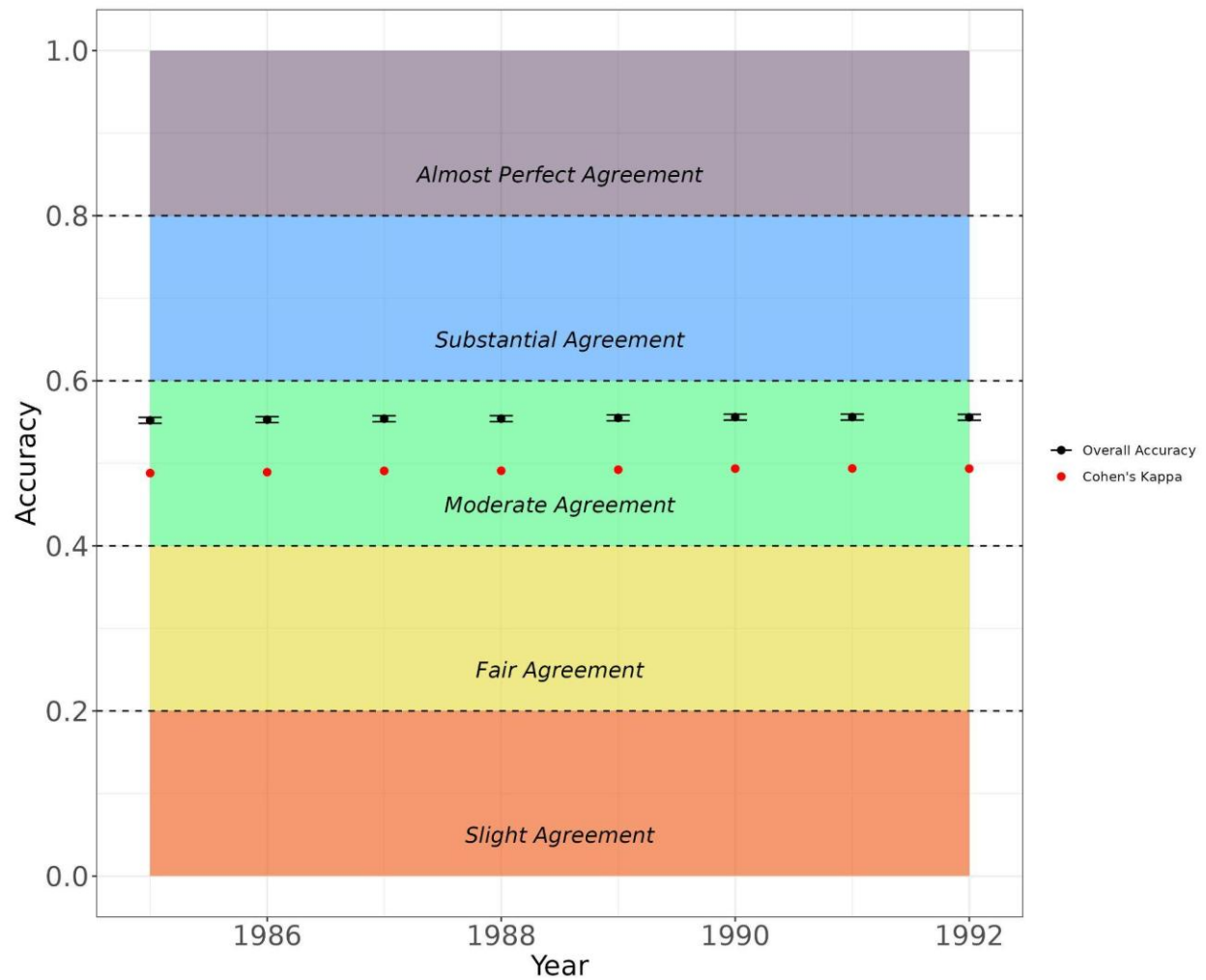


Figure S3.

Overall accuracy and Cohen's Kappa statistic for each year of overlap between National Land Cover Database land cover maps and historical land-cover scenario maps revealed only moderate agreement across 13 land-cover classes when comparing 1000 random points per spatial polygon.

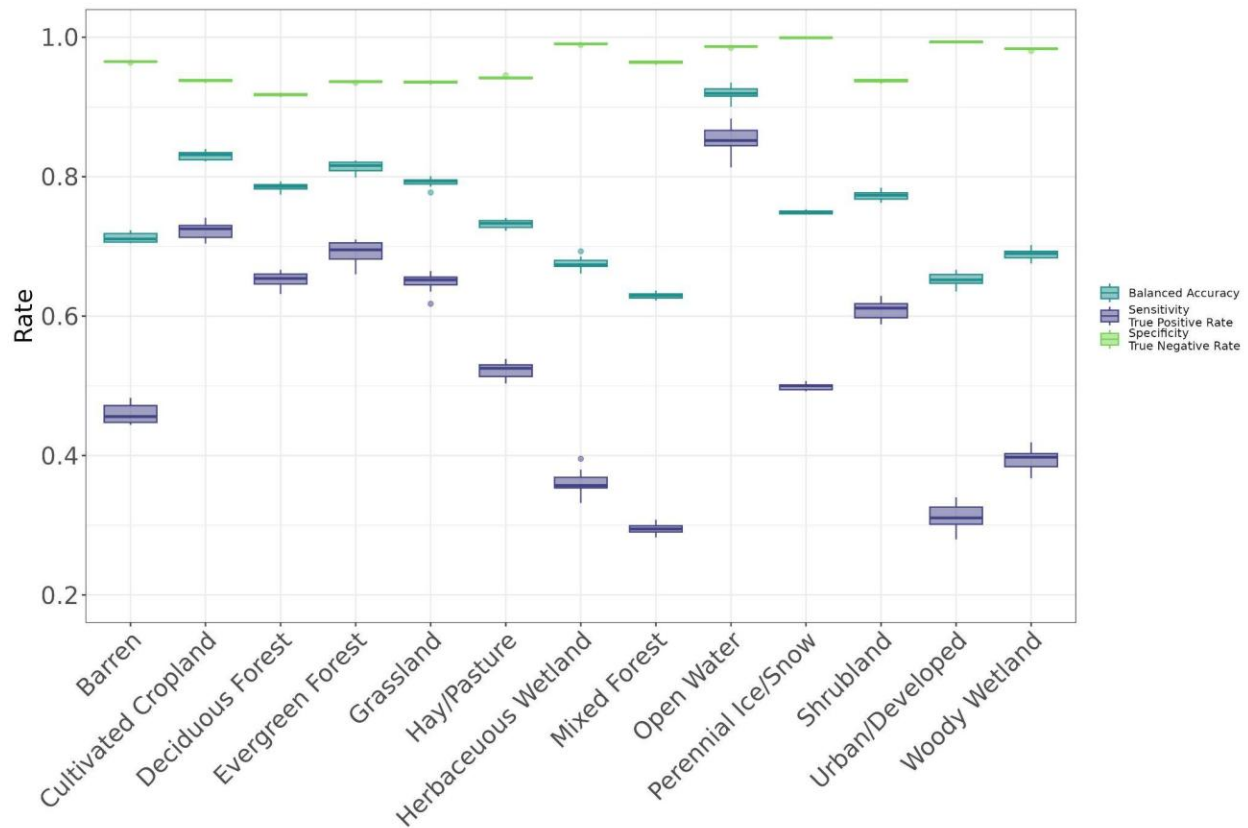


**Figure S4.**

Sensitivity (true positive rate), specificity (true negative rate), and balanced accuracy (average of sensitivity and specificity) for each land-cover class showing how the cover classes in the historical land-cover scenario product matched those in the National Land Cover Database when comparing 1000 random points per cover class for the

contiguous

United

States.

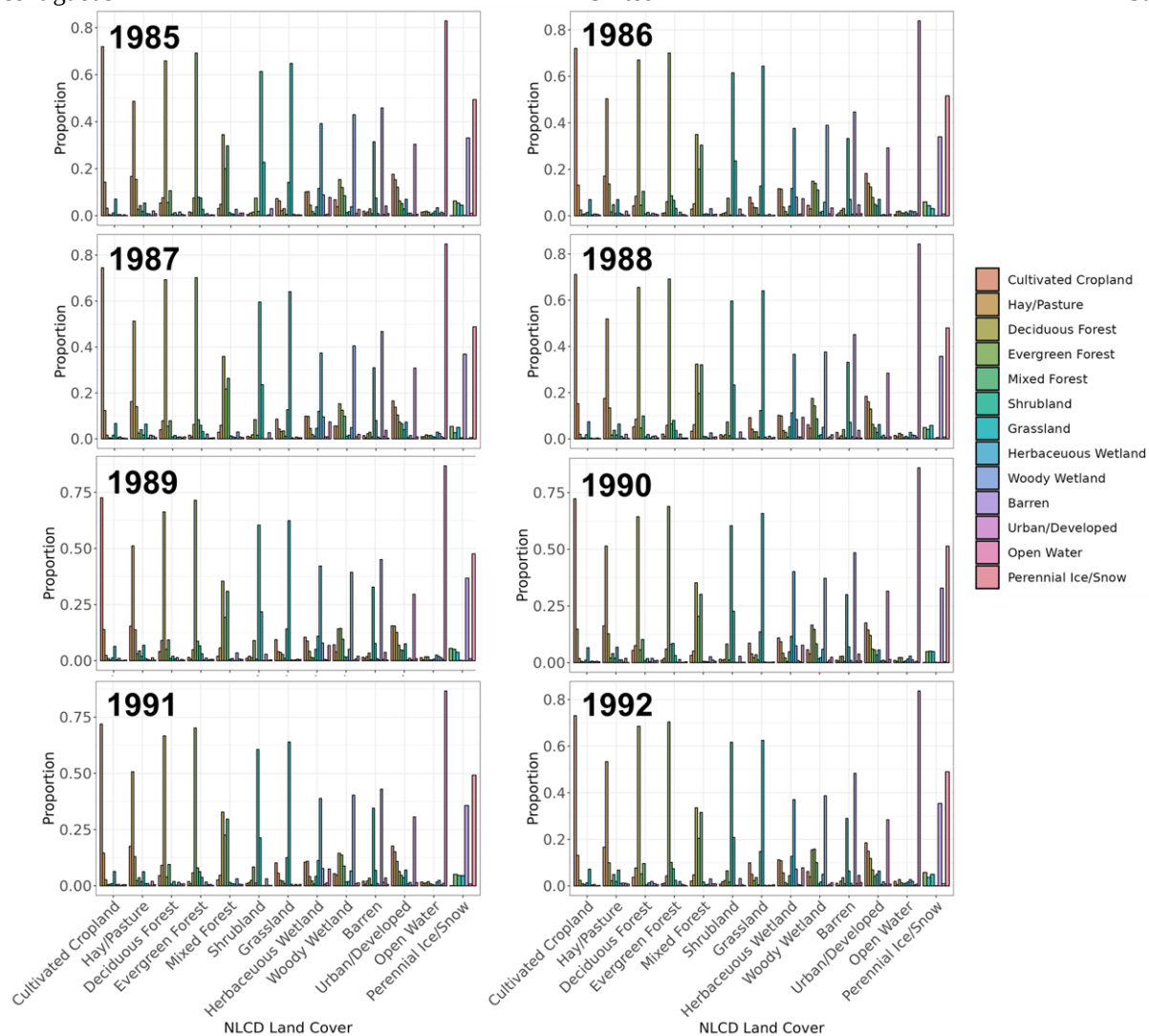


**Figure S5.**

Systematic misclassifications between historical land-cover and NLCD maps for 1000 random points per cover class. For each NLCD land-cover category on the x-axis and each year of overlap between the two products, the proportion of pixels correctly and incorrectly identified as belonging to that category is shown. For example, hay/pasture is represented by an orange bar, and across each year of overlap we see that hay/pasture was correctly identified in about 50% of the points. For all years we also see that the proportion of hay/pasture that was incorrectly identified as cultivated cropland (red bar) is about 20%, indicating a systemic misclassification between these two classes.

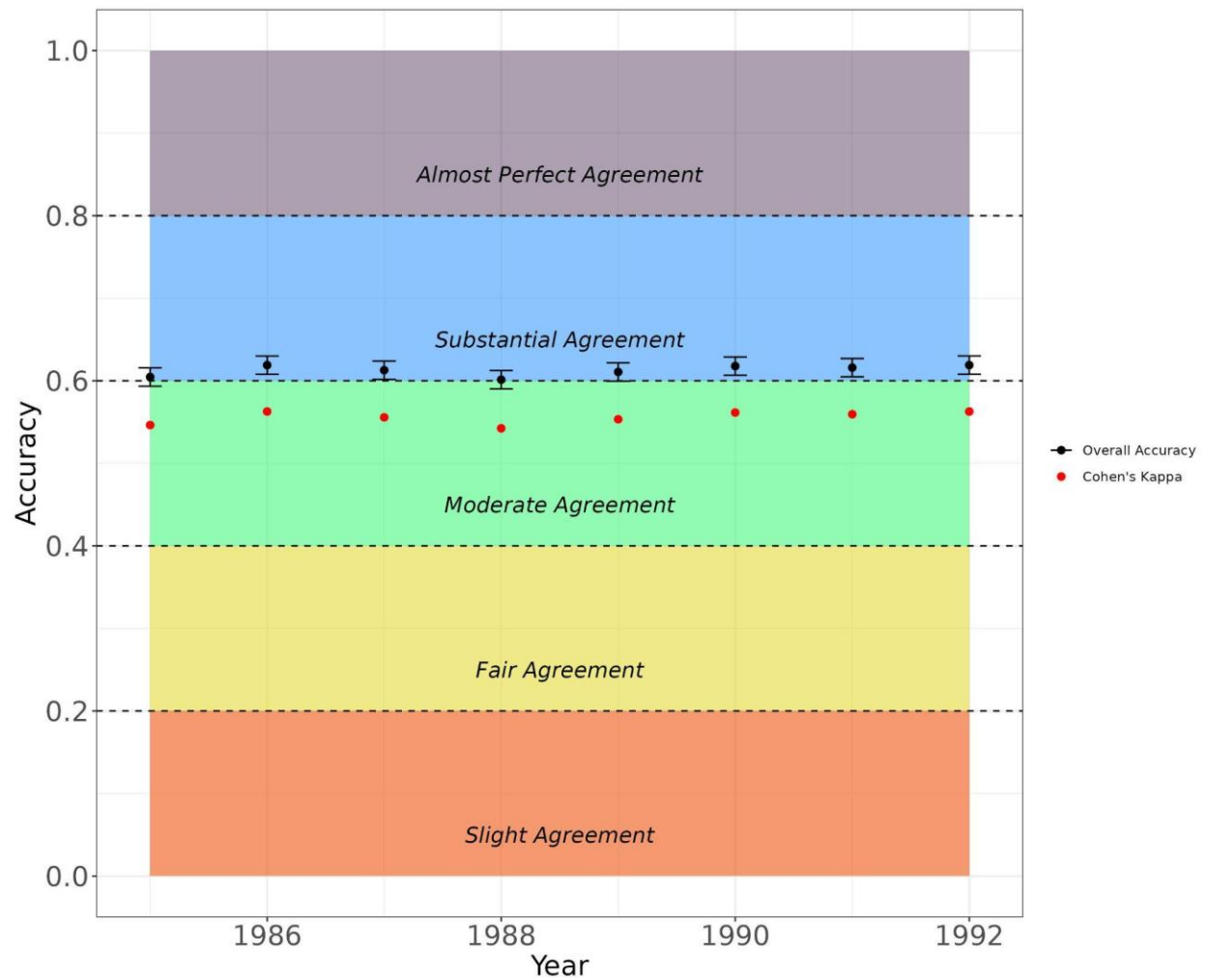


**Figure S6.**

Overall accuracy and Cohen's Kappa statistic for each year of overlap between National Land Cover Database land cover maps and historical land-cover scenario maps revealed moderate to substantial agreement when comparing 1000 random points per cover class for the contiguous United States and further aggregating land-cover classes.

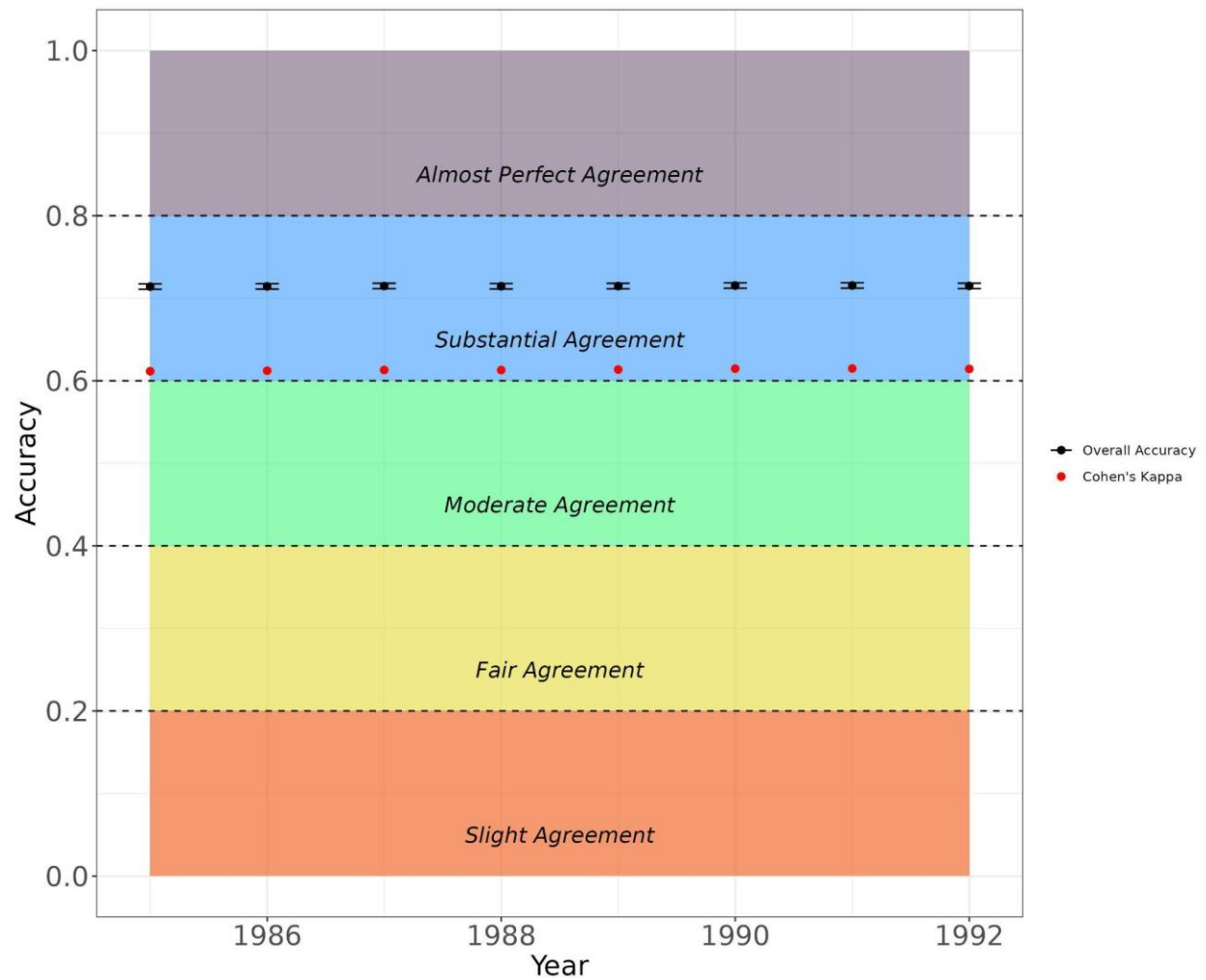


**Figure S7.**

Overall accuracy and Cohen's Kappa statistic for each year of overlap between National Land Cover Database land cover maps and historical land-cover scenario maps showed substantial agreement when comparing 1000 random points per spatial polygon and aggregating the original 13 land-cover classes to eight.

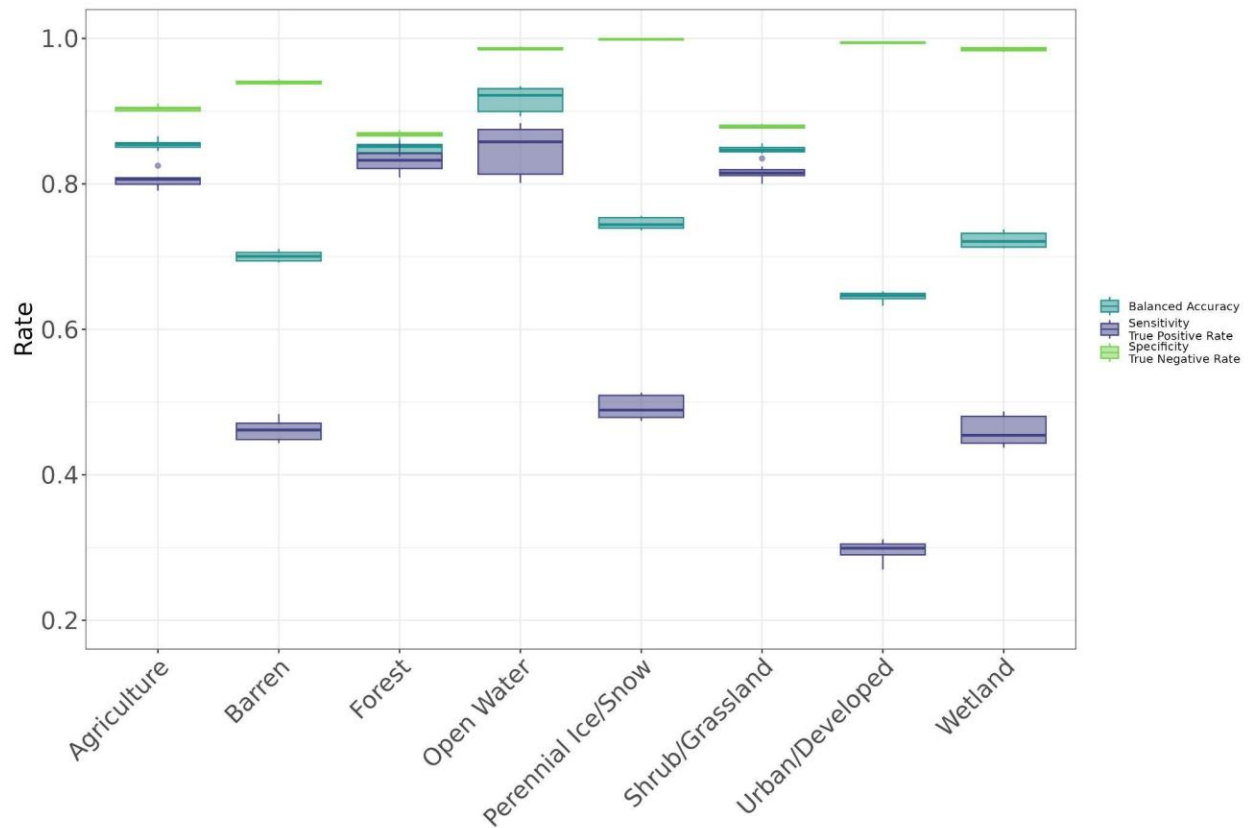


**Figure S8.**

Sensitivity (true positive rate), specificity (true negative rate), and balanced accuracy (average of sensitivity and specificity) for each land-cover class showing the improvement between the accuracy of matching the land-cover classes in historical land-cover scenario product and the National Land Cover Database after aggregating the 13 original classes to eight and when comparing 1000 random points per cover class for the contiguous United States. The improvement was especially strong for agriculture, forest, and shrub/grassland.

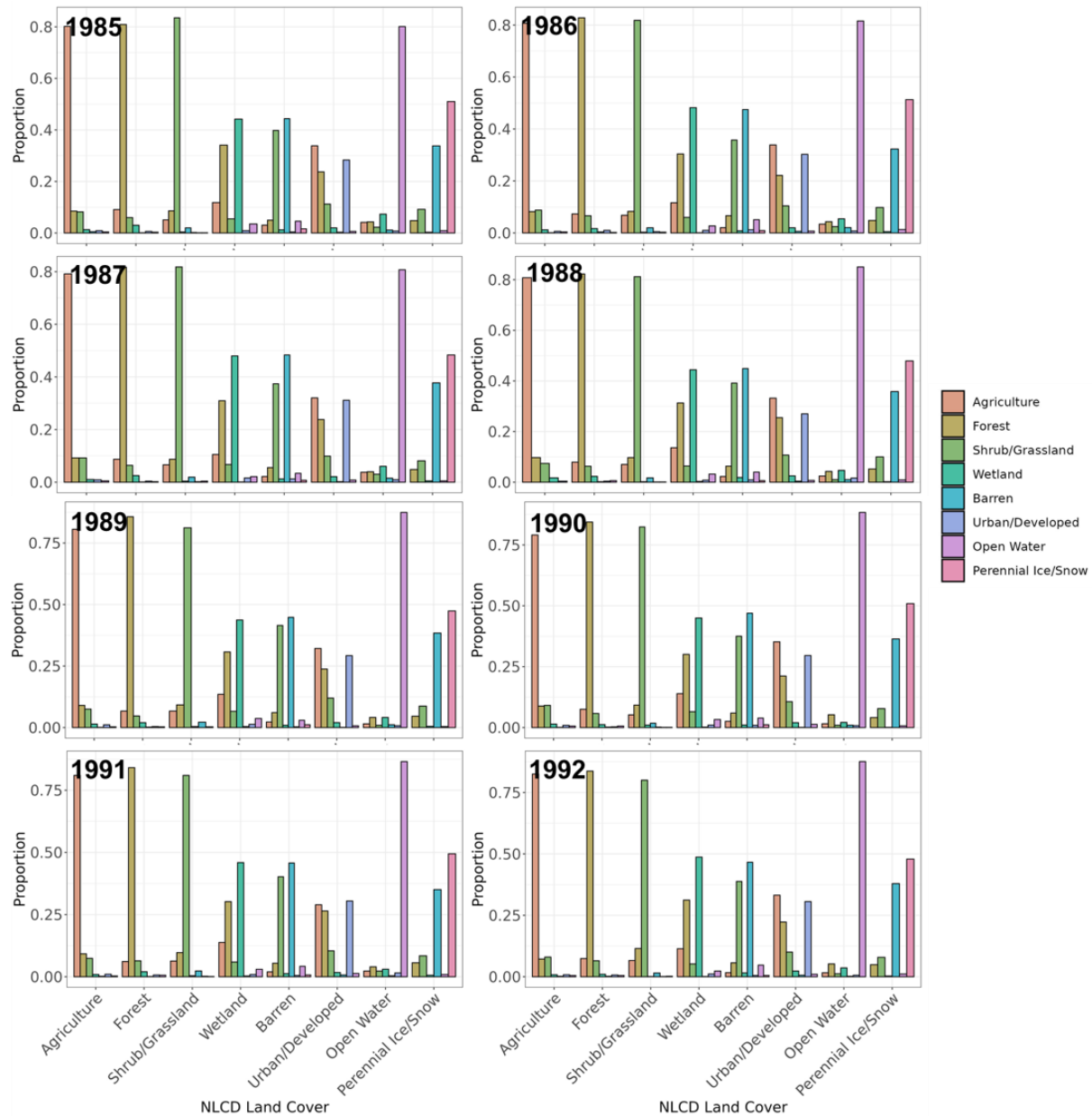


**Figure S9.**

Remaining systematic misclassifications between historical land-cover and NLCD maps for 1000 random points per cover class after aggregating the original 13 cover classes to eight. For each NLCD land-cover category on the x-axis and each year of overlap between the two products, the proportion of pixels correctly and incorrectly identified as belonging to that category is shown. While aggregating the original 13 classes into eight improved classifications, there were still systemic misclassifications for the wetland, barren, and urban classes. For example, wetlands (aqua) were often misclassified as forest (gold) or shrub/grassland (light green).

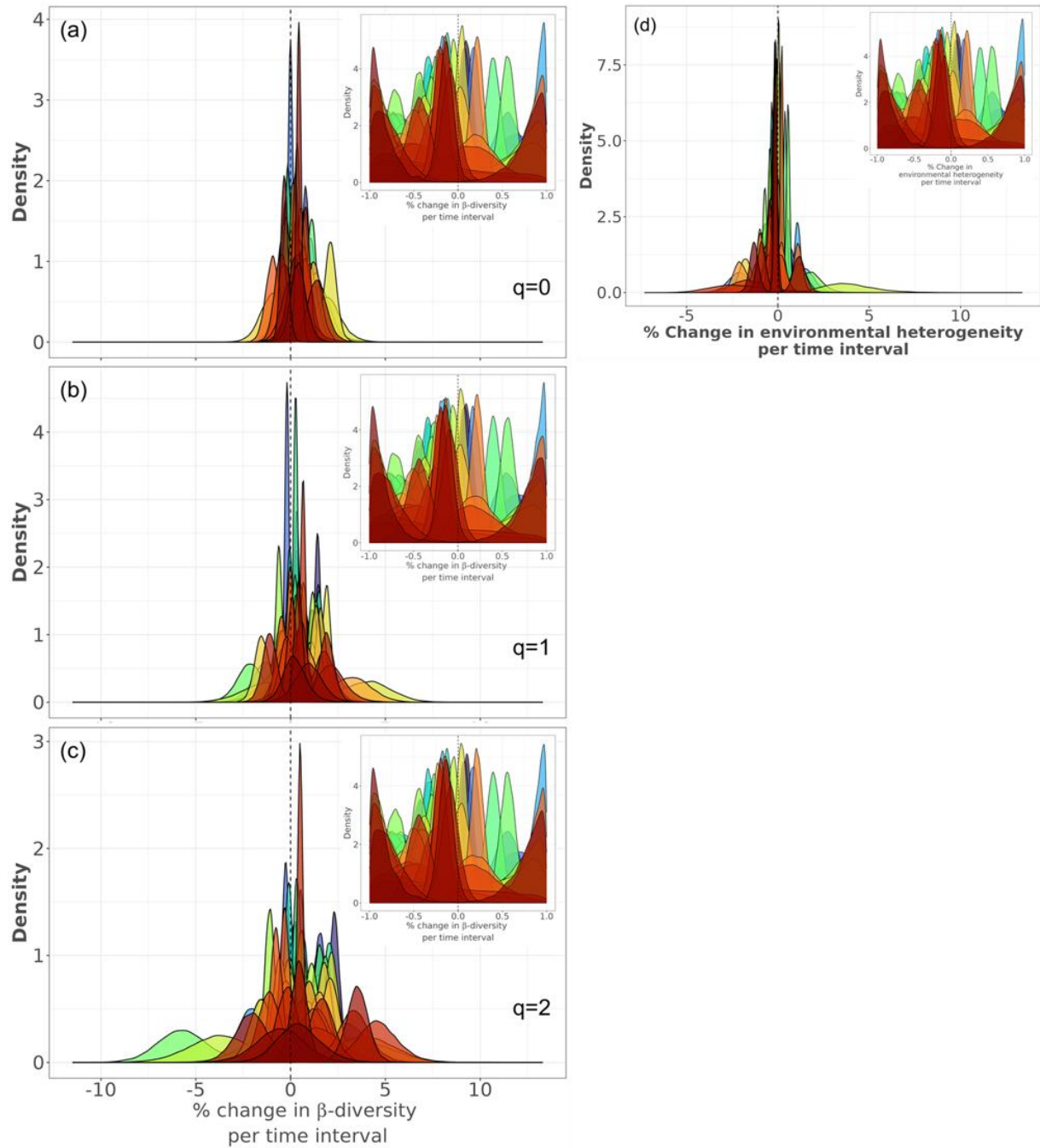


**Figure S10.**

Rate of change in beta diversity and environmental heterogeneity. Posterior distributions of the percent change in  $\beta$ -diversity per 4-year interval from 1973-2021 for  $q=0$  (a),  $q=1$  (b), and  $q=2$  (c) and the percent change in environmental heterogeneity (d) per 4-year interval.

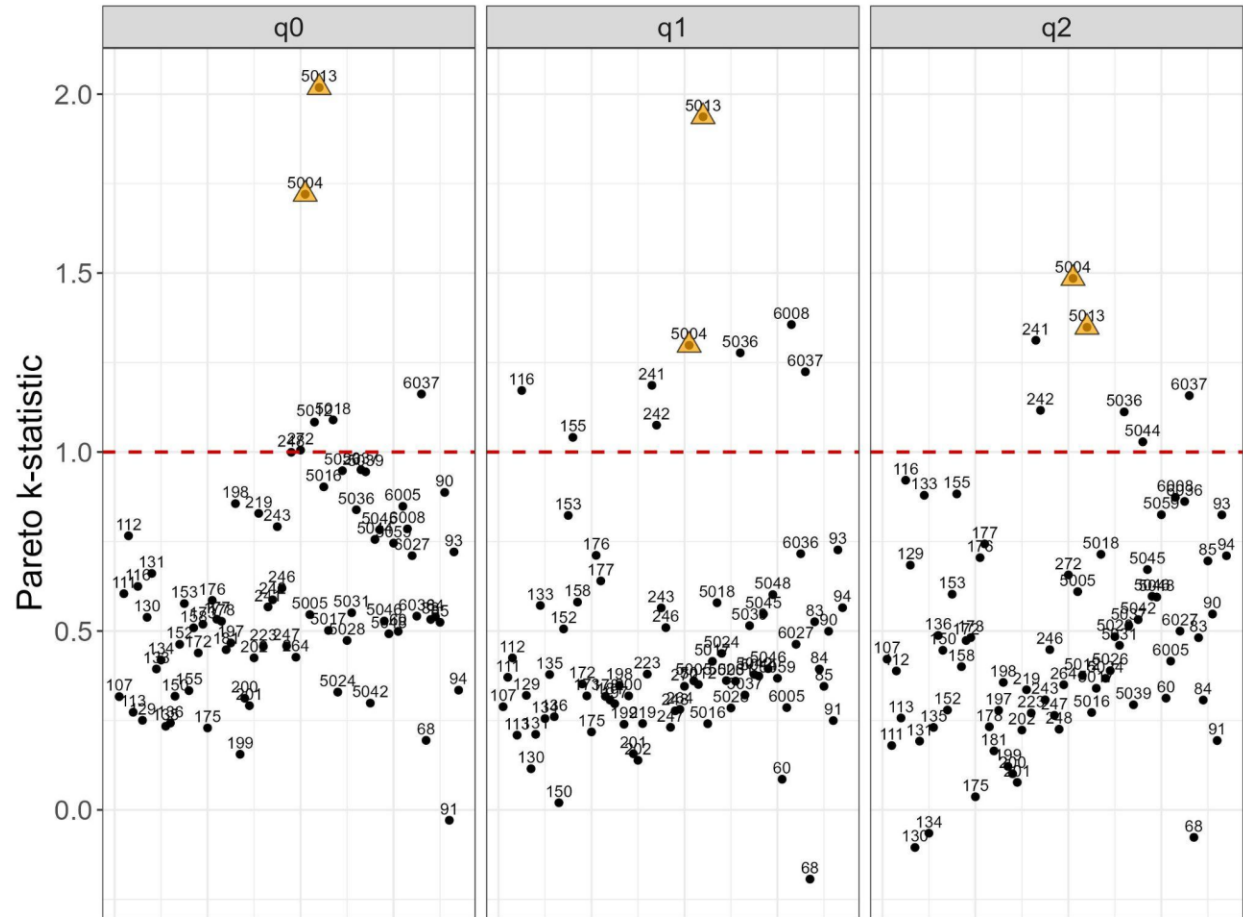


**Figure S11.**

Pareto k-statistics highlighting highly influential spatial polygons in Bayesian hierarchical models fit using  $\beta$ -diversity and EH values calculated from pairs of routes within spatial polygons. Panels show the Pareto k-statistics for each fitted model. Each point represents a spatial polygon, with orange triangles highlighting the two spatial polygons that showed a Pareto k-statistic  $\geq 1.5$  in at least two out of the three models.

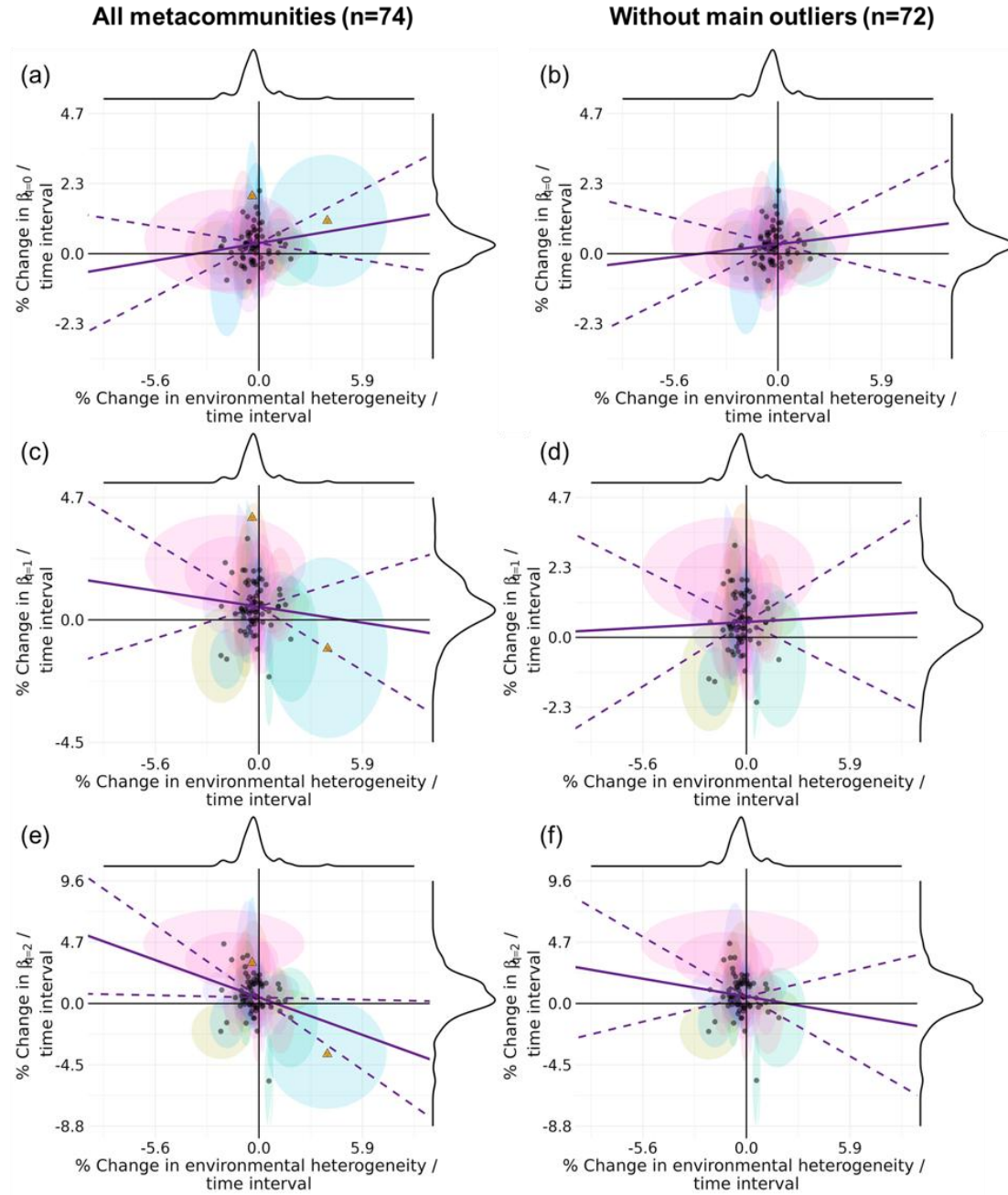


**Figure S12.**

Percent change in  $\beta$ -diversity per 4-year time interval as a function of the percent change in environmental heterogeneity per time interval for  $q=0$  (a, b),  $q=1$  (c, d), and  $q=2$  (e, f), where  $\beta$ -diversity was calculated as the average value across pairs of routes within each spatial polygon. The overall trend and 95% credible intervals are shown in solid and dashed lines, respectively; while the values of each spatial polygon are shown as grey points, with colored ellipses for the 95% credible intervals of each spatial polygon. (a), (c), and (e) mirror the results in the main text and include all spatial polygons ( $n=74$ ). The two orange triangles represent the spatial polygons which were flagged as potential outliers with Pareto-k analysis (Fig S11). (b), (d), and (f) show model predictions after removing these two outliers.

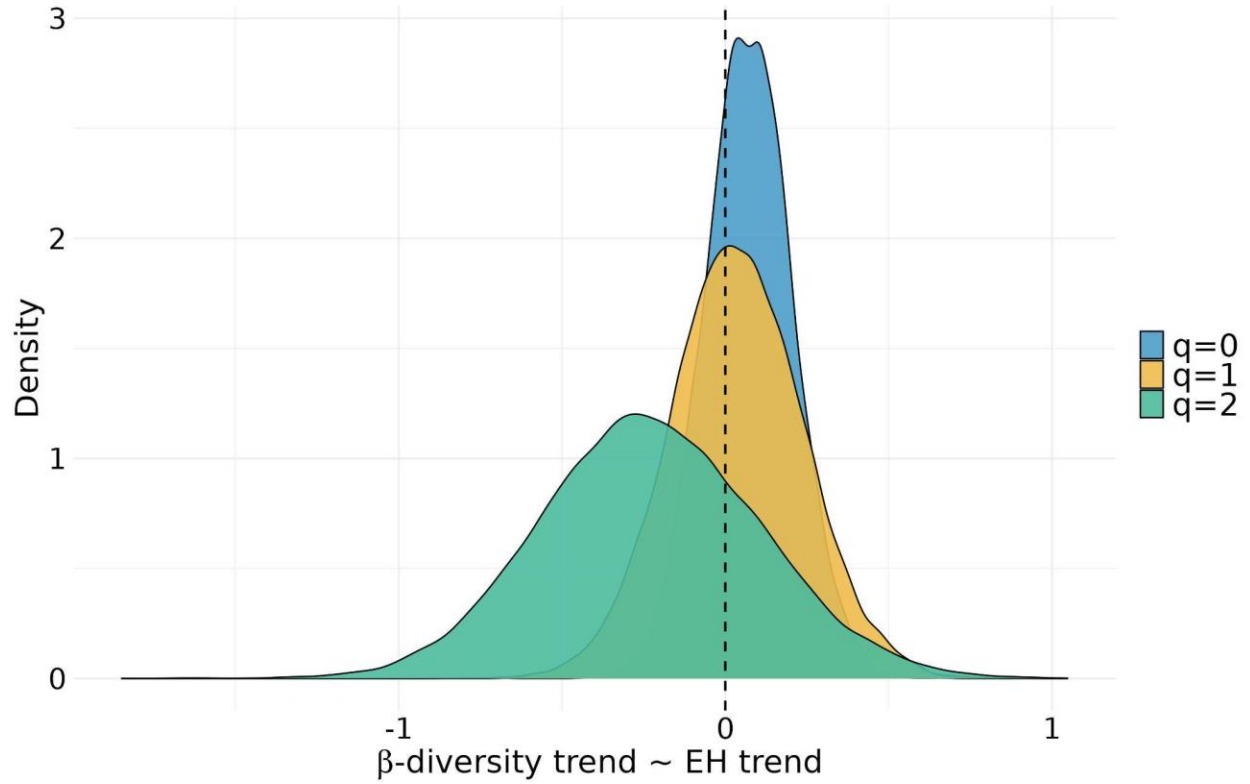


**Figure S13.**

Posterior distributions of the regression slopes relating change in  $\beta$ -diversity to change in environmental heterogeneity for three Hill numbers ( $q=0$ ,  $q=1$ ,  $q=2$ ), with two influential metacommunities (see Figure S11 and S12) removed. Removing these metacommunities shifted the posterior means closer to zero for all  $\beta$ -diversity metrics; however,  $q=0$  and  $q=2$  still exhibited opposing relationships with EH: the probability of drawing a value from the posterior distribution greater than 0 for  $q_0 = 0.71$ ; the probability of drawing a value from the posterior distribution less than 0 for  $q_2 = 0.76$  (Table S1).

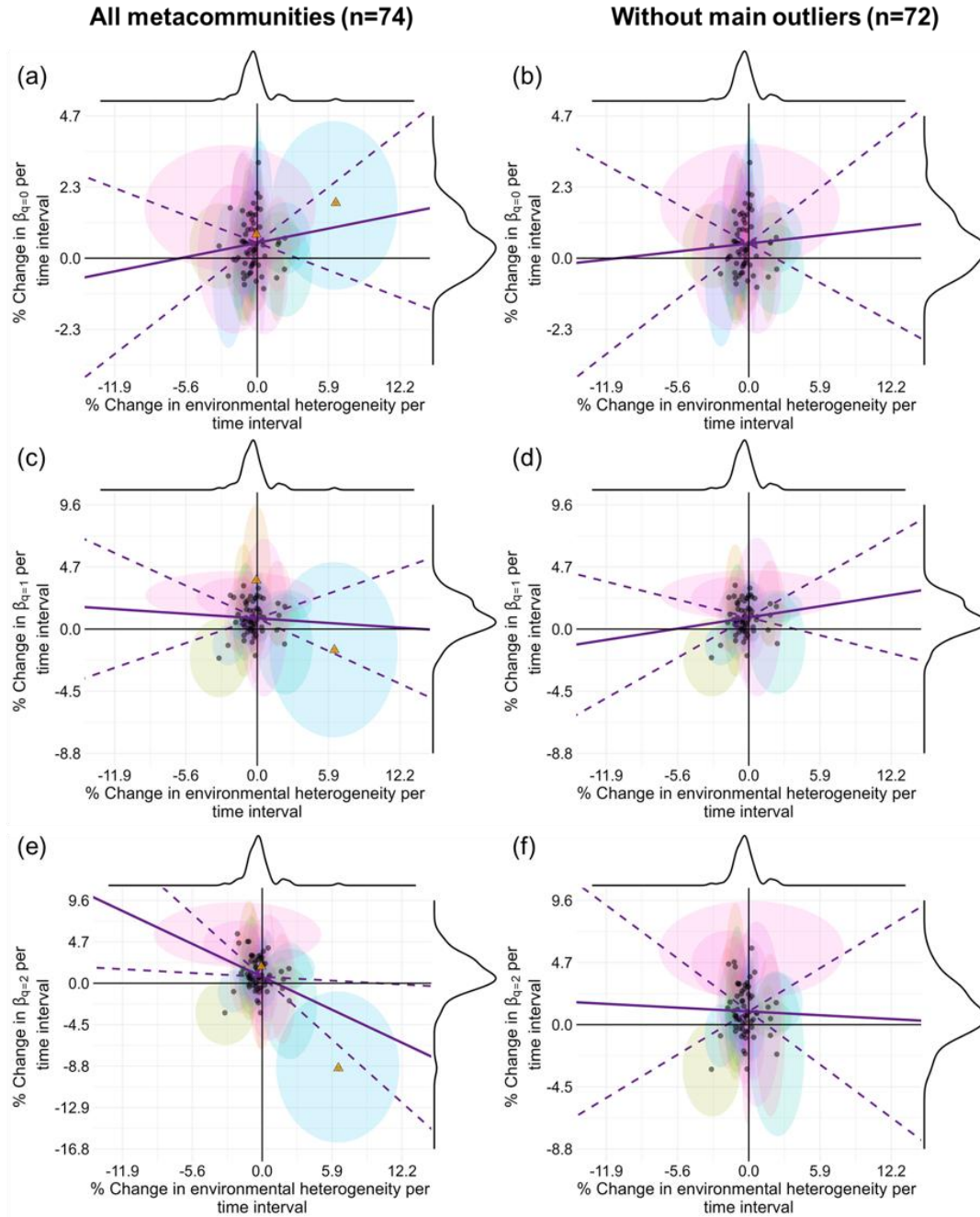


**Figure S14.**

Percent change in  $\beta$ -diversity per 4-year time interval as a function of the percent change in environmental heterogeneity per time interval for  $q=0$  (a, b),  $q=1$  (c, d), and  $q=2$  (e, f), where  $\beta$ -diversity was calculated as the average value across draws of four routes within each spatial polygon. The overall trend and 95% credible intervals are shown in solid and dashed lines, respectively; while the values of each spatial polygon are shown as grey points, with colored ellipses for the 95% credible intervals of each spatial polygon. (a), (c), and (e) include all spatial polygons ( $n=74$ ). The two orange triangles represent the spatial polygons which were flagged as potential outliers with Pareto-k analysis (Fig S12). (b), (d), and (f) show model predictions after removing these two outliers.

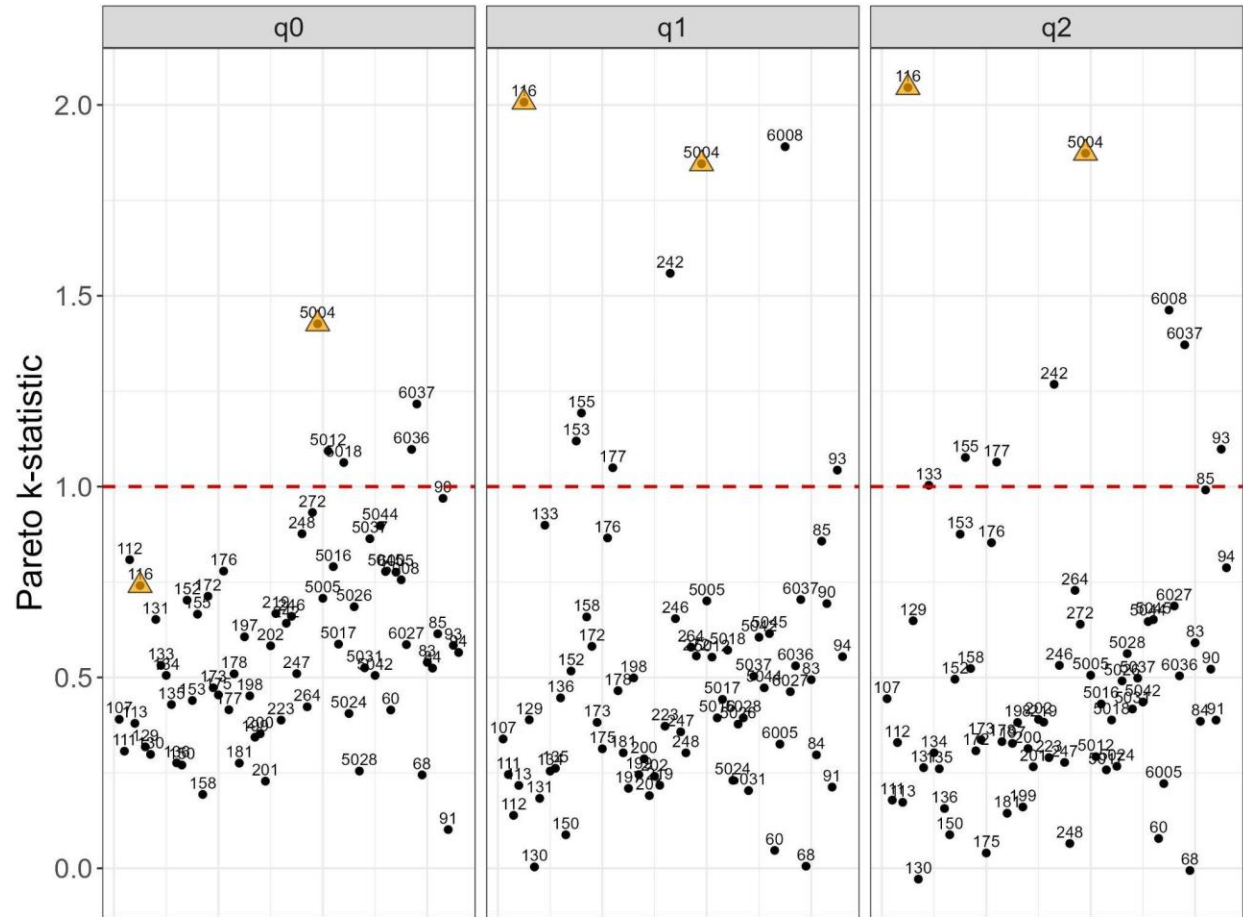


**Figure S15.**

Pareto k-statistics highlighting highly influential spatial polygons in Bayesian hierarchical models fit using  $\beta$ -diversity and EH values calculated from repeated random sampling of 4 routes within spatial polygons. Panels show the Pareto k-statistics for each fitted model. Each point represents a spatial polygon, with orange triangles highlighting the two spatial polygons that showed a Pareto k-statistic  $\geq 1.5$  in at least two out of the three models.

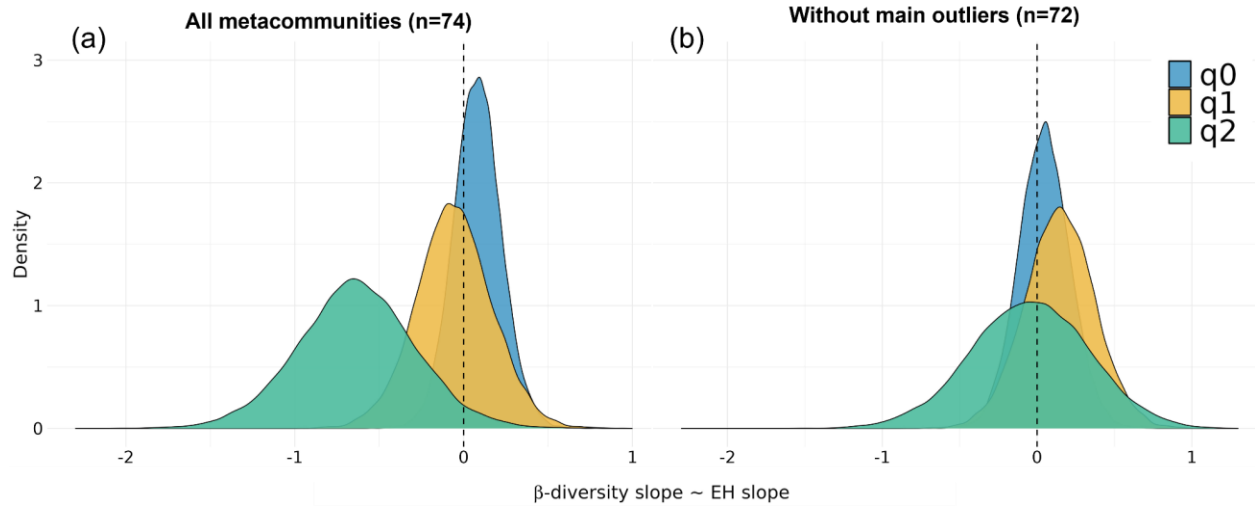


**Figure S16.**

Posterior distributions of the regression slopes relating change in  $\beta$ -diversity to change in environmental heterogeneity, where beta diversity was calculated as the average value from random draws of 4 routes in each metacommunity for three Hill numbers ( $q=0$ ,  $q=1$ ,  $q=2$ ). (a) represents all metacommunities ( $n=74$ ), while (b) shows the posterior distributions after refitting the models without 2 influential metacommunities identified through a Pareto-k test (see Figure S15). The results with all metacommunities included are similar to the main results (Figure 2), with a probability of drawing a value from the posterior distribution greater than 0 for  $q_0 = 0.72$  and  $q_1 = 0.39$ , and the probability of drawing a value from the posterior distribution less than 0 for  $q_2 = 0.97$  (Table S1). Alternatively, removing the two influential metacommunities nullified the opposing relationship between  $q_0$  and  $q_2$ : the probability of drawing a value from the posterior distribution greater than 0 for  $q_0 = 0.61$  and  $q_1 = 0.75$ , and the probability of drawing a value from the posterior distribution less than 0 for  $q_2 = 0.55$  (Table S1).

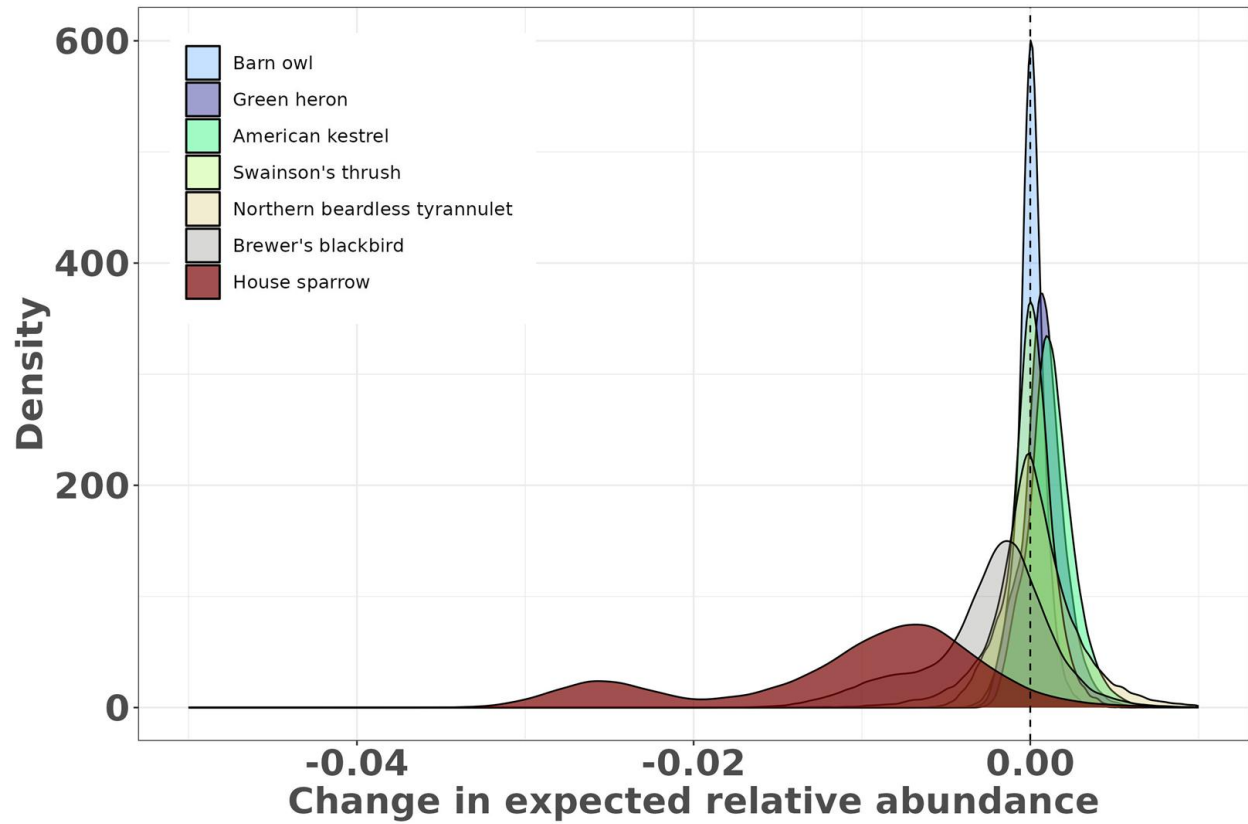


**Figure S17.**

Posterior distributions showing the expected change in relative abundance between 1973–1976 and 2017–2020 for seven bird species with six habitat associations (i.e., extreme generalists). Positive values indicate higher (expected) relative abundance in 2017–2020 than in 1973–1976, whereas negative values indicate that (expected) relative abundance was higher in 1973–1976. Declines in the relative abundance of the house sparrow were strongest in magnitude

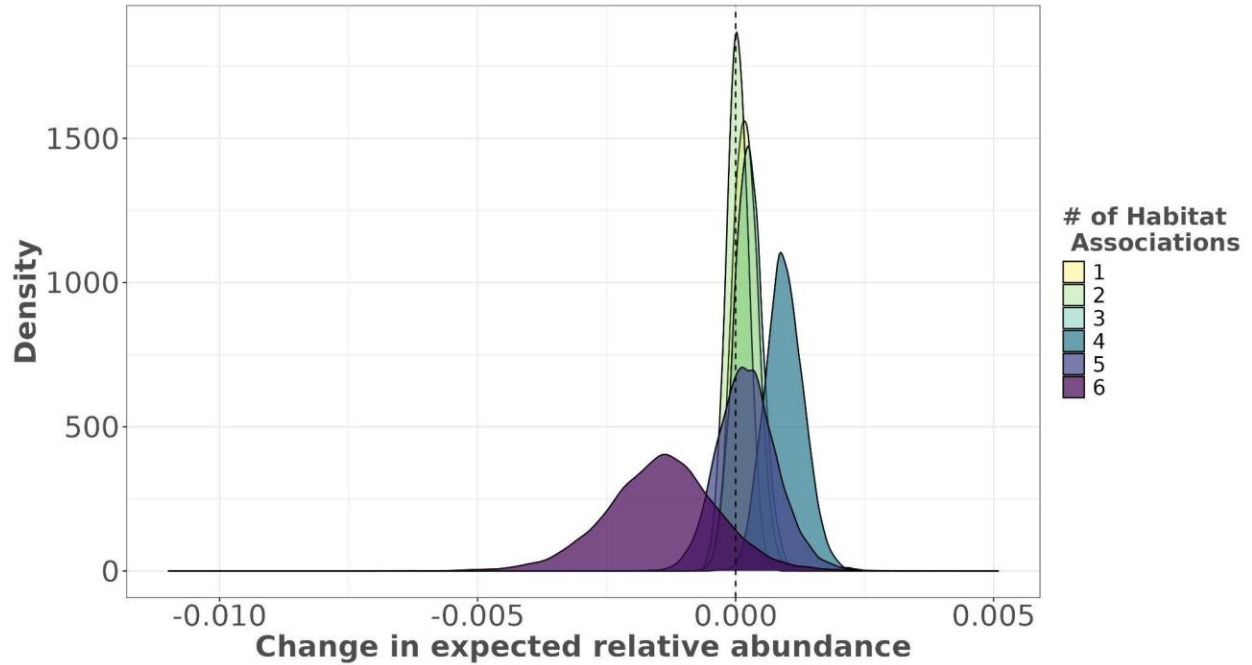


**Figure S18.**

Posterior distributions showing the expected change in relative abundance between 1973–1976 and 2017–2020 for 480 bird species with one (specialists) to six (generalists) habitat associations. Positive values indicate higher (expected) relative abundance in 2017–2020 than in 1973–1976, whereas negative values indicate that (expected) relative abundance was higher in 1973–1976. The model predictions illustrated here resulted from testing the sensitivity of the model predictions shown in the main text (Figure 3) by removing the house sparrow (*Passer domesticus*), which had six habitat associations and declined substantially between 2017–2020 and 1973–1976 (Figure S17). Despite removal of this species, model predictions still show that species with 6 habitat associations declined in their relative abundance in 2017–2020, relative to 1973–1976, and relative to groups of species with different numbers of habitat associations.

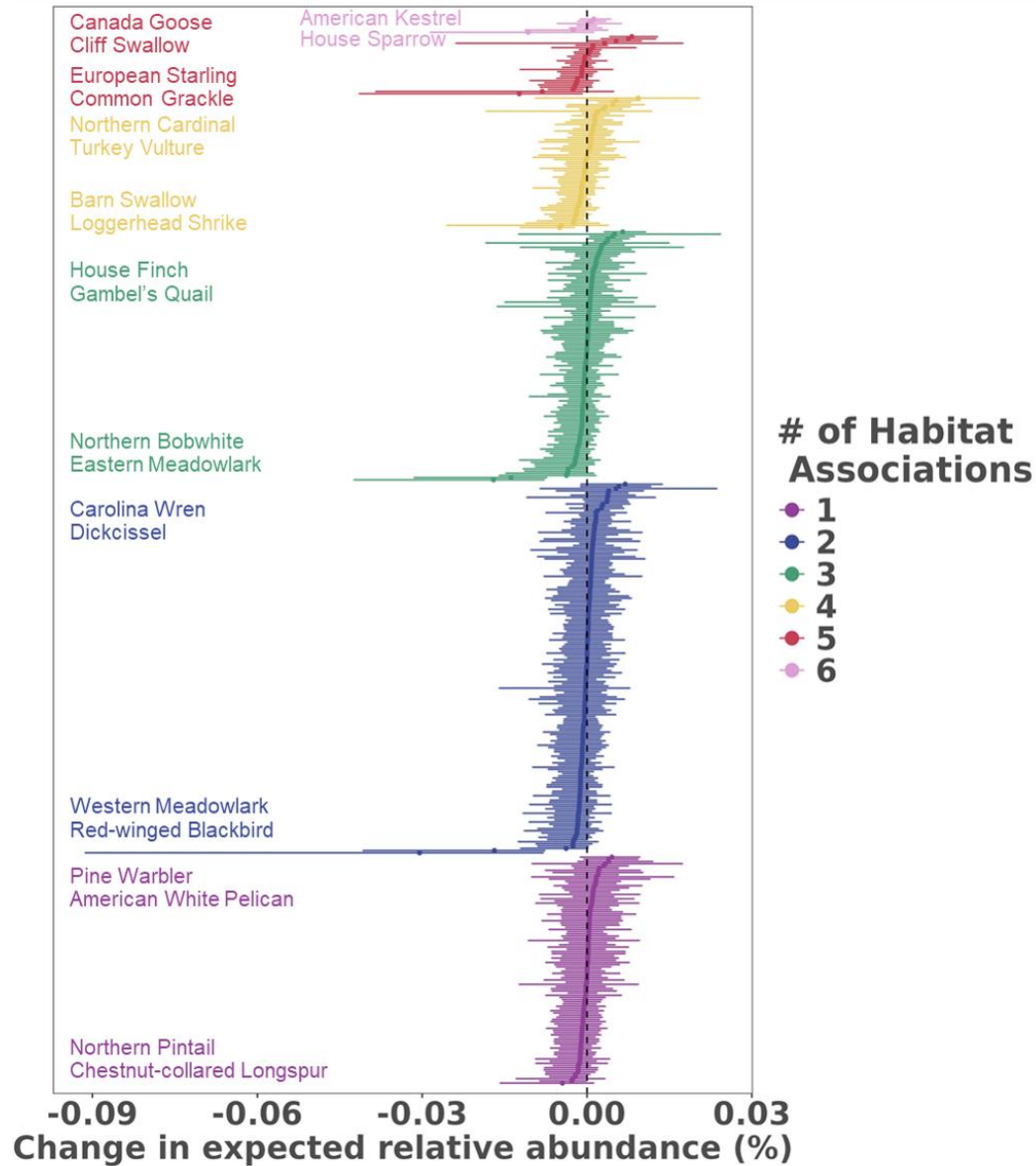


**Figure S19.**

Predicted change in relative abundance between 2017–2020 and 1973–1976 for 481 species detected across 74 metacommunities in the contiguous US with one (i.e., specialists) to six (i.e., extreme generalists) habitat associations. Each point and line represent one species. Points are the posterior mean of predicted values and the lines span the 95% credible interval. Positive posterior mean values indicate higher relative abundance in 2017–2020 than in 1973–1976, whereas negative values indicate that relative abundance was higher in 1973–1976. For habitat associations one through five, the two species with the highest and lowest posterior means are labeled. For species with six habitat associations, only the species with the highest and lowest posterior mean are labelled.

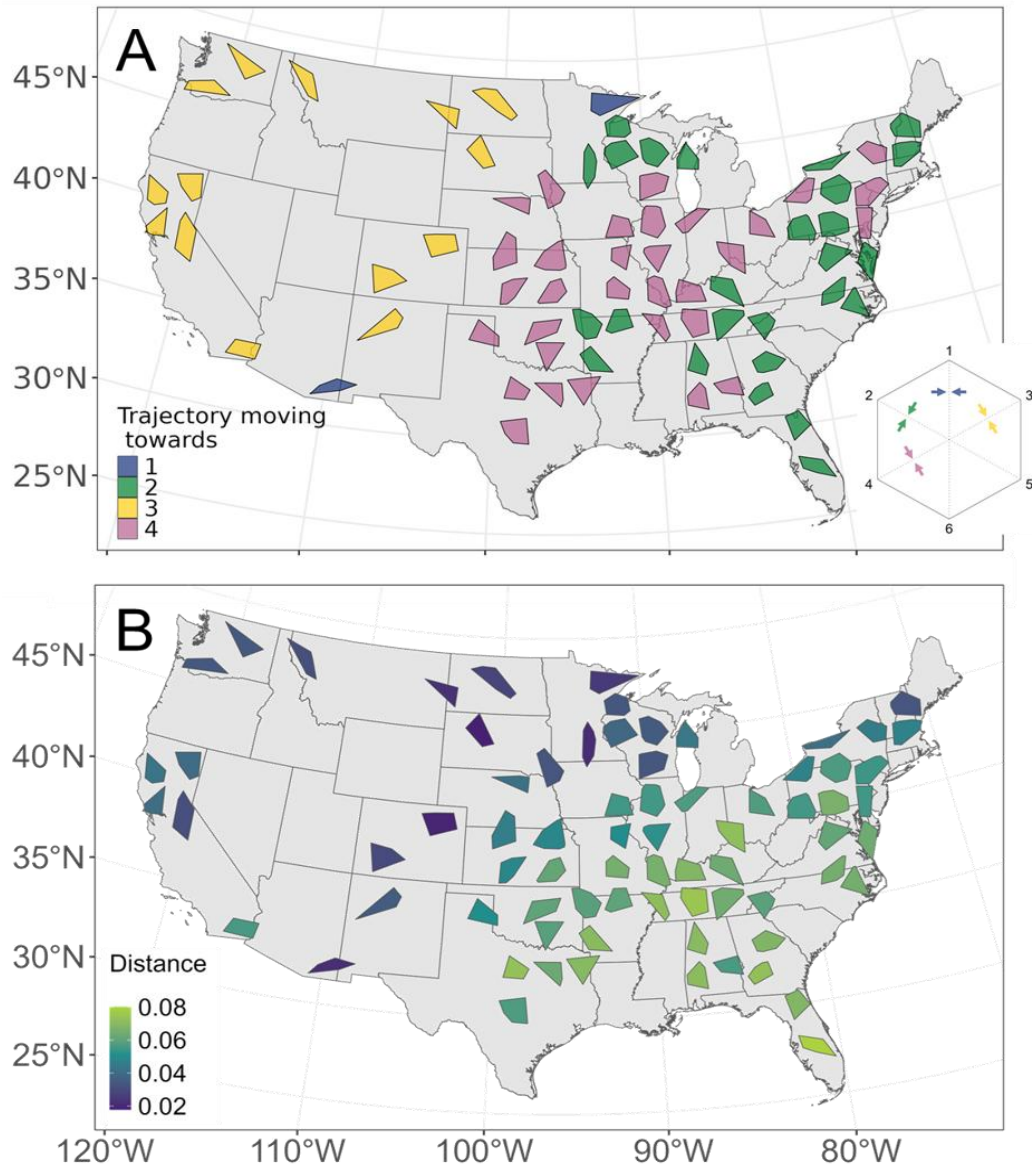


**Figure S20.**

Direction and distance of composition change in habitat breadth for bird metacommunities between 1973-1976 and 2017-2020. A In the 6-dimensional space composed of different numbers of habitat associations (i.e. 1: specialist, 6: extreme generalist), the majority of metacommunities moved towards habitat-breadth compositions that favored more intermediate to broad generalists. B The distance of each metacommunity shift in this 6-dimensional space revealed that relative to other metacommunities, those in the southeast were most different in 2017-2020, relative to their 1973-1976 baseline.

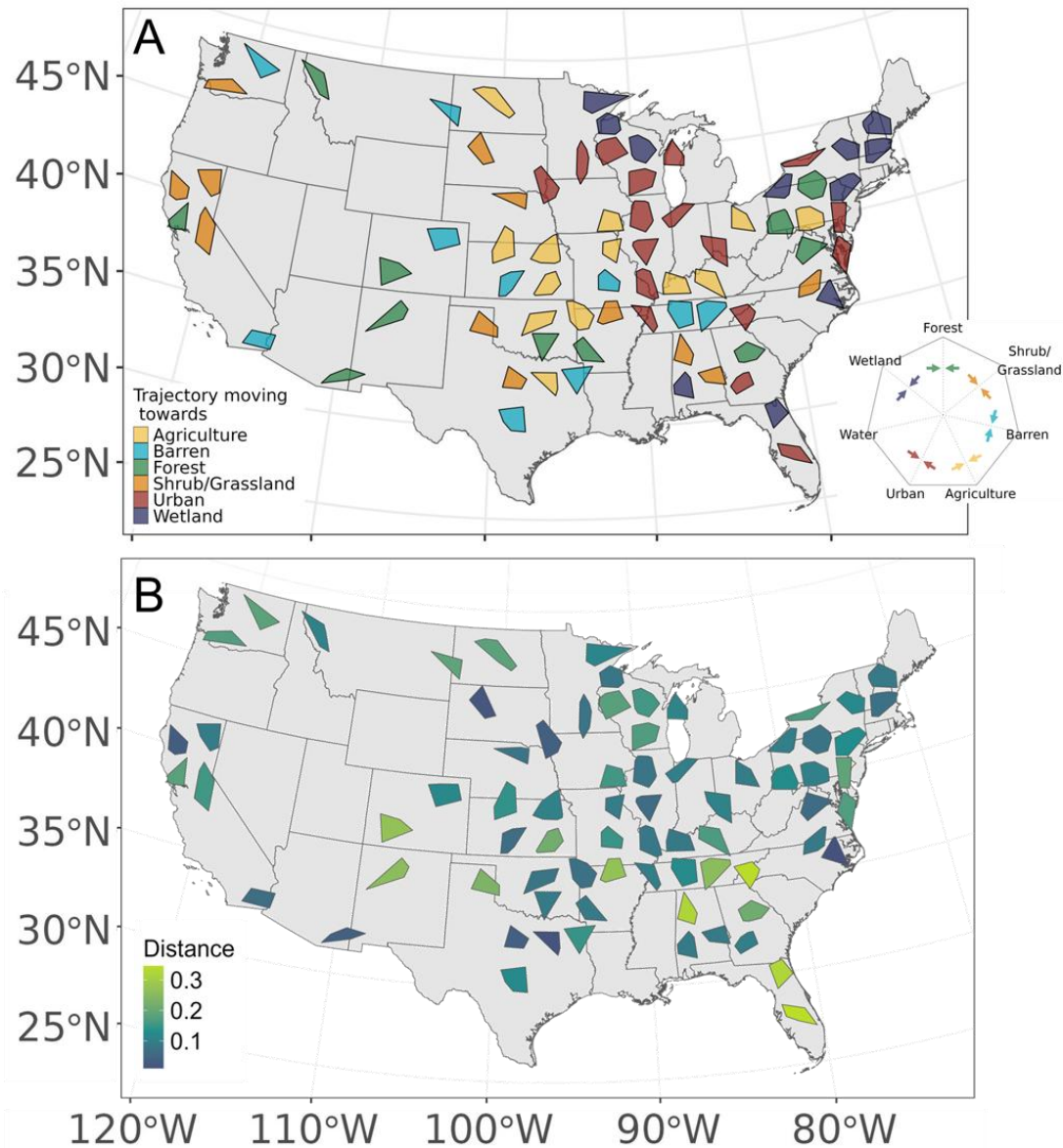


**Figure S21.**

Direction and distance of composition change in land cover for metacommunities between 1973-1976 and 2017-2020. A In the 7-dimensional space composed of different land-cover categories, metacommunities exhibited variation in which category their trajectory shifted towards, but with about 30% of them moving towards compositions with more agriculture and urban land. B Although metacommunities in the southeast shifted most in their land-cover composition, overall there was no clear geographic pattern in compositional shift.

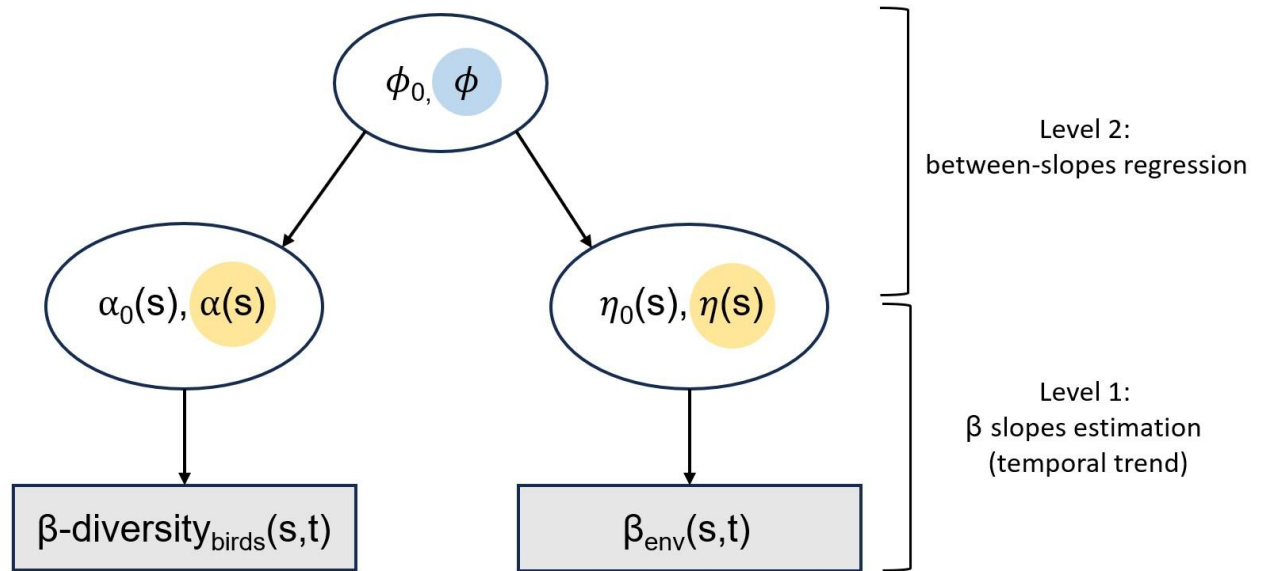
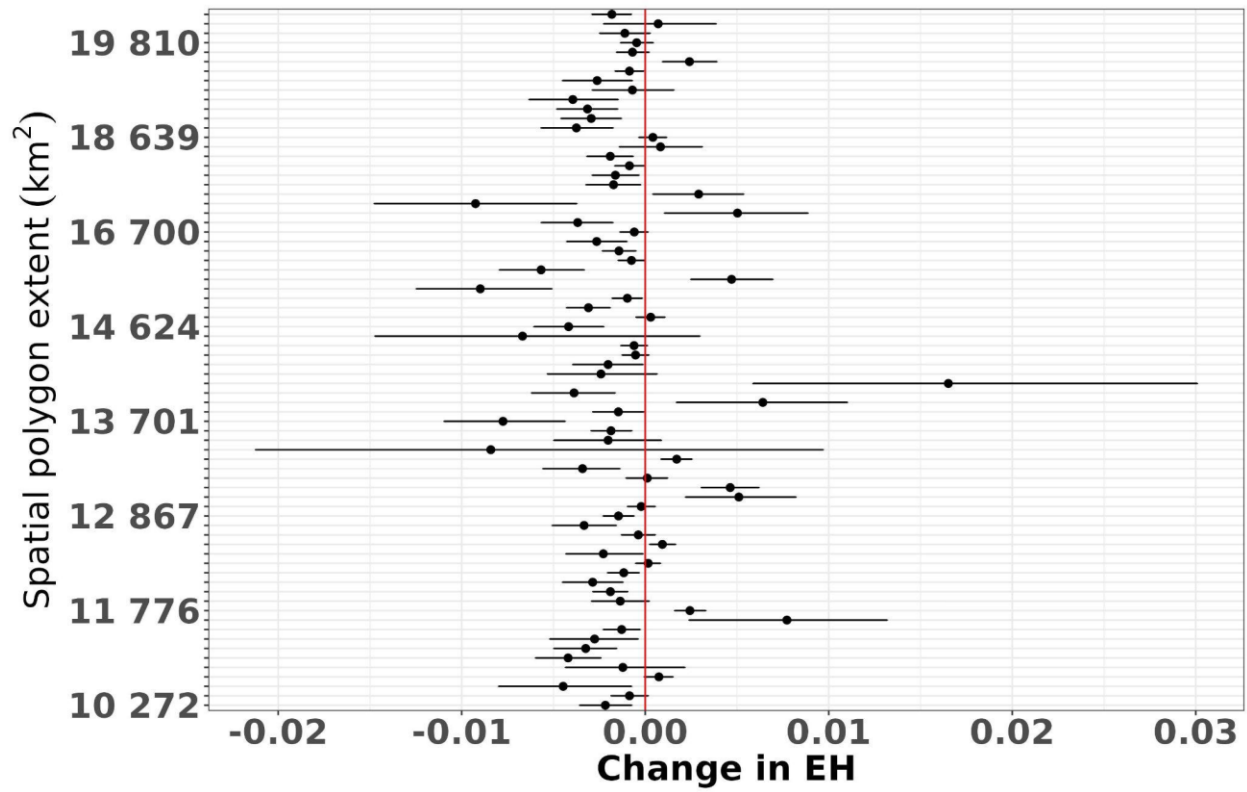


**Figure S22.**

Graphical representation of the Bayesian hierarchical model. The first level of the hierarchy estimates temporal trends for bird  $\beta$ -diversity ( $\beta\text{-diversity}_{\text{birds}}$ ) and environmental heterogeneity ( $\beta_{\text{env}}$ ). In the second level, we infer how the rate of change in environmental heterogeneity affects the rate of change in  $\beta$ -diversity. This approach allows the uncertainty in the estimation at the level 1 to be correctly propagated to level 2, as opposed to a 2-step procedure.

1



2

3

### Figure S23:

4

Change in environmental heterogeneity as a function of spatial polygon extent. Change in environmental heterogeneity comes from the model predictions from the first level of the Bayesian hierarchical model relating trends in  $\beta$ -diversity to trends in environmental heterogeneity. Points represent the mean change in EH for each spatial polygon and error bars represent the 95% credible interval.

5

6

7

8

9

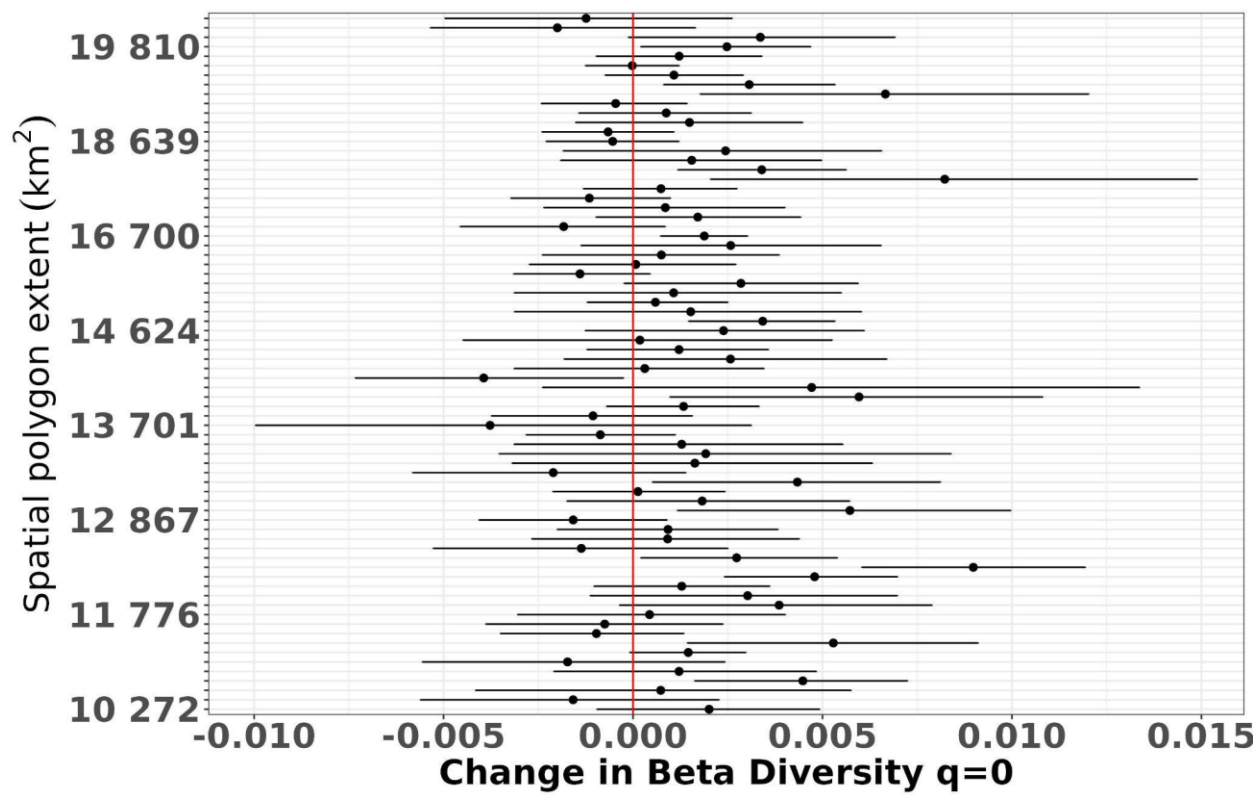
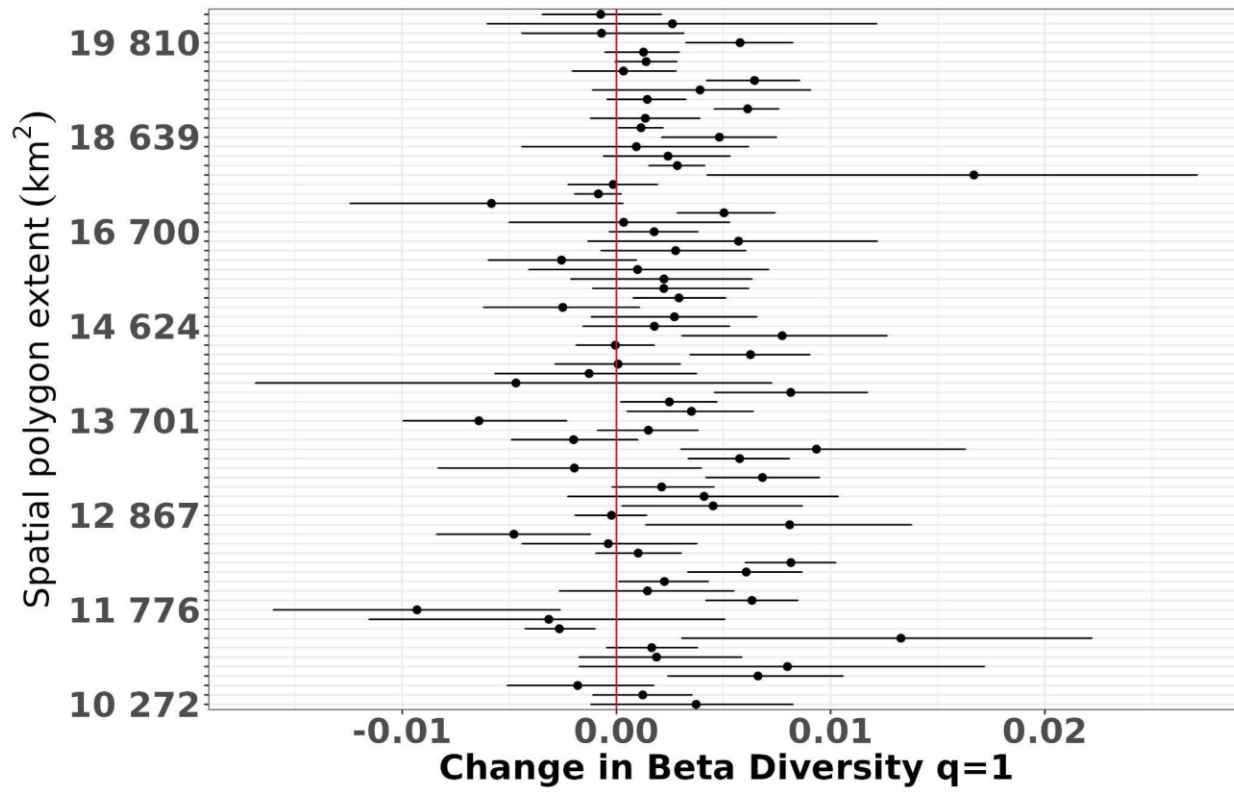


**Figure S24:**

Change in  $\beta$ -diversity, where  $q=0$ , as a function of spatial polygon extent. Change in  $\beta$ -diversity, where  $q=0$ , comes from the model predictions from the first level of the Bayesian hierarchical model relating trends in  $\beta$ -diversity to trends in environmental heterogeneity. Points represent the mean change in  $\beta$ -diversity for each spatial polygon and error bars represent the 95% credible interval.

17

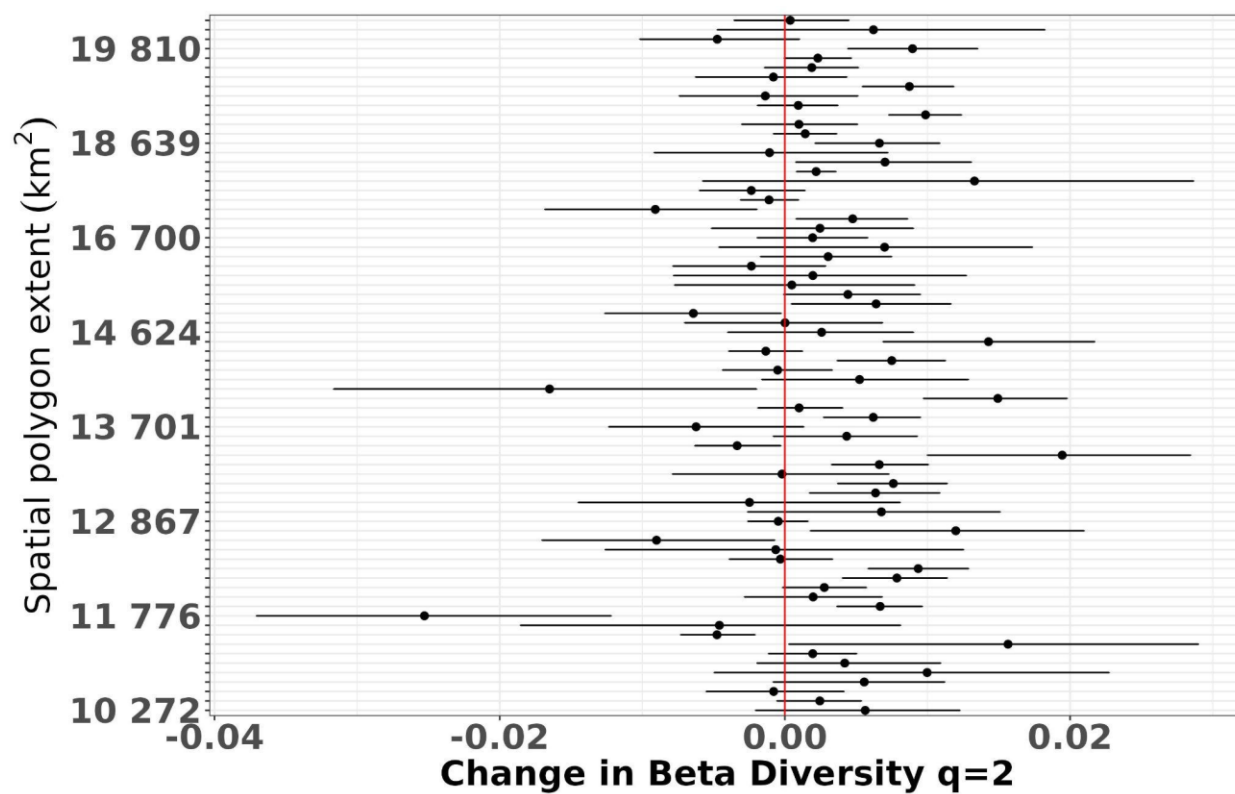


18

19 **Figure S25:**

20 Change in  $\beta$ -diversity, where  $q=1$ , as a function of spatial polygon extent. Change in  $\beta$ -diversity, where  $q=1$ , comes  
 21 from the model predictions from the first level of the Bayesian hierarchical model relating trends in  $\beta$ -diversity to trends  
 22 in environmental heterogeneity. Points represent the mean change in  $\beta$ -diversity for each spatial polygon and error bars  
 23 represent the 95% credible interval.  
 24

25



26

27

28

29

30

31

32

**Figure S26:**

Change in  $\beta$ -diversity, where  $q=2$ , as a function of spatial polygon extent. Change in  $\beta$ -diversity, where  $q=2$ , comes from the model predictions from the first level of the Bayesian hierarchical model relating trends in  $\beta$ -diversity to trends in environmental heterogeneity. Points represent the mean change in  $\beta$ -diversity for each spatial polygon and error bars represent the 95% credible interval.

Table S1.

Results from hierarchical Bayesian models relating the change in  $\beta$ -diversity per 4-year time interval to the change in environmental heterogeneity per 4-year time interval from 1973–2020 for a group of 74 metacommunities in the contiguous United States. Model descriptions refer to the way in which  $\beta$ -diversity was calculated for each of three Hill numbers ( $q = 0, 1, 2$ ): for the 2-route average model and the 2-route average without influential metacommunities model,  $\beta$ -diversity is the average value of all possible pairs of routes within a metacommunity; for the 4-route average and 4-route average without influential outlier model,  $\beta$ -diversity is the average of 99 randomly drawn samples consisting of four routes per metacommunity.

| Model                                                | n  | q value | Posterior Mean | Lower 95% CI | Upper 95% CI | Probability of posterior draw > 0 | Probability of posterior draw < 0 |
|------------------------------------------------------|----|---------|----------------|--------------|--------------|-----------------------------------|-----------------------------------|
| 2-route average                                      | 74 | 0       | 0.10           | -0.14        | 0.35         | 0.79                              | 0.21                              |
|                                                      |    | 1       | -0.10          | -0.47        | 0.27         | 0.30                              | 0.70                              |
|                                                      |    | 2       | -0.48          | -1.03        | 0.08         | 0.05                              | 0.95                              |
| 2-route average, without influential metacommunities | 72 | 0       | 0.07           | -0.17        | 0.34         | 0.71                              | 0.29                              |
|                                                      |    | 1       | 0.04           | -0.36        | 0.44         | 0.57                              | 0.43                              |
|                                                      |    | 2       | -0.23          | -0.88        | 0.44         | 0.24                              | 0.76                              |
| 4-route average                                      | 74 | 0       | 0.08           | -0.19        | 0.37         | 0.72                              | 0.28                              |
|                                                      |    | 1       | -0.06          | -0.50        | 0.39         | 0.39                              | 0.61                              |
|                                                      |    | 2       | -0.64          | -1.33        | 0.05         | 0.04                              | 0.96                              |
| 4-route average, without influential metacommunities | 72 | 0       | 0.05           | -0.28        | 0.37         | 0.61                              | 0.39                              |
|                                                      |    | 1       | 0.15           | -0.30        | 0.58         | 0.75                              | 0.25                              |
|                                                      |    | 2       | -0.05          | -0.81        | 0.69         | 0.45                              | 0.55                              |

33  
34

## Table S2.

Marginal predictions of the change in relative abundance between 2017-2020 and 1973-1976 for species detected in 74 metacommunities across the contiguous United States and associated with different numbers of habitats. Positive values indicate higher predicted relative abundance in 2017–2020 than in 1973–1976, whereas negative values indicate that predicted relative abundance was higher in 1973–1976. A species with one habitat association corresponds to a specialist, while a species with six habitat associations corresponds to an extreme generalist. Based on the substantial loss in the house sparrow's (*Passer domesticus*) relative abundance, we tested the sensitivity of the model that included all species by refitting it without the house sparrow. n = total number of species included in the model

| Model                 | n   | # Habitat Associations | Posterior Mean | Lower 95% CI | Upper 95% CI | Probability of posterior draw > 0 | Probability of posterior draw < 0 |
|-----------------------|-----|------------------------|----------------|--------------|--------------|-----------------------------------|-----------------------------------|
| All species           | 104 | 1                      | 0.000          | -0.000       | 0.001        | 0.77                              | 0.23                              |
|                       | 169 | 2                      | 0.000          | -0.000       | 0.000        | 0.57                              | 0.43                              |
|                       | 114 | 3                      | 0.000          | -0.000       | 0.001        | 0.81                              | 0.19                              |
|                       | 60  | 4                      | 0.001          | 0.000        | 0.002        | 0.99                              | 0.01                              |
|                       | 27  | 5                      | 0.000          | -0.000       | 0.002        | 0.66                              | 0.34                              |
|                       | 7   | 6                      | -0.003         | -0.006       | -0.001       | 0.01                              | 0.99                              |
| Without house sparrow | 104 | 1                      | 0.000          | -0.000       | 0.001        | 0.77                              | 0.23                              |
|                       | 169 | 2                      | 0.000          | -0.000       | 0.001        | 0.56                              | 0.44                              |
|                       | 114 | 3                      | 0.000          | -0.000       | 0.001        | 0.82                              | 0.18                              |
|                       | 60  | 4                      | 0.001          | 0.000        | 0.002        | 0.99                              | 0.01                              |
|                       | 27  | 5                      | 0.000          | -0.001       | 0.001        | 0.65                              | 0.35                              |
|                       | 6   | 6                      | -0.001         | -0.004       | 0.001        | 0.08                              | 0.92                              |

## Table S3:

Land-cover classes from the National Land Cover Database (NLCD) and Historical land-cover. As a first step, we reclassified the NLCD classes to match those within the Historical Land Cover product by aggregating the developed NLCD classes into one urban/developed class.

| National Land Cover Database |               |                   | Historical Land Cover |      |
|------------------------------|---------------|-------------------|-----------------------|------|
| Class                        | Original Code | Reclassified Code | Class                 | Code |
| Open Water                   | 11            | 1                 | Open Water            | 1    |
| Perennial Ice/Snow           | 12            | 17                | Perennial Ice/Snow    | 17   |
| Developed, Open Space        | 21            | 2                 | Urban / Developed     | 2    |
| Developed, Low Intensity     | 22            | 2                 |                       |      |
| Developed, Medium Intensity  | 23            | 2                 |                       |      |
| Developed, High Intensity    | 24            | 2                 |                       |      |
| Barren Land (Rock/Sand/Clay) | 31            | 7                 | Barren                | 7    |
| Deciduous Forest             | 41            | 8                 | Deciduous Forest      | 8    |
| Evergreen Forest             | 42            | 9                 | Evergreen Forest      | 9    |
| Mixed Forest                 | 43            | 10                | Mixed Forest          | 10   |
| Shrub/Scrub                  | 52            | 12                | Shrubland             | 12   |
| Grassland/Herbaceous         | 71            | 11                | Grassland             | 11   |
| Pasture/Hay                  | 81            | 14                | Hay/Pasture           | 14   |
| Cultivated Crops             | 82            | 13                | Cultivated Cropland   | 13   |
| Woody Wetlands               | 90            | 16                | Woody Wetland         | 16   |
| Emergent Herbaceous Wetlands | 95            | 15                | Herbaceous Wetland    | 15   |
|                              |               |                   | Mining                | 6    |

# Table S4.

Reclassification of IUCN habitat-association subcategories to the eight land-cover classes from the harmonized land-cover data.

| Habitat association | IUCN Detailed Subcategory                                                                    |
|---------------------|----------------------------------------------------------------------------------------------|
| Forest              | 1.1. Forest - Boreal                                                                         |
| Forest              | 1.2. Forest - Subarctic                                                                      |
| Forest              | 1.4. Forest - Temperate                                                                      |
| Forest              | 1.5. Forest - Subtropical/tropical dry                                                       |
| Forest              | 1.6. Forest - Subtropical/tropical moist lowland                                             |
| Forest              | 1.7. Forest - Subtropical/tropical mangrove vegetation above high tide level                 |
| Forest              | 1.8. Forest - Subtropical/tropical swamp                                                     |
| Forest              | 1.9. Forest - Subtropical/tropical moist montane                                             |
| Shrub/Grassland     | 2.1. Savanna - Dry                                                                           |
| Shrub/Grassland     | 2.2. Savanna - Moist                                                                         |
| Shrub/Grassland     | 3.1. Shrubland - Subarctic                                                                   |
| Shrub/Grassland     | 3.3. Shrubland - Boreal                                                                      |
| Shrub/Grassland     | 3.4. Shrubland -Temperate                                                                    |
| Shrub/Grassland     | 3.5. Shrubland - Subtropical/tropical dry                                                    |
| Shrub/Grassland     | 3.6. Shrubland - Subtropical/tropical moist                                                  |
| Shrub/Grassland     | 3.7. Shrubland - Subtropical/tropical high altitude                                          |
| Shrub/Grassland     | 3.8. Shrubland - Mediterranean-type shrubby vegetation                                       |
| Shrub/Grassland     | 4.1. Grassland - Tundra                                                                      |
| Shrub/Grassland     | 4.2. Grassland - Subarctic                                                                   |
| Shrub/Grassland     | 4.4. Grassland - Temperate                                                                   |
| Shrub/Grassland     | 4.5. Grassland - Subtropical/tropical dry                                                    |
| Shrub/Grassland     | 4.6. Grassland - Subtropical/tropical seasonally wet/flooded                                 |
| Shrub/Grassland     | 4.7. Grassland - Subtropical/tropical high altitude                                          |
| Wetland             | 5.1. Wetlands (inland) - Permanent rivers/streams/creeks (includes waterfalls)               |
| Wetland             | 5.2. Wetlands (inland) - Seasonal/intermittent/irregular rivers/streams/creeks               |
| Wetland             | 5.3. Wetlands (inland) - Shrub dominated wetlands                                            |
| Wetland             | 5.4. Wetlands (inland) - Bogs, marshes, swamps, fens, peatlands                              |
| Wetland             | 5.5. Wetlands (inland) - Permanent freshwater lakes (over 8 ha)                              |
| Wetland             | 5.6. Wetlands (inland) - Seasonal/intermittent freshwater lakes (over 8 ha)                  |
| Wetland             | 5.7. Wetlands (inland) - Permanent freshwater marshes/pools (under 8 ha)                     |
| Wetland             | 5.8. Wetlands (inland) - Seasonal/intermittent freshwater marshes/pools (under 8 ha)         |
| Wetland             | 5.9. Wetlands (inland) - Freshwater springs and oases                                        |
| Wetland             | 5.10. Wetlands (inland) - Tundra wetlands (inc. pools and temporary waters from snowmelt)    |
| Wetland             | 5.13. Wetlands (inland) - Permanent inland deltas                                            |
| Wetland             | 5.14. Wetlands (inland) - Permanent saline, brackish or alkaline lakes                       |
| Wetland             | 5.15. Wetlands (inland) - Seasonal/intermittent saline, brackish or alkaline lakes and flats |
| Wetland             | 5.16. Wetlands (inland) - Permanent saline, brackish or alkaline marshes/pools               |
| Wetland             | 5.17. Wetlands (inland) - Seasonal/intermittent saline, brackish or alkaline marshes/pools   |
| Barren              | 6. Rocky Areas (e.g., inland cliffs, mountain peaks)                                         |

|                 |                                                             |
|-----------------|-------------------------------------------------------------|
| Barren          | 7.1. Caves and Subterranean Habitats (non-aquatic) - Caves  |
| Barren          | 8.1. Desert - Hot                                           |
| Barren          | 8.2. Desert - Temperate                                     |
| Barren          | 8.3. Desert - Cold                                          |
| Open Water      | 9.1. Marine Neritic - Pelagic                               |
| Wetland         | 9.2. Marine Neritic - Subtidal rock and rocky reefs         |
| Wetland         | 9.3. Marine Neritic - Subtidal loose rock/pebble/gravel     |
| Wetland         | 9.4. Marine Neritic - Subtidal sandy                        |
| Wetland         | 9.5. Marine Neritic - Subtidal sandy-mud                    |
| Wetland         | 9.7. Marine Neritic - Macroalgal/kelp                       |
| Wetland         | 9.9 Seagrass (Submerged)                                    |
| Wetland         | 9.10 Estuaries                                              |
| Open Water      | 10.1 Epipelagic (0-200 m)                                   |
| Open Water      | 10.2 Mesopelagic (200-1,000 m)                              |
| Wetland         | 12.1 Rocky Shoreline                                        |
| Wetland         | 12.2 Sandy Shoreline and/or Beaches, Sand Bars, Spits, etc. |
| Wetland         | 12.3 Shingle and/or Pebble Shoreline and/or Beaches         |
| Wetland         | 12.4 Mud Shoreline and Intertidal Mud Flats                 |
| Wetland         | 12.5 Salt Marshes (Emergent Grasses)                        |
| Wetland         | 12.6 Tidepools                                              |
| Wetland         | 13.1 Sea Cliffs and Rocky Offshore Islands                  |
| Wetland         | 13.3 Coastal Sand Dunes                                     |
| Wetland         | 13.4 Coastal Brackish/Saline Lagoons/Marine Lakes           |
| Wetland         | 13.5 Coastal Freshwater Lakes                               |
| Agriculture     | 14.1 Arable Land                                            |
| Agriculture     | 14.2 Pastureland                                            |
| Agriculture     | 14.3 Plantations                                            |
| Urban/Developed | 14.4 Rural Gardens                                          |
| Urban/Developed | 14.5 Urban Areas                                            |
| Forest          | 14.6 Subtropical/Tropical Heavily Degraded Former Forest    |
| Open Water      | 15.1 Water Storage Areas [over 8 ha]                        |
| Open Water      | 15.2 Ponds [below 8 ha]                                     |
| Open Water      | 15.3 Aquaculture Ponds                                      |
| Barren          | 15.4 Salt Exploitation Sites                                |
| Barren          | 15.5 Excavations (open)                                     |
| Urban/Developed | 15.6 Wastewater Treatment Areas                             |

37  
38  
39  
40