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CONCEPTS, REVIEWS AND SYNTHESES

Making sense of metacommunities: dispelling the mythology of a metacommunity typology

Bryan L. Brown[1] · **Eric R. Sokol**[2] · **James Skelton**[3] · **Brett Tornwall**[1]

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Abstract Metacommunity ecology has rapidly become a dominant framework through which ecologists understand the natural world. Unfortunately, persistent misunderstandings regarding metacommunity theory and the methods for evaluating hypotheses based on the theory are common in the ecological literature. Since its beginnings, four major paradigms—species sorting, mass effects, neutrality, and patch dynamics—have been associated with metacommunity ecology. The Big 4 have been misconstrued to represent the complete set of metacommunity dynamics. As a result, many investigators attempt to evaluate community assembly processes as strictly belonging to one of the Big 4 types, rather than embracing the full scope of metacommunity theory. The Big 4 were never intended to represent the entire spectrum of metacommunity dynamics and were rather examples of *historical* paradigms that fit within the new framework. We argue that perpetuation of the Big 4 typology hurts community ecology and we encourage researchers to embrace the full inference space of metacommunity theory. A related, but distinct issue is that the technique of variation partitioning is often used to evaluate the dynamics of metacommunities. This methodology has produced its own set of misunderstandings, some of which are directly a product of the Big 4 typology and others which are simply the product of poor study design or statistical artefacts. However, variation partitioning is a potentially powerful technique when used appropriately and we identify several strategies for successful utilization of variation partitioning.

Keywords Metacommunity · Species sorting · Mass effects · Neutral theory · Patch dynamics · Variation partitioning

Introduction

In 1999, John Lawton opined that the single largest barrier to the progress and success of community ecology was "… its overwhelming emphasis on localness" (Lawton 1999). In the intervening 17 years, community ecologists have answered Lawton's challenge, and the collective direction of community ecology has notably steered toward multi-scale perspectives on the assembly and structure of communities. This progress has occurred largely through the development of metacommunity theory (Holyoak et al. 2005; Leibold et al. 2004). Metacommunity theory posits that it is not only the local processes of species interactions and interactions with local environmental conditions that dictate community composition, but that composition also depends on regional-scale processes such as the movement of organisms on a landscape (Leibold et al. 2004). Today, metacommunity ecology is no longer a fringe discipline within community ecology, but has rapidly become a dominant framework through which ecologists understand the natural world.

Unfortunately, despite the widespread and growing focus on multi-scale ecology, persistent misunderstandings

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✉ Bryan L. Brown
stonefly@vt.edu

[1] Department of Biological Sciences, Virginia Tech, Blacksburg, VA 24061, USA

[2] Institute of Arctic and Alpine Research, University of Colorado, Boulder, USA

[3] School of Forest Resources and Conservation, University of Florida, Gainesville, USA

regarding metacommunity theory and the methods for evaluating hypotheses based on the theory are common in the ecological literature. Based on our observations from published papers, meeting presentations, and manuscript reviews, some of these misconceptions appear to be increasing in frequency, rather than decreasing as metacommunity ecology matures. Here, we discuss two major sources of misapprehension about metacommunities. The first is "the Big 4" metacommunity paradigms, i.e., species sorting, neutral dynamics, patch dynamics, and mass effects. The second is variation partitioning as a method for evaluating metacommunity dynamics. We stress that neither the Big 4 paradigms nor variation partitioning are intrinsically unsound, but misunderstandings and disagreements about how to properly test neutral and niche-based hypotheses have nevertheless persisted around both (Gilbert and Bennett 2010; Logue et al. 2011; Smith and Lundholm 2010). While each of these topics present different sources of misunderstanding, they are also linked conceptually since variation partitioning is often used as an analysis of empirical evidence that attempts to distinguish between the Big 4 paradigms (Cottenie 2005). Below, we focus not only on some persistent misunderstandings, but also on how the Big 4 and variation partitioning can be powerful conceptual and statistical tools when used appropriately.

Problems with the Big 4 metacommunity paradigms

Four classic models of community dynamics and structure are strongly associated with metacommunity theory: species sorting, patch dynamics, mass effects, and neutral dynamics (Chase 2005; Leibold et al. 2004). These paradigms are all representatives of metacommunity theory because all four paradigms combine the process occurring at local (i.e., patch-level) scales with processes occurring at regional scales, driven by the movement of organisms among patches. Each of the Big 4 is distinguished by the amount of emphasis they place on a combination of local processes, regional processes, disturbance, and the degree to which species are equivalent in their traits. Species sorting is a classic niche-based paradigm emphasizing local processes in which species occupy locales that best suit them based on environmental tolerances and their interactions with other species (Whittaker 1962). The patch dynamics paradigm largely ignores the specific properties of local patches, and local diversity is primarily dictated by differences in species' dispersal while regional dynamics are a product of extinctions and colonization (Levin 1974; Levins and Culver 1971; Skellam 1951). Mass effects present the perspective that source-sink dynamics at high rates of regional dispersal can swamp out local processes (Brown and Kodric-Brown 1977; Shmida and Wilson 1985) and neutral dynamics model community composition through species losses, gains, and probabilistic colonization, without respect to differences in traits between species (Bell 2001; Hubbell 2001).

The problem with the Big 4 is not an inherent issue with any of the four paradigms. Each of the Big 4 is a historically respected—though not always agreed upon—theory of community assembly. Each of the Big 4 is also clearly representative of metacommunity theory, since it involves phenomena occurring at both local and regional scales. Rather, the problem is that "the Big 4 have been widely misconstrued to represent the entire inference space of metacommunities and to describe all possible metacommunity dynamics*"*. If this representation were accurate, then all metacommunities could be classified as either belonging to one of the Big 4 or as occupying some middle ground between extremes represented by the Big 4. However, this representation is incorrect for two reasons. First, the Big 4 paradigms are not mutually exclusive. They are not mutually exclusive regarding the mechanisms they invoke for structuring communities, nor are they exclusive in the predictions they make regarding measurable metacommunity variables (Chase et al. 2005; Leibold et al. 2004; Logue et al. 2011; Winegardner et al. 2012). Second, the Big 4 do not constitute the entire inference space of metacommunity theory (Brown et al. 2011; Logue et al. 2011; Winegardner et al. 2012). This issue is very effectively illustrated in Fig. 1 of Logue et al. 2011 which shows that the Big 4 occupy only a limited space within the total metacommunity inference space defined by three axes: species equivalence, influence of dispersal, and environmental heterogeneity (Logue et al. 2011). The most serious consequence of these misunderstandings is that many studies expressly define their goal as identifying which of the Big 4 are responsible for structuring a system of interest. Unfortunately, these studies are in many ways nonsensical because they begin with the false premise that a community of interest can always, and exclusively, be classified as one of the Big 4. As a result, many studies ignore the swath of inference space that lies outside of the Big 4 paradigms and fail to recognize metacommunity inference space as continuous and multidimensional (Logue et al. 2011).

These issues arose from widespread misunderstanding of two key publications that catalyzed the emergence of metacommunity theory: Leibold et al. (2004) and Holyoak et al. (2005). Both works prominently featured the Big 4 paradigms and used them extensively as points of discussion regarding metacommunity theory. Many readers incorrectly interpreted these uses of the Big 4 to mean that metacommunities were explicitly defined by these four categories of dynamics. However, a careful reading of either work clearly reveals that the Big 4 were never intended by the authors to typify all possible metacommunities or to represent mutually exclusive types of metacommunities. Rather, the four paradigms were presented as historically prominent models of community assembly that fit within the broader framework of metacommunity theory: "To date, theoretical and empirical work on metacommunities falls along four broad lines or approaches…" (Leibold et al. 2004), clearly indicating that the authors viewed the Big 4 as perspectives shared by researchers rather than types of metacommunities. Additionally, in Leibold et al. (2004), a five-paragraph section describing explicitly why the Big 4 do *not* constitute the proper inference space of metacommunity theory directly follows brief descriptions of the Big 4 paradigms (found in the section "The Role of Trade-Offs Among Species Traits in Metacommunities"). Unfortunately, early misunderstandings were unintentionally perpetuated by prominent publications demonstrating how empirical patterns could distinguish among types of metacommunity dynamics using the Big 4 as examples (e.g., Chase et al. 2005; Cottenie 2005). Ultimately, conceptual misapprehensions combined with procedural knowledge to produce studies whose stated purpose was to test which of the Big 4 paradigms described assembly of a particular system.

We do not suggest that the Big 4 metacommunity paradigms have no utility. They serve as useful perspectives that emphasize different sets of metacommunity dynamics and provide a convenient shorthand for discussing metacommunity scenarios. However, as metacommunity theory continues to develop, we suggest that investigators embrace a metacommunity concept that is more flexible, inclusive, and continuously defined than a typological classification scheme based on the Big 4. Logue et al. (2011) provide one such example in their Fig. 1 by defining metacommunity inference space along 3 axes: species equivalence, dispersal, and environmental heterogeneity. While this definition is an example of a more inclusive approach, it is only one of many possibilities and other investigators may decide to include other important axes, for example disturbance (Brown et al. 2011), metacommunity openness, niche breadth, metacommunity size, and scale of environmental heterogeneity (Sokol et al. 2015). Some investigators may find these conceptions of metacommunities unsatisfying because they are less delineated and sharply defined than simply having four categories of metacommunity, and because there is no consensus on what the exact axes are that define metacommunity space. However, these flexible and continuous conceptions are both more accurate than the Big 4 with regard to making inferences about metacommunity dynamics, and potentially more useful because they are more adaptable to particular scenarios or empirical problems. These conceptions are also more true to the original intent of metacommunity theory which was never intended to be defined by four simplistic categories of dynamics (Leibold et al. 2004; Winegardner et al. 2012). Thus, the ideas presented here are more reminder than revolutionary.

Issues with variation partitioning

There is a long history in the ecology of investigators inferring underlying processes from patterns documented in observational studies, for example, the concept of niche-based species sorting stems, in large part, from Hutchinson (1959) inferring competitive exclusion dynamics as the underlying process that created the distribution and co-occurrence patterns he observed for corixid species in ponds. Similarly, species' dispersal capabilities are often invoked to explain distance-decay patterns in community similarity with stronger limitations on dispersal being inferred from steeper distance-decay patterns (Nekola and White 1999). With the ever-increasing availability of observational data, computing power, and analytical software, many ecologists and environmental scientists are eager to embrace a framework by which they can use biodiversity patterns to infer underlying community assembly processes. Careful consideration of the observed patterns have contributed much to our understanding of the natural world; however, maybe the most important lesson from Hutchinson's corixids was that there are limits on how much we can learn about ecological processes from observational studies alone, and mechanistic inferences based on observed patterns should be carefully scrutinized (Simberloff and Boecklen 1981).

A major appeal of the metacommunity concept is that it potentially offers a framework to disentangle the roles of niche-based and dispersal-based dynamics in different community assembly scenarios that are thought to produce different emergent biodiversity patterns (e.g., Chase and Myers 2011; Diniz-Filho et al. 2012; Gil-Tena et al. 2013; Meynard et al. 2013; Moritz et al. 2013). Shortly after the Big 4 were framed as alternative metacommunity scenarios that could emerge under different combinations of dispersal, habitat heterogeneity, and ecological neutrality (i.e., lack of functional diversity in the regional species pool), "variation partitioning" was co-opted as a quantitative tool to diagnose metacommunity type from observational data (Logue et al. 2011). Many empirical studies were modeled after a meta-analysis by Cottenie (2005), which suggested that variation partitioning outcomes could be used to infer underlying metacommunity dynamics when biodiversity data are accompanied by environmental and geospatial data.

The general concept of variation partitioning (reviewed in detail in Dray et al. 2012; Peres-Neto and Legendre 2010) was first introduced in community ecology by Borcard et al. (1992) as a method to quantify how much among-site variation in community composition was correlated with environmental and spatial variables. There are two general methodological approaches to variation partitioning. The first is the raw data method (Legendre et al.

2005, 2008; Legendre and Fortin 2010) in which constrained ordinations (e.g., CCA, RDA, dbRDA) are used to quantify the proportion of variation in community composition in a site by species matrix (*Y*) that can be explained by variables represented in a site by environmental data matrix (*E*) and a matrix of spatial variables (*S*) used to model different scales of spatial heterogeneity. Spatial variables that make up *S* (i.e., spatial predictors) are derived from geographic coordinates (e.g., latitude and longitude) and are used to detect spatial patterns in community composition, such as the scale of autocorrelation. Non-linear spatial relationships have been modeled with quadratic functions (Borcard et al. 1992), but more flexible methods based on Moran eigenvector maps (MEM) have been developed and are now widely used to model spatial structure in variation partitioning studies (described by Peres-Neto et al. 2006; Peres-Neto and Legendre 2010; Legendre et al. 2012; see Sokol et al. 2013, 2014 for examples). In a typical raw data variation partitioning analysis, coefficients of determination [R^2 or adjusted R^2 values (Blanchet et al. 2008)] estimated from multivariate models are used to split variation in *Y* into four components, where [a] is the pure environmental component (R^2 $E|S$), [b] represents variation in *Y* that corresponds to both *E* and *S* (R^2 E intersect S), [c] is pure spatial variation (R^2 $S|E$), and [d] is unexplained variation (1—[$a + b + c$]) (see Fig. 1 in Peres-Neto et al. 2006).

The second approach is the distance-based method, which is used to assess correlations between triangular site-by-site distance matrices, D_Y, D_E, and D_S. These distance matrices are calculated from raw data matrices *Y*, *E*, and *S* (where *S* is a matrix of site coordinates, such as latitude and longitude), respectively. Linear multiple regression on distance matrices (Smouse et al. 1986; Legendre and Legendre 1998) is used to calculate how much variation in the distances represented in D_Y can be explained by among-site environmental differences (D_E) and geographic distance (D_S) (Duivenvoorden et al. 2002; Tuomisto et al. 2003). It is important to note that the raw data approach explains variation in community composition, whereas the distance approach explains variation in community dissimilarity (but does not predict composition). While these two analyses are related, their application to testing metacommunity hypotheses, such as predictions of neutral theory, is controversial (Legendre et al. 2005, 2008, 2009; Tuomisto and Ruokolainen 2006; Laliberté 2008; Tuomisto and Ruokolainen 2008; Tuomisto et al. 2012).

Cottenie (2005) outlined three postulates to describe how the presence or absence of different, statistically significant variation partitioning components in a metacommunity could provide insight into the underlying community assembly dynamics:

1. An [a] that is very high relative to [c] indicates a metacommunity was organized purely by species sorting because community composition must be empirically linked to environmental variation if "everything is everywhere, but, the environment selects" (Becking 1934). Further, such a metacommunity is assumed to be panmictic and any spatial variation in community composition must result from species sorting along a spatially structured environmental gradient and thus fall in the [b] component.
2. The presence of significant [a] and [c] indicates a scenario in which species sorting and mass effects organized metacommunity biodiversity. Under such source sink dynamics, species are expected to be most abundant in patches that most closely match their fundamental niche, thereby creating an expectation for a significant [a] component. However, individuals are also expected to disperse to and maintain nearby sink populations where the local habitat does not represent their fundamental niche, thus, creating spatial patterns in species turnover that are not explained by environmental variables, resulting in a significant [c] component.
3. The absence of [a] and presence of [c] indicates a lack of species sorting and a metacommunity in which species turnover patterns were organized by stochastic dispersal dynamics that occurred independent of environmental gradients. However, spatial patterns in community composition (e.g., autocorrelation) that occur independent of environmental variation can be predicted by both neutral models and patch dynamics.

These postulates represent an important contribution to the discipline of community ecology, because they provide a heuristic framework to link empirical data to metacommunity theory. Like Leibold et al. (2004), Cottenie emphasized that the Big 4 and their empirical evaluation using variation partitioning are particular manifestations of metacommunities in a larger continuum spanning from scenarios influenced by environmental drivers to scenarios organized by spatial processes, but his organization of these concepts is often misinterpreted as producing mutually exclusive predictions about community assembly. These publications have had a profound influence over how ecologists use metacommunity theory to interpret biodiversity patterns, as there have been over 150 metacommunity publications indexed in the Web of Science during each of the past 4 years (2011–2014) and over 80% of those published in 2014 still cited both Leibold et al. (2004) and Cottenie (2005). However, a decade of research has demonstrated that ecologists should be cautious when drawing links between variation partitioning outcomes and the underlying metacommunity dynamics.

Weak inference

While Leibold et al. (2004) and Cottenie (2005) used the Big 4 as reference points in metacommunity parameter space which are recognizable because they are rooted in classical ecological theory, many subsequent studies misinterpreted the above postulates as alternative, mutually exclusive hypotheses and attempted to use them in a strong inference approach (sensu Platt 1964) to identify the community assembly processes underlying observed biodiversity patterns (reviewed in Logue et al. 2011). Major criticisms of the strong inference approach include questions about whether it is possible to know if alternative hypotheses accurately characterize all alternative scenarios and whether alternative hypotheses will actually produce mutually exclusive outcomes (problems with equifinality) (O'Donohue and Buchanan 2001; Tuomisto et al. 2012), and these caveats do indeed apply to the Big 4. For example, a significant [c] component is used to infer a spatial pattern in community turnover is influenced by limits on dispersal (sensu Nekola and White 1999). However, the alternative hypothesis to such a conclusion is that there could be a spatially autocorrelated environmental gradient that was not measured that is driving species sorting in the metacommunity. This alternative hypothesis is not falsifiable and therefore poses a significant problem to the application of strong inference to infer metacommunity characteristics from variation partitioning outcomes.

Do variation partitioning outcomes mean what we think they mean?

Generally, ecology is a complex science and it is necessary for investigators to use creative and innovative methods to infer process from pattern and to distinguish causation from correlation (Shipley 2002). The three postulates described above, which provide the foundation for linking variation partitioning to underlying metacommunity dynamics, assume that R^2 values for each of the variation components respond monotonically to shifts in the balance of environmental and spatial influences over community composition. However, simulation studies have shown that variation partitioning outcomes may be more sensitive to choices an investigator makes regarding statistical methods and sampling design rather than underlying community assembly dynamics (Gilbert and Bennett 2010; Steinbauer et al. 2012; Tuomisto 2012).

Tuomisto et al. (2012) demonstrated how a scaling mismatch between community turnover and environmental gradients can result in a disconnect between the statistical and ecological assumptions that are used to link variation partitioning to metacommunity theory. For example, if species sorting is driving community turnover among sites arranged along an environmental gradient, then community dissimilarity is assumed to increase monotonically along the transect as sites represent increasingly dissimilar habitats from the original sampling location. At some distance along the transect, community composition will have turned over completely (no species in common with the original reference point), at which point most dissimilarity metrics reach their maximum value. As the study transect is extended along the environmental gradient, measures of environmental dissimilarity from the original sampling location will continue to increase, yet most community dissimilarity metrics will have plateaued at their maximum possible value, a phenomenon termed dissimilarity saturation. Using simulations, Tuomisto et al. demonstrated how increasing the extent of an observational study to include multiple community turnovers, which increases dissimilarity saturation (i.e., the number of pairwise comparisons a study with the maximum dissimilarity value), can lead to non-intuitive variation partitioning outcomes that do not match the framework described above.

While the relationships between variation partitioning outcomes and metacommunity dynamics described by Cottenie (2005) cannot be assumed to be ubiquitously applicable, the framework can still prove useful in the right context. For example, Tuomisto et al. (2012) developed a dissimilarity metric that can capture multiple species turnovers and performs well when dissimilarity saturation is <60%. Other alternatives of community turnover, such as dissimilarity metrics based on phylodiversity (Webb et al. 2002) or functional traits (e.g., Ricotta and Moretti 2010; Sokol et al. 2011), offer alternative measures of community turnover that do not have the same sensitivity to the dissimilarity saturation as traditional taxonomy-based measures of community composition. Lastly, simulation-based approaches can be used to identify the contexts under which it is appropriate to assume variation partitioning components respond predictably (i.e., monotonically) to changes in metacommunity dynamics. Tuomisto et al. (2012) demonstrated that variation partitioning outcomes reflected metacommunity dynamics, as expected, when dissimilarity saturation was low (<20%) and sampling effort was sufficiently high to reduce noise from sampling error in the data set. Additionally, simulation studies may potentially be used to identify when it is appropriate to make assumptions about how diversity metrics will respond to environmental and spatial predictors (Sokol et al. In Review; Stegen and Hurlbert 2011).

A confusion of continuums

Leibold et al. (2004) emphasized that the metacommunity concept outlines a continuum of community assembly dynamics. Indeed, many studies have used variation partitioning outcomes to characterize where a metacommunity falls along a continuum of influential factors; however, community ecologists do not appear to agree on what exactly the continuum is. For example, Cottenie's (2005) meta-analysis ranked metacommunities along a continuum of environmental to spatial influence. Other studies have described metacommunity continuums bookended with the deterministic vs. stochastic, niche vs. neutral, niche vs. dispersal, and local vs. regional dichotomies (e.g., Cottenie 2005; De Bie et al. 2012; Thompson and Townsend 2006). While there are common themes among each of these continuums, they are not interchangeable.

Generally, niche-based species sorting is equated with "local" and "deterministic" community assembly process that results in a strong link between environmental variables and community composition, assumed to be driven by environmental filtering. However, the perception of species sorting is scale dependent (Steinbauer et al. 2012; Tuomisto et al. 2012). To detect species sorting, an observational study must have a resolution such that species and environmental factors vary across the landscape at a similar scale and the extent of the study must encompass sufficient environmental heterogeneity for community composition to vary along an environmental gradient, but the study extent must not be so large as to encompass multiple community turnovers (described above). Given these constraints, variation partitioning outcomes indicative of species sorting are more likely to be detected for species that are the least "local", such as small-bodied widely dispersed organisms (De Bie et al. 2012; Soininen 2012). Conversely, specialist species that are similarly adapted to local habitat conditions often do not coexist locally, and niche-based competitive exclusion may weaken the perceived link between a habitat and species composition (Grime 2006). Thus, niche-based processes that structure metacommunities may not necessarily be "local" or "deterministic".

On the other hand, spatial patterns such as distance decay patterns in community similarity are often equated with dispersal-based community assembly processes, neutral metacommunity dynamics, stochasticity (e.g., priority effects and ecological drift), and regional scale influences over community assembly. Dispersal-based dynamics do not necessarily need to be neutral. "Neutrality" refers to the assumption that all species in the metacommunity are assumed to be ecologically equivalent (Bell 2001; Hubbell 2001), and thus have similar dispersal capabilities. Community turnover can arise in neutral metacommunities from stochastic demographic processes, but dispersal, colonization, and speciation dynamics can vary widely in a neutral metacommunity, producing a wide range of diversity outcomes. Alternatively, species dispersal abilities may vary, violating the assumption of ecological equivalence, which can affect variation partitioning outcomes (De Bie et al. 2012).

Current and best-practice use of variation partitioning

In 2014, 20 of the 153 peer-reviewed metacommunity studies indexed in the Web of Science were research articles that employed variation partitioning techniques that cited methods described in Borcard and Legendre (2002) and/or Peres-Neto et al. (2006). The majority of these papers (>80%) referenced the Cottenie and Leibold et al. papers that have served as a foundation for linking variation partitioning outcomes to metacommunity theory, but also demonstrate how the application of variation partitioning has evolved beyond a simple characterization of the relative influence of spatial and environmental factors. Given the previously expressed cautions, how is the technique of variation partitioning best used? Below, we outline several prudent and informative ways to apply variation partitioning to observational data sets to answer biologically meaningful questions, though it is certainly not an exhaustive list.

1. Use a sensitivity analysis to understand how decisions about study design can create bias in analytical outcomes (Sokol et al. 2016). A single variation partitioning on a single system will inevitably produce results, but there are limits to the inferences that can be drawn from those results. The technique is sensitive to a variety of study-specific issues including analytical choices like distance metrics and transformations, as well as the variables selected for the analysis, both measured and unmeasured. Repeated analyses using multiple sets of analytical choices may reveal how robust the observed results are to variation of such choices. For example, Legendre et al. (2009) showed that variation partitioning outcomes are sensitive to patch grain size. A survey conducted using small patches will be biased toward lower patch-level richness (alpha diversity) and variation in community composition will tend to be attributed more heavily to pure spatial components [c] in the variation partition analysis. Alternatively, aggregating observations into larger patches will show stronger links between environment and community composition.
2. Strategically subset data, and compare variation partitioning outcomes among groups to answer specific questions. It is important to be aware that simulation studies have shown many factors (e.g., dispersal dynamics, patch topology, different levels of functional diversity) can elicit similar changes in variation partitioning outcomes (Stegen and Hurlbert 2011; Gilbert and Bennett 2010; Smith and Lundholm 2010, Sokol et al. accepted). One approach is to divide the species matrix (Y) based on traits and compare vari-

ation partitioning outcomes among groups. This provides a method to control for the influence of landscape structure and patch topology over variation partitioning outcomes. For example, Szekely and Langenheder (2014) showed that generalists, relative to specialists, responded more strongly to environmental gradients at the landscape scale. Other studies (De Bie et al. 2012; Rádková et al. 2014) reported evidence that passive dispersers, relative to active dispersers, exhibited more spatial structure in their biodiversity patterns.

3. A number of studies have had success testing community assembly hypotheses by comparing outcomes from alternative analytical approaches. One approach is to reanalyze data sets using different methods for quantifying spatial relationships. For example, stream ecologists have embraced study designs that compare variation partitioning outcomes based on overland and watercourse distances to address hypotheses about the implications of aerial and aquatic dispersal in dendritic networks (Meier and Soininen 2014; Padial et al. 2014; Zhang et al. 2014; Canedo-Arguelles et al. 2015). A second approach is to supply different measures of community composition to variation partitioning analyses and compare the outcomes. Mismatches between the scale of turnover in functional, phylogenetic, and/or taxonomic diversity that are detected in variation partitioning analyses can provide insight into controls of biodiversity at the local and regional scales (Sokol et al. 2011; Biswas et al. 2016). Importantly, analyses based on functional trait data can identify the influence of regional environmental filters that would otherwise be missed in an analysis of taxonomic turnover (Sokol et al. 2011).
4. Use simulations to expand sensitivity analyses beyond what is possible with empirically collected data and explore if variation partitioning metrics respond as expected to changes in metacommunity dynamics. Mouquet and Loreau (2003) used simulations to show how increased dispersal in a metacommunity can cause a decrease in beta-diversity. Similarly, investigators have used simulated data sets to assess how variation partitions respond to shifts in metacommunity dynamics, and outcomes from such studies demonstrate that extreme caution is warranted when making inferences from variation partitioning outcomes (e.g., Gilbert and Bennett 2010; Smith and Lundholm 2010). Alternatively, simulations can provide robust tools to understand the contingencies under which one can infer underlying community assembly processes from observed patterns (e.g., Stegen and Hurlbert 2011; Münkemüller et al. 2012) or as a null model for hypothesis testing (e.g., Sokol et al. 2015). For example, we have used simulations to identify a range of niche-breadth values and metacommunity configurations for which we can expect Cottenie (2005) postulates to hold true for specific raw data variation partitioning methods (Sokol et al. 2016).
5. Despite the criticisms of variation partitioning based on simulation studies (Gilbert and Bennett 2010; Smith and Lundholm 2010) and ambiguous results in experimental studies (Logue et al. 2011), meta-analyses have shown that there are clear empirical trends in variation partitioning outcomes across ecosystem and organism types (Cottenie 2005; Soininen 2016). It is important to document such empirical trends and identify when they are pervasive in ecology. While metacommunity theory and simulation models suggest variation partition response curves may not be monotonic or easy to interpret across the entirety of mathematically possible community assembly scenarios, the range of ecologically plausible community assembly scenarios may be more restricted. Simulation-based approaches can be used in combination with in situ observations to identify the ecologically plausible subset of the mathematically possible metacommunity parameter space (e.g., Sokol et al. 2015). Further, strong empirical, monotonic relationships between variation partitioning outcomes and metacommunity characteristics observed in a meta-analysis might suggest simulation models are more complicated than that needed to answer practical questions. Overall, a balance between modeling and empirical study is crucial for understanding complex systems such as metacommunities. Models allow us to understand how response variables should be expected to behave, but empirical studies and meta-analyses are necessary to identify ecologically relevant ranges of values for variables of interest.
6. Assessing temporal variability is crucial for understanding metacommunity dynamics. Variation in metacommunity structure through time can be tied to underlying metacommunity community assembly mechanisms (Seymour et al. 2015; Hubert et al. 2015, Jabot and Lohier 2016). Studies covering a broad spatial scope will likely need to account for evolutionary controls over community assembly in addition to the contemporary dynamics (Hubert et al. 2015). Furthermore, conclusions in many variation partitioning studies rely on the assumption that metacommunities are in equilibrium; however, controls over community assembly likely shift seasonally or in the wake of disturbance (e.g., Fernandes et al. 2014; Datry et al. 2016). Thus, investigators should be weary when inferring community assembly processes based on a snapshot in time. When temporal resolution is avail-

able, temporal heterogeneity can be modeled similarly to spatial heterogeneity and incorporated into variation partitioning analyses (Legendre and Gauthier 2014).

Summary

Despite misunderstandings and misapplications, we reiterate that both the Big 4 metacommunity paradigms and the technique of variation partitioning are potentially useful tools in the investigation of metacommunity patterns. The Big 4 paradigms are all historical approaches to community assembly that clearly fall under the purview of metacommunity ecology, and each is foundational theory in its own right. However, recognizing that the mechanistic space represented by metacommunity theory both exceeds the Big 4 paradigms and is continuous in nature is necessary to truly realize the potential of the metacommunity concept. Likewise, variation partitioning may be a valuable tool for investigation of metacommunity patterns, particularly from observational data. However, recent studies suggest caution with regard to interpreting the results of variation partitioning and insist that the technique not be approached blithely. Careful consideration of the data used in variation partitioning studies, of the specific choices made by investigators, and of the inferences to be drawn from variation partitioning are necessary for robust outcomes based on the method.

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