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Research article

Functional and phylogenetic convergence of winter and breeding bird communities in the northeastern US

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Around the world, ecological communities are becoming more similar to one another in a process known as biotic homogenization – an increase in similarity among communities over time. While biotic homogenization has been widely studied among spatial communities, very little attention has been paid to beta diversity between seasonal communities, especially in terms of functional or phylogenetic diversity. In temperate ecosystems, seasonality plays a major role in structuring ecological communities, but anthropogenic pressures are altering community composition. We analyze 40 years of data to study changes in beta diversity between winter and breeding bird communities in the northeastern US. We find evidence of taxonomic, phylogenetic, and functional homogenization between winter and breeding bird communities driven by decreasing turnover. Changes in phylogenetic diversity largely mirrored changes in taxonomic diversity, but functional diversity did not, with functional richness increasing in both seasons despite species richness increasing only in winter. Functional homogenization was driven by 1) decreasing occurrence of winter boreal finches and breeding season aerial insectivores, which reduced the functional space unique to either season, and 2) increasing occurrence of raptors, mergansers, wild turkey, and other functionally distinct species, which expanded the total functional space of both seasons and the shared functional space between seasons. Together, these shifts demonstrate a decline in the distinctiveness of functional space between seasons. Our study is one of the first to describe functional and phylogenetic homogenization between seasons and highlights the importance of considering seasonal homogenization and of using multiple facets of diversity to describe and understand biotic homogenization.

Keywords: beta diversity, biotic homogenization, climate change, functional traits, phylogenetic diversity, seasonality

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Introduction

Anthropogenic pressures such as climate change, land-use change, habitat fragmentation, and the introductions of non-native species are altering the ecological and evolutionary dynamics which maintain biodiversity (Singh 2002, IPBES 2019, Jaureguiberry et al. 2022). Consequently, many species assemblages in human-modified landscapes are experiencing biotic homogenization – increasing similarity among multiple assemblages over time (McKinney and Lockwood 1999, Olden 2006). Biotic homogenization, which can be quantified as a decrease in beta diversity, may apply to changes in taxonomic, phylogenetic, or functional diversity (Fig. 1), and evaluating these aspects concurrently can provide insight into the underpinnings of community responses (Olden 2006, Baiser and Lockwood 2011, Baselga and Orme 2012).

The beta diversity metrics used to characterize taxonomic, phylogenetic, and functional biotic homogenization all correspond to commonly used alpha diversity metrics (Fig. 1). Species richness is one of the most widely used taxonomic alpha diversity metrics (Whittaker et al. 2001), and taxonomic beta diversity metrics such as the Sørensen dissimilarity index use the same species presence–absence data to describe the degree to which species are shared between communities (Sørensen 1948). Phylogenetic richness (also known as Faith's phylogenetic diversity) describes the sum of phylogenetic branch lengths represented in a community (i.e. the total sum of evolutionary history; Faith 1992). Phylogenetic beta diversity, then, describes the degree of shared evolutionary history between communities (Leprieur et al. 2012). Functional richness, one common metric for quantifying functional alpha diversity, describes the volume of functional space filled

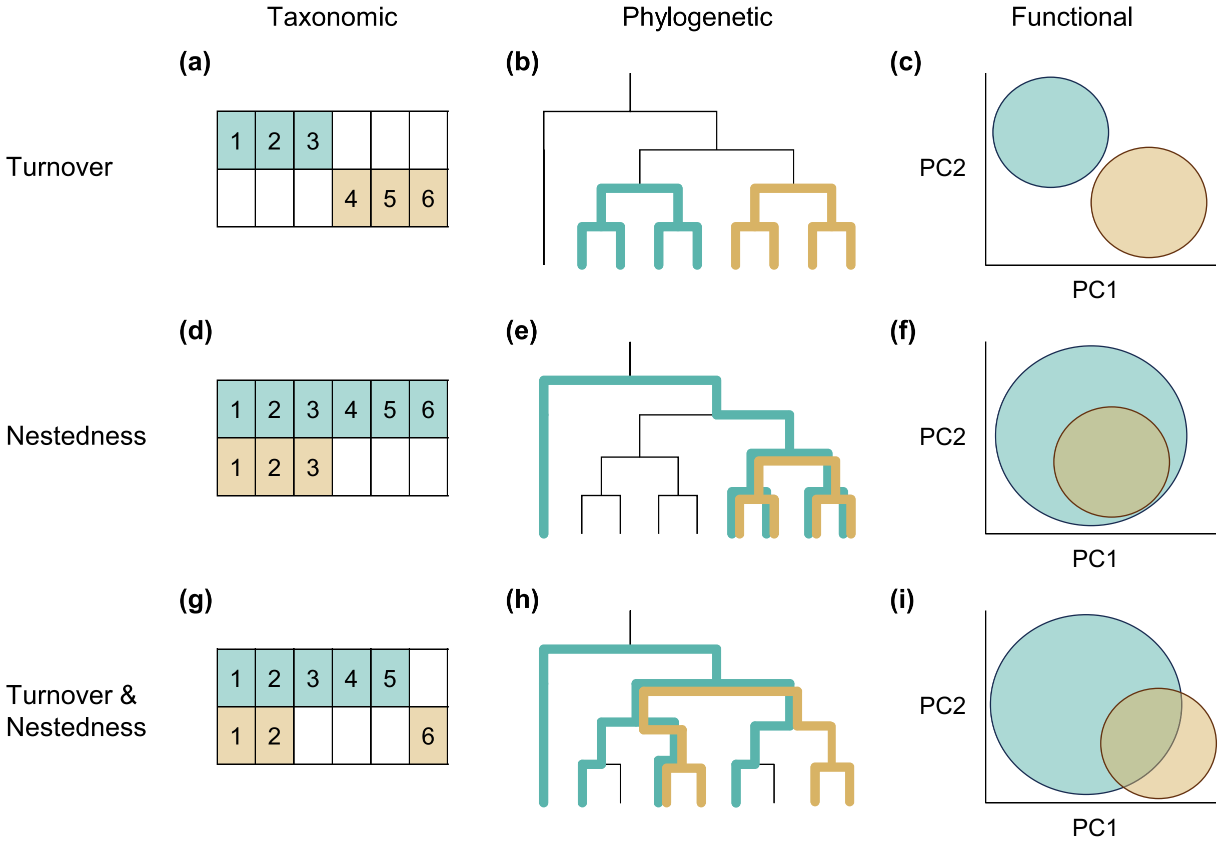

Figure 1. Taxonomic, phylogenetic, and functional beta diversity, with examples of turnover and nestedness. Taxonomic beta diversity (a, d, g) describes shared species between a pair of communities, such as a winter community and a breeding community. Phylogenetic beta diversity (b, e, h) describes shared evolutionary branches between a pair of communities. Functional beta diversity (c, f, i) describes shared functional space between a pair of communities, i.e. the overlap in the functional space occupied by communities. Turnover (a–c) quantifies dissimilarity between communities due to replacement. In these examples, the two communities have equal species richness, phylogenetic richness, and functional richness, but there are no shared species, branches, or functional space between communities. All species, branches, and functional space are replaced between the pair of communities. Nestedness (d–f) quantifies dissimilarity between communities due to differences in richness. In these examples, one community is entirely nested within the other, yet the communities are dissimilar because they differ in species richness, phylogenetic richness, and functional richness. Beta diversity is usually a combination of both turnover and nestedness (g–i). In these examples, richness of one community is higher than the other (nestedness), yet there are still unique species, branches, and functional spaces of the community with lower richness that are not nested within the community with higher richness (turnover).

by a community (i.e. the volume filled by a convex hull in multidimensional functional space; Cornwell et al. 2006). Functional beta diversity describes the overlap of functional spaces filled by a given pair of communities (Villéger et al. 2013). Homogenization is then the increasing proportion of shared species (taxonomic homogenization), shared branches (phylogenetic homogenization), or shared functional space (functional homogenization) over time (Olden 2006).

Additionally, taxonomic, phylogenetic, and functional beta diversity can all be decomposed into their respective components of turnover and nestedness (Baselga 2010, Cardoso et al. 2014). Turnover here refers to the replacement of species, phylogenetic lineages, or functional space between communities (Fig. 1a–c). Nestedness, in contrast, refers to differences in richness between communities (Fig. 1d–f). Biotic homogenization, then, may be driven by either decreasing turnover (a decrease in unique species, branches, or functional space, after accounting for differences in richness) or decreasing nestedness (a reduction in the discrepancy of richness). Partitioning out these components allows a better understanding of the drivers behind biotic homogenization (Baeten et al. 2012).

Biotic homogenization has been widely observed in terms of decreasing beta diversity across space (Baiser et al. 2012, Finderup Nielsen et al. 2019), but it has rarely been examined in terms of beta diversity across seasons (Curley et al. 2024). Seasonality is responsible for major changes in ecological communities throughout the year, as species distributions shift in response to abioticallydriven cyclic changes in resource availability (Ng et al. 2022). Seasonal cycles of temperature, precipitation, and other abiotic factors are particularly important for migratory species which respond to seasonal cues to undergo these journeys (Youngflesh et al. 2021). In the face of rapid environmental change, individual species have responded by changes in the timing of migratory phenology (phenological mismatches), shifts in migration routes, and changes in breeding phenology, as well as poleward and elevational shifts (Parmesan et al. 1999, Tøttrup et al. 2008, Thomas 2010, Visser et al. 2012). At the community level, these species-specific responses may lead to novel species interactions, such as new competitive interactions for resources in breeding or non-breeding habitats (Stralberg et al. 2009, Princé and Zuckerberg 2015). For example, climate change has led to increased direct competition between resident great tits *Parus major* and migratory European pied flycatchers *Ficedula hypoleuca* (Samplonius and Both 2019). These novel interactions can reduce the stability of historical competitive interactions and have cascading impacts on establishment and local extinction or extirpation dynamics (Jiguet et al. 2011, Blois et al. 2013).

Over recent decades, the taxonomic composition of wintering and breeding avian communities in North America has changed substantially (Princé and Zuckerberg 2015, Curley et al. 2022). Winter and breeding communities are both increasingly composed of bird species associated with warmer temperatures and changing precipitation patterns (Princé and Zuckerberg 2015, Curley et al. 2022, Anderson et al. 2023). For example, species such as Carolina wren *Thryothorus ludovicianus*, northern cardinal *Cardinalis cardinalis*, and tufted titmouse *Baeolophus bicolor* have increased in their abundances while also expanding their breeding ranges northward in the eastern US, presumably tracking changes in temperature and precipitation as well as increasing supplemental feeding at bird feeders (Robb et al. 2008, Curley et al. 2022). However, these shifts in distribution are not uniform across all bird species. Generalist species are shifting their ranges faster than less-adaptable specialist species (Huang et al. 2023). This process can lead to the homogenization of bird communities, where the same few adaptable species become increasingly dominant across wider regions (Gaüzère et al. 2020). Furthermore, winter communities are changing more rapidly than breeding communities (Curley et al. 2020, Lehikoinen et al. 2021). These ongoing changes may be contributing to an increasing similarity in species composition (taxonomic homogenization) between wintering and breeding communities that has been observed over the last several decades (Curley et al. 2024).

While Curley et al. (2024) observed seasonal taxonomic homogenization, it remains unclear how these changes in taxonomic diversity translate into changes at the phylogenetic or functional levels. As species composition changes, phylogenetic and functional composition also necessarily change, so taxonomic, phylogenetic, and functional diversity are often highly correlated, yet differences among these diversity metrics provide a fuller picture of how diversity is changing (Baiser and Lockwood 2011, Schipper et al. 2016, Tsianou et al. 2021). For example, phylogenetic homogenization may be stronger than taxonomic homogenization when the species that are lost are evolutionarily unique (Nowakowski et al. 2018). Differences in phylogenetic richness usually reflect differences in evolutionary history among regions (Voskamp et al. 2017, Le Bagousse-Pinguet et al. 2019), but winter and breeding birds occupy in the same region, so it is unclear whether there would be phylogenetic biases in changing seasonal species composition. It is more likely, though still untested, that there would be functional biases in changing seasonal species composition (Baiser and Lockwood 2011). Functional diversity of North American birds is strongly seasonal, but seasonal patterns of functional and taxonomic diversity are decoupled (Jarzyna and Stagge 2023). For example, in the eastern US, species richness declines in winter while functional richness increases (Jarzyna and Stagge 2023). Northern American winter avian communities have undergone significant functional reorganization in recent decades (Quimbayo et al. 2024), though it is unclear whether these functional changes are leading to convergence with breeding communities. Seasonal functional beta diversity is highest among bird communities where climate seasonality is strongest (Keyser et al. 2024), but warming winters that decrease climate seasonality could erode seasonal functional differences and lead to functional homogenization. Comparing taxonomic, phylogenetic, and functional beta diversity can provide a more nuanced understanding of the consequences of homogenization on community resilience, particularly under the continued and accelerated pressures of human-induced environmental change (Baiser and Lockwood 2011, Oliver et al. 2015). Furthermore, understanding which ecological functions are changing is important for managing avian communities. Yet no studies of homogenization between seasons (e.g. comparing winter versus breeding communities) have analyzed phylogenetic or functional homogenization.

Here, we use two community science datasets, the National Audubon Society Christmas Bird Count (CBC; National Audubon Society 2020) and the North American Breeding Bird Survey (BBS; Sauer et al. 2021), to quantify changes in taxonomic, phylogenetic, and functional beta diversity in the northeastern US, where CBC and BBS data have been collected consistently for more than 40 years. Building on previous work that observed taxonomic seasonal homogenization in this region (Curley et al. 2024), we assess how phylogenetic and functional homogenization compare to taxonomic homogenization, using a more spatially explicit approach which allows us to estimate spatial variation in homogenization within the Northeast. We further investigate which components of beta diversity (turnover and nestedness) and which species (including which types of species) are contributing most to these trends. We predict that changes in species composition will be functionally biased but not phylogenetically biased, so phylogenetic homogenization will reflect trends in taxonomic homogenization while functional homogenization will differ from taxonomic homogenization patterns. We also investigate which species and which ecological functions are driving changes in functional diversity.

Material and methods

Bird survey data

We used data from the National Audubon Society Christmas Bird Count (CBC) and the North American Breeding Bird Survey (BBS) for our winter and breeding bird assemblages, respectively. Each of these monitoring programs collects long-term data on avian abundances and offers broad geographic coverage, though they differ in survey design and effort. CBC count surveys are conducted annually in late December through early January within designated count circles, which are non-randomly selected and proposed by local coordinators. The number of participants in CBC circles varies widely, and participant skill levels range from beginner to expert. Each count circle is centered at a latitude and longitude point with a diameter of 24.14 km (Soykan et al. 2016). BBS surveys are roadside transect surveys conducted annually between May and June, meant to coincide with the peak of the breeding season of North American birds. Locations are typically randomized within delineated physiographic regions to ensure balanced coverage between different habitat types. Each route is approximately 39.4 km long and partitioned into 50 evenly spaced 3-min point count locations, where 1–2 trained observers record all individual birds seen or heard within a 0.4 km radius of their location (Pardieck et al. 2020). We confined our analysis to the northeastern US including Connecticut, Delaware, Maine, Maryland, Massachusetts, New Hampshire, New Jersey, New York, Pennsylvania, Rhode Island, and Vermont (Fig. 2). We selected this region because of the consistency with which CBC and BBS data were collected. We used 40 years of CBC and BBS data, from the winter season of 1979–1980 (December–January) through the breeding season (May–June) of 2019. Due to the interruption of data collection in 2020 due to the COVID-19 pandemic, we did not include surveys from 2020 onward.

We cross-referenced common and scientific names between BBS and CBC and created a combined standardized species list following the eBird taxonomy, removing all hybrids and unidentified individuals. Subspecies were grouped at the species level. While CBC and BBS both collect count data that can be used to calculate relative abundance, relative abundance is only comparable among surveys using the same methodology, so CBC relative abundance and BBS relative abundance are not directly comparable. Despite this limitation, the longevity of CBC and BBS make these excellent datasets for studying seasonal homogenization. To directly compare CBC and BBS data, we converted CBC and BBS species abundances to presence–absence data, which was later used to model occurrence in both seasons.

Grid cell assemblages

We created a grid of equal-area hexagons with 50 km edges (approximately 6495 km^2 in area) that fully covered the states in our study region. We retained cells that had at least one winter survey and at least one breeding survey for each of the 40 years, which left us with 57 cells, 9052 CBC winter surveys, and 10 099 BBS breeding surveys (Fig. 2).

We used presence–absence data from surveys to model occurrence for each grid cell and each year, running single-species occurrence models for both winter and breeding. To exclude very rarely detected species, we ran winter occurrence models on species detected in $> 1\%$ of included CBC surveys, and we ran breeding occurrence models on species detected in $> 1\%$ of included BBS surveys.

For each species, the winter occurrence model was a logistic regression with species presence in a survey (0 or 1) as the response variable, log party hours as a covariate, and random intercepts for year, grid cell, and survey location. These models were based on standard models used to account for detection in CBC data (Soykan et al. 2016, Saunders et al. 2022). We ran mixed effects models using the 'glmmTMB' package ver. 1.1.7 (Brooks et al. 2017). Then, using predicted occurrence probability from these models and the 'pROC' package ver. 1.18.4 (Robin et al. 2011), we identified optimal species-specific occurrence probability thresholds. For each combination of cell and year, we calculated the mean occurrence probability of each species for all surveys in that cell and year. We then used our species-specific thresholds to categorize each species as 'present' or 'absent' for each combination of

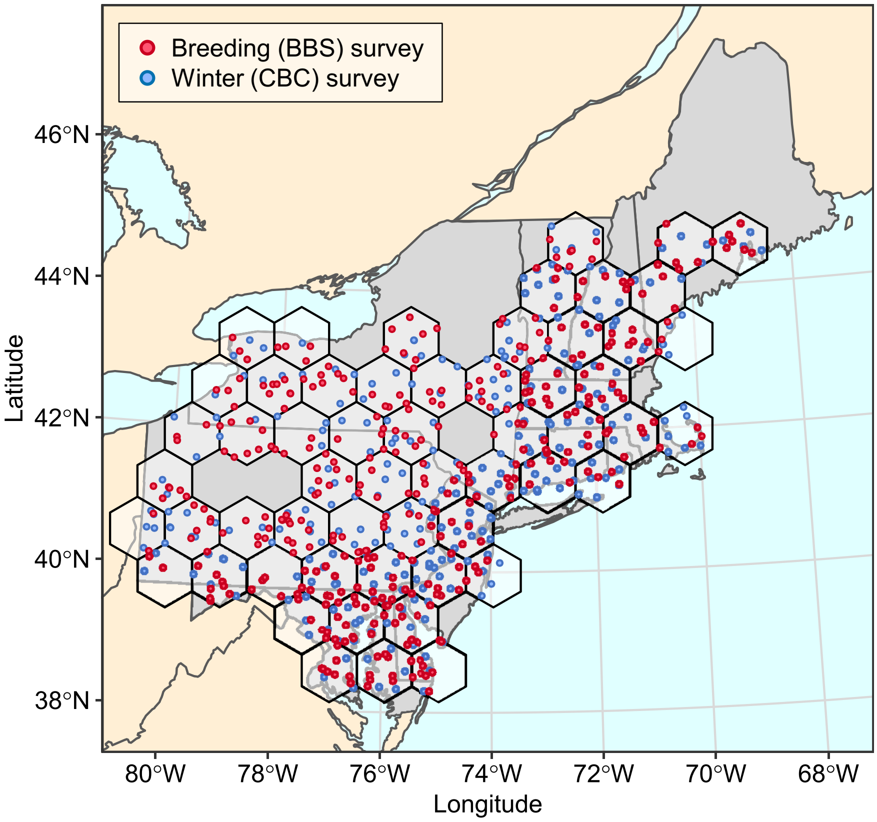

Figure 2. Hexagonal grid cell assemblages in the northeastern US. Cells were retained that had at least one BBS breeding survey and at least one CBC winter survey for each year from 1980 through 2019.

cell and year. This provided the grid cell-level winter species assemblages that we used for further analyses. These analyses and all subsequent analyses were performed using R ver. 4.2.1 (www.r-project.org).

Our process for calculating grid cell-level breeding species assemblages was similar to our process for winter assemblages. For each species, the breeding occurrence model was a logistic regression with species presence in a survey (0 or 1) as the response variable, whether it was the observer's first year on the route (0 or 1) as a covariate, and random intercepts for year, grid cell, and each combination of route and observer. These models were based on standard models used to account for detection in BBS data (Sauer and Link 2011). As with the winter data, we used ROC curves to identify species-specific thresholds, calculated mean occurrence probability of each species for all surveys in a given cell and year, and used the threshold to define present and absent species for each combination of cell and year. This provided the grid cell-level breeding species assemblages that we used for further analyses.

Phylogenetic and functional data

We created an ultrametric consensus tree (including consensus branch lengths) based on 1000 credible phylogenies of all bird species (Jetz et al. 2012), which we used to calculate phylogenetic diversity metrics. For functional traits, we used three types of trait data from three databases: 1) seasonal diet data from SAviTraits (Murphy et al. 2023), 2) foraging strata data from EltonTraits (Wilman et al. 2014), and 3) morphological traits from AVONET (Tobias et al. 2022). SAviTraits includes diet category percentage data varying by month. We calculated breeding and winter diets as the average diet percentages between May and June (BBS survey months) or December and January (CBC survey months), respectively, using eight diet categories: invertebrates, fish, vertebrates, carrion, fruit, nectar, seeds, and other plant parts. EltonTraits includes percentage data for seven foraging strata categories: water below surf, water around surf, ground, understory, mid to high forest levels, canopy, and aerial. AVONET includes morphological traits which are associated with ecological niches and which influence the diet, locomotion, and foraging of a species (Tobias et al. 2022). Because most of these traits are strongly correlated with body mass, we calculated relative traits as the residuals of linear regressions of log-transformed traits against log-transformed body mass. The eleven morphological traits we used were: log body mass, relative beak length (culmen), relative beak length (nares), relative beak width, relative beak depth, relative tarsus length, relative Kipps distance, hand-wing index, relative wing length, relative secondary length, and relative tail length. Thus, we had a total of 26 functional traits. While there are many additional traits we could have chosen, such as life history traits, we selected these traits because they best capture the role and function of species within a community

(Wilman et al. 2014), especially in terms of trophic interactions, rather than the demographic performance of individuals. That is, we are interested in describing the functions of communities, rather than the functions of individuals. We used the 'gawdis' package ver. 0.1.5 (de Bello et al. 2021) to analytically calculate a distance matrix of species using our 26 functional traits. Then, we used the 'mFD' package ver. 1.0.5 (Magneville et al. 2022) to create a four-dimensional functional trait PCoA of all bird species (Fig. 3). Because each species has both breeding diet data and winter diet data,

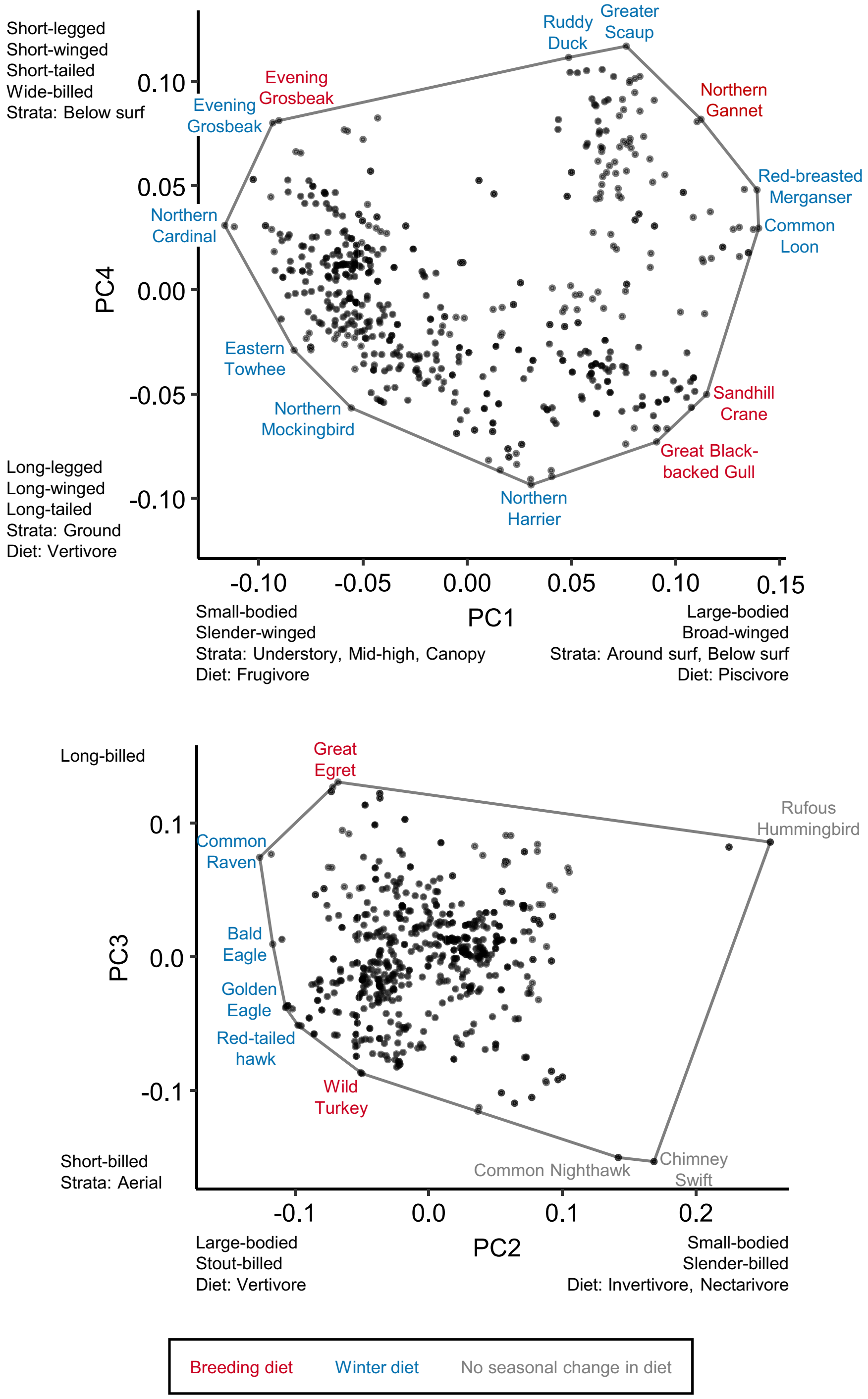

Figure 3. Functional PCoA space used to calculate functional diversity. Axes are labeled with the traits associated with these functional axes. Traits used to calculate functional space included 8 diet categories, 7 foraging strata categories, and 11 morphological traits. Diet data varied by season, so each species is plotted both with its breeding diet and with its winter diet. Functional space is 4-dimensional, but only certain pairs of axes are shown here. Vertex species for the convex hull of all species are labeled.

species with seasonally varying diets have different breeding and winter PCoA coordinates. We used four dimensions as including more dimensions was computationally intractable. This functional space was then used to calculate functional beta diversity and functional richness.

Beta diversity

We calculated taxonomic, phylogenetic, and functional beta diversity between the winter assemblage and the breeding assemblage for each combination of grid cell and year. We calculated taxonomic beta diversity using the *beta.pair* function from the 'betapart' package ver. 1.5.6 (Baselga and Orme 2012). We calculated phylogenetic beta diversity using the *phylo.beta.pair* function, also from the 'betapart' package. We calculated functional beta diversity using the *beta.fd.multidim* function from the 'mFD' package ver. 1.0.5 (Magneville et al. 2022). In all cases, we used the Sørensen family of dissimilarity indices. We calculated total beta diversity, turnover, and nestedness for all three facets of diversity (Fig. 1), resulting in nine beta diversity metrics (Fig. 4).

To assess changes in beta diversity over time, we ran mixed-effects models with year as a covariate and grid cell as a random effect with random slopes and intercepts. We ran nine separate models for each combination of diversity facet (taxonomic, phylogenetic, functional) and beta diversity component (total beta diversity, turnover, nestedness) as response variables. We ran all these models as beta regressions because all values were between 0 and 1 and linear regressions did not fit the data well. Taxonomic nestedness included true zeros (when winter and breeding species richness were equal), which beta regression does not allow, so we ran a zero-inflated beta regression for this metric.

Richness

To help interpret beta diversity trends, we calculated taxonomic, phylogenetic, and functional richness for each combination of grid cell and year for both winter and breeding. We calculated phylogenetic richness using the *pd* function in the 'picante' package ver. 1.8.2 (Kembel et al. 2010), and we calculated functional richness using the *alpha.fd.multidim* function in the 'mFD' package ver. 1.0.5 (Magneville et al. 2022). We ran linear mixed-effects models with year as a covariate and grid cell as a random effect with random slopes and intercepts. We ran six separate models for each combination of season (breeding, winter) and richness metric (species richness, phylogenetic richness, functional richness) as response variables.

Occurrence trends and functional changes

To understand which species might contribute most to changes in beta diversity, we modeled winter and breeding occurrence trends for each species. We ran logistic regressions with occurrence (presence or absence in the winter or breeding grid cell assemblage) as the response variable and year

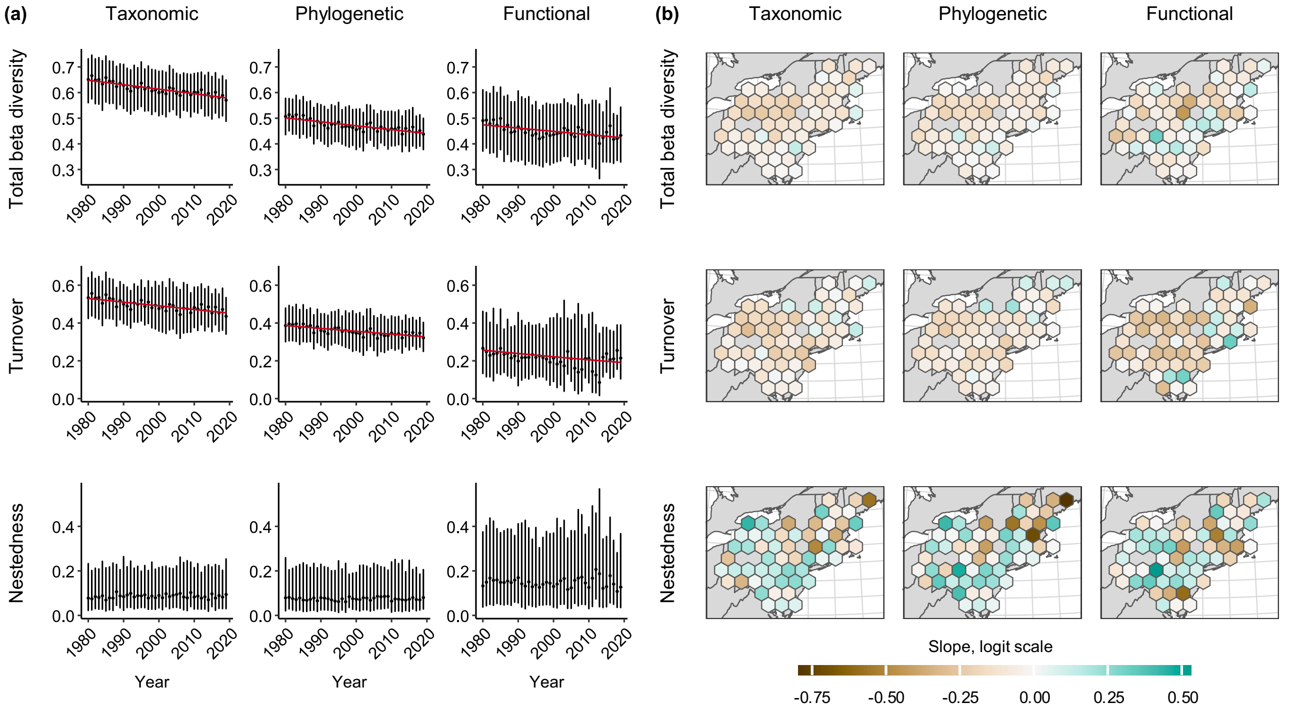

Figure 4. Changes in beta diversity between winter and breeding communities over 40 years. (a) Beta diversity trends over time. Significant decreases in beta diversity (homogenization) are indicated by red lines. For each year, mean beta diversity values across cells are plotted, with error bars representing standard deviation, transformed back from the logit scale. (b) Beta diversity trends among grid cells. The slopes for each grid cell are the random slopes in the mixed-effects models, representing the predicted change in beta diversity between winter and breeding communities within the grid cell.

as a linear covariate. Due to the high number of tests, we identified significantly increasing or decreasing species using a Bonferroni correction, with α set to 0.05 divided by the total number of species in our dataset (269 species).

We identified shifts in functional space by plotting the convex hulls of winter and breeding assemblages in the first and last decade of our study. For each cell, we created assemblages consisting of species which occurred in the cell for the majority of either the first or last decade (i.e. ≥ 5 years). Then, we plotted the two-dimensional convex hulls for each assemblage, where darker regions represent greater overlap of convex hulls and a higher proportion of assemblages occupying that region of functional space (Supporting information). By comparing the density of occupied functional space, we identified differences in functional diversity between winter and breeding assemblages as well as shifts in functional space between the first and last decade.

To distinguish which species were responsible for changes in functional space, we ran a post hoc analysis to determine which species served as vertices for assemblage convex hulls more or less often over time. For each combination of year and cell, and for both winter and breeding, we used the 'mFD' package ver. 1.0.5 (Magneville et al. 2022) to obtain a list of the species at the vertices of the convex hull for that assemblage. Then, for each species, we ran logistic regressions with vertex (0 or 1) as the response variable and year as a covariate, with separate models for winter and breeding. As with occurrence, we used a Bonferroni correction to assess significance. Species that serve as vertices more often over time and which also have increasing occurrence trends are likely responsible for the expansion of functional space over time, while species that serve as vertices less often over time and which also have decreasing occurrence trends are likely responsible for the contraction of functional space. Certain species are highlighted in the main text figures, but all vertex species are plotted in the Supporting information.

Results

Taxonomic homogenization

Across the northeastern US, taxonomic beta diversity decreased from 1980 to 2019 (–0.086 ± 0.011, $p < 0.001$; Fig. 4a) driven by decreasing turnover (–0.090 ± 0.014, $p < 0.001$; Fig. 4a), meaning that fewer species are being replaced between seasons. Birds that only occur in the breeding season have become rarer, while birds that occur in both the breeding season and winter are occurring have become more common in both seasons (Supporting information). The steepest declines in taxonomic beta diversity and turnover were in inland regions, specifically northern Pennsylvania and southwestern New York (Fig. 4b). Species richness of winter communities increased (2.93 ± 0.34, $p < 0.001$), while species richness of breeding communities did not significantly change across the region as a whole (0.00 ± 0.53, $p = 0.999$; Fig. 5a), though breeding species richness increased in the

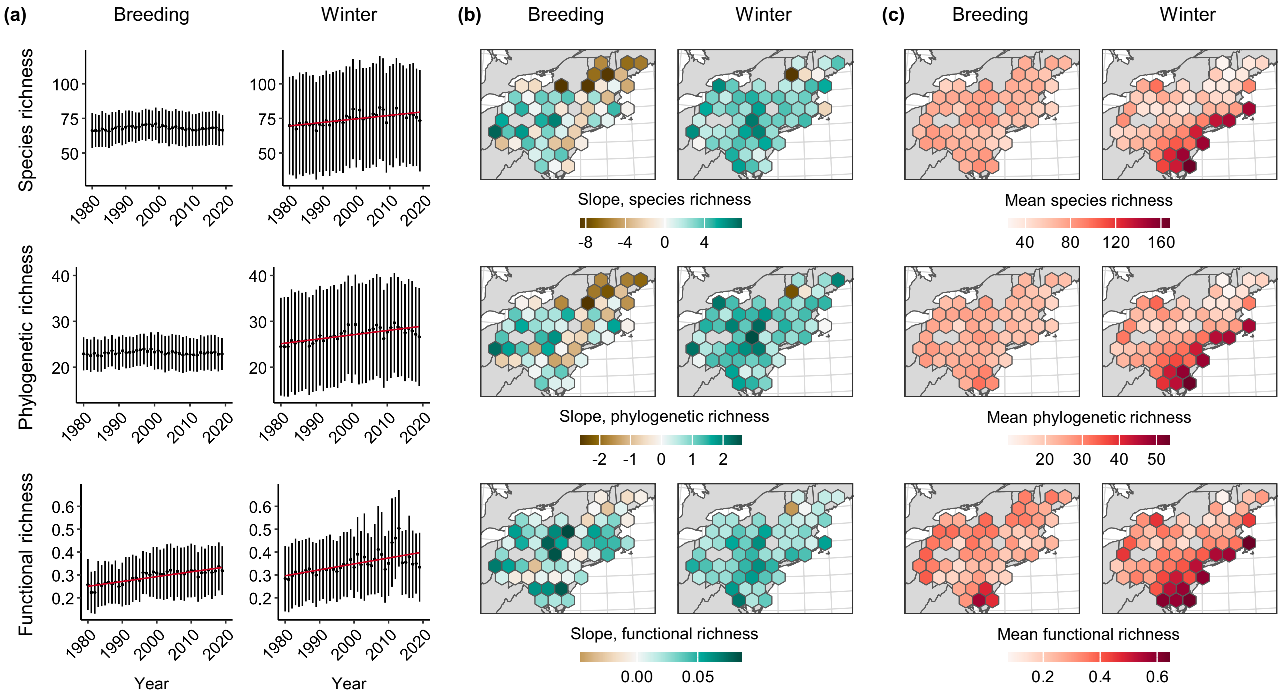

Figure 5. Temporal and spatial richness patterns of breeding and winter communities. (a) Richness trends over time. Significant increases in richness are indicated by red lines. For each year, mean richness values across cells are plotted, with error bars representing standard deviation. (b) Richness trends among grid cells. The slopes for each grid cell are the random slopes in the mixed-effects models. These slopes represent the predicted change in richness within the grid cell over 1 standard deviation of years (~11 years). (c) Mean richness across all years.

southwestern portion of our study area and decreased in the northeastern portion (Fig. 5b). Along the coast, species richness tends to be higher in winter than in the breeding season, though breeding species richness is higher than winter species richness in inland New England (Fig. 5c). The difference in species richness between breeding and winter communities did not significantly change over time, so there was no change in taxonomic nestedness across the region (0.005 ± 0.031, p = 0.863; Fig. 4).

Phylogenetic homogenization

Phylogenetic beta diversity decreased from 1980 to 2019 (–0.071 ± 0.010, p < 0.001), driven by decreasing turnover (–0.076 ± 0.013, p < 0.001) rather than nestedness (–0.006 ± 0.039, p = 0.871; Fig. 4a). Phylogenetic richness increased in winter (1.11 ± 0.11, p < 0.001) but did not change in the breeding season (0.00 ± 0.16, p = 0.982; Fig. 5a). Among grid cell assemblages, patterns of mean phylogenetic richness, change in phylogenetic richness, and change in phylogenetic beta diversity are all strikingly similar to corresponding taxonomic metrics (Fig. 4–5).

Functional homogenization

Functional beta diversity decreased from 1980 to 2019 (–0.060 ± 0.019, p = 0.002) driven by decreasing turnover (–0.111 ± 0.025, p < 0.001) rather than nestedness (–0.010 ± 0.036, p = 0.779; Fig. 4a). Functional richness increased in both the breeding season (0.024 ± 0.004, p < 0.001) and winter (0.030 ± 0.003, p < 0.001), even though species richness only increased in winter (Fig. 5a). For functional richness to increase without increasing species richness, functionally unique species must replace functionally redundant species. Many of the breeding species being lost are small passerine invertivores (Supporting information), while the species that are expanding the functional space of breeding assemblages include raptors, waterfowl, wild turkey *Meleagris gallopavo*, common raven *Corvus corax* and ruby-throated hummingbird *Archilochus colubris* (Fig. 6). Most of these species have also become more common in winter and are expanding the functional space of winter assemblages as well (Fig. 6). Functional richness increased in both seasons, but the gap in functional richness between breeding and winter assemblages did not change over time, so nestedness did not change.

Decreasing functional turnover indicates that functional space unique to breeding or winter assemblages (after accounting for differences in richness) is decreasing. This can happen in two ways: 1) contraction of functional space unique to one season, or 2) expansion of functional space shared by both seasons. We observe both of these phenomena. Seasonally unique functional space has contracted for both winter and the breeding season. For winter assemblages, species such as evening grosbeak *Coccothraustes vespertinus*, pine grosbeak *Pinicola enucleator*, and purple finch *Haemorhous purpureus* filled a region of functional space that was not usually filled by breeding assemblages, but these species are occurring less often in this region, so the volume of winter-only functional space has decreased (Fig. 6a, Supporting information). Similarly, short-billed aerial invertivores such as chimney swift *Chaetura pelagica* and common nighthawk *Chordeiles minor* filled a region of functional space in breeding assemblages that winter assemblages did not fill, but these species have declined, so the volume of breeding-only functional space has decreased (Fig. 6b, Supporting information).

Functional turnover has also decreased due to the expansion of shared functional space between seasons. Raptors were originally more common in winter assemblages, but species such as Cooper's hawk *Astur cooperii* and red-tailed hawk *Buteo jamaicensis* have increased in the breeding season (Fig. 6, Supporting information), so this region of functional space that was often winter-only is now increasingly shared by both seasons. In addition, functionally unique species such as bald eagle *Haliaeetus leucocephalus*, common merganser *Mergus merganser*, wild turkey, and common raven are increasing in both seasons and are expanding functional space in both seasons. (Fig. 6, Supporting information). As these species increase shared functional space, the proportion of unshared functional space has decreased, and functional turnover has decreased.

In addition to the species described above, hummingbirds are contributing to changes in functional diversity. Ruby-throated hummingbird is increasing in the breeding season and thus increasing the volume of functional space unique to the breeding season, though this is partially counteracted by the increase of rufous hummingbird *Selasphorus rufus* in winter. (Fig. 6b, Supporting information). Hummingbirds are so functionally distinctive that they play an outsized role in driving functional diversity patterns. In 2013, rufous hummingbird occurred in every grid cell, resulting in particularly high winter functional richness and low functional turnover that year (Fig. 4a–5a, Supporting information). If we remove rufous hummingbird from the analysis, total functional beta diversity still decreases (–0.063 ± 0.018, p < 0.001), but functional turnover does not significantly decrease (–0.029 ± 0.030, p = 0.326), as the rise of ruby-throated hummingbird in the breeding season counteracted increasing similarity in other regions of functional space. If we remove both hummingbirds, total functional beta diversity and turnover both decrease (–0.106 ± 0.023, p < 0.001; –0.199 ± 0.025, p < 0.001) due to the other functional changes described above.

Discussion

Building on previous research that identified taxonomic homogenization between winter and breeding bird communities in the northeastern US (Curley et al. 2024), we find that phylogenetic and functional beta diversity have also decreased over the last four decades. The decreasing seasonal turnover that we observed for taxonomic, phylogenetic, and functional diversity indicates that fewer species, evolutionary lineages, and functional traits are unique to either winter or breeding assemblages and are instead increasingly shared by assemblages in both seasons. While phylogenetic homogenization closely mirrors taxonomic homogenization, functional

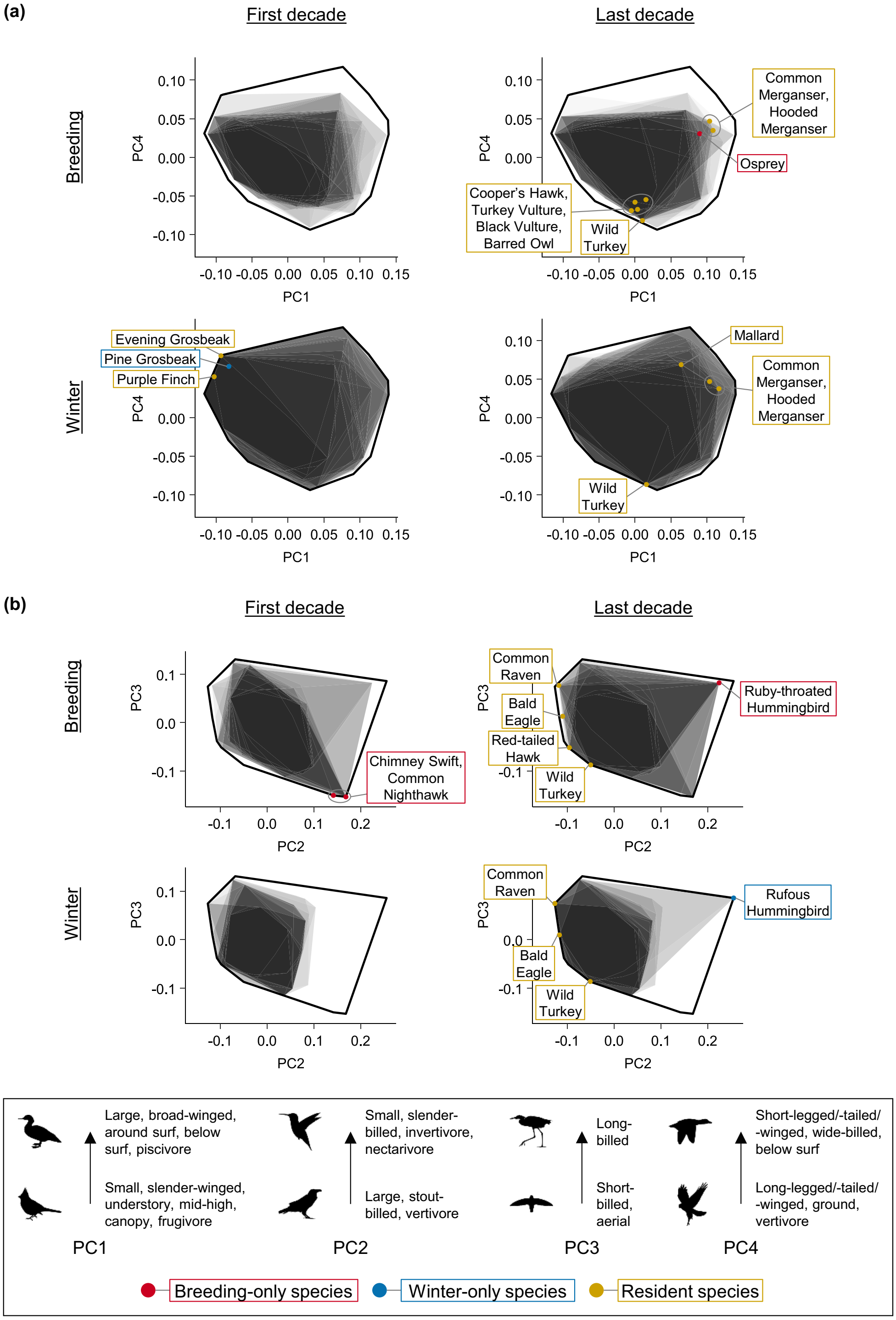

Figure 6. These plots illustrate the functional space filled by breeding and winter communities, with overlapping polygons representing grid cell assemblages from that decade and season. Each polygon represents the convex hull of an assemblage composed of species occurring within a given grid cell for ≥ 5 years of the decade, either 1980–1989 or 2010–2019. The darker regions where multiple assemblages overlap are regions of functional space that are more often filled in that decade and season. Comparing the shaded areas between first and last decade indicates shifts in functional space from the 1980s to the 2010s. Comparing the shaded areas between breeding and winter indicates seasonal differences in functional space. Black outlines indicate the convex hull for all bird species (Fig. 3). Labeled species are some of the species associated with changes in functional space, either declining species associated with the contraction of functional space (first decade column) or increasing species associated with the expansion of functional space (last decade column). Functional space was calculated as a four-dimensional PCoA, with axes 1 and 3 (a) and axes 2 and 4 (b) shown here. See the Supporting information for additional combinations of axes. Public domain silhouettes from PhyloPic.

homogenization manifests in distinct ways that are important to unpack. Loss of specialized functions specific to a season may have cascading effects on biodiversity, similar to the consequences of other types of biotic homogenization where specialists have decreased and generalists have increased (Davey et al. 2012, van Der Plas et al. 2016), and the loss of functional diversity could impact ecosystem resilience and health (Flynn et al. 2009, Matuoka et al. 2020). In order to understand the effects of functional homogenization, though, it is important to know which functions are changing.

The contrast between taxonomic and functional diversity provides insight into how seasonal assemblages are changing. Although species richness of breeding communities is stable, the functional richness of these breeding communities is increasing, as small-bodied invertivores unique to the breeding season are replaced by functionally distinct species which also occur in winter assemblages, such as bald eagle *Haliaeetus leucocephalus*, Cooper's hawk *Astur cooperii*, common merganser *Mergus merganser*, common raven *Corvus corax*, turkey vulture *Cathartes aura*, and wild turkey *Meleagris gallopavo*. As taxonomic homogenization increases the proportion of shared species between seasons, the proportion of functional space shared between seasons should also increase, but the relationship between these diversity metrics is not straightforward. The assemblages with the steepest declines in taxonomic beta diversity are not the same assemblages with the steepest declines in functional beta diversity (Fig. 4b). Some assemblages with increasing taxonomic turnover (less shared species) have decreasing functional turnover (more shared functional space), and vice versa. Therefore, changes in functional composition are not merely a side effect of changes in taxonomic composition (Baiser and Lockwood 2011). Studies of biotic homogenization across space have also found different trends for taxonomic and functional beta diversity (Sonnier et al. 2014, White et al. 2018, Tsianou et al. 2021). Though many studies of functional homogenization find trends of increasing generalists and decreasing specialists (McKinney and Lockwood 1999, 2001, Clavel et al. 2011, Davey et al. 2012), we instead find increasing functional richness in both seasons as functionally distinct species become more common. Yet this leads to homogenization because these species are increasingly shared between winter and the breeding season.

Many of the functionally unique species shared between seasons have increased thanks to human efforts. Species such as bald eagle and wild turkey have increased populations as the result of decades of successful conservation (Watts et al. 2008, Hughes and Lee 2015). Increases in raptors and waterfowl – including species such as Cooper's hawk, hooded merganser *Lophodytes cucullatus*, and common merganser – also reflect successful reversals of earlier declines thanks to effective conservation and management (Rosenberg et al. 2019). As these species have increased in both seasons, both the total volume of functional space and the proportion of functional space shared by both seasons has increased, resulting in higher functional richness in both winter and the breeding season and lower functional turnover between seasons. Some of the homogenization we observe, therefore, may in fact be a positive indicator, reflecting the recovery of species that increasingly occur year-round.

Human actions have also boosted populations of hummingbirds, particularly through the spread of feeders (Greig et al. 2017, Meehan et al. 2020). Ruby-throated hummingbird *Archilochus colubris* has become much more common since the 1980s, though in our study area it only occurs in the breeding season. As ruby-throated hummingbird increases the volume of functional space unique to breeding assemblages, it contributes to functional differentiation – rather than homogenization – between seasons. However, this differentiation is partially counteracted by rufous hummingbird *Selasphorus rufus*, a western North American species which has been increasingly documented in the eastern US over the last several decades (Conway and Drennan 1979, Hill et al. 1998, Mitra and Bochnik 2001). If rufous hummingbird continues to spread in the Northeast, then hummingbirds will occur in both the breeding season and in winter, representing an important aspect of functional convergence between these two seasons.

Less positive anthropogenic effects, including climate change, are also likely responsible for functional homogenization between seasons. Species, such as turkey vulture and black vulture *Coragyps atratus*, have become increasingly common in the northern US in winter as ranges shift north in response to climate change (Zimmerman et al. 2019, Marneweck et al. 2023), increasing functional space shared by winter and breeding season assemblages. At the same time that some species are shifting their ranges into our study area, other species are shifting their ranges out of our study area. The decreasing occurrences we observed for evening grosbeak *Coccothraustes vespertinus* and pine grosbeak *Pinicola enucleator* are likely due to poleward shifts in their winter ranges (Widick et al. 2023). Boreal finches occupy functional space unique to winter, so the loss of these species reduces the seasonal differences between bird assemblages. Breeding-only functional space is also decreasing due to declines in aerial invertivores such as common nighthawk *Chordeiles minor* and chimney swift *Chaetura pelagica*. Declines of aerial insectivores are well documented and are likely the result of multiple cascading impacts, including phenological mismatches of prey, decline of insect prey due to pesticide use, and habitat loss (Spiller and Dettmer 2019, Garrett et al. 2022). Therefore, while functional homogenization is partially driven by the conservation success of resident species such as bald eagle and wild turkey, functional homogenization is also driven by anthropogenic population declines of seasonal species that represent seasonally unique functions.

We observe phylogenetic homogenization between seasons, meaning winter and summer communities have increasingly similar pools of evolutionary history, but this phylogenetic homogenization appears to merely reflect taxonomic homogenization. The same assemblages show the greatest decreases in both taxonomic and phylogenetic beta diversity (Fig. 4b), and assemblages that have either increased or decreased species richness show the same trends for phylogenetic richness (Fig. 5b). In other systems, however, phylogenetic and taxonomic homogenization are not always so tightly linked. Global amphibian assemblages show much stronger phylogenetic than taxonomic homogenization when comparing natural and converted habitats, because the amphibians lost in converted habitats tend to be evolutionarily unique (Nowakowski et al. 2018), and non-native plant introductions on oceanic islands have shown much stronger taxonomic than phylogenetic homogenization because introduced and native species tend to be closely related (Yang et al. 2021). In our study, though, changes in species composition do not seem to be phylogenetically biased.

Our study is the first to quantify functional and phylogenetic homogenization between seasons, illustrating how evaluating biotic homogenization across multiple metrics offers a more comprehensive view of community changes. We find evidence of homogenization between winter and breeding bird communities in the northeastern US, and we identify the functional shifts contributing to functional homogenization. As the pressures of continued and accelerated global change continue to drive biotic homogenization worldwide, understanding patterns of seasonal homogenization and its drivers is crucial for future bird conservation, as conservation strategies often target specific periods of the annual cycle, such as the breeding season or migration. Consequently, traditional conservation approaches may need re-evaluation, and more flexible, dynamic management strategies that account for changing bird populations may be required.

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Author contributions

Peter J. Williams: Conceptualization (equal); Data curation (equal); Formal analysis (lead); Methodology (lead); Visualization (lead); Writing – original draft (equal); Writing – review and editing (equal). **Shannon R. Curley**: Conceptualization (equal); Data curation (equal); Methodology (supporting); Writing – original draft (equal); Writing – review and editing (equal).

Transparent peer review

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Data availability statement

Data and code used in this study are available from the Zenodo Digital Repository: https://doi.org/10.5281/zenodo.15538337 (Williams and Curley 2025) and from the GitHub Repository: https://github.com/pwilliams0/Bird_biotic_homogenization.

Supporting information

The Supporting information associated with this article is available with the online version.

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