## Research

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# Local species diversity, β-diversity and climate influence the regional stability of bird biomass across North America

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Biodiversity often stabilizes aggregate ecosystem properties (e.g. biomass) at small spatial scales. However, the importance of species diversity within communities and variation in species composition among communities (β-diversity) for stability at larger scales remains unclear. Using a continental-scale analysis of 1657 North American breeding-bird communities spanning 20-years and 35 ecoregions, we show local species diversity and β-diversity influence two components of regional stability: local stability (stability of bird biomass within sites) and spatial asynchrony (asynchronous fluctuations in biomass among sites). We found spatial asynchrony explained three times more variation in regional stability of bird biomass than did local stability. This result contrasts with studies at smaller spatial scales—typically plant metacommunities under 1 ha—that find local stability to be more important than spatial asynchrony. Moreover, spatial asynchrony of bird biomass increased with bird β-diversity and climate heterogeneity (temperature and precipitation), while local stability increased with species diversity. Our study reveals new insights into the scale-dependent processes regulating ecosystem stability, providing evidence that both local biodiversity loss and homogenization can destabilize ecosystem processes at biogeographic scales.

## 1. Introduction

Biodiversity loss can decrease the stability of key ecosystem properties such as total biomass and primary productivity [1–6]. To date, evidence linking biodiversity and ecosystem stability comes primarily from small-scale experiments in grasslands and aquatic microcosms [7–9]. However, the extent to which local species diversity contributes to ecosystem stability at large scales remains unclear. This scale mismatch has fuelled controversy regarding the consequences of biodiversity loss [10–14], especially in light of recent studies showing the number of plant, fish and terrestrial animal species does not appear to be declining at small scales [10,15,16]. By contrast, the species composition of ecological communities is becoming homogenized due to myriad processes including biological invasions, climate change, intensifying land use and selective responses of species to human and natural disturbance [15,17–24].

Despite decades of interest in diversity–stability relationships, key gaps remain in our understanding of how and why biodiversity at different scales—from species diversity within local communities (local diversity) to variation in species composition among communities (β-diversity)—contributes to ecosystem stability at larger scales [25–28]. Recent theory predicts that ecosystem stability at large scales depends on how biodiversity influences two key components of regional stability: the temporal stability of ecosystem properties within sites (local stability) (figure 1a,b) and how much ecosystem properties among sites in a region fluctuate asynchronously (spatial asynchrony) (figure 1c) [25,29]. At small scales, local species diversity can increase local stability when co-occurring species differ in their responses to environmental conditions [2,3,30–36] or when diversity is
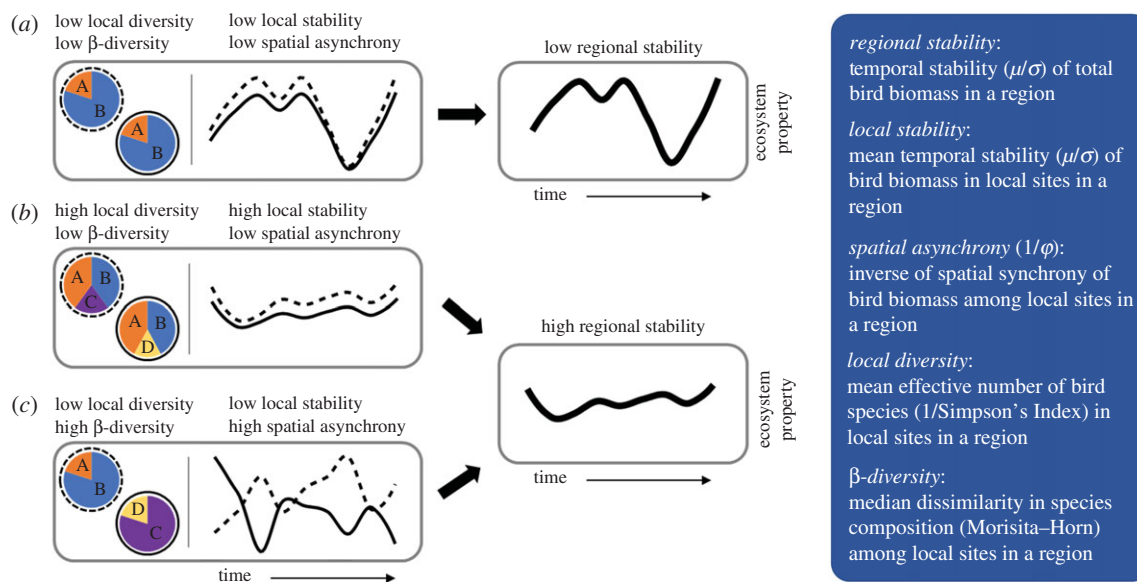
**Figure 1.** Conceptual diagram showing hypothesized effects of biodiversity on the stability of an aggregate ecosystem property, like total biomass. The dashed and solid lines indicate different sites within a region, with letters for species and colours for their relative abundance within sites. There are two paths to regional stability: local stability (average temporal stability of locations in a region) and spatial asynchrony (temporal asynchrony among locations within a region). In scenario (*a*), low β-diversity (same species composition in both sites) causes low spatial asynchrony, and low local species diversity (*S* = 2 species) causes local biomass to be unstable; thus, regional biomass is unstable. (*b*) Low β-diversity causes low spatial asynchrony, but higher local species diversity (*S* = 3) stabilizes local biomass; thus, regional biomass is stable. (*c*) High β-diversity causes high spatial asynchrony, compensating for low local species diversity (*S* = 2) and instability in local biomass; thus, regional biomass is stable. (Online version in colour.)

maintained by spatial processes like dispersal [37,38]. Yet, local stability can vary non-monotonically with local diversity—yielding positive, negative or neutral relationships [39,40]—making it unclear how important local diversity is to stability at larger scales. At larger scales, ecosystem stability can be attained, even when local species diversity is low, if β-diversity increases spatial asynchrony (figure 1*c*) [25,29]. In seagrass ecosystems, for example, β-diversity of crustacean grazers caused spatially variable effects of herbivory, thus causing spatial asynchrony that stabilized plant biomass [41].

The ecological mechanisms underlying spatial asynchrony are difficult to discern because spatial asynchrony may result from β-diversity, environmental heterogeneity or the interplay of both [25]. Environmental heterogeneity and β-diversity can jointly increase spatial asynchrony when species sort among communities that differ in abiotic (e.g. climate, resource availability) or biotic (competitors, natural enemies) conditions [42,43]. Alternatively, environmental heterogeneity can cause spatial asynchrony without directly altering β-diversity [25,44]. For example, ecosystem processes like productivity can vary spatially when abiotic conditions mediate energy inputs or the strength of species interactions [45]. However, most prior tests of the importance of β-diversity and spatial asynchrony come from studies of plant communities at relatively small scales—metacommunities less than 1 ha in size (median 0.5 ha) and/or single grasslands [26,46,47]—which may not contain the abiotic heterogeneity or variation in species composition necessary to drive spatial asynchrony. Consistent with these expectations, these studies typically found local stability was more important than plant β-diversity or spatial asynchrony for stabilizing biomass at larger scales [26,47]. The lack of studies across heterogeneous ecosystems or outside of plant communities limits our understanding of how and why biodiversity contributes to ecosystem stability at large, regional scales.

We evaluated the importance of bird species diversity, β-diversity and climate heterogeneity for stabilizing regional bird biomass across North America. We evaluated these hypotheses using continental-scale data from the North American Breeding Bird Survey (BBS: www.pwrc.usgs.gov/) [48,49]. The spatial and temporal scale covered by BBS provides an opportunity to test theory about regional diversity–stability relationships over a range of conditions that are difficult to emulate within the constraints of controlled experiments. Specifically, we used data for 342 species of breeding birds collected over 20 years at 1657 local sites distributed across 35 large regions ($5 \times 10^4$–$1 \times 10^8$ ha) with diverse biogeographic histories, climates and ecotypes (see electronic supplementary material, figure S1 and table S1). Additionally, the stability of total bird biomass may indirectly reflect numerous ecosystem processes because birds are supported by lower trophic levels, are critical seed dispersers, and major consumers of insect herbivores that limit primary production [50]. Our analysis proceeded through two hierarchical steps. First, we partitioned variation in the stability of regional bird biomass across regions into components explained by local stability and spatial asynchrony to quantify their relative importance. Second, we developed a structural equation model integrating key predictions for how local bird species diversity, β-diversity, and climate heterogeneity contribute to local stability, spatial asynchrony, and regional stability of total bird biomass. Our results reveal new evidence suggesting that variation in species composition and spatial asynchrony may be among the most important drivers of stability when scaling up from local communities to regional ecosystems.

## 2. Material and methods

### (a) Breeding Bird Survey data processing
BBS data provide an opportunity to evaluate the importance of biodiversity for stability at regional scales because of their extensive spatial and temporal replication, and standardized data-collection

methods that yield sound comparisons of bird relative abundances across space and time. Birds are censused annually during the height of the breeding season along *ca* 4100 routes (hereafter 'sites') distributed across North America, primarily north of Mexico. Each site is a *ca* 40 km route with 50 stops separated by *ca* 800 m. At each stop, trained observers conduct 3-min point counts to record birds heard or seen within 400 m. BBS sites occur within larger regional units with boundaries defined using the North American Bird Conservation Initiative's Bird Conservation Regions (hereafter 'regions'). Each region was defined by ecoregions representing areas with distinct species compositions and biogeographic histories [51–53]. The standardized BBS sampling scheme has some limitations that can affect the detection of particular species [54]. To reduce potential detection bias, we follow standard practices and excluded species not well sampled by point-count techniques during sampling periods, removed sites with low temporal replication, aggregated bird counts across years to increase sample coverage, and used estimates of diversity that focus on relative abundance of common species that are well-represented in the data (these steps are detailed below).

First, we excluded observations for individual sites that do not satisfy the minimum BBS requirements for trends analyses (e.g. when observations were made outside the breeding season, activity period or during inclement weather). Next, we quantified the total number of sites that were surveyed at least 16 years during 20-year windows occurring between 1966 and 2016. We used a minimum 80% sample coverage (16–20 years) to maximize the number of regions available for our analyses ($n = 35$); thus, extending geographical extent to the contiguous U.S., Alaska, and southern provinces of Canada (electronic supplementary material, table S1). Furthermore, this cut-off increased spatial replication within regions, allowing more accurate estimates of biodiversity and stability components. We chose a 20-year times series because this ensures stability is estimated over multiple generations [55] and is less prone to variability or transient dynamics that may dominate shorter time series. The 1994–2013 period provided the most sites satisfying the trade-off between temporal and spatial coverage; $n = 1657$ (electronic supplementary material, figure S1) (mean/median = 47/30 sites per region).

We focus on passerine species (order Passeriformes) because (i) they are the most-diverse clade of birds in North America; (ii) they have relatively similar body sizes which reduces detection bias [56,57]; and (iii) passerines are particularly suited to point-count techniques used by the BBS [58]. Our analysis includes 342 species of passerines (mean per region = 107; range = 43–153 species).

## (b) Quantifying biodiversity and climate heterogeneity

Within each site, we summed the abundances for each species across all 50 stops and all 20 years; therefore, each site-level diversity estimate is a more complete sample which minimizes the role of detection bias in diversity estimates [54]. We calculated local and regional species diversity as the effective number of species using the Inverse Simpson's Index, i.e. Simpson's diversity. Simpson's diversity has a number of useful properties that make it ideal for this study: (i) it integrates species' richness and relative abundance, (ii) has high precision, and (iii) is not sensitive to differences in sample size [57]. We averaged Simpson's diversity across sites to calculate the mean local species diversity for each region. We calculated β-diversity for each region as the median dissimilarity in species composition among sites using the Morisita–Horn index. Morisita–Horn dissimilarity is ideal for our study because it down-weights rare species that may be prone to detection bias and accurately reflects differences in the relative abundance of dominant species [57]. Dominant species are expected to contribute disproportionately to variation in biomass because energy is transferred primarily through common species [59,60]. Although different β-diversity metrics may reflect slightly different

processes, Morisita–Horn dissimilarity was significantly correlated with both Bray–Curtis dissimilarity ($r = 0.99$, $p < 0.01$) and the multiplicative partitioning of Simpson's diversity ($r = 0.52$, $p < 0.001$). We calculated local diversity and β-diversity using the 'vegan::diversity()' and 'vegan::vegdist()' functions [61], respectively, in R v. 3.4.1. Using mixed models, we ensured that aggregating local diversity and β-diversity across all years for each region was reasonable because neither mean local diversity, spatial β-diversity, nor species compositions at the regional scale showed general trends over the time period of this study (electronic supplementary material, figure S2).

Climate, especially precipitation and temperature, are among the strongest drivers of bird biomass and fitness; both directly through stress to birds and indirectly by influencing behaviour, foraging quality, resource availability and net-primary production [53,62–64]. Heterogeneity in climate conditions is also influenced by variation in topography, and thus serves as a gross metric encompassing a broader set of interrelated environmental drivers [65]. We calculated climate heterogeneity for each region as the multivariate dispersion of annual mean temperature and precipitation among sites. Climate variables for each site were obtained from the Climatic Research Unit's high-resolution data (version CRU TS3.10) based on monthly observations from 1994 to 2013 interpolated to $0.5° × 0.5°$ latitude/longitude grid cells [66]. These data are free and publicly available at www.cru.uea.ac.uk. First, we standardized (centred and scaled) the climate variables across all 1657 sites within the study extent. Next, for each region, we calculated the mean square of the Euclidean distances from each site to that region's spatial median in multivariate (climate) principal coordinate space. This is similar to calculating the climate niche space of each region using the outlying mean index [67,68].

## (c) Quantifying stability

We summed bird counts across all years to calculate mean local diversity and β-diversity for each region, which we then relate to temporal variability in an emergent property—bird biomass—consistent with other diversity–stability studies [1,26]. Stability of total bird biomass at the regional scale (hereafter 'regional stability') can be partitioned into two components: local stability and spatial asynchrony [29]. For each region we calculated regional stability, mean local stability and spatial asynchrony (figure 1) of total bird biomass using equations for partitioning stability across scales [25,29] and R code from Wilcox *et al.* [26]. We inverted all equations to convert them from temporal variability to stability [26]. First, we calculated the total yearly biomass for each site and each region by summing the total abundance for each species at these respective scales, then multiplying by their mean body mass (g) [69]. In any given year, over 91% of the sites in each region were sampled on average, with no systematic bias in sampling frequency across sites or regions [48,49]. We then calculated regional stability as the invariability of biomass over time using the inverse temporal coefficient of variation:

$$\left(\frac{\sigma_R}{\mu_R}\right)^{-1},$$

where $\mu_R$ and $\sigma_R$ are the mean and standard deviation across years, respectively, of summed biomass for each region $R$. We calculated the mean local stability in each region by first calculating the invariability of total biomass for each site and then taking the mean across all sites within the region, weighted by each site's total biomass:

$$\left(\sum_i \frac{\mu_i}{\mu_R} \times \frac{\sigma_i}{\mu_i}\right)^{-1},$$

where $\mu_i$ and $\sigma_i$ are the mean and standard deviation across years, respectively, in the *i*th site and $\mu_R$ is the regional mean biomass.
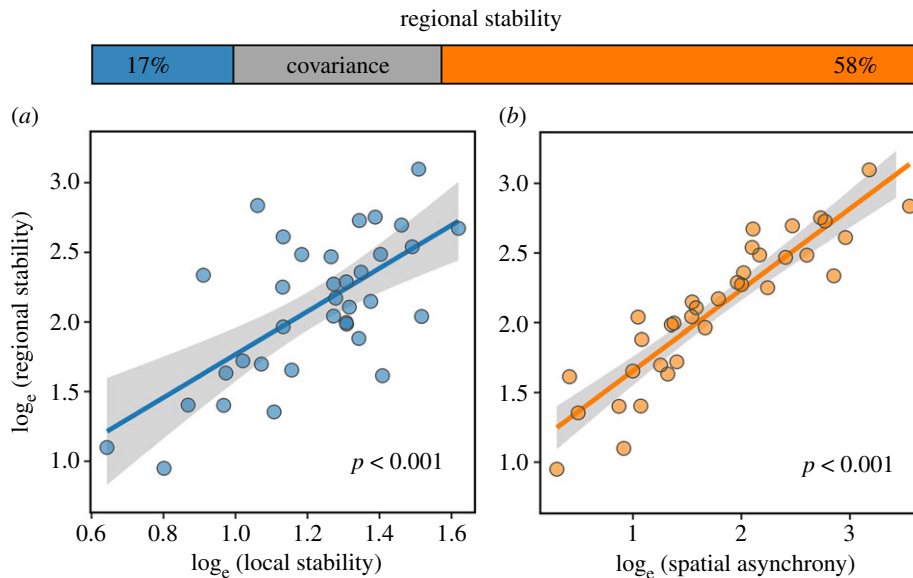
**Figure 2.** The relative importance of local stability of bird biomass and spatial asynchrony of bird biomass for regional stability of bird biomass across 35 conservation regions in North America. Local stability and spatial asynchrony are defined and illustrated in figure 1. Percentages are the proportion of variation in regional stability attributed uniquely to local stability (blue) and spatial asynchrony (orange). Plots show the bivariate association (linear regressions) between regional stability and (a) mean local stability and (b) spatial asynchrony (n = 35). All variables were natural-log (log$_e$) transformed to linearize relationships. (Online version in colour.)

Weighting each site by its total biomass is necessary to accurately estimate the contribution of average local stability to regional stability when the total biomass in a region is not evenly distributed across sites [29].

Spatial asynchrony is the degree to which the total biomass of local sites fluctuates differently with respect to one another through time (figure 1c), which we calculate as the inverse of spatial synchrony ($\varphi$) following others [25,26,29]:

$$\frac{1}{\varphi} = \left( \frac{\sum_{i,j} w_{ij}}{\left( \sum_i \sqrt{w_{ii}} \right)^2} \right)^{-1},$$

where $w_{ij}$ is the temporal covariance of biomass between sites $i$ and $j$, and $w_{ii}$ is the temporal variance of biomass for site $i$. Because spatial synchrony ranges from 0 (no synchrony) to 1 (perfect synchrony), larger values of $1/\varphi$ indicate greater spatial asynchrony. One especially useful property of this measure of spatial asynchrony is that it is equivalent to (regional stability/local stability) [29]. Therefore, the square root of spatial asynchrony is a scalar linking local and regional stability; hereafter called the spatial stabilization factor *sensu* Wilcox et al. [26]. The spatial stabilization factor quantifies how much more stability is generated at the regional scale by spatial asynchrony compared to local stability. Values greater than 2 indicate spatial asynchrony more than doubles (contributes more than half) stability moving from the local to the regional scale.

## (d) Statistical analyses

To determine the relative importance of each stability component to stability at larger scales, we partitioned the variation in regional stability among regions into fractions explained by mean local stability and spatial asynchrony. We then tested whether mean local stability and spatial asynchrony were important predictors of regional stability by fitting linear regressions (figure 2). All variables in this analysis were natural-log (log$_e$) transformed to linearize relationships for variation partitioning. To ensure the relative importance of local stability and spatial asynchrony were not simply related to differences in sampling effort among regions, we partitioned out variation attributed to differences in the number of sites (electronic supplementary material, table S2).

The total number of sites per region was positively correlated with the total area of a region ($r = 0.62$). Therefore, the number of sites reflects the net effect of sampling effort and other ecological processes that vary with region area [29,70,71]. We performed variation partitioning using vegan::varpart() in R.

Next, we developed a structural equation model to evaluate hypotheses regarding the direct and indirect effects of biodiversity and climate heterogeneity for explaining local stability, spatial asynchrony and regional stability. First, we used recent theory and empirical studies on diversity–stability relationships [25,29,70] to guide the specification of our initial structural equation model (electronic supplementary material, figure S3). We natural-log (log$_e$) transformed spatial asynchrony and the number of sites in each region to satisfy the assumptions for linear models (i.e. linear relationships, normally distributed residuals and homogeneous error). Second, we evaluated model-data consistency with a $\chi^2$-test comparing our model to a saturated model [72,73]. Our initial model, however, was inconsistent with the data (i.e. poor model fit, $\chi^2$ with 14 d.f. = 34.45, $p < 0.001$). Third, we considered whether any biologically reasonable links were omitted based on modification indices produced from residual covariances [72,73]. We thus added links from the total number of sites to β-diversity, and from β-diversity to local stability. There was not support for additional links between any other variables in the final model. Fourth, we removed statistically non-significant links ($p > 0.05$) only if this improved model parsimony ($\Delta$AIC $\geq 2$). This resulted in removing mean pair-wise distance among sites (initially included to account for variation in the spatial arrangement of sites within regions that could influence the covariance component of asynchrony and β-diversity). The structural equation model was fit and evaluated using global estimation using maximum likelihood (figure 3; electronic supplementary material, table S3) in R using the lavaan package v. 0.6-3 [74]. Although bird species richness can be spatially autocorrelated [75], we confirmed there was no residual spatial autocorrelation for local stability, spatial asynchrony and regional stability by assessing spatial trends in Moran's $I$ [76] and comparing support for models with different spatial autocorrelation terms (electronic supplementary material, figure S4 and table S4). Bivariate partial regression plots show the relationships between all links in the final model (electronic supplementary material, figure S5).
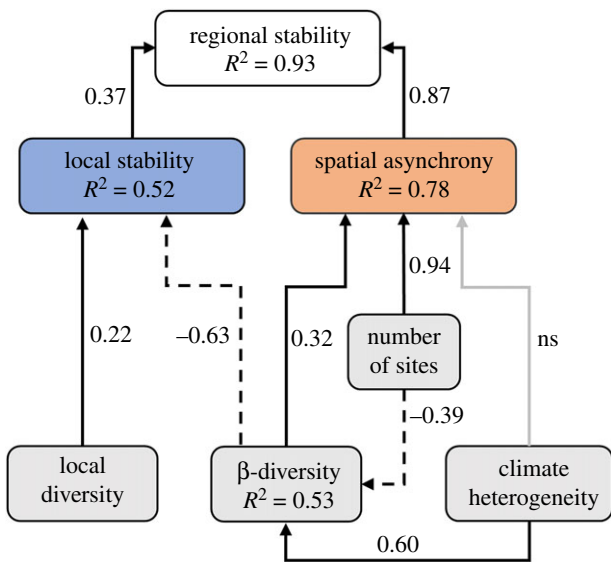
**Figure 3.** Structural equation model showing effects of mean local bird species diversity (Inverse Simpson's Index) within regions, bird β-diversity (Morisita–Horn dissimilarity) within regions and climate heterogeneity (annual mean temperature and precipitation) within regions on regional stability of bird biomass, local stability and spatial asynchrony across 35 conservation regions in North America. Local stability and spatial asynchrony are defined and illustrated in figure 1. Solid arrows represent positive effects, dashed arrows represent negative effects and the grey arrow represents effects where $p > 0.1$. Effects are relative (standardized) effects sizes. The structural equation model was fit using global estimation and maximum likelihood; test statistic $= 8.57$ with 9 d.f. and $p = 0.48$ (indicating good model-data fit). Unstandardized effects, standard errors and significance for each link are provided in electronic supplementary material, table S3. 'Number of sites' and 'spatial asynchrony' were log-transformed to satisfy linear model assumptions. (Online version in colour.)

In addition to shorter-term fluctuations in biomass, long-term trends in regional biomass could also contribute to differences in stability across regions. We tested for trends in each region using a generalized linear model with a first-order temporal correlation structure (electronic supplementary material, figure S6). We then performed a sensitivity analyses by refitting the final structural equation model after excluding regions with significant ($p < 0.05$) trends (electronic supplementary material, table S5). Finally, to assess the total effect of diversity on stability at the regional scale (naive of the influence of local and β-diversity on local stability and spatial asynchrony), we fit a linear model for the bivariate relationship between regional diversity and regional stability.

## 3. Results

Local stability and spatial asynchrony were both positively associated with regional stability, but spatial asynchrony explained over three times more variation in regional stability (58%) than local stability (17%) (figure 2). Among the 35 regions, regional stability of total bird biomass ranged an order of magnitude from 2.59 to 22.14 (median 8.57). Regional stability of total bird biomass was positively log-linearly related to both mean local stability of bird biomass (slope $1.55 \pm 0.31$ [s.e.m], $p < 0.0001$; figure 2a) and spatial asynchrony of bird biomass (slope $0.58 \pm 0.05$ [s.e.m], $p < 0.0001$; figure 2b) among regions. Among regions, spatial asynchrony increased regional relative to local stability by an average by 263% (range $= 16$–590%; electronic supplementary material, figure S7).

Local bird species diversity, β-diversity and climate heterogeneity contributed to regional stability through their relationships with local stability and spatial asynchrony (figure 3; electronic supplementary material, table S3). β-diversity, climate heterogeneity and the number of sites in a region accounted for 78% of the variation in spatial asynchrony (figure 3). Spatial asynchrony increased with β-diversity (*standardized (std.) effect* $= 0.32$, $p = 0.005$) and the number of sites in a region (*std. effect* $= 0.94$, $p < 0.001$), but was not directly related to climate heterogeneity ($p = 0.28$). The positive relationship between β-diversity and spatial asynchrony was qualitatively similar when measuring β-diversity using a partition of Simpson's diversity ($p < 0.001$). Additionally, climate heterogeneity and the number of sites in a region indirectly contributed to spatial asynchrony through their positive and negative associations, respectively, with β-diversity (*std. effects* $= 0.60$ and $-0.39$, $p < 0.001$).

Together, β-diversity and local species diversity accounted for 52% of the variation in local stability among regions. Local stability increased with local diversity (*std. effect* $= 0.22$, $p = 0.069$), but decreased with higher β-diversity (*std. effect* $= -0.63$, $p < 0.001$). The negative link between β-diversity and local stability was not predicted by theory [25,29] and thus not included in our initial model (electronic supplementary material, figure S3), but was strongly supported by the data (see Material and methods). We found that four regions exhibited significant long-term trends in total biomass (electronic supplementary material, figure S6); however, a sensitivity analysis demonstrates that all links in the structural equation model are robust (maintain qualitatively similar effects and statistical significance) to the inclusion/exclusion of these regions (electronic supplementary material, table S5). Regional stability was not directly related to regional diversity ($p = 0.32$) after controlling for differences in the number of sites.

## 4. Discussion

Despite decades of interest in diversity–stability relationships, the relative importance of mechanisms that stabilize aggregate ecological properties at different spatial scales remains poorly understood. Our study provides some of the first evidence to suggest that at macroscales, biomass is stabilized more by spatial variation in biomass fluctuations and species composition than average local stability or species diversity. Moreover, our results suggest recent theory on scaling biodiversity–stability relationships [25,29] (which has mostly been tested with sessile organisms like plants [26,46,47,71]) can be generalized to more mobile consumers like birds.

We found that spatial asynchrony of bird biomass among sites was the strongest predictor of regional stability of total bird biomass, explaining three times more variation in regional stability than local stability (figure 2). This finding contrasts with recent studies in grasslands that found local stability of aboveground plant biomass was the primary force stabilizing plant productivity at larger scales [26,47]. In these studies, spatial scales were relatively small—ranging from $0.5 \text{ m}^2$ (median) grassland plots at the local scale to 0.5 ha metacommunities at the regional scale. In stark contrast, spatial scales in our study were significantly larger—ranging from $6\,300\,000 \text{ m}^2$ sites at the local scale to $2.8 \times 10^5$ ha (median) regions (electronic supplementary material, table

S1). Spatial asynchrony is predicted to increase with region area, as larger regions tend to contain a greater diversity of environments and higher species turnover associated with a greater number of local communities (sites) [29]. The number of sites per region in our study was positively correlated with region area ($r = 0.62$) and was the strongest predictor of spatial asynchrony and stability of regional bird biomass (figure 3). Our study confirms that the importance of spatial asynchrony increases with region size and contributes to a stability–area relationship [29,70,71].

Moreover, our study shows that bird β-diversity and climate heterogeneity appear to be key drivers of spatial asynchrony in bird biomass (figure 3; electronic supplementary material, figure S5). This finding provides perhaps the strongest evidence to date for theory predicting that spatial variation in biodiversity and the environment may be among the most important ecological factors scaling stability to large regional ecosystems [25,29]. We found that much of the variation in bird β-diversity across regions was related to variation in climate, which is one of the largest drivers of turnover in bird species composition across North America [65]. Regions that span greater latitudinal and/or elevational gradients, such as the Mojave and Sonoran Deserts or Great Basin in the western United States, tend to be those with greater bird β-diversity and climate heterogeneity (electronic supplementary material, figure S8)—suggesting an important role for species sorting as a driver of spatial asynchrony. Spatial asynchrony could also occur in regions with low environmental heterogeneity when historical contingencies and/or demographic stochasticity among isolated populations increase variation in species composition [42,43]. Historical contingencies may be more likely in productive regions [77], such as those in the eastern United States characterized by low elevational variation and humid oceanic and temperate climates.

At smaller scales, bird species diversity increased the stability of local bird biomass (figure 3; electronic supplementary material, figure S5). This finding is consistent with expectations for when co-occurring species differ in their responses to similar environmental conditions or differ in population growth rates [1–8]. However, our structural equation model revealed a link not explicitly predicted by theory—a strong negative association between local stability and β-diversity (figure 3; electronic supplementary material, figure S5). This link may reflect a negative effect of β-diversity on local stability, or latent/unmeasured variables that determine the negative correlation between local stability and β-diversity. For example, western regions that have high β-diversity are also likely to have low local stability (electronic supplementary material, figure S8) due to high interannual variability in rainfall or El Niño effects that cause variability in bird fitness [64]. Although less likely for mobile species like birds, β-diversity could also decrease local stability if dispersal limitation contributes to variation in species composition across communities (high β-diversity), but decreases rescue effects that maintain species diversity and local stability in variable environments [37,38]. Therefore, differences in the relative importance of environmental and spatial mechanisms of community assembly among regions may contribute to geographical patterns of spatial asynchrony and stability.

Our study using BBS data provides unique insights into the roles that different dimensions of biodiversity play in stabilizing ecosystems at large scales—effectively extending inferences generally gleaned from smaller metacommunities [26,46,47,71] to macroecological scales. However, the large extent of BBS data presents a trade-off between the emergence of general patterns at broad scales and the loss of resolution at fine spatial and/or temporal scales. For example, variation in land use or habitat within sites (i.e. along routes) could influence interspecific interactions and metapopulation dynamics that influence local stability in ways that are not necessarily captured by local diversity [26]. Additionally, long time series may not be stationary, potentially complicating interpretations of the relationships between diversity and stability when variability is partly a consequence of long-term trends. We found total biomass declined in four regions (Gulf Coast Prairies, Mid Atlantic Coasts, Central Hardwoods and Eastern Tallgrass Prairies) (electronic supplementary material, figure S6), consistent with a recent study demonstrating bird population declines over that past 50 years appear strongest in coastal and grassland ecosystems [78]. Importantly, our results are not sensitive to trends in these regions (electronic supplementary material, table S5). However, continued population declines could eventually cause localized extinctions that decrease local stability and alter spatial variation in both bird species composition and asynchrony. Finally, some birds are exhibiting small declines in body mass, coupled with increases in wing length that can alter metabolic costs and dispersal abilities [79]. Therefore, integrating intraspecific morphological change and biodiversity change offers an emerging opportunity to further understand how global change may influence ecosystem stability across scales.

# 5. Conclusion

Our study has broad implications for unresolved questions at the interface of ecology and global-change biology. The biogeographic scale of our study complements similar studies at local and metacommunity scales [26,38,41,70,80,81], together generalizing the importance of spatial processes for stabilizing ecosystems at larger scales. However, our study differs from those at local and metacommunity scales by demonstrating spatial asynchrony related to variation in community composition (β-diversity) and climate (temperature and precipitation) appears to the strongest driver of stability at macroscales. Global environmental changes that result in biotic homogenization [15,17–23] and/or environmental homogenization [25] may destabilize ecosystems by synchronizing local communities, even under scenarios with no net change in local diversity. These findings support arguments that biodiversity–ecosystem function research remains critical for anticipating the consequences of biodiversity change at large scales [10–14]. Changes in biodiversity at different scales—from species diversity within local communities to variation in community composition—may be critical for anticipating the consequences for ecosystem stability across scales relevant to nature and people [82–85].

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