Decoupled spatiotemporal patterns of avian taxonomic and functional diversity

Marta Jarzyna[1] and James Stagge[1]

[1]The Ohio State University

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Abstract

Each year, seasonal bird migration leads to an immense redistribution of species occurrence and abundances, with pervasive, though unclear, consequences for patterns of multi-faceted avian diversity. Here, we uncover stark disparities in spatiotemporal variation between avian taxonomic and functional diversity across the continental US. In the eastern US, the temporal patterns of taxonomic and functional diversity are diametrically opposed, with functional richness highest in winter despite seasonal loss of species, and the remaining most abundant species amassed in a few regions of the functional space that likely reflect the resources available in winter. In contrast, in the western US, both species and functional richness are high during the breeding season, and species' abundances are regularly distributed and widely spread across the functional space. We anticipate that the uncovered complexity of spatiotemporal associations among avian diversity measures will be the catalyst for adopting an explicitly temporal framework for multi-faceted biodiversity analysis.

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Authors: Marta A. Jarzyna[1,2,*] and James H. Stagge[3]

Affiliations:

[1]Department of Evolution, Ecology and Organismal Biology, The Ohio State University

[2]Translational Data Analytics Institute, The Ohio State University

[3]Department of Civil, Environmental and Geodetic Engineering, The Ohio State University

*Corresponding author

Email addresses:

Marta A. Jarzyna: jarzyna.1@osu.edu

James H. Stagge: stagge.11@osu.edu

Corresponding author:

Marta A. Jarzyna, Department of Evolution, Ecology and Organismal Biology, The Ohio State University, 318 W. 12th Ave., 300 Aronoff Laboratory, Columbus, OH, 43210

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ABSTRACT

Each year, seasonal bird migration leads to an immense redistribution of species occurrence and abundances, with pervasive, though unclear, consequences for patterns of multi-faceted avian diversity. Here, we uncover stark disparities in spatiotemporal variation between avian taxonomic and functional diversity across the continental US. In the eastern US, the temporal patterns of taxonomic and functional diversity are diametrically opposed, with functional richness highest in winter despite seasonal loss of species, and the remaining most abundant species amassed in a few regions of the functional space that likely reflect the resources available in winter. In contrast, in the western US, both species and functional richness are high during the breeding season, and species' abundances are regularly distributed and widely spread across the functional space. We anticipate that the uncovered complexity of spatiotemporal associations among avian diversity measures will be the catalyst for adopting an explicitly temporal framework for multi-faceted biodiversity analysis.

INTRODUCTION

Pinpointing the mechanisms responsible for maintenance of biodiversity relies on accurate evaluations of biodiversity patterns (Pereira *et al.* 2013; Jetz *et al.* 2019), but those often reflect the static conditions of one, often breeding, season (Callaghan *et al.* 2021; Jarzyna *et al.* 2021; Hughes *et al.* 2022) and ignore seasonal variability inherent in the full annual cycle of species (Marra *et al.* 2015). The availability of resources, however, shows strong intra-annual variability, particularly in temperate regions, that causes many animals to engage in seasonal short- and long-distance migration or hibernation (Somveille et al. 2013), ultimately leading to seasonal patterns of species richness and abundance (Ng et al. 2022).

No other taxonomic group shows stronger intra-annual geographic redistribution of species occurrence and abundance than birds. Each year, billions of individuals (Hahn *et al.* 2009; Dokter *et al.* 2018) of an estimated 1,855 species (19% of all extant bird species; Kirby *et al.* 2008, a percentage that strongly increases with latitude; Somveille *et al.* 2013) migrate toward lower latitudes in autumn and higher latitudes in spring in response to seasonal fluctuations in resource availability (Strong *et al.* 2015; Thorup *et al.* 2017; Ng *et al.* 2022) and unfavorable weather conditions given some species' physiological limitations (Pfeifer *et al.* 2018). These migratory movements produce seasonal patterns of biomass, abundance, and species richness (Ng *et al.* 2022). Unexplored, however, are the implications of this seasonal redistribution of bird occurrence and abundance for other facets of biodiversity, such as functional diversity, the diversity and distribution of functional traits within an assemblage of species (Safi *et al.* 2011; Cardoso *et al.* 2014; Gagic *et al.* 2015). Functional diversity is vital for understanding community assembly (Cavender-Bares *et al.* 2009; Kraft *et al.* 2015), niche packing, expansion, and complementarity (Pigot *et al.* 2016; Pellissier *et al.* 2018), ecosystem functioning, services, and stability (Cadotte *et al.* 2011; Jarzyna *et al.* 2022), and conservation prioritization (Thuiller *et al.* 2015; Pollock *et al.* 2017; Mazel *et al.* 2018).

Seasonality of avian functional diversity is likely to deviate from that of taxonomic diversity because migratory and resident birds likely present with different trait characteristics. For example, migratory and resident birds have been shown to differ in traits such as body mass (Hein *et al.* 2012; Soriano-Redondo *et al.* 2020) and clutch size (Jetz *et al.* 2008). Migrants often show stronger habitat (Martin & Fahrig 2018;

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Zurell *et al.* 2018; but see Reif *et al.* 2016), diet (Boyle *et al.* 2011; Fristoe 2015), and climate (Gómez *et al.* 2016; but see Dufour *et al.* 2020) specialization than partial migrants or resident species, who are often generalists that possess a broader spectrum of trait values conferring tolerance to harsh winter conditions of temperate regions. Furthermore, seasonality in resource availability leads to a disproportionate decrease in the occurrence of species that depend on resources typically unavailable during winter (Somveille *et al.* 2015) such as obligate insectivores (Fristoe 2015). Such disproportionate redistribution of trait characteristics likely leads to decoupling of spatiotemporal patterns of avian functional from taxonomic diversity, but the magnitude and direction of such decoupling have not been previously elucidated.

Here, we present the first broad-scale assessment of commonalities among seasonal patterns in avian taxonomic and functional diversity. We leverage abundance estimates during the full annual cycle for > 600 North American bird species from eBird Status and Trends (Fink *et al.* 2021) to quantify taxonomic diversity (species richness, SR). We combine these with avian trait databases (Wilman *et al.* 2014) to quantify three independent and complementary components of functional diversity—functional richness (FRic), functional evenness (FEve), and functional dispersion (FDis) (Villéger *et al.* 2008a). A species-corrected version of functional richness (cFRic) that better reflects true breadth of occupied functional space is included, raising the total metrics considered to five, measured across the continental US at weekly temporal resolution. Our study offers, to our knowledge, the first comprehensive characterization of the seasonality in taxonomic and functional diversity for any taxonomic group, with an unprecedented level of detail that can yield invaluable insights into spatiotemporal dynamics of avian communities.

MATERIALS AND METHODS

Species distributions and abundances. We used bird species occurrence and relative abundance estimates from eBird Status and Trends (S&Ts) 2019 data published by the Cornell Lab of Ornithology (Fink *et al.* 2021). 2019 eBird S&Ts provides modeled estimates of weekly occurrence and abundance for 807 species. Species' occurrence and abundance estimates in S&Ts are obtained using the spatiotemporal exploratory model (STEM)—i.e., an ensemble model designed to include essential information about spatial and temporal scales (Fink *et al.* 2010) and account for intra-annual variability in species distributions. Relative abundance in eBird S&Ts is defined as the count of individuals of a given species detected by an expert eBirder on a 1 hour, 1 kilometer traveling checklist at the optimal time of day. Relative abundance predictions are optimized for search effort, user skill, and hourly weather conditions, specific for the given region, season, and species. For each species, occurrence and abundance predictions are made at a weekly temporal resolution and a spatial resolution of appr. 8.4 km, using raw eBird records and high-resolution satellite imagery. The relative abundance estimates from eBird S&Ts thus allow for obtaining estimates of avian diversity across North America without having to model raw eBird records. We note that some species are necessarily poorly detectable in the field, and their abundance might thus remain underestimated by STEM. However, this underestimation—if present—should be consistent across space and time because STEM optimizes for detection covariates such as effort, observer, and weather. Consequently, patterns of spatiotemporal variation in avian diversity should not be biased by potential underestimation of poorly detectable species (Daniel Fink, personal communication). eBird S&Ts data used here were downloaded in February 2022 and reflect species abundance estimates of 2019 (data version 2020, released in 2021; Fink *et al.* 2021). Data version 2021 was not available at the time of the analysis and submission.

Before quantifying bird diversity, we removed pelagic species, which are typically poorly sampled by eBird observers. To decrease the computational cost and ensure taxonomic completeness—crucial for robust estimation of assemblage composition—we truncated the data to the continental US and only considered species that were recorded in the continental US during at least one week in a year. Ultimately, we included 630 bird species.

Avian taxonomic and functional diversity. We quantified species richness (SR) as the count of all species whose relative abundances were greater than zero (Ng *et al.* 2022). We based estimates of all functional diversity metrics on a compilation of function-relevant (i.e., reflecting species' functional role in an ecosystem; Kissling *et al.* 2012; Junker *et al.* 2019) traits in Wilman *et al.* (2014), with four trait categories: body

mass, diet, foraging niche, and activity time. Diet and foraging niche categories included seven axes each: proportions of invertebrates, vertebrates, carrion, fruits, nectar and pollen, seeds, and other plant materials in species' diet (diet); proportional use of water below surface, water around surface, terrestrial ground level, understory, mid canopy, upper canopy, and aerial (foraging niche). Activity time included two axes: diurnal and nocturnal. We acknowledge that bird dietary characteristics might change across seasons, but currently such higher temporal resolution data are not available for most species included in this analysis.

To gain a comprehensive understanding of functional diversity of each assemblage across space and time, we quantified three dimensions of functional diversity: functional richness (FRic), functional evenness (FEve), and functional dispersion (FDis). FRic describes the total breadth of trait diversity present in an assemblage; FEve reflects the regularity of the distribution of species' abundances within the functional trait space; FDis summarizes the overall spread and relative distribution of species' abundances in an assemblage, relative to the centroid of the functional trait space (Laliberté & Legendre 2010; Villéger *et al.* 2010). To obtain all three indices we first calculated species' multivariate functional dissimilarities using corrected Gower's distance as implemented in the 'gawdis' package (de Bello *et al.* 2021a), which better balances the contribution of traits (and trait groups) to overall dissimilarity and is especially important when using highly dimensional data and fuzzy coded traits (de Bello *et al.* 2021b). We optimized trait weights using the 'optimization' method for 300 iterations (the default), with equal weights for individual traits within manually designated trait groups (i.e., fuzzy coded diet and foraging stratum, binary activity time, and a continuous body mass). The resulting functional distance matrix was used to calculate all three indices of functional diversity (FRic, FDis, FEve) using the 'dbFD' function in package 'FD' (Laliberté *et al.*2014). FRic was calculated as the convex hull volume and based on the first three PCoA axes (Villéger *et al.* 2008b). Reduction to three dimensions was necessary for FRic because the construction of convex hulls requires more species than traits (here represented by PCoA axes) and we used four as the lowest number of species necessary for functional diversity to be obtained. Additionally, using more than three PCoA axes was not computationally feasible. We standardized FRic by the 'global' FRic that includes all species so that it was constrained by 0 and 1 and comparable across the spatiotemporal domain. FEve was calculated as the regularity of species functional distances along the minimum spanning tree (Villéger *et al.* 2008b). FDis was calculated as the mean distance of species to their collective centroid in functional trait space (Laliberté & Legendre 2010). We chose FDis (Laliberté & Legendre 2010) instead of closely related functional divergence (FDiv; Villéger *et al.* 2008b) or Rao's quadratic entropy (Botta-Dukát 2005) because it better estimates the dispersion of species in trait space (Laliberté & Legendre 2010). Calculation of FEve and FDis was based on all PCoA axes. Both FEve and FDis integrate information on species' relative abundances; FDis is constrained by 0 but has no upper limit, while FEve is constrained by 0 and 1. We used the 'sqrt' correction for negative eigenvalues.

All avian diversity indices were computed for each 8.4 x 8.4 km grid cell across the contiguous US and for each week, resulting in a total of > 52M values per avian diversity metric. We used statistical software R v3.6.0 for all analyses and utilized Ohio Supercomputer Center (OSC) Pitzer cluster to run all calculations and models, for a total of approximately 11,000 hours of runtime.

Species richness-controlled avian functional diversity. Functional richness is strongly related to species richness and its interpretation benefits from statistically controlling for this association. To control for species richness, we regressed log-transformed FRic against log-transformed SR using a simple linear regression and used residuals of this regression as SR-corrected values of FRic (cFRic). Residuals quantify deviations of FRic from the expectation given SR (Mason *et al.* 2005; Safi *et al.* 2011; Zupan *et al.* 2014; Gaüzère *et al.* 2022), with positive residuals indicative of surplus and negative residuals indicative of deficits in functional richness given species richness of that assemblage (Gaüzère *et al.* 2022). While another common method to obtain SR-corrected values of functional diversity calls for a randomization procedure wherein species identities are shuffled hundreds of times (Swenson 2011; Jarzyna & Jetz 2018), such a procedure would require 100s of times the aforementioned run time (> 1,000,000 hours) and was not computationally feasible. FDis and FEve are based on relative abundance and are thus independent of species richness and do not require a correction (Villéger *et al.* 2008b; Laliberté & Legendre 2010).

Spatiotemporal variation in avian diversity. We applied Principal Component Analysis (PCA) to identify the dominant components of temporal (here, seasonal) variation in avian diversity, find regions characterized by similar seasonal patterns of avian diversity, and identify commonalities in spatiotemporal signatures across the different indices of avian diversity. Below we provide a brief description of the principles of PCA in the context of biodiversity change analysis; for a more thorough explanation we refer the reader to (Jarzyna & Stagge, In review).

We first created a 2-dimensional matrix $\mathbf{Y}$ [t, ij] where each row t is a time step (i.e., week), and each column holds values of an avian diversity index, j (here, $j =5$: SR, FRic, cFRic, FEve, and FDis) measured at location i . Matrix $\mathbf{Y}$is then subject to PCA, which transforms these multivariate data into a dataset measured along new orthogonal axes organized in such a way that the first axis, or Principal Component (PC), captures the largest proportion of variance in the data. The second PC (PC2) captures the second largest proportion of variance, measured orthogonally to PC1, and so on. These new PCs are orthogonal, i.e., uncorrelated with each other. Since one of the primary goals of PCA is dimensionality reduction, we typically only consider the most important PCs—i.e., those that capture a significant amount of variance in the data or are functionally important.

PCA decomposes the original matrix $\mathbf{Y}$ [t, ij] into two new matrices, referred to as PC loadings, $\mathbf{U}$, and PC scores,

$\mathbf{V}$

$$\mathbf{Y} = \ \mu + U\ \mathbf{V^t}\sigma \text{(Eq. 1)}$$

where the loading matrix $\mathbf{U}$ has dimensions equal to ij x k, or the number of measurements across all sites and indices by the number of principal components, k . The score matrix $\mathbf{V}$ has dimensions of t x k where t is the number of time steps. All avian diversity indices were first centered and normalized independently for each site and metric by calculating the long-term mean, μ, and standard deviation, σ, for each column of the original $\mathbf{Y}$matrix.

PC scores describe the temporal expression of each PC, centered around the long-term mean, μ. In the context of our analysis, PC scores capture the dominant seasonal pattern of avian diversity. For example, a transition of PC scores from strongly negative at the beginning of the year to strongly positive in the summer and strongly negative again towards the end of the year captures breeding-winter season variation in avian diversity. PC loadings indicate how strongly, positively or negatively, the temporal pattern given by PC scores is expressed at a given location. Strong positive loadings mean that the average temporal pattern given by PC scores is expressed strongly in that region, strong negative loadings indicate the temporal pattern given by PC scores is expressed strongly in the opposite direction, and loadings near zero indicate that the temporal pattern given by PC scores is barely expressed, producing values of biodiversity near the mean. Loadings maps can be produced for all k PCs, with later PCs often capturing increasingly random spatial variation. Note that the true temporal pattern of avian diversity will always be a combination of the principal modes, but the stronger loadings on a given PC the stronger the effect of that particular Principal Component on avian diversity (see below); PC loadings can thus be thought of as weights indicating the contribution of each PC to the true temporal pattern.

Once we calculated the PC scores and loadings and selected the number of PCs to consider, we used subset versions of the loading and score matrices, $\mathbf{U}$ and $\mathbf{V,}$ to show the effect of each PC as well as the cumulative effect of all considered PCs together on avian diversity over time, at selected sites. To accomplish this, we multiplied $\mathbf{U}$ by the transpose of the score matrix,$\mathbf{V^t}$, to produce a matrix in 'normalized space'. Because we originally chose to normalize the data,$\mathbf{UV^t}$ must be multiplied by the standard deviation, σ, and added to the mean, μ, to obtain reconstructions of the original avian diversity metrics (Eq. 2). For a single site and$k$ $^\text{th}$ PC, this becomes:

$$\text{Div}_{i,j,k}[t] = \ \mu_{i,j} + \ \sigma_{i,j} \times [U_{i,j,k} \times V_k[t]] \text{(Eq. 2)}$$

where $U_{i,j,k}$ is a single loading value for PC_k and a given site/avian diversity metric; $V_k[t]$ is a score vector for

PCk which changes over time. The long-term mean and standard deviation of an avian diversity metric j at location i are given by $\mu_{i,j}$ad $\sigma_{i,j}$, respectively. PC loadings and scores therefore work together to reconstruct the original avian diversity at each site and time step by calculating the number of standard deviations from the long-term mean. Lastly, we compared the reconstructed values of avian diversity metrics with true avian diversity time series for select locations.

We conducted Principal Component Analysis using function 'prcomp' from a package 'stats' in R.

Spatial congruence in seasonality of avian taxonomic and functional diversity. To assess agreement in spatiotemporal patterns of all avian diversity metrics, we first evaluated correlations among loadings for the first three PCs (which together accounted for ca. 65% of variance in the data; Fig. S1) for each pair-wise association of avian diversity metrics (SR, FRic, cFRic, FEve, FDis). To better synthesize findings from the three PCs and identify regions characterized by similar temporal patterns of avian diversity, we conducted a clustering procedure using the k-means clustering algorithm. The k-means algorithm partitions observations into k clusters in which each observation belongs to the cluster with the nearest mean in q-dimensional space, where the q axes represent the number of measurements. For this example, q = 15 because clustering was based on loading values from the five diversity metrics and three principal components. We first performed a k-means clustering procedure on a training dataset (a subset of 20,000 locations) and used a goodness-of-fit metric (maximum silhouette width) to select the most appropriate number of clusters (Fig. S2). We then used function 'kcca' from package 'flexclust' to partition observations into clusters with the closest k-centroid. Repeated tests with random samples produced stable cluster estimates, increasing confidence in the use of a training subset rather than the full dataset. All code will be available on GitHub and archived with zenodo (doi: to be provided upon acceptance of the manuscript).

RESULTS

Spatiotemporal variation in avian diversity. We identify three Principal Components (PCs) that together explain 65% of weekly variance for the five taxonomic and functional diversity metrics across the continental US (Fig. S1). The first Principal Component (PC1; 47% variance explained; Fig. S1), separates the breeding (positive score) from the wintering (negative score) season, with two distinct, lesser peaks likely associated with the temporary addition of transient species during seasonal migration (Fig. 1a). The second Principal Component (PC2, 11% variance explained; Fig. S1) further isolates migration (primarily, spring migration; positive score) from periods of wintering and breeding (negative score; Fig. 1a). The third Principal Component (PC3, 8% variance explained; Fig. S1) further emphasizes the signal of autumn migration (positive score; Fig. 1a). Each subsequent PC explains $< 5\%$ of the total variance (Fig. S1) and captures mostly stochastic fluctuations, without a clear seasonal signature (Fig. S3). Seasonal patterns of avian diversity can thus be approximated for each grid cell as the weighted combination of three principal modes: breeding/winter season (PC1), spring (PC2), and autumn (PC3) migration, where the weights (i.e., importance of each PC at different locations) are shown by the PC loading maps (Fig. 1b).

Avian diversity shows clear spatial patterns in the strength (loading) of temporal variation (score) patterns, but there are notable differences among the five diversity metrics in how these patterns are expressed (Figs. 1,2a,S4). Seasonality of species richness demonstrates a strong latitudinal gradient, with the northern US (n=693,160 grid cells, ~74% of study region) characterized by high breeding season SR and low winter SR (strongly positive PC1 loadings; Figs. 1,2a). Along the Gulf of Mexico coast, SR instead peaks during winter (n=48,251, ~5%; strongly negative PC1 loadings). Known migratory staging areas across the South, Southeast, Southwest, and California (n=159,452, ~17%) experience spring and autumn peaks in SR (strongly positive PC2 and PC3 loadings; Figs. 1,2a), with some spatial differences between PC2 (spring) and PC3 (autumn) loading. A few patches in the Southeast (n=32,298, ~4%) instead experience autumn troughs in SR (Figs. 1,2a). Raw functional richness, FRic, expectedly shows fairly strong spatiotemporal congruence with SR, with only small deviations for parts of Texas and the Midwest where FRic peaks during the breeding season and autumn migration, respectively (Fig. 1,2b).

In stark contrast to the strongly correlated SR and FRic, corrected functional richness, cFRic, peaks during

winter across most of the East, Midwest, and the Pacific Coast (strongly negative PC1 loadings; n=265,851, ˜29%; Figs. 1,2c). This temporal signature implies that the total breadth of functional space occupied by a bird assemblage is higher during winter than would be expected after accounting for seasonal declines in species richness due to migration, but lower during summer when migrants are back on their breeding grounds. In contrast, breeding season peaks in cFRic (strongly positive PC1 loading) are common across northern Michigan, Florida, Texas, the Rocky Mountains, and California's Central Valley (n=240,285, ˜26%; Figs. 1,2c). For Florida and Texas in particular, this suggests that the influx of short-distance migrants from northern latitudes during winter leads to assemblage-wide declines in functional richness. Importantly, passage migrants strongly influence the seasonality of cFRic. Specifically, the high plateaus of the Intermountain West experience spring troughs in cFRic (strongly negative PC2 loadings; n=144,797, ˜15%; Figs. 1,2c), while parts of the Southwest, Southeast, and New England see spring and autumn peaks (strongly positive PC2 and PC3 loadings; n=188,824, ˜20%; Figs. 1,2c).

Seasonality of functional evenness, FEve, broadly displays an east-west gradient (Figs. 1,2d), with breeding season peaks (strongly positive PC1 loadings) common east of the Rocky Mountains, in parts of the Great Basin, and along the Pacific Coast (n=642,027, ˜69%; Figs. 1,2d). Such a temporal pattern indicates an even distribution of species' abundances in the functional space during the breeding season. In winter, however, species' abundances amass in a few regions of the functional space. Passage migrants influence seasonality of FEve particularly strongly in high elevation and topographically varying regions. The Intermountain West high plateaus, parts of the Rocky Mountains, and the Sierras experience irregular distribution of species' abundances within the functional space (low FEve) during spring (negative PC2 loadings; n=108,813, ˜12%) and the breeding season (negative PC1 loadings; n=34,122, ˜4%), while parts of the Rocky, Chisos, Ozark, and Appalachian Mountains (n=100,862, ˜11%) see functional evenness peak in spring and autumn (Fig 1,2d).

Strong breeding-wintering seasonality characterizes functional dispersion, FDis, across most of the continental US (n=745,939; ˜80%; Figs. 1,2e), with peaks typically observed during the breeding season (strongly positive PC1 loadings). This temporal signature implies that during the breeding season abundant species are spread further away from the centroid of the functional space relative to rare species, but in winter they are positioned near the centroid. The only regions with winter peaks in FDis (negative PC1 loadings) are the northern Rocky Mountains and lower Peninsular Florida (n=32,980, ˜4%; Figs. 1,2e). Passage migrants strongly increase the dispersion of species' abundances in the functional space in spring and autumn (strongly positive PC2 and PC3 loadings) in the Appalachian Mountains, the Great Lakes region, and upper Peninsular Florida (n=52,619, ˜6%), but lower it (strongly negative PC2 and PC3 loadings) in the Intermountain West high plateaus, the Sierras, and the Midwest (n=101,588, ˜10%; Figs. 1,2e).

Spatial congruence in seasonality of avian taxonomic and functional diversity. We identify seven distinct spatiotemporal clusters (Figs. 3,S2). Broadly, Clusters 1 (n=140,846, ˜15% of continental US) and 2 (n=140,967, ˜15%) represent locations where species richness and functional diversity peak during the breeding season and migration, except for cFRic, which alone declines during the breeding season (Fig. 3b). Together, Clusters 1 and 2 cover much of the eastern US (Fig. 3a), with Cluster 1 representing the higher elevation Appalachian region and southeastern plateaus and Cluster 2 representing the low lying plains and prairies of the Lower Great Lakes. Parts of California and the Pacific Northwest also show characteristics of Clusters 1 and 2 (Fig. 3a).

Cluster 3 (n=120,658, ˜13%) is broadly defined by breeding season peaks in avian diversity, across nearly all measures, and declines during winter, spring, and autumn (Fig. 3b). cFRic is again an exception to this pattern as it instead peaks in spring and plummets in autumn (Fig. 3b). Cluster 3 comprises high elevation, cold winter, forested regions of the Rocky Mountains, New England, upstate New York, and the Upper Great Lakes (Fig. 3a). Cluster 4 (n=99,342, ˜11%) is characterized by low SR but high functional diversity during the breeding season (Fig. 3b) and covers the southernmost regions of Texas, Florida and inland California (Fig. 3a), areas typically characterized by warm winters.

Broadly, Clusters 5 (n=190,523, ˜21%) and 6 (n=115,681, ˜12%) experience peaks in avian diversity during

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the breeding season and troughs during winter, spring, and autumn (Fig. 3b) and cover medium (Cluster 5) to high (Cluster 6) elevation plateaus of the western US (Fig. 3a). Finally, Cluster 7 (n=123,113, ~13%) identifies locations where SR peaks during both the breeding and migration seasons and functional diversity peaks in the breeding season (Fig. 3b). Cluster 7 comprises mostly the deserts of the Southwest and extends into the prairies along the Front Range (Fig. 3a). Remarkably, we find a close agreement between these emergent spatiotemporal clusters and Bird Conservation Regions (BCRs; Fig 3a,c)—independently and qualitatively derived regions that are ecologically distinct in terms of their bird communities, habitat types, and resource management issues (Babcock *et al.* 1998).

DISCUSSION

We show strong spatial and seasonal decoupling for multiple facets of avian diversity across the continental US. The seasonality of species richness expectedly follows a latitudinal gradient, associated with north-south migratory movements of hundreds of bird species, corroborating findings from others (Ng *et al.* 2022). In the northern US, species richness is expectedly highest in the breeding season, but that temporal pattern reverses along the Gulf of Mexico coast, where species richness instead peaks in winter, likely driven by seasonal influx of short-distance migrants into these wintering grounds (Ng *et al.* 2022). Across the South, Southeast, Southwest, and California, migrants further contribute strongly to spring and autumn peaks in species richness, with spatial differences between spring and autumn patterns potentially indicative of loop migration (La Sorte *et al.* 2014).

The seasonality of functional diversity manifests a more complex spatial variation, characterized by a stronger east-west gradient, further latitudinal variation superimposed on it, and some apparent topographical effect. The diametrically opposed temporal patterns of taxonomic and functional diversity are most apparent in the eastern US, where bird assemblages in the breeding season are characterized by a tightly packed functional space that leads to lower overall functional richness, an even distribution of species' abundances in that space and a wide spread of abundant species in relation to the space centroid. Such a pattern suggests an effective use of the entire range of available resources (Mason *et al.* 2005) despite the lower overall functional richness of bird assemblages. During winter, functional richness increases despite species loss, suggesting that migratory birds do not contribute disproportionately to the breadth of the functional space occupied by bird assemblages. The remaining most abundant species, however, are confined to one or a few regions of the functional space that are likely associated with the limited resources available during winter. Likewise, along the Gulf of Mexico, multi-faceted functional diversity peaks during the breeding season despite declines in species richness, again suggesting that short-distance migrants do not disproportionately expand the functional breadth of bird assemblages while wintering in that region.

Across the western US, discrepancies in temporal signatures of avian diversity measures are somewhat less pronounced. There, bird assemblages during the breeding season are characterized by high functional richness, and a regular distribution and a wide spread of species' abundances in the functional space, a pattern that reverses in winter. Superimposed onto this broad pattern in the western US is a latitudinal gradient that reveals the importance of passage migrants, wherein more northerly regions are increasingly characterized by spring and autumn declines in avian diversity. This might partly result from the differential timing of migration, wherein northerly latitudes see earlier departure (in autumn) and later arrival (in spring) dates than southerly regions. Additionally, birds across the western US are known to travel shorter distances as they often combine elevational with latitudinal migration movements, a direct result of high topographic relief (Boyle 2017), which might ultimately lead to a more pronounced north-south gradient.

Stark differences in seasonality of functional richness suggest differential contributions of migratory and resident birds to functional diversity across the east-west gradient. In the western US, migratory birds seemingly play a more important role in maintaining functional diversity by contributing unique trait characteristics outside the trait spectrum represented by resident species. Indeed, dietary and habitat specialization are higher in the western US than in the east (Belmaker *et al.* 2012) and narrow-ranged, and thus potentially more specialized (Botts *et al.* 2013; Slatyer *et al.* 2013), migratory birds make up a greater proportion of avian communities in the western US (Somveille *et al.* 2013). For example, of 15 species of hummingbirds

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found in the US, only one—the Ruby-throated hummingbird (*Archilochus colubris)* —breeds in the eastern US, and is additionally considered a niche generalist compared to hummingbirds of the western US. A seasonal loss of these and other functionally unique species is likely to have an outsized effect on assemblage functional diversity, particularly functional richness. In the eastern US, higher levels of generalization in resident birds (Belmaker *et al.* 2012) ensure that most regions of the functional space remain occupied during winter, albeit scarcely. There, the primary contribution of migratory birds to functional diversity is through increasing the evenness and dispersion of abundances within the functional space, which ensures a high degree of niche differentiation and thus a more efficient resource use (Mason *et al.* 2005; Villéger *et al.* 2008b).

The uncovered complexity of spatiotemporal associations among the different facets of avian diversity illustrates the importance of isolating unique seasonal signals of biodiversity. Our findings, paired with the evidence for strong temporal non-stationarity of the effects of environmental drivers on biodiversity (Wolkovich *et al.* 2014; Zuckerberg *et al.* 2016) and seasonally varying projections of regional climate change (Abatzoglou & Redmond 2007; Wuebbles *et al.* 2014; Pendergrass *et al.* 2017; Dunn *et al.* 2020), reinforce the pressing need to place the investigations of biodiversity in an explicitly temporal context to ensure sound forecasting, conservation, and management of biodiversity.

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FIGURE CAPTIONS

Figure 1. Intra-annual variability in avian diversity—measured as species richness (SR), raw functional richness (FRic), species richness-corrected functional richness (cFRic), functional evenness (FEve), and functional dispersion (FDis)—is well captured by three primary modes (Principal Components, PCs). The scores (temporal seasonal patterns) are illustrated in (a). The seasonal patterns of scores of the first mode (PC1) captures differences in avian diversity between breeding (high score) and wintering (low score) season; the second mode (PC2) separates migration (particularly, spring migration; high score) from periods of wintering and breeding (low score); the third mode (PC3) further emphasizes the signal of autumn migration (high score). (b) PC loading maps show how strongly, positively (red hues) or negatively (blue hues), the temporal pattern given by scores for each PC is expressed at a given location: PC1 (left column), PC2 (middle column), and PC3 (right column). The loading maps demonstrate strong and contrasting spatial variation in seasonality of each avian diversity measure.

Figure 2. The ability of the first three Principal Components (PCs) to explain the intra-annual variability in avian species richness (SR; a), raw functional richness (FRic; b), species richness-corrected functional richness (cFRic; c), functional evenness (FEve; d), and functional dispersion (FDis; e) varies across space and among diversity metrics. We computed an empirical reconstruction of true avian diversity time series (dependent variable) as a linear model of the time series recreated by each PC's scores and loadings (independent variable; see Materials and Methods for more details). The coefficient of determination, R^2, of these reconstructed diversity models was used as a measure of the variation explained by each PC. In purple are regions where PC1 explains the most variation in avian diversity. In green and yellow are regions where PC2 and PC3, respectively, explain the most variation in avian diversity. Dark and light hues indicate positive and negative PC loadings, respectively. Inset boxes indicate % of the study area falling within each category. Avian diversity at select sites (right panels) show seasonal patterns broadly consistent with those recreated by the PC that explains the most variation for that location.

Figure 3. We identified seven unique spatiotemporal clusters that are characterized by similar temporal patterns of avian diversity (a). These are indicated on the map by colour, unique to each cluster. Cluster identities are listed in (b) where the cluster colour is indicated by the colored column at the left edge of each cluster's bar graph. The spatiotemporal clusters coincide strongly with the Bird Conservation Regions (BCRs), indicated by white boundaries and a numbered tag in (a). Box plots in (b) show distribution of loadings for each Principal Component (PC) and each avian diversity metric (species richness, SR; raw functional richness, FRic; species richness-corrected functional richness, cFRic; functional evenness, FEve; and functional dispersion, FDis) for locations that fall within each cluster; blue-and-red heat maps in (b) summarize the direction of PC loadings, with red (blue) indicating those loadings/avian diversity metric combinations whose interquartile range is positive (negative) and does not overlap zero, and grey indicating that the interquartile range overlaps zero. Bar graphs in (c) show proportion of each cluster falling within each BCR. BCRs in (a) follow numbering consistent with their official designation[41] and are as follows: 5) Northern Pacific Rainforest, 9) Great Basin, 10) Northern Rockies, 11) Prairie Potholes, 12) Boreal Hardwood Transition, 13) Lower Great Lakes/St. Lawrence Plain, 14) Atlantic Northern Forests, 15) Sierra Nevada, 16) Southern Rockies Colorado Plateau, 17) Badlands and Prairies, 18) Shortgrass Prairie, 19) Central Mixed Grass Prairie, 20) Edwards Plateau, 21) Oaks and Prairies, 22) Eastern Tallgrass Prairie,

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23) Prairie Hardwood Transition, 24) Central Hardwoods, 25) West Gulf Coastal Plain/Ouachitas, 26) Mississippi Alluvial Valley, 27) Southeastern Coastal Plain, 28) Appalachian Mountains, 29) Piedmont, 30) New England/MidAtlantic Coasts, 31) Peninsular Florida, 32) Coastal California, 33) Sonoran and Mojave Deserts, 34) Sierra Madre Occidental, 35) Chihuahuan Desert, 36) Tamaulipan Brushlands, 37) Gulf Coastal Prairie.
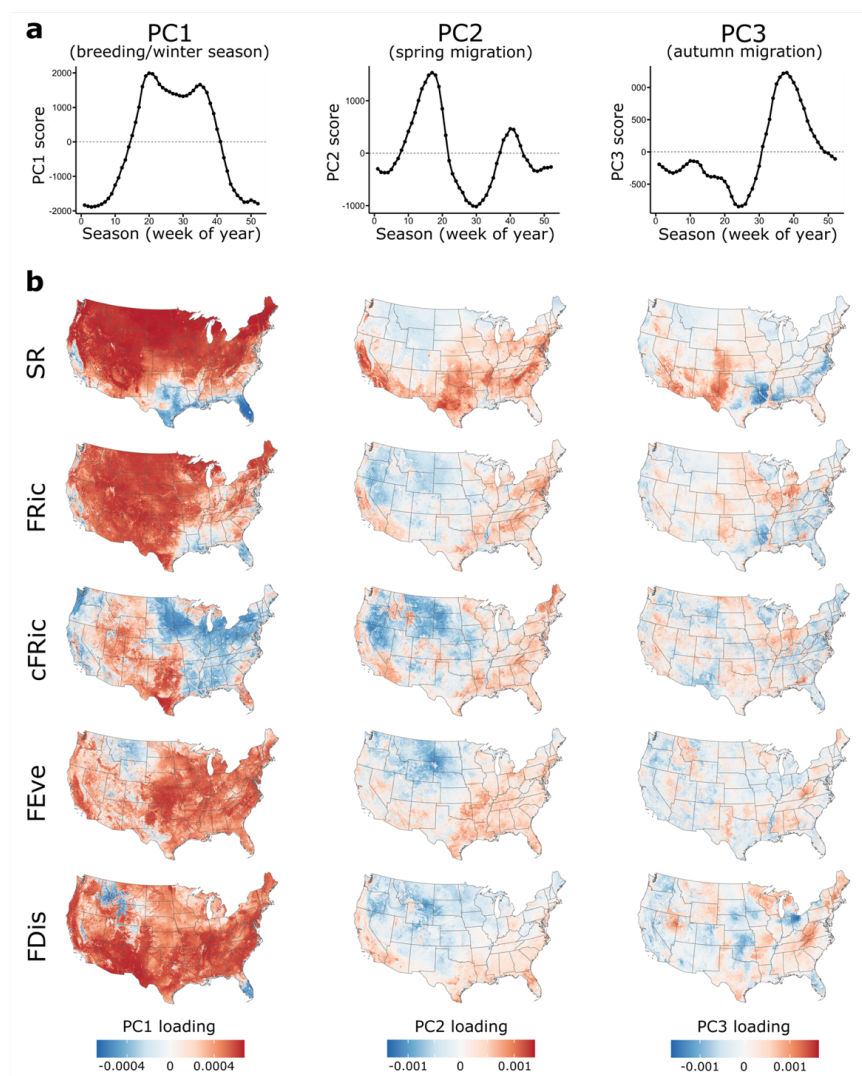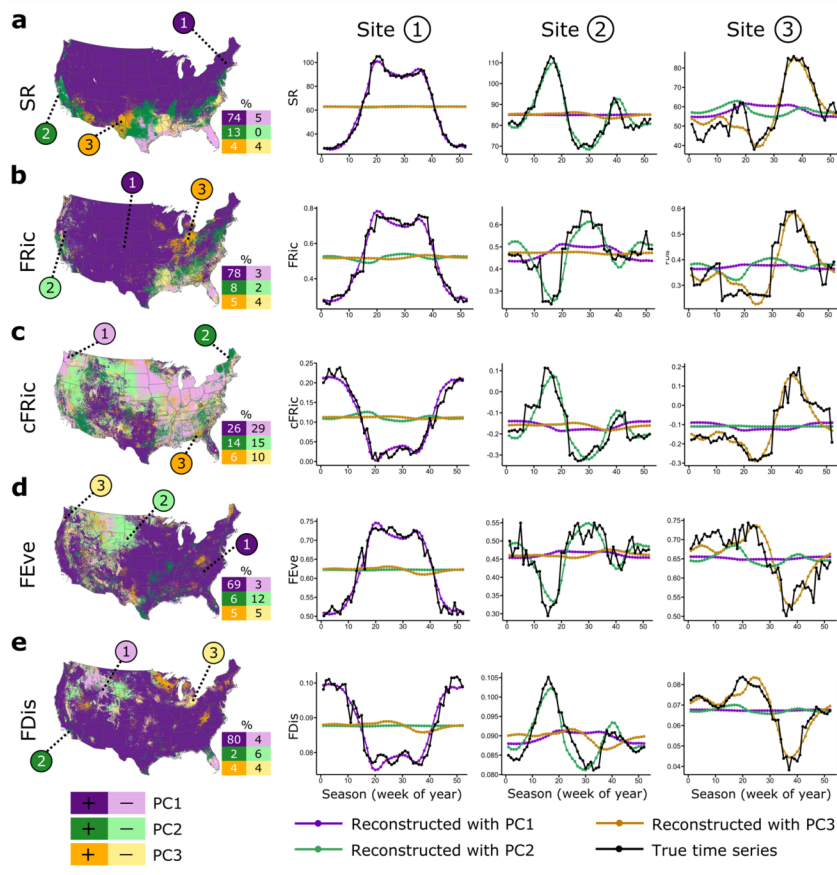
FIGURES

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