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Title: The dual nature of metacommunity variability

Running head: Metacommunity variability

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Abstract

It is well recognized that within local communities, fluctuations of constituent species over time can alter both aggregate (e.g., total abundance or biomass) and compositional community properties. At broader spatial scales, recent evidence shows how spatial asynchrony can further stabilize aggregate properties at the regional, or metacommunity, scale. Yet, apparent lack of variability in aggregate metacommunity properties can mask changes in metacommunity composition, and a framework acknowledging such dual nature of metacommunity variability is still lacking. Here, we present an approach to characterize metacommunity variability that integrates both aggregate and compositional properties. We demonstrate that the compositional variability of a metacommunity critically depends on the degree of spatial synchrony in the compositional trajectories over time among local communities. We develop two methods, available in the *ltmc* R package, to quantify such spatial compositional synchrony and apply them to a case study of understory macroalgal communities inhabiting shallow rocky reefs off the coast of Santa Barbara, California. We found that moderate spatial asynchrony reduced variability in aggregate metacommunity biomass, whilst masking synchronous, and potentially destabilizing, compositional variability at the metacommunity scale. These results highlight the need to consider both aspects of metacommunity variability simultaneously in order to fully understand variability over broad spatial scales.

Keywords: biodiversity, metacommunity, scale, stability, variability, long-term ecological research.

Introduction

Understanding the processes that influence the temporal variability of ecological communities is a fundamental aim of ecology (MacArthur 1955, May 1973, Grimm and Wissel 1997, Ives and Carpenter 2007). Decades of study have identified several important factors that can stabilize aggregate properties (e.g., total abundance or biomass) of local communities, such as dampened population fluctuations and compensatory dynamics among species (Tilman 1999, Yachi and Loreau 1999, Gonzalez and Loreau 2009, Brown et al. 2016). However, local communities do not exist in isolation; they are connected across space via the dispersal of constituent species to form metacommunities. This connectivity reflects important processes acting across spatial scales that ultimately determine variability of the aggregate properties at the metacommunity scale (Leibold et al. 2004, Leibold and Chase 2018). Understanding variability at the metacommunity scale is particularly important for managing complex landscapes in the context of current environmental changes.

Recent theoretical (Wang and Loreau 2014, 2016) and empirical (Wilcox et al. 2017, Wang et al. 2017, 2019) contributions have shown that aggregate community variability decreases with increasing spatial scale, depending on the degree of spatial synchrony. Aggregate community variability at the regional scale, quantified as the square of the coefficient of variation of aggregate metacommunity property (CV_γ^2), can be multiplicatively partitioned as $CV_\gamma^2 = CV_\alpha^2 \times \varphi$ (see equations in Table 2; Wang and Loreau 2014). Here, CV_α^2 is the average

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local aggregate community variability and φ is the spatial aggregate synchrony, which serves as a scaling factor for aggregate community variability from local to regional scales. φ ranges between zero and one, with higher φ indicating more spatially synchronous fluctuations in the aggregate community property among local communities. Values of φ close to zero indicate that local communities fluctuate in such a way that aggregate metacommunity variability is null. A low degree of spatial aggregate synchrony across local communities reduces the variability of an aggregate property at the metacommunity scale (hereafter, 'aggregate metacommunity variability'), which provides spatial insurance effects (Loreau et al. 2003, Wang and Loreau 2014, 2016). For example, if the total biomass of two local communities fluctuate in perfect asynchrony, these fluctuations cancel each other out, resulting in no variability in metacommunity biomass through time (Figure 1).

However, fluctuations in an aggregate property at the metacommunity scale represents only one facet of temporal metacommunity variability (*sensu* Micheli et al. 1999). A second facet is 'compositional metacommunity variability', which is the temporal variability in species composition at the metacommunity scale. Temporal fluctuations in aggregate metacommunity properties can arise with or without corresponding fluctuations in compositional metacommunity variability (Figure 1A vs. 1B). Similarly, a lack of aggregate metacommunity variability can mask important temporal changes in the composition and relative abundance of the species that comprise the metacommunity. For instance, a spatial insurance effect can stabilize total biomass of the metacommunity due to spatially asynchronous fluctuations among local communities (i.e., low aggregate metacommunity variability; Figure 1C). However, if one species becomes dominant over time at the metacommunity scale, this compositional change could remain undetected with aggregate properties (Figure 1D), which however has important implications for the maintenance of biodiversity at large spatial scales.

There have been few empirical investigations of the mechanisms that influence the degree of variability across scales (e.g., Wilcox et al. 2017), partly due to a lack of theoretical development and long-term, large-scale community datasets (Oliver et al. 2010, Donohue et al. 2013, Wang and Loreau 2014, 2016). To address these gaps, we provide a conceptual and methodological framework to apply measures of compositional variability at the metacommunity scale. These measures can be implemented in the *ltmc* package for R (available at https://github.com/sokole/ltermetacommunities/tree/master/ltmc). We then use long-term data from kelp forest communities in the Santa Barbara Channel off the coast of California, USA, to empirically demonstrate the dual nature of metacommunity variability—compositional and aggregate. Lastly, we discuss this dual nature in light of dispersal, environmental heterogeneity, and species interactions, shedding new light on the processes that promote the resilience of ecosystems across spatial scales.

Incorporating composition into temporal metacommunity variability

Compositional differences in community structure have been studied extensively in a spatial context (e.g., beta diversity and community assembly) (Chase 2010, Anderson et al. 2011), but much less attention has been given to how these properties vary over time (Adler et al. 2005, Magurran et al. 2018, De Cáceres et al. 2019). A common approach to assess variation in species composition among samples collected across space is to measure beta diversity (Tuomisto

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2010a, b, Anderson et al. 2011, Legendre and De Cáceres 2013). Beta diversity metrics have also been used to quantify compositional variability through time (e.g., Hillebrand et al. 2010, De Cáceres et al. 2019, Legendre 2019), but there is currently no framework to understand how temporal compositional variability scales with space. Although beta diversity can be assessed based on any pairwise dissimilarity index (Anderson et al. 2011, Legendre and Legendre 2012), many of these indices depend on differences in aggregate properties, such as total community biomass, across samples (Legendre 2014, but see Lamy et al. 2015). To ensure that measures of compositional variability can reveal new insights that are not already captured in aggregate variability, quantification of compositional variability in the metacommunity context should be based on indices that rely on species' relative frequencies (of biomass or abundance for instance). Three pairwise dissimilarity indices fulfill this "density invariance" property (Jost et al. 2011): Whittaker's index of association (Whittaker 1952), the Chord distance (Orloci 1967) and the Hellinger distance (Rao 1995). Here, we discuss the Hellinger distance and a new time-independent Hellinger normalization to measure compositional variability across space.

Quantifying temporal compositional variability

The compositional variability (Table 1 and 2) of a single local community *i* composed of *s* species surveyed *n* times can be computed as beta diversity (BD) under the variance framework of Legendre and De Cáceres (2013). In this framework, the compositional variability of local community *i* represents the total variance in species composition observed over time and is computed as:

$$BD_i = SST_i/(n-1) \ \#(1)$$

where SST_i is the total sum of squares in species composition, $SST_i = \sum_j^s \sum_t^n (X_{itj} - \bar{X}_{i.j})^2$, with $(X_{itj} - \bar{X}_{i.j})^2$ the square of the difference between the biomass of species *j* at time *t*, and the temporal mean biomass of species *j* ($\bar{X}_{i.j} = \sum_t^n X_{itj}/n$). This definition of BD corresponds to the Euclidean distance, which was shown to be inappropriate for beta diversity assessment (Wolda 1981, Legendre and Gallagher 2001) and does not fulfill the density invariance property, described previously (Jost et al. 2011). To make this measure appropriate for calculating compositional variability, we compute a value of SST corresponding to the Hellinger distance by computing the Hellinger transformation on the original data (Table 2). Compositional variability based on the Hellinger transformation (BD^h; where *h* stands from Hellinger) is calculated from the square root of species relative frequencies and provides a measure of compositional variability that is independent from the differences in aggregate community property (Table 2). Compositional variability of local community *i* based on the Hellinger distance is:

$$BD_i^h = \sum_j^s v_{ij}^h \ \#(2)$$

where $v_{ij}^h = \frac{\sum_t^n (X_{itj}^h - \bar{X}_{i.j}^h)^2}{n-1}$ is the temporal variance of the Hellinger-transformed biomass of species *j* in the local community *i*. Here, X_{itj}^h represents the Hellinger transformation of the biomass, or abundance, of species *j* in community *i* at time *t* (Table 2). Greater sums of species variances (v_{ij}^h) lead to greater compositional variability (BD_i^h). The advantage of BD_i^h is that it is comparable among taxonomic groups because it ranges between zero, when species composition is constant over time, and one, when species composition is unique at each time point (Legendre and De Cáceres 2013).

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However, using BD_i^h to understand compositional variability across space has one particular limitation. It yields a spatial compositional synchrony metric that does not truly behave as its aggregate counterpart φ (*i.e.* ranging from zero to one) as BD_i^h does not necessarily decrease with increasing spatial scale (whereas aggregate variability always does so). Therefore, we derive a new compositional variability metric that is more appropriate when dealing with multiple spatial scales as it will yields a synchrony metric ranging from zero to one. This metric corresponds to a time-independent version of the Hellinger transformation (BD_i^{hT}; where hT stands from Hellinger time-independent). Our modified Hellinger transformation represents a time-independent normalization of the original data. That is, species' frequencies are computed relative to total biomass within a community across all time steps:

$$X_{itj}^{hT} = \sqrt{X_{itj}/X_{i..}} \#(3)$$

Where X_{itj} is the biomass of species *j* at time *t* in local community *i*, and $X_{i..}$ corresponds to the total community biomass observed across all time steps in local community *i* ($X_{i..} = \sum_j^s \sum_t^n X_{itj}$). Instead of normalizing the biomass of each species by the total community biomass observed at each time step, we normalize species biomass by the total community biomass observed across all time steps in a given local community. Compositional variability based on the time-independent Hellinger transformation of a local community *i* is:

$$BD_i^{hT} = \frac{\sum_j^s v_{ij}^{hT}}{X_{i..}} \#(4)$$

where $v_{ij}^{hT} = \frac{\sum_t^n \left(\sqrt{X_{itj}} - \overline{\sqrt{X_{i.j}}}\right)^2}{n-1}$ is the temporal variance of the square root coefficient biomass of species *j* in local community *i*. Contrary to BD_i^h, the time-independent measure of compositional variability, BD_i^{hT}, can exceed one but it always scales negatively with space.

To summarize, direct interpretation of local and regional scale Hellinger-transformed compositional variability, BD_i^h, can be more intuitive, but this metric does not scale negatively with space and therefore the resulting synchrony metric does not lie between zero and one. On the contrary, the interpretation of local and regional scale *time-independent* Hellinger-transformed compositional variability, BD_i^{hT} always scales negatively with space and therefore yields a more realistic synchrony metric. In the next section we show how BD_i^{hT} can be used to link compositional variability across spatial scales. In the supplementary material we show a similar computation for BD_i^h. Both metrics can be calculated using the 'temporal_BD' function in the *ltmc* (long-term metacommunity analysis) package for R (available at https://github.com/sokole/ltermetacommunities/tree/master/ltmc).

Linking aggregate and compositional variability across spatial scales

Both aggregate and compositional variability measured over a large spatial extent (γ variability) can be hierarchically partitioned in a multiplicative way into a local-scale (α) variability and a spatial component (φ). The spatial component (φ) corresponds to the spatial aggregate synchrony and the spatial compositional synchrony that quantify how aggregate and compositional variability, respectively, scale up from the local to the metacommunity scale. The partitioning of both aggregate and compositional community variability can be easily applied to

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a wide variety of ecosystems surveyed through both space and time, and we provide R functions in the *ltmc* package for R to facilitate its application.

For a given metacommunity, we assume each local community is sampled in a similar way, such that *m* local communities (or sites) are sampled over *n* time steps. During each survey, the total abundance or biomass of *s* species is recorded (for clarity we will use biomass as an example hereafter). Hence, data can be summarized as a community array **X**, where X_{itj} represents the abundance or biomass of species *j* in community *i* at time *t*. The aggregate community metric (total community biomass) is obtained by summing the values of these variables across the *s* species. The metacommunity corresponds to the largest spatial scale and is defined by summing the values of the aggregated community metric across the *m* local communities (Table 1). This will produce a vector of length *n* for the aggregate metacommunity metric (total metacommunity biomass), and a $n \times s$ time-by-species matrix containing the biomass of each species over time at the regional scale. We have already discussed the multiplicative relationship between local- and regional-scale aggregate variability (CV_α^2 and CV_γ^2, respectively; Table 2), and we will now demonstrate the multiplicative relationship between local- and regional-scale compositional variability (BD_α and BD_γ, respectively).

Local scale compositional variability

Mean local scale compositional variability is computed as the weighted average of compositional variability across the *m* local communities calculated using BD_i^{hT} (see SM1 for BD_i^h), the time-independent Hellinger transformation:

$$BD_\alpha^{hT} = \sum_i^m \frac{X_{i..}}{X_{...}} BD_i^{hT} = \frac{\sum_i^m \sum_j^s v_{ij}^{hT}}{X_{...}} \#(5)$$

with $\frac{X_{i..}}{X_{...}}$ the weight of local community *i*. Local communities are weighted by their contributions to the overall metacommunity biomass with $X_{...} = \sum_i^m \sum_t^n \sum_j^s X_{itj}$ and $X_{i..} = \sum_t^n \sum_j^s X_{itj}$. In eq. 5, v_{ij}^{hT} represents the temporal variance of the square root coefficient of abundance (or biomass) of species *j* in local community *i*.

Regional scale compositional variability

We define the regional scale compositional variability based on the time-independent Hellinger transformation (see SM1 for BD_γ^h) as:

$$BD_\gamma^{hT} = \frac{\sum_j^s \sum_t^n \left(X_{.tj}^{hT} - \bar{X}_{..j}^{hT}\right)^2}{(n-1)} = \frac{\sum_j^s v_{Tj}^{hT}}{X_{...}} \#(6)$$

where $X_{.tj}^{hT} = \sqrt{\sum_i^m X_{itj}/X_{...}}$ is the square root of the regional frequency of species *j* relative to the total metacommunity biomass, and $\bar{X}_{..j}^{hT} = \frac{\sum_t^n X_{.tj}^{hT}}{n}$s, is the temporal mean of the square root of the frequencies of species *j* in the regional pool relative to total metacommunity biomass, and $v_{Tj}^{hT} = \frac{\sum_t^n \left(\sqrt{X_{.tj}} - \overline{\sqrt{X_{..j}}}\right)^2}{n-1}$ is the temporal variance of the square root of the regional biomass of species *j*. Thus, greater variability of individual species biomasses at the regional scale,

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regardless of spatial location, contributes to greater regional scale compositional variability (i.e., larger values of BD_{γ}^{hT}).

Linking compositional variability across multiple spatial scales: the spatial asynchrony components

Similar to aggregate variability (see Introduction), we propose that compositional variability at the regional scale (BD_{γ}) can be partitioned multiplicatively into a local scale (BD_{α}) and a spatial component (BD_{φ}) as $BD_{\gamma} = BD_{\alpha} \times BD_{\varphi}$. Spatial compositional synchrony, BD_{φ}, reflects how compositional variability scales up from the local to the regional scale. BD_{φ} increases as temporal compositional changes become more spatially synchronous among local communities. The time-independent Hellinger transformation yields the relationship $BD_{\gamma}^{hT} = BD_{\alpha}^{hT} \times BD_{\varphi}^{hT}$, with BD_{φ}^{hT} the spatial component (see SM1 for details about BD_{φ}^{h}). First, BD_{φ}^{hT} can be rewritten as:

$$BD_{\varphi}^{hT} = \frac{BD_{\gamma}^{hT}}{BD_{\alpha}^{hT}} = \frac{\sum_{j}^{s} v_{Tj}^{hT}}{\sum_{i}^{m}\sum_{j}^{s} v_{ij}^{hT}} \#(7)$$

by substituting the equations for BD_{α}^{hT} and BD_{γ}^{hT} given above. Next, we define the spatial synchrony of species *j* ($\varphi_{(j)}^{hT}$) as the ratio between its temporal variance in square root biomass at the regional scale (v_{Tj}^{hT}) and the sum across all patches of its local temporal variance in square root biomass ($\sum_{i}^{m} v_{ij}^{hT}$), which yields:

$$\varphi_{(j)}^{hT} = \frac{v_{Tj}^{hT}}{\sum_{i}^{m} v_{ij}^{hT}} \#(8)$$

By substituting this species-specific spatial synchrony index ($\varphi_{(j)}^{hT}$) into the measure of spatial compositional synchrony (BD_{φ}^{hT}), we obtain:

$$BD_{\varphi}^{hT} = \frac{\sum_{j}^{s}\sum_{i}^{m} v_{ij}^{hT} \cdot \varphi_{(j)}^{hT}}{\sum_{i}^{m}\sum_{j}^{s} v_{ij}^{hT}} = \sum_{j}^{s} \frac{\sum_{i}^{m} v_{ij}^{hT}}{\sum_{i}^{m}\sum_{j}^{s} v_{ij}^{hT}} \cdot \varphi_{(j)}^{hT} = \sum_{j}^{s} w_j \cdot \varphi_{(j)}^{hT} \#(9)$$

with $w_j = \sum_{i}^{m} v_{ij}^{hT} / \sum_{j}^{s}\sum_{i}^{m} v_{ij}^{hT}$ representing a weighting term for each species. Therefore, our suggested definition of spatial compositional synchrony, BD_{φ}^{hT}, corresponds to the weighted average of species-level spatial synchrony ranging between the minimum and maximum $\varphi_{(j)}^{hT}$ observed in the metacommunity.

Both the aggregate and compositional variability metrics and their respective scaling coefficients described here can be calculated using the *metacommunity_variability* function in the *ltmc* package for R. See supplemental material SM2 for an example.

Our species-specific metric of spatial synchrony, $\varphi_{(j)}^{hT}$, ranges between zero and one. However, it differs from the classic definition of Loreau and de Mazancourt (2008), which takes the form $v_X / \left(\sum \sqrt{v_x}\right)^2$, that is used to define spatial aggregate synchrony (Wang and Loreau 2014). A notable difference is that species biomasses are square-root transformed before computing their temporal variances in the case of our new metric. The denominator of $\varphi_{(j)}^{hT}$, $\sum_{i=1}^{m} v_{ij}^{hT}$, corresponds to the sum across all local populations of the temporal variances of square root biomass of species *j*, and the numerator, v_{Tj}^{hT} corresponds to the temporal variance of the

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square root of its summed biomass across all local communities. Wang et al. (2019) provided an integrative framework in which metacommunity variability can be expressed as the product of local-scale population variability and two synchrony indices. Metacommunity variability can be partitioned in two ways, either (i) from individual local populations to local communities and from local communities to the metacommunity or (ii) from individual local populations to metapopulations and from metapopulations to the metacommunity (Wang et al. 2019). Here, BD_{φ}^{hT}, represents an integrative measure of synchrony that directly scales individual local populations to the metacommunity.

The quantitative partitioning of variability into local-scale (α), regional-scale (γ), and spatial (φ) components of aggregate and compositional variability suggests the existence of a common currency to investigate metacommunity stability. Notably, φ and BD_{φ}^{hT} are essential components to understand the spatial insurance of natural communities. Both aggregate and compositional variability may be highly variable at the local scale, but a strong spatial insurance effects may dampen these fluctuations at the regional level (e.g., Figure 1D).

Illustrating the dual nature of metacommunity variability: a case study

We used a case study of understory macroalgal communities inhabiting shallow rocky reefs off the coast of Santa Barbara, California, USA to illustrate the dual nature of metacommunity variability. These data were collected as part of the Santa Barbara Coastal Long Term Ecological Research program (http://sbc.lternet.edu; Reed 2018) and are publicly available on the EDI data portal (https://doi.org/10.6073/pasta/d5fd133eb2fd5bea885577caaf433b30). We focused on 14-year time series (2004–2017) of species-specific biomass of 53 macroalgae surveyed across 10 shallow (4–12 m depth) rocky reefs. Abundance data were measured at 27 fixed 80 m^2 (40 m × 2m) plots distributed across the 10 rocky reefs, and then converted to biomass density (g decalcified dry mass m^{-2}) using species-specific allometries (Harrer et al. 2013, Reed 2018). Detailed methods for calculating metacommunity variability can be found in SM2.

Consistent with theoretical predictions, local-scale fluctuations in aggregate biomass (CV_{α}^{2} = 0.182) were reduced by a factor of ~5.5 at the metacommunity scale (CV_{γ}^{2} = 0.033) (Figure 2C). This reduction in aggregate metacommunity variability occurred due to relatively low spatial synchrony in total biomass across local communities (φ = 0.182). However, compositional variability only decreased by a factor of 2 from the local community scale (BD_{α}^{hT} = 0.019) to the whole metacommunity (BD_{γ}^{hT} = 0.01). This was due to a higher degree of spatial compositional synchrony (BD_{φ}^{hT} = 0.498), suggesting that local compositional trajectories were not spatially independent (Figure 2A). That is, local communities partly followed similar compositional trajectories over time, which translated to compositional variability at the metacommunity scale (Figure 2B). This cross-scale comparison of aggregate and compositional variability suggests that spatial insurance effects were stronger on aggregate variability than compositional variability.

To further investigate compositional variability across spatial scales, we assessed the temporal compositional dynamics of local communities and of the metacommunity. The nonmetric multidimensional scaling (NMDS) of Hellinger distances illustrated both substantial compositional heterogeneity among local communities overall (i.e., spatial beta diversity) and temporal changes within each local community during the 14-year period (Figure 2D). When

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visualized along the first two NMDS axes, many local communities had similar community structure at the beginning of the time series (in the upper left quadrant of the NMDS plot). Over the next 14 years, local community dynamics were similar across these sites in the metacommunity, resulting in comparable temporal trajectories along NMDS-axis 2 (ended in the lower left quadrant of the NMDS). As a result, the overall metacommunity tracked these local dynamics along NMDS-axis 2, but metacommunity variability was slightly dampened due to present, but weak, spatial compositional asynchrony.

Discussion

Scaling variability from local to regional scales has posed an exciting challenge for ecologists. With regard to aggregate variability, recent theory (Wang and Loreau 2014, 2016, Wang et al. 2019) have provided the foundation to better understand the factors that contribute to reduced aggregate metacommunity variability. For instance, spatial insurance effects can reduce aggregate metacommunity variability of plant assemblages (Wilcox et al. 2017) and higher beta diversity was linked to a lower degree of spatial aggregate synchrony (Wang et al. 2019, 2021). As more long-term spatio-temporal surveys become available (Hughes et al. 2017, Record et al. 2021), it will become increasingly feasible to gain new insights into processes suspected of reducing aggregate variablity over broader scales. Yet, such an aggregate perspective overlooks the compositional component of community dynamics, which characterizes an important dimension of metacommunity variability (Micheli et al. 1999). The framework presented here fills this knowledge gap by providing a means to quantify the aggregate and compositional properties of metacommunity variability.

Compositional insight into metacommunity variability

Wang et al. (2019) proposed a framework to partition metacommunity aggregate variability as the product of local-scale population variability and two synchrony indices that capture the temporal coherence across species and space. In other words, local-scale population variability scales up to the metacommunity either through aggregate properties of local communities or through the metapopulations of constituent species. The framework of Wang et al. (2019) ties together the variability of local populations, metapopulations, local communities, and the metacommunity. The metrics of compositional variability and spatial compositional synchrony we presented here is a more integrative measure that directly quantifies how variability scales from local-scale populations to the metacommunity directly. It captures the degree of synchrony in the compositional trajectories of local communities and could provide insights into the mechanisms that stabilize aggregate properties across scales.

High compositional spatial synchrony is not necessarily destabilizing but instead can provide insight into the stabilizing mechanisms that dampen aggregate metacommunity variability. For example, in our case study of an understory marine macroalgal metacommunity, compositional spatial synchrony was higher than its aggregate counterpart (Figure 2C). As a result, compositional variability of the metacommunity mirrored that of local communities, which exhibited large compositional shifts that would have been undetected from aggregate properties alone (Figure 2B). Indeed, this higher compositional spatial synchrony captures the fact that most local communities underwent similar trajectories, in particular, major declines of the dominant species that were partly compensated for by the rise of the three sub-dominant

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species (Lamy et al. 2019). Consequently, the metacommunity underwent a similarly large shift in composition as the dominant species was replaced by the sub-dominant species (Figure 2B). Our approach demonstrates the key point that invariability in aggregate metacommunity properties can mask compositional changes occurring from local to regional scales. In particular, we identified how community dynamics contributed to low aggregate variability at the metacommunity scale.

The relationship between compositional and aggregate variability across spatial scales reflects the underlying metacommunity processes that influence spatial synchrony of community trajectories. The degree of compositional spatial synchrony emerges from the combined effects of species interactions, dispersal, and environmental variation across space and time in the metacommunity (Amarasekare 2003, Leibold et al. 2004, Shoemaker and Melbourne 2016). For example, high dispersal rates can lead to increased spatial synchrony in composition that increases compositional metacommunity variability (Gouhier et al. 2010). Similarly, region-wide environmental forcing can also induce spatial synchrony in community dynamics (Steiner et al. 2013). For example, if changes in local environmental conditions are similar across patches, local community composition might follow similar trajectories, leading to high compositional metacommunity variability (Figure 3A). This is probably the mechanism driving the metacommunity change observed in the case study of understory algae as the consistent replacement of the dominant species by a few sub-dominant species was linked to large-scale variations in sea surface temperature and nutrient concentration along the coast of California (Lamy et al. 2019). However, if environmental change is not strongly correlated in space, if dispersal is limited, or if community dynamics are largely stochastic, spatial compositional synchrony may be low, resulting in reduced compositional metacommunity variability (Figure 3B; Micheli et al. 1999, Gonzalez and Loreau 2009). Metacommunity variability may also be reduced by relatively stable local environmental conditions (Figure 3C), or if local environmental conditions diverge and shift local community composition in opposite directions (Figure 3D). Thus, metacommunity variability may be stabilized by low-to-intermediate dispersal rates, low environmental variability over time, or spatially asynchronous environmental variability that reduce compositional spatial synchrony (Chalcraft 2013).

Diagnosing the effects of environmental change on aggregate variability

Scenarios in which aggregate metacommunity variability is unaccompanied by synchronous compositional changes may indicate the effects of external forcing. For example, community composition may be stable at local and metacommunity scales (e.g., Figure 3C), but aggregate properties of the metacommunity could be variable (e.g., Figure 1A). This situation could arise when community composition is unaffected by shifting environmental conditions, but some aspect of the environment (e.g., disturbance, climatic change) limits total biomass production uniformly across all species or differentially in a subset of vulnerable species. The net result would be a metacommunity with variability in an aggregate property (e.g., declining total biomass) despite little change in composition. In this scenario, the driver of aggregate metacommunity variability may be incorrectly attributed to spatial compositional synchrony, but our approach would eliminate this possible explanation, instead pointing to non-compositional changes that limit productivity and contribute to aggregate metacommunity variability.

When considering how environmental variables affect metacommunity variability (e.g., via compositional changes or by acting directly on aggregate properties), it may be informative

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to analyze the degree of spatial autocorrelation in environmental variation. For example, spatially autocorrelated environmental changes may increase metacommunity variability by increasing spatial aggregate and compositional synchrony. Any disturbance that increases the synchrony in environmental fluctuations across the landscape will destabilize communities at large spatial scales (Moran 1953). Therefore, the spatial scale of environmental fluctuations determines how many patches of the metacommunity are likely to be experiencing similar environmental conditions at any given time. This suggests a distinction between local-extent fluctuations and large-extent fluctuations, such that large-extent fluctuations may increase metacommunity variability more strongly than fluctuations at the local scale by inducing spatial synchrony in a larger portion of the metacommunity (Ruhi et al. 2018). Recent increases in large-extent disturbances (e.g., regional land use, global climate change; Foley et al. 2005), are especially troubling because they are more likely to synchronize variability among communities and destabilize metacommunities.

Our framework clarifies multiple scales of metacommunity variability and is thus relevant for conservation planners who are increasingly tasked with implementing local- and regional-scale strategies to minimize biodiversity loss (e.g., Gimona et al. 2012, Socolar et al. 2016). While the importance of spatial processes (e.g. colonization–extinction and source–sink dynamics) for conservation planning has been widely acknowledged (Margules and Pressey 2000), explicit use of the metacommunity concept has been rare, but effective. For example, application of the metacommunity framework to lowland heathland conservation showed that coordinated efforts among local sites could increase regional-scale conservation success (Diaz et al. 2013). In addition, this study recognized the importance of suboptimal patches for the maintenance of regional biodiversity, an aspect of conservation that is often overlooked, but would be important for identifying which and how many sites should be targeted for conservation (Socolar et al. 2016).

Conclusions

Metacommunity temporal variability has two complementary dimensions: aggregate and compositional. Partitioning aggregate and compositional variability across spatial scales yields a quantitative estimate of the degree of spatial aggregate synchrony and spatial compositional synchrony, thus facilitating the comparison between the two dimensions of community variability across spatial scales. Our framework links aggregate variability, based on previous work, and compositional variability across spatial scales to deepen our understanding of the mechanisms underlying metacommunity variability. Our marine metacommunity case study illustrates how the joint focus on aggregate and compositional variabilities reveals important compositional changes at broad spatial scales, mainly due to synchronous compositional trajectories among local communities, which would have been overlooked if the focus had been solely on the aggregate components of the metacommunity. Our approach contributes to relevant conservation and management issues by yielding insight into the ecological processes that may stabilize or destabilize aspects of biodiversity at large spatial scales.

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Supplementary material

SM1 (Supplementary material 1): Derivation of compositional variability for BD_{α}^{h}, BD_{γ}^{h}, and BD_{φ}^{h}

SM2 (Supplementary material 2): R code to reproduce the example in Fig 2 is available at https://github.com/sokole/ltermetacommunities/tree/master/Manuscripts/MS2-Supp-Info/supp-info-example-agg-by-site-rev20191121

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Legend to Figures

Figure 1. Conceptual figure illustrating the dual nature of metacommunity variability. Each panel displays a scenario of low (C, D) and high (A, B) aggregate metacommunity variability and low (A, C) and high (B, D) compositional metacommunity variability. Scenarios are based on two local communities (community 1 and 2) composed of two species surveyed for 15 years (x-axis of inset panels). Within each local community, dashed red and blue lines represent the biomass of the two species, and the solid grey line represents the aggregate community property (total community biomass). At the metacommunity scale, dashed red and blue lines represent the metapopulation biomass of the two species, and the solid grey line the aggregate metacommunity property (the total biomass of the whole metacommunity).

Figure 2. Case study of macroalgae that inhabit shallow rocky reefs (data package ID: knb-lter-sbc.50.7). Representation of the community structure of (A) the 10 local communities and (B) the metacommunity. Each color corresponds to one species. (C) Comparison of the partitioning of aggregate and compositional variability. Each color represents one of the three methods. (D) Compositional trajectories of each local community and the metacommunity based on NMDS. The compositional trajectory of the metacommunity is pictured as a thick black line and each color represents the compositional trajectory of one of the 10 local communities.

Figure 3. Conceptual framework for integrating compositional metacommunity variability. Each sub-figure represents the temporal trajectory over nine time steps (from t1 to t9) of a metacommunity composed of two local communities (X and O) in a two-dimensional compositional space. We propose four conceptual scenarios for the compositional variability in a metacommunity. These scenarios are based on the original framework proposed by Micheli et al. (1999), but extended to scale compositional variability from local communities up to the regional scale. They correspond to (A) synchrony, (B) asynchrony, (C) stasis, and (D) compensation, and depend on the degree of local scale temporal compositional variability and spatial compositional synchrony. When the two local communities follow similar compositional trajectories, such strong spatial compositional synchrony increases regional-scale compositional variability (Scenario A: ‘synchrony’). Conversely, if the two local communities follow perfectly reverse compositional trajectories the metacommunity exhibits no compositional change (Scenario D: ‘compensation’). If the two local communities undergo weakly correlated compositional changes over time, the reduced spatial compositional synchrony partly reduces regional-scale compositional variability but, in contrast to scenario D, does not buffer it entirely (Scenario B: ‘*asynchrony*’). Finally, when the two local communities do not undergo any compositional change, the metacommunity compositional variability is also null (Scenario C: ‘*stasis*’).

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Table 1. Glossary

Term	Definition
Local scale	Local communities delimited within "patches" (or sites) within the metacommunity.
Regional scale	The collection of all local communities. Also referred to as the metacommunity.
Metacommunity	A set of local communities connected by the dispersal of potentially interacting species.
Temporal variability	The fluctuation in time of a given metric. Here, we focus on the temporal variability of both aggregate (e.g. total community biomass) and compositional metrics of communities.
Compositional variability	Variability in time in the relative frequencies of the species that make up local communities or the whole metacommunity. Independent of aggregate variability.
Aggregate variability	Temporal variability in the aggregate metric of a community or of the whole metacommunity (e.g. total community biomass).
Spatial aggregate synchrony	The degree of synchrony in aggregate community metrics among local communities.
Spatial compositional synchrony	The degree of synchrony in compositional change among local communities.
Environmental synchrony	The degree of synchrony in environmental change among local communities.

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Table 2. Notations summary for aggregate and compositional metacommunity variability across spatial scales. Temporal compositional variability is computed based on the time-independent Hellinger transformation. Note that "." are used to define sums (e.g. $X_{it.} = \sum_j^s X_{itj}$) while $\overline{\sqrt{X_{i.j}}} = \sum_t \sqrt{X_{itj}}/n$ is the temporal mean of the square root coefficient biomass.

Symbol	Description
X_{itj}	Biomass, or abundance, of species *j* in community *i* at time *t*
$X_{it.} = \sum_j^s X_{itj}$	Total aggregate metric of community *i* at time *t*
$X_{itj}^h = \sqrt{X_{itj}/X_{it.}}$	Hellinger transformation of the biomass, or abundance, of species *j* in community *i* at time *t*, corresponding to the square root coefficient of species relative
$X_{i..} = \sum_t^n \sum_j^s X_{itj}$	Total aggregate metric of community *i*
$X_{itj}^{hT} = \sqrt{X_{itj}/X_{i..}}$	Time-independent Hellinger transformation of the biomass, or abundance, of species *j* in community *i* at time *t*, corresponding to the square root coefficient of species relative frequencies with respect to the total aggregate metric of community *i*
Local scale aggregate variability	
σ_{Ti}	Temporal standard deviation of the aggregate metric in community *i*
$CV_\alpha^2 = \left(\frac{\sum_i^m \sigma_{Ti}}{\mu_{TT}}\right)^2$	Local scale aggregate variability, defined as the square coefficient of the weighted average of aggregate variability across communities
Local scale compositional variability	
$v_{ij}^{hT} = \frac{\sum_t^n \left(\sqrt{X_{itj}} - \overline{\sqrt{X_{i.j}}}\right)^2}{n-1}$	Temporal variance of the square root coefficient biomass of species *j* in community *i*
$BD_i^{hT} = \frac{\sum_j^s v_{ij}^{hT}}{X_{i..}}$	Temporal compositional variability of community *i*, corresponding to the beta diversity based on the time-independent Hellinger transformation of community *i*
$BD_\alpha^{hT} = \frac{\sum_i^m \sum_j^s v_{ij}^{hT}}{X_{...}}$	Local scale aggregate variability, defined as the weighted average of local compositional changes based on the time-independent Hellinger transformation
Regional scale aggregate variability	
σ_{TT}	Temporal standard deviation of the aggregate metric of the whole metacommunity
μ_{TT}	Temporal mean of the aggregate metric of the whole metacommunity
$CV_\gamma^2 = \left(\frac{\sigma_{TT}}{\mu_{TT}}\right)^2$	Regional scale aggregate variability, or aggregate variability of the whole metacommunity
Regional scale compositional variability	
$X_{.tj} = \sum_i^m X_{itj}$	Total aggregate metric of species *j* at time *t* in the whole metacommunity
$X_{..j} = \sum_i^m \sum_t^n X_{itj}$	Total aggregate metric of species *j* in the whole metacommunity
$X_{...} = \sum_i^m \sum_t^n \sum_j^s X_{itj}$	Total aggregate metric of the whole metacommunity
$v_{Tj}^{hT} = \frac{\sum_t^n \left(\sqrt{X_{.tj}} - \overline{\sqrt{X_{..j}}}\right)^2}{n-1}$	Temporal variance of the square root coefficient of the regional biomass of species *j*
$BD_\gamma^{hT} = \frac{\sum_{j=1}^s v_{Tj}^{hT}}{X_{...}}$	Regional scale compositional variability, or compositional variability of the whole metacommunity, corresponding to the beta diversity based on the time-independent Hellinger transformation of the whole metacommunity

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Spatial aggregate and compositional synchrony

$\varphi = \left(\frac{\sigma_{TT}}{\sum_i^m \sigma_{Ti}}\right)^2$	Spatial aggregate synchrony, defined following Wang and Loreau (2014) and the synchrony definition of Loreau and de Mazancourt (2008)
$\varphi_{(j)}^{hT} = \frac{v_{Tj}^{hT}}{\sum_i^m v_{ij}^{hT}}$	Species-level spatial synchrony, defined as the spatial synchrony of the square root coefficient of the biomass of species *j*. This synchrony index differs from the definition of Loreau and de Mazancourt (2008). Instead of the ratio between the total variance over the square coefficient of the summed standard deviations, we here use the ratio between the total variance over the sum of local variances
$BD_{\varphi}^{hT} = \sum_{j=1}^{s} w_j \cdot \varphi_{(j)}^{hT}$, where $w_j = \sum_i^m v_{ij}^{hT} / \sum_{j=1}^{s} \sum_{i=1}^{m} v_{ij}^{hT}$	Spatial compositional synchrony, corresponding to weighted average of species-level spatial synchrony. Different from the synchrony definition of Loreau and de Mazancourt (2008)

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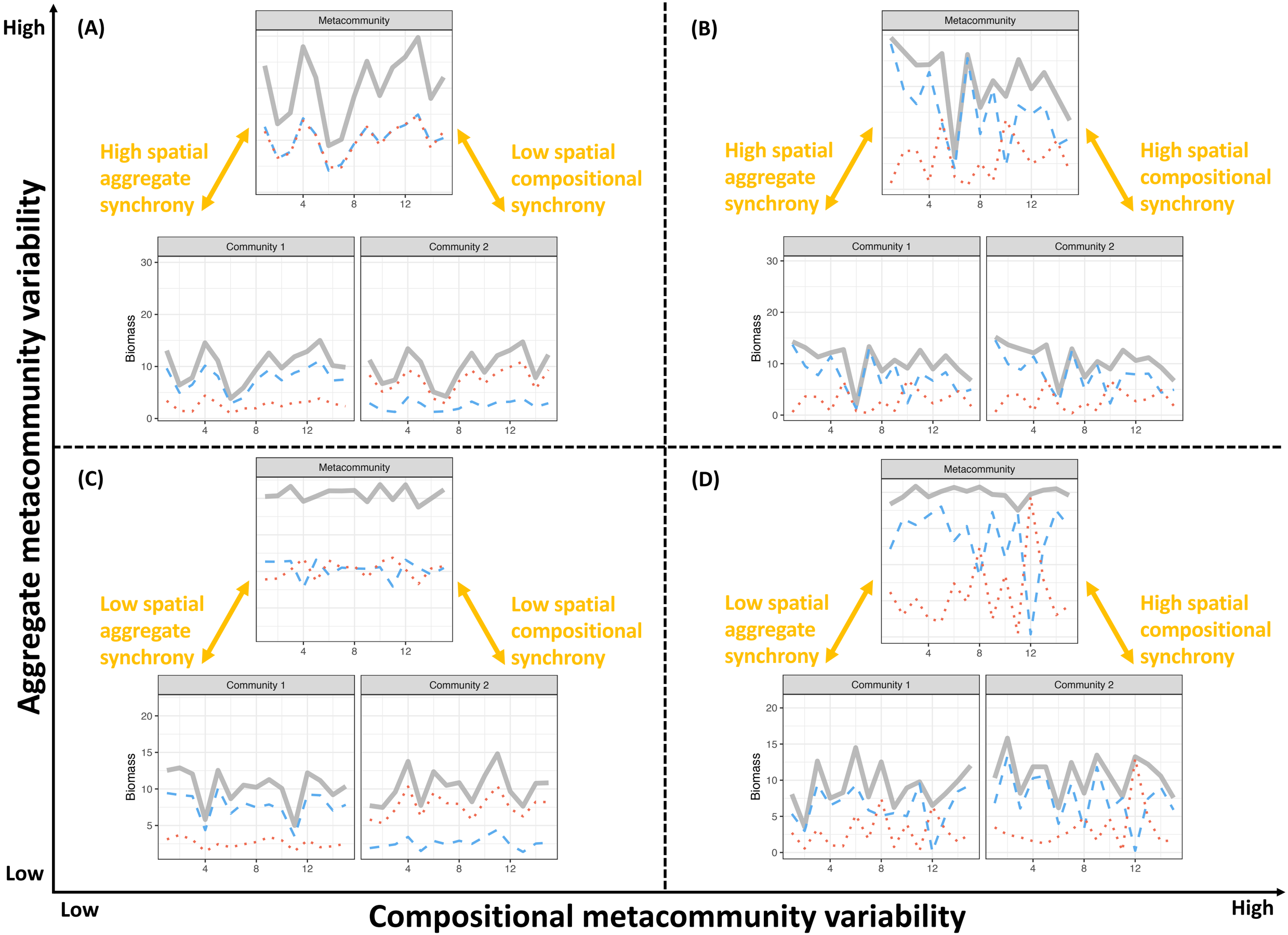
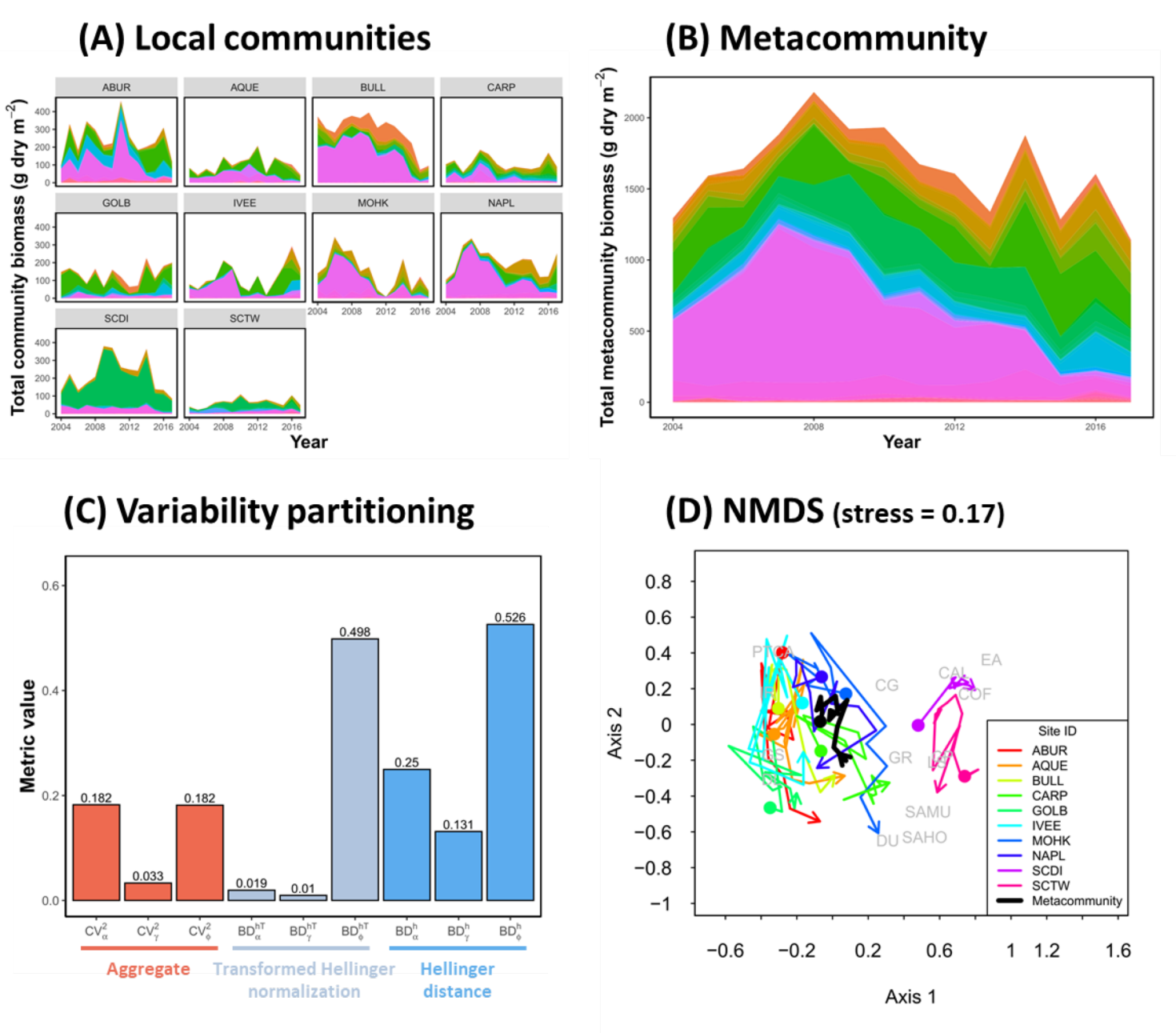
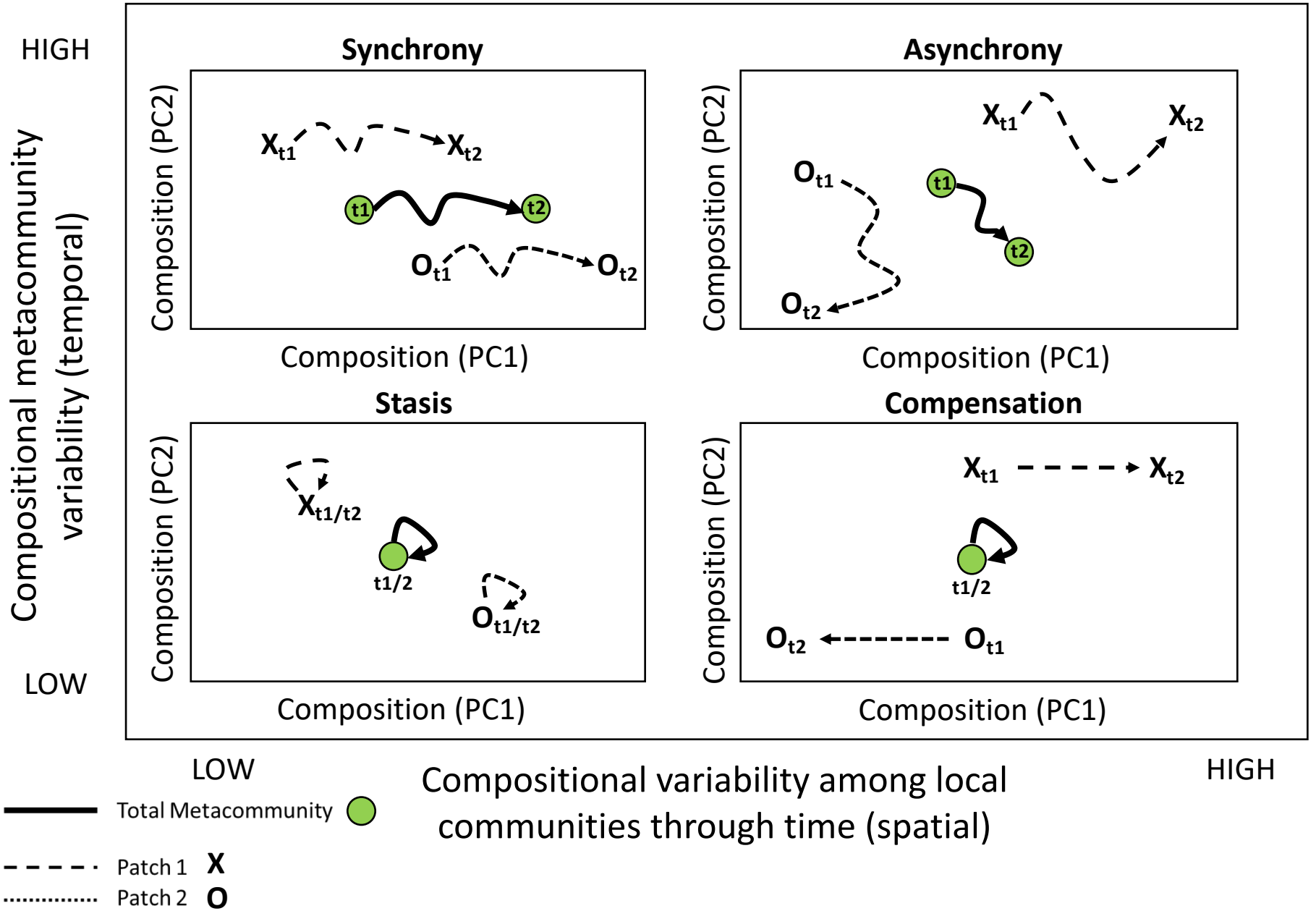

High
Low
Aggregate metacommunity variability
Low
High
Compositional metacommunity variability
(A)
Metacommunity
High spatial aggregate synchrony
Low spatial compositional synchrony
Community 1
Community 2
Biomass
(B)
Metacommunity
High spatial aggregate synchrony
High spatial compositional synchrony
Community 1
Community 2
Biomass
(C)
Metacommunity
Low spatial aggregate synchrony
Low spatial compositional synchrony
Community 1
Community 2
Biomass
(D)
Metacommunity
Low spatial aggregate synchrony
High spatial compositional synchrony
Community 1
Community 2
Biomass


(A) Local communities
ABUR
AQUE
BULL
CARP
GOLB
IVEE
MOHK
NAPL
SCDI
SCTW
Total community biomass (g dry m^{-2})
Year
(B) Metacommunity
Total metacommunity biomass (g dry m^{-2})
Year
(C) Variability partitioning
Metric value
0.182
0.033
0.182
0.019
0.01
0.498
0.25
0.131
0.526
CV^2_α CV^2_γ CV^2_ϕ BD^{hT}_α BD^{hT}_γ BD^{hT}_ϕ BD^h_α BD^h_γ BD^h_ϕ
Aggregate
Transformed Hellinger normalization
Hellinger distance
(D) NMDS (stress = 0.17)
Axis 2
Axis 1
CG
CAL
EA
COF
GR
SAMU
DU
SAHO
Site ID
ABUR
AQUE
BULL
CARP
GOLB
IVEE
MOHK
NAPL
SCDI
SCTW
Metacommunity


HIGH
LOW
Compositional metacommunity variability (temporal)
Synchrony
Asynchrony
Stasis
Compensation
Composition (PC2)
Composition (PC1)
X_{t1}
X_{t2}
O_{t1}
O_{t2}
t1
t2
$X_{t1/t2}$
$O_{t1/t2}$
t1/2
LOW
HIGH
Compositional variability among local communities through time (spatial)
Total Metacommunity
Patch 1 X
Patch 2 O