Multi-scale biodiversity drives temporal variability in macrosystems

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High temporal variability in environmental conditions, populations, and ecological communities can result in species extinctions and outbreaks of agricultural pests and disease vectors, as well as impact industries dependent on reliable provisioning of ecosystem services. Yet few empirical studies have focused on testing hypotheses about the drivers of ecological temporal variability at large spatial and temporal scales. Using decadal datasets that span aquatic and terrestrial macrosystems and structural equation modeling, we show that local temporal variability and spatial synchrony increase temporal variability for entire macrosystems. These mechanisms are influenced by environmental heterogeneity, habitat-level species diversity, spatial scale, and the size of the regional species pool. This analysis is among the first to provide a quantitative argument for the value of regional species diversity. Moreover, our conceptual model is generalizable and may help guide management efforts to reduce temporal variability for conservation or service provisioning in other macrosystems.

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Populations, communities, and ecosystem functions all rise and fall through time in accordance with seasonal patterns, year-to-year changes in weather, and regulation through internal processes like predator–prey cycles (Levin 1992). These patterns, which we refer to as *temporal variability*, may also be influenced by human activities. Temporal variability that becomes exaggerated (ie higher peaks and lower lows) increases the risk for local extinction of animal and plant populations (Heino *et al.* 1997; Schindler *et al.* 2010), as well as outbreaks of pests and disease vectors (Bolker and Grenfell 1996; Sabo 2005). Similarly, socioeconomic systems can be impacted by unexpected temporal variability, particularly when these fluctuations occur at large spatial scales. For example, a particularly bad year for fisheries production can reduce food security and result in unsustainable harvests (Badjeck *et al.* 2010; Moore and Schindler 2010). Likewise, greater unreliability of pollinator services can heighten the risk of crop failure in bad years (Slingo *et al.* 2005; Ray *et al.* 2015). Understanding the drivers of temporal variability in spatially structured ecosystems is therefore critically important for both conservation planning and sustaining human livelihoods and economies.

In a nutshell:

- Maintaining the stability of harvests, species populations, and ecological communities are common management objectives, but the processes thought to control temporal fluctuations in ecosystems have been poorly studied at regional to continental scales
- Local and regional biodiversity along with spatial variation in the environment were found to reduce fluctuations in ecosystem stocks (biomass, abundance) at the landscape scale
- Analysis and synthesis of long-term, spatially replicated datasets will enhance our understanding of the drivers of stability at different scales, and improve stewardship of species, communities, and ecosystem services

Improving knowledge about temporal variability requires consideration of how drivers interact directly and indirectly with one another across spatial scales. The emerging subdiscipline of *macrosystems ecology* explicitly focuses on the study of ecological dynamics at large scales, with patterns being driven by multiple factors that interact across scales (Heffernan *et al.* 2014). Empirical evidence suggests that temporal variability can be influenced by local and regional factors (Tilman and Downing 1994; Schindler *et al.* 2010), and there is growing consensus that cross-scale interactions are also important for understanding variability (Wang and Loreau 2014; Wilcox *et al.* 2017). For example, the Moran theorem suggests that large-scale synchronous environmental fluctuations lead to large-scale synchronous fluctuations in population abundance (Moran 1953). Synchronized subpopulations in a connected system may be more vulnerable to punctuated natural or anthropogenic disturbances (Wang and Loreau 2014). Here, we review the literature on drivers of temporal variability at multiple scales, identify testable hypotheses (Table 1), and provide new evidence from our own analyses. Our purpose is to illustrate how progress can be made to understand the drivers

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Table 1. Hypothesized direct and indirect drivers of γ-variability*

Hypothesis	Rationale	Implications for managers seeking to reduce regional temporal variability
(1) γ-variability is positively related to α-variability	Fluctuations in the local environment will scale to large-scale fluctuations	See recommendations for hypotheses (3) and (4)
(2) γ-variability is positively related to spatial synchrony	Reductions in spatial synchrony reduce the degree to which local fluctuations translate into large-scale fluctuations	See recommendations for hypotheses (5), (6), and (7)
(3) γ-variability is negatively related to α-richness	Local diversity acts on γ-variability by reducing α-variability via response diversity	Increase local biodiversity through restoration and conservation
(4) γ-variability is negatively related to γ-richness	Regional diversity acts on γ-variability by increasing local diversity, acting on γ-variability through α-variability	Conserve local biodiversity, diversity of habitats in the region, and connectivity between habitats
(5) γ-variability is negatively related to spatial scale	Scale increases γ-richness and environmental heterogeneity (a) while reducing population connectivity (b), ultimately acting on γ-variability through both spatial synchrony and α-variability	Increase the size of managed and protected areas through land acquisition and preservation of corridors between habitats
(6) γ-variability is negatively related to environmental heterogeneity	Environmental heterogeneity increases γ-richness (a) and β-diversity (b) while reducing spatial synchrony via the Moran effect (c), ultimately acting on γ-variability through both spatial synchrony and α-variability	Preserve or restore landscape environmental heterogeneity
(7) γ-variability is negatively related to β-diversity	β-diversity reduces spatial synchrony, which decreases γ-variability	Prevent or reduce environmental homogenization and the spread of invasive species

Notes: *Numbers and letters correspond to the main text and Figure 2.

Table 2. Definitions for variability and biological diversity across scales

Name	Definition	Example
α-variability	The temporal standard deviation (SD) divided by the temporal mean of a time series measured in a single habitat	For an annual record of fish abundance in a single pond, this is the SD of fish abundance in that pond among years divided by the average number of fish in a pond
Spatial synchrony	Degree to which temporal fluctuations of ecosystem components among multiple locations are similar to one another, measured as covariance among time series	The degree of similarity in year-to-year changes between two annual time series of fish present in two separate ponds
γ-variability	The temporal SD divided by the temporal mean of a time series composed of summed measurements among sites in the defined region	For a dataset of fish abundance in ten ponds sampled annually through time; total fish among ponds are summed each year to create an aggregate time series, then the SD of that series is divided by the mean of that series
α-richness	The number of different species found within a single location	The number of fish species observed within a single pond
β-diversity	The dissimilarity in species composition among multiple locations; may be calculated using a variety of metrics; here calculated as mean pair-wise Bray-Curtis dissimilarity among sites	The difference in the types of fish found within two or more ponds
γ-richness	The number of different species found across all locations in a region	The total number of fish species found among all ponds on a landscape

of macrosystem variability, so that we may anticipate the effects of human activities on the temporal variability in ecosystems and the services they provide.

We begin by defining key terms for understanding temporal variability (Table 2). Ecological temporal variability can be defined as the frequency and magnitude of fluctuations in ecosystem structure (eg standing stocks of resources, species abundance) or ecosystem function (eg production, decomposition rate). Wang and Loreau (2014) demonstrated that temporal variability can be partitioned into local (α), landscape (β), and regional (γ) components, echoing concepts for biological diversity (Whittaker 1972). Following the definitions provided by Wilcox (2017), we define α-variability as the standard deviation of a time series from a local habitat divided by the mean of the time series (Table 2); regional γ-variability as the standard deviation of the summation of time series from all locations in the region divided by the mean of the summed time series (Table 2); and the β portion of variability as spatial synchrony, or the degree of covariation in fluctuations through time among all locations in the region (Table 2).

A core set of hypotheses in the literature is that γ-variability is driven by spatial synchrony (Table 1, row 1) and α-variability (Table 1, row 2). Increases in α-variability directly enhance γ-variability by increasing the magnitude of fluctuations (Figure 1), while reductions in spatial synchrony allow differences in patterns of fluctuations among locations to cancel each other out, thereby reducing γ-variability (Figure 1). If these core hypotheses are correct, then understanding the drivers of

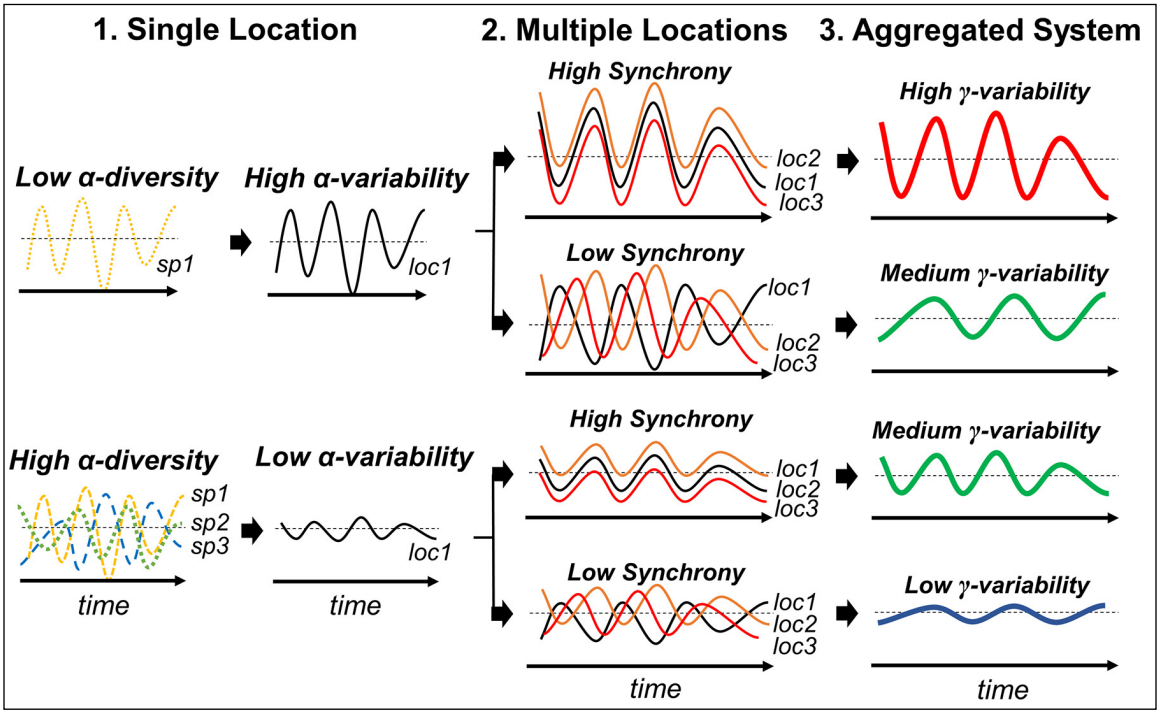

Figure 1. Conceptual diagram illustrating how variability propagates across spatial scales. Labels include trend lines for each of several hypothetical species (sp1, sp2, and sp3) and for the multispecies total abundance at each of several different locations (loc1, loc2, and loc3) in the landscape. The diagram shows (1) how higher local diversity is predicted to reduce α-variability, (2) different scenarios for combinations of α-variability and spatial synchrony in multisite landscapes, and (3) the predicted effect of these combinations on γ-variability.

α-variability and spatial synchrony will enhance our understanding of controls on γ-variability (Wilcox *et al.* 2017).

For decades, ecologists have focused on the drivers of local α-variability, which include fluctuations in precipitation and temperature (Andrewartha and Birch 1954), species or trait diversity (Tilman and Downing 1994; Tilman *et al.* 2006), and species interactions (McCann 2000). Greater species diversity allows for a greater diversity of responses to environmental change, allowing for compensatory dynamics that reduce variability in ecosystem functions like total plant production in grassland plots (Tilman *et al.* 2006). Reductions in species diversity can therefore increase species synchrony and subsequently α-variability in aggregated biomass (Tilman *et al.* 2006), the aggregate of which may in turn induce greater γ-variability (Table 1, row 3).

A number of other pathways may then act on γ-variability through their effect on α-richness. For example, α-richness is constrained by the number of species in the regional species pool (γ-richness; Crist and Veech 2006; Ulrich *et al.* 2016), and therefore we predict that γ-richness should be negatively related to both α-variability and γ-variability (Table 1, row 4). This implies that declines in regional biological diversity will increase temporal variability across spatial scales (Hooper *et al.* 2012). Spatial scale and environmental heterogeneity can also act on these mechanisms. Theories concerning species–area relationships predict that species pools should increase with spatial scale and that the relationship should strengthen with environmental heterogeneity (Palmer and White 1994). Consequently, larger spatial scales and greater environmental heterogeneity reduce γ-variability via effects cascading through γ-richness and α-richness (Table 1, row 5a and row 6a).

Spatial synchrony, the other hypothesized driver of γ-variability, is in turn also regulated by several direct and indirect factors. For example, it is expected that β-diversity (ie differences in community composition among local habitats) will reduce spatial synchrony (Wang *et al.* 2019) and subsequently diminish regional γ-variability (Wang and Loreau 2016) as a result of a decrease in organismal response diversity (Elmqvist *et al.* 2003) (Table 1, row 7). Environmental heterogeneity acts indirectly on spatial synchrony via this pathway by providing opportunities to increase the β-diversity of species, traits, and life stages (Hilborn *et al.* 2003), and should therefore act to lower γ-variability by reducing spatial synchrony (Table 1, row 6b). However, environmental heterogeneity may also act directly on spatial synchrony. In homogenous landscapes, large-scale events (eg drought) should alter local environmental conditions in similar ways, leading to greater spatial synchrony among responses and enhancing the Moran effect (McCluney *et al.* 2014). As a result, landscape homogenization (eg agricultural fields in the midwestern US, dammed rivers in the Colorado River basin) should lead to increased macrosystem γ-variability (Table 1, row 6c).

Spatial synchrony also depends on dispersal of organisms between local ecosystems – a combination of geographic distance, dispersal ability, and barriers to movement. Therefore, even when the environment does not vary, changes in

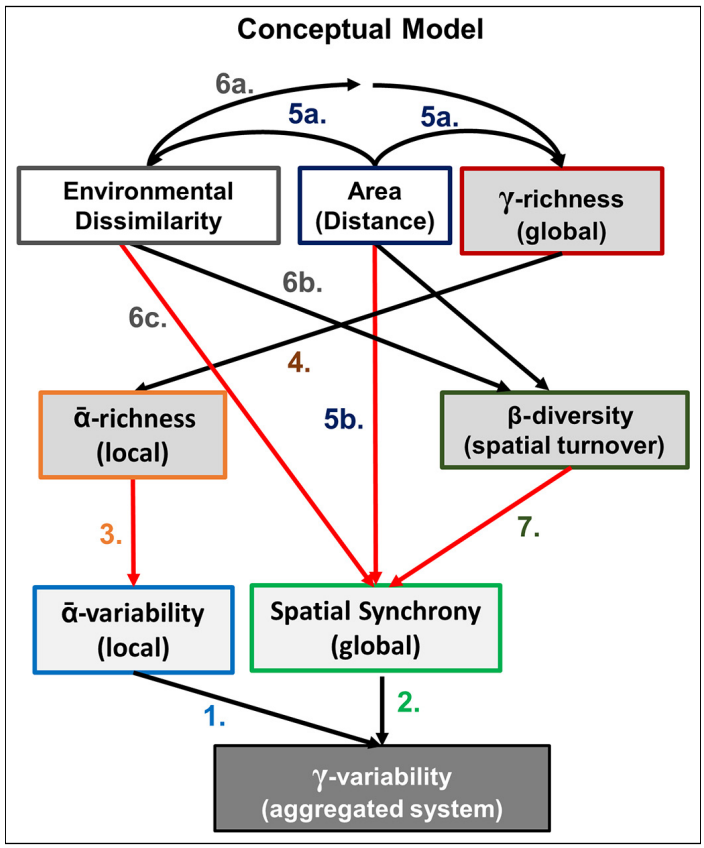

Figure 2. Hypothesized network of drivers influencing system variability. Descriptions of the hypotheses and their rationales are presented in Table 1. Black and red arrows indicate positive and negative effects, respectively. Biological diversity measures are shown in medium gray and proximate drivers of γ-variability are shown in light gray. The model predicts that spatial synchrony and ᾱ-variability will increase γ-variability, and that these factors are negatively influenced by ᾱ-richness and β-diversity, spatial scale, and environmental dissimilarity via a series of direct and indirect effects. Directional effects are numbered and color-coded to correspond to the hypothesis, rationale, and suggested management activities in Table 1.

organismal fluxes across habitats may alter local and regional dynamics (Gouhier *et al.* 2010). Generally, reduced dispersal, driven by the presence of physical barriers or greater geographic distance, should lower spatial synchrony by promoting dissimilar community dynamics (Table 1, row 5b). However, we note that dispersal barriers can also lead to extinctions of migratory species and reduce dispersal-driven rescue effects, lowering diversity. Consequently, the effects of dispersal on γ-variability are likely complex and nonlinear.

We identified seven distinct hypotheses about drivers of γ-variability (Table 1). Many of these hypotheses include cascading or indirect paths of causality (eg α-richness) or multiple mechanisms (eg environmental heterogeneity). Although these hypotheses have been evaluated individually, and in some cases comparatively (Wilcox *et al.* 2017), additional assessments of their relative importance may improve understanding of how they interact across scales in a diversity of systems and landscapes, and how these concepts could be operationalized for management purposes. In Figure 2, we connect the hypotheses presented in Table 1 in a conceptual framework to illustrate the relative importance of the factors driving macrosystems variability, and their potential interactions. Using this graphical model as a guide, we used spatially explicit decadal data from four macrosystems to test the conceptual model and individual hypotheses.

Methods

The methodological procedures and datasets used in our analysis are described in greater detail in WebPanel 1.

Datasets

Terrestrial beetles were previously collected in Phoenix, Arizona, with nine yearly (2006–2014) estimates of abundance of multiple taxa from 24 sites across 20,000 km^2 (Grimm *et al.* 2018). Data consisted of pit-fall traps in groups, typically of four (mean ± standard deviation; 3.7 ± 0.7), trapped quarterly, with all individuals identified to family (50 families included in the dataset). Covariate data included percent land use in a 500-m radius circle surrounding the trapping locations, taken from the 2006 National Land Cover Database (Fry *et al.* 2011). We also included minimum–maximum temperature and precipitation data from downscaled PRISM data (PRISM Climate Group 2016).

Submerged vegetation was surveyed at 95 subestuaries (smaller estuaries within the larger Chesapeake Bay estuary) with 30 yearly (1984–2009, except 1988) estimates of density-weighted coverage distributed across Chesapeake Bay, in Maryland and Virginia (Patrick and Weller 2015). Species composition (25 taxa across bays) within each embayment was derived from ground observations (Patrick *et al.* 2017). Covariate data included estuary morphology, salinity, tidal range, benthic substrate, watershed land cover, and shoreline armoring and structures (see Patrick *et al.* [2017] for further explanation of all variables and sources). The subestuaries were divided into two distinct groups, upper bay and lower bay, in accordance with designations applied by the Chesapeake Bay Program, a partnership of states in the Chesapeake Bay watershed and federal agencies led by the US Environmental Protection Agency (Batiuk 2000).

Stream fish composition (56 species observed) and abundance were identified from annual (2000–2012) electrofishing surveys conducted in 27 Maryland streams (Southerland *et al.* 2005). Abundance was converted to biomass (grams, g) by multiplying the mean length of each taxa by species-specific allometric scaling equations (www.fishbase.org). Covariate data included water chemistry and quality (pH, conductivity, temperature, dissolved organic carbon, total nitrogen, total phosphorus, orthophosphate, ammonium, and nitrate), habitat quality metrics, canopy cover, stream morphology (width, depth, drainage area), velocity, and watershed land cover taken from the 2006 National Land Cover Database (Fry *et al.* 2011).

Analyses

Structural equation models (SEMs) were used to test the conceptual model (Figure 2), which allows for statistical evaluation of direct and indirect effects cascading through multiple endogenous and exogenous variables (Grace *et al.* 2012). SEMs are appropriate for testing our conceptual model because drivers of within-site variability and spatial synchrony may co-vary, and indirect effects are possible. Metrics calculated for each factor in the conceptual model included environmental heterogeneity, spatial area, diversity at multiple scales (γ, α, and β), and variability at multiple scales (γ, α, and β). Metrics were calculated within multiple circular regions of varying spatial grain, allowing for a multi-scale analysis within each system.

Metrics used in the analysis consisted of *environmental heterogeneity*, measured as mean dissimilarity in environmental conditions among sites in a ring (multivariate Euclidian distance in *z*-score environmental data), and *spatial area*, which referred to the spatial grain. Diversity metrics for sites within the ring included $\bar{\alpha}$-*richness* (average number of species within local habitats), β-*diversity* as mean Bray-Curtis dissimilarity, and γ-*richness* (total count of species within the ring). Temporal metrics included (1) $\bar{\alpha}$-*variability*, calculated as the average temporal coefficient of variation (CV) within sites within the ring; (2) γ-*variability*, calculated as the temporal CV of all locations in the ring summed together; and (3) *spatial synchrony*, calculated as the variance explained by the first temporal mode of variation extracted from empirical orthogonal function (EOF) analysis of the time series within the ring (Patrick and Weller 2015).

The complete aggregate dataset was analyzed as two separate models consisting of a "general model", where study system was not considered a factor, and a "multigroup model", where study system ($n = 4$) was included as a categorical predictor (Grace 2003). The purpose of the two models was to develop a common model shared by all systems and then evaluate the variation in model coefficients among individual systems and the goodness of fit for the general model within individual systems. We estimated and corrected for spatial autocorrelation within systems in accordance with the procedures established by Harrison and Grace (2007) and Matteson *et al.* (2013) (see WebPanel 1 for more details). SEM goodness of fit was assessed using the global covariance method, where the covariance matrix of the data is compared to the covariance matrix implied by the model using a chi-square (χ^2) test, with a significant result ($P < 0.05$) indicating that the data were not likely to have been produced by the model (ie a poor fit). Total effects of each predictor on γ-variability were calculated by summing all of the coefficients of each path from the predictor to the response variable. Coefficients for paths that cascade through mediating variables were calculated by multiplying the path coefficients together (Grace 2003). A summary of the results and total effects is presented below; full results and model outputs are presented in WebPanel 1.

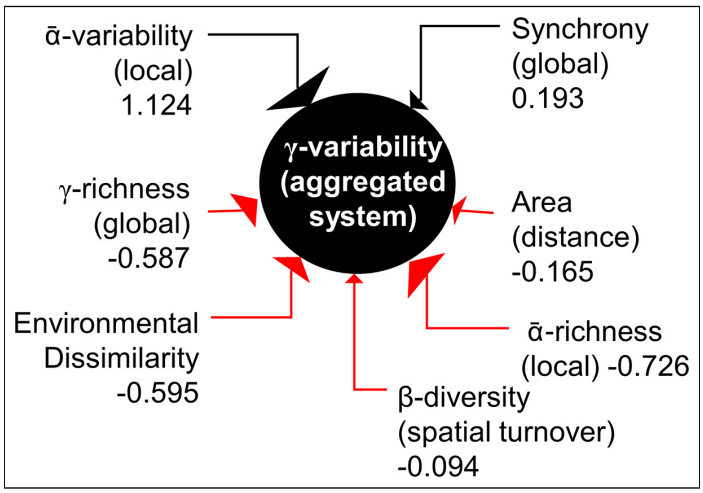

Figure 3. Total effect sizes of each driver on γ-variability in the general structural equation model. Red arrows indicate negative relationships; black arrows indicate positive relationships. Numbers are the total effect (sum of direct and indirect effects).

Results

We found support for our general model across all systems (ie no difference between the covariance matrix of the general model and the data; $P = 0.956$, $\chi^2 = 0.003$; Figure 3). However, the general model was not an equally good fit across all systems, suggesting variation in the relative importance of each pathway in different systems (ie significant differences between the multigroup model covariance matrix and the data; $P < 0.001$, $\chi^2 = 142.404$; WebFigure 3).

For the general model, both $\bar{\alpha}$-variability and spatial synchrony among locations increased γ-variability, and together these factors explained 86% of the variation in γ-variability (WebFigure 2). The effect of $\bar{\alpha}$-variability on γ-variability was six times larger than the effect of synchrony (Table 3). The total effects of γ-richness, $\bar{\alpha}$-richness, β-diversity, environmental dissimilarity, and spatial scale on γ-variability were all negative (Figure 3; Table 3).

In the multigroup model comparing differences among systems, $\bar{\alpha}$-variability increased γ-variability in all study systems, and spatial synchrony increased γ-variability in all systems with the exception of the high salinity lower Chesapeake Bay (Table 3). The total effects of biodiversity metrics (α, β, γ) on γ-variability were generally negative or nearly neutral across models, with several exceptions. For the ground beetle dataset, both local richness (α) and regional richness (γ) had negative total effects on γ-variability (similar to most models), but β-diversity had a positive total effect on γ-variability (different from most models; Table 3). For the high salinity lower Chesapeake Bay, all measures of biodiversity had positive total effects on γ-variability, differing from most models (Table 3).

Table 3. Total effects of predictor variables on γ-variability across models

Predictor variable	General model	Upper Chesapeake Bay	Lower Chesapeake Bay	Stream fish	Ground beetles	Expected (+ or –)
Environmental dissimilarity	–0.595	0.070	0.155	–0.721	–0.234	–
Area (distance)	–0.165	–0.339	0.184	0.319	–0.383	–
γ-richness (global)	–0.587	0.019	0.183	–0.591	–0.721	–
$\bar{\alpha}$-richness (local)	–0.726	–0.026	0.235	–0.754	–0.276	–
β-diversity (spatial turnover)	–0.094	–0.003	0.016	–0.002	0.123	–
$\bar{\alpha}$-variability	1.124	0.240	0.704	1.263	0.372	+
Spatial synchrony	0.193	0.518	–0.406	0.017	0.599	+

Discussion

Here we synthesized putative drivers of temporal variability in entire macrosystems (γ-variability; Figure 2) and tested their relative importance by analyzing empirical data on four distinct systems. Agreeing with predictions, we found that variability within locations (eg α-variability) and spatial synchrony among locations increased temporal macrosystem γ variability, whereas biodiversity ($\bar{\alpha}$-richness, β-diversity, and γ-richness), environmental dissimilarity, and spatial scale reduced γ-variability. However, we did not expect $\bar{\alpha}$-richness, γ-richness, and environmental dissimilarity to be the most important determinants of γ-variability. If this pattern is general, it bears important implications for conservation planning and ecosystem management. The result indicates that preservation of multiple components of biodiversity (local, regional, habitat) is needed to ensure macrosystem stability; regional management plans should therefore address all of these components. Our results also demonstrate that ongoing environmental homogenization represents an emerging threat because it can increase macrosystem variability by reducing habitat diversity, which enhances the Moran effect and reduces variation in sets of "filtered" communities (β-diversity), both of which synchronize temporal dynamics among ecosystems.

The stabilizing effects of $\bar{\alpha}$-richness and γ-richness were important components of most models. Species-rich communities (α-richness), which are constrained by the diversity of the regional species pool (γ-richness), have more ways to respond to disturbance (Elmqvist *et al.* 2003; Angeler and Allen 2016). At the scale of an individual habitat or patch, greater taxonomic or functional richness then leads to compensatory dynamics, with multispecies (or multitrait) aggregations displaying reduced variability (Tilman and Downing 1994; Tilman *et al.* 2006).

Strong support for the theoretically predicted importance of biodiversity is a key difference between our results and those of Wilcox *et al.* (2017), who found little evidence for relationships between α-richness and either α-variability or γ-variability. The differences may result from choice of study units; whereas we focused on landscape- to regional-scale datasets (>1 million ha each) that included >8 years of data collected from 18–65 sampling locations, Wilcox *et al.* (2017) focused on much smaller areas (0.024–144 ha) and included data from fewer sampling locations (3–18), with many of those datasets composed of data covering time frames less than 8 years. Thus, one reason we may have found a greater influence of diversity on temporal variability may have been having larger gradients of diversity, related to larger spatial areas with more replicates. In addition, although diversity typically increases ecosystem functioning at local scales (Hooper *et al.* 2005), there are many exceptions (Loreau and de Mazancourt 2013). Larger regional-scale datasets would be less influenced by rarer local sites that may exhibit negative relationships between diversity and function; moreover, Wilcox *et al.* (2017) suggested in shorter time series that disturbance patterns among sites may overshadow diversity effects. These results may indicate that the importance of biodiversity for temporal variability may be more apparent over longer time periods and at greater spatial scales (Levin 1992).

Our data suggest that environmental heterogeneity acts on system fluctuations through multiple pathways, the strongest of which is the positive relationship with γ-richness. However, there were also effects of heterogeneity on spatial synchrony. Local populations subject to the same environmental regime typically exhibit more similar fluctuations in abundance (Moran 1953). Environmental homogenization can therefore synchronize population dynamics among taxa in disparate locations (Wang and Loreau 2016), increasing γ-variability. The importance of heterogeneity in reducing system fluctuations is relevant given ongoing environmental homogenization caused by natural and anthropogenic stress. For example, widespread dam construction and operational practices like hydropeaking (releasing dammed water in short regular intervals to meet electricity demands) are increasing flow similarity among rivers across regions (Poff *et al.* 2007). Hydropeaking can also synchronize population dynamics among riverine invertebrates across sites distributed downstream from hydroelectric dams (Ruhi *et al.* 2018). Likewise, increasingly frequent large-scale extreme events linked to climate change, such as droughts or tropical cyclones (Diffenbaugh *et al.* 2015), can temporarily increase environmental similarity across distant habitats.

The weak relationship between spatial synchrony and γ-variability in the general model reflects system-specific

differences in the relationship between spatial synchrony and γ-variability. Previous work has shown that species and spatial synchrony increases γ-variability across spatial scales; for example, within a local habitat, grassland production is stable when production patterns are asynchronous among co-occurring species (Tilman and Downing 1994). At larger scales encompassing multiple habitats, a positive relationship was found between spatial synchrony among local communities and γ-variability of plant (Wilcox *et al.* 2017) and salmon (Schindler *et al.* 2010) biomass production.

We expected spatial synchrony to be positively related to γ-variability in our model, and although it was in most cases, the results for Chesapeake Bay macrophyte communities did not support our hypothesis. There are several potential reasons for the unexpected relationships in this system. Following the approach of the Chesapeake Bay Program monitoring and assessment strategy, we divided the system into upper bay and lower bay sections, because these regions contain very different macrophyte communities and are controlled by very different environmental drivers (Batiuk 2000). In total, 26 macrophyte species occur in Chesapeake Bay, ranging from freshwater taxa in the upper Potomac River and Susquehanna Flats, mesohaline taxa throughout the middle bay, and marine seagrasses in the lower bay. Species diversity declines along the salinity gradient, from 13 freshwater species to only two marine species (Patrick *et al.* 2017). Although our general hypotheses were supported in the species-rich upper bay (Figure 4a), spatial synchrony had a *negative* relationship with γ-variability in the lower bay (Figure 4b).

Two marine species, eelgrass (*Zostera marina*) and widgeon grass (*Ruppia maritima*), are dominant in the lower bay subestuaries (Figure 5), and their life histories provide an explanation for the counterintuitive negative relationship between spatial synchrony and γ-variability. Eelgrass forms expansive meadows and populations are stable under good growing conditions. Interannual fluctuations in eelgrass, when they occur, are controlled by broad climate forcing and may lead to heat-stress-induced die-offs (Moore and Jarvis 2008), events that are typically synchronized across the lower portion of the Chesapeake Bay (Patrick and Weller 2015). In contrast, widgeon grass may form large meadows in certain years but is primarily characterized by asynchronous boom–bust population cycles (Patrick *et al.* 2017). We interpret this to mean that in this low diversity system, high spatial synchrony is indicative of eelgrass, the species less prone to fluctuations in density and cover. Overall, we infer that when spatial synchrony is mechanistically linked with $\bar{\alpha}$-variability through species-specific life history characteristics, such as those of widgeon grass and eelgrass, the relationship between spatial synchrony and γ-variability may not be positive. Extrapolating the results across ecosystems, these types of effects are most likely when biodiversity is low and system stability can be determined by the inherent "life-history" stability of single dominant species.

The weak effects of spatial synchrony on γ-variability partially explain the surprisingly weak effects of β-diversity on γ-variability, but β-diversity also had weaker-than-expected effects on spatial synchrony itself. Intuitively, variation in species identity among communities should reduce synchronicity of dynamics among those communities. While the negative relationship between β-diversity and spatial synchrony was first reported by Wang *et al.* (2019), Wilcox *et al.* (2017) also found poor support for a link between β-diversity and spatial synchrony, and suggest that a measure of β-diversity based to a greater degree in functional rather than taxonomic differences among communities may yield better support. Indeed, Wang *et al.* (2019) included species with very different functional traits (eg woody shrubs, grasses), which could maximize the possible stabilizing effects of increasing β-diversity; moreover, their study was conducted across smaller spatial scales that may have conferred less environmental variability, increasing the detectability of β-diversity effects. In addition, a metric of β-diversity that is focused on the portion purely explained by turnover rather than differences in richness may have had a stronger relationship (Legendre 2014). It is possible, however, that at broad scales, environmental heterogeneity is simply a

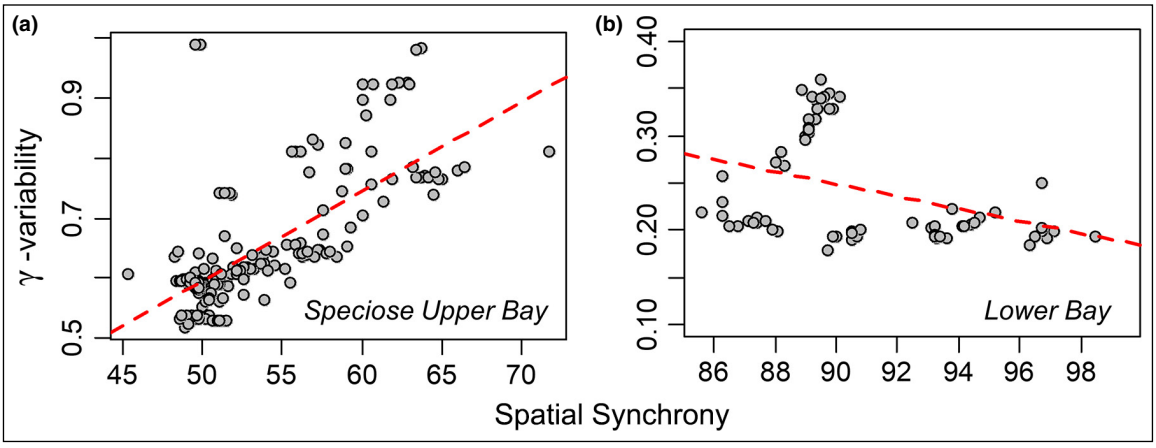

Figure 4. Relationship between spatial synchrony and γ-variability in (a) high-diversity upper Chesapeake Bay and (b) low-diversity lower Chesapeake Bay. Relationship is positive as expected in the upper bay (a) but negative in the lower bay (b).

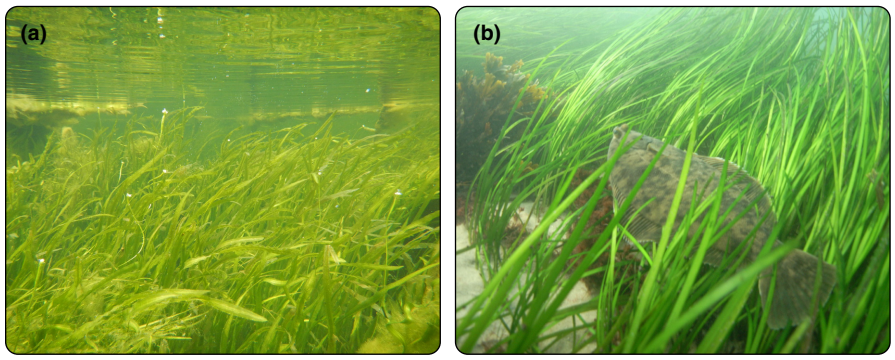

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Figure 5. Examples of the differing composition of submerged aquatic vegetation (SAV) found in Chesapeake Bay. (a) Mixed species composition SAV meadow in the tidal fresh Susquehanna Flats of upper Chesapeake Bay. (b) Eelgrass (*Zostera marina*) monoculture providing shelter to a summer flounder (*Paralichthys dentatus*) in the high salinity lower Chesapeake Bay.

much stronger driver of variation in temporal dynamics among localities (ie via variation in microclimates) than community composition.

Overall, understanding the interplay between the ultimate and proximate controls of macrosystem variability may aid in the design of more effective conservation actions, management practices, and monitoring networks. The results of our analysis suggest that preservation of biodiversity – including landscape heterogeneity – is key to achieving these goals. Biodiversity conservation is already a major goal of ecosystem management (Sodhi and Ehrlich 2010), but our results bolster the argument for diversity conservation by indicating that multi-scale diversity is critically important for temporal stability in the delivery of ecosystem services at macrosystem scales. Notably, the framework suggests that regional γ-richness plays an important role by providing a mechanistic link between biodiversity at conservation-relevant spatial scales and ecosystem functioning, a relationship that biodiversity–ecosystem functioning experiments have at times failed to detect (Hooper *et al.* 2005).

Future directions

As the use of big data in ecology continues to advance, there are a growing number of datasets that cover increasingly larger spatial and temporal scales. These expansive datasets offer new opportunities. For example, the proliferation of affordable remote-sensing data at increasingly high frequencies and broad scales offers a powerful resource for evaluating patterns of variability and spatial synchrony in vegetation dynamics across a wide range of spatial scales. Existing publicly funded programs focused on boots-on-the-ground research provide another source for valuable long-term and large-scale data. For instance, coastal monitoring programs funded by state and federal agencies (eg the National Estuarine Research Reserve Network) provide access to decades of high-frequency data on coastal processes from dozens of sites along the US coastline. Similarly, the US National Science Foundation (NSF)-funded Long Term Ecological Research Network and Lotic Intersite Nitrogen Experiment programs have amassed numerous macrosystem-level datasets. Because of the size, distribution, and longevity of those projects, they offer an opportunity for examining macrosystem processes. More recently, in 2012, NSF developed the National Ecological Observatory Network (NEON) to characterize long-term ecological changes at large scales, by integrating local- to continental-scale measurements at 20 core terrestrial and 20 core aquatic sites, supplemented by 41 relocatable sites. Data generated from these efforts would be especially useful for understanding how macrosystem processes like metacoupling and teleconnections influence temporal variability (see Tromboni *et al.* [2021]). For example, knowledge of migratory patterns of waterfowl along the Atlantic, Mississippi, Central, and Pacific flyways could provide information on long distance telecommunications for both avian and invertebrate taxa (eg fairy shrimp) that can travel on the feathers or in the guts of migratory birds, or by wind. Dispersal via these pathways may influence stability relationships within ephemeral wetlands (O'Neill and Thorp 2014). Combining multiple sources of data can improve knowledge about the relative importance of drivers of temporal variability, including dispersal and climate, from local to continental scales. The approaches we describe here could be applied to data collected on plants, animals, soil, nutrients, biogeochemistry, and atmospheric characteristics across multiple sites, identifying important controls of variability at different spatiotemporal scales for a wide range of ecosystems.

Conclusions

Our results demonstrate that organism and landscape diversity can influence variability across scales, including at the macrosystem level. Research on biodiversity–ecosystem functioning relationships has historically formed one argument for conserving global biodiversity to maintain ecosystem functions and services (Hooper *et al.* 2005). However, much of the earlier work on such relationships suffered from disconnects between small-scale experiments and the type of diversity loss that occurs at larger spatial scales. Our case study highlights the importance of large-scale diversity (γ) to macrosystem stability, and provides a clear link between local-scale taxonomic diversity (α), local-scale temporal variability, and macrosystem variability. We hope that this line of inquiry will further advance macrosystems theory, and guide the preservation of biodiversity – and the provision of ecosystem functions and services – across spatiotemporal scales.

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FrontiersEcoPics

Nocturnal crickets disperse seeds

Both ants and crickets are abundant in tropical and temperate ecosystems. In general, ants are seed dispersers, whereas crickets are seed consumers. However, while conducting field research on *Stemona tuberosa* (a medicinal plant that relies on wasps and ants to disperse its seeds), we observed nocturnal foraging crickets (*Teleogryllus mitratus*) consuming the outer covering (aril) of *S tuberosa* seeds and then dispersing the seeds into suitable microhabitats.

Typically, ants forage collectively and discard plant seeds near their nests, which leads to small-scale spatial aggregations of seeds. In contrast, crickets often forage individually, which could result in multidirectional seed dispersal and effectively reduce seed aggregation. Consequently, the potential benefits of seed dispersal by crickets could promote "seed escape" from predators, pathogens, and competing seedlings.

Given the abundance and diversity of crickets worldwide, and that there are more than 11,000 flowering plant taxa known to be ant-dispersed, seed dispersal by crickets may be more common than currently recognized. Yet, several questions remain: whether olfactory cues from seeds mediate cricket behavior, whether seed dispersal distance is related to cricket life stage or sex, and why crickets prefer to disperse seeds of primarily ant-dispersed plants.

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