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Diversity–stability relationships across organism groups and ecosystem types become decoupled across spatial scales

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Abstract

The relationship between biodiversity and stability, or its inverse, temporal variability, is multidimensional and complex. Temporal variability in aggregate properties, like total biomass or abundance, is typically lower in communities with higher species diversity (i.e., the diversity–stability relationship [DSR]). At broader spatial extents, regional-scale aggregate variability is also lower with higher regional diversity (in plant systems) and with lower spatial synchrony. However, focusing exclusively on aggregate properties of communities may overlook potentially destabilizing compositional shifts. It is not yet clear how diversity is related to different components of variability across spatial scales, nor whether regional DSRs emerge across a broad range of organisms and ecosystem types. To test these questions, we compiled a large collection of long-term metacommunity data spanning a wide range of taxonomic groups (e.g., birds, fish, plants, invertebrates) and ecosystem types (e.g., deserts, forests, oceans). We applied a newly developed quantitative framework for jointly analyzing aggregate and compositional variability across scales. We quantified DSRs for composition and aggregate variability in local communities and metacommunities. At the local scale, more diverse communities were less variable, but this effect was stronger for aggregate than compositional properties. We found no stabilizing effect of γ-diversity on metacommunity variability, but β-diversity played a strong role in reducing compositional spatial synchrony, which reduced regional variability. Spatial synchrony differed among taxa, suggesting differences in stabilization by spatial processes. However, metacommunity variability was more strongly driven by local variability than by spatial synchrony. Across a broader range of taxa, our results suggest that high γ-diversity does not consistently stabilize aggregate properties at regional scales without sufficient spatial β-diversity to reduce spatial synchrony.

KEYWORDS
community variability, diversity–stability relationship, metacommunity, spatial insurance hypothesis, stability

INTRODUCTION

Temporal variability (or its inverse, stability) in the distribution and abundance of species has important implications for the maintenance of biodiversity and ecosystem functions (McCann, 2000; Tilman et al., 2014). Ecological communities can vary through time along multiple dimensions, including species composition and aggregate properties (like total abundance or biomass) that ignore composition (Cottingham et al., 2001; Hillebrand et al., 2018; Hillebrand & Kunze, 2020; Micheli et al., 1999). Various mechanisms have been proposed to explain why variability in aggregate properties is often lower in species-rich communities than in species-poor communities,

a pattern known as the diversity–stability relationship (DSR) (Craven et al., 2018; Ives & Carpenter, 2007; McCann, 2000; Tilman, 1999). This reduced variability can arise from portfolio effects that relate to the statistical and ecological benefits of high species richness for ecosystem functioning (Doak et al., 1998; Thibaut & Connolly, 2013; Tilman et al., 1998; Yachi & Loreau, 1999) or from compensatory dynamics that occur when populations fluctuate asynchronously through time (Brown et al., 2016; Gonzalez & Loreau, 2009; Klug et al., 2000). Empirically, the DSR has been well studied in local communities, but it is less clear how temporal variability is regulated at the broader spatial extents where ecosystem management decisions are made and spatial dynamics operate (Chen et al., 2022; Gonzalez et al., 2020;

Lamy et al., 2021; Loreau et al., 2003; Wang et al., 2019; Wang & Loreau, 2016; Wilcox et al., 2017).

Temporal aggregate variability at regional scales depends on the variability of local communities and the degree of spatial synchrony among communities (Wang et al., 2019; Wang & Loreau, 2014, 2016). For example, regional-scale fluctuations in total biomass or abundance can be reduced through a dampening of local fluctuations (e.g., through local portfolio effects or compensatory dynamics) or through a reduction in spatial synchrony (Wang et al., 2019). Low spatial synchrony implies that community variability is weakly spatially correlated, which can dampen variability at the regional scale through a process called the spatial insurance effect (Catano et al., 2020; Howeth & Leibold, 2010; McGranahan et al., 2016; Steiner et al., 2011; Wang et al., 2021; Wilcox et al., 2017). Spatial insurance may be strengthened by environmental heterogeneity, which generates contrasting population dynamics among communities, or by dispersal rates that are low enough to prevent spatial homogenization that could cause patches to fluctuate similarly across the metacommunity (Daleo et al., 2023; Gouhier et al., 2010; Lamy et al., 2019; Loreau et al., 2003; Thompson et al., 2015).

The strength and direction of the DSR can differ across spatial scales because variability and diversity both change with spatial extent (Aragón et al., 2011; Gonzalez et al., 2020; Liang et al., 2022; Wang et al., 2019, 2021; Wang & Loreau, 2014, 2016). At regional scales, higher γ-diversity is sometimes associated with lower variability in total metacommunity biomass (Aragón et al., 2011; Wang et al., 2019; Wang & Loreau, 2016). For example, in a desert grassland community, both local and regional variability decreased as α- and γ-diversity increased, respectively (Chalcraft, 2013). However, broader surveys of plant communities have shown mixed evidence of a regionally stabilizing effect of γ-diversity (Liang et al., 2022; Wang et al., 2021; Wilcox et al., 2017). Instead, spatial turnover in species composition (β-diversity) has been shown to have a stronger stabilizing effect at the regional scale by reducing spatial synchrony in community dynamics, which dampens biomass fluctuations in the metacommunity (Catano et al., 2020; Delsol et al., 2018; Liang et al., 2022; Qiao et al., 2022). However, the stabilizing effects of β-diversity on aggregate variability are not always to be expected, and may depend on complex interactions between environmental heterogeneity, species traits, and dispersal (van der Plas et al., 2023).

Regional-scale studies of the DSR have largely overlooked the relationship between diversity and compositional variability (Lamy et al., 2021). Quantifying compositional and aggregate variability together is important because a lack of variability in total metacommunity biomass can conceal broad-scale changes in composition (Lamy et al., 2021; Micheli et al., 1999; Xu et al., 2022). Furthermore, compositional studies can reveal species combinations that are important for the conservation of biomass across spatial scales (Arranz et al., 2022). It is not yet clear how different facets of biodiversity relate to compositional variability at local and regional scales. For example, species-rich plant communities often have higher variability in composition due to increased biotic interactions and niche partitioning (e.g., which drive compensatory dynamics), in addition to the stochastic fluctuations of communities with smaller average population sizes (Hector et al., 2010; Tilman, 1999; Tilman et al., 2006; Wang et al., 2019). But this positive relationship between richness and compositional variability is not universal (Chalcraft, 2013; Cottingham et al., 2001). Extending this relationship to the regional scale suggests that metacommunities with higher γ-diversity could be more compositionally variable, but empirical studies have found the lowest compositional variability at intermediate γ-diversity (Chalcraft, 2013). Compositional DSRs at both local and regional spatial scales merit additional study across ecosystems and taxonomic groups to assess their generality and transferability.

Using a large compilation of long-term metacommunity time series data ($n = 29$; Table 1), from a range of ecosystem types (e.g., deserts, forests, coral reefs) and taxonomic groups (e.g., birds, fish, plants, algae), we quantified diversity–stability relationships at multiple spatial scales. Specifically, we examined community variability (both aggregate and compositional) at both local (observational unit, such as a sampling plot) and regional (study scale, such as a Long-Term Ecological Research [LTER] site) spatial scales, alongside changes in diversity, to address three questions. First (Q1), how does local diversity relate to aggregate and compositional variability within communities, and do broader relationships emerge across ecosystems and organisms? Second (Q2), does sustained β-diversity reduce spatial synchrony? And third (Q3), how are aggregate and compositional variability at the metacommunity scale related to local and spatial components of biodiversity and variability? Our synthesis found support for local DSRs, with wide variability among systems in compositional DSRs; strong evidence that spatial β-diversity reduces both compositional and aggregate spatial synchrony; and that β-diversity is important for reducing aggregate variability at regional scales through reductions in compositional spatial synchrony.

METHODS

Data acquisition, processing, archiving

We acquired 29 data sets spanning a wide range of ecosystems and organismal groups represented primarily by

TABLE 1 Summary of datasets included in the synthesis of diversity–stability relationships in metacommunities.

Dataset ID	Site code	Organismal group	Location	Initial year	Duration (years)	Spatial sites	Taxa sampled
and-birds	AND	Birds	Oregon, USA	2009	5	184	81
and-plants	AND	Plants	Oregon, USA	1989	21	12	85
bes-birds	BES	Birds	Maryland, USA	2005	5	52	33
cap-birds	CAP	Birds	Arizona, USA	2001	16	35	104
cap-herps	CAP	Herps	Arizona, USA	2013	5	7	18
cdr-grasshopper	CDR	Grasshopper	Minnesota, USA	1989	18	19	50
cdr-plantsABC	CDR	Plants	Minnesota, USA	1982	23	18	128
cdr-plantsD	CDR	Plants	Minnesota, USA	1982	23	5	128
fce-diatoms	FCE	Diatoms	Florida, USA	2005	10	30	193
fce-fish-Dry	FCE	Fish	Florida, USA	2006	11	10	56
fce-fish-Wet	FCE	Fish	Florida, USA	2011	6	14	56
gce-mollusc	GCE	Mollusc	Georgia, USA	2000	14	18	9
hays-plants	HAYS	Plants	Kansas, USA	38	35	14	139
jrn-lizards	JRN	Lizards	New Mexico, USA	1990	16	9	18
jrn-plants	JRN	Plants	New Mexico, USA	1915	18	10	113
knz-grasshopper	KNZ	Grasshopper	Kansas, USA	1996	19	13	43
luq-snails	LUQ	Snails	Puerto Rico	1991	27	40	19
mcr-algae	MCR	Algae	Moorea, French Polynesia	2006	10	6	73
mcr-coral	MCR	Coral	Moorea, French Polynesia	2005	13	6	31
mcr-inverts	MCR	Inverts	Moorea, French Polynesia	2005	17	6	17
sbc-algae	SBC	Algae	California, USA	2001	18	9	59
sbc-fish	SBC	Fish	California, USA	2001	18	9	64
sbc-mobileInverts	SBC	Mobile	California, USA	2001	18	9	34
sbc-sessileInverts	SBC	Sessile	California, USA	2001	18	9	71
sev-arthropods	SEV	Arthropods	New Mexico, USA	1992	13	10	316
sev-grasshopper	SEV	Grasshopper	New Mexico, USA	1992	22	10	54
sev-plants	SEV	Plants	New Mexico, USA	2003	13	8	157
sgs-plants1	SGS	Plants	Colorado, USA	1999	8	6	84
sgs-plants2	SGS	Plants	Colorado, USA	1995	14	6	58

Note: Dataset ID refers to the identifier used in the analysis and referred to in Appendix S1. Duration and spatial sites represent the data included in the analysis after passing the criteria described in the methods.

the LTER Network, with data obtained from the Environmental Data Initiative (EDI) portal (https://portal.edirepository.org). We used time series of species assemblages containing abundance, percent cover, or biomass data using the ecocomDP model (O'Brien et al., 2021). We kept data sets with at least five spatial and at least five temporal sampling locations to ensure sufficient spatial and temporal resolution. We then filtered and aggregated each data set to ensure homogeneous sampling, and consistent taxonomic identification, and to make sure that each data set represented a collection of potentially interacting species (i.e., our data sets focus on competitive metacommunities).

To ensure homogeneous sampling, we retained only the spatial locations that were sampled at every time step. If some locations were not sampled annually, we retained only the portion of the data set with uninterrupted, annual temporal sampling while still retaining at least five sites and five time points. When a data set was sampled twice or more per year, we computed annual averages, summations, or maximums of species abundances, depending on the best approach for the survey method, to aid in comparison across data sets (Appendix S1).

We aggregated or filtered data to ensure homogeneous taxonomic identification. Our taxonomic information was

provided mostly at the species level, but some data sets contained information at the genus, family, or order level. This posed an issue only when individuals were identified at both the genus level and at the level of species nested within that genus. For example, some individuals were identified as simply belonging to a genus (e.g., "*Carex* sp."), while most individuals were identified as a species of said genus (e.g., "*Carex phoetida*"). Such heterogeneous identification in the data suggested that species identification was inconsistent. As a general rule, if taxa identified at the genus level comprised a small portion of the individuals within a genus (i.e., <5% of records were identified at the genus rather than species level), we removed the genus-level data from the data set. Conversely, if >5% of individuals were identified at the genus level, we assumed this reflected inconsistent identification. In this case, we lumped taxonomic identification at the genus level. We used a cutoff of 5% in most cases (Appendix S1). We removed all species with an undetermined identification.

We identified potential metacommunities by retaining data sets with shared, potentially interacting species among local sites. For example, when a data set contained two or more distinct taxonomic groups (e.g., fish, sessile invertebrate, and algal assemblages in the Santa Barbara Coastal LTER), we treated these groups as separate data sets. When a data set contained sites that shared <5% of species, we investigated these sites further (by looking at species identities and the spatial distribution of species among sites) and excluded sites if they were geographically separate from or shared few/no species with other sites in the metacommunity. We plotted species accumulation curves, time series of species abundance, spatiotemporal replication, and the number of species shared between spatial locations. Information about the data sets is given in Appendix S1. All analyses were conducted in the R statistical computing environment, v.4.2.1 (R Core Team, 2022).

Quantifying aggregate and compositional variability

To quantify variability at local and regional scales in our metacommunity data sets, we used two multiplicative partitioning frameworks, one for aggregate (Wang & Loreau, 2014, 2016) and one for compositional (Lamy et al., 2021) variability.

We used the aggregate partitioning approach to analyze temporal variability in the total abundance/biomass of each local community and of the metacommunity. This was computed as a weighted average of the variability in local communities

$$\mathrm{CV}_\alpha^2 = \left(\frac{\sum_i^m \sigma_{Ti}}{\mu_{TT}}\right)^2, \tag{1}$$

and the variability of all communities in the metacommunity

$$\mathrm{CV}_\gamma^2 = \left(\frac{\sigma_{TT}}{\mu_{TT}}\right)^2, \tag{2}$$

where μ_{TT} is the temporal mean total abundance/biomass of all m sites in the metacommunity; σ_{Ti} is the standard deviation of total abundance/biomass in community i, and σ_{TT} is the standard deviation of the whole metacommunity (Wang & Loreau, 2014).

We used the compositional partitioning approach to calculate the average temporal variability in species relative abundances within local communities (BD_α^h) and the temporal variability in relative abundances at the metacommunity scale (BD_γ^h), thereby capturing both changes in richness and relative abundance. To compute BD_α^h, we first calculated the temporal variance in the Hellinger-transformed relative abundance of each species within each community, summed these variances across all species in the community, then calculated the weighted average of all local community variabilities weighted by their total abundances (Lamy et al., 2021):

$$\mathrm{BD}_\alpha^h = \sum_i^m w_i \sum_j^S v_{ij}^h, \tag{3}$$

where w_i is the relative weight of community i and v_{ij}^h is the temporal variance of species j in community i after Hellinger transformation (h superscript), summed across S species and all m communities. Regional compositional variability was computed as the sum of variances for species at the regional scale:

$$\mathrm{BD}_\gamma^h = \sum_j^S v_{Tj}^h, \tag{4}$$

where v_{Tj}^h is the temporal variance of the Hellinger-transformed total abundance of species j summed across all communities in the metacommunity. The compositional metrics extend the BD metric of the variance-based approach to beta diversity (Legendre & De Cáceres, 2013).

For each metacommunity data set, we partitioned the regional-scale variability into its components of mean local variability (described above) and spatial synchrony. We obtained spatial synchrony components for both aggregate (ϕ) and compositional (BD_ϕ^h) dimensions of variability in metacommunities, where $\phi = \mathrm{CV}_\gamma^2 / \mathrm{CV}_\alpha^2$ and $\mathrm{BD}_\phi^h = \mathrm{BD}_\gamma^h / \mathrm{BD}_\alpha^h$ (Lamy et al., 2021). Values of 0 for ϕ or BD_ϕ^h indicate no synchrony and a complete dampening of variability at regional scales, while 1 indicates perfect

synchrony and no spatial stabilization. Thus, these spatial synchrony terms serve as scaling factors that link local- and regional-scale variability.

Testing multiscale diversity–stability relationships

We compared the relationships between variability (aggregate and compositional) and diversity at different scales in the metacommunity. For every moment in time, we partitioned regional γ-diversity with a multiplicative approach ($\gamma = \beta \times \alpha$), where γ was metacommunity richness, α was mean local richness, and $\beta = \gamma / \alpha$ for each metacommunity time series in our data set. Then, α, β, and γ components of diversity were averaged through time, yielding long-term estimates of mean local ($\overline{\alpha}$), among-site ($\overline{\beta}$), and regional ($\overline{\gamma}$) diversity for each metacommunity. With these calculations, we addressed three main questions about DSRs in metacommunities.

Question 1 (Q1): How does local diversity relate to aggregate and compositional variability within communities, and do broader relationships emerge across ecosystems and organisms?

To investigate local-scale DSRs, we focused on within and among-metacommunity patterns. At the local scale, we predicted that plots with higher species richness would be less variable in their aggregate properties, but that species richness would show a potentially weaker, positive relationship with compositional variability. Within each metacommunity, we first computed the z-score for richness to ease comparisons across metacommunities, rescaling richness relative to other sites in the same metacommunity. We then computed the temporal average of z-transformed α-diversity of each plot and the temporal variability of (1) total community abundance, $CV = \sigma_{Ti}/\mu_{Ti}$, where μ_{Ti} is the mean total abundance for community i, and (2) composition, $BD = \sum_j^S v_{ij}^h$, the unweighted form of Equation (3).

We then tested whether species-rich plots in each metacommunity were more or less variable through time in their aggregate or compositional properties using linear mixed effects models in the *lme4* R package v. 1.1-32 (Bates et al., 2015). We modeled plot-level CV or BD as the response variable and plot-level mean richness as the predictor. We used a random intercepts and random slopes model, such that different metacommunities could have different DSRs, while contributing to the among-group mean intercept and slope (Harrison et al., 2018).

We estimated the fixed effects of mean richness to identify emergent trends across the datasets. To quantify the extent to which metacommunities differed in their DSRs, we computed the variance explained by the time-averaged local richness using the marginal (without the random effects) and conditional (including the random effects) R^2 approach for (G)LMMs (Nakagawa & Schielzeth, 2013).

Question 2 (Q2): Does sustained β-diversity reduce spatial synchrony?

The scaling factors that link local variability to metacommunity variability (ϕ, BD_ϕ^h) are interpreted as spatial synchrony components. We compared the scaling of compositional and aggregate variability to assess the relative magnitude of spatial stabilization within and across different ecosystem types and organismal groups. We visualized the reduction in variability from the local scales to the regional scale. For each metacommunity, we compared the aggregate (ϕ) and compositional (BD_ϕ^h) spatial synchrony among all the metacommunities, and computed Spearman's rank correlation to quantify the association between compositional and aggregate spatial synchrony. When $\phi \gg BD_\phi^h$, aggregate properties were weakly stabilized by space compared with compositional properties; when $\phi \ll BD_\phi^h$, composition was weakly stabilized by space compared with aggregate properties.

To test whether these synchrony values were related to spatial differences in community composition, we compared them with a temporal average of spatial β-diversity in each metacommunity. This temporally averaged spatial β-diversity captures sustained compositional heterogeneity among plots in the metacommunity, a putative driver of decreased spatial synchrony. We predicted compositional spatial synchrony would decrease with β-diversity faster than aggregate spatial synchrony due to the more direct relationship between β-diversity and compositional synchrony than with aggregate properties like total abundances. We evaluated this prediction using Bayesian linear mixed effects models. We used a Bayesian approach to avoid boundary issues with maximum likelihood methods for mixed models (Chung et al., 2015), and we fit models using the "stan_lmer()" function in the R package *rstanarm* v.2.21.4 (Goodrich et al., 2020). We fitted random slope and random intercepts models using LTER site as a random factor. We used weakly informative priors (Chung et al., 2015) and sampled posterior distributions with MCMC using four chains of 5000 iterations each (with a burn-in of 1000 samples). We assessed chain convergence with visual inspection of trace plots, temporal autocorrelation, and the $\widehat{R}$ metric (where $\widehat{R} = 1$ indicates convergence among chains) (Vehtari et al., 2021). We confirmed that

observed data points fell within posterior prediction intervals, and estimated posterior medians and 95% credible intervals using Highest Density Intervals.

Question 3 (Q3): How are aggregate and compositional variability at the metacommunity scale related to local and spatial components of biodiversity and variability?

We then evaluated whether diversity and variability were related at the metacommunity scale and how variability propagates across spatial scales. We predicted that increased γ-diversity and increased β-diversity would dampen aggregate metacommunity variability. However, the relationship with compositional metacommunity variability was predicted to be less clear given the range of compositional DSRs previously described at local and regional scales. We hypothesized that higher β-diversity would reduce compositional variability at regional scales, while α- and γ-diversity could increase compositional metacommunity variability. We used random slopes and intercepts Bayesian linear mixed effects models to assess the relationships between variability at the metacommunity scale and $\overline{\alpha}$-, $\overline{\beta}$-, and $\overline{\gamma}$-diversity, with LTER site as a random factor to account for nonindependence in co-located metacommunities. We used weakly informative priors and sampled the posterior distribution with four MCMC chains with 5000 iterations each and checked models with the same approaches as described for Q2.

Because variability at the metacommunity scale can come from local variability or spatial synchrony, we used structural equation modeling (SEM) to partition the pathways contributing to metacommunity variability. We partitioned the contributions of diversity, variability, and synchrony to compositional and aggregate metacommunity variability using the *piecewiseSEM* R package v.2.3.0 (Lefcheck, 2016). We computed the χ^2 and Fisher's C statistics to assess model fit (rejecting models with p-values below 0.05, which indicate that the SEM model has a poor fit to the data). We present the final model with significant paths only, showing standardized regression coefficients. Code to reproduce the analysis is located in a Zenodo archive (Wisnoski, 2023).

RESULTS

We found general support for local-scale diversity–stability relationships. Sites with more species in the metacommunity tended to have much lower variability in total community abundance or biomass (Figure 1a; fixed effects: intercept $= 0.596 \pm 0.0497$ SE, $t = 11.99$; $\beta = -0.052 \pm 0.017$ SE, $t = -3.065$). While not all communities showed this expected DSR (e.g., algae and some invertebrates), it did emerge as a general pattern across studies (Appendix S2: Table S1). The random effects explained a substantial amount of variation in local variability ($R_m^2 = 0.024$; $R_c^2 = 0.717$), indicating large differences in DSR slopes and intercepts among metacommunities. We present the slopes and intercepts for each dataset in Appendix S2: Table S2. We found weaker support for a relationship between compositional variability and local species richness (Figure 1b). There was a negative effect of richness on compositional variability when looking across ecosystems and organisms (fixed effects: intercept $= 0.316 \pm 0.029$ SE, $t = 10.76$; $\beta = -0.023 \pm 0.011$ SE, $t = -2.07$), but some individual metacommunities showed strong positive relationships between richness and compositional variability, as evidenced by differences in the slopes across taxa and organism groups (Appendix S2: Table S3). Accounting for these among-dataset differences explained much more of the variation in local compositional variability ($R_m^2 = 0.014$; $R_c^2 = 0.725$), demonstrating a range of local DSRs detected for compositional properties.

Metacommunities with higher sustained spatial β-diversity over time exhibited lower spatial synchrony (Figure 1c,d). We detected negative relationships between β-diversity and compositional synchrony (fixed effects estimate: -0.09, $[-0.15, -0.03]$ 95% credible interval) and aggregate synchrony (estimate: -0.12, $[-0.19, -0.06]$ 95% CI). Full model results are provided in Appendix S2: Tables S4 and S5.

Overall, we found a positive, but moderate, correlation ($\rho = 0.47$) between aggregate (ϕ) and compositional (BD_ϕ^h), synchrony, indicating that metacommunities with lower compositional spatial synchrony also tended to have less aggregate synchrony (Figure 2). However, metacommunities differed in the relative degree of spatial synchrony in aggregate and compositional variability (i.e., deviations from the 1:1 line in Figure 2). In other words, some metacommunities showed a greater reduction in aggregate—but not compositional—properties across scales, and vice versa. Plants and invertebrate communities tended to have the highest spatial synchrony, in both compositional and aggregate dimensions (Appendix S2: Figure S1). In contrast, bird metacommunities showed consistently low spatial synchrony. Animals with slightly lower dispersal abilities (e.g., fish, herps) exhibited intermediate synchrony values between birds and plants. Interestingly, fish showed low spatial synchrony in aggregate properties, but higher spatial synchrony in composition.
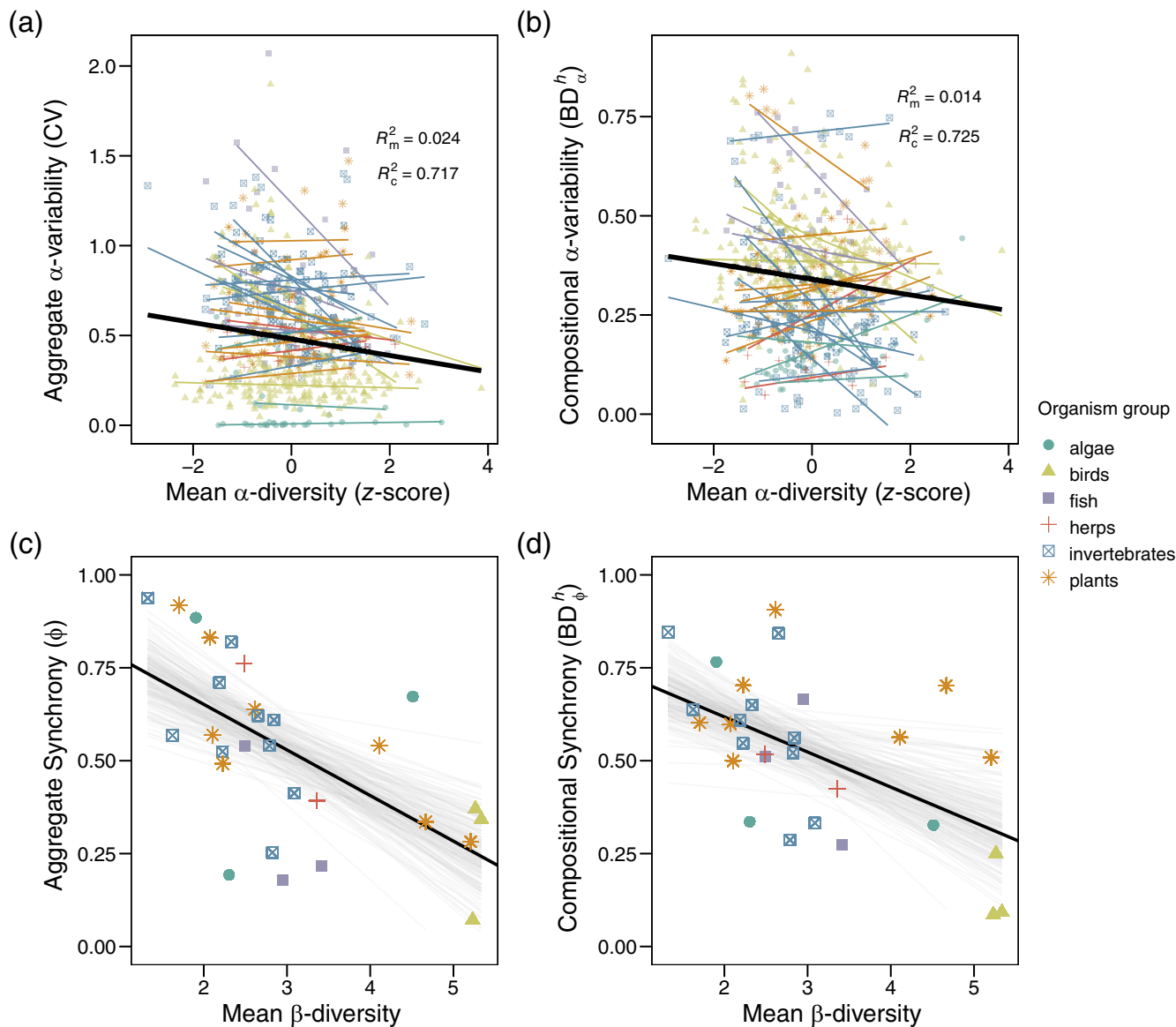
FIGURE 1   Local (a, b) and spatial (c, d) diversity–stability relationships. Relationship between mean α-diversity and (a) local aggregate variability and (b) local compositional variability. Bold black lines represent the fixed effects of α-diversity and thinner colored lines the relationships within each metacommunity. R_m^2 represents the variance explained by the fixed effects only, while R_c^2 represents the variance explained by the fixed and random effects. Mean spatial β-diversity was significantly negatively related to spatial synchrony in (c) aggregate and (d) compositional properties. Solid line represents the fixed effects from a Bayesian linear mixed effects model. Gray lines depict fixed effects from a sample of posterior models.

Variability in total metacommunity abundance showed no relationship with γ- or α-diversity (Figure 3a,e), but was negatively related to β-diversity (Figure 3c; estimate: −0.06, [−0.13, −0.01] 95% CI). Compositional metacommunity variability was unrelated to γ- or β-diversity (Figure 3b,d), but was positively related to α-diversity (Figure 3f; estimate: 0.01, [0, 0.02] 95% CI). Plants tended to have high compositional, but low aggregate variability, while invertebrates had high aggregate but low compositional variability; herpetofauna, birds, and algae had low metacommunity variability (Appendix S2: Figure S1). Variability and

synchrony partitions for all datasets are shown in Appendix S2: Figure S2.

Diversity, synchrony, and variability influenced variability at the regional scale through multiple direct and indirect pathways (Figure 4; $\chi^2 = 8.53$, $p = 0.577$, $df = 10$; Fisher's $C = 8.523$, $p = 0.86$, $df = 14$). In general, α-, β-, and γ-diversity had significant direct effects on compositional variability and synchrony, which, in turn, had direct effects on aggregate variability and synchrony. Thus, diversity effects on aggregate properties occurred indirectly, mediated by compositional changes. Compositional metacommunity
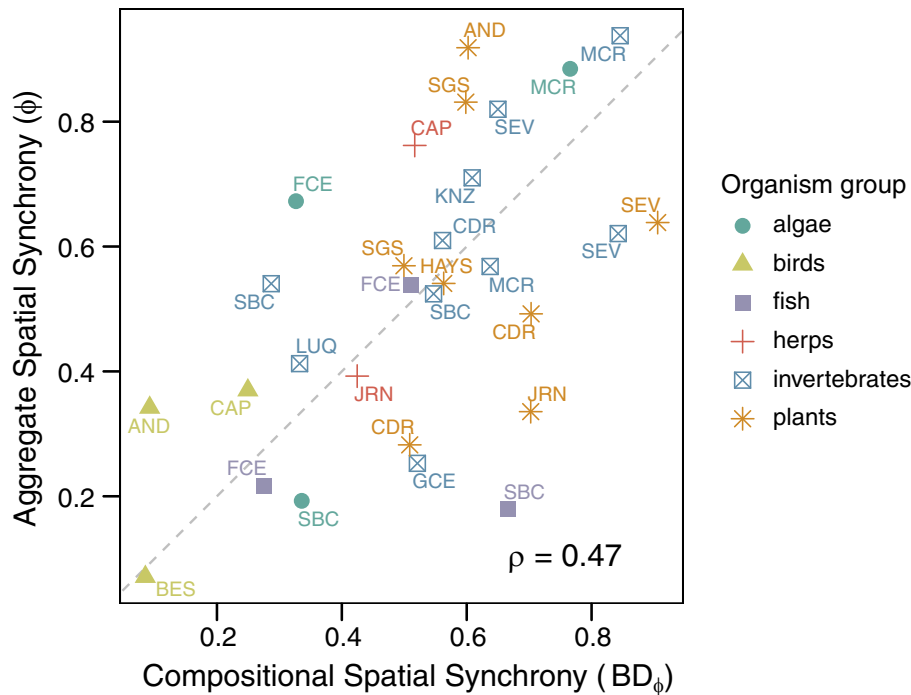
FIGURE 2 The relationship between compositional and aggregate spatial synchrony for all metacommunities (Spearman's $\rho = 0.47$). Metacommunities above the 1:1 line had a smaller reduction in aggregate than compositional variability from local to regional scales, while those below the 1:1 line had a relatively greater reduction in aggregate than compositional variability.

variability was significantly positively related to compositional spatial synchrony (0.488, standardized path coefficients reported here and for the following relationships) and local compositional variability (0.725). Compositional spatial synchrony was significantly negatively related to average beta diversity (−0.716) and positively related to local compositional variability (0.419), which was significantly related to α (1.595) and β (1.110) diversity. In contrast, aggregate metacommunity variability was significantly related to aggregate spatial synchrony (0.642) and local aggregate variability (0.829). Aggregate spatial synchrony was positively related to compositional synchrony (0.456), while local aggregate variability was positively related to local compositional variability (0.496). Indirect effects of diversity on compositional and aggregate metacommunity variability differed in sign depending on different pathways. For example, β-diversity had negative effects on compositional and aggregate metacommunity variability mediated by compositional spatial synchrony, but it also had positive effects that acted through increased local compositional variability (Figure 4).

with higher species richness had lower variability in aggregate properties and (to a lesser degree) community composition. Q2: Metacommunities with higher spatial β-diversity had lower spatial synchrony for both compositional and aggregate properties. Q3: At the metacommunity scale, aggregate variability was unrelated to γ-diversity, but negatively related to β-diversity. Compositional metacommunity variability was positively related to mean α-diversity. Metacommunity variability was more strongly influenced by local variability than by spatial synchrony. β-Diversity was the primary driver of regional stability by reducing spatial synchrony, but it could also indirectly promote regional variability by increasing local compositional variability. Thus, aggregate stability shifted from being driven by α-diversity at local scales to β-diversity at broader scales, while β-diversity had opposing indirect effects on compositional metacommunity variability. Overall, our study suggests that, across a wide range of taxonomic groups, DSRs established at local scales may become decoupled at broader spatial scales.

DISCUSSION

We analyzed the multiscale relationships between diversity and variability in empirical metacommunities and addressed three main questions. Q1: At the local scale, sites

Diversity–stability relationships at the local scale

We observed a variety of diversity–stability relationships at the local scale. In general, we found support for the
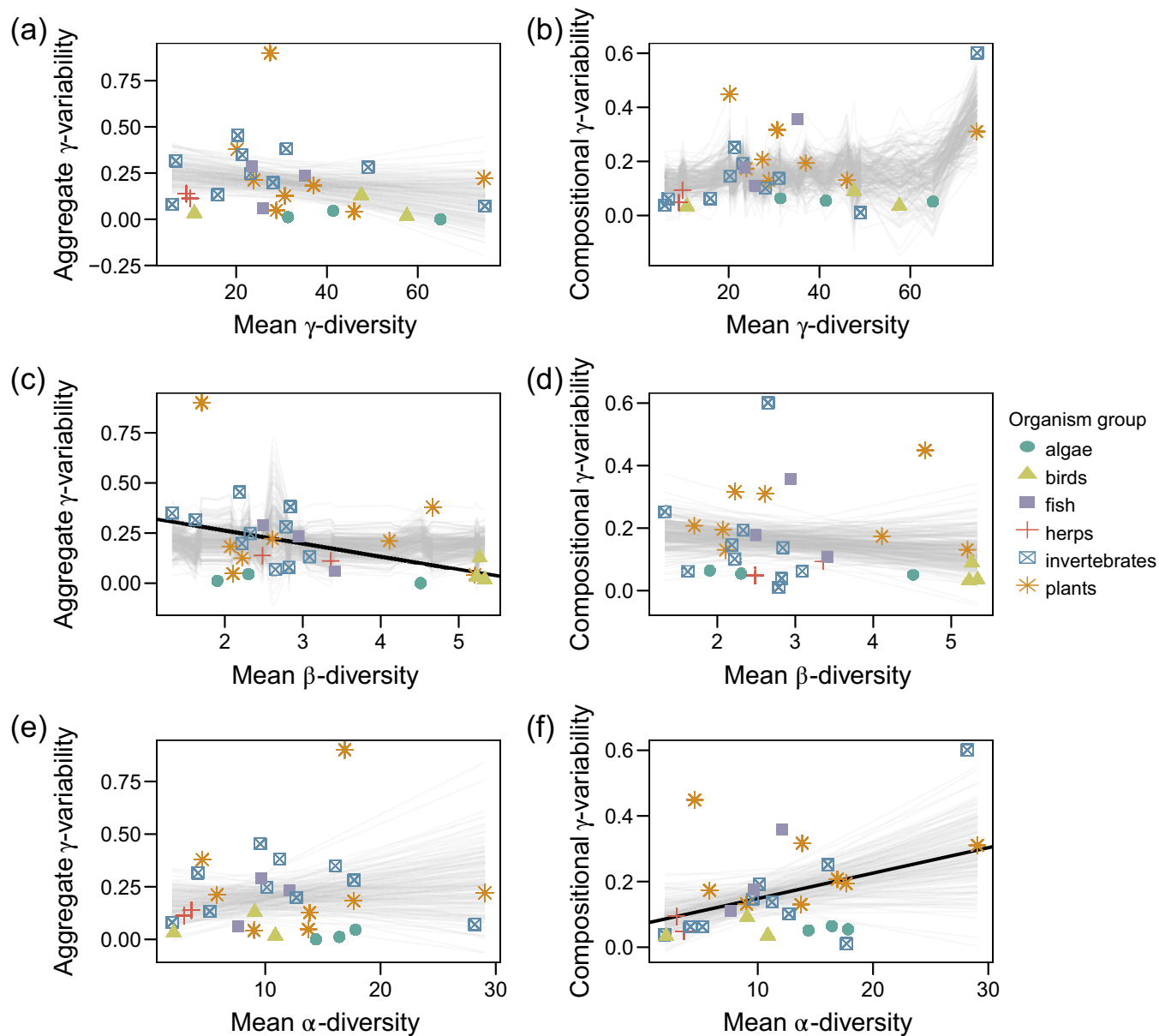
FIGURE 3 Diversity–stability relationships for aggregate (left column) and compositional (right column) variability at the metacommunity scale, in relation to the temporal average of regional gamma-diversity (a, b), the temporal average of spatial beta diversity (c, d), and the temporal average of mean alpha-diversity (e, f). Solid line represents the fixed effects from a Bayesian linear mixed effects model, shown only when the 95% credible intervals exclude zero. Gray lines depict fixed effects from posterior possible models.

stabilizing effect of α-diversity on aggregate variability (e.g., total community biomass) (Figure 1a). However, there was variation in DSR slopes among organismal groups. For example, several invertebrate communities did not follow a negative relationship between diversity and aggregate variability, but instead showed a positive relationship. Fish, bird, and most plant communities supported a stabilizing effect of biodiversity. Relative to the numerous studies analyzing DSRs in plant communities, our broader analysis suggests there could be deviations from predicted DSRs that depend on the organisms in the community.

We found more heterogeneous relationships between diversity and compositional variability (Figure 1b). Overall, there was a negative relationship between richness and compositional variability across all metacommunities. However, within metacommunities, we often found strong positive or negative relationships between average site richness and compositional variability. For example, in many (but not all) invertebrate communities, communities with higher α-diversity were less variable in their composition over time, as we observed with bird and fish communities. In contrast, algae and plant communities with higher average richness tended to be more compositionally
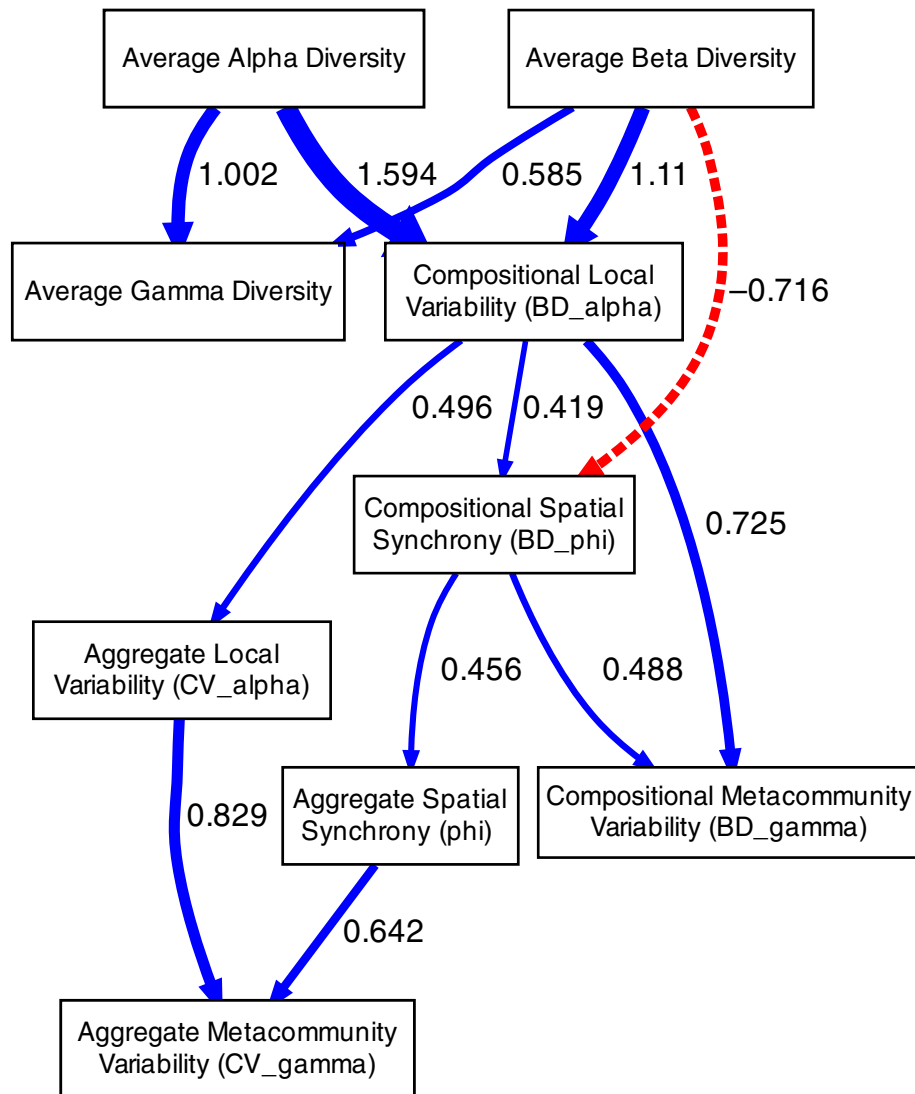
FIGURE 4 Structural equation model (SEM) showing the significant paths and standardized coefficients. Blue solid lines indicate significant positive relationships and the red dashed line indicates significant negative relationships. Nonsignificant relationships are not shown. Widths of the arrows are proportional to the standardized path coefficients.

variable (Figure 1b). This positive relationship is consistent with the predictions established in other plant communities (Hector et al., 2010; Tilman, 1999; Tilman et al., 2006; Wang et al., 2019). It may arise from competing species that respond differently to environmental fluctuations, such that environmental shifts that decrease the abundances of some species allow competing species to increase, generating high compositional variability (Tilman, 1996). Our broader synthesis suggests that this positive relationship may not translate to communities of other organisms, especially animal communities.

β-Diversity reduces spatial synchrony

The strongest and most consistent relationship that emerged in our study was the negative relationship between mean spatial β-diversity and spatial synchrony (Figures 1c,d and 4). This pattern emerged across metacommunities spanning a range of ecosystem types and organismal groups, including species with different dispersal capabilities. Moreover, because spatial synchrony in both composition and total abundance declined with β-diversity, this suggests that aggregate metacommunity variability generally declined due to spatially distinct community dynamics, rather than noncompositional factors like asynchronous fluctuations in community abundance or biomass. However, this was not always the case. For example, the fish metacommunity at the SBC LTER had low aggregate variability due to low aggregate spatial synchrony, but high spatial synchrony in composition (Figure 2). This pattern may indicate that reductions in regional variability were not due to spatial insurance effects, but instead due to external factors, such as spatially

asynchronous environmental variation (Lamy et al., 2021). Across all ecosystems, the effects of β-diversity tended to flow from diversity to compositional synchrony, to aggregate synchrony, and to aggregate metacommunity variability (Figure 4).

Our results support the prediction that β-diversity is important for reducing aggregate metacommunity variability due to its effects on reducing compositional synchrony (Figures 3c and 4). Recent empirical work in temperate forests across northern China further supports this prediction by showing that reducing spatial synchrony was more important than reducing local variability for stabilizing aggregate properties at broad spatial scales (Qiao et al., 2022). In our analysis, however, local variability was a slightly stronger pathway to regional variability than spatial synchrony, and higher β-diversity was also associated with increased local variability (Figure 4). The positive association between β-diversity and local variability is likely to be due to dispersal from compositionally different communities, which facilitates local turnover. Understanding these direct and indirect pathways is important because the long-term maintenance of spatial ecological processes that promote asynchrony in the metacommunity could be desirable for management and conservation (Harrison et al., 2020; Socolar et al., 2016).

Taxonomic patterns in aggregate and compositional spatial synchrony

In our analysis, bird metacommunities had the lowest compositional spatial synchrony, while plant metacommunities tended to have the highest (Figure 2; Appendix S2: Figure S1). One possible explanation for this result might relate to dispersal capacity and habitat selection. Birds are strong dispersers with the potential for habitat selection, allowing environmental tracking (i.e., seeking favorable habitats for reproduction) across a spatially heterogeneous landscape (e.g., Catano et al., 2020). The bird metacommunity from the Baltimore Ecosystem Survey (BES) had the largest reduction in variability from local to regional scales for both total abundance and composition, followed by birds in the Andrews Experimental Forest (AND) and the Central Arizona Phoenix (CAP) urban ecosystem (Figure 2). High β-diversity and low compositional spatial synchrony in these metacommunities suggests that local community dynamics counteracted each other at the regional scale (Figure 1c,d), reducing metacommunity variability. At the local scale, bird communities were less variable in their total abundances but more variable in composition than other taxa (Appendix S2: Figure S1), a pattern consistent with local compensatory dynamics

(Brown et al., 2016). Together, this suggests that bird metacommunities may be stabilized by reduced compositional spatial synchrony and local aggregate variability.

In contrast, plant metacommunities tended to have high spatial synchrony in both compositional and aggregate properties (Figure 2; Appendix S2: Figure S1). Such high spatial synchrony suggests that spatial processes contribute little to the reduction in variability from local to regional scales. High spatial synchrony could occur if plants are not dispersal limited and respond similarly to environmental fluctuations across the landscape. The spatial heterogeneity of the grassland sites included in this analysis could also be insufficient to generate the high β-diversity necessary to confer regional stability. Indeed, several plant metacommunities had low β-diversity, which may explain their high spatial synchrony (Figure 1c,d). High spatial synchrony may also be due to a comparatively small spatial extent of the region studied (Liang et al., 2022), suggesting that spatial extent may contribute to differences among metacommunities. Even among plant metacommunities, some were more spatially synchronous than others (Appendix S2: Figure S2), which may be due to differences in plant demographic traits in relation to environmental variability. Understanding the interplay of spatiotemporal heterogeneity and dispersal for species diversity and community dynamics at different scales could be especially relevant for conservation (Andrade et al., 2020; Chase et al., 2020), and our analysis suggests there could be key differences among taxa that must be taken into consideration before implementation.

Diversity–stability relationships at the regional scale

Our results suggest a transition in how DSRs scale up from local to metacommunity scales. While α-diversity tended to reduce aggregate fluctuations at the local scale (Figure 1a), we found no evidence that higher γ-diversity reduced the variability of total metacommunity abundance (Figures 3a and 4). Although γ-diversity reduced aggregate variability at the regional scale in recent syntheses of plant biodiversity experiments focusing on within-ecosystem patterns (Liang et al., 2022; Wang et al., 2019, 2021), our results suggest that this relationship may not hold more broadly across a wider collection of organisms and ecosystems. The absence of a regional DSR across ecosystems may occur because different numbers of species may be needed to stabilize different ecosystems, making γ-diversity a poor predictor of variability.

In contrast with theoretical predictions that γ-diversity should stabilize aggregate properties at broad

spatial scales, metacommunities may exhibit additional sources of variability that dilute the strength of this predicted relationship among ecosystems. Other dimensions of community structure, such as evenness (Craven et al., 2018; Valencia et al., 2020) or the spatial synchrony of richness (Walter et al., 2021), may also be relevant for community variability beyond species richness alone. Likewise, species identity may be an important consideration, as some metacommunities with low γ-diversity had low aggregate variability (Figure 3a), possibly indicating that a few well adapted species may be sufficient to stabilize regional abundances. Environmental variability is also likely to be important, with some metacommunities existing in relatively constant environments, while others exhibit higher temporal or spatial heterogeneity. These additional factors could explain why our results were consistent with those of other syntheses, which found weak relationships between diversity and biomass production at metacommunity scales (Wilcox et al., 2017).

Compositional metacommunity variability was positively related to mean α-diversity (Figure 3f). This relationship could arise because of the strong positive relationship between mean α-diversity and local compositional variability, and the strong influence of local compositional variability on metacommunity variability (Figure 4). In other words, a metacommunity where a large proportion of sites has high α-diversity may indicate that regionally, the metacommunity has high variability due to numerous highly variable local communities, such as in strongly competing plant communities (Hector et al., 2010; Tilman, 1996). These local fluctuations could scale up to the metacommunity scale if they are not sufficiently offset by decreases in spatial synchrony due to dispersal limitation or spatial environmental heterogeneity. However, it is worth noting that average local richness may also be driven by a few sites with high richness, and local sites with high α-diversity were not always the most compositionally variable (Figure 1b). Therefore, mean α-diversity emerges as a useful predictor of higher compositional metacommunity variability at the regional scale even if individual sites within metacommunities do not always show the same relationship.

β-Diversity was the primary stabilizing force that reduced metacommunity variability. However, while we found a significant negative relationship between β-diversity and aggregate metacommunity variability, we did not find one with compositional variability. One explanation for these differences comes from the indirect effects of β-diversity. When accounting for all the indirect pathways (Figure 4), the total effects of β-diversity on aggregate metacommunity variability were sufficiently negative. In contrast, for compositional metacommunity variability, the stabilizing effects of β-diversity (by reducing spatial synchrony) can be counterbalanced by its destabilizing

effects (by increasing local variability). In other words, DSRs become decoupled at the metacommunity scale because of increased direct and indirect pathways that modify relationships between biodiversity and variability.

Overall, our study demonstrates a range of aggregate and compositional DSRs (varying in strength and direction) beyond the patterns established in plant communities at the local scale. Our results suggest that, at regional spatial scales, β-diversity helps to stabilize metacommunities through system-specific pathways. In some cases, β-diversity could enable local turnover that drives local aggregate fluctuations, which directly increases metacommunity variability, while in other cases, the strong reduction in compositional spatial synchrony with β-diversity is enough to overcome any potentially destabilizing effects. β-Diversity also appears to have a stronger stabilizing effect on aggregate than compositional metacommunity properties, perhaps because regional aggregate stability can occur through regional compositional fluctuations (Lamy et al., 2021). While our analysis is focused on broad patterns across systems, future investigations into the relationships between species traits and environmental variation, conducted at appropriate spatial scales, will be crucial for disentangling the local and regional metacommunity processes that generate variability and for managing specific habitats for biodiversity conservation.

AUTHOR CONTRIBUTIONS

Nathan I. Wisnoski led the analysis, made the figures, and wrote the first draft of the manuscript. All authors contributed to data processing, conceptualization of the study, analysis, figures, and writing/edits.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data sets are publicly available; the list of data sources can be found in Appendix S1: Section S1. Code (Wisnoski 2023) is available on Zenodo at https://doi.org/10.5281/zenodo.8066470.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.