A comprehensive framework for the evaluation of metacommunity structure

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The metacommunity framework is a powerful platform for evaluating patterns of species distribution in geographic or environmental space. Idealized patterns (checkerboard, Clementsian, evenly spaced, Gleasonian and nested distributions) give the framework shape. Each pattern represents an area in a multidimensional continuum of metacommunity structures; however, the current approach to analysis of spatial structure of metacommunities is incomplete. To address this, we describe additional non-random structures and illustrate how they may be discerned via objective criteria. First, we distinguish three distinct forms of species loss in nested structures, which should improve identification of structuring mechanisms for nested patterns. Second, we define six quasi-structures that are consistent with the conceptual underpinnings of Clementsian, Gleasonian, evenly spaced and nested distributions. Finally, we demonstrate how combinations of structures at smaller spatial extents may aggregate to form Clementsian structure at larger extents. These refinements should facilitate the identification of best-fit patterns, associated structuring mechanisms, and informative scales of analysis and interpretation. This conceptual and analytical framework may be applied to network properties within communities (i.e. structure of interspecific interactions) and has broad application in ecology and biogeography.

The metacommunity concept substantively advanced understanding of meso- and large-scale ecology as well as the distribution of organisms along environmental gradients (Holyoak et al. 2005). Two interrelated and complementary avenues of investigation have been followed to understand spatial variation in species composition: one focusing on mechanism (Cottenie 2005), and one focusing on pattern (Leibold and Mikkelson 2002). The mechanistic approach to understand variation in site composition considers the roles of patch dynamics, species sorting, mass effects and neutrality (Leibold et al. 2004, Holyoak et al. 2005). In contrast, the pattern-based approach evaluates characteristics of species distributions along environmental gradients that emerge as a result of those mechanisms and manifest as particular metacommunity structures (e.g. random, checkerboard, nested, evenly-spaced, Gleasonian, or Clementsian patterns; sensu Leibold and Mikkelson 2002). To date, research largely has focused on one or the other of these approaches, with little coupling of mechanism and structure. Development of a more comprehensive framework for the evaluation of spatial structures should facilitate the integration of these complementary approaches.

Several conceptual models of spatial structure have been developed to describe patterns of species distribution. Clements (1916) described an idealized metacommunity structure comprising communities with distinctive species

compositions based on shared evolutionary history and inter-dependent ecological relationships, resulting in coincident range boundaries and compositional unity along different portions of the environmental gradient. In contrast, Gleason (1926) described a structure based on idiosyncratic species-specific responses to the environment, with coexistence resulting from chance similarities in requirements or tolerances. In situations where strong interspecific competition exists, tradeoffs in competitive ability may manifest as distributions that are more evenly spaced along environmental gradients than expected by chance (Tilman 1982). Alternatively, strong competition may result in checkerboard patterns produced by pairs of species with mutually exclusive ranges (Diamond 1975). If mutually exclusive pairs occur at random with respect to other such pairs, checkerboards will manifest at the metacommunity level. Finally, species-poor communities may form nested subsets of increasingly more species-rich communities (Patterson and Atmar 1986), with predictable patterns of species loss associated with variation in species-specific characteristics (e.g. dispersal ability, habitat specialization, tolerance to abiotic conditions).

Early research on spatial structures primarily was descriptive (Clements 1916, Gleason 1926, Whittaker 1956, 1960, 1965, Terborgh 1971, 1977). Because analytical approaches did not exist to distinguish among hypothetical patterns, controversies about the ubiquity of particular structures

remained unresolved, with only modest advancement of ecological understanding. More recently, a number of quantitative tests were developed that distinguish between nested and non-nested structures (Patterson and Atmar 1986, Wright and Reeves 1992, Wright et al. 1998, Jonsson 2001, Ulrich et al. 2009). Importantly, these approaches are restricted to analyses along gradients of richness and do not distinguish among non-random patterns that are not nested. In contrast, Leibold and Mikkelson (2002) developed a rigorous quantitative approach to simultaneously distinguish among multiple hypothetical patterns of species distribution based on an empirical species incidence matrix. This approach combines evaluation of three elements of metacommunity structure – coherence, range turnover and range boundary clumping – to identify which idealized structure (i.e. checkerboard, nested, Clementsian, Gleasonian, evenly spaced, or random distributions) most accurately characterizes an empirical metacommunity. Each non-random structure assumes that species distributions are molded by biotic interactions (e.g. competition, habitat associations) or responses to abiotic factors (e.g. temperature, rainfall) that vary among sites that constitute an environmental gradient. Importantly, the theoretical underpinnings of each idealized structure are unique (Clements 1916, Gleason 1926, Diamond 1975, Tilman 1982, Patterson and Atmar 1986), allowing analyses to simultaneously evaluate multiple hypotheses associated with spatial structure of a metacommunity.

Despite the ability of Leibold and Mikkelson's (2002) approach to identify emergent spatial structures in a metacommunity, it has been little used and researchers frequently fail to take advantage of its most powerful aspect, determination of the best-fit structure and identification of associated structuring mechanisms that are consistent with its theoretical underpinnings (Zimmerman 2006, Bloch et al. 2007, Werner et al. 2007, Barone et al. 2008). Three reasons likely exist. First, the six idealized structures do not describe all possible combinations of coherence, range turnover, and boundary clumping. Second, these idealized structures represent only portions of a multidimensional continuum of structural attributes that characterize empirical metacommunities. Third, spatial scale of analysis often is ignored; thereby, confounding attempts to identify environmental gradients that mold metacommunity structure or mechanisms that operate at particular spatial scales. From a different perspective, Lewinsohn et al. (2006) recognized each of these problems with current approaches to identify spatial structures along gradients, as well as the need for a "comprehensive procedure to address the full range of possible patterns."

We ameliorate this situation by introducing three conceptual refinements for analyses of metacommunity structure (sensu Leibold and Mikkelson 2002), thereby developing a comprehensive framework for the evaluation of structures along environmental gradients. Our goals are four-fold. First, we briefly describe the conceptual approach of Leibold and Mikkelson (2002). Second, we demonstrate how analysis of boundary clumping can distinguish among three distinct forms of species loss in nested subsets, a particularly common structure along richness gradients. Third, we describe six quasi-structures that are conceptually related to six of the idealized structures. Finally, we outline

a hierarchical approach for evaluating metacommunity structure at multiple spatial extents, an approach that is particularly useful for metacommunities with distinctive groups of species along portions of an environmental gradient (i.e. compartments).

Conceptual framework and idealized structures

A fundamental principle in ecology is that the abundances of species are Gaussian: modal in form with continuous distributions with respect to an underlying environmental gradient (Gauch and Whittaker 1972, Whittaker 1975, Austin 1985). More specifically, if a species can occur at values of x_1 and x_2 along some gradient, then it also should be able to occur at all values of the gradient between x_1 and x_2. Consequently, species should occupy a coherent range of sites along environmental gradients in metacommunities (i.e. no holes should exist in the n-dimensional hypervolume that defines the fundamental niches of species). For an entire metacommunity to exhibit coherence, the ranges of a majority of species must be molded in this fashion and in response to the same environmental gradient. Nonetheless, the nature of responses to the gradient may differ among species (i.e. the modes in abundance or extents of occurrence differ among species). If species, as a group, do not respond to the same environmental gradient, distributions will not form a coherent structure (Leibold and Mikkelson 2002). This does not necessarily mean that species occur at random. If species distributions are associated with different gradients, they would fail to exhibit coherence along a single common gradient. Because metacommunity analyses generally are restricted to a group of co-occurring species defined by taxon (assemblages), function (guilds), or both (ensembles; Fauth et al. 1996), and because of ecological similarities among members of such restricted groups, coherence likely is a pervasive attribute of well sampled metacommunities that span modest to large environmental gradients. Indeed, the vast majority of evaluated metacommunities exhibited coherence (Kusch et al. 2005, Zimmerman 2006, Bloch et al. 2007, Burns 2007, Werner et al. 2007, Barone et al. 2008, Presley et al. 2009, Presley and Willig 2010, Presley et al. unpubl.), including 24 of 35 metacommunities in Leibold and Mikkelson (2002). Most non-coherent metacommunities have had few species (< 10), few sites, or both; thereby, providing little statistical power to adequately evaluate coherence along a gradient via a randomization approach.

Prior to analysis of structure, a site-by-species incidence matrix is ordered according to the primary axis extracted via reciprocal averaging (i.e. simple correspondence analysis), arguably the best indirect ordination procedure (Gauch et al. 1977, Pielou 1984) to discern variation in response to latent environmental gradients (i.e. variation in unmeasured environmental characteristics). Reciprocal averaging maximizes the proximity of species with similar distributions as well as the proximity of sites with similar species compositions. In doing so, reciprocal averaging maximizes the coherence of species distributions and the coherence of community compositions. This reorganization of data matrices is analogous to species-packing algorithms that produce maximal nestedness in an empirical metacommunity prior to quantifying the number of deviations from perfect nestedness as a

measure of significance (Patterson and Atmar 1986). Because the order of sites and species in matrices affect the magnitude of metrics that represent deviations from an idealized state (e.g. perfect coherence), a standardized approach to order sites and species is necessary for a reliable statistical test via randomization procedures.

Many null model algorithms are available to generate null distributions for statistical evaluations of metrics that are based on incidence matrices (Gotelli 2000, Leibold and Mikkelson 2002). These models differ in susceptibility to errors of type I (rejecting the null hypothesis when it is true) and type II (failing to reject the null hypothesis when it is false) that arise from row and column constraints associated with randomization procedures. In the original methodology (Leibold and Mikkelson 2002), two null model options that represent ends of a spectrum from highly liberal (Random 0) to highly conservative (Random 4) were used for demonstration purposes. Random 0 assigns equiprobable occurrences throughout the matrix. Because null models such as this have little structure, they are highly prone to type I errors (Gotelli 2000). In contrast, Random 4 fixes row and column totals (i.e. species occurrences and site richnesses) to equal empirical values. Highly constrained null models such as this may incorporate the ecological mechanisms under examination, which can create an unrealistically small null space and an analysis with little statistical power, resulting in a high likelihood of type II errors (Gotelli and Graves 1996). The magnitude of these problems with fixed-fixed null models is contingent on matrix size, with power decreasing and type II error rates increasing with decreasing matrix size (Hausdorf and Hennig 2007, Ulrich and Gotelli 2007). These problems may arise because the null model does not allow sufficient randomization of matrix aspects associated with the structure under evaluation, resulting in exceedingly low statistical power and a high susceptibility to type II errors. This problem also can occur with the application of a fixed-fixed null model in analyses o coherence (Leibold and Mikkelson 2002). In addition to matrix size, matrix fill can affect the power of null model approaches (Ulrich and Gotelli 2007). Importantly, the total number of species occurrences in each of these null model approaches is constrained to equal the total number of occurrences in the empirical metacommunity (i.e. matrix fill is fixed).

An ecological concern when selecting a null model is that it only allows the factor of interest to occur at random, while constraining all other parameters. The range of a species is defined by the number and identity of sites at which the species occurs, and occurrences are determined by species-specific characteristics that combine to define the ranges of species. Consequently, these factors (number and location of species occurrences) should be allowed to occur at random in the null model when assessing the degree of range coherence in a metacommunity. In contrast, site characteristics (area, number of habitats, sampling intensity) and passive sampling affect the number of species (though not necessarily the identity of those species) that are recorded from each site. For these reasons, we suggest a null model that constrains species richness of each site to equal empirical richness, with equiprobable occurrences for each species. This null model has a more desirable combination of type I and type II error properties than does Random 0 or Random 4 (Gotelli and

Graves 1996, Gotelli 2000) and has been applied successfully to analyses of coherence (Presley et al. 2009, Presley and Willig 2010). Moreover, we view each type of error (I and II) to be of equal concern and do not recommend the use of highly conservative null models that are more likely to classify truly coherent metacommunities as random.

Coherence is measured by counting the number of embedded absences (i.e. interruptions in the distributions of species or in the compositions of sites) in a matrix that has been reordered via reciprocal averaging. In an ordinated matrix, absences that have a presence toward each extreme in a row or in a column are termed embedded absences. A metacommunity with perfect coherence has no embedded absences. The number of embedded absences is compared statistically to a null distribution created by randomizing elements of the observed data matrix, counting the number of embedded absences, and repeating the procedure for 1000 iterations. If the number of empirical embedded absences is not significantly different from that expected by chance, species do not respond to the same latent environmental gradient and the metacommunity is deemed to have random structure. Metacommunities with more embedded absences than expected by chance (negative coherence) have checkerboard distributions (Fig. 1), with strong interspecific competition that results in mutual exclusion as the implied structuring mechanism. Metacommunities with positive coherence have fewer embedded absences than expected by chance and include a number of structures that are distinguished via assessment of range turnover and boundary clumping. Importantly, the validity of conclusions concerning range turnover or boundary clumping is contingent on an accurate assessment of coherence. In a non-coherent metacommunity, for which a single gradient is not important to a preponderance of species, occurrences and absences are scattered along the latent environmental gradient such that metrics of species turnover and range boundary clumping do not effectively reflect the concepts that they represent in coherent metacommunities.

Species range turnover is measured as the number of times one species replaces another between two sites (i.e. number of replacements) for each possible pair of species and for each possible pair of sites. A replacement between two species (A and B) occurs when the range of A extends beyond that of B at one end of the gradient and the range of B extends beyond that of A at the other end of the gradient. Because replacements associated with embedded absences are not related to the primary axis of correspondence, they can be misleading in evaluations of turnover along that axis. Consequently, each species range is made perfectly coherent by 'filling in' any embedded absences prior to evaluation of turnover. The observed number of replacements in a metacommunity is compared to a distribution of randomly generated values based on a null model that randomly shifts entire ranges of species (Leibold and Mikkelson 2002). Significantly low (negative) turnover is consistent with nested distributions (Fig. 1, 2). Significantly high (positive) turnover is consistent with Gleasonian, Clementsian, or evenly spaced distributions, requiring analysis of boundary clumping to distinguish among them (Fig. 1, 2). Significance of boundary clumping is evaluated via a χ^2 goodness-of-fit test that compares the observed distribution to an expected (equiprobable)
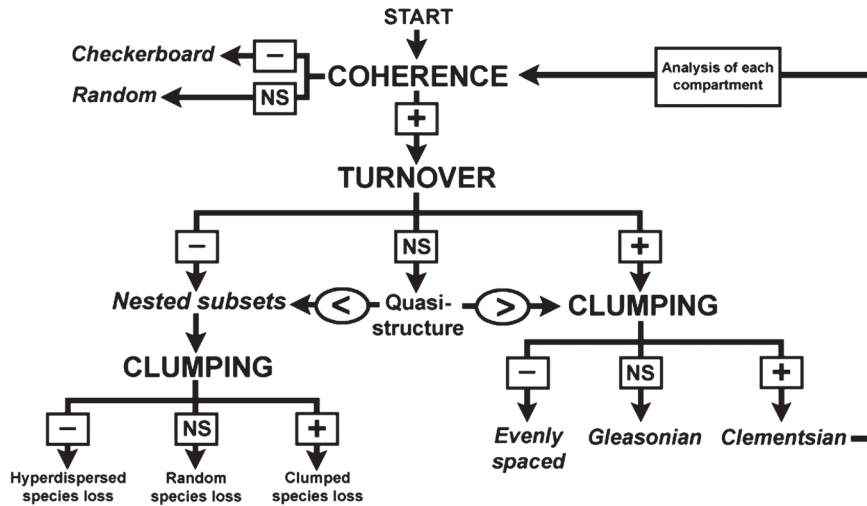
Figure 1. Diagrammatic representation of the hierarchical approach based on analysis of elements of metacommunity structure and combinations of results that are consistent of each of six idealized structures (Leibold and Mikkelson 2002), three patterns of species loss for nested subsets, six quasi-structures, and structures of compartments within Clementsian distributions. Boxes designate statistical results; ovals indicate direction of non-significant turnover.

distribution of range boundary locations (Hoagland and Collins 1997, Leibold and Mikkelson 2002). When the χ^2-test is significant, Morisita's (1971) index (I) is used to determine if results represent clumped (I > 1.0) boundaries, indicating Clementsian structure, or if results represent hyperdispersed (I < 1.0) boundaries, indicating evenly spaced distributions. Metacommunities with randomly distributed boundaries indicate individualistic responses of species that characterize Gleasonian structure.

In concert, analyses of coherence, turnover, and boundary clumping can identify more than the six structures outlined here and in Leibold and Mikkelson (2002). More specifically, at least 12 possible coherent structures exist (Fig. 2) based on these three elements of metacommunity

structure. Nonetheless, only four of these coherent structures have been described previously, with the remaining patterns not explored or not associated with particular structuring mechanisms. Better resolution and distinction of coherent structures defined by combinations of range turnover and boundary clumping will enhance pattern recognition and coupling of pattern with mechanism.

Patterns of species loss in nested metacommunities

Classically, nested subsets describe a pattern of metacommunity structure in which taxa found in species-poor sites are subsets of those found in species-rich sites. Because the focus of the Leibold and Mikkelson (2002) approach is on

Figure 2. Twelve coherent metacommunity structures defined by range turnover and boundary clumping. Quasi-structures are shaded; nested structures that are distinguished by patterns of species loss are stippled. Significant positive results, +; significant negative results, –; non-significant clumping, NS, non-significant turnover but with more replacements than the average number in randomly generated metacommunities, NS (>); non-significant turnover but with fewer replacements than the average number in randomly generated metacommunities, NS (<).

distributions of species and not species richness of communities, nested structures describe a pattern in which the ranges of species with restricted distributions along an environmental gradient are contained within the ranges of species that are more widely distributed along the gradient. Regardless of the conceptual approach, the manifest structure is the same. Nested structures are characterized by a predictable pattern of species loss among sites, with species absent from a particular site also absent from all sites with fewer species. During the last two decades, many studies have documented empirical patterns of nestedness. Despite the apparent ubiquity of nested subsets, the assignment of structuring mechanisms to particular examples of nestedness has been rare. Indeed, multiple mechanisms may give rise to nested subsets, and assigning mechanisms to particular patterns is difficult. However, the expected pattern of species loss along the gradient in a nested metacommunity may be distinct for each mechanism. Consequently, identification of distinctive forms of species loss should facilitate the identification of mechanisms associated with particular nested structures.

A nested metacommunity may exhibit hyperdispersed, stochastic, or clumped species loss among sites (Fig. 1–3), which can be distinguished via analysis of range boundary clumping. Each pattern of species loss in a nested metacommunity is analogous to evenly spaced, Gleasonian, or Clementsian structure, except that the dispersion of range boundaries is only at one end of the gradient. Nonetheless, to avoid confusion between metacommunity structures and patterns of species loss in nested structures, we refer to negative range boundary clumping in a nested structure as hyperdispersed species loss, non-significant range boundary clumping in a nested structure as stochastic species loss, and positive range boundary clumping in a nested structure as clumped species loss (Fig. 2).

To evaluate the efficacy of the analysis in detecting differences in range boundary dispersion in nested structures, we created all possible combinations of clumped boundaries in a perfectly nested metacommunity defined by 20 sites and 20 species, beginning with hyperdispersed boundaries (Fig. 3A) and progressively increasing the clumping of boundaries. Because range boundaries may be clumped in multiple groups, as well as in groups of different sizes, we began with a single group of the smallest possible size (i.e. two clumped boundaries) and incrementally increased the number of clumped boundaries in that one group until boundaries changed from significantly hyperdispersed, to random, to significantly clumped. Similarly, we incrementally increased the number and the sizes of groups of clumped boundaries until the progression of possible results was complete (i.e. from hyperdispersed, to random, to clumped) for each permutation of numbers and sizes of groups (Table 1). Additional details of analytical approaches appear elsewhere (Leibold and Mikkelson 2002, Presley et al. 2009, Presley and Willig 2010). Herein, analyses of coherence, turnover, and boundary clumping of exemplar metacommunities were conducted with algorithms written in Matlab 7.5.0.342 (script files available at <www.tarleton.edu/~higgins/EMS.htm>). All analyses were performed from the "range" perspective sensu Leibold and Mikkelson (2002).

Requirements for hyperdispersed species loss in nested structures (Fig. 3A) were relatively stringent. There are few ways (sometimes only one) to maximally disperse species boundaries in a metacommunity. In contrast, there are many ways that boundaries can occur at random or in clumps. This may explain why evenly spaced structures are documented less often than are Gleasonian or Clementsian structures, and also may indicate that hyperdispersed species loss in nested structures occur infrequently.

Metacommunities with only a modest number of clumped boundaries (from one group of four boundaries to five groups of two boundaries) were characterized by stochastic species loss (Table 1). For a metacommunity with nested structure to evince clumped species loss (Fig. 3C), a single group of six clumped boundaries (30% of species), five groups of three clumped boundaries (involving 75% of species), or some intermediate combination of numbers of groups and sizes of groups were required (Table 1). The exemplar metacommunities (Fig. 3, Table 1) were relatively small, allowing only a modest amount of variation in boundary location. Nonetheless, multiple instances were consistent with each form of species loss (Table 1), indicating that this
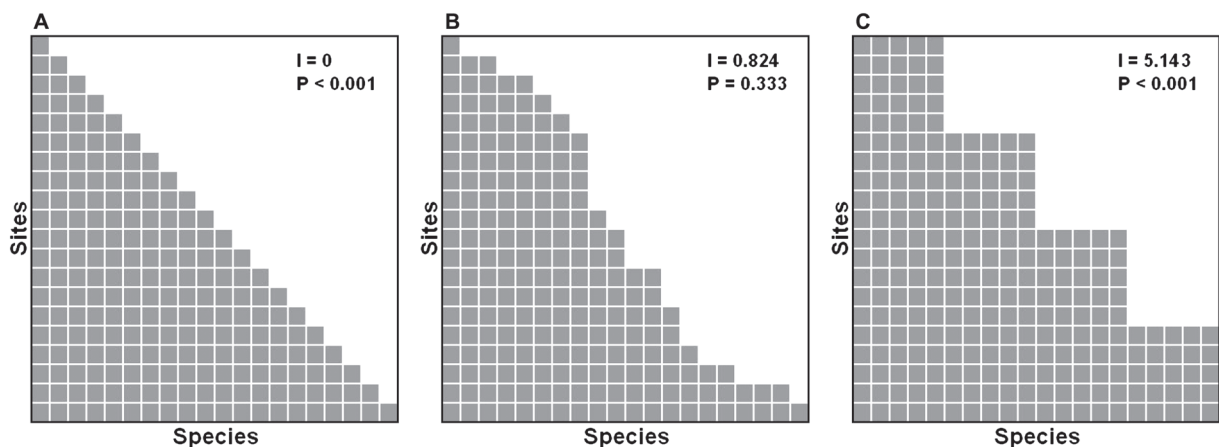

Figure 3. Three perfectly nested metacommunities that exhibit different patterns of species loss that can be distinguished via analysis of range boundary clumping. Shaded cells represent species presences. Species in metacommunity A exhibit hyperdispersed species loss (no clumping), species in metacommunity B exhibit stochastic species loss (one group of three and four groups of two clumped boundaries), and species in metacommunity C exhibit clumped species loss (five clumped boundaries in each of four groups). Morisita's index, I.

Table 1. Assessments of boundary clumping (Morisita's index, I, and associated p-values) for perfectly nested metacommunities comprising 20 species and 20 sites. Exemplars differ in the number of groups of clumped range boundaries and in the number of species boundaries clumped within each group. For each row of analyses, the number of boundaries in the first group increases from left to right. Significant (p ≤ 0.05) results with values of I < 1.0 indicate hyperdispersed species loss and are in italics. Significant results with values of I > 1.0 indicate clumped species loss and are in bold.

Total number of clumped groups	Number of clumped boundaries in other groups	Number of clumped boundaries in first group									
		2		3		4		5		6	
		I	p	I	p	I	p	I	p	I	p
One group											
	0	*0.12*	*<0.001*	*0.35*	*0.0068*	0.71	0.1999	1.18	0.2742	**1.76**	**0.026**
Two groups											
	2	*0.24*	*<0.001*	*0.47*	*0.0335*	0.82	0.3329	1.29	0.1847	**1.88**	**0.015**
	3	*0.47*	*0.0335*	0.71	0.1999	1.06	0.3888	1.53	0.0745	**2.12**	**0.005**
	4	0.82	0.3329	1.06	0.3888	1.41	0.1194	**1.88**	**0.015**	**2.47**	**<0.001**
	5	1.29	0.1847	1.53	0.0745	**1.88**	**0.015**	**2.35**	**0.0013**	**2.94**	**<0.001**
Three groups											
	2, 2	*0.35*	*0.0068*	0.59	0.0964	0.94	0.4762	1.41	0.1194	**1.89**	**0.013**
	2, 3	0.59	0.0964	0.82	0.3329	1.18	0.2742	**1.65**	**0.0449**	**2.24**	**0.003**
	2, 4	0.94	0.4762	1.18	0.2742	1.53	0.0745	**2.00**	**0.0084**	**2.59**	**<0.001**
	2, 5	1.41	0.1194	**1.65**	**0.0449**	**2.00**	**0.0084**	**2.47**	**<0.001**	**3.06**	**<0.001**
	3, 3	0.82	0.3329	1.06	0.3888	1.41	0.1194	**1.88**	**0.015**	**2.47**	**<0.001**
	3, 4	1.18	0.2742	1.41	0.1194	**1.76**	**0.0263**	**2.24**	**0.0025**	**2.82**	**<0.001**
Four groups											
	2, 2, 2	*0.47*	*0.0335*	0.71	0.1999	1.06	0.3888	1.53	0.0745	**2.12**	**0.005**
	2, 2, 3	0.71	0.1999	0.94	0.4762	1.29	0.1847	**1.76**	**0.026**	**2.35**	**0.001**
	2, 2, 4	1.06	0.3888	1.29	0.1847	**1.65**	**0.0449**	**2.12**	**0.0046**	**2.71**	**<0.001**
	2, 3, 3	0.94	0.4762	1.18	0.2742	1.53	0.0745	**2.00**	**0.0084**	**2.59**	**<0.001**
	2, 3, 4	1.29	0.185	1.53	0.075	**1.88**	**0.015**	**2.35**	**0.001**	**2.94**	**<0.001**
	3, 3, 3	1.18	0.274	1.41	0.119	**1.76**	**0.026**	**2.24**	**0.003**	**2.82**	**<0.001**
Five groups											
	2, 2 ,2, 2	0.59	0.096	0.82	0.333	1.18	0.274	1.56	0.062	**2.24**	**0.003**
	2, 2, 2, 3	0.82	0.333	1.06	0.389	1.41	0.119	**1.88**	**0.015**	**2.47**	**<0.001**
	2, 2, 2, 4	1.18	0.274	1.41	0.119	**1.76**	**0.026**	**2.24**	**0.003**	**2.82**	**<0.001**
	2, 2, 3, 3	1.06	0.389	1.29	0.185	**1.65**	**0.045**	**2.12**	**0.005**	**2.71**	**<0.001**
	2, 3, 3, 3	1.29	0.185	1.53	0.075	**1.88**	**0.015**	**2.35**	**0.001**	**2.94**	**<0.001**
	3, 3, 3, 3	1.53	0.075	**1.76**	**0.026**	**2.12**	**0.005**	**2.59**	**<0.001**	**3.18**	**<0.001**

test is capable of distinguishing among these three forms of species loss in nested or in quasi-nested structures.

In a metacommunity context, patterns of species loss for nested structures evaluate the form of species loss only along the latent environmental gradient, which may not be completely coincident with gradients of species richness, as in classical analyses of nestedness. As such, appropriate explanations for species loss must be restricted to environmental variation associated with the latent gradient (i.e. order of sites along primary axis of correspondence). Indeed, ascribing mechanisms to explain nested patterns along gradients of richness may be difficult if an obvious environmental gradient is not correlated with species richness. For nested subsets, reciprocal averaging discerns inter-site variation in response to a latent environmental gradient. This directly places analyses of nested structures in an environmental context, possibly enhancing the ability of researchers to associate mechanisms with nested structures.

To demonstrate how analysis of species loss can provide insight, we use a hypothetical fauna from an elevational gradient as a model. Environmental characteristics (e.g. temperature, precipitation, vegetational composition) to which species respond change with elevation in predictable fashions. Although elevational changes in abiotic characteristics and associated vegetation are predictable, they differ from each other in form. Abiotic characteristics generally change in a gradual fashion with elevation (Jacobson 2005), whereas vegetation associations have more-or-less discrete boundaries (ecotones) between habitat types (Whittaker 1956, 1960, 1965, Terborgh 1971, 1977). Along this hypothetical elevational gradient, all species occur at lower elevations where environmental conditions are less stressful and resources are multifarious, with species richness declining with increases in elevation, resulting in nested structure. If species-specific environmental tolerances determine species range boundaries, the metacommunity likely will evince stochastic species loss (Fig. 3B) or perhaps hyperdispersed species loss (Fig. 3A) if tradeoffs between competitive ability and environmental tolerance exist. If habitat specializations determine the locations of species range boundaries, the metacommunity likely will evince a clumped pattern of species loss, with range boundaries clumped and coincident with ecotones (Fig. 3C). In an empirical example similar to this hypothetical system, the bat metacommunity on an eastern slope of the Andes was nested with clumped species loss (Presley et al. unpubl.). In addition, range boundaries of bats were clumped at ecotones, revealing a distinct pattern of species loss associated with changes in habitat type along the elevational gradient.
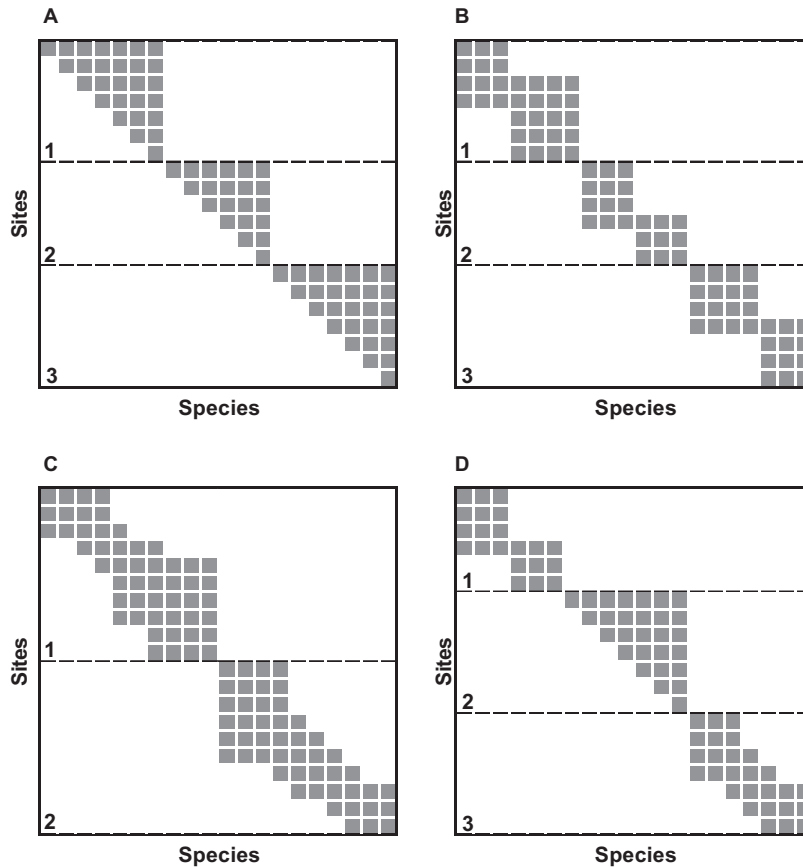
Figure 4. Four metacommunities (20 species and 20 sites) that evince Clementsian structure (perfect coherence, positive turnover, and clumped range boundaries; Table 2), but that exhibited different types of structure within compartments. Shaded cells represent species presences. Compartments within each metacommunity are delineated by dashed horizontal lines. Species in metacommunity A exhibit nested structure (negative turnover) with evenly spaced species loss in each compartment, species in metacommunity B exhibit Clementsian structure (positive turnover and clumped boundaries) in each compartment, species in metacommunity C exhibit Gleasonian structure (positive turnover and randomly distributed boundaries) in each compartment, and species in metacommunity D exhibit Clementsian (compartment 1), nested (compartment 2), or Gleasonian (compartment 3) structure (Table 2).

Without consideration of patterns of species loss, ecological understanding of Andean bat metacommunity structure would have been less complete.

Quasi-structures

Metacommunities with positive coherence and non-significant turnover have a non-random structure that has not been considered in the literature. Nonetheless, these structures are quite common. For example, 9 of the 24 coherent metacommunities in Leibold and Mikkelson (2002) evinced this pattern. Other studies have detected this pattern in a variety of taxa, including snails in a tropical rainforest (Presley unpubl.), moths in temperate forests (Kusch et al. 2005), birds in montane tropical habitats (Presley et al. unpubl.), bats in various biomes of Paraguay (Presley et al. 2009), and bats inhabiting islands of the Caribbean (Presley and Willig 2010).

We propose the recognition of six quasi-structures, each of which has a foundation that is consistent with the conceptual underpinning of Clementsian, evenly spaced, or Gleasonian distributions, or with those of each form of species loss for nested distributions. Each quasi-structure has the same basic

characteristics as its associated idealized structure, except that range turnover is indistinguishable from random (Fig. 2). Although some expectation of turnover is associated with non-random structures, significantly positive or negative turnover is not a fundamental characteristic of Gleasonian, evenly spaced, or nested distributions. For example, because distributions of restricted-range species are contained within those of wide-ranging species in nested structures, one would expect nested distributions to have negative turnover (i.e. fewer replacements than the average in randomly generated matrices); however, turnover need not result in statistical significance for a nested pattern to best describe a metacommunity. Similarly, some positive turnover is a fundamental character of Gleasonian or evenly spaced distributions, but statistically significant positive turnover is not required for such patterns to best describe a metacommunity. Nonetheless, the level of significance associated with turnover may indicate the strength of structuring mechanisms, with quasi-structures resulting from weaker structuring forces than those effecting structures in which turnover is significant.

A coherent metacommunity with turnover that is random, but with fewer replacements than the average number that occurs in randomly generated metacommunities

Table 2. Results of analyses of species turnover and boundary clumping (Morisita's index, I) for each of four illustrative metacommunities and associated extents (Fig. 4). Significant (p ≤ 0.05) results are bold.

Metacommunity	Compartment	Species turnover Replacements Observed	Mean	p	Boundary clumping I	p	Structure
A		2303	2007	**0.029**	2.21	**< 0.001**	Clementsian
	1	0	25	**0.015**	0.00	**< 0.001**	nested
	2	0	13	**0.033**	0.00	**< 0.001**	nested
	3	0	23	**0.017**	0.00	**< 0.001**	nested
B		2816	2544	**0.030**	1.74	**0.001**	Clementsian
	1	72	36	**0.006**	2.14	**0.028**	Clementsian
	2	54	27	**0.013**	4.00	**< 0.001**	Clementsian
	3	108	52	**0.003**	5.00	**< 0.001**	Clementsian
C		4110	3268	**0.012**	1.45	**0.026**	Clementsian
	1	420	208	**< 0.001**	1.58	0.064	Gleasonian
	2	390	222	**0.007**	1.33	0.139	Gleasonian
D		2404	2128	**0.020**	1.78	**< 0.001**	Clementsian
	1	54	27	**0.014**	4.00	**< 0.001**	Clementsian
	2	0	24	**0.020**	0.00	**< 0.001**	nested
	3	103	52	**0.008**	1.07	0.343	Gleasonian

(i.e. non-significant negative turnover), has species distributions that resemble nested subsets. Because the degree of nestedness in such metacommunities is not strong, but is more consistent with nested subsets than with other idealized structures, we term these structures quasi-nested. Similar to nested structure, quasi-nested structures may exhibit hyperdispersed, stochastic, or clumped species loss (Fig. 1–3). The remaining quasi-structures have random turnover with more replacements than the average number present in randomly generated matrices (i.e. non-significant positive turnover). Similar to the approach for distinguishing among idealized structures, each of the remaining quasi-structures is defined by the degree of range boundary clumping (Fig. 2).

A coherent metacommunity with non-significant positive turnover and random clumping of boundaries is consistent with the individualistic responses of Gleasonian structure. Individualistic responses of species with smaller niche breadths (relative to the extent of the gradient) likely result in greater positive turnover and Gleasonian structure, whereas species with larger niche breadths may result in non-significant positive turnover and quasi-Gleasonian structure. Turnover is not a defining characteristic of Gleason's concept of community organization; therefore, each of these structures represents a manifestation of the same phenomenon.

A coherent metacommunity with non-significant positive turnover and negative boundary clumping is consistent with the evenly spaced distributions generated by tradeoffs associated with strong interspecific competition. The amount of niche space in which each species is competitively dominant will determine the degree of turnover in the metacommunity. The amount of positive turnover in evenly spaced structures is determined by the proportion of the gradient in which each species is dominant. Consequently, species are dominant along larger proportions of the gradient in

evenly-spaced structures than are species in quasi-evenly spaced structures.

A coherent metacommunity with non-significant positive turnover and positive boundary clumping has quasi-Clementsian structure. Often, range boundaries for quasi-Clementsian structures are clumped at the termini of the latent environmental gradient, with the majority of species spanning a large portion of the gradient. In such cases, this quasi-structure indicates that a metacommunity is characterized by compositional unity along most of the gradient. Quasi-Clementsian structures may arise because of truncation in two circumstances. If variation in environmental characteristics along an empirical gradient is small compared to the niche breadths of species in the metacommunity, a quasi-Clementsian structure likely will arise with most species occupying most of the empirical gradient. Alternatively, if only a part of an empirical gradient is sampled, then any observed structure may be an artifact as environmental distributions of species may extend beyond the bounds of the truncated gradient. The investigator must determine the plausibility of each potential reason for distributions that appear to be truncated.

A hierarchical approach for Clementsian metacommunities

The crucial aspects of scale in the context of metacommunity analysis are that the focus (i.e. site) and extent (i.e. metacommunity) must be consistent with the conceptual issues that are explored in the analysis, and with spatial variation in environmental characteristics addressed via supplementary analyses. Moreover, the scale at which structuring mechanisms operate must be consistent with the scale used to observe patterns. Focal scale and extent are critical a priori considerations because metacommunities may evince

distinctive structures at multiple spatial extents, with different underlying mechanisms associated with each extent (Presley and Willig 2010).

Clementsian metacommunities are defined by coincidence of species boundaries, with their locations defining the limits along the environmental gradient for sites that have shared species compositions. Such groups of sites are termed compartments (Lewinsohn et al. 2006). Because compartments form self-similar groupings of sites and likely represent non-arbitrary units for analysis along environmental gradients, the structure of each compartment may be analyzed independently of each other and of the larger extent(s) within which it is embedded. Indeed, metacommunities may evince an overall structure that results from the agglomeration of distinctive structures associated with multiple compartments along the environmental gradient (Fig. 4). Visual inspection of the ordinated matrix and a vector of the number of range boundaries that occur at each site facilitate the determination of the limits of each compartment. More specifically, large numbers of range boundaries at sites indicate likely locations of turnover (e.g. ecotones) between compartments. Alternatively, natural biogeographic divisions may be used as a basis for identifying compartments. In some cases, identification of compartments may be difficult. Once identified, analyses of metacommunity structure (i.e. coherence, turnover, boundary clumping) within each compartment can provide additional information about ecological organization.

To demonstrate hierarchical structure of Clementsian metacommunities, we constructed four exemplars, each with Clementsian structure along the full gradient (Table 2, Fig. 4). For simplicity, each of the exemplars was created with perfect coherence (i.e. zero embedded absences), which does not affect analyses of range turnover or range boundary clumping. To make delineation of constituent compartments clear, no species occurred in more than one compartment within each metacommunity. Exemplars differed in the structure evinced by each compartment, including nested (Fig. 4A), Clementsian (Fig. 4B), Gleasonian (Fig. 4C), or a mix of structures (Fig. 4D, Table 2). A similar hierarchical approach has been proposed for Clementsian structures in which each compartment has nested structure (as in Fig. 4A) and was called compound structures (Lewinsohn et al. 2006); however, this concept can be extended to include any type of structure, not just those that are nested.

Hierarchical structures are not simply a theoretical construct. Presley and Willig (2010) analyzed metacommunity structure of Caribbean bats at multiple spatial extents that were defined by biogeographic characteristics. At the extent of the entire Caribbean Basin, bats exhibited Clementsian structure with distinctive species compositions associated with each of three biogeographic regions (Bahamas, Greater Antilles and Lesser Antilles). Moreover, each biogeographic region evinced a unique structure: the Bahaman metacommunity exhibited quasi-Gleasonian structure, the Greater Antillean metacommunity exhibited nested structure (with clumped species loss), and the Lesser Antillean metacommunity exhibited Clementsian structure (not unlike Fig. 4D). Distinct mechanisms were associated with structure at each extent. More specifically, proximity and number of mainland sources of colonization were invoked to explain Clementsian structure for the entire Caribbean Basin, whereas species-specific environmental tolerances, habitat specializations, and physical attributes of islands were identified as likely structuring mechanisms for compartments (for details see Presley and Willig 2010). Similarly, Lewinsohn et al. (2006) evaluated the structure of insect–plant interactions in southeastern Brazil and found Clementsian structure (compartmentation) in which each compartment exhibited a nested pattern of species interactions. In each case, the hierarchical and scale-dependent approach revealed aspects of structure that would not have been evident otherwise.

Concluding statements

Development of conceptual frameworks and analytical tools to evaluate metacommunity structure is ongoing. A multidimensional continuum of structure exists in which idealized structures based on distinct conceptual foundations represent only a fraction of possible structures. Nested patterns are easily identified, but may represent multiple structures (each with unique conceptual underpinnings) that masquerade as one. Identification of patterns of species loss in nested structures facilitates the association of mechanism with pattern. The introduction of quasi-structures increases the volume of the structural continuum that is associated with particular concepts. Finally, the ability to detect and interpret emergent properties of species distributions, such as metacommunity structure, depends on recognition of appropriate scales of analysis. Because multiple mechanisms may operate at different spatial scales to determine compositions of local communities, analysis of metacommunity structure at multiple scales or extents may be required to comprehensively understand the dynamics of metacommunity composition. In addition to analysis of metacommunity structure, this conceptual framework may be applied to other types of systems such as plant-animal interaction assemblages (Lewinsohn et al. 2006) or networks of community-level interspecific interactions (Burns 2007).

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