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Stability and synchrony across ecological hierarchies in heterogeneous metacommunities: linking theory to data

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Ecography
42: 1200–1211, 2019
doi: 10.1111/ecog.04290

Subject Editor: Pedro Peres-Neto
Editor-in-Chief: Miguel Araújo
Accepted 31 January 2019

Understanding stability across ecological hierarchies is critical for landscape management in a changing world. Recent studies showed that synchrony among lower-level components is key to scaling temporal stability across two hierarchical levels, whether spatial or organizational. But an extended framework that integrates both spatial scale and organizational level simultaneously is required to clarify the sources of ecosystem stability at large scales. However, such an extension is far from trivial when taking into account the spatial heterogeneities in real-world ecosystems. In this paper, we develop a partitioning framework that bridges variability and synchrony measures across spatial scales and organizational levels in heterogeneous metacommunities. In this framework, metacommunity variability is expressed as the product of local-scale population variability and two synchrony indices that capture the temporal coherence across species and space, respectively. We develop an R function 'var.partition' and apply it to five types of desert plant communities to illustrate our framework and test how diversity shapes synchrony and variability at different hierarchical levels. As the observation scale increased from local populations to metacommunities, the temporal variability of plant productivity was reduced mainly by factors that decreased species synchrony. Species synchrony decreased from local to regional scales, and spatial synchrony decreased from species to community levels. Local and regional species diversity were key factors that reduced species synchrony at the two scales. Moreover, beta diversity contributed to decreasing spatial synchrony among communities. We conclude that our new framework offers a valuable toolbox for future empirical studies to disentangle the mechanisms and pathways by which ecological factors influence stability at large scales.

Keywords: hierarchical levels, metacommunity, organizational level, partitioning, spatial scale, synchrony

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Introduction

Understanding ecological stability is key to developing management strategies that maintain ecosystem services in a changing world (Donohue et al. 2016). During the past decades, numerous studies have been devoted to clarifying the mechanisms underlying ecosystem stability. Community ecologists developed experimental and theoretical approaches to investigate the stability of ecosystem functioning, and in particular its relation with biodiversity (McCann 2000, Tilman et al. 2006, Ives and Carpenter 2007, Hector et al. 2010). While stability has been defined in many different ways in the ecological literature, temporal variability, as measured by the temporal coefficient of variation of some ecosystem property, is most commonly used in empirical studies and is increasingly investigated by theoreticians (Donohue et al. 2016). In this approach, ecosystems with lower variability are considered to be more stable. Recent theory showed that ecosystem variability can be expressed as the product of species-level variability and the synchrony among species (Thibaut and Connolly 2013). This result clarifies the link between variability at two organizational levels, i.e. species and communities. Species-level and community-level variability, however, can exhibit different responses to ecological factors, mediated by their effects on species synchrony. For instance, several empirical studies showed that plant diversity decreased species synchrony, and thus community-level variability, but at the same time increased species-level variability (Tilman et al. 2006, Hector et al. 2010, Hautier et al. 2014).

On the other hand, population ecologists have focused on the persistence and stability of populations, often in a spatial context (i.e. metapopulations) (Ranta et al. 2006). The variability of a metapopulation can also be expressed as the product of the variability and spatial synchrony of its component local populations (Wang and Loreau 2014, Wang et al. 2015). Clarifying the drivers of spatial synchrony is thus key to understanding the stability of metapopulations. Previous studies have investigated the effects of spatial correlation in the environment and dispersal on the spatial synchrony and their consequences for metapopulation stability (Kendall et al. 2000, Liebhold et al. 2004, Ranta et al. 2006, de Roissart et al. 2015). In particular, dispersal can stabilize local populations while at the same time increasing spatial synchrony, such that its net effect on metapopulation stability can be either positive or negative (Earn et al. 2000, Abbott 2011, Wang et al. 2015).

While all these studies have provided insights into the stability of local communities and metapopulations, landscape management calls for a synthetic framework to understand stability in complex communities at large scales, e.g. metacommunities (Gravel et al. 2016, Wang et al. 2017). A metacommunity can be regarded either as a set of local communities at different locations or as a set of metapopulations belonging to different interacting species (Liebhold et al. 2004, Holyoak et al. 2005). Therefore, the stability of a metacommunity can arise from asynchrony across both species and space, and the ecological factors that regulate species and spatial synchrony all affect the stability of the whole metacommunity (Wang and Loreau 2014). One important unresolved question is what form of asynchrony (between species or across space) is more important for metacommunity stability. Furthermore, within a metacommunity, species synchrony can be measured at both the local and regional scales, just as spatial asynchrony can be measured at both the species and community levels, generating four different synchrony measures. It remains largely unknow how synchrony changes across spatial scales and organizational levels, and how they are regulated by different ecological factors, such as species diversity and dispersal. Disentangling the drivers of synchrony across ecological hierarchies should greatly improve our understanding of the scaling properties and ecological drivers of metacommunity stability.

Addressing these issues requires consistent definitions of synchrony that enable comparison across different hierarchical levels. Here we define a hierarchical level as the combination of a specific spatial scale (e.g. local or regional) and a specific organizational level (e.g. species or community). In the special case where local communities all have the same number and abundance of species, recent studies proposed definitions for two synchrony indices, i.e. species synchrony at the local scale and spatial synchrony among communities, and clarified their relations to metacommunity variability (Jørgensen and Nielsen 2013, Wang and Loreau 2014). These indices, however, are hardly applicable to empirical studies, due to the ubiquitous spatial heterogeneity in species composition and ecosystem properties in natural landscapes. An extended framework that is applicable to heterogeneous metacommunities is critically needed for application to real-world ecosystems (Wilcox et al. 2017).

In this paper, we develop a partitioning framework that links variability and synchrony indices at four hierarchical levels in heterogeneous metacommunities (i.e. populations, communities or metapopulations, metacommunities). Such a framework provides consistent measures of variability and synchrony across spatial scales and organizational levels, which offers new opportunities to clarify the pathways through which ecological factors regulate metacommunity stability. To illustrate our framework, we applied it to a long-term dataset of fifteen different Chihuahuan desert plant communities. Results showed that factors contributing to reducing species synchrony played a more important role in metacommunity stability, compared with those reducing spatial synchrony. Moreover, species synchrony decreased with spatial scale and spatial synchrony decreased with organizational level. At both local and regional scales, species diversity was a key factor that significantly decreased species synchrony and increased ecosystem stability. Beta diversity, or the spatial turnover of species composition, decreased the spatial synchrony among communities. We conclude that our framework provides a new practical tool to understand variability and synchrony in heterogeneous metacommunities, which may stimulate novel empirical research into the mechanism of ecosystem stability at large scales and their relations with biodiversity across scales.

Theory

In this section, we develop a partitioning framework that links temporal variability across spatial scales and organizational levels within a heterogeneous metacommunity, i.e. local population as the lowest level, local community or metapopulation as the intermediate level, and metacommunity as the highest level (Fig. 1). This framework, which is built upon recent theory that partitions stability across two spatial scales (e.g. our Eq. 1, 2, 5 are basically the square-root transformation of the respective metrics in Wang and Loreau 2014), offers critical extensions (Fig. 1) that enables applications to multi-level partitioning in realistic, heterogeneous metacommunities. Furthermore, our approach can be applied to an arbitrarily high number of hierarchical levels (Supplementary material Appendix 1).

Consider a metacommunity that consists of a number of local patches and includes a number of species. We denote $X_{i,k}(t)$ as the biomass (or any other population or ecosystem property) of species i in patch k at time t, $\mu_{i,k}$ as the temporal mean biomass of species i in patch k, and $v_{ij,kl}$ as the temporal covariance between species i in patch k and species j in patch l. Both $\mu_{i,k}$ and $v_{ij,kl}$ can be easily calculated from time-series data (Table 1). Note that $\mu_{i,k} = v_{ij,kl} = 0$ if species i is never recorded in patch k during the study period. Based on $\mu_{i,k}$ and $v_{ij,kl}$, we define a number of variability and synchrony indices that correspond to different spatial scales and organizational levels (Table 1 for a summary).

Defining variability at multiple hierarchical levels

We define variability at a given hierarchical level as the coefficient of variation of biomass. As we will see, such a definition makes the mathematical expressions and interpretations easier, as compared with the squared coefficient of variation used in recent studies (Wang and Loreau 2014). Specifically, metacommunity variability is defined as the coefficient of variation of total metacommunity biomass ($CV_{C,R}$ with the subscripts 'C' and 'R' representing 'community-level' and 'regional-scale' respectively; Table 1):

$$CV_{C,R} = \frac{\sqrt{v_{\Sigma,\Sigma}}}{\mu_{\Sigma,\Sigma}} \tag{1}$$

where $\mu_{\Sigma,\Sigma} = \sum_{i,k} \mu_{i,k}$ and $v_{\Sigma,\Sigma} = \sum_{i,j,k,l} v_{ij,kl}$ are the temporal mean and variance of total metacommunity biomass, respectively.

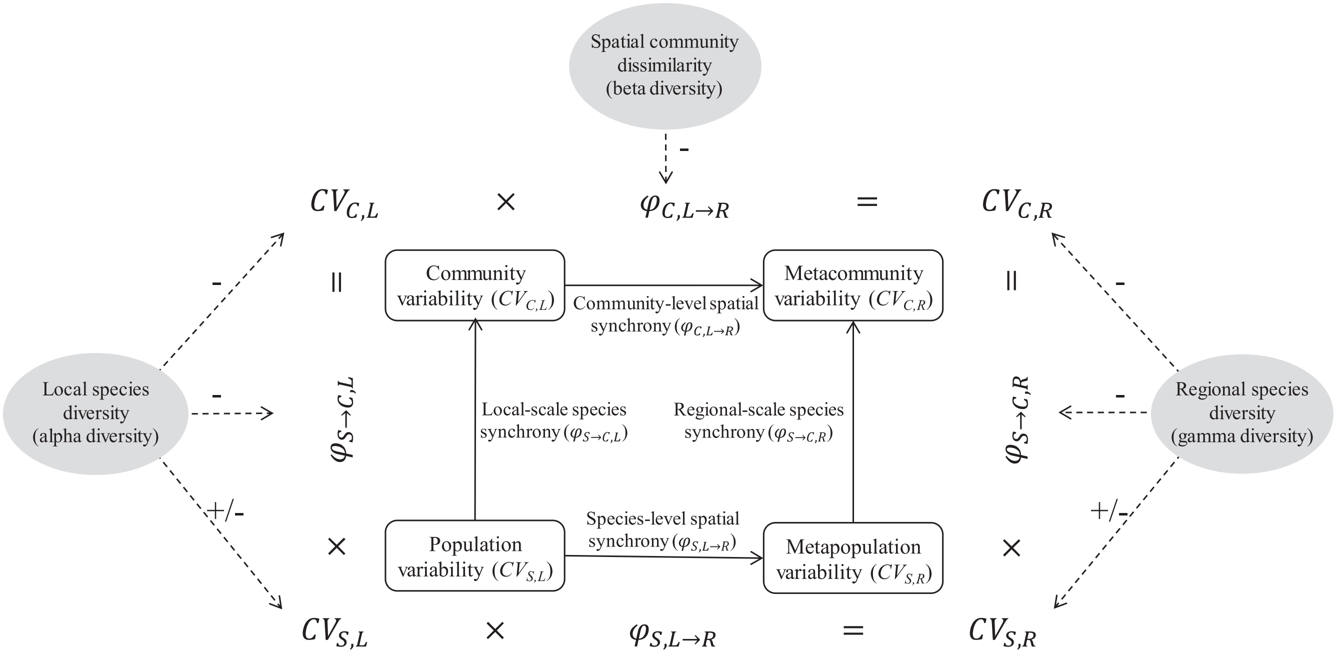

Figure 1. A partitioning framework of metacommunity variability into its lower-level components. Two alternative ways exist for scaling up variability from local species (bottom-left corner; $CV_{S,L}$) to metacommunities (top-right corner; $CV_{C,R}$). The first is to aggregate populations within each local community (top-left corner; $CV_{C,L}$) first and then aggregate local communities to metacommunities. The second is to aggregate populations within each species (bottom-right corner; $CV_{S,R}$) first and then aggregate metapopulations to metacommunities. See mathematical definitions in Table 1. Note that the link between community and metacommunity variability (i.e. $CV_{C,R} = CV_{C,L} \times \varphi_{C,L\to R}$) had been clarified in Wang and Loreau (2014). The dashed arrows describe hypothesized relationships between species diversity and variability or synchrony across hierarchical levels ('−' on the arrows indicates a negative relationship, and '+/−' indicates an either positive or negative relationship).

Table 1. Temporal variability and synchrony across spatial scales and organizational levels within a metacommunity.

Symbol	Description	Related hypotheses (and reference)
Temporal mean and variance		
$X_{i,k}(t)$	The biomass of species *i* in patch *k* at time *t*	
$\mu_{i,k} = \frac{\sum_{t=1}^{T} X_{i,k}(t)}{T}$	Temporal mean biomass of species *i* in patch *k*	
$v_{ij,kl} = \frac{\sum_{t=1}^{T} \left(X_{i,k}(t) - \mu_{i,k}\right)\left(X_{j,l}(t) - \mu_{j,l}\right)}{T-1}$	Temporal covariance between species *i* in patch *k* and species *j* in patch *l*	
$\mu_{i,\Sigma} = \sum_{k} \mu_{i,k}$	Temporal mean metapopulation biomass of species *i*	
$\mu_{\Sigma,k} = \sum_{i} \mu_{i,k}$	Temporal mean community biomass of patch *k*	
$\mu_{\Sigma,\Sigma} = \sum_{i,k} \mu_{i,k}$	Temporal mean biomass of the whole metacommunity	
$v_{ij,\Sigma} = \sum_{k,l} v_{ij,kl}$	Temporal covariance between metapopulation biomass of species *i* and *j*	
$v_{\Sigma,kl} = \sum_{i,j} v_{ij,kl}$	Temporal covariance between total community biomass of patches *k* and *l*	
$v_{\Sigma,\Sigma} = \sum_{i,j,k,l} v_{ij,kl} = \sum_{k,l} v_{\Sigma,kl} = \sum_{i,j} v_{ij,\Sigma}$	Temporal variance of the whole metacommunity	
Variability metrics		
$CV_{i,k} = \frac{\sqrt{v_{ii,kk}}}{\mu_{i,k}}$	Temporal variability of species *i* within the patch *k*	
$CV_{i,R} = \frac{\sqrt{v_{ii,\Sigma}}}{\mu_{i,\Sigma}}$	Temporal variability of the metapopulation biomass of species *i*	
$CV_{C,k} = \frac{\sqrt{v_{\Sigma,kk}}}{\mu_{\Sigma,k}}$	Temporal variability of total community biomass of patch *k*	
$CV_{S,L} = \sum_{i,k} CV_{i,k} \times \frac{\mu_{i,k}}{\mu_{\Sigma,\Sigma}} = \frac{\sum_{i,k} \sqrt{v_{ii,kk}}}{\mu_{\Sigma,\Sigma}}$	Local-scale average species variability, defined as the weighted average of local population variability ($CV_{i,k}$) across species and patches	Local species diversity (alpha diversity) can either increase or decrease the local-scale species variability (Tilman et al. 2006, Thibaut and Connolly 2013)
$CV_{S,R} = \sum_{i} CV_{i,R} \times \frac{\mu_{i,\Sigma}}{\mu_{\Sigma,\Sigma}} = \frac{\sum_{i} \sqrt{v_{ii,\Sigma}}}{\mu_{\Sigma,\Sigma}}$	Regional-scale average species variability, defined as the weighted average of metapopulation variability ($CV_{i,R}$) across species	Metacommunity diversity (gamma diversity) can either increase or decrease the regional-scale species variability (this study; sensu Tilman et al. 2006, Thibaut and Connolly 2013)
$CV_{C,L} = \sum_{k} CV_{C,k} \times \frac{\mu_{\Sigma,k}}{\mu_{\Sigma,\Sigma}} = \frac{\sum_{k} \sqrt{v_{\Sigma,kk}}}{\mu_{\Sigma,\Sigma}}$	Local-scale average community variability, defined as the weighted average of community variability ($CV_{C,k}$) across patches, the square of which corresponds to the alpha variability in Wang and Loreau (2014, 2016)	Local species diversity (alpha diversity) can decrease the local-scale average community variability (Tilman et al. 2006)
$CV_{C,R} = \frac{\sqrt{v_{\Sigma,\Sigma}}}{\mu_{\Sigma,\Sigma}} = \frac{\sqrt{\sum_{i,j,k,l} v_{ij,kl}}}{\mu_{\Sigma,\Sigma}}$	Regional-scale community variability or metacommunity variability, the square of which corresponds to the gamma variability in Wang and Loreau (2014, 2016)	Metacommunity diversity (gamma diversity) can decrease the metacommunity variability (Wang and Loreau 2016)

(*Continued*)

Table 1. (Continued)

Symbol	Description	Related hypotheses (and reference)
Species synchrony		
$\varphi_{S\to C,k} = \frac{\sqrt{v_{\Sigma,kk}}}{\sum_i \sqrt{v_{ii,kk}}}$	Synchrony among species within the patch *k*, which follows the definition in Loreau and de Mazancourt (2008) but in a square root version	
$\varphi_{S\to C,L} = \sum_k \omega'_k \times \varphi_{S\to C,k}$ where $\omega'_k = \frac{\sum_i \sqrt{v_{ii,kk}}}{\sum_{i,k} \sqrt{v_{ii,kk}}}$	Average local-scale species synchrony, defined as the weighted average of species synchrony across patches	Local species diversity can decrease local-scale species synchrony (Loreau and de Mazancourt 2008)
$\varphi_{S\to C,R} = \frac{\sqrt{v_{\Sigma,\Sigma}}}{\sum_i \sqrt{v_{ii,\Sigma}}} = \frac{\sqrt{\sum_{i,j} v_{ij,\Sigma}}}{\sum_i \sqrt{v_{ii,\Sigma}}}$	Regional-scale species synchrony	Regional species diversity can decrease regional-scale species synchrony (this study; sensu Loreau and de Mazancourt 2008)
Spatial synchrony		
$\varphi_{i,L\to R} = \frac{\sqrt{v_{ii,\Sigma}}}{\sum_k \sqrt{v_{ii,kk}}}$	Spatial synchrony among populations of species *i*	
$\varphi_{S,L\to R} = \sum_i \omega_i \times \varphi_{i,L\to R}$ where $\omega_i = \frac{\sum_k \sqrt{v_{ii,kk}}}{\sum_{i,k} \sqrt{v_{ii,kk}}}$	Average species-level spatial synchrony, defined as the weighted average of spatial population synchrony across species	
$\varphi_{C,L\to R} = \frac{\sqrt{v_{\Sigma,\Sigma}}}{\sum_k \sqrt{v_{\Sigma,kk}}}$	Community-level spatial synchrony, defined as the spatial synchrony of total community biomass across patches. The reciprocal of its square corresponds to the beta variability in Wang and Loreau (2014, 2016)	Community-level spatial synchrony decreases with beta diversity (Wang and Loreau 2016)
Synchrony ratio across levels		
$\lambda = \frac{\varphi_{S\to C,R}}{\varphi_{S\to C,L}} = \frac{\varphi_{C,L\to R}}{\varphi_{S,L\to R}}$	Ratio of regional-scale species synchrony to the local-scale one, or of community-level spatial synchrony to the species-level one	The synchrony ratio is smaller than 1 because synchrony decreases with the hierarchical level (this study) The synchrony ratio decreases with the beta diversity (this study)

Similarly, we define the variability of each local community *k* as $CV_{C,k} = \sqrt{v_{\Sigma,kk}} / \mu_{\Sigma,k}$, where $\mu_{\Sigma,k} = \sum_i \mu_{i,k}$ and $v_{\Sigma,kk} = \sum_{i,j} v_{ij,kk}$ are the temporal mean and variance, respectively, of total community biomass in patch *k*. We then define local-scale average community variability as the weighted average of community variability across patches:

$$CV_{C,L} = \sum_k CV_{C,k} \times \frac{\mu_{\Sigma,k}}{\mu_{\Sigma,\Sigma}} = \frac{\sum_k \sqrt{v_{\Sigma,kk}}}{\mu_{\Sigma,\Sigma}} \tag{2}$$

We also define the variability of the total metapopulation biomass of each species *i* as $CV_{i,R} = \sqrt{v_{ii,\Sigma}} / \mu_{i,\Sigma}$, where $\mu_{i,\Sigma} = \sum_k \mu_{i,k}$ and $v_{ii,\Sigma} = \sum_{k,l} v_{ii,kl}$ are the temporal mean and variance of the metapopulation biomass of species *i*. We then define regional-scale average species variability as the weighted average of metapopulation variability across species:

$$CV_{S,R} = \sum_i CV_{i,R} \times \frac{\mu_{i,\Sigma}}{\mu_{\Sigma,\Sigma}} = \frac{\sum_i \sqrt{v_{ii,\Sigma}}}{\mu_{\Sigma,\Sigma}} \tag{3}$$

Finally, we define the local population variability of species *i* in patch *k* as $CV_{i,k} = \sqrt{v_{ii,kk}} / \mu_{i,k}$, and local-scale average species variability as the weighted average of local population variability across species and patches:

$$CV_{S,L} = \sum_{i,k} CV_{i,k} \times \frac{\mu_{i,k}}{\mu_{\Sigma,\Sigma}} = \frac{\sum_{i,k} \sqrt{v_{ii,kk}}}{\mu_{\Sigma,\Sigma}} \tag{4}$$

Defining synchrony at multiple hierarchical levels

We define synchrony following Loreau and de Mazancourt's (2008) definition but use a square-root transformation of their metric to simplify mathematical expression and interpretation. Specifically, community-level spatial synchrony ($\varphi_{C,L\rightarrow R}$ with the subscript '*C*' representing 'community-level' and '*L*→*R*' indicating that this synchrony metric serves as a scaling factor from local to regional scales; see the next section) is defined as the spatial synchrony of total community biomass among local patches:

$$\varphi_{C,L\rightarrow R} = \frac{\sqrt{v_{\Sigma,\Sigma}}}{\sum_k \sqrt{v_{\Sigma,kk}}} \tag{5}$$

where the metacommunity variance $v_{\Sigma,\Sigma}$ represents the sum of covariances of total community biomass between patches *k* and *l* ($v_{\Sigma,kl}$): $v_{\Sigma,\Sigma} = \sum_{k,l} v_{\Sigma,kl}$.

Similarly, we define the spatial synchrony of populations for each species *i* as $\varphi_{i,L\rightarrow R} = \sqrt{v_{ii,\Sigma}} \Big/ \sum_k \sqrt{v_{ii,kk}}$, where $v_{ii,\Sigma} = \sum_{k,l} v_{ii,kl}$ is the variance of the total metapopulation biomass of species *i*. We then define the average species-level spatial synchrony as the weighted average of spatial synchrony across species:

$$\varphi_{S,L\rightarrow R} = \sum_i \omega_i \times \varphi_{i,L\rightarrow R} \tag{6}$$

where the weight is given by the relative contribution of species *i* to the summed standard deviation of all populations within the metacommunity: $\omega_i = \sum_k \sqrt{v_{ii,kk}} \Big/ \sum_{i,k} \sqrt{v_{ii,kk}}$ (thus $\sum_i \omega_i = 1$).

We also define the synchrony among different species at different spatial scales. At the regional scale, we define the regional-scale species synchrony as the synchrony among different metapopulations:

$$\varphi_{S\rightarrow C,R} = \frac{\sqrt{v_{\Sigma,\Sigma}}}{\sum_i \sqrt{v_{ii,\Sigma}}} \tag{7}$$

where the total metacommunity variance $v_{\Sigma,\Sigma}$ represents the sum of covariances of total metapopulation biomass between species *i* and *j* ($v_{ij,\Sigma}$): $v_{\Sigma,\Sigma} = \sum_{i,j} v_{ij,\Sigma}$.

Finally, we define the species synchrony within each local patch *k* as $\varphi_{S\rightarrow C,k} = \sqrt{v_{\Sigma,kk}} \Big/ \sum_i \sqrt{v_{ii,kk}}$, where $v_{\Sigma,kk} = \sum_{i,j} v_{ij,kk}$ is the variance of total biomass of patch *k*. The average local-scale species synchrony is then the weighted average of species synchrony across patches:

$$\varphi_{S\rightarrow C,L} = \sum_k \omega'_k \times \varphi_{S\rightarrow C,k} \tag{8}$$

where the weight is given by the relative contribution of patch *k* to the summed standard deviations of all populations within the metacommunity: $\omega'_k = \sum_i \sqrt{v_{ii,kk}} \Big/ \sum_{i,k} \sqrt{v_{ii,kk}}$ (thus $\sum_k \omega'_k = 1$).

Linking variability and synchrony across hierarchical levels

Based on above definitions, we obtain the following equations that partition metacommunity variability into lower-level components of variability and synchrony (Supplementary material Appendix 1):

$$CV_{C,R} = CV_{C,L} \times \varphi_{C,L\rightarrow R} = CV_{S,L} \times \varphi_{S\rightarrow C,L} \times \varphi_{C,L\rightarrow R} \tag{9}$$

$$CV_{C,R} = CV_{S,R} \times \varphi_{S\rightarrow C,R} = CV_{S,L} \times \varphi_{S,L\rightarrow R} \times \varphi_{S\rightarrow C,R} \tag{10}$$

Equation 9, 10 provide two alternative ways to scale up variability from local populations to metacommunities in heterogeneous landscapes (Fig. 1). The first aggregates populations within each local patch first, and then aggregates local patches into a metacommunity (Eq. 9). The second aggregates populations within each species first, and then aggregates metapopulations into a metacommunity (Eq. 10). In both partitions, variability is scaled up by a combination of spatial and species synchrony. Synchrony at a specific hierarchical level quantifies how much variability is maintained at the higher level. In other words, asynchrony (i.e. one minus synchrony) quantifies how much variability is reduced because of processes generating compensatory dynamics at this level.

Material and methods

Data

We applied the above framework to analyse the stability of plant biomass production across spatial scales and organizational levels in desert grassland communities. Plant communities were surveyed as part of the Jornada Long Term Ecological Research (LTER) program located in the Jornada del Muerto Basin in southern New Mexico (Huenneke et al. 2002, Peters et al. 2012). Fifteen plots covering five different vegetation zones (i.e. Creosotebush shrubland, Black grama grassland, Playa, Tarbush shrubland and Mesquite dune) were surveyed from 1990 to 2012 (Supplementary material Appendix 3 Table A1). Each plot consists of 49 1-m^2 quadrats evenly distributed in a 70×70 m^2 area, except for the COLL plot that includes 48 1-m^2 quadrats evenly distributed in a 30×160 m^2 area). In each quadrat, the biomass of each species was estimated in spring, fall and winter. Annual productivity of each species was then derived by summing its net growth between seasons (Huenneke et al. 2002). In total, 353 species were encountered in the survey. In our analyses, we regarded each plot as a metacommunity (i.e. regional scale) and each quadrat as a local community (i.e. local scale).

Calculating variability, synchrony and diversity across hierarchical levels

At each spatial scale and organizational level, we calculated the temporal variability and synchrony as defined by Eq. 1–8. To do so, we developed an R function 'var.partition', which takes the raw data of time series of species biomass at each location as input and returns variability and synchrony metrics at different hierarchical levels (Supplementary material Appendix 2). Based on these metrics, we calculated the ratio of regional- to local-scale species synchrony and that of community- to species-level spatial synchrony, which are equal to each other as implied by Eq. 9, 10:

$$\frac{\varphi_{S\to C,R}}{\varphi_{S\to C,L}} = \frac{\varphi_{C,L\to R}}{\varphi_{S,L\to R}} \triangleq \lambda \tag{11}$$

For convenience, we refer to these ratios as the synchrony ratio across hierarchical levels and denote them by λ.

We also computed local species richness (i.e. alpha diversity) as the average number of species sampled per quadrat, and regional species richness (i.e. gamma diversity) as the total number of species sampled across quadrats for each plot. We assessed community dissimilarity across quadrats within each plot (i.e. beta diversity) as the ratio of gamma to alpha diversity (Whittaker 1972). All diversity metrics were calculated for each year and temporal means were used in subsequent analyses.

Statistical analyses

We investigated variability and synchrony across spatial scales and organization levels and their relationship with species diversity. First, we explored how the patterns of variability and synchrony across hierarchical levels varied among vegetation zones. In particular, we compared the values of species synchrony and spatial synchrony and examined whether factors influencing species or spatial synchrony played a more important role in the stability of metacommunity productivity.

Second, we examined how species synchrony changed between spatial scales or, equivalently, how spatial synchrony changed between organization levels. Specifically, across the 15 plots (or metacommunities), we performed Pearson correlation tests to investigate whether a plot exhibiting a higher species-level spatial synchrony also had a higher community-level spatial synchrony, and whether a plot exhibiting a higher local-scale species synchrony also had a higher regional-scale species synchrony. Paired t-tests were then conducted to investigate whether spatial synchrony increased from species to community levels, and whether species synchrony increased from local to regional scales.

Lastly, we performed linear regressions to investigate how species diversity influences variability and synchrony at different hierarchical levels (Fig. 1). Specifically, how does local species diversity (i.e. alpha diversity) affect local-scale species and community variability and local-scale species synchrony? Similarly, how does regional species diversity (i.e. gamma diversity) affect metapopulation variability, metacommunity variability and regional-scale species synchrony? Besides, we also used a linear regression model to examine how the community-level spatial synchrony was related with beta diversity.

Data accessibility

The data that support the findings of this study are available on request from the Jornada Basin Long-Term Ecological Research (LTER) project (<https://jornada.nmsu.edu/content/npp-study-quadrat-biomass-data>). The R scripts can be found in the R package codyn (<https://github.com/NCEAS/codyn>).

Results

Different vegetation zones exhibited different patterns of variability and synchrony across hierarchical levels (Fig. 2 and 3). Creosotebush and Tarbush exhibited the lowest variability at both local and regional scales and at both species and community levels. Creosotebush plots also had low spatial synchrony and relatively low species synchrony, implying strong stabilizing effects along both axes (i.e. spatial scales and organizational levels). In contrast, Mesquite dune and the Playa exhibited the highest variability at both scales and both organizational levels. Plots of both Mesquite dune and Tarbush had intermediate species and spatial synchrony, implying intermediate stabilizing effects along both axes. On the other hand, Playa plots had high species and spatial synchrony, implying weak stabilizing effects along both axes. Finally, Black grama grassland plots had high species-level variability, but relatively low community-level variability at both spatial scales. The latter could be explained by the low species synchrony in grassland plots, which implied a strong stabilizing effect of species diversity and complementary dynamics. Overall, species synchrony (mean and SD across 15 plots: 0.50 ± 0.086 at the regional scale and 0.55 ± 0.082 at the local scale) was generally smaller than spatial synchrony (mean and SD across 15 plots: 0.70 ± 0.13 at the community level and 0.76 ± 0.091 at the species level) (see also Fig. 2).

Synchrony itself also varied across scales and organizational levels. Spatial synchrony was strongly correlated between species and community levels ($p < 0.001$), and so was species synchrony at local and regional scales ($p < 0.001$; Fig. 3). Furthermore, community-level spatial synchrony ($\varphi_{C,L\to R}$) was generally smaller (12 out of 15 plots) than species-level spatial synchrony ($\varphi_{S,L\to R}$), and regional-scale species synchrony ($\varphi_{S\to C,R}$) was generally smaller (12 out of 15 plots) than local-scale species synchrony ($\varphi_{S\to C,L}$) (paired t-test: $p < 0.01$ for both) (Fig. 3). As a consequence, the synchrony ratio across hierarchical levels (λ) was generally smaller than 1.

At both local and regional scales, species diversity exhibited no significant relationships with species-level variability

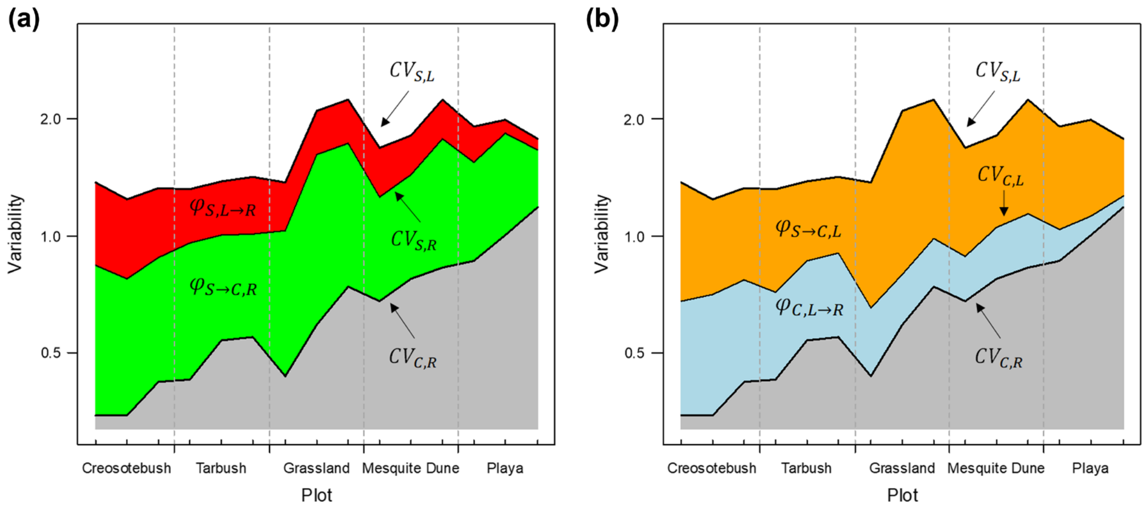

Figure 2. Temporal variability and synchrony of plant productivity at different spatial scales and organizational levels in the 15 plots at the Jornada site: (a) population ($CV_{S,L}$) – metapopulation ($CV_{S,R}$) – metacommunity ($CV_{C,L}$), and (b) population ($CV_{S,L}$) – community ($CV_{C,L}$) – regional community ($CV_{C,R}$). Note that the y-axis is logarithm transformed. According to Eq. 9, 10, $\log_{10} CV_{C,R} = \log_{10} CV_{S,L} + \log_{10} \varphi_{S\to C,L} + \log_{10} \varphi_{C,L\to R}$ and $\log_{10} CV_{C,R} = \log_{10} CV_{S,L} + \log_{10} \varphi_{S,L\to R} + \log_{10} \varphi_{S\to C,R}$. Thus, the width of the shades indicates how much variability is reduced from lower to higher hierarchical levels due to the asynchronous dynamics at the corresponding level.

($r^2 < 0.1$ and $p > 0.3$ at both scales; Fig. 4e–f), but strong negative relationships with species synchrony ($r^2 = 0.7$ and $p < 0.001$ at both scales; Fig. 4c–d). Consequently, species diversity provided stabilizing effects on total biomass mainly by reducing the synchrony among species, rather than by affecting species-level variability. This relationship emerged by scaling up over spatial scales: while the relationship between species diversity and community variability was negative at the regional scale ($r^2 = 0.29$ and $p = 0.04$; Fig. 4b), this relationship was weak and non-significant at the local scale ($r^2 = 0.16$ and $p = 0.14$; Fig. 4a). In other words, the stabilizing effect of plant diversity on community productivity became stronger at larger spatial scales. Besides, community-level spatial synchrony and the synchrony ratio (λ) both decreased with the beta diversity within the metacommunity (Fig. 5).

Discussion

Hierarchy and drivers of metacommunity stability

Our proposed framework provides a quantitative tool to partition variability across multiple hierarchical levels in heterogeneous metacommunities. It extends and integrates

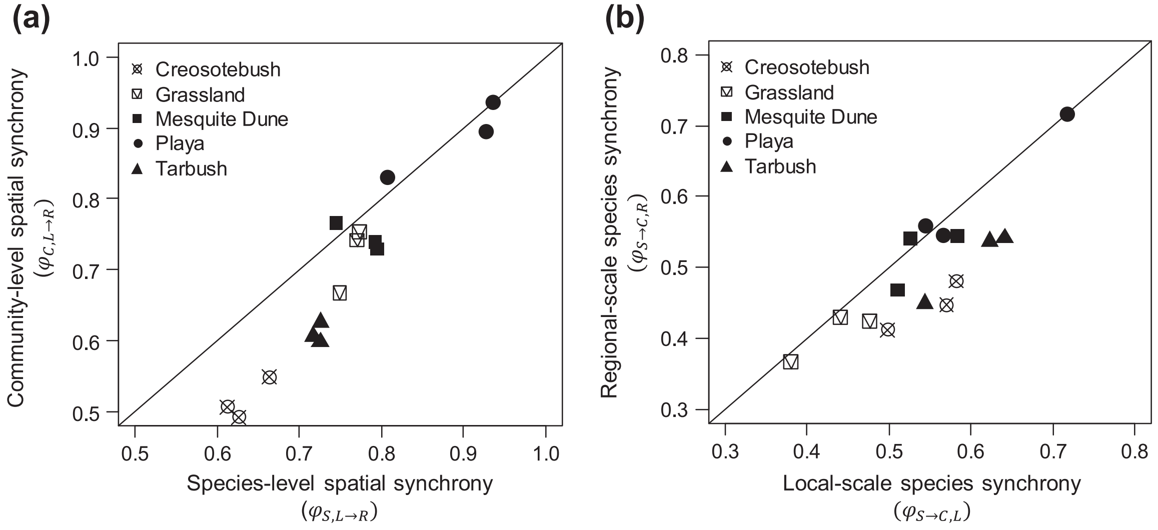

Figure 3. (a) Spatial synchrony across organizational levels and (b) species synchrony across scales. Different symbols represent different vegetation types, and the line represents the 1:1 line. Note that the two panels have different ranges of axis, and the spatial synchrony (a) has on average larger values than species synchrony (b). Note also that spatial synchrony decreases from species to community levels (i.e. points are generally below the 1:1 line (a)), and species synchrony decreases from local to regional scales (b).

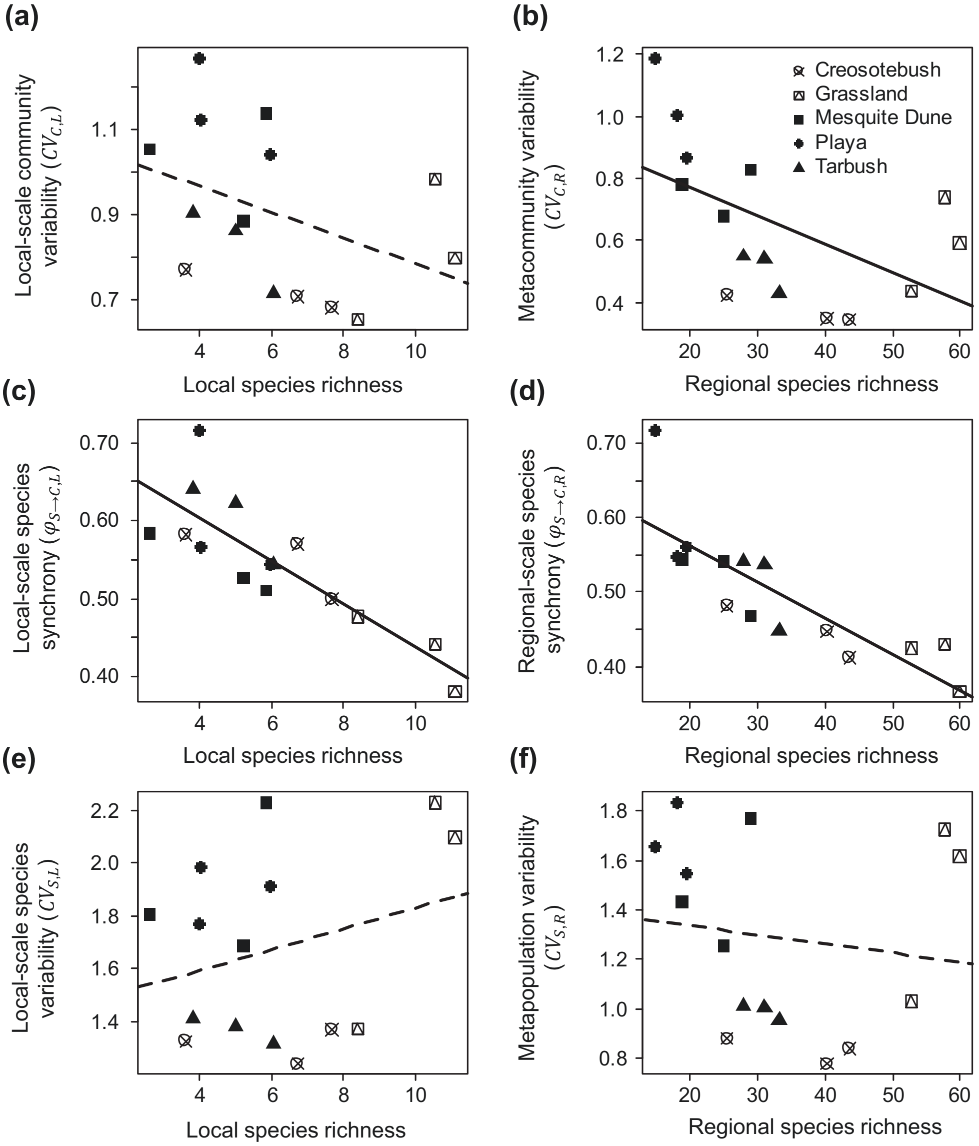

Figure 4. Relationships between species diversity and community variability (a–b), species synchrony (c–d) and species variability (e–f) at local (a, c, e) and regional (b, d, f) scales. Different symbols correspond to different vegetation types. Lines represent least-square regressions. Solid lines are statistically significant ($p < 0.05$) and dashed lines are not ($p > 0.05$).

previous frameworks that apply only to two hierarchical levels (either spatial scales or organizational levels) (Thibaut and Connolly 2013, Wang and Loreau 2014). Given the complexity and heterogeneity of real-world ecosystems, our new framework is critical for applications to empirical data. In particular, it clarifies the appropriate weights to be used in averaging lower-level variability and synchrony measures in order to link them to metacommunity variability. Specifically, the lower-level variability should be weighted by each component's relative contribution to the total biomass of the metacommunity, and the lower-level synchrony should be weighted by each component's relative contribution to the summed standard deviation of populations within the metacommunity (Table 1). Such a weighted averaging approach has also been used to study species diversity across scales when variation in species abundance is accounted for (Lande 1996). Recent studies have used other weightings when calculating lower-level variability and synchrony (Chalcraft 2013, Wilcox et al. 2017). This leads to metrics that differ from our partitioning, and that do not directly link to metacommunity stability. Our framework therefore extends previous work, and proposes a consistent set of metrics that should prove valuable in future empirical studies.

Application of the framework to data reveals patterns that align with the natural history of the Jornada Vegetation zones (Fig. 2). Creosotebush and Tarbush plots are dominated by woody perennials and thus exhibit stable biomass production at different hierarchical levels. In contrast,

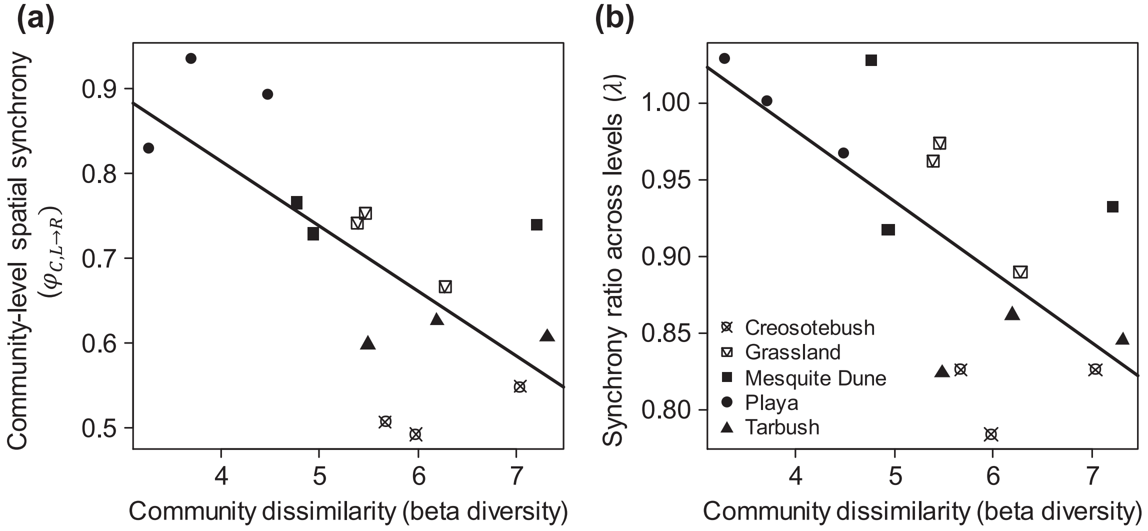

Figure 5. Relationship between beta diversity and community-level spatial synchrony (a) and the synchrony ratio across levels (b). Lines represent least-square regressions, both of which are statistically significant ($p < 0.05$).

vegetation zones characterized by strong environmental drivers, such as Mesquite dune which is structured by 'moving dunes' and the Playa which experiences periodic floods (Havstad et al. 2006), exhibited low stability at different levels. The periodical flooding at the Playa acts to synchronize species growth over space and time, leading to high species and spatial synchrony. The grassland plots exhibit low species synchrony, which aligns with vegetation dynamics in this zone: the dominant grass, *Bouteloua eriopoda*, exhibits high variability in cover depending on rainfall availability, but other species can dominate when *Bouteloua* declines (e.g. *Sporobolus flexuisus*, *Aristida purpurea*, *S. contarctus*; Havstad et al. 2006).

The partitioning framework clarifies that a lower synchrony among populations of either different species or different patches can contribute to stabilizing metacommunity dynamics. In our data, species synchrony is generally lower than spatial synchrony, suggesting that the decrease in variability from local populations to metacommunities was attributed mainly to processes that reduces species synchrony, e.g. species diversity and compensatory dynamics (Loreau and de Mazancourt 2008, 2013). The high spatial synchrony could be the result of the relatively small spatial extent of our metacommunities (~5000 m^2). At such a scale, local communities experience very similar environments, have high dispersal and have similar species composition, which all lead to higher spatial synchrony (Liebhold et al. 2004, Wang and Loreau 2016).

Synchrony across hierarchical levels

Our partitioning framework provides consistent measures of synchrony across hierarchical levels, which offers a unique opportunity to investigate the scale-dependence of synchrony metrics. Our empirical analysis reveals, for the first time to our knowledge, the patterns of synchrony across hierarchical levels: species and spatial synchrony at higher hierarchical levels (i.e. regional-scale species synchrony and community-level spatial synchrony) are highly correlated with, but lower than, their lower-level counterparts (i.e. local-scale species synchrony or species-level spatial synchrony). The high correlation may be explained by the shared drivers of synchrony across hierarchical levels. Two important drivers of spatial synchrony are environmental correlation and dispersal (Liebhold et al. 2004). These two factors operate at both the species and community levels, which may explain the correlation in spatial synchrony between the two levels. On the other hand, species diversity is an important driver of species synchrony (Fig. 3; Loreau and de Mazancourt 2008), and the high correlation between local and regional species synchrony may therefore be explained by the correlation of species diversity across scales (Supplementary material Appendix 3 Fig. A2).

The decrease of synchrony with hierarchical level suggests that the stabilizing effect of biodiversity increases from local to regional scales, and the stabilizing effect of spatial heterogeneity increases from species to community levels. The decrease in species synchrony with spatial scale may occur because the number of species increases from local to regional scales (Supplementary material Appendix 3 Fig. A2). The decrease in spatial synchrony with organizational level may occur because spatial community turnover or beta diversity adds a new (biotic) dimension of spatial heterogeneity, which should further reduce the spatial synchrony of communities relative to that of species (Wang and Loreau 2016, Delsol et al. 2018). Both explanations suggest that the magnitude of the decrease in synchrony across hierarchical levels should increase with beta diversity, which is supported by our data (Fig. 5b).

The stabilizing effect of biodiversity across hierarchical levels

By decomposing metacommunity variability into lower-level components, our framework provides an opportunity to clarify the different pathways by which biodiversity may provide stabilizing effects (Fig. 1). Previous studies have shown that species diversity generally reduces the variability of community-level properties (Loreau and de Mazancourt 2013, Wang and Loreau 2016), while it may either increase or decrease the species-level variability (Tilman et al. 2006, Thibaut and Connolly 2013). Our empirical results are generally consistent with these previous findings and with a recent study on the same system using a shorter time series (i.e. 12 yr; Chalcraft 2013) (Fig. 3 and Supplementary material Appendix 3 Fig. A1). However, due to the small sampling size (i.e. $n = 15$), the relationship between diversity and community variability is not significant at the local scale (Fig. 3). Our additional analysis examining their relation across quadrats revealed an overall negative correlation; more specifically, local species diversity and community variability are negatively correlated in 9 out of 15 plots, with the other 6 plots showing no correlation (Supplementary material Appendix 3 Fig. A1).

Recent theory has suggested that species diversity can decrease species synchrony (Loreau and de Mazancourt 2008, Thibaut and Connolly 2013). Our results confirm this prediction at both local and regional scales. Theory also predicts that beta diversity can decrease spatial synchrony, thereby enhancing metacommunity stability (Wang and Loreau 2016). A recent meta-analysis failed to find such a relation across a large number of plant ecosystems (Wilcox et al. 2017). However, in the dataset used by Wilcox et al. (2017), environmental conditions and spatial scales vary across ecosystems, which might obscure the relation between beta diversity and spatial synchrony. By using data collected in the same region and based on the same survey regime, our study provides a more rigorous test that supports the predicted negative relation between these two variables. Overall, our analysis demonstrates the multiple pathways that biodiversity reduce synchrony and thereby provide stabilizing effects on metacommunity dynamics.

Conclusion

Our partitioning framework establishes an explicit link among variability and synchrony metrics across ecological hierarchies. When moving from low to high hierarchical levels, variability decreases consistently and the magnitude of this decrease is determined by the degree of synchrony among lower-level components. Our framework offers new research opportunities to understand the mechanisms underlying ecosystem stability at large scales, e.g. by investigating the scaling patterns of synchrony across hierarchical levels and the relationship between lower-level variability and synchrony and ecological drivers (e.g. species diversity) (Levin 1992). Our application of the framework to a long-term dataset of desert plant communities reveals novel patterns and drivers of the change in synchrony with hierarchical levels, which may shed new light on the scale-dependence of the mechanisms of stability. It also demonstrates that different components of biodiversity (e.g. alpha, beta and gamma diversity) can contribute to the reduction of synchrony and variability at different hierarchical levels, in line with recent theories (Thibaut and Connolly 2013, Wang and Loreau 2016). Future analysis can develop structural equation models (SEM) to clarify how ecological factors affect metacommunity stability through different pathways by affecting its lower-level components. We anticipate that our framework will offer a useful toolbox for future empirical studies of ecological stability across scales in natural ecosystems.

Acknowledgements – We thank Bart Heageman and Lei Zhao for helpful comments on earlier versions of the manuscript.

Funding – This work was supported by the National Key Research and Development Program of China (2017YFC0503906), the National Natural Science Foundation of China (31870505) and the CAS Interdisciplinary Innovation Team (JCTD-2018-06). Ideas were developed in part during a LTER Synchrony working group funded by the Long-term Ecological Network Communication Office. TL was supported by the National Aeronautics and Space Administration, Biodiversity and Ecological Forecasting Program (grant NNX14AR62A), the Bureau of Ocean Energy Management, Environmental Studies Program (BOEM Agreement MC15AC00006) and the National Oceanic and Atmospheric Administration in support of the Santa Barbara Channel Marine Biodiversity Observation Network. ML was supported by the TULIP Laboratory of Excellence (ANR-10-LABX-41) and by the BIOSTASES Advanced Grant, funded by the European Research Council under the European Union's Horizon 2020 research and innovation programme (grant agreement no. 666971). Data sets were provided by the Jornada Basin Long-Term Ecological Research (LTER) project. Funding for these data was provided by the U.S. National Science Foundation (Grant DEB-1235828).

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Supplementary material (available online as Appendix ecog-04290 at <www.ecography.org/appendix/ecog-04290>). Appendix 1–3.