Different beta-diversity frameworks reveal contrasting roles of species abundance distributions and spatial aggregation

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Abstract

Aim

Determining why community composition changes from place-to-place (spatial β-diversity) is central to advancing biodiversity theory and conservation of threatened species. Spatial β-diversity can occur most simply, due to random sampling effects from the larger species-pool, such as the random placement and distribution of individuals and species. However, ecological processes can also generate intraspecific aggregation changes that also produce changes in spatial β-diversity. We decomposed changes in β-diversity among birds in geographically isolated wetlands to understand the relative contributions of intraspecific aggregation and random sampling processes. Specifically, we compared two analytical approaches from the Measurement of Biodiversity framework: multi-metric vs multi-scale. We also examined how estimates of β-diversity are sensitive to changes in spatial extent and environmental context.

Location

Continental United States.

Time Period

2010-2024

Major Taxa Studied

Birds.

Methods

We integrated a dataset of n=207 geographically isolated wetlands with eBird data from 2010-2024 from across the continental United States to investigate how β-diversity changes in these wetland systems at two different spatial extents: (1) within ecoregions and (2) between wetlands continentally, regardless of ecoregion. We used both the multi-metric and the multi-scale approaches of the Measurement of Biodiversity framework which account for changes in abundance and the species-abundance distribution, to test if β-diversity in these systems reflects intraspecific aggregation across ecoregions.

Results

The multi-metric β-diversity approach was largely consistent with random sampling effects due to variation in community size and the species-abundance distribution at both ecoregion and continental extents evidenced by low β_C. However, our multi-scale β-diversity analysis using spatially explicit rarefaction curves revealed a strong divergence from the random sampling effects indicating that β-diversity is also due to intraspecific aggregation generated by ecological processes both at the ecoregion and continental extents.

Main Conclusions

Our two analytical frameworks uncovered different explanations for spatial β-diversity in wetlands. The β-diversity metrics did not differ from random sampling presumably due to the homogenous distribution of a few hyperabundant species. However, the spatial accumulation of species was slower than expected under random sampling which indicates that ecological processes, such as environmental filtering and/or dispersal limitation, are driving nearby

wetlands to have more similar composition than expected. Both of these signals were present within and across ecoregions, highlighting the need for a pluralistic approach to analyzing β-diversity and disentangling these non-mutually exclusive processes.

Keywords: birds, beta diversity, wetland biodiversity, species turnover, geographically isolated wetlands; Measurement of Biodiversity (MoB) framework

Introduction

β-diversity is a measure of species assemblage change through space and time due to species turnover (Condit et al. 2002; Whittaker 1972). Species turnover can be driven by two non-mutually exclusive processes: sampling effects and ecological processes (McGlinn et al. 2025). Ecological processes, such as niche-based environmental filtering, are commonly invoked when turnover between different communities is encountered, that generate species clumping, or intraspefic aggregation changes (Myers et al. 2013; Veech et al. 2005). However, random turnover can also be generated by stochastic sampling effects from a regional species pool where the number of observed species or individuals is limited by incomplete sampling (Adler et al. 2005; Stegen et al. 2013). Because communities are finite in size, estimated turnover between communities can be encountered due to random sampling of individuals from the much larger regional pool and/or by changes in the shape of the regional species-abundance distribution (SAD) without any need to invoke site-specific differences in biotic or abiotic conditions (Coleman et al. 1982; Kraft et al. 2011; McGlinn and Palmer 2009). Depending on the shape of the species-abundance distribution and the total community abundance, these sampling effects can artificially deflate β-diversity if there is a hyperabundance of common species, or inflate β-diversity by randomly sampling too few individuals in an even hypothetical regional species pool. However, intraspecific aggregation changes due to dispersal or species-sorting can be invoked after controlling for sampling effects, to reveal non-random clumping of species through space and/or time (Myers et al. 2013). Sampling effects are always present when comparing ecological communities but, we can remove the effects of both total community abundance and the species-abundance distribution to isolate the ecological processes that generate non-random mechanistic changes in community composition which we are seeking to understand with different measures of β-diversity (McGlinn and Palmer 2009; McGlinn et al. 2019; 2025). High β-diversity can emerge from both sampling effects and ecological processes (Anderson et al. 2011; Chase 2007; 2010), in order to truly uncover the process(es) driving β-diversity requires disentangling the impacts of both drivers of turnover through space and time.

While conceptually straightforward, β-diversity is complicated to quantify and is calculated using an ever-growing number of metrics, each aimed at capturing and decomposing some facet of community structure. Recently, the use of the Measurement of Biodiversity (MoB) framework has emerged to disentangle the impacts of random sampling effects, such as abundance (N) and the species-abundance distribution (SAD) from intraspecific aggregation changes that are more likely to reflect ecological processes (Blowes et al. 2020; McGlinn et al. 2019; 2025; Veech 2005). MoB provides two complementary approaches for examining β-diversity, the multi-scale and multi-metric. Yet, it is unclear if these both yield the same qualitative results in different systems. Such a framework allows the testing of whether β-diversity is driven by random sampling effects, and/or ecological assembly processes like environmental filtering and dispersal limitation (Baselga 2010; Legendre 2014; Reu et al. 2022). MoB compares a regional scale (gamma) rarefaction curve (generated by pooling all sites) to the average local scale (alpha) rarefaction curve. Differences between the regional and average local rarefaction curves can then be used to assess the impact of local community size (i.e., number of individuals) and the shape of the SAD (i.e., size of species pool and evenness) on turnover (Fig 1). If communities have high β-diversity at the tail end of the curve due to a large number of relatively rare species, but we see low β-diversity at the base of the curve due to high abundances of common species, hyperabundance of common species may drive β-diversity (ter Steege et al. 2013). Using

individual-based rarefaction curves, we can calculate multiple metrics of β-diversity along the rarefaction curve to account for each of the random-sampling effects outlined above to also uncover how composition is impacted variably by each (Fig. 1B).

In addition to the decomposition of β-diversity into sampling effects and ecological processes through multiple metrics, we also have to account for how these processes may change across spatial extents (Chase et al. 2018; Jarzyna and Jetz 2018). β-diversity generally increases as distance between samples increases, in other words as we go from local scale species turnover, to biogeographical species turnover the signal may increase, or decrease depending on the ecological processes and sampling effects at play. These signal changes can be due in part to changes in the size of the regional species pool (sampling effect), the abundance of rare and common species (sampling effect), or due to changes in environmental heterogeneity (ecological process) (Engel et al. 2021). Embracing scale-dependence is key for uncovering how β-diversity signals may flip as our scale of analysis increases, and the ecological mechanisms potentially mediating species turnover change between sites (Chase et al. 2018). Given that β-diversity interpretation is quite nuanced, the MoB approach using a combination of individual and spatial sampling-based rarefaction can help us separate the impacts of random sampling effects from ecological processes (intraspecific aggregation changes) at multiple spatial extents (Fig. 1C). By combining a multi-metric and multi-scale approach, we can uncover the ecological processes and random sampling effects that impact estimates of biodiversity in systems with continental distributions.

Birds are a globally distributed taxa, with robust publicly available data from community science platforms like eBird. Birds are well-documented biodiversity components of geographically isolated wetlands (GIWs) across their continental distribution (Comer et al. 2005; Tiner 2003), including as breeding habitat in prairie potholes of the Midwest (Ballard et al. 2021; Bartzen et al. 2017), as wintering habitat in the high plains of Texas (Fern et al. 2023; Ray et al. 2003), and as migratory stopover points for a whole host of species in the Eastern United States (McKinney and Paton 2009; Gnass Giese et al. 2018). Their contributions to bird biodiversity are well-documented, yet most studies on birds and GIWs focus on single β-diversity metrics (Daniel et al. 2019) at a single spatial extent (Barratt Heitmann et al. 2025), which ignore the biodiversity value of these systems above the meta-community level. Without analyzing these data using multiple metrics, at multiple spatial extents, it is unclear what processes are driving their biodiversity and whether conservation importance of potentially unique assemblages is necessary or if ecoregions with low wetland cover have more homogenous or heterogenous communities compared to their high wetland cover counterparts. Consequently, GIWs provide an ideal system for simultaneously evaluating β-diversity inference and understanding how bird communities are structured across broad geographic extents.

Here, we use bird communities across GIWs of the United States to investigate how different approaches to β-diversity decomposition influence ecological inference. We have two complementary objectives. First, we evaluate whether alternative β-diversity frameworks within the Measurement of Biodiversity (MoB) framework yield consistent conclusions regarding the relative importance of sampling effects and non-random spatial aggregation in generating species turnover. We do so by comparing both multi-metric and multi-scale approaches across broad geographic extents. Second, we apply these approaches to determine whether bird assemblages

occupying GIWs exhibit evidence of non-random spatial structuring across ecoregions and at continental extents, providing insight into the biodiversity value and uniqueness of these wetlands. We hypothesize that inference regarding the drivers of β-diversity will depend on the analytical framework employed, with metrics that account for different components of community structure potentially yielding contrasting interpretations of turnover. We further expect β-diversity to increase with spatial extent as species pools, environmental conditions, and wetland characteristics vary across the continent, resulting in stronger signals of spatial aggregation and community differentiation among wetlands.

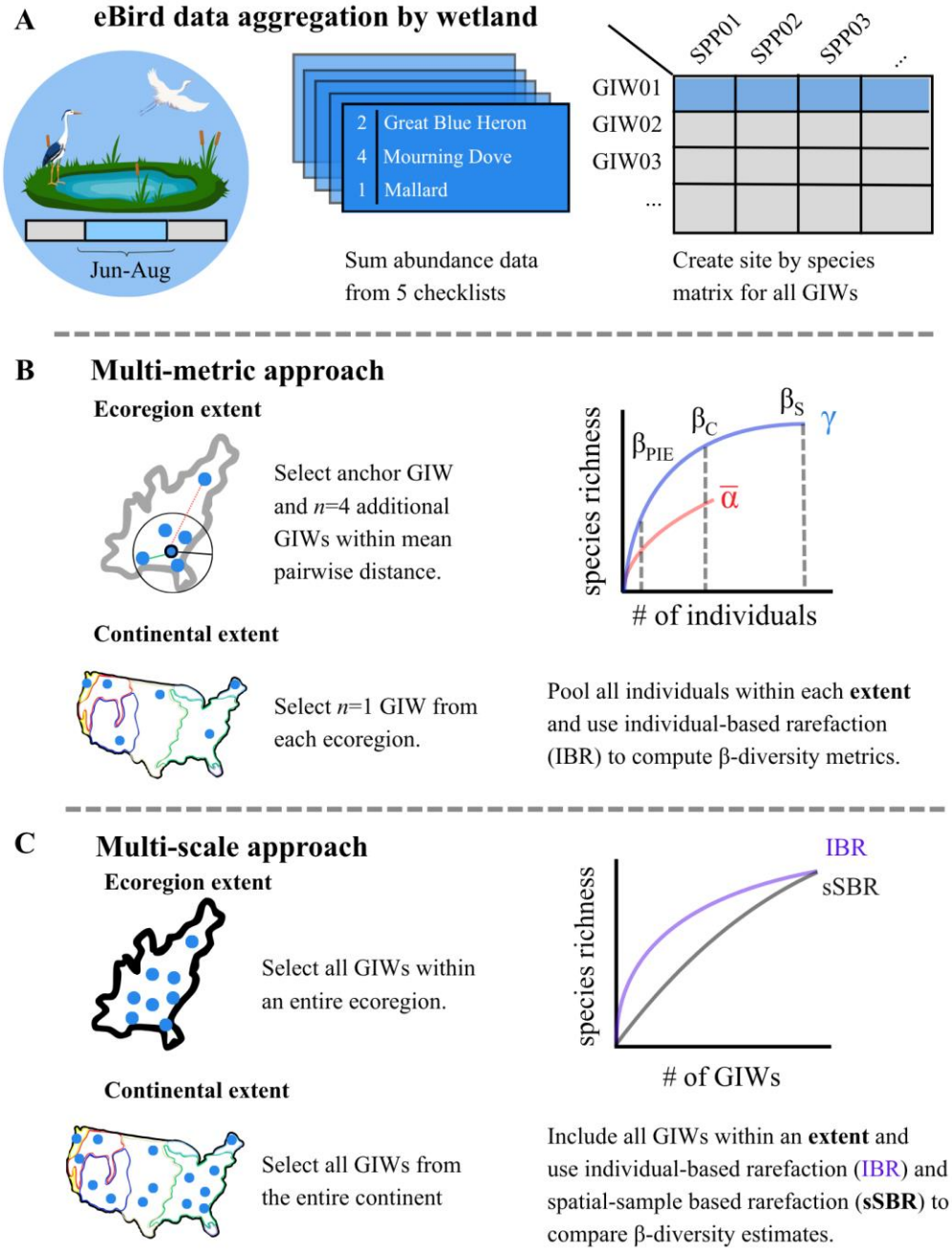

Figure 1. **Conceptual framework for calculating spatial β-diversity using a multi-metric and multi-scale approach**. **A**) eBird data aggregation for for each GIW (study grain) by randomly aggregating 5 submitted checklists. **B**) *Multi-metric approach*: *Ecoregion extent* calculated using individual-based rarefaction (IBR) only, by randomly selecting an anchor GIW, then selecting 4 additional GIWs within the mean pairwise distance between all sites within each EPA level I ecoregion, bootstrapped *n*=99 times per ecoregion. *Continental extent* calculated by comparing *n*=1 randomly selected GIW from each ecoregion, bootstrapped *n*=99 times. **C)** *Multi-scale approach*: *Ecoregion extent* calculated by using all GIWs within an ecoregion, and comparing the individual based rarefaction (IBR), and spatial-based sample rarefaction (sSBR). *Continental extent* calculated by including all GIWs across the entire continental United States, and comparing the individual based rarefaction (IBR) and spatial-based sample rarefaction (sSBR).

Methods

GIW selection and delineation

To select and delineate GIWs with bird biodiversity data from eBird, we began by downloading all eBird hotspots that contained the word "wetland" or "Wetland" in the hotspot name. Using the generic term "wetland" gave us the best opportunity to select the greatest number of hotspots that could potentially satisfy the GIW criteria from Tiner (2002). We only considered eBird hotspots with ≥ 100 submitted checklists (Callaghan et al. 2022; Freckleton 2002), as a conservative measure to ensure we had adequate sampling coverage.

We then visually inspected and assessed *n*=534 unique eBird hotspot locations by overlaying National Agriculture Imagery Program (NAIP) imagery from 2010 to 2022 (Earth Resources Observation and Science (EROS) Center 2017), the most recent National Wetlands Inventory (NWI) data (US Fish and Wildlife Service 2022), and Google Earth Imagery from 1985-2022 (Google Earth 1985-2022). We inspected these various imagery products to identify standing water and relative surface-level water connectivity. While we agree that these systems are no doubt connected through below-ground hydrology, we identified GIWs as any wetland surrounded completely by upland habitat (Cohen et al. 2016; Mushet et al. 2015; Tiner 2003). After reviewing each eBird hotspot our final dataset included a total of *n*=207 GIWs.

eBird data filtering

eBird is a semi-structured, community science effort organized by the Cornell Lab of Ornithology starting in 2002 with over 2 billion bird observations globally (Sullivan et al. 2009). eBird uses a semi-automated data quality control where especially rare, or high abundance species are flagged, and subsequently reviewed by a regional expert before being integrated into eBird (Gilfedder et al. 2019). We started by downloading the eBird basic dataset (ebird_vrs_June2024) for *n*=207 geographically isolated wetlands from a dataset published by Barratt Heitmann et al. (2025) (Fig. 2)—see above section for delineation criteria. First, we filtered this dataset to only include 'complete checklists' where the primary activity of the eBird user was birding. We only included a single checklist from group birding activities those that had a 'Group Identifier') using *dplyr::sample_n* (Wickham, François, et al. 2025) to avoid re-sampling the same eBird checklist more than once. We also filtered out checklists that contained

an ‘X’ in the abundance column, as we could not perform sample-based rarefaction without abundance estimates for all species within a checklist (see **Multi-metric approach** below).

To deal with potential confounding temporal effects on spatial β-diversity, we subsequently analyzed all of our data nested within each year and season (Winter, Spring, Summer, and Fall) (Martin 2018). We also filtered checklists to have only a single checklist submitted at an isolated wetland on a single day (i.e., for eBird hotspot: L9798114 on 06-01-2010 we randomly selected 1 unique checklist) to remove possible non-independent samples. All β-diversity calculations were constrained within year and season, to make spatial comparisons between GIWs robust to effects of migration and season on species richness of birds in North America. For clarity, when we computed β-diversity we always aggregated data at each GIW (sampling grain) from 5 random checklists to keep sampling effort consistent (Fig 1A). Given that typical wetland bird counting involves 3 repeated visits in the breeding season (Barratt Heitmann et al. 2025; Scheffers et al. 2006; Sorace et al. 2000), we felt that 5 random checklists was sufficient.

Table 1. Multi-metric and multi-scale β-diversity metrics captured effects and interpretations.

Multi- Metric		
Metric	*Effects captured*	*Interpretation*
β_S	None	Changes in communities are due to some combination of N, SAD, and spatial aggregation. This metric is most sensitive to rare species.
β_{SPIE}	N, Aggregation	Reflects the number of distinct communities at a given scale and is impacted strongly by common species.
β_C	Aggregation	Reflects changes in aggregation between communities, and accounts for changes in N and the SAD between sites.
Multi-scale		
Curve	*Effects captured*	*Interpretation*
IBR	SAD	Effects of the SAD remain, but all spatial and density effects at each wetland are removed. This becomes the expectation if species are randomly distributed amongst sites.
sSBR	N, SAD, Aggregation	This includes the impacts of N, the SAD, and spatial aggregation changes. The accumulation of entire sites here retains the density of individuals at each wetland, meaning that it would converge with the IBR if no spatial aggregation changes are observed.

Multi-metric approach

We computed three β-diversity metrics at two different spatial extents using the *mobr* framework (McGlinn et al. 2019). We computed a quantitatively equivalent measure to Whittaker's β as γ/α bar (β_S), evenness, or the effective number of species based on Hurlbert's PIE (β_{SPIE}), and coverage based β-diversity computed at γ-coverage of 75% (β_C) (Table 1). β_S captures species turnover as a result of random sampling (abundance (*N*) and the species-abundance distribution (SAD) as well as aggregation. This is because β_S is calculated at the end of the rarefaction curve, (i.e., including all individuals from all species) and is quite sensitive to rare species with only one individual for example (Fig. 1). β_{SPIE} highlights the number of distinct communities and is the most sensitive metric to the number of common species. β_{SPIE} effectively controls for variation in *N* but captures changes in evenness and aggregation across communities, β_C eliminates the contributions of N and the SAD, and isolates the impacts of aggregation solely on turnover between sites, allowing us the opportunity to directly comment on how mechanisms may impact β-diversity. For β_C we always set the γ-coverage in *target_gamma_C* to 0.75, or 75% coverage (McGlinn et al. 2019). Due to our self-imposed temporal sampling scheme, we had a varying number of samples within each year at the different extents (Fig S1). Our β-diversity metrics were quite similar across all seasons, so we only present those results in the supplementary material, and our results focus *only* on the summer season (Fig S2-S5, Table S1-S9). For the purposes of our study, we use computed confidence intervals (quantiles: 2.5% and 97.5%) to determine whether β-diversity metrics deviated significantly from 1–which indicates little to no species turnover. Our interpretation of β-diversity is based on confidence interval overlap and deviation from y=1, which indicates total overlap in bird communities.

We computed the aforementioned β-diversity metrics at 2 different spatial extents: ecoregion and continental (Fig 1B). When calculating β-diversity we made some consistent choices, which we then sensitivity analyzed (see *Sensitivity analysis* section). For our multi-metric approach, our β-diversity metrics are computed using individual-based rarefaction (IBR). This approach pools all individuals and species within a specified extent and pulls them at random to construct a gamma curve (all GIW samples), and alpha bar curve (average GIW), and subsequently compares the difference in expected species along those curves at various sampling efforts (# of individuals).

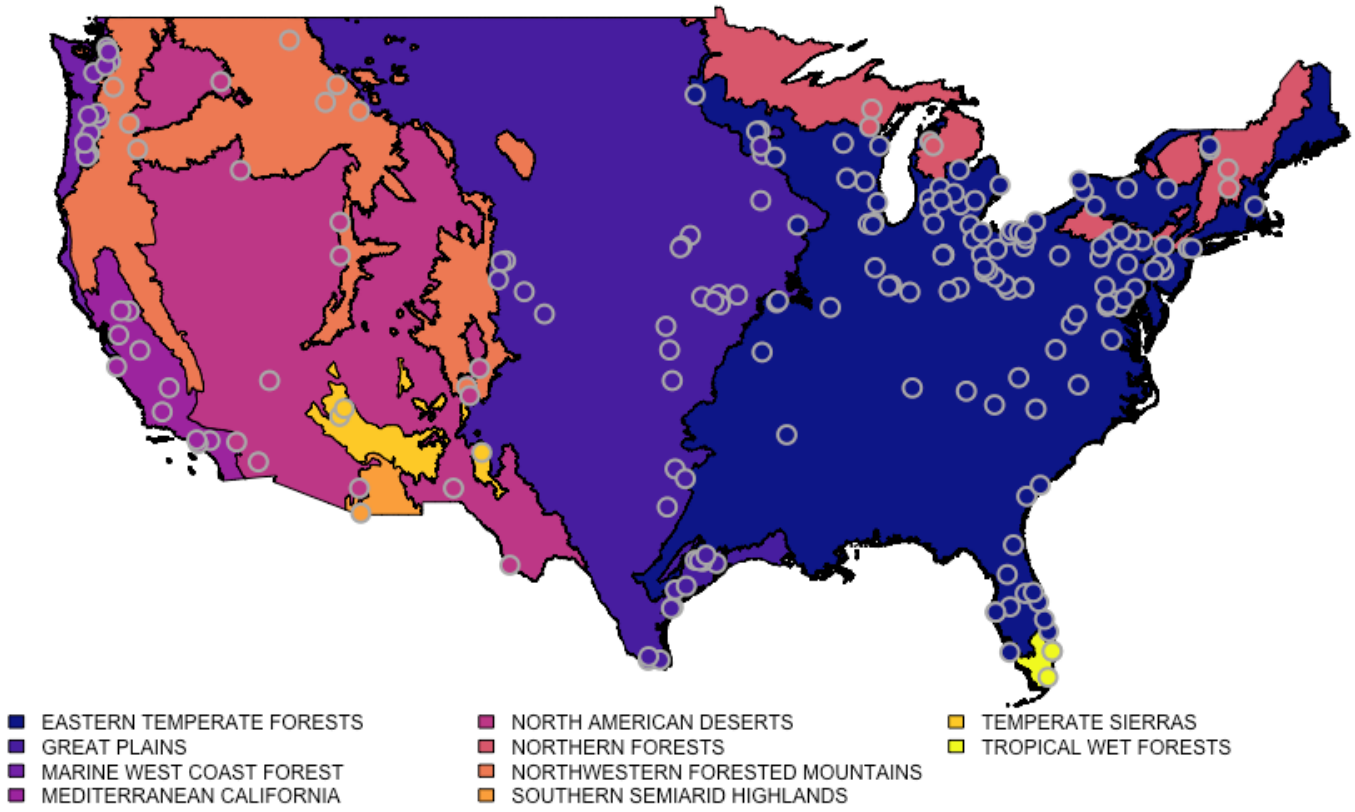

Figure 2. Map of GIWs (*n*=207) and EPA Level I ecoregion. Eastern Temperate Forests (*n* = 114), Great Plains (*n* = 34), Marine West Coast Forest (*n* = 16), North American Deserts (*n* = 12), Mediterranean California (*n*=10), Northwestern Forested Mountains (*n*=8), Northern Forests (*n*=6), Temperate Sierras (*n*=3), Tropical Wet Forests (*n*=3), and Southern Semiarid Highlands (*n*=1).

Ecoregion extent

Throughout this study, the geographically isolated wetland (GIW) represents the sampling grain for all analyses. What differs between our analyses is the spatial extent over which wetlands are compared, either within ecoregions or across the continental United States. We calculated β-diversity metrics at the ecoregion extent if they had *n* >= 5 GIWs with at least 5 submitted checklists within a season of a given year. In order to deal with the impact of the distance-decay function (Nekola and White 1999) we devised a sampling scheme to compare GIWs within ecoregions. We first computed the mean-pairwise distance between all GIWs within an ecoregion (during a given year, since the number of sampling sites increased over time due to increasing checklist submission). We nested our mean-pairwise distance calculation within an ecoregion to deal with a differing number of GIW samples per ecoregion (Fig. 2) and because ecoregions varied dramatically in wetland cover, an ecological reason we wanted to control potential variation in (Lane and D'Amico 2016). Then, we randomly selected an 'anchor' GIW, and randomly selected 4 other sites within that mean-pairwise distance that also had at least 5 submitted checklists. We then aggregated 5 random checklists in each GIW, and computed our

β-diversity metrics using the *mobr* function *calc_comm_div.* If an 'anchor' GIW did not satisfy the above requirements, we skipped it, and randomly selected another 'anchor' GIW. We set the maximum number of 'anchor' GIW attempts at *n*=99 per ecoregion, and bootstrapped this process *n*=99 times within each ecoregion, within each season and year. The extent for this multi-metric approach was therefore confined to only *n*=5 GIWs in any given ecoregion–but we allowed the distance between these GIWs to vary by ecoregion.

Continental extent

We calculated β-diversity across the entire United States to gauge if there were strong impacts on aggregation at the continental extent. We calculated the three β-diversity metrics by selecting a single GIW from each ecoregion that satisfied the sampling requirements (*n* >= 5 GIWs with an ecoregion and at least 5 submitted checklists), and bootstrapped this process *n*=99 times within each year. We selected only a single GIW from each ecoregion due to the uneven number of GIWs within each ecoregion (Fig. 2). Variation in the number of submitted checklists within each year at GIWs meant that we did not have the same sampling size within each year (see Fig S1), however, variation between years was quite small so we visualized and analyzed the data across all years together (Fig S6-S7). The extent for this approach was confined to at most *n*=9 GIWs, since we only ever selected a single GIW from any one ecoregion.

Multi-scale approach

Rarefaction analysis

To determine if β-diversity was being impacted by ecological processes that would cause spatial clustering of species, we constructed and compared individual-based rarefaction curves (IBR) and spatial sample-based rarefaction curves (sSBR) (Gotelli and Colwell 2001). We compared our random individual-based rarefaction curves (IBR) used to calculate our β-diversity metrics to spatial sample-based rarefaction (sSBR) where samples (GIWs) are accumulated using k-nearest neighbor accumulation (Fig 1C). Using this approach, we pooled all available GIWs within each ecoregion and continental extent, respectively, within each year and season (just as we did in our multi-metric approach). However, the key difference with this approach is that the sampling extent included all available GIWs at the given extent, and we accumulated samples through individuals (*N*) (IBR) and samples (GIWs) (sSBR), separately. This is in essence the multi-scale nature of this analysis; we changed the sampling scale to see if β-diversity was impacted differently depending on whether we sampled individuals (*N*) or entire communities (GIW) to construct our rarefaction curves.

At the ecoregion extent, we computed curves using all available GIWs in ecoregions with >5 GIWs. We started by randomly selecting a summer-year-GIW combination, and aggregating the data from *n*=5 random checklists. Using this approach, we do accumulate samples (GIWs) within ecoregions from different years, as random selection of summer-year combinations could result in different years between samples. We plot this combination of 5 GIWs together on a single rarefaction curve, and when we sensitivity tested this with all the sites from the same summer-year combinations, the curves looked very similar (Fig S2). We computed confidence intervals around each of the IBR curves using the *mobr::rarefaction* function, but we found that they were not visually distinguishable from the average curve and therefore we do not display them below. At the continental extent, we aggregated and selected sample data the same way, but instead of

constraining sample selection within ecoregions, we pulled them from all available GIWs continentally, regardless of whether the ecoregion had >5 samples.

At each extent, we computed each rarefaction curve individually using the *mobr::rarefaction* function. We had to rescale the individual-based rarefaction curve (IBR) by the average abundance per GIW when plotting it alongside the sSBR. This approach differed explicitly from our multi-metric approach as we included *all* possible GIWs across an entire extent (larger spatial scale) rather than using our subsetted approaches employed in the multi-metric approach. We also built these rarefaction curves to explicitly compare β-diversity between the IBR and the sSBR, the latter of which accounts for changes in distance between samples and accumulates species per GIW, not per individual. This multi-scale approach allows us to decompose β-diversity signals as spatial extent increases, and distance between samples increases, and treat GIWs as spatially-accumulated samples compared to our null model IBR curves–where species assemblages are not accumulated spatially. For our rarefaction analysis no overlap between the IBR and sSBR curves denote significant differences between the null assumptions of no spatial arrangement of species (IBR) and spatially explicit arrangement of species (sSBR).

Statistical analysis

Sensitivity analysis

After inspecting the total number of birds counted (*N*) for each species at each of our extents of analysis, we decided to filter out the 5 most abundant species and re-run all of the above multi-metric and multi-scale analyses to see if rarer species had more of an impact on β-diversity when ignoring the impact of the most hyperabundant species (Figs S6-S9). We computed the total number of birds counted (*N*) from n=5 submitted checklists at each GIW within each season, and then subsequently removed all of these species from each checklist. The results were qualitatively similar to our main analyses, and so we only discuss these results in the discussion section.

We also performed some additional analyses and visualization to assess 1) our multi-metric approach to traditional β-diversity dissimilarity indices (Bray-Curtis, Jaccard's, and Sorensen's) (Fig S15-16) and 2) the relative contributions of the species-abundance distribution (SAD) compared to aggregation in our multi-scale approach (Fig S13-14). We wanted to assess whether more classic β-diversity metrics are able to capture the dramatic differences in estimated β-diversity between β_S, β_{SPIE} and β_C in the MoB framework we employed. Furthermore, we wanted to gauge how aggregation was contributing to our overall β-diversity signals at both extents compared to the SAD. These results are mentioned in the discussion but are not included as figures in the main text here.

Modeling

At the ecoregion extent we built GLMM model using the glmmTMB::*glmmTMB* function (Brooks et al. 2025) with a gamma family argument and a log link function and checked model fit with the *performance::check_model* function (Lüdecke et al. 2021). At this extent, we explicitly tested for significant differences among ecoregions, and so we included this as a fixed effect with season, and at this extent only had year as a random effect. We then performed Tukey's Honest Significant Difference Tests (HSD) to determine significant differences between

ecoregions (Fig S8). Below is the model structure we employed for all 3 metrics at the ecoregion extent:

$$\beta \sim \text{Season} + \text{Ecoregion} + (1|\ \text{Year})$$

At the continental extent we also built a GLMM model using the glmmTMB::*glmmTMB* function (Brooks et al. 2025) with a gamma family argument and a log link function and checked model fit with the *performance::check_model* function (Lüdecke et al. 2021). At this extent, we simplified the model by removing ecoregion from the model, as we were explicitly testing for differences among ecoregions. We included just a single fixed effect season, and one random effect for year. Below is the model structure we employed for all 3 metrics at the continental extent:

$$\beta \sim \text{Season} + (1|\ \text{Year})$$

Data analysis and availability

Our workflow relied heavily on *tidyverse* to clean and tidy our data (Wickham, Vaughan, et al. 2025). We visualized all of our data using *ggplot2* (Wickham et al. 2016) and *patchwork* (Pedersen 2025). We used *R* version 4.5.1. Raw eBird data can be accessed here: https://ebird.orf/data/download. Code and data to reproduce our analyses are available here: Anonymous GitHub repository.

Results

Overall, we had a total of 28,218 checklists from 195 unique isolated wetlands across 9 EPA level I ecoregions in the United States in the summer season. Eastern Temperate Forests had by far the greatest number of GIWs n=114, followed by the Great Plains with n=16 (Fig. 2). We had a total of 497 species and total birds counted (N) of 4,053,763 birds. The 5 most abundant species across all wetland sites were Red-winged Blackbird *Agelaius phoeniceus* 362,064 (8.9% of total birds counted), European Starling *Sturnus vulgaris* 271,212 (6.7% of total birds counted), Mallard *Anas platyrhynchos* 265,533 (6.5% of total birds counted), Canada Goose *Branta canadensis* 212,149 (5.2% of total birds counted), and Purple Martin *Progne subis* 55,710 (4.0% of total birds counted) (Fig S9). Together these 5 species represented <1% of our total species but made up ~31% of total birds counted. Through our random sampling approach, all individual birds counted (N) and species were not necessarily captured in each respective extent (ecoregion and continental). However, our total dataset of checklists and individual birds represents the entirety of the bird community from which we sampled our data at our two spatial extents and their respective extents.

Our β-diversity metrics were statistically different between seasons for all metrics (β_S, β_{PIE}, β_C), at both extents (ecoregion, continental). However, the statistical significance is likely a product of our bootstrapping process increasing the sample size, not a true ecological difference (Martínez-Abraín 2008), as the mean and standard errors around our estimates are extremely small (<0.1 in every case) (Tables S1-S9). Therefore, we only discuss these results briefly in the discussion, and will only display our results from the summer season in the Results section.

Multi-metric approach

β-diversity metrics were quite similar in all ecoregions, with small differences in β_S and β_C (Fig. 3). Notably, all ecoregions had high β_S, but after accounting for sampling effects (N and the SAD) β_C confidence intervals did not overlap 1 in North American Deserts (m=1.40, 95% CI: 1.17-1.80), Marine West Coast Forests (m=1.26, 95% CI: 1.13-1.43), and Northwestern Forested Mountains (m=1.34, 95% CI: 1.08-1.50). However even in those ecoregions, mean and 95% CIs were exceedingly close to 1. Ecoregions did differ significantly in β-diversity metrics (Fig S8, Table S1-S9), although β values themselves were only significantly different from 1 for β_S in all ecoregions, and β_C in Marine West Coast Forests, North American Deserts, and Northwestern Forested Mountains. Therefore, strong differences in β-diversity metrics were not observed between ecoregions.

At the continental extent, β_S was higher than 1 (β_S = 4.31, 95% CI: 3.42-5.78) and after accounting for changes in evenness (β_{SPIE} = 1.77, 95% CI: 1.14-2.29), the impacts of aggregation (β_C = 1.51, 95% CI: 1.01-2.13) were still present albeit much lower than β_S (Fig 5A). We also analyzed this data at a larger extent using all GIWs within each year, as opposed to our subsetted approach using n=5 GIWs. We found very similar results and so we only include those in the supplementary material (Fig S2).

Multi-scale approach

Using our multi-scale approach, we disentangled our β-diversity signals using two different rarefaction curves: the individual-based rarefaction (IBR) and spatial sample-based rarefaction. Contrary to our multi-metric approach, our multi-scale approach showed strong evidence of spatial clustering within ecoregions as the sSBR curve fell well below the IBR curve in all ecoregions (Fig 4). This relationship was relatively consistent amongst ecoregions, regardless of the number of GIWs within that ecoregion, the mean-pairwise distance between GIWs, or the size of the ecoregion.

At the continental extent, we found similar evidence that spatial clustering exists in bird communities in GIWs (Fig 5B). The spatial sample-based rarefaction curve (sSBR) again fell well below the individual-based rarefaction curve (IBR), with a distinct bump ~125 samples due to the East-West divide in the regional-species pool. Similar to our ecoregion extent, when we accumulated GIWs spatially, species richness fell below the null expectations from the IBR curve, that assumes no spatial arrangement of species.

However, when we estimated the relative contributions of the SAD and aggregation to observed spatial β-diversity at both extents; we found that the SAD was responsible for most of this observed difference, not aggregation even after accounting for the relative abundances of species at each site (Fig S13-14).

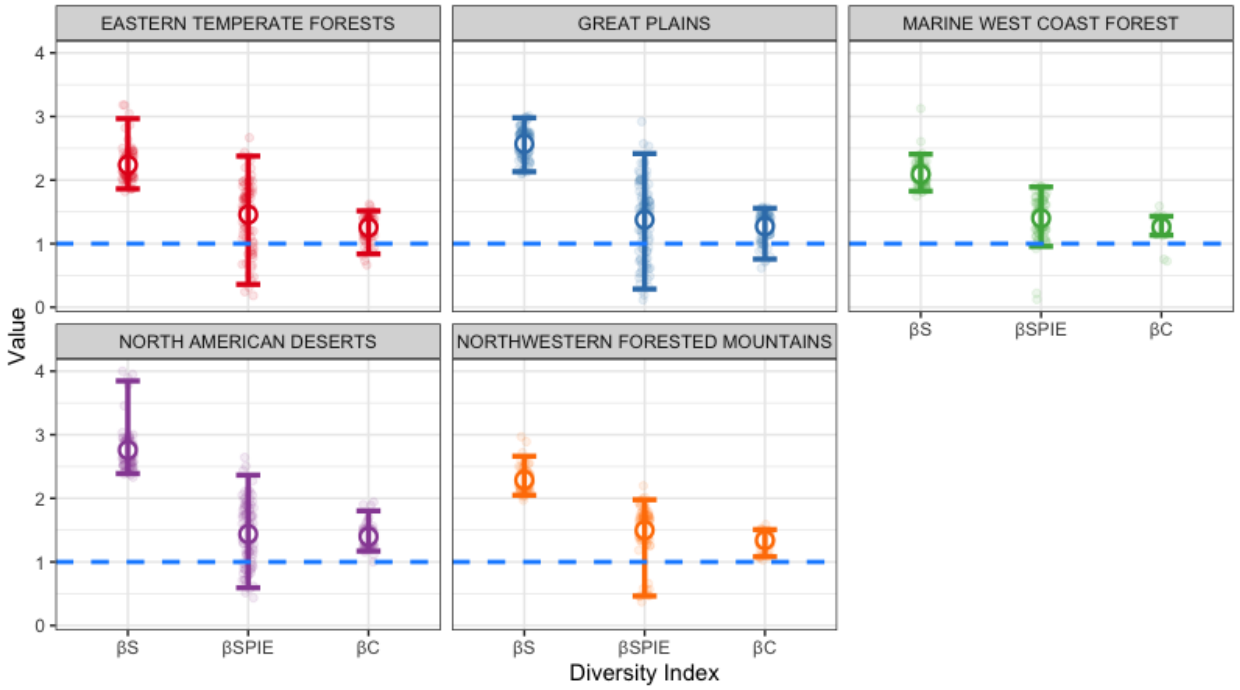

Figure 3. β-diversity indices between GIWs at the ecoregion extent. White points represent mean values and error bars display 95% confidence intervals. Confidence intervals overlapping 1 (dashed blue line) indicate little to no change in β-diversity.

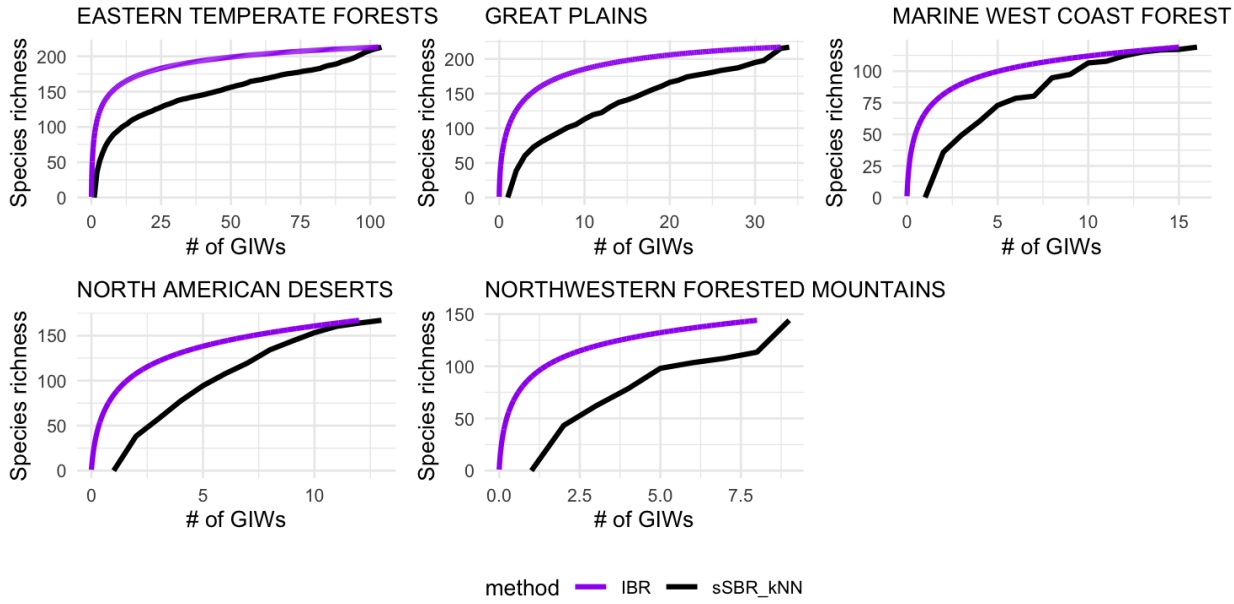

Figure 4. Individual and spatial rarefaction curves within ecoregions: (purple) random individual-based rarefaction (IBR) used to calculate all of our β-diversity metrics, (black) spatial sample-based rarefaction where samples are accumulated using k-nearest neighbor (sSBR_kNN). Our IBR curve is rescaled by the average abundance at each GIW within the ecoregion and is accumulated using random pulls of individuals, not samples (GIWs) as with our spatial curves.

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501
502

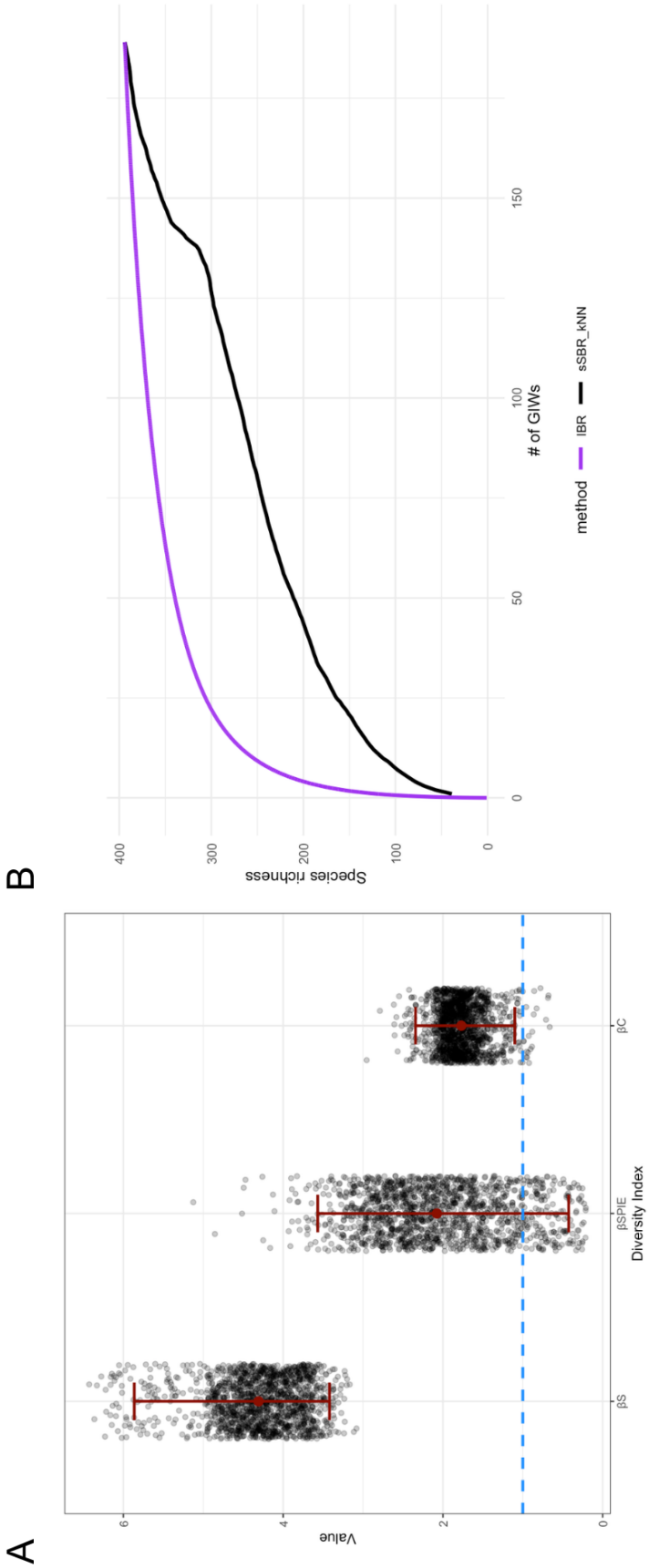
A
Value
0
2
4
6
βS
βSPIE
βC
Diversity Index
B
Species richness
0
100
200
300
400
0
50
100
150
# of GIWs
method
IBR
sSBR_kNN

Figure 5. β-diversity indices between GIWs at the continental extent. A) Multi-metric approach bootstrapped *n*=99 times with only *n*=1 GIW per ecoregion, per year. Red points represent mean values and error bars display 95% confidence intervals. Confidence intervals overlapping 1 (dashed blue line) indicate little to no change in β-diversity. **B**) Multi-scale approach using individual and spatial rarefaction curves across the continent: (purple) random individual-based rarefaction (IBR) used to calculate all of our β-diversity metrics, (black) random spatial based rarefaction (SBR). Our IBR curve is rescaled by the average abundance across all GIWs and is accumulated using random pulls of individuals, not samples (GIWs) as with our spatial curves.

Discussion

Our primary finding is that different approaches to quantifying β-diversity yielded different interpretations of the same bird communities occupying geographically isolated wetlands throughout the United States. Our multi-metric approach showed evidence of strong sampling effects, most importantly that hyperabundance of common species was driving compositional similarity between GIWs within ecoregions and across the continent evidenced by relatively low β_C. But in contrast, our multi-scale approach revealed departures from expectations under random placement, with spatial sample-based rarefaction curves falling below individual-based rarefaction curves, indicating non-random spatial structuring of communities. Broadly, our study illustrates the importance of carefully considering how the abundance structure of communities influences β-diversity inference, especially when leveraging large community-science datasets such as eBird.

Different β-diversity frameworks yield different ecological interpretations

Focusing on our multi-metric approach, our β-diversity signals were primarily driven by random sampling effects, due to changes in the species-abundance distribution (SAD). β_S was high within each ecoregion and at the continental extent, but β_S is sensitive to rare species. After rarefying richness by moving towards the base of the rarefaction curve–which is less sensitive to rare species–and controlling for differences in sample coverage between ecoregions, our β_C signal was not significantly different from 1 in any of our ecoregions or at the continental extent indicating minimal species turnover (Engle et al. 2021; McGlinn et al. 2025) Although β_C was statistically higher than 1 at the continental extent and in ⅗ ecoregions, the values were consistently lower than both β_S and β_{SPIE}. Our multi-metric approach indicates that although GIWs are supporting high α-diversity (Barratt Heitmann, Mason, et al. 2025; Barratt Heitmann, Folk, et al. 2025; Riffell et al. 2006; Scheffers et al. 2006); at both spatial extents differences between bird communities are largely changing because of shifts in the SAD ($\beta_S > \beta_C$). We supplemented this analysis by calculating 3 other classic β-diversity metrics (Bray-Curtis, Jaccard's, and Sorensen's Dissimilarity Indices), and all of them acted universally similar to β_S even though each is designed to be sensitive to high abundances (Bray-Curtis), shared species (Jaccard's), and rare species (Sorensen's). Each of these metrics overestimates turnover due to stochastic changes in relatively rare species between sites, because they do not use rarefaction to directly control for changes in the total community abundance, or the SAD, like β_C (Fig S15-16).

Using even a combination of those three classic metrics ignores the importance of the SAD, which when accounted for explains most of the variation compared to the minimal importance of intraspecific aggregation (Fig S13-14). This result does mimic some previous work that showed the SAD accounted for much of the β-diversity signal in fish (Budnick et al. 2019; Schroeder and Jenkins 2018). In these cases, classic β-diversity metrics developed on Barro Colorado Island, Panama (Condit et al. 2002, 2012) may underestimate or undercount the true dominance of a select few species. The MoB framework being applied here to a novel citizen-science dataset (eBird) uncovers this contribution with multiple sensitivity tests for the SAD, the total number of individuals, evenness, to compute meaningfully the contributions of ecological processes that underpin intraspecific aggregation changes—of which we had little. Even in our multi-scale approach, when we dissected the aggregation versus SAD signal, we found that aggregation actually contributed significantly less to the overall β-diversity signal compared to the impacts of the SAD (Fig S13-14) (Blowes et al. 2020). Previous work using this MoB framework typically

focused on one of the two frameworks we outlined above, with evidence of changes in β-diversity due to evenness in fish (Blowes et al. 2020), due to environmental filtering as spatial grain is coarsened in arthropods (McGlinn et al. 2020), and due mostly to random placement in birds (McGlinn et al. 2025). We extended this work by directly using multiple frameworks simultaneously to test how random sampling effects and aggregation impact bird communities in GIWs. In our case, sampling modulates much of the β-diversity signal with smaller contributions from aggregation, but this is only revealed when considering the duality of the multi-metric and multi-scale approaches.

There is strong evidence for scale-dependence in β-diversity measurements (Chase and Knight 2013; Chase et al. 2018), yet our metrics did not change as we coarsened spatial extent, nor did they change between ecoregions. We expected ecological mechanisms like environmental filtering to, to generate intraspecific aggregation changes (Myers et al. 2013; Veech et al. 2005) and alter our β-diversity metrics (especially β_C) between ecoregions, given the variety of environmental conditions and changes in wetland cover across the United States (i.e., Eastern Temperate Forests versus North American Deserts) (Lane and D'Amico 2016). Importantly, we do not directly test the mechanisms support for ecological processes that generate aggregation changes, but rather document if there are departures from sampling alone. Our multi-scale approach using rarefaction analysis showed stronger evidence for spatial clustering of species at the ecoregion and continental extents, but this contribution was dramatically lower than the contributions of the SAD (Fig S13-14). Our multi-metric β-diversity approach appeared to contradict some previous work on wetland birds, which found strong evidence for high β-diversity metrics due to species replacement (an ecological process) (Liu et al. 2024; Si et al. 2015). We advocate for a pluralistic approach to analyzing β-diversity because our multi-scale analysis indicates that wetlands do not conform purely to random distributions of species, as wetlands do become more distinct as the distance between them increases. Although seemingly at odds, β-diversity is multi-faceted, being driven in part by intraspecific aggregation changes and predominantly by sampling effects due to hyperabundance, within and among ecoregions.

GIWs have consistently similar bird communities across broad geographic extents

While our first objective focused on how different β-diversity frameworks influence ecological inference, our second objective was to understand how bird communities occupying geographically isolated wetlands are structured across broad geographic extents. We expected that β-diversity would be quite different within and between ecoregions of the continental United States. However, we found that both the multi-metric and multi-scale approaches remained relatively consistent within ecoregions and across the entire continent. This suggests that bird communities occupying GIWs may be governed by broadly similar assembly dynamics across environmental contexts, resulting in consistent abundance structures and spatial organization of communities throughout their continental distribution. We speculate that one possible ecological reason for this is that because GIWs are relatively small habitats (*median area of our study was* 0.16 km^2) their landscape contexts don't produce different β-diversity signatures, regardless of their ecological context (Daniel et al. 2019; Niemuth and Solberg 2003; Rendón et al. 2008). Although aggregation contributed substantially less than the SAD, spatially explicit rarefaction consistently departed from random expectations. This suggests that GIWs are not merely random subsets of regional avifauna and instead contain unique assemblage components that accumulate through space. A further possible reason for the consistent β-diversity among wetlands, despite

different contexts, was that dominant widespread species (e.g., Canada Goose, Red-winged Blackbird) are obscuring turnover among specialist species (dos Anjos et al. 2019). Furthermore, eBird data is skewed towards urban locations, that are best suited to generalist species with larger body sizes (Callaghan et al. 2020; Neate-Clegg et al. 2023), that may become hyperdominant in human-dominated landscapes. Although, when we removed the 5 most dominant species in a supplementary analysis, our results were qualitatively similar (Fig S11-S12, meaning that only when we include incredibly rare species do we start to see meaningful differences in community composition between wetlands.

Considerations for using eBird data for β-diversity analyses in the future

The impacts of different β-diversity frameworks using community or citizen-science collected data like eBird, require extensive testing moving forward. Accounting for sampling effects is not new in β-diversity analyses as many scholars have developed methods to try and account for sampling effects through rarefaction, random sampling of individuals, partitioning of nestedness and turnover, and stochastic versus ecological processes (Baselga 2010; Legendre 2014; Chase 2007; McGlinn et al. 2019). But, with citizen science data, we begin to move towards sampling saturation in habitats that receive high count effort to uncover the many species that occur in them. Our wetland sites have alpha-diversity estimates of up to 300 species and thousands of individuals, and therefore the number of individuals that make up the most common sets of species are exponentially larger than what could be generated from field counts. So, detecting signals between wetlands becomes incredibly difficult when they share these sets of common species. In our study, bird community turnover was dominated by common species with extremely high abundances, but these communities are still subject to intraspecific aggregation changes when we move beyond the sampling grain of an individual and consider entire communities as the sampling grain, but this is likely due to changes in rare species that make up a very small proportion of the entire community. Future consideration needs to be paid to the dataset being used, the sampling grain, and sampling duration by observes, when considering how to calculate various *for β-diversity* metrics.

Conservation implications

Our results suggest GIWs deserve conservation attention throughout their continental distribution, especially given their threat of destruction from recent legal proceedings in the United States (Simmons et al. 2024). It is prudent to highlight that β-diversity research using citizen science data, may estimate higher total abundances of avifauna in our case than in more structured professional survey techniques with strict temporal cutoffs (Hutto et al. 1986). An important consideration for those aiming to use eBird data to measure β-diversity, should be prudent to consider how the SAD and individual abundances contribute to β-diversity versus aggregation changes. Our framework outlined above helps achieve this goal. Furthermore, when sampling effort reaches such a high saturation level, it is possible that conservation managers may look to alpha diversity to identify more important habitats for conservation, given that β-diversity is driven almost entirely by hyperabundant species (ter Steege et al. 2013) that do not need conservation attention. eBird data does also skew sampling towards urban areas, which may also homogenize communities by filtering out many specialist species and including some invasive/non-native species (Liu et al. 2024). β-diversity metrics may also be impacted by local and regional demography, by altering the relative abundances of a select few hyperabundant species with large niche-widths and high urban-tolerance (Callaghan et al. 2021; Callaghan et al.

2020; Neate-Clegg et al. 2023). But, the β-diversity signals in our study do seem to mimic similar macroecological work on birds using the Breeding Bird Survey (Di Cecco and Hurlbert 2021), suggesting that the changes in extent and changes in the number of individuals of common species are responsible for community turnover in birds. In our case, this makes conservation prioritization of these habitats straight forward, they're equally important regardless of spatial context, making them incredibly valuable in all environmental contexts for birds, and likely biodiversity more generally (Comer et al. 2005; Snodgrass et al. 2000).

To conclude, our observed β-diversity signals are predominantly driven by sampling effects due to the SAD and in part by aggregation changes due to rare species clumping in GIWs at both the ecoregion and continental extents. β-diversity metrics in eBird data are influenced heavily by sampling effects due to hyperabundance of a few shared generalist species. While, β-diversity signals in our multi-scale rarefaction analysis were much more sensitive to rarer specie sin the community, revealing some spatial clumping of species, but this was a small contribution compared to the SAD. Multiple metrics and extents of analysis are required when analyzing β-diversity changes, and they are likely to be contingent on the taxonomic group in question, their respective life-history traits, and the source of the data (field collected versus community science data).

Data and code availability

Data and code to recreate all figures and analyses are available on https://doi.org/10.5281/zenodo.21362560.

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Conflict of interest statement

The authors declare no conflicts of interest.

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Supplementary Information

Wetland extent analysis

Table S1. Generalized-linear mixed effect model outputs for β_S at the Wetland extent. Reference level is Fall for Season.

effect	component	term	estimate	std.error	statistic	p.value
fixed	cond	(Intercept)	0.975	0.039	24.698	0
fixed	cond	Spring	-0.031	0.005	-5.894	0
fixed	cond	Summer	-0.099	0.006	-16.956	0
fixed	cond	Winter	-0.047	0.006	-7.873	0

Table S2. Generalized-linear mixed effect model outputs for β_{PIE} at the Wetland extent. Reference level is Fall for Season.

effect	component	term	estimate	std.error	statistic	p.value
fixed	cond	(Intercept)	0.244	0.039	6.207	0.000
fixed	cond	Spring	0.028	0.015	1.920	0.055
fixed	cond	Summer	0.021	0.016	1.282	0.200
fixed	cond	Winter	-0.004	0.016	-0.216	0.829

Table S3. Generalized-linear mixed effect model outputs for β_C at the Wetland extent. Reference level is Fall for Season.

effect	component	term	estimate	std.error	statistic	p.value
fixed	cond	(Intercept)	0.276	0.036	7.628	0.000
fixed	cond	Spring	0.016	0.007	2.442	0.015
fixed	cond	Summer	-0.016	0.007	-2.214	0.027
fixed	cond	Winter	-0.016	0.007	-2.078	0.038

Ecoregion extent analysis

Table S4. Generalized-linear mixed effect model outputs for β_S at the Ecoregion extent. Reference levels are Eastern Temperate Forests and Fall for Ecoregion and Season, respectively.

effect	component	term	estimate	std.error	statistic	p.value
fixed	cond	(Intercept)	0.934	0.025	36.839	0.000
fixed	cond	GREAT PLAINS	0.124	0.006	21.495	0.000
fixed	cond	MARINE WEST COAST FOREST	-0.097	0.006	-16.730	0.000
fixed	cond	NORTH AMERICAN DESERTS	0.146	0.006	25.054	0.000
fixed	cond	NORTHWESTERN FORESTED MOUNTAINS	-0.009	0.007	-1.302	0.193
fixed	cond	Spring	-0.040	0.005	-7.584	0.000
fixed	cond	Summer	-0.069	0.005	-13.159	0.000
fixed	cond	Winter	-0.054	0.006	-9.580	0.000

Table S5. Generalized-linear mixed effect model outputs for β_{PIE} at the Ecoregion extent. Reference levels are Eastern Temperate Forests and Fall for Ecoregion and Season, respectively.

effect	component	term	estimate	std.error	statistic	p.value
fixed	cond	(Intercept)	0.336	0.032	10.548	0.000
fixed	cond	GREAT PLAINS	0.072	0.031	2.342	0.019
fixed	cond	MARINE WEST COAST FOREST	0.011	0.031	0.345	0.730
fixed	cond	NORTH AMERICAN DESERTS	0.094	0.031	3.031	0.002
fixed	cond	NORTHWESTERN FORESTED MOUNTAINS	0.104	0.034	3.042	0.002
fixed	cond	Spring	0.070	0.028	2.496	0.013
fixed	cond	Summer	0.100	0.028	3.607	0.000
fixed	cond	Winter	0.055	0.030	1.813	0.070

Table S6. Generalized-linear mixed effect model outputs for β_C at the Ecoregion extent. Reference levels are Eastern Temperate Forests and Fall for Ecoregion and Season, respectively.

effect	component	term	estimate	std.error	statistic	p.value
fixed	cond	(Intercept)	0.285	0.016	17.341	0.000
fixed	cond	GREAT PLAINS	0.047	0.010	4.755	0.000
fixed	cond	MARINE WEST COAST FOREST	-0.021	0.010	-2.093	0.036
fixed	cond	NORTH AMERICAN DESERTS	0.090	0.010	9.035	0.000
fixed	cond	NORTHWESTERN FORESTED MOUNTAINS	0.031	0.011	2.757	0.006
fixed	cond	Spring	-0.001	0.009	-0.070	0.945
fixed	cond	Summer	0.003	0.009	0.341	0.733
fixed	cond	Winter	0.001	0.010	0.062	0.951

Continental extent analysis

Table S7. Generalized-linear mixed effect model outputs for β_S at the Continental extent. Reference level is Fall for Season.

effect	component	term	estimate	std.error	statistic	p.value
fixed	cond	(Intercept)	1.442	0.033	43.572	0
fixed	cond	Spring	0.022	0.003	8.144	0
fixed	cond	Summer	0.014	0.003	5.165	0
fixed	cond	Winter	0.016	0.003	5.839	0

Table S8. Generalized-linear mixed effect model outputs for β_{PIE} at the Continental extent. Reference level is Fall for Season.

effect	component	term	estimate	std.error	statistic	p.value
fixed	cond	(Intercept)	0.526	0.037	14.111	0

effect	component	term	estimate	std.error	statistic	p.value
fixed	cond	Spring	0.135	0.019	7.080	0
fixed	cond	Summer	0.187	0.019	9.790	0
fixed	cond	Winter	0.083	0.019	4.377	0

Table S9. Generalized-linear mixed effect model outputs for β_C at the Continental extent. Reference level is Fall for Season.

effect	component	term	estimate	std.error	statistic	p.value
fixed	cond	(Intercept)	0.467	0.024	19.200	0
fixed	cond	Spring	0.057	0.007	8.278	0
fixed	cond	Summer	0.101	0.007	14.755	0
fixed	cond	Winter	0.036	0.007	5.202	0

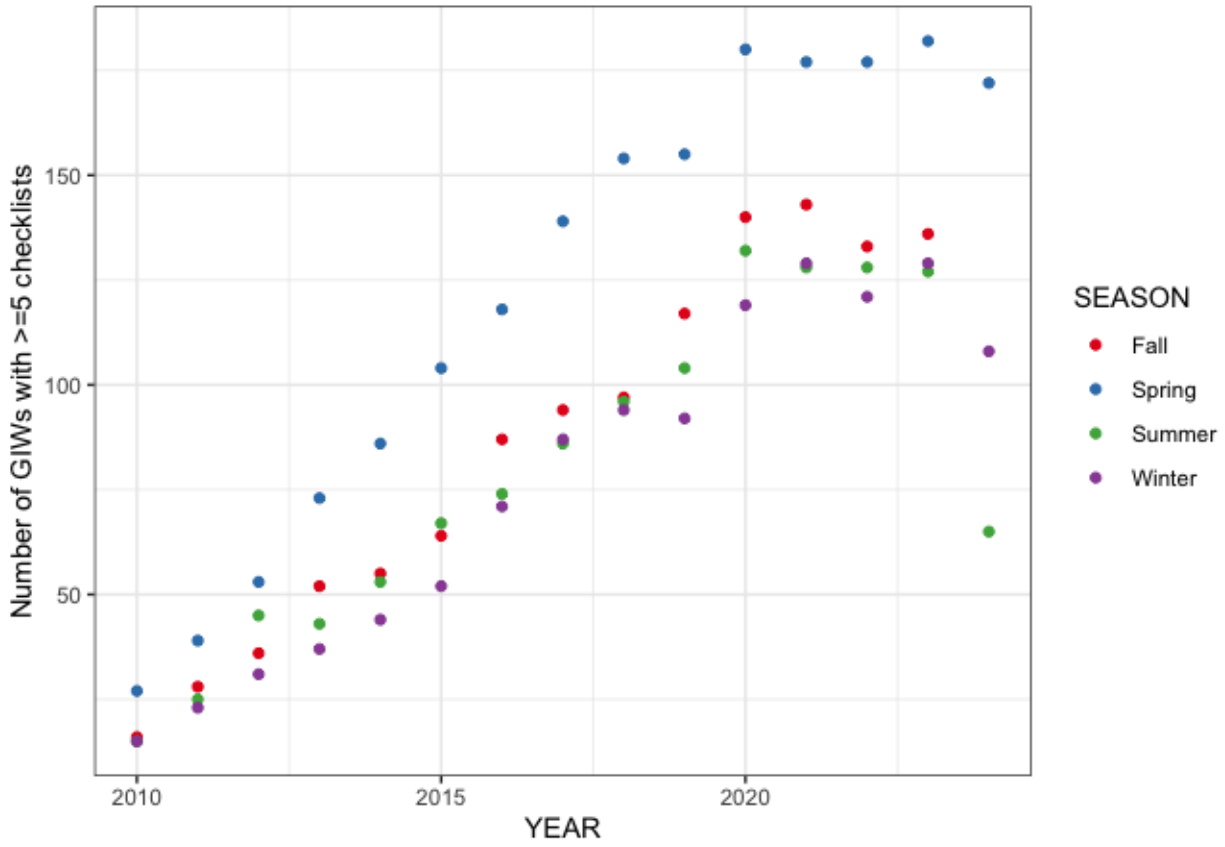


Figure S1. Number of GIW that meet sampling requirements of at least 5 submitted checklists each year and season.

Seasonal differences in β-diversity

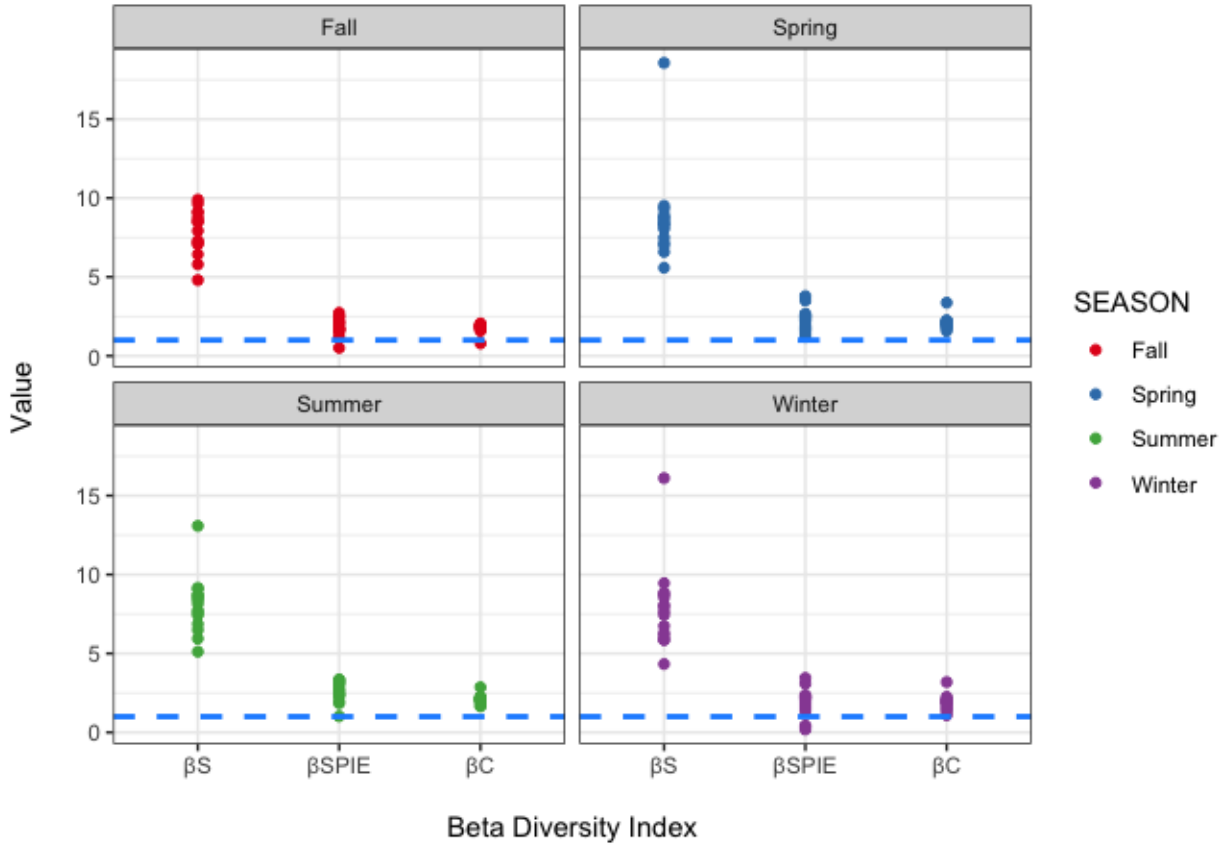


Figure S2. Seasonal β-diversity indices between all GIWs at the continental extent. Higher deviation in either direction of the dashed red line (y=1) indicates higher β-diversity. Different points represent different years.

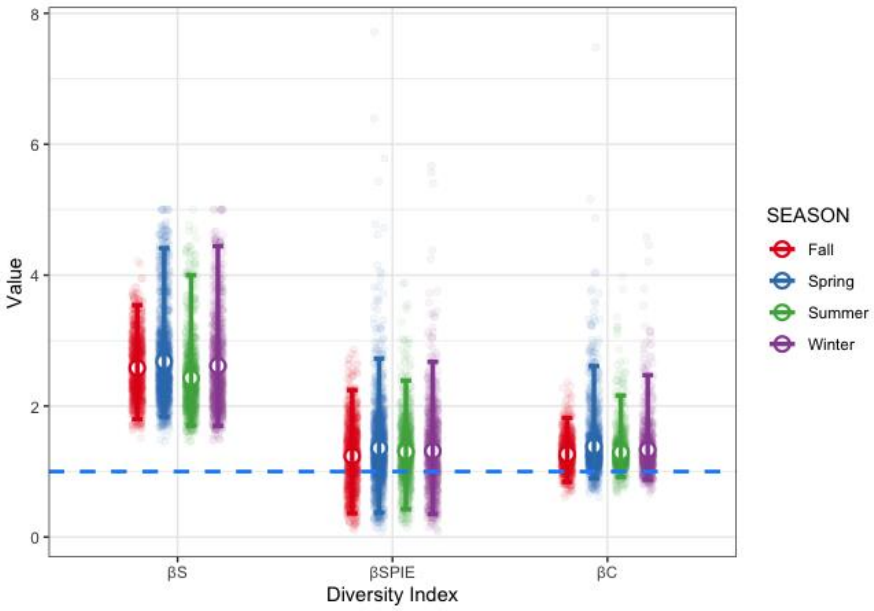


Figure S3. Seasonal β-diversity indices between all GIWs at the wetland extent. White points represent mean values and error bars display 95% confidence intervals. Confidence intervals overlapping 1 (dashed blue line) indicate little to no change in β-diversity.

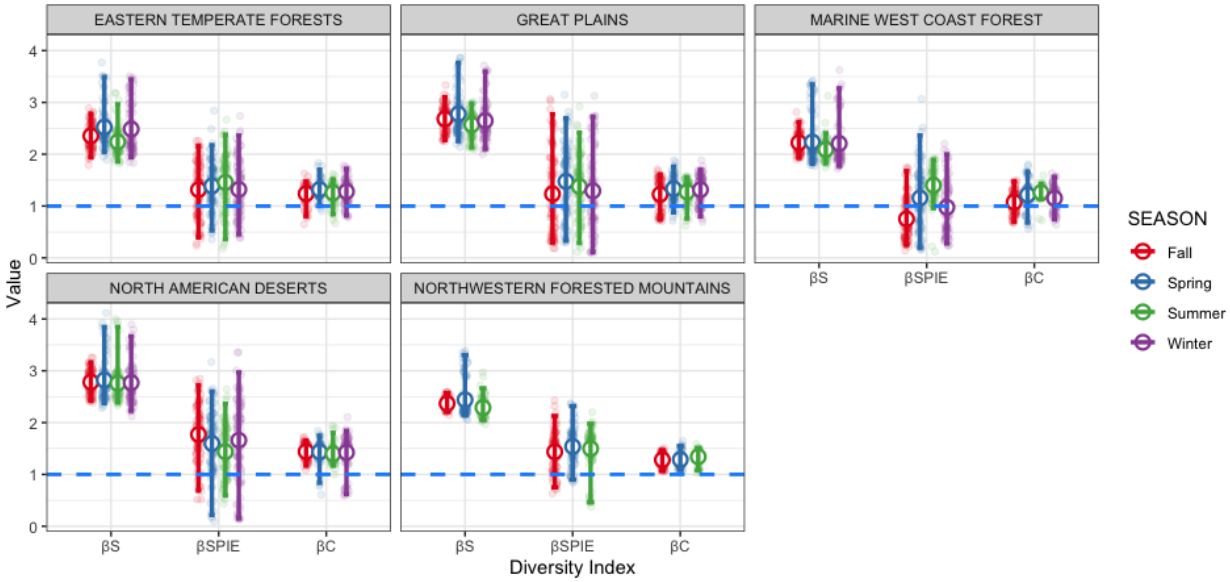


Figure S4. Seasonal β-diversity indices between GIWs at the ecoregion extent. White points represent mean values and error bars display 95% confidence intervals. Confidence intervals overlapping 1 (dashed blue line) indicate little to no change in β-diversity.

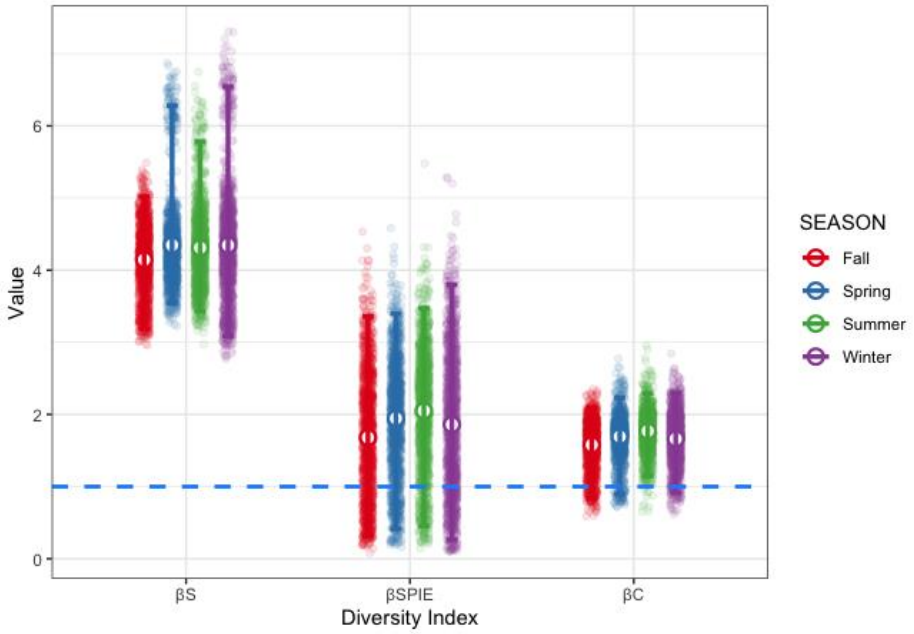


Figure S5. Seasonal β-diversity indices between all GIWs at the continental extent bootstrapped *n*=99 times with only *n*=1 GIW per ecoregion per year. White points represent mean values and error bars display 95% confidence intervals. Confidence intervals overlapping 1 (dashed blue line) indicate little to no change in β-diversity.

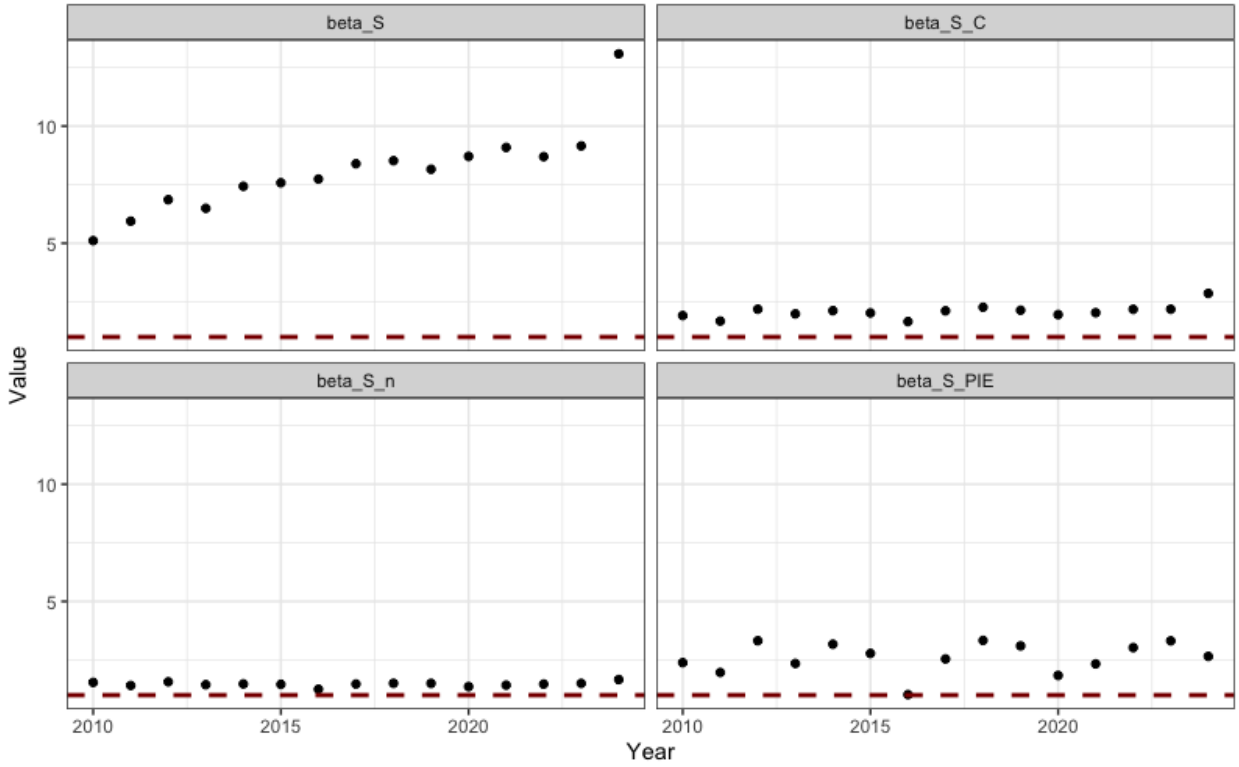


Figure S6. β-diversity at the continental extent broken up by year for summer only. Higher deviation in either direction of the dashed red line (y=1) indicates higher β-diversity.

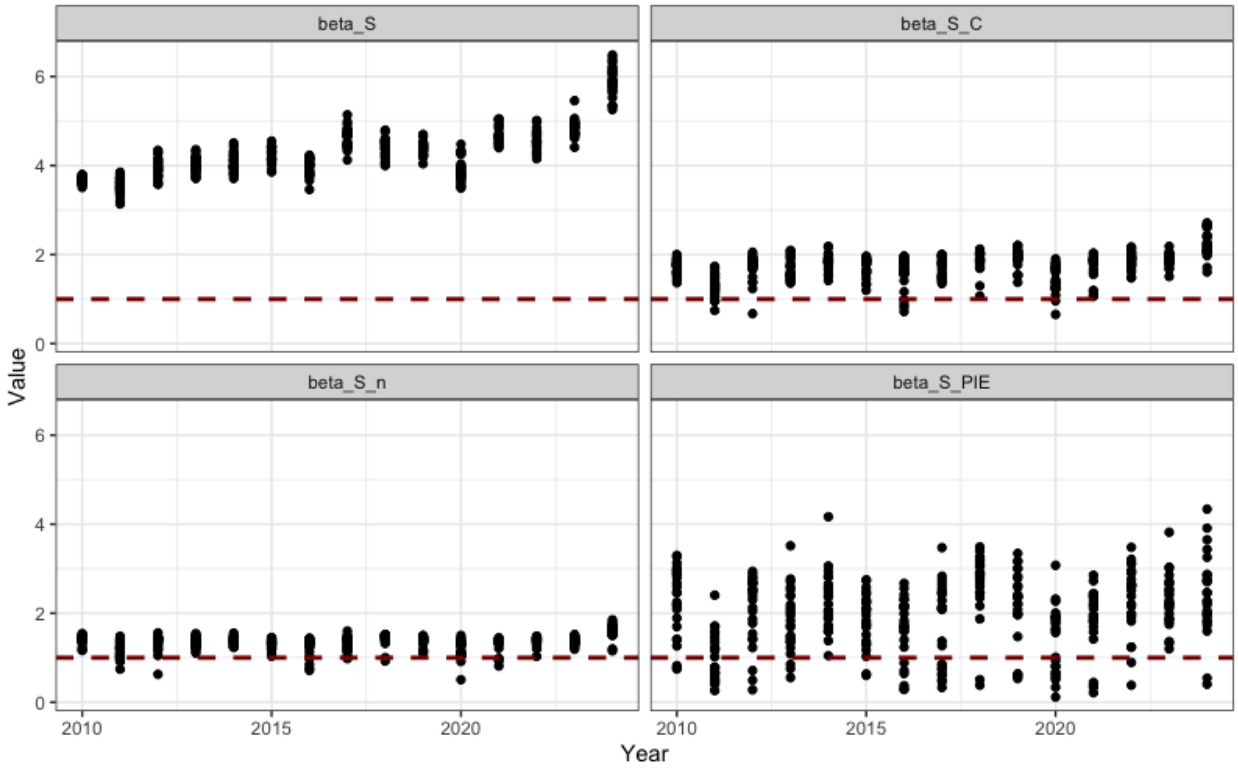
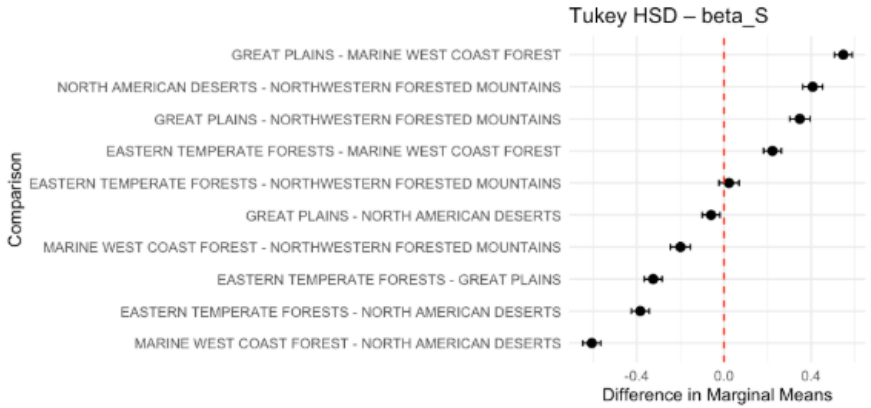
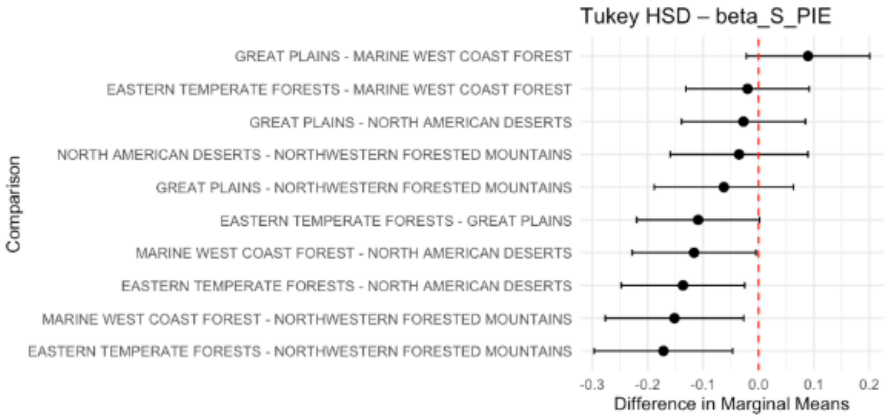


Figure S7. β-diversity bootstrapped at n=1 GIW per ecoregion at the continental extent broken up by year for summer only. Higher deviation in either direction of the dashed red line (y=1) indicates higher β-diversity.

A


Tukey HSD – beta_S
GREAT PLAINS - MARINE WEST COAST FOREST
NORTH AMERICAN DESERTS - NORTHWESTERN FORESTED MOUNTAINS
GREAT PLAINS - NORTHWESTERN FORESTED MOUNTAINS
EASTERN TEMPERATE FORESTS - MARINE WEST COAST FOREST
EASTERN TEMPERATE FORESTS - NORTHWESTERN FORESTED MOUNTAINS
GREAT PLAINS - NORTH AMERICAN DESERTS
MARINE WEST COAST FOREST - NORTHWESTERN FORESTED MOUNTAINS
EASTERN TEMPERATE FORESTS - GREAT PLAINS
EASTERN TEMPERATE FORESTS - NORTH AMERICAN DESERTS
MARINE WEST COAST FOREST - NORTH AMERICAN DESERTS
Comparison
-0.4
0.0
0.4
Difference in Marginal Means

B


Tukey HSD – beta_S_PIE
GREAT PLAINS - MARINE WEST COAST FOREST
EASTERN TEMPERATE FORESTS - MARINE WEST COAST FOREST
GREAT PLAINS - NORTH AMERICAN DESERTS
NORTH AMERICAN DESERTS - NORTHWESTERN FORESTED MOUNTAINS
GREAT PLAINS - NORTHWESTERN FORESTED MOUNTAINS
EASTERN TEMPERATE FORESTS - GREAT PLAINS
MARINE WEST COAST FOREST - NORTH AMERICAN DESERTS
EASTERN TEMPERATE FORESTS - NORTH AMERICAN DESERTS
MARINE WEST COAST FOREST - NORTHWESTERN FORESTED MOUNTAINS
EASTERN TEMPERATE FORESTS - NORTHWESTERN FORESTED MOUNTAINS
Comparison
-0.3
-0.2
-0.1
0.0
0.1
0.2
Difference in Marginal Means

C

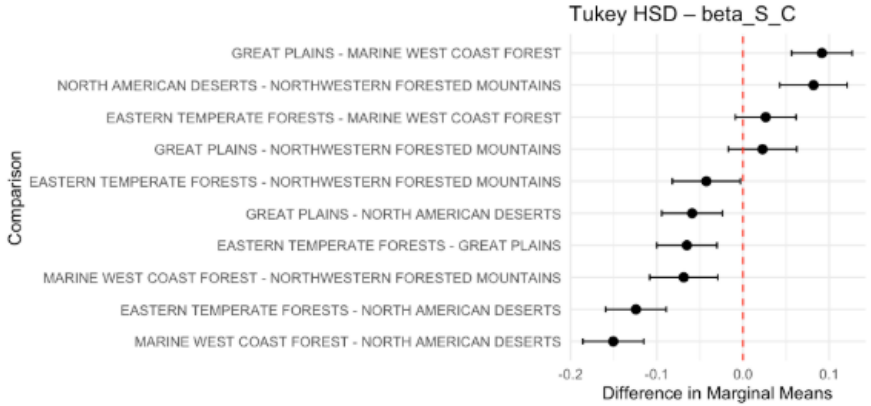

Tukey HSD – beta_S_C
GREAT PLAINS - MARINE WEST COAST FOREST
NORTH AMERICAN DESERTS - NORTHWESTERN FORESTED MOUNTAINS
EASTERN TEMPERATE FORESTS - MARINE WEST COAST FOREST
GREAT PLAINS - NORTHWESTERN FORESTED MOUNTAINS
EASTERN TEMPERATE FORESTS - NORTHWESTERN FORESTED MOUNTAINS
GREAT PLAINS - NORTH AMERICAN DESERTS
EASTERN TEMPERATE FORESTS - GREAT PLAINS
MARINE WEST COAST FOREST - NORTHWESTERN FORESTED MOUNTAINS
EASTERN TEMPERATE FORESTS - NORTH AMERICAN DESERTS
MARINE WEST COAST FOREST - NORTH AMERICAN DESERTS
Comparison
-0.2
-0.1
0.0
0.1
Difference in Marginal Means

Figure S8. Tukey Honest significant difference test results for ecoregion β-diversity indices.

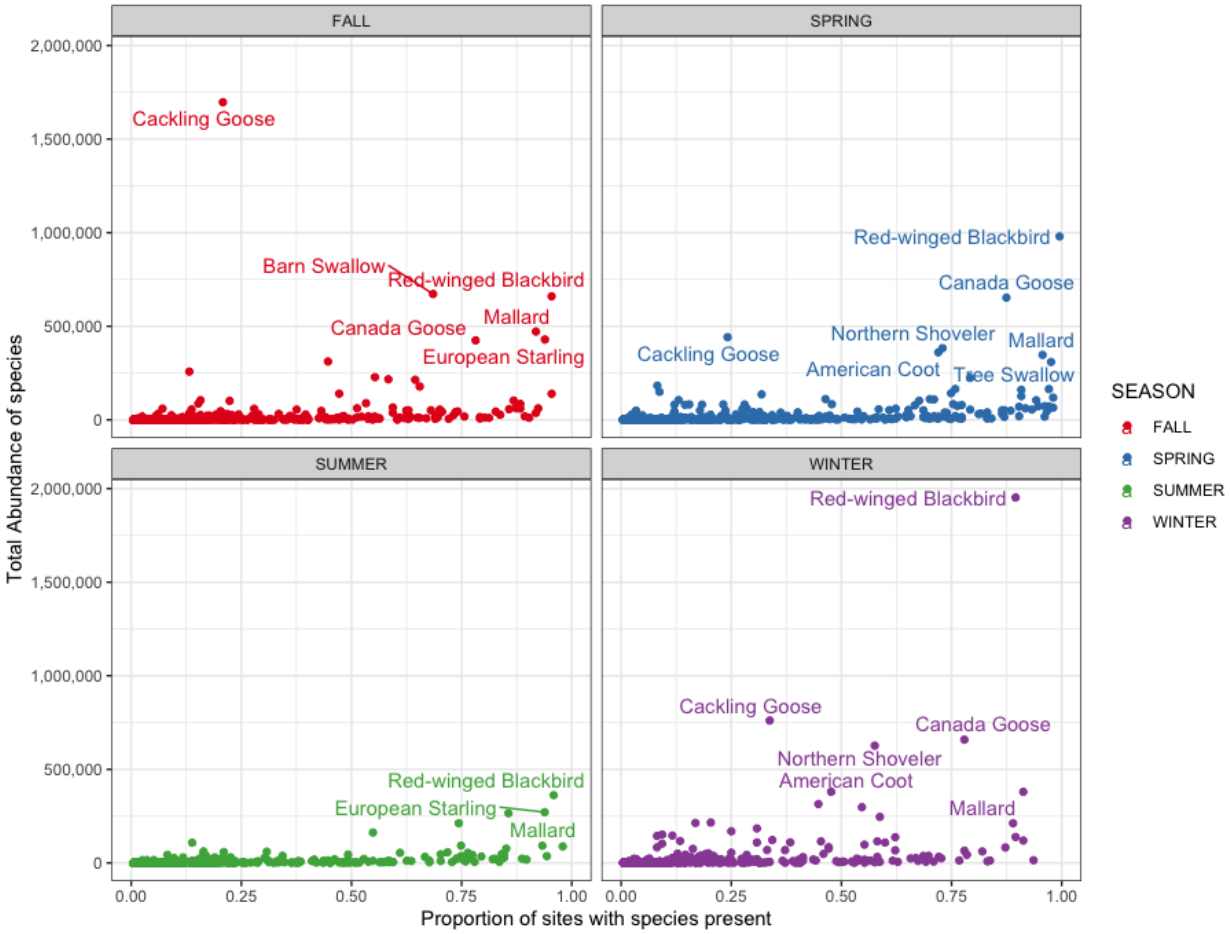


Figure S9. Total abundance of all *n*=587 species present across all isolated wetland sites from each season (Winter *n*=172, Spring *n*=207, Summer *n*=195, Fall *n*=197) with the proportion of wetland sites (%) they were present in.

Hyperabundant Species Removed

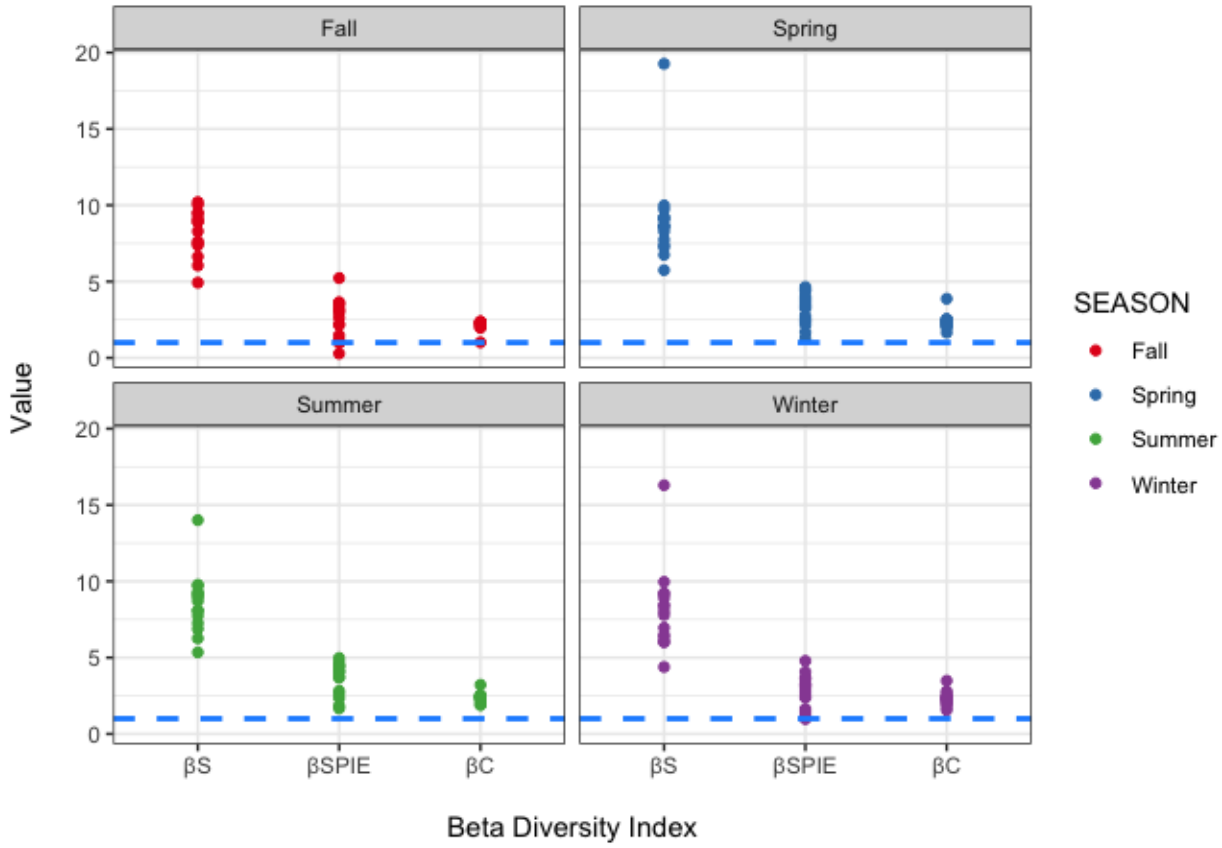


Figure S10. β-diversity indices between all GIWs at the continental extent with *n*=5 most abundant species removed. Higher deviation in either direction of the dashed red line (*y*=1) indicates higher β-diversity. Different points represent different years.

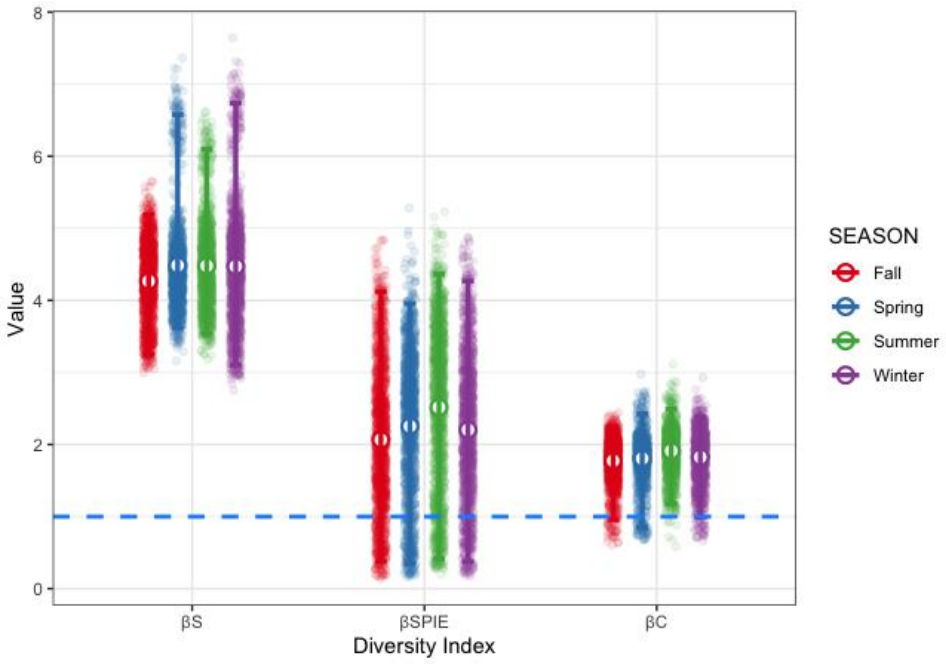


Figure S11. β-diversity indices between GIWs at the continental extent bootstrapped *n*=99 times with only *n*=1 GIW per ecoregion per year, with *n*=5 most abundant species removed. White points represent mean values and error bars display 95% confidence intervals. Confidence intervals overlapping 1 (dashed blue line) indicate little to no change in β-diversity.

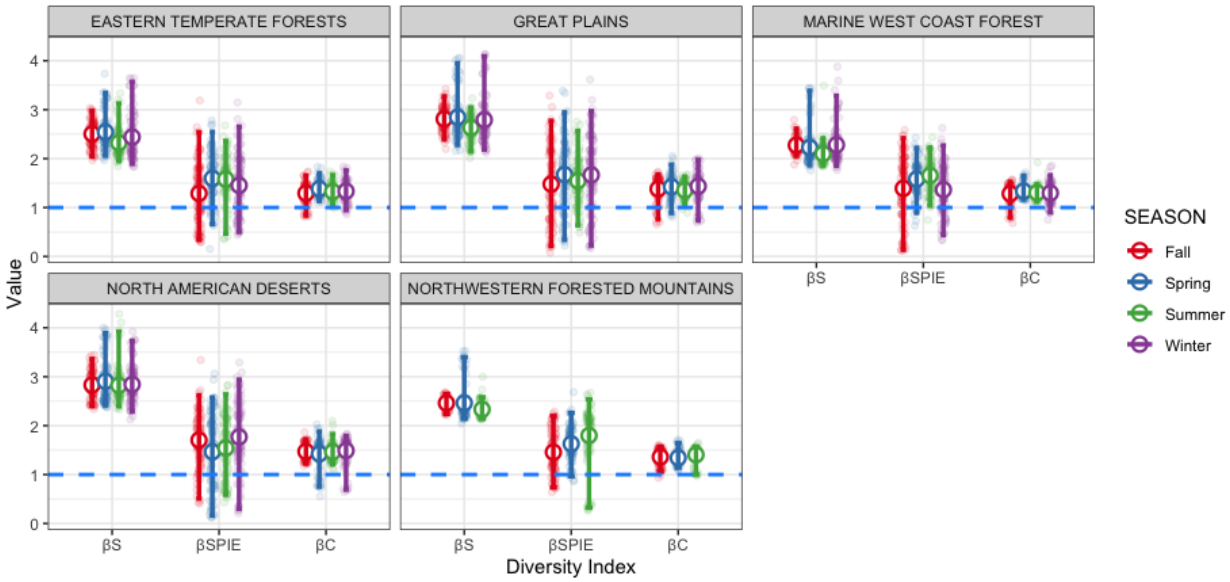


Figure S12. β-diversity indices within ecoregions, with *n*=5 most abundant species removed. Black points represent mean values, and black error bars display 95% confidence intervals. Confidence intervals overlapping 1 (dashed red line) indicate little to no change in β-diversity. Letters above error bars denote whether indices differ between ecoregions.

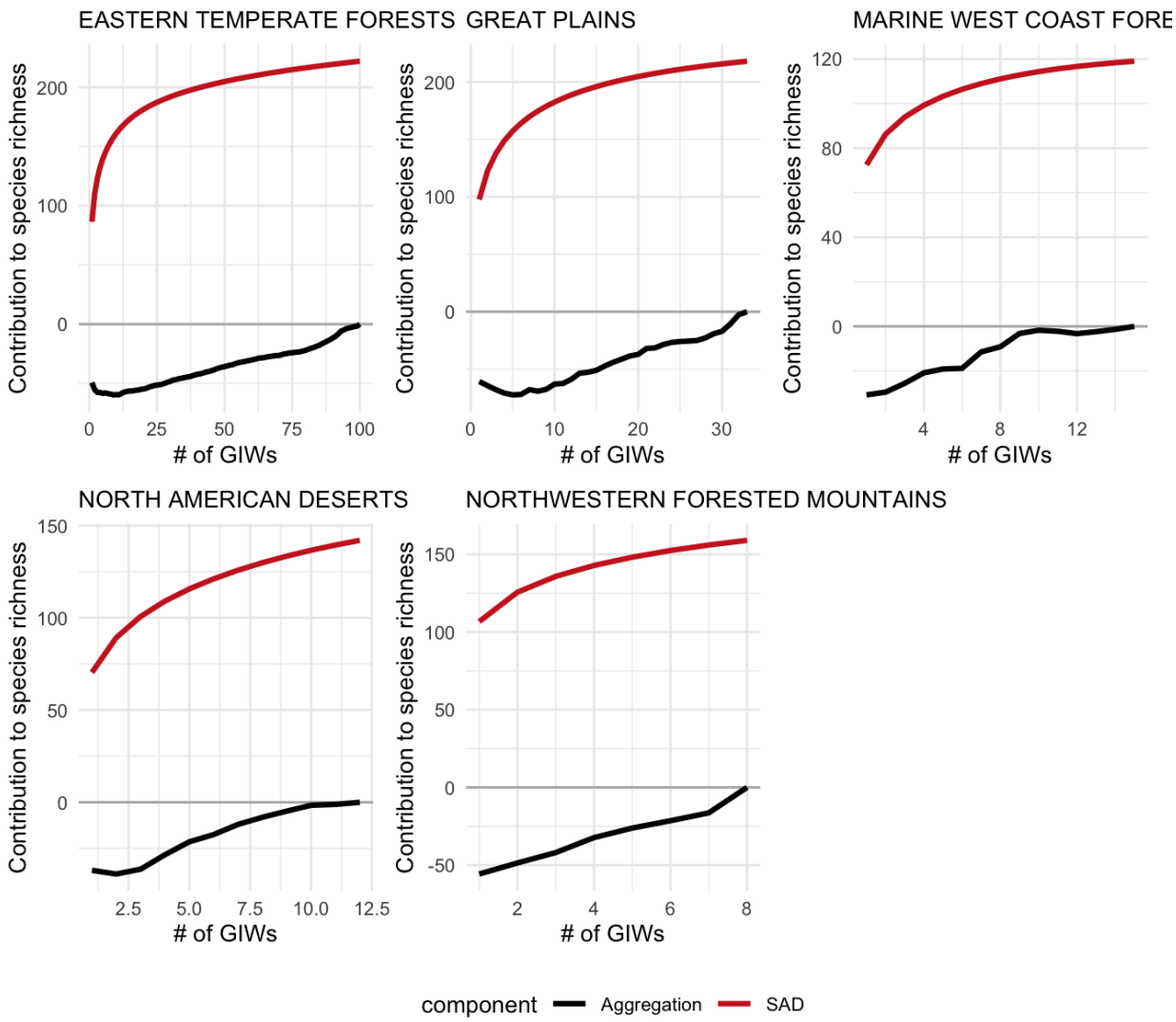


Figure S13. Contribution of the species-abundance distribution (SAD) and aggregation to β-diversity at the ecoregion extent. Curves are relative to one another, with proportional increases positively associated with higher-than-expected contributions to β-diversity and vice-versa.

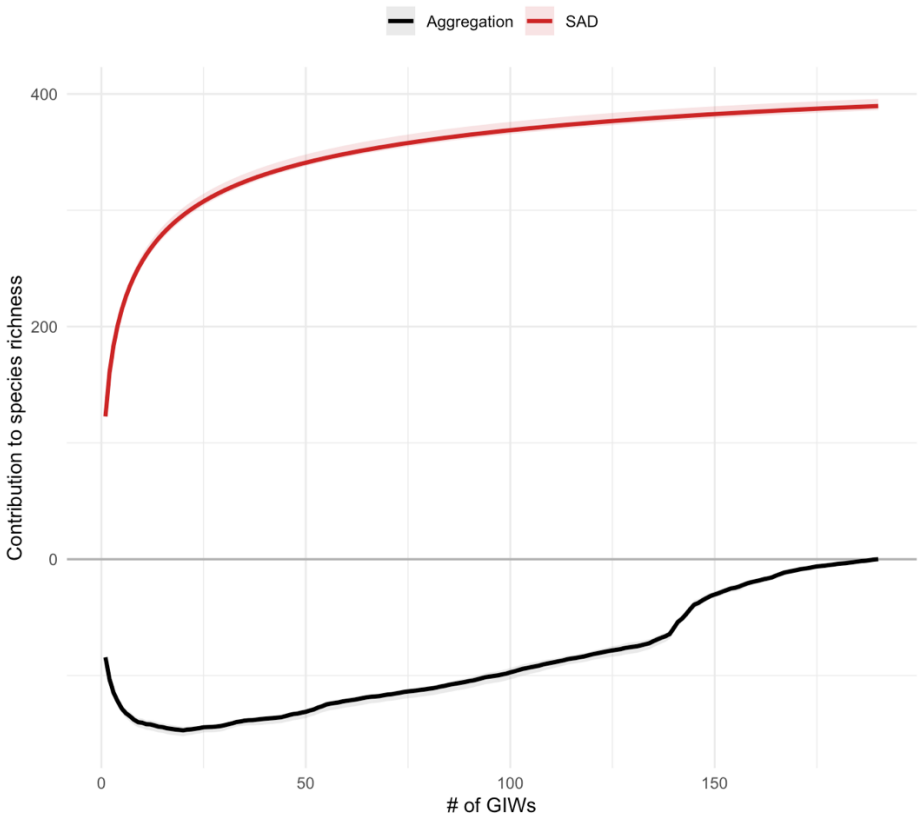


Figure S14. Contribution of the species-abundance distribution (SAD) and aggregation to β-diversity at the continental extent. Curves are relative to one another, with proportional increases positively associated with higher-than-expected contributions to β-diversity and vice-versa.

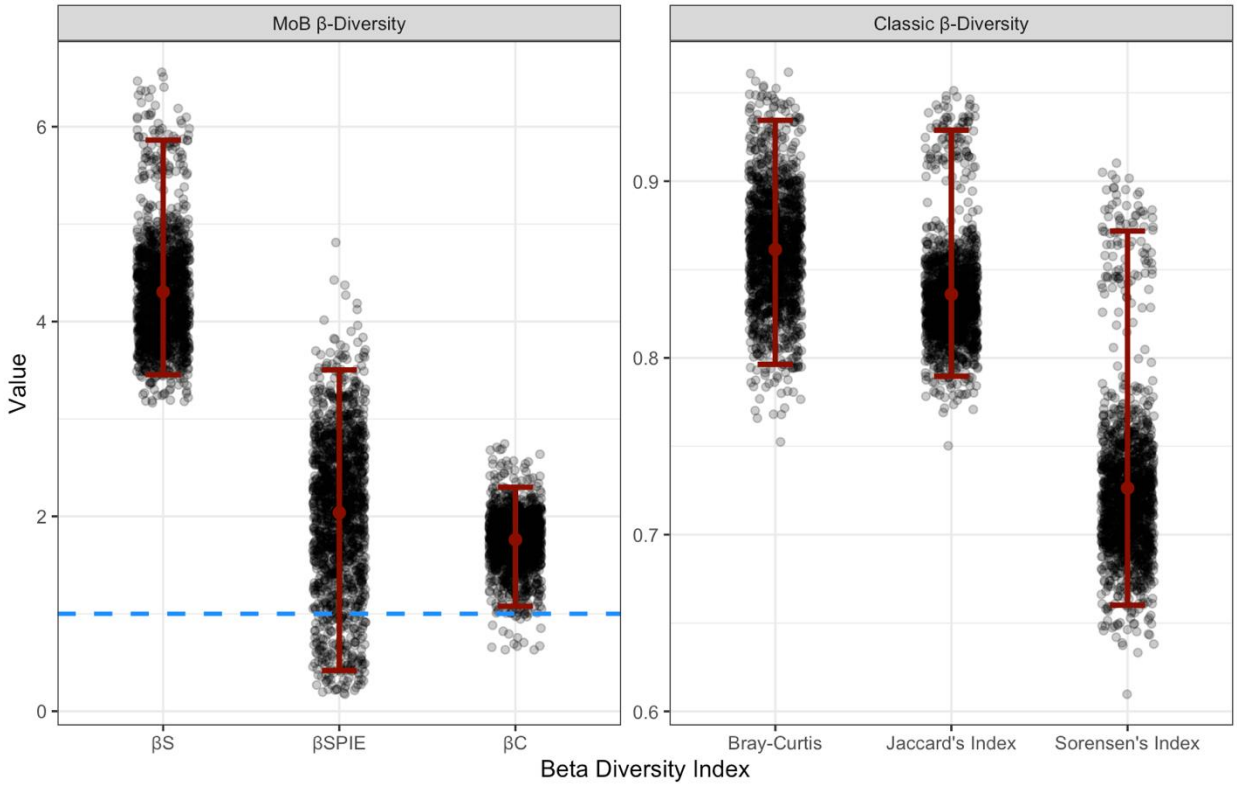


Figure S15. Multi-metric approach with 3 additional classic beta diversity metrics at the continental extent. The Classic B-diversity metrics panel consists of 3 metrics (Bray-Curtis Dissimilarity, Jaccard's Dissimilarity, and Sorensen's Dissimilarity Indices) all of which are on a scale of 0-1, 1 being completely dissimilar and 0 being completely the same.

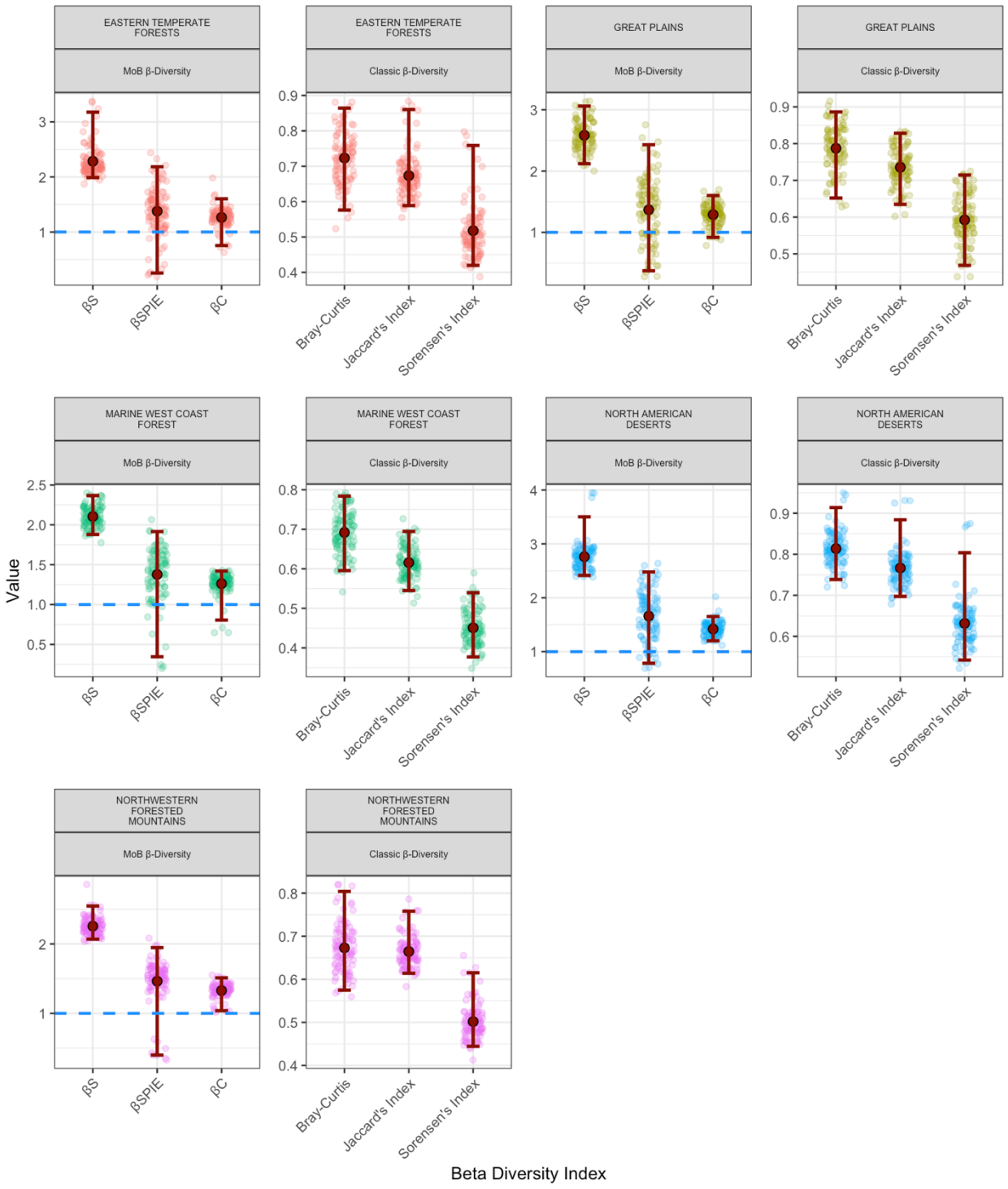


Figure S16. Multi-metric approach with 3 additional classic beta diversity metrics at the continental extent. The Classic B-diversity metrics panel consists of 3 metrics (Bray-Curtis Dissimilarity, Jaccard's Dissimilarity, and Sorensen's Dissimilarity Indices) all of which are on a scale of 0-1, 1 being completely dissimilar and 0 being completely the same.