

RESEARCH ARTICLE

Heterogeneity, Productivity, and Migration Drive Continental Evenness Patterns of Bird Assemblages

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ABSTRACT

Aim: Evenness quantifies similarities in abundances among species in an assemblage and may influence processes such as species coexistence and the supply of ecosystem services. Previous work has failed to identify generalised patterns of how productivity and habitat heterogeneity influence evenness and moreover has not considered seasonal variation in evenness arising from migration. Therefore, our goal was to quantify the interplay of productivity, habitat heterogeneity, and migration on evenness patterns of bird assemblages.

Location: Contiguous United States.

Time Period: Contemporary.

Group: Birds (613 species).

Methods: Using relative abundance maps from eBird, we computed evenness of bird assemblages for 27 × 27 km grid cells at weekly temporal resolution. We used generalized linear mixed-effects models to evaluate the influences of productivity (normalized difference vegetation index), habitat heterogeneity (Shannon diversity of land cover), and the dominance of migratory species on evenness.

Results: Productivity and heterogeneity interacted to influence evenness such that there was a positive productivity–evenness relationship in high-heterogeneity landscapes but no relationship in low-heterogeneity landscapes. Evenness was highest during the pre-breeding and breeding seasons when migratory taxa were present, but a high dominance of migrants reduced evenness and generally dampened evenness–productivity relationships.

Main Conclusions: Evenness increased with productivity in high-heterogeneity—but not low-heterogeneity—landscapes, indicating that hypotheses relating to energy availability and niche partitioning should be considered jointly. Higher evenness during the growing season likely reflects the presence of low-abundance migrant taxa, whereas the negative effects of migrant dominance on evenness are likely driven by one or few high-abundance species. The dampening effect of migrant dominance on evenness–productivity relationships in many situations supports the notion that migrants concentrate in high-productivity landscapes.

1 | Introduction

Abundances of species within assemblages are variable. Typically, a few species are common and many are uncommon or rare (McGill et al. 2007). Ecologists summarise this variability using evenness—a measure of the similarity of abundances. Assemblages with low evenness have less equal abundances, meaning many species are rare while a small number are dominant, whereas assemblages with high evenness have more equal abundances among species. Evenness can influence ecosystem function and the supply of ecosystem services, and thus understanding its patterns can lead to improved management and conservation of natural systems (Hooper et al. 2005; Barbaro et al. 2017; Graves et al. 2017; Hordijk et al. 2023). Moreover, evenness may modulate ecological processes such as species coexistence, and thus quantifying spatiotemporal variation in evenness may transform our understanding of the structure and function of ecological communities (Hillebrand et al. 2008; Rohr et al. 2016; Brooks et al. 2023). Despite the potential role of evenness in basic and applied ecology, relatively few studies quantify environmental influences on evenness, and those that do often find conflicting results (Hurlbert 2004; Pautasso et al. 2011; Sandal et al. 2024). Here, we evaluate influences of productivity,

habitat heterogeneity, and migration on the evenness of avian assemblages at a continental scale.

Primary productivity sets limits on energy availability and is linked to population, community, and ecosystem processes (Wright 1983; Currie 1991; Brown et al. 2004; Evans et al. 2005; Storch et al. 2018). The classic and well-substantiated “more individuals hypothesis” suggests that increasing productivity supports more individuals and thus higher species richness (Hurlbert 2004; Chiari et al. 2010; Seoane et al. 2017). However, the “more individuals” logic may also apply to evenness patterns. One idea, which we call the “rising-abundances-lift-all-species hypothesis”, suggests that increasing productivity adds individuals randomly among species, making it less likely that any one species will dominate and creating positive productivity–evenness relationships (Figure 1a,b). A competing idea, which we call the “rich-get-richer hypothesis”, suggests that increasing productivity apportions individuals to already-dominant species, accentuating abundance inequities among species and creating negative productivity–evenness relationships (Figure 1c,d). Empirical support for these ideas is mixed: previous studies of productivity–evenness relationships have found positive (Hurlbert 2004),

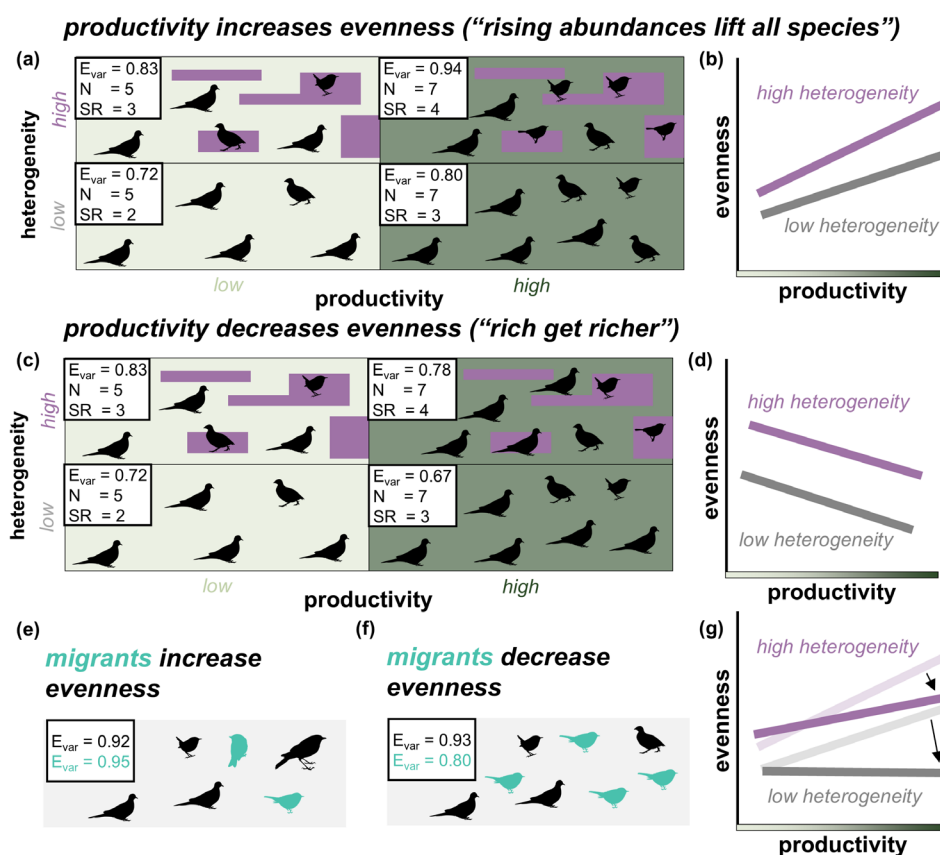


FIGURE 1 | (a, b) One hypothesis is that increasing productivity supports more individuals which are randomly apportioned among species (“rising abundances lift all species”), leading to increasing evenness; heterogeneity is also expected to expand niche space for partitioning and increase evenness. Numbers in top-left corners of the landscapes are the evenness values (E_{var}), total number of individuals (N), and species richness (SR) for the bird assemblage. (c, d) A competing hypothesis is that the additional individuals are added to already-abundant species (“rich get richer”), leading to lower evenness in high-productivity scenarios; heterogeneity is still expected to support higher evenness. (e) The presence of migrants (aquamarine) could increase the evenness of an assemblage by increasing the number of rare species. (f) Alternatively, migrants could decrease the evenness of an assemblage if some migrant species occur in large numbers. (e) We hypothesized that migrant species occur in disproportionately large numbers in productive landscapes, leading to (g) a dampening of relationships between evenness and productivity.

hump-shaped (Bae et al. 2018), negative (Pautasso et al. 2011), and unclear (Pautasso and Gaston 2005; Sandal et al. 2024) relationships. This uncertainty may arise because productivity alone is insufficient to explain evenness patterns.

Habitat heterogeneity may also contribute to broad-scale evenness patterns. Habitat heterogeneity promotes niche partitioning and co-existence of species (MacArthur 1958; Huffaker 1958), and heterogeneity could increase evenness by limiting the monopolisation of dominant species (Estrada-Carmona et al. 2022). In birds, this positive relationship between evenness and habitat heterogeneity has been supported by empirical studies (Cotgreave and Harvey 1994; Hurlbert 2004; Symonds and Johnson 2008; Bae et al. 2018). Like productivity, however, habitat heterogeneity alone may be insufficient to explain evenness patterns.

We hypothesized that productivity and habitat heterogeneity co-influence evenness patterns, a perspective that encourages an explicit seasonal perspective due to intra-annual fluctuations in productivity. Imagine a diverse landscape in a region with harsh winters; in the winter, energy availability is limited (low productivity), and few individuals occur in the landscape. This may result in high evenness (if the few individuals are apportioned among equally rare species) or low evenness (if the low productivity is such a strong environmental filter that only one or a few species occur and reach high abundances), despite the high heterogeneity. Because many species track resources through the seasons, explicitly evaluating seasonal shifts in abundance patterns among species represents a crucial nuance in understanding associations between evenness, productivity, and heterogeneity (Alatalo and Alatalo 1980; Craig and Klaver 2013).

Birds offer a good system for studying seasonal evenness dynamics given the dramatic migrations that many species undertake. Migrants could conceivably decrease or increase

assemblage evenness (Figure 1e,f). Uniformly small numbers of migrants might increase the evenness of an assemblage by increasing the number of rare species with similarly low numbers of individuals (Figure 1e), whereas large concentrations of one or a few migrant species may reduce assemblage evenness (Figure 1f). Furthermore, because migration is an adaptation to track resources in space and time (Salewski and Bruderer 2007; Fristoe 2015; Cohen et al. 2021; Guo et al. 2023), we hypothesized that large numbers of migrants are disproportionately likely to occur in high-productivity landscapes, which might lead to a dampening of relationships between evenness and productivity (Figure 1g). We did not have a priori expectations of whether these effects would be stronger in low- or high-heterogeneity landscapes. A high-heterogeneity landscape might host large numbers of both forest-associated and grassland-associated migrants, increasing the chances that one or a few species will occur in high abundances, thereby reducing evenness and dampening evenness–productivity relationships. Conversely, if birds demonstrate flexibility in habitat use during migration (Zuckerberg et al. 2016) or if many species share habitat preferences while migrating (e.g., forest; Buler et al. 2007), low-heterogeneity landscapes could show similar or stronger dampening effects compared to high-heterogeneity ones.

Our objective was to quantify the interplay of productivity, habitat heterogeneity, and migration on evenness patterns of bird assemblages at a continental scale. Using eBird relative abundance maps (613 species, weekly temporal resolution, 27×27 km spatial resolution), we calculated assemblage evenness and the dominance of migratory species (Figure 2). We then analysed evenness in relation to productivity (normalised difference vegetation index), habitat heterogeneity (Shannon diversity of land cover classes), and migrant dominance. By jointly considering productivity, heterogeneity, and migration, our work provides a synthesis of several perspectives (species–energy theory, resource partitioning, migratory ecology) to resolve evenness

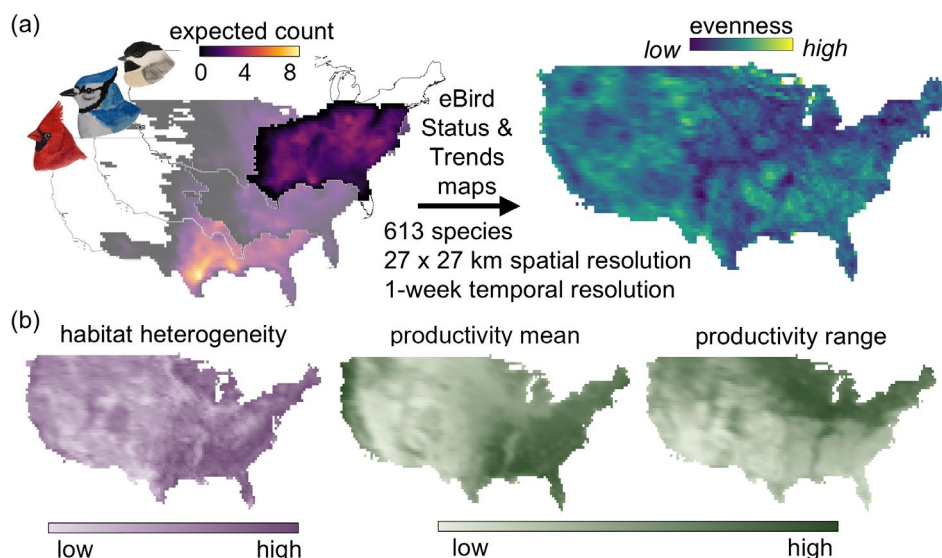


FIGURE 2 | Overview of data used in paper. (a) We used relative abundance maps of 613 species (stacked maps of three example species shown) generated by eBird to calculate evenness at weekly temporal resolution and 27×27 km spatial resolution. Maps for three example species—Northern Cardinal (*Cardinalis cardinalis*), Blue Jay (*Cyanocitta cristata*), Carolina Chickadee (*Poecile carolinensis*)—and evenness are from 4 January 2022. (b) We used Shannon diversity of land cover classes as a measure of habitat heterogeneity (static across the year) and normalised difference vegetation index (NDVI) as a measure of productivity (mean and range across the year are shown; 16-day temporal resolution).

patterns at a continental scale and provide a seasonal perspective in macroecology, which traditionally has relied on static or single-season data (Hurlbert 2004).

2 | Materials and Methods

2.1 | Evenness From eBird Abundance Maps

We downloaded eBird relative abundance rasters specific to the year 2022 for all species for which data were available for the contiguous United States using the *ebirdst* R package version 3.2023.0 (Fink et al. 2022; Strimas-Mackey et al. 2022). This material uses data from the eBird Status and Trends Project at the Cornell Lab of Ornithology, [eBird.org](https://ebird.org). Any opinions, findings, and conclusions or recommendations expressed in this material are those of the authors and do not necessarily reflect the views of the Cornell Lab of Ornithology. These data products have weekly temporal resolution and 27×27 km spatial resolution. The abundance maps are based on eBird, a global community science project in which observers submit checklists of birds they detect (Sullivan et al. 2009). The data are semi-structured, meaning that metadata such as effort (time of day, distance travelled) are captured but that sampling locations are not randomised (Sullivan et al. 2009). Prior to being modelled, these data are subjected to strict filtering rules to retain only checklists that report counts of all bird species detected, have complete effort information, are 6 h or less in duration, and cover less than 10 km; the data are then spatially subsampled to minimise bias from non-random sampling (Fink et al. 2010; Johnston et al. 2021). The machine-learning models used to predict relative abundance incorporate environmental variables (e.g., land cover, elevation) that influence bird abundance, as well as variables accounting for detection and observer behaviour (e.g., time-of-day, weather, observer skill; Fink et al. 2010). The resulting predictions of relative abundance can be interpreted as the expected count of a species by an experienced birdwatcher during a 1-h, 1-km checklist during the morning hours on a day with favourable weather conditions at a random location within a given 27 × 27 km pixel (Strimas-Mackey et al. 2022).

We calculated the evenness for each grid cell and week of 2022 based on the relative abundance estimates of all species occurring in a cell during a given week (Figure 2). We used the E_{var} metric (Camargo 1993; Smith and Wilson 1996), which describes variation in abundance across species based on proportional differences in abundances, and is calculated with the following formula:

$$E_{var} = 1 - \frac{2}{\pi} \arctan \left(\frac{\sum_{s=1}^S \left(\ln(x_s) - \sum_{s=1}^S \ln(x_s) / S \right)^2}{S} \right), \quad (1)$$

where S is the total number of species (s) in a community and x_s is the abundance of each species. The index varies from 0 to 1, with larger values representing more even communities and 1 representing a community with identical abundances of all species. We only calculated evenness for cell-week combinations that had relative abundance estimates > 0 for at least two species. This gave us 571,064 unique evenness measures (across 10,982 unique 27-km grid cells and 52 unique weeks).

2.2 | Calculating Dominance of Migratory Species

We calculated the migratory status of the species in our analysis using sedentary versus non-sedentary species classifications provided by the eBird Status and Trends data product (Strimas-Mackey et al. 2022). For each species, the eBird range maps consist of either one polygon (for sedentary species that are year-round residents) or four polygons that delineate a species' distribution during the nonbreeding, pre-breeding migration, breeding, and post-breeding migration seasons; these seasons have eBird-defined species-specific start and end dates (Strimas-Mackey et al. 2022). For each grid cell and week, we calculated the dominance of migratory species as the proportion of total assemblage abundance comprised of non-sedentary species. Thus, our migratory classification includes both passage migrants (those that are only temporarily passing through a location) as well as migratory species on their breeding or non-breeding grounds. In supplemental analyses (see Appendix S1), we also calculated the dominance of passage migrants alone (i.e., not including migratory species on their breeding or non-breeding grounds) and species richness, and we fit additional models replacing migrant dominance with either passage migrant dominance or species richness.

2.3 | Productivity and Habitat Heterogeneity Data

We used the normalised difference vegetation index (NDVI) as a measure of productivity and Shannon diversity of land cover as a measure of habitat heterogeneity (Figure 2). We acquired NDVI data from the Moderate Resolution Imaging Spectroradiometer (MODIS) 16-Day Global Vegetation Indices product, which provides a measure of vegetation greenness at 16-day intervals and 0.05° spatial resolution (Didan 2015). We aggregated the NDVI data to match the spatial resolution of the eBird evenness metric by calculating the mean NDVI value (median: 0.38; range: −0.11, 0.91) within the 27 × 27 km eBird grid cell and matched the date of the NDVI observation to the nearest date of the evenness data. For land cover, we downloaded the 2021 National Land Cover Database (NLCD) land cover product from the Multi-Resolution Land Characteristics Consortium (Dewitz 2023), which provides land cover classifications (16 unique classes) at 30 m spatial resolution. We calculated the Shannon diversity of NLCD classes within each 27 × 27 km eBird grid cell; larger values represent more heterogeneous landscapes (median: 1.25; range: 0.02, 2.46). Correlation between productivity and heterogeneity was moderate (Pearson's $r = 0.49$) but below commonly used thresholds to disqualify predictor variables from being included together in multiple regressions (Dormann et al. 2013). While land cover and heterogeneity are used to predict abundance in eBird Status & Trends models, we do not think it is redundant to use them in our analysis because our response variable is an emergent, assemblage-level parameter (evenness), not abundance of a single species.

2.4 | Analysis: Quantifying Interactive Effects of Productivity, Heterogeneity, and Migrants

We analysed these data using a generalised linear mixed-effects model with a beta response (because evenness is bounded by 0 and 1) and a logit link. The response variable was evenness of the

avian assemblage (all species) for a given 27×27 km grid cell and week. The predictor variables (all continuous) were productivity (mean within the 27×27 km grid cell), Shannon diversity of land cover (within the 27×27 km grid cell), and migrant dominance; we included all two-way and three-way interactions between predictors in the model. To account for spatiotemporal variation in evenness beyond that captured by our predictor variables, we included a random intercept for a grouping of week and the 0.5° grid cell that contained a given 27×27 km grid cell (median number of 27×27 km grid cells within a 0.5° cell: 3; range 1–6). We fit the models using the R package glmmTMB (Brooks et al. 2017; R Core Team 2025). To interpret model results, we visualise and report model predictions across a continuous range of values for productivity, the minimum and maximum values of habitat heterogeneity, and the minimum, mean, and maximum values of migrant dominance (see Figure 3). To aid in interpretation of the results, we also report the percent difference in predicted evenness between the lowest and highest observed values of productivity for different combinations of heterogeneity and migrant dominance. A supplemental analysis (Appendix S1) of model residuals to assess possible latitudinal variation in evenness patterns beyond that explained by our model structure did not find systematic latitudinal variation in model residuals (Figure S3).

2.5 | Analysis: Visualising Spatial and Seasonal Variability of Evenness

In addition to the primary analysis described above, we mapped productivity, evenness, and migrant dominance for four dates representing non-breeding season (1 January), pre-breeding migration (10 May), breeding season (28 June), and post-breeding migration (20 September). Moreover, we classified each 27×27 km grid cell as low, medium, or high seasonality. To do so, we calculated seasonality as the range of productivity values per cell over the year and divided the range of seasonality into three

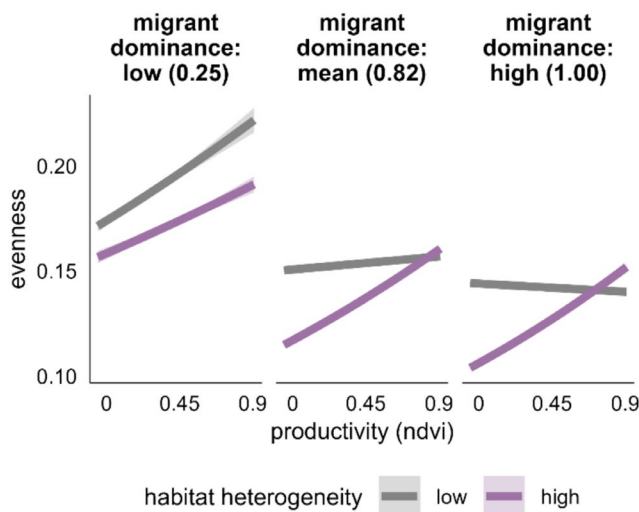


FIGURE 3 | Productivity, habitat heterogeneity, and migrant dominance co-influence evenness of bird assemblages. The three columns show model predictions for minimum observed (left), average (middle), and maximum observed (right) values of migrant dominance. The colours represent model predictions for minimum observed (low, grey) and maximum observed (high, purple) values of habitat heterogeneity.

equally sized intervals. We then fit generalised additive models (Wood 2017; Pedersen et al. 2019) in which the responses were productivity, evenness, or migrant dominance, predicted by a smooth of date (cyclic-cubic spline with 6 knots), with separate smooths for low, medium, and high-seasonality cells.

3 | Results

Productivity and habitat heterogeneity jointly increased assemblage evenness (Figure 3). Holding migrant dominance at its mean value, bird assemblages were the most even in heterogeneous, high-productivity landscapes (Figure 3, middle panel). Productivity had a positive effect on evenness (0.05 ± 0.0005 , $p < 0.01$), while habitat heterogeneity had an unexpected negative effect (-0.03 ± 0.0004 , $p < 0.01$), and the two terms showed a positive interaction (0.02 ± 0.0004 , $p < 0.01$) to produce the strongest productivity–evenness relationships for high-heterogeneity landscapes (Figure 3). For low-heterogeneity scenarios, evenness was predicted to be 4.3% higher in the most-productive relative to the least-productive landscapes, compared to 33.2% higher in the high-heterogeneity landscapes (Figure 3).

Migrant dominance reduced evenness and mediated effects of productivity and heterogeneity (Figure 3). Holding productivity and habitat heterogeneity at their mean values, evenness was predicted to be 31.4% lower under high migrant dominance compared to low migrant dominance (main effect of migrant dominance: -0.05 ± 0.0005 , $p < 0.01$). At low migrant dominance, both low- and high-heterogeneity landscapes showed similar positive relationships between productivity and evenness: evenness was predicted to be 19.9% and 25.6% higher in the most-productive compared to the least-productive landscapes for low- and high-heterogeneity, respectively. The impact of migrant dominance on evenness–productivity relationships was contingent on heterogeneity: at high migrant dominance, the positive evenness–productivity relationship was accentuated in high-heterogeneity landscapes (37.5% higher evenness in most- versus least-productive landscapes) but reversed to a weak negative relationship in low-heterogeneity scenarios (2.9% lower evenness in most- versus least-productive landscapes; Figure 3).

A supplemental model (Appendix S1) with passage migrant dominance (i.e., dominance of species in migration, not including migratory species on their breeding or wintering ranges) identified qualitatively similar results to the model with the broader migrant variable presented in the main text (Figure S1). A supplemental model (Appendix S1) with species richness identified a weak negative effect of species richness on evenness and interactions that implied that, as richness increased, associations between evenness and productivity pivoted from positive to negative, and that this shift happened faster in low- compared to high-heterogeneity landscapes (Figure S2).

3.1 | Seasonal Variation in Productivity, Evenness, and Migrant Dominance

The growing season wave of productivity (Figure 4a) is reflected in higher assemblage evenness during the pre-breeding

migration and breeding seasons (Figure 4b). This seasonal shift in evenness is particularly apparent for regions that experience strong productivity seasonality (i.e., regions that oscillate between cold winters and warm, humid summers); during the winter, evenness was lowest in the north-central United States (Figure 4b). Particularly in high-seasonality environments, this spring–summer peak in evenness presumably is the outcome of the arrival of migratory species tracking resources (for which productivity is a proxy). Conversely, the departure of high-abundance migratory species wintering in low-seasonality regions may also contribute to spring–summer peaks in evenness in these low-seasonality regions (Figure 4b,c). Thus, the addition of low-abundance migrant species (i.e., abundances similar to those of sedentary species) may increase evenness during the growing season in high-seasonality environments. This may seem to contradict the previously reported negative influence of migrant dominance on evenness (Figure 3); however,

the negative influence of dominance is likely the signal of one or a few extremely abundant species (e.g., flocks of waterfowl). Indeed, the proportion of migratory species (rather than dominance) showed very weak positive correlation (Pearson's $r=0.03$) with evenness, supporting the idea that one or a few dominant migrant species strongly influence the estimated effects of migrant dominance. Moreover, the proportion of highly abundant (relative abundance > 5) species generally decreased from January to June (Figure S4), supporting the idea that the addition of many low-abundance migrant species leads to growing-season increases in evenness. Finally, the dominance of migrants showed strong seasonal and spatial patterns; in strongly seasonal environments (e.g., the north-central United States), migrant dominance was low in the winter but high in the summer, and in less seasonal environments (e.g., the south-eastern coastal plain), migrant dominance was highest in the winter (Figure 4c).

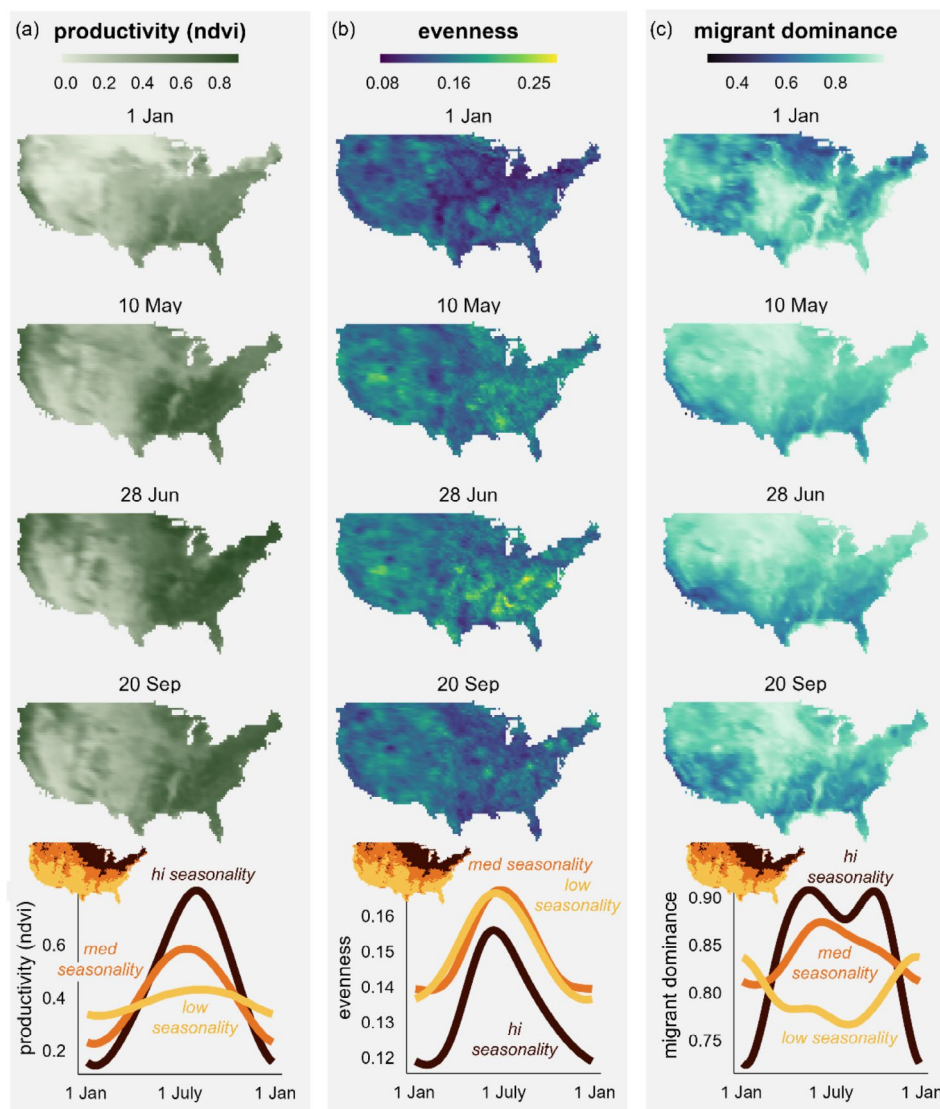


FIGURE 4 | Seasonal and spatial patterns in (a) productivity, (b) evenness, and (c) migrant dominance. In the bottom row, the curves are produced by a generalised additive model with a cyclic cubic regression spline for date, with separate smoothers for regions with high (brown), medium (orange), and low (yellow) productivity seasonality (see bottom inset map).

4 | Discussion

The key aim of our paper was to quantify influences of productivity, habitat heterogeneity, and migrant species on the evenness of bird assemblages at a continental scale. We found an interdependence between productivity and habitat heterogeneity in shaping the abundance structure of bird assemblages: evenness increased with productivity, but only in landscapes with moderate-to-high habitat heterogeneity. This result suggests that the more-individuals and niche-partitioning hypotheses in isolation are not sufficient to explain patterns of abundance within avian assemblages. Productivity likely increases evenness by supporting more low-abundance species (“rising-abundances-lift-all-species” hypothesis; Figure 1a), many of which are migrants; however, highly dominant migrant species reduce evenness and dampen evenness–productivity relationships across all levels of habitat heterogeneity (Figure 3). Moreover, the pivot to negative evenness–productivity relationships under high species richness (Figure S2) may be a further signal of the effect of migrants, as the highest values of species richness (> 220 species) were observed late April–early May (peak of pre-breeding migration in species-rich southern parts of the United States) and September (peak of post-breeding migration for many species). Considered altogether, these results indicate that the abundance structures of avian assemblages vary spatially and seasonally, with possible implications for processes such as ecosystem function and the supply of ecosystem services.

Birds provide ecosystem services and disservices which may be influenced by evenness (Gaston et al. 2018). For example, more even bird communities have been linked to higher rates of pest control in agricultural landscapes (Barbaro et al. 2017). This effect may emerge if communities with higher evenness show higher functional diversity, for example in terms of foraging strategy, such that even communities include similar abundances of species that glean foliage, forage on the ground, and hawk flying insects, leading to greater pest control than communities dominated by species with one foraging strategy. Birds also provide cultural ecosystem services by enriching the lives of birdwatchers, hunters, gardeners, and others (Gaston et al. 2018). Experimental work in other systems (wildflowers and intertidal communities) demonstrates that nature enthusiasts prefer biotic communities with high evenness over communities with low evenness (Graves et al. 2017; Fairchild et al. 2022); thus, locations with high avian richness and evenness may be particularly valued by birdwatchers and other nature enthusiasts. Beyond these benefits, birds may provide disservices such as destruction of crops (Peisley et al. 2015) or the transmission of pathogens to humans or livestock (Harvey et al. 2023). Evenness may moderate these disservices; for example, outbreaks of avian influenza often occur in locations with large congregations of one or a few species (Harvey et al. 2023); such locations would have low evenness. Thus, evenness may facilitate forecasts of disease dynamics and spillover (Keasing et al. 2010).

Migrant dominance reduced evenness, but counterintuitively, evenness was highest during the pre-breeding and breeding seasons, times when migrant dominance was generally high (Figures 3 and 4). This seemingly counterintuitive result likely arises because the random intercept in our model adjusts for

seasonal shifts in evenness. Within a given week, locations with high migrant dominance tended to have lower evenness, perhaps the signature of one or a few highly abundant species, for example, large flocks of passage migrants (Castro and Myers 1993). The generally higher evenness during the growing season may reflect the presence of many low-abundance migrant species or a more uniform dispersion of individuals during the breeding season; for example, the American Robin (*Turdus migratorius*) roves in large flocks during the winter but spreads out to defend territories in the spring and summer (Vanderhoff et al. 2020). Supporting these ideas, the proportion of highly abundant species in representative assemblages decreased from the non-breeding to breeding season, while evenness increased (Figure S4). Moreover, broad-scale seasonal shifts in demography—particularly among-species variation in survival or fecundity—may influence evenness patterns; for example, migrant traffic is lower in the pre-breeding migration compared to the post-breeding migration due to overwinter mortality (Dokter et al. 2018). Finally, beyond direct effects of migrants on evenness, we found evidence that migrants mediate evenness–productivity–heterogeneity relationships (Figure 3).

While our main analysis considered migratory species broadly (encompassing both passage migrants and migratory species on their breeding and non-breeding grounds), a supplemental analysis (Appendix S1) that evaluated dominance of passage migrants revealed similar results (Figure S1). The dampening influence of passage migrants on evenness–productivity relationships for high-heterogeneity scenarios (Figure S1) supports the notion that migrants concentrate in high-productivity landscapes. The only deviation was that evenness–productivity relationships were stronger in high-heterogeneity landscapes compared to low-heterogeneity landscapes for passage migrants but not for the broader migrant grouping (Figures S1 and 3). This mild discrepancy may be explained by differences in the residence times between these groups. While neither group permanently occupies a location, passage migrants generally occur over shorter timespans (days to weeks), compared to longer timespans (e.g., entire seasons, or weeks to months) for migratory species on their breeding or non-breeding grounds (Schlägel et al. 2020). Landscapes may be able to support excess numbers of individuals for brief periods of time, and thus ephemeral concentrations of passage migrants may lower evenness and weaken relationships with productivity, whereas migratory species on their breeding/non-breeding grounds may follow the predictions of a joint “more individuals–niche partitioning” hypothesis (Alonso et al. 1994; Holdo et al. 2011; Schlägel et al. 2020). Considered more broadly, the effects of migratory species highlight a need for seasonal, full-annual-cycle perspectives in macroecology (Marra et al. 2015; Keyser et al. 2024), which has historically emphasised static data such as range maps and surveys from individual seasons (e.g., the North American Breeding Bird Survey; Hurlbert 2004).

One of the results that surprised us most was the negative main effect of habitat heterogeneity on evenness; together with the interaction with productivity, this resulted in positive evenness–heterogeneity relationships in high-productivity landscapes but negative evenness–heterogeneity relationships in low-productivity landscapes. This contradicted our expectation that heterogeneity would generally be associated with higher

evenness (Figure 1b,d) and counters previous studies that identified higher evenness in more heterogeneous environments (Cotgreave and Harvey 1994; Hurlbert 2004; Symonds and Johnson 2008; Bae et al. 2018). This contradiction may have an analytical explanation: for example, if heterogeneous landscapes tend to have higher productivity (Pearson's $r=0.49$ in our dataset), an analysis that includes heterogeneity but not productivity might identify stronger and more universally positive associations between evenness and heterogeneity (Cotgreave and Harvey 1994; Hurlbert 2004). Productivity and heterogeneity are likely intrinsically related in many cases; for example, warm and wet conditions that allow the growth of forests with abundant structural heterogeneity also result in high productivity. Because of this strong covariation, we suggest that productivity and heterogeneity effects on abundance structures should not be considered in isolation. Additionally, there may be a biological explanation for the surprising heterogeneity result; for example, if low productivity is such a strong environmental filter that only one or a small number of specialists can reach high abundances, evenness will be low even if the landscape has high heterogeneity (Symonds and Johnson 2008).

Studying the abundance structures of biological assemblages at a continental scale is a challenging undertaking: each species has its unique phenology and distribution in space, and so any general conclusions about environmental influences on abundance structures will be mired by spatial and temporal heterogeneity (Magurran and Henderson 2003). The eBird Status & Trends data product provides a step forward in understanding macroecological abundance structures by offering weekly relative abundance estimates at fine spatial scales for many species. But challenges remain in understanding spatiotemporal variability in abundance structures of birds at continental scales. For example, the values reported in these data products represent *relative* abundance and are interpreted as expected counts of species reported by observers; thus, the estimated values for difficult-to-detect species (e.g., owls) may be skewed based on observer behavior and effort (Callaghan et al. 2024). Furthermore, scale is also an issue, as using different grain sizes could lead to different results (Cohen and Jetz 2025); because both species richness and the number of individuals increases with area, we might predict lower estimates of evenness if finer grains are evaluated since with fewer species and individuals, it is increasingly likely that one or a few species will dominate. And finally, the task of differentiating migratory and sedentary populations is complicated by species undertaking small-scale migrations or performing nomadic movements: for example, northern populations of Hairy Woodpeckers (*Leuconotopicus villosus*) regularly move southward into the northeastern United States in the autumn (Griscom 1935). Some migratory species show considerable overlap between breeding, wintering, and migratory distributions: the American Robin, for example, breeds in almost all of North America north of the Isthmus of Tehuantepec, and southerly populations may be breeding while non-breeding migrants from northern regions are still present (Vanderhoff et al. 2020). Despite these challenges, the production of continental-scale relative abundance maps for many species facilitates broad-scale insights into how abundances are distributed across species and how the environment influences that process.

5 | Conclusions

Evenness of bird assemblages increased with productivity in high-heterogeneity, but not low-heterogeneity, landscapes, indicating that energy and niche availability must be considered interdependently when assessing abundance structures of bird assemblages. Evenness was at its highest during the growing season when migratory species were present, particularly in highly seasonal regions (Figure 4). However, high dominance of migratory species was associated with lower evenness, which may reflect differing life-history strategies of sedentary versus migratory species (e.g., one or very few high-abundance migrant species lower evenness when present). Finally, migrant dominance influenced evenness–productivity relationships; the dampened evenness–productivity relationships in many scenarios may reflect concentrations of migrants in high-productivity areas. All told, our analysis reflects that the distribution of abundances across species in an assemblage is influenced both by the environment and the identities of the species making up the assemblage and emphasises the need for seasonal perspectives in macroecology.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Data and code are available on Dryad at the following anonymized link: <http://datadryad.org/share/5ADpsBVIEN3QqpbYTs-RfnzUKtIJT TqUMtB5uFkAog0>.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Figure S1:** Effects of productivity, habitat heterogeneity, and passage migrant dominance on evenness of bird assemblages. **Figure S2:** Species richness modulates relationships between productivity, habitat heterogeneity, and evenness of bird assemblages. **Figure S3:** Correlation between latitude and model residuals for the main text model (top) and the species richness model (bottom). **Figure S4:** Cells representing extremes of productivity seasonality and habitat heterogeneity used for interpretation.