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# Seasonality Structures Avian Functional Diversity and Niche Packing Across North America

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## ABSTRACT

Assemblages in seasonal ecosystems undergo striking changes in species composition and diversity across the annual cycle. Despite a long-standing recognition that seasonality structures biogeographic gradients in taxonomic diversity (e.g., species richness), our understanding of how seasonality structures other aspects of biodiversity (e.g., functional diversity) has lagged. Integrating seasonal species distributions with comprehensive data on key morphological traits for bird assemblages across North America, we find that seasonal turnover in functional diversity increases with the magnitude and predictability of seasonality. Furthermore, seasonal increases in bird species richness led to a denser packing of functional trait space, but functional expansion was important, especially in regions with higher seasonality. Our results suggest that the magnitude and predictability of seasonality and total productivity can explain the geography of changes in functional diversity with broader implications for understanding species redistribution, community assembly and ecosystem functioning.

## 1 | Introduction

Seasonality, the intraannual, periodic change of the environment (Williams et al. 2017), affects species spatial distributions, behaviour and physiology (John and Post 2022; Winger et al. 2019). When species move in response to seasonality, assemblages go through a dramatic reshuffling leading to shifts in geographic patterns of diversity (Mellard, Audoye, and Loreau 2019). Globally, more than 2000 species (~20%) of birds migrate (Eyres, Böhning-Gaese, and Fritz 2017) and, in North America alone, 5 billion birds (ca. 700,000 t of biomass) are estimated to migrate annually (Cox 1985; Fristoe 2015; Rappole 1995) resulting in a 10-fold change in local species richness in some regions (Somveille, Rodrigues, and Manica 2015). This mass flux of migrating birds is a vast redistribution of biomass and diversity that culminates in striking changes in assemblage composition (Martin 2018; Ng et al. 2021; Somveille, Rodrigues, and Manica 2015). Yet, the environmental factors and underlying ecological processes driving seasonal changes in the structure and diversity of assemblages remain poorly understood (Jarzyna and Stagge 2022).

A key challenge is that both the magnitude and predictability of seasonality vary greatly across space (Figure 1A), and this variation may have different effects on animal assemblages. It has been hypothesised that regions characterised by both strong and predictable seasonality in climate and productivity should

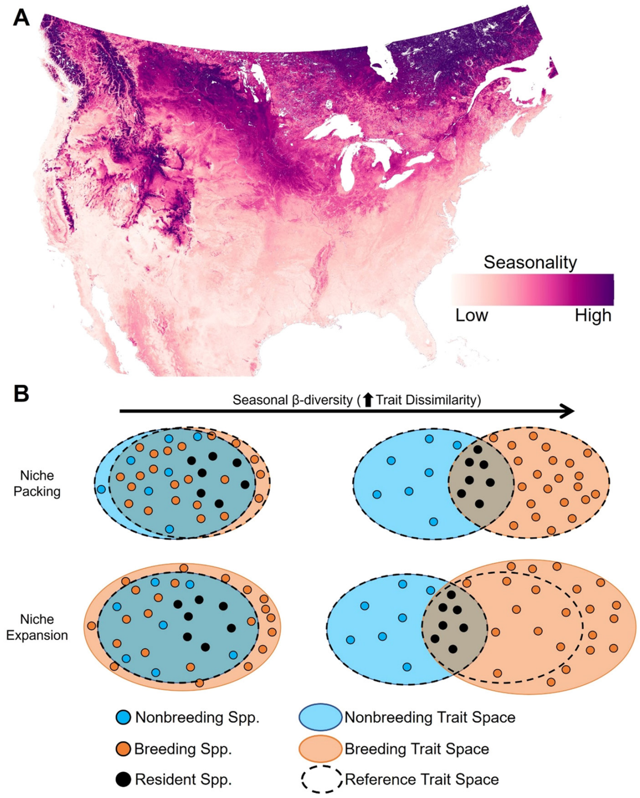


**FIGURE 1** | Conceptual model of how seasonality relates to seasonal β-diversity and niche packing versus expansion. (A) Seasonality has strong latitudinal and elevational gradients and varies substantially across North America. Map shows the annual coefficient of variation of NDVI (DHIvar) across the study extent from 2005 to 2020 with dark purple regions exhibiting stronger seasonality. (B) Seasonal β-diversity is expected to increase as seasonality increases (left to right). Concurrent changes in seasonal richness may be facilitated via niche packing (top row) or via niche expansion (bottom row). For example, seasonal environments may promote increasing seasonal β-diversity (right column), concurrent with the increase in summer species richness. Species richness may be packed into the volume of the winter assemblage (points inside black dashed circle; top right) or increased richness may increase the breeding volume relative to nonbreeding (points outside black dashed circle; bottom right). Conversely, assemblages in regions of low seasonality are expected to experience low seasonal β-diversity (left column). However, despite relatively low change in functional diversity, changes in richness may still be facilitated via packing (top left) and expansion (top right) differentially.

induce both high *temporal species diversity* and *seasonal species turnover* (Tonkin et al. 2017) in communities (Figure 1B). This is because strong seasonal environmental variation should select seasonal specialists and promote coexistence through temporal niche availability (Chesson 2000; Tonkin et al. 2017), especially when these fluctuations are predictable (Riotte-Lambert and Matthiopoulos 2020; Tonkin et al. 2017). Predictable ecosystems should return to a given state consistently (i.e., contingency), remain unchanged (i.e., constancy) or both (Colwell 1974). Thus, seasonally predictable systems exhibit consistent interannual variation in environmental conditions (e.g., deciduous green-up) whereas unpredictable systems do not (e.g., desert green-up). At the same time, regions that support higher and more stable productivity should also harbour diverse species assemblages (Mellard, Audoye, and Loreau 2019), but be less likely to experience turnover. Together, this suggests that patterns of seasonal diversity across space should be driven by different aspects of seasonality, such as its magnitude and predictability.

A second issue is that most studies on seasonal-diversity responses have focused solely on species richness and turnover (e.g., Martin 2018; Mellard, Audoye, and Loreau 2019). However, these alone provide an incomplete characterisation of community structure as it ignores the ecological functions and roles that species occupy within an ecosystem (Cadotte, Carscadden, and Mirotchnick 2011; Petchey and Gaston 2002). The occupation and size of ecological niche space can be studied by quantifying functional diversity—the variation and composition of species' traits that determine their response to, or effects on, the environment (Cadotte, Carscadden, and Mirotchnick 2011). There is a strong emphasis on studying spatial functional diversity patterns (Violle et al. 2014) but accompanying temporal dynamics are often overlooked, especially at seasonal scales. Recent work demonstrates that seasonal patterns of bird functional and taxonomic diversity are decoupled across the United States, with pronounced longitudinal gradients in seasonal functional diversity (Jarzyna and Stagge 2022). This suggests that the patterns and processes that explain seasonal changes in taxonomic richness may be different from those underlying functional diversity.

Seasonal changes in species richness could theoretically result from two related processes: niche packing and niche expansion (Macarthur 1965; Figure 1B). Niche packing occurs when the additional species entering the assemblage are functionally similar to the species present in the assemblage before, resulting in a denser packing of trait space. Conversely, niche expansion occurs when the additional species entering the assemblage are ecologically unique and are thus associated with an increase in the volume of functional trait space (Pigot, Trisos, and Tobias 2016). Thus, trait expansion may reflect a greater breadth of ecological opportunities and resource use whereas trait packing suggests that increased niche specialisation or overlap facilitates increases in species richness. Global analyses comparing assemblages across spatial environmental gradients suggest that while more speciose assemblages occupy larger volumes of niche space, increases in species richness are primarily associated with greater niche packing (Pellissier et al. 2018). However, it remains unclear how niche packing and expansion interact with seasonality to facilitate increases in species richness (Pellissier et al. 2018; Pigot, Trisos, and Tobias 2016). If there is variation in the prevalence of niche packing and expansion between seasons, then understanding the underlying environmental drivers may reveal how diversity is maintained in seasonal assemblages.

We examined the role of seasonality on functional diversity and niche packing using an example of large-scale assemblage change: avian migration. Avian migration is an ideal ecological phenomenon to examine the role of seasonality in functional trait dynamics because it is a ubiquitous phenomenon (ca. 20% of bird species migrate; Eyres, Böhning-Gaese, and Fritz 2017) that is strongly associated with variation in primary productivity and climate (Gudex-Cross et al. 2022; Somveille, Rodrigues, and Manica 2015). Furthermore, the comprehensive availability of bird trait data with well-established links to ecological functions (Pigot et al. 2020; Tobias et al. 2022), and the critical ecosystem services these support (Sekercioglu 2006), enables quantification of the functional trait space occupied by birds at continental scales and high resolution.

Using North American bird migration as our model system, we posed the following questions:

a. What are the geographical patterns of seasonal changes in functional diversity (seasonal β-diversity) across North America and what are the key trait dimensions along which changes in functional diversity occur?

b. To what extent do seasonal changes in primary productivity and climate predict observed patterns of seasonal changes in functional diversity?

c. What is the relative importance of niche packing and expansion in seasonal changes in species richness?

We hypothesised that if species functional traits respond to environmental characteristics, then environments that experience strong, but predictable, fluctuations should foster shifts in seasonal functional diversity (i.e., high functional β-diversity). Furthermore, we hypothesised that if seasonality increases the breadth of ecological opportunities (e.g., increasing resource diversity) then increases in species richness will be associated with greater niche expansion, especially where seasonality is greatest. Conversely, if species richness is limited more by seasonal resource availability (i.e., density) then we predicted niche packing to be the dominant process associated with seasonal increases in species richness.

## 2 | Methods

### 2.1 | Species Data and Distribution Models

We estimated seasonal bird assemblage composition using species distribution models (SDMs) from eBird Status and Trends (Fink et al. 2022) for the breeding and nonbreeding seasons. We removed pelagic specialists, species with ranges outside of our sampled locations, and species with estimated distributions known to have extensive areas of extrapolation and/or omission across its range, resulting in 524 species considered in the analysis. We then reconstructed potential local assemblage composition from stacked-SDMs for each species at 3-km resolution within the conterminous United States and southern Canada (25°–55° N and 59°–128° W). We randomly selected 5000 locations (pixels) to limit computational burden and extracted the seasonal mean occurrence probability for each species during breeding and nonbreeding seasons to create a site-by-species matrix for calculating functional diversity metrics. We repeated our analyses on the passerine-only assemblage to assess the generalities of our findings (see Supporting Information: Supplementary Methods).

### 2.2 | Functional Trait Data and Hypervolume Estimation

We analysed bird functional trait data from AVONET (Tobias et al. 2022), which provides measurements for key ecomorphological traits for all bird species included in our analysis. Prior to functional diversity estimation we log-transformed and reduced nine primary morphological traits into orthogonal axes using principal components analysis (PCA) for hypervolume estimation (Blonder 2018; Mammola et al. 2021). These nine morphological traits are body mass, beak depth, beak width, beak length from the culmen, beak length from the nares, wing length, length to the secondary flight feather, tail length and tarsus length. These traits capture bird trophic niche space including diet, foraging substrate and foraging manoeuvres (Pigot et al. 2020; Ricklefs 2012). We selected the first three PC axes that describe 93% of the variation in North American bird morphology for functional trait space estimation (Supporting Information, Table S1).

We estimated the volume ($SD^3$) of functional trait space, hereafter referred to as 'trait volume', around the 95% probabilistic kernel density estimate enclosing the hypervolume (Blonder 2018) using the R package 'hypervolume' (Blonder et al. 2018; Supporting Information, Table S2). We estimated a fixed bandwidth using traits from the entire species pool to construct hypervolumes estimated using the 'plug-in' estimator and included species' probability of occurrence at weights. We estimated trait volumes at each location for both breeding and nonbreeding seasons.

### 2.3 | Seasonal Functional Diversity and Niche Packing/Expansion

Based on the estimated trait volumes, we calculated various components of seasonal functional diversity. We estimated functional richness as the volume of the breeding and nonbreeding trait volumes (FRic), in units of $SD^n$ where $n$ is the number of trait dimensions. We visualised the density of species in trait space by calculating the mean pairwise distance (MPD; Weiher, Clarke, and Keddy 1998) among species within each seasonal assemblage using the 'mFD' package (Magneville et al. 2022). To control for species richness in our functional diversity metrics we calculated the standardised effect size (SES). We estimated SES by randomising the species in an assemblage 100 times based on a random sample of all species in the study extent for each given season while maintaining site-level species richness using the R packages 'vegan' (Oksanen et al. 2022). Our null model permits species occurrence anywhere within the spatial extent but accounts for the fact that species may depart the study extent in the breeding or nonbreeding season, effectively controlling for species richness at the site level for each respective season.

Seasonal functional β-diversity, hereafter 'seasonal β-diversity', captures the degree of seasonal differences in multidimensional trait volumes. We calculated seasonal β-diversity ($\beta_{Total}$) between seasonal trait volumes using the R package 'BAT' (see Supporting Information: Functional Diversity Metrics; Mammola and Cardoso 2020). Finally, we calculated SES seasonal β-diversity, which captures how functionally dissimilar assemblages are to the distribution of seasonal β-diversity estimated for 100 random assemblages at each site.

Seasonal β-diversity captures the overall dissimilarity of the trait volumes between seasons but does not indicate whether increases in species richness are associated with an expansion or packing of functional trait space. This is because functional β-diversity combines information on both the size and position of trait volumes and partitioning the contribution of expansion and packing requires methods that are insensitive to the position of trait volumes. For example, a more speciose seasonal assemblage could occupy a largely distinct region of trait space compared to the more species-poor season and thus exhibit high β-diversity, but the additional species may result from a denser packing of an equivalent trait volume (e.g., top row Figure 1B). While expansion necessitates increased β-diversity, the proportion of species contributing to expansion will not be captured by β-diversity alone.

We quantified how seasonal changes in species richness are facilitated by the packing and expansion of functional trait space following Pigot, Trisos, and Tobias (2016). We defined $A_1$ as the assemblage with greater species richness, and $A_2$ as the reference assemblage. Note that $A_1$ is usually (~88% of sites), but not always, the breeding assemblage (Figure 2A). Thus, we set $A_1$ to always represent the more speciose season for each site. Species unique at $A_1$ (i.e., absent in $A_2$) are sequentially removed (and then reinstated) to determine the species whose removal results in the largest volume decline. This species is then permanently removed, and the process continues until the volume of $A_1$ is less than or equal to the volume of $A_2$. The number (Ne) of unique species removed from $A_1$ divided by the number (Nu) of unique species in $A_1$ represents the proportion of species in the more speciose assemblage that is associated with expansion (Figure S1). The complement to this is the proportion of species in the more speciose assemblage that is associated with packing. We note that the algorithm we use for sequentially removing species

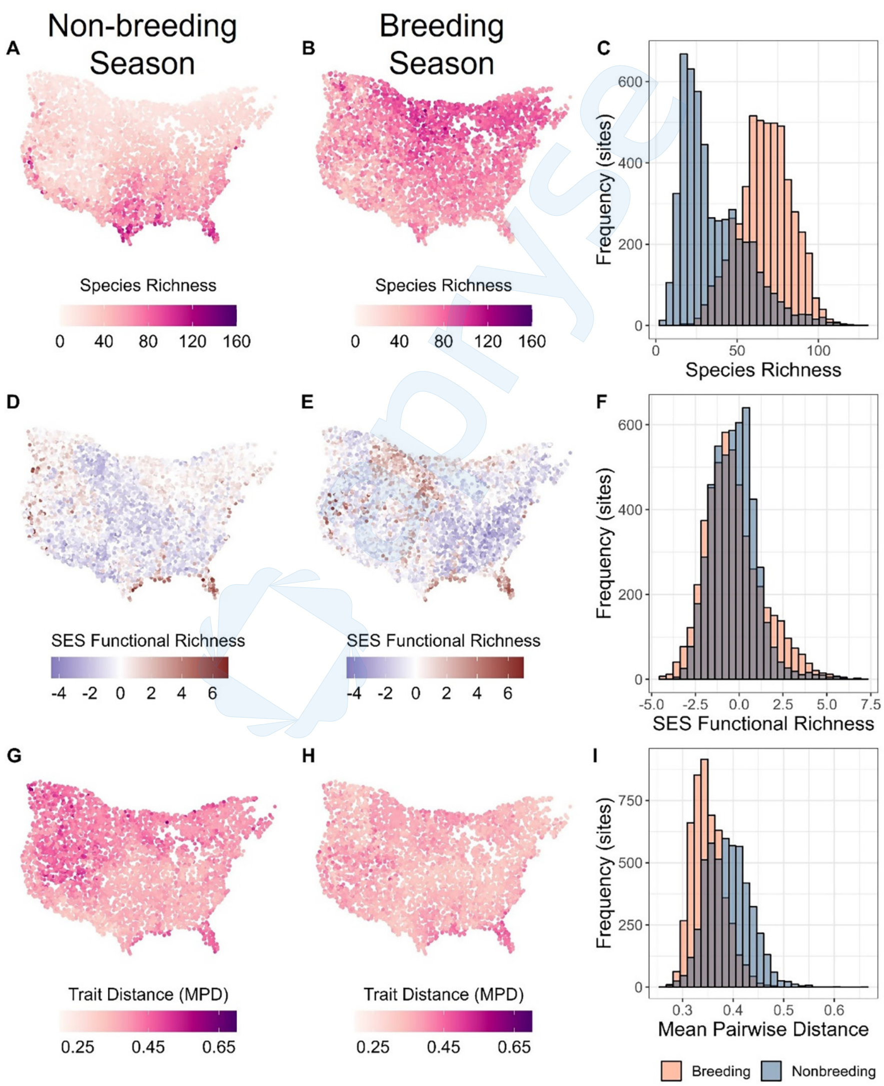


**FIGURE 2** | Spatial patterns of components of seasonal functional diversity. (A, B) Patterns in taxonomic bird richness in the breeding and nonbreeding seasons for our 5000 study locations. Generally, species richness is greater in the breeding season (C). (D, E) Mapped patterns of SES functional richness for the nonbreeding (D) and breeding (E) seasons. Blue colour denotes sites with less trait diversity than random and red colour denotes sites with greater trait diversity than random. (F) Histograms show relatively low differences in the overall distribution of SES functional richness. Mean pairwise distance across the 5000 assemblages for the nonbreeding (G) and breeding (H) seasons. Colour gradient corresponds to shifts from assemblages that are more densely clustered in functional trait space (lighter) to assemblages comprised of species with greater distance to one another (darker). (I) Histograms suggest species are less densely clustering in trait space during the nonbreeding season.

is simply to determine the number of species associated with the expansion and packing of niche space rather than implying any ecological process. Note, if the reference assemblage $A_2$ occupies a larger volume than $A_1$ the assemblage, Ne = 0, and the increase in richness in $A_1$ would be facilitated entirely through packing.

### 2.4 | Environmental Predictors of Seasonal Functional Diversity

To test the relative influence of environmental drivers on seasonal β-diversity and niche packing we selected seasonally relevant environmental predictors. We captured dynamic productivity using remotely sensed data on annual productivity seasonality ($Sea_P$) and accumulated productivity ($Tot_P$) from the Dynamic Habitat Indices (DHIs; Hobi et al. 2017). We used the average NDVI-based, DHI products calculated from 2000 to 2020 (Hobi et al. 2017). To capture climate seasonality, we calculated the average annual temperature range (TR) using daily mean temperature from Daymet (Thornton et al. 2022) for the breeding season (June—August) and nonbreeding season (December—February). We chose these periods because they overlapped with >97% of species breeding and nonbreeding seasons while corresponding to defined meteorological seasons. To capture environmental predictability we used Colwell's predictability metrics (Colwell 1974). The original metrics capture two components of predictability: constancy and contingency. For our analysis, we defined predictability as the sum of contingency and constancy. Thus, in our analysis sites are relatively predictable when they exhibit consistent yearly recurrence of the seasonal state, constant seasonal state, or a mixture of both. For productivity predictability (PrP) we calculated monthly mean productivity from MODIS Terra NDVI 16-day global 500-m product (Didan 2015). For temperature predictability (PrT) we averaged the monthly summaries calculated from Daymet. We then calculated predictability using the monthly averages of mean temperature and NDVI from 2005 to 2020 using the R package 'hydrostats' (Bond 2022; Figure S2). MODIS and Daymet data were summarised and extracted from a 3-km buffer around the point to match eBird SDMs using Google Earth Engine (Gorelick et al. 2017). DHI values were extracted in R using the 'terra' (Hijmans 2023) and 'exactextractr' (Baston 2022) packages.

### 2.5 | Statistical Modelling

We modelled seasonal β-diversity as a function of both seasonality of temperature and productivity, predictability of temperature and productivity and total productivity. We built three models: (1) a null, spatial-only model, (2) a model that included our predictors as additive terms only and (3) a model that allowed interactions between seasonality and predictability of both temperature and productivity. We retained total productivity as an additive term in that model. For niche packing models we used predictors for total available energy, seasonal productivity and temperature range. We excluded measures of predictability in niche packing models because we focused on model inference and lacked a priori hypotheses on the effects of predictability on niche packing (Tredennick et al. 2021).

To account for spatial dependence, we fitted geospatial models under a Bayesian framework using integrated nested Laplace approximation (INLA) with the R package 'INLA' (Martins et al. 2013; Rue, Martino, and Chopin 2009) and stochastic partial differential equations (SPDE) using a triangulated mesh across the study extent (Lindgren, Rue, and Lindström 2011; Figure S3). For details see Supporting Information: Spatial Modelling.

We modelled seasonal β-diversity and niche packing using spatial beta regression. Niche packing metrics had values at the extremes (i.e., [0, 1]) and did not match a beta distribution. Therefore, we transformed values within the bounds of the beta distribution (Smithson and Verkuilen 2006; Zuur and Ieno 2018). We modelled SES seasonal β-diversity with a Gaussian response. We used the default priors set by R-INLA. We centred and scaled all predictors to facilitate the interpretation of the relative importance of different environmental predictors and to aid model convergence. We assessed collinearity between predictors with variance inflation factor and found no issues (VIF < 3). We determined important predictors in our models using 95% Bayesian credible intervals (CI) where predictors with CI overlapping zero were deemed unimportant. We visualised parameter posterior distributions, and residual spatial autocorrelation with semi-variograms, plotted the spatial field and checked model diagnostics. We found no apparent issues (Figures S4 and S5). Finally, we validated our models using an 80/20 split of our sites for training and testing to examine the model's predictive performance. All analyses were performed using R version 4.2.2 (R Core Team 2022).

### 2.6 | Trait-Specific Contributions of Seasonal Diversity

To visualise how changes in individual trait axes correspond with functional turnover we mapped changes in the individual trait axes. We calculated the difference in the assemblage weighted mean trait axis using the species PC scores and compared the direction of change between the nonbreeding and breeding seasons. We then plotted mean trait change with seasonal β-diversity as bivariate maps to examine broad geographical patterns in changes in individual traits.

## 3 | Results

### 3.1 | Seasonal Functional Diversity Patterns

Bird taxonomic and functional diversity differed between seasons, but the magnitude of difference varied across North America (Figure 2). During the nonbreeding season, both taxonomic and functional richness were highest in the southeastern United States, the Gulf Coast region and the Central Valley of California (Figure 2A). After controlling for species richness, regions with higher functional richness included the northern temperate and boreal forests, intermountain west, central Pacific and parts of the southeastern U.S. (Figure 2D). During the breeding season, areas of high species and functional richness shifted to northern latitudes and montane regions, but many coastal regions remained functionally diverse.

Summer SES and raw functional richness patterns were similar (Figure 2B). Nonbreeding assemblages consisted of birds that were more functionally different from one another in high latitudes, topographically complex regions and coastal regions in the Southeast (Figure 2G,I). During the breeding season, species were often more functionally clustered in trait space and spatial variation of trait density was more homogeneous (Figure 2H).

Seasonal β-diversity ranged from relatively low to nearly complete change (range $\beta = 0.2–0.9$; $\text{mean}_\beta = 0.5$, $SD_\beta = 0.12$; Figure 3B). The highest overall seasonal β-diversities occurred at mid-to-high latitudes and in mountainous regions (Figure 3A). Further, the dominance of seasonal niche packing also varied spatially (Figure 3A). Niche packing was the dominant process facilitating seasonal increases in species richness ($\text{mean}_{Pack} = 0.84$, $SD_{Pack} = 0.15$; Figure 3C), and was observed in all bird assemblages. However, niche expansion contributes to increases in species richness across 80% of assemblages, suggesting both processes were important. Generally, assemblages where niche expansion had a larger contribution were those with greater seasonal β-diversity (e.g., yellow regions in Figure 3A), whereas assemblages with lower seasonal β-diversity experienced stronger packing (e.g., blue regions in Figure 3A). Patterns of passerine seasonal β-diversity and niche packing were generally similar, but we found higher niche packing in the boreal regions of eastern Canada. See the supplementary information for patterns of passerine-only seasonal diversity (Table S3; Figures S6 and S7).

### 3.2 | Seasonal Environment-Functional Diversity Relationships

Environmental seasonality, predictability and total productivity were all important predictors of seasonal β-diversity (Figure 4A). The interactive model outperformed both the null and the additive model (Figure S8), suggesting an important interaction between the magnitude and predictability of seasonal primary productivity in addition to temperature range and total productivity (Figure 4A). Seasonal β-diversity was higher in regions with strong temperature seasonality ($\beta_{TR} = 0.14$, 95% CI: [0.09–0.19]; Figure 3B). Furthermore, seasonal β-diversity was higher in regions with high productivity seasonality, but this relationship was contingent on the predictability of productivity ($\beta_{SeaP:PrP} = 0.033$, 95% CI: [0.022–0.045]; Figure 3C). That is, seasonal β-diversity was maximised in regions with strong, yet predictable seasonal productivity dynamics (Figure 4C). Seasonal β-diversity was lowest in regions with high annual productivity ($\beta_{TotP} = -0.16$, 95% CI: [−0.18 to −0.14]; Figure 4D). Overall, seasonal β-diversity was highest in regions with strong, predictable seasonality, such as north temperate grasslands, boreal forests and mountainous ecosystems (Figure 3A). Our spatial model for seasonal β-diversity suggested spatial dependence on an average of ca. 4500 km ($\text{Range}_\mu = 1.53$, 95% CI: [1.33–1.75]). We did not detect an important influence of either temperature predictability ($\beta_{PrT} = 0.012$, 95% CI: [−0.007–0.031]; Figure 4A) or the interaction between temperature range and predictability ($\beta_{TR:PrT} = 0.012$, 95% CI: [−0.001–0.024]; Figure 4A). Model validation suggested predictive performance was strong (Figure S9). SES seasonal β-diversity models exhibited consistent qualitative results (Table S4; Figure S10). However, we found an important, positive influence of temperature predictability ($\beta_{PrT} = 0.096$, 95% CI: [0.007–0.18]; Table S4) in SES seasonal β-diversity models. The best-performing SES seasonal β-diversity model demonstrated moderate predictive performance (Figure S11). Finally, results for the passerine-only analysis were largely consistent but we found deviations in the importance of temperature seasonality and predictability (Tables S8 and S9).

The degree of seasonal niche packing versus expansion depended on both productivity and climate. Niche expansion was more common in regions characterised by strong seasonality in temperature ($\beta_{TR} = -0.71$, 95% CI: [−0.85 to −0.58]; Figure 5) and productivity ($\beta_{SeaP} = -0.065$, 95% CI: [−0.11 to −0.016]; Figure 5). However, the effect of seasonal productivity was reversed in our

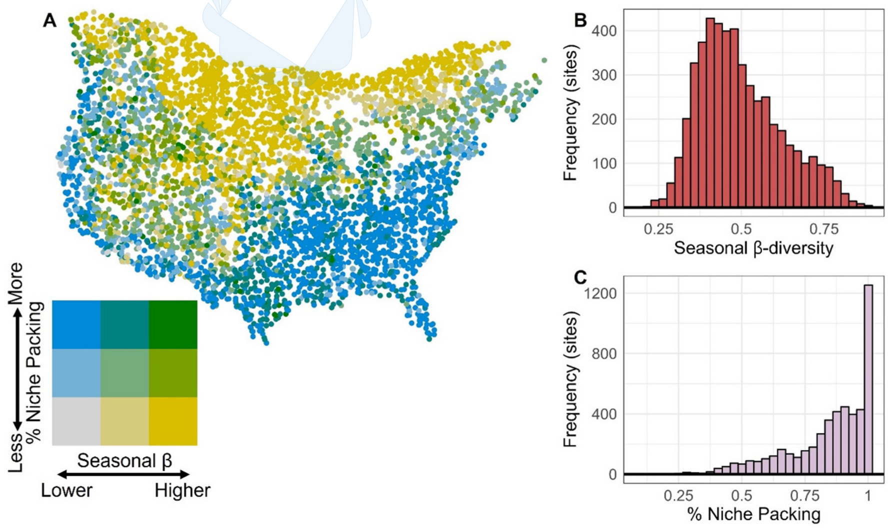


**FIGURE 3** | Spatial patterns of seasonal β-diversity and niche packing. (A) Map represents bivariate relationship between % packing and seasonal β-diversity. Moving from left to right on the *x*-axis of the legend denotes higher seasonal β-diversity, whereas bottom to top on the *y*-axis denotes a higher proportion of niche packing. (B–C) Histograms of seasonal β-diversity and % niche packing respectively. Note the colours correspond to quantiles of the empirical distributions of values in panels B and C.

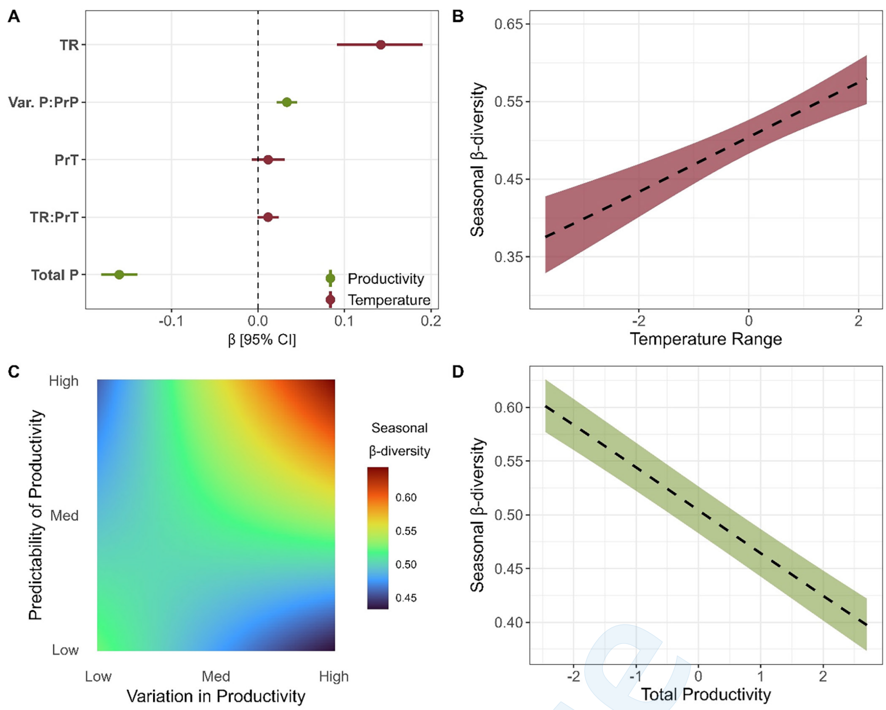


**FIGURE 4** | Productivity and climate explain patterns of seasonal β-diversity. (A) Effects plot for important predictors showing median beta estimate and the 95% Bayesian credible interval (BCI) estimates. Predictors tested in the model included the average temperature range between the breeding and nonbreeding season (TR), coefficient of variation in NDVI (Var. P), Colwell's predictability for interannual NDVI (PrP), Colwell's predictability for interannual temperature (PrT) and annual total productivity (Total P). (B) Marginal effects of the influence of temperature range on seasonal β-diversity with 95% BCI. (C) Marginal interaction plot between productivity seasonality and predictability. Colour ramp shows lower (cooler colours) to higher (warmer colours) seasonal β-diversity. (D) Marginal effect between seasonal β-diversity and total productivity with 95% BCI. We do not show fixed effects for terms that were significant as interactions (see Supporting Information for full model output).

passerine-only analysis (Figure S12). Conversely, niche packing was more prevalent in regions with greater overall productivity ($\beta_{TotP}$ = 0.11, 95% CI: [0.048–0.16]; Figure 4). The niche packing models had spatial dependence at similar scales to seasonal β-diversity and exhibited strong model predictive performance (Figure S13).

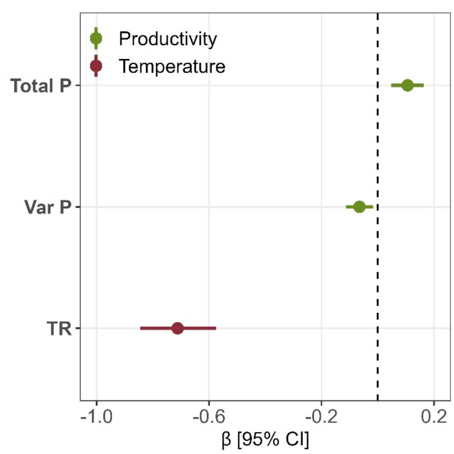


**FIGURE 5** | Productivity and climate explain patterns in niche packing. Effects plot for beta estimates in spatial models of niche packing. Labels on the *y*-axis correspond to annual total productivity (Total P), coefficient of variation in NDVI (Var. P) and temperature range between the breeding and nonbreeding season (TR). Dots represent mean parameter estimates and the bars are the 95% Bayesian credible intervals. Bars overlapping zero (dashed line) were deemed unimportant in the niche packing model.

## 3.3 | The Geography of Seasonal Changes in Trait Axes

Seasonal changes in principal component (PC) axes captured divergent patterns in the change of trait composition. PC1 captured overall body size and the seasonal change in this axis demonstrated a latitudinal gradient (Figure 6A). Bird assemblages exhibited seasonal reductions in mean body size from winter to summer across most of North America (Figure 6A), but these were most common in mid-to-high latitudes and montane regions. These findings were consistent for the passerine-only assemblage (Figure S14A). PC2 captured bill to tail length ratio, representing a transition from species with short bills and long-tails (e.g., chickadees) in winter to long-billed, short-tailed species (e.g., hummingbirds) in summer. Like body size, the seasonal shift in these traits was associated with the greatest changes in seasonal β-diversity in the Western United States. (Figure 6B). Finally, PC3 captured differences in species with wide, deep beaks and those with narrow beaks. The spatial patterns in PC3 were more variable with increases in birds with narrow beaks in boreal forests and mountainous regions (e.g., warblers), and the reverse transition in high latitude, open ecosystems, the southeastern United States and the west coast (e.g.,

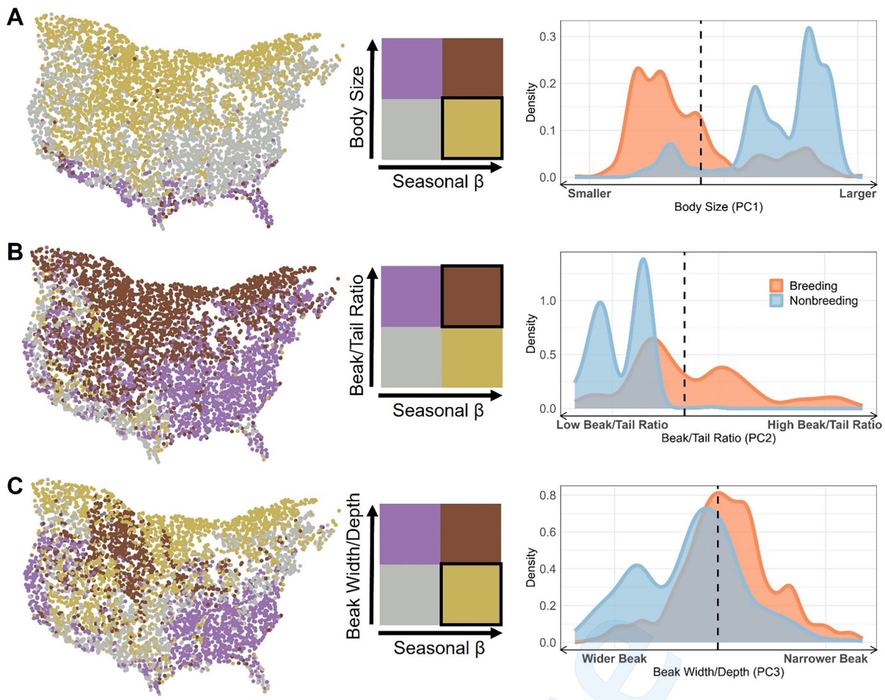


**FIGURE 6** | Seasonal shifts in individual trait axes. Bivariate maps between seasonal β-diversity and individual trait axes: (A) PC1, (B) PC2 and (C) PC3. Density plots provide examples from assemblages that fall into the dominant spatial patterns (outlines in black on the map legends) and the dashed line denotes mean occurrence weighted trait values (PC scores) for these assemblages. Positive changes of the PC axes that correspond with relatively high seasonal β-diversity are represented by the top right quadrant (i.e., brown) whereas negative changes but high seasonal β-diversity are in the lower right quadrant (i.e., gold).

sparrows; Figure 6C). See supplemental information for corresponding passerine-only results (Figure S14).

## 4 | Discussion

Avian migration fosters dramatic changes in both taxonomic and functional diversity over vast geographies. Across North America, we found that the seasonal reshuffling of birds prompted widespread changes in functional diversity with regional differences imposed by variations in the magnitude and predictability of productivity and temperature. The model underlying seasonal changes in species richness—niche packing and expansion—also varied regionally with the relative importance of each process depending on the geography of seasonality. Our findings confirm strong seasonal shifts in bird functional diversity (Jarzyna and Stagge 2022) and provide new insights into the role of environmental variation on community dynamics across space and time.

Greater seasonality generally induced greater seasonal functional β-diversity. This is expected if seasonality impacts niche availability and selects for distinct functional assemblages between seasons (Chesson et al. 2004; Tonkin et al. 2017). Seasonality encompasses shifts in environmental conditions including variation in primary productivity and temperature. Temperature shapes morphology in many species (Clavel and Morlon 2017), contributing to latitudinal and temporal gradients in morphology (Danner and Greenberg 2015; Youngflesh et al. 2022). From a seasonal perspective, shifting thermal limits may generate observed functional turnover (e.g., body size). For example, we found a transition from larger birds in winter to smaller birds in summer across most sites for the full and passerine-only bird assemblage, providing a seasonal reflection of well-known biogeographic patterns (e.g., Bergmann's Rule; Olson et al. 2009). Likewise, shifting resources may select for species with a subset of traits, such as species with winter-specialised foraging strategies (e.g., granivores) or generalist morphology (Jarzyna and Stagge 2022). Highly seasonal regions experience a burst of primary productivity in summer, creating niche space that permits a more diverse assemblage of species with diverse trait combinations (e.g., aerial insectivores, aquatic herbivores; Hughes et al. 2022; Pigot et al. 2020) and allow migrants to fill vacant niche space (Hurlbert and Haskell 2003). However, bird traits often evolve in response to diverse selective pressures (Tobias, Ottenburghs, and Pigot 2020). For example, the bill is multifunctional as an adaptive feature to variations in climate, resources and communication (Bosse et al. 2017; Friedman et al. 2019; Miller, Latimer, and Zuckerberg 2018). Further studies should attempt to disentangle how seasonal temperature and productivity interact with additional factors to shape functional trait composition.

While seasonality sets the stage for changes in functional diversity, predictability mediates this response. Indeed, seasonal specialists may synchronise life histories to reliable seasonal variation (Mellard, Audoye, and Loreau 2019; Tonkin et al. 2017). Our results support this hypothesis by demonstrating that sites with greater predictability in seasonal productivity had higher seasonal β-diversity, but this relationship weakened and even reversed when the environment was unpredictable. This result was robust to differences in species richness for both the full bird and passerine-only assemblages. Migratory birds represent substantial trait variation and are dominant components of northerly assemblages (Fristoe 2015), likely explaining latitudinal clines of higher seasonal β-diversity. Thus, predictable fluctuations in resources are likely a precursor for the evolution of migration (Riotte-Lambert and Matthiopoulos 2020; Winger et al. 2019) and promote the incoming of seasonal specialists with unique traits (Tonkin et al. 2017; Williams et al. 2017). Though functional and phylogenetic diversity need not be related (Jarzyna, Quintero, and Jetz 2021; Swenson et al. 2012), evolutionary conservatism in both traits and migratory tendencies suggests phylogenetic and functional turnover are coupled (Ricklefs 2012; Winger, Lovette, and Winkler 2011).

Productive regions host more functionally similar assemblages between seasons. These regions support greater year-round functional diversity facilitated by the constant availability of resources that may reduce competition (Pigot et al. 2018) and promote a wider range of trait combinations (Barnagaud et al. 2019; Gorczynski et al. 2021). For example, southeastern coastal regions support functionally diverse assemblages year-round and the departure of migratory species has a relatively low impact on trait dissimilarity (Jarzyna and Stagge 2022). This is further supported by the dominance of niche packing in these regions, suggesting that changes in taxonomic diversity accumulated via an increase in niche specialisation or overlap rather than the loss or gain of unique traits.

Overall, niche packing was the dominant route facilitating increases in species richness associated with the influx of migrants. This indicates that migratory species are largely 'filling in' regions of trait space already occupied in the more species-poor season (Yaxley, Skeels, and Foley 2023). This is consistent with the strong central tendency (Ricklefs 2012) and convergence of avian morphology globally (Cooney et al. 2017; Pigot et al. 2020). For example, on average only 42% of species in an assemblage are required to capture 80% of the functional diversity across the year confirming the strong functional trait similarity among most North American birds (Figure S15). These factors, coupled with environmental filters, likely explain why most assemblages exhibited lower seasonal β-diversity than expected.

Despite the overall dominance of seasonal niche packing, assemblages also exhibit niche expansion (in some cases > 50%; Figure 3C). Niche expansion increases with seasonality, suggesting differences in seasonal richness are partially associated with the emergence of novel trait combinations and thus ecological niches. For the full assemblage, seasonal productivity may coincide with alternative resources (e.g., open water) providing opportunities for functionally unique migrants (e.g., waterbirds). However, this effect was contingent on the taxonomic group analysed. While the effect of temperature seasonality was consistent between the full and passerine-only analysis, we found that greater seasonality in productivity prompted greater packing in passerines (Figure S12). Thus, for passerines, fluctuations in productivity may facilitate migrants via greater resource *availability* rather than *breadth*.

Generally, more productive ecosystems promote greater niche packing. The constant availability of resources may fix trait volumes between seasons and accommodate migrants via reduced competition, increased niche overlap, or finer niche partitioning (Pellissier et al. 2018; Pigot, Trisos, and Tobias 2016). The increased importance of niche expansion in the most seasonal regions is consistent with patterns observed in previous studies analysing spatial gradients in productivity, and where niche expansion contributes most when comparing assemblages in the least to the most productive sites. Taken together, our results support niche packing as the dominant pattern facilitating increases in richness between assemblages (Pellissier et al. 2018; Pigot, Trisos, and Tobias 2016) but extend this generality across time (i.e., seasons) as well as space.

Seasonality is a critical determinant of biodiversity patterns (Janzen 1967), and our study reveals how this component of environmental variability drives changes in the bird functional diversity at a continental scale. Incorporating the dynamics of functional diversity within seasonal assemblages comprised of migratory, but functionally important species (Bauer and Hoye 2014; Dybala, Truan, and Engilis 2015), will be critical for reliable biodiversity projections under ongoing and future environmental change. We show that both the magnitude and predictability of seasonality induce changes in bird functional diversity across the annual cycle. The dominance of niche packing suggests that niche partitioning or overlap underlies the increase in species richness of birds during the northern summer and hints at the resilience of these assemblages to species losses. Yet, the greater importance of niche expansion in more northerly and montane regions suggests that an expansion in the breadth of ecological opportunity is also critical in highly seasonal environments and that the functional integrity of these regions will be more vulnerable to the extirpation of functionally unique species (Ali et al. 2023; Tobias, Ottenburghs, and Pigot 2020). The importance of both seasonality and predictability in determining seasonal changes in functional diversity has broad implications for understanding community responses to climate change. A key component of climate change is increasing climate variability and reduced predictability (John and Post 2022; Tan, Gan, and Horton 2018), which will affect the environmental cues that species use for seasonal movements. Ultimately, this may lead to reductions in functional turnover, potentially compromising ecosystem functionality and resilience.

## Author Contributions

Spencer R. Keyser, Jonathan N. Pauli and Benjamin Zuckerberg conceived and designed the study. Spencer R. Keyser performed all analyses. Daniel Fink assisted with curating bird occurrence data. Alex L. Pigot provided code and assistance on niche packing and expansion. Volker C. Radeloff provided remotely sensed productivity metrics. Spencer R. Keyser produced figures with assistance from Jonathan N. Pauli, Alex L. Pigot and Benjamin Zuckerberg. Spencer R. Keyser led the writing of the manuscript. All authors contributed important insights on drafts and gave final approval for publication.

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## Data Availability Statement

All data used in this analysis are publicly accessible. Avian seasonal distribution models were accessed from the Cornell Lab of Ornithology Status and Trends Project (https://science.ebird.org/en/status-and-trends). Avian morphological data were sourced from the publicly available AVONET database (https://figshare.com/s/b990722d72a26b5bfead). Remotely sensed information on the dynamic habitat indices is provided by the SILVIS Lab at the University of Wisconsin-Madison (https://silvis.forest.wisc.edu/data/dhis/). Temperature data were provided by Daymet and accessed freely using Google Earth Engine (https://developers.google.com/earth-engine/datasets/catalog/NASA_ORNL_DAYMET_V4). Code and data supporting the results are available for peer-review on Dryad: https://datadryad.org/stash/share/Et7uSpo71BPaaj0ZQlw5Eb0H_3bt8wV2Kvk_S-5mcqA. Code and data will be published publicly upon acceptance on Dryad: https://doi.org/10.5061/dryad.2547d7wzq.

## Peer Review

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## Supporting Information

Additional supporting information can be found online in the Supporting Information section.