

# Chapter 15

## Gradients and the Structure of Neotropical Metacommunities: Effects of Disturbance, Elevation, Landscape Structure, and Biogeography



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### 15.1 Introduction

The metacommunity concept explicitly recognizes that the composition of local communities, as well as spatial variation in composition among communities, are influenced by local (e.g., biotic interactions, environmental tolerances, habitat preferences) and regional (e.g., dispersal, habitat fragmentation, landscape structure) processes (Leibold et al. 2004). In contrast, research that focuses on local communities typically ignores aspects of spatial variation, making it difficult to detect mechanisms that mold patterns of local coexistence and that operate at larger spatial scales (Ricklefs 2008). Consequently, examining species distributions along salient environmental gradients represents a complementary approach to the perspective that focuses on arbitrarily circumscribed “local communities” (Ricklefs 2006). This focus on the distributions of species, rather than the coexistence of species, has formed the basis for an evolving framework to evaluate community and metacommunity structure. Moreover, understanding the contributions of regional factors to local community assembly (i.e., how species from a regional species pool are filtered at local spatial scales) has changed perceptions of the community concept to expand it beyond the simple definition of a localized group of interacting species to one in which environmental or spatial distributions of species have become a greater focus for understanding patterns of co-occurrence and local biodiversity (Ricklefs 2008).

Even though the term “metacommunity” had not been coined at the time, early metacommunity work was conducted in the Neotropics to understand patterns of biodiversity (Terborgh 1977) and distribution (Terborgh 1971; Terborgh 1985) of birds along extensive elevational gradients in the Andes. High biodiversity, a

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complex biogeographical history, and a heterogeneous topography associated with orogenic events combine to make the Neotropics an ideal test bed for theories related to ecological gradients and the assembly of communities. In this chapter, we define and use the term “metacommunity structure” to mean an emergent pattern defined by relationships among the distributions of species along a latent environmental gradient (*sensu* Leibold and Mikkelsen 2002; Presley et al. 2010).

Our goals are fourfold: (1) to introduce the conceptual underpinnings of metacommunity ecology, especially as they relate to latent environmental gradients; (2) to outline the methods used to detect metacommunity structures (*sensu* Leibold and Mikkelsen 2002) as well as complementary approaches for identifying the processes that give rise to them; (3) to provide a selective summary of research along gradients in the Neotropics, with a focus on those related to disturbance, elevation, landscape structure and fragmentation, and biogeographical history; and (4) to make recommendations for advancing ecological understanding derived from research on Neotropical metacommunities.

## 15.2 Metacommunity Ecology

A metacommunity perspective provides ecological insight into spatiotemporal dynamics, because it explicitly considers the structure and organization of communities along environmental gradients, and seeks to understand the local and regional processes that generate these larger-scale patterns (Leibold and Chase 2018). More specifically, a metacommunity is a network of communities that are potentially connected to each other via dispersal of individuals among constituent communities (Leibold and Mikkelsen 2002). Local emigration and immigration, when coupled with other spatially explicit ecological processes such as species sorting, habitat filtering, priority effects, or interspecific competition, imbue the network with an emergent structure that corresponds to underlying environmental gradients (Leibold et al. 2004; Leibold 2011).

Since its inception, the domain, theories, and hypotheses associated with metacommunity ecology have received increasing attention, amplification, and refinement (Leibold and Chase 2018). In general, two complementary approaches exist for studying metacommunities: one focuses on processes and the other focuses on patterns. The framework of the process-based approach is built on four archetypal mechanistic models (*i.e.*, neutral theory, patch dynamics, species sorting, mass effects). These models differ in their assumptions about the role of particular processes (*e.g.*, competition, dispersal) and sources of variation (*e.g.*, habitat heterogeneity, species-specific capacity) to make predictions about community composition (Leibold and Chase 2018). The pattern-based approach focuses on patterns of species distributions (*e.g.*, nestedness, Clementsian, Gleasonian) along environmental gradients (Leibold and Mikkelsen 2002; Presley et al. 2010). It is predicated on the idea that it is generally useful to identify emergent patterns before hypothesizing the relative importance of mechanisms that give rise to those patterns.

The four archetypical models forming the basis for a mechanistic framework evaluate the contributions of patch heterogeneity (i.e., local processes) and community connectivity (i.e., regional processes) to variation in the composition of communities (Leibold 2011). Species sorting models assume that species are highly responsive to among-site variation in environmental characteristics, and that dispersal is insufficient to support persistence in habitats with negative population growth (Tilman 1982; Chase and Leibold 2003), resulting in species composition being determined exclusively by local environmental factors. Mass effects models also assume that species respond to environmental variation among sites, but that dispersal allows species to persist in less suitable habitats via source-sink dynamics (Holt 1993), resulting in species composition being determined by a combination of local environmental characteristics and their spatial structure. The neutral model (Hubbell 2001) makes predictions about community composition based on the premise that all species are “ecologically equivalent” and do not differ greatly in rates important to metacommunity dynamics (e.g., dispersal, competitive ability, birth rates, death rates). Consequently, species should not exhibit strong associations with local environmental factors and spatial variation among sites should be determined only by spatial processes. Like the neutral model, patch dynamics recognizes the importance of spatial processes in determining the composition of local communities, but patch dynamics incorporates tradeoffs between dispersal and competitive abilities, resulting in temporally dynamic species composition in local communities (Yu et al. 2001). In general, processes and mechanisms associated with multiple archetypical models combine to determine the composition of local communities and variation in composition among local communities (Leibold and Chase 2018).

Metacommunity structure is an emergent property that reflects ecological processes operating at different spatiotemporal scales to mold species distributions along a geographical or environmental gradient (Leibold and Mikkelsen 2002; Presley et al. 2010). Throughout the history of ecology, several conceptual models of spatial structure have been identified that describe patterns of species distribution along spatial or environmental gradients. Clements (1916) described an idealized metacommunity structure based on shared evolutionary history and inter-dependent ecological relationships, resulting in coincident range boundaries for groups of species along different portions of an environmental gradient. Each set of communities that harbor a distinct group of species represents a compartment (Lewinsohn et al. 2006), with compartments replacing one another along an environmental gradient. In contrast, Gleason (1926) described a structure arising from species-specific responses to the environment, with local coexistence being a byproduct of similarities in ecological requirements or abiotic tolerances and with species range boundaries occurring idiosyncratically along an environmental gradient. In situations where interspecific competition exists, trade-offs in competitive ability may result in distributions that are more evenly spaced along environmental gradients than are expected by chance (Tilman 1982). Finally, species-poor communities may form nested subsets of increasingly species-rich communities (Patterson and Atmar 1986), with predictable patterns of species gain associated with variation in species-specific characteristics (e.g., dispersal ability, habitat specialization, abiotic

tolerance). These idealized structures form the framework representing a continuum of possible structures, from those with high species turnover (e.g., as described by Clements or Gleason) to those with low species turnover (e.g., nested subsets), and from those structures characterized by coincident range boundaries (i.e., as described by Clements) to those characterized by hyperdispersed range boundaries (i.e., as described by Tilman).

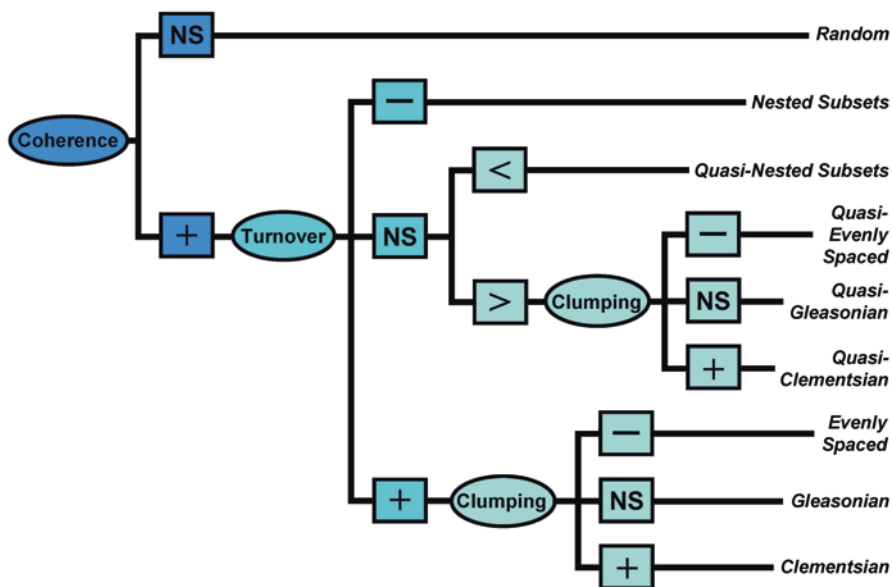
As metacommunity ecology endeavors to evaluate how local and regional processes combine to structure local communities and generate variation among them, analytical approaches that use communities as replicates to understand variation in characteristics of communities (e.g., species presences, species abundances, biodiversity) in response to environmental variation (e.g., temperature, precipitation, seasonality, vegetative structure, soil nutrient concentration) or spatial structure (e.g., Moran's eigen vector maps, pairwise distances between sites, elevation) are useful for exploring metacommunity dynamics. These include methods such as canonical correspondence analysis (CCA) (Ter Braak 1986; Ter Braak and Prentice 1988), variation partitioning (Cottenie 2005; Peres-Neto et al. 2006; Peres-Neto et al. 2012), hierarchical partitioning of biodiversity (Jost 2007), and elements of metacommunity structure (Leibold and Mikkelsen 2002; Presley et al. 2010, Presley et al. 2019b; Presley 2020). We focus on elements of metacommunity structure (EMS) as a means of exploring how a single approach can elucidate different patterns and structuring mechanisms associated with various gradients and can do so at multiple spatiotemporal scales. Nonetheless, EMS represents a point of departure for understanding spatial structure. Supporting (e.g., canonical correspondence analysis, hierarchical partitioning of biodiversity, general linear models) and complementary (e.g., variation partitioning) analyses are required to determine the nature of environmental gradients along which the metacommunity is structured, the number and locations of compartments, or the relative influence of potential structuring mechanisms. Therefore, we first outline the EMS approach, and then highlight approaches that are commonly used to understand metacommunity structures in empirical examples selected from the Neotropics.

### 15.3 Elements of Metacommunity Structure

The common conceptual aspect to all nonrandom metacommunity structures is that the ranges of species in these metacommunities are molded by a common environmental gradient, with sites reflecting environmental variation along this gradient. Similarly, a fundamental principle in ecology is that species occurrences along an environmental gradient represent underlying continuous distributions. More specifically, species should occupy sites that represent a coherent range of the underlying environmental gradient (i.e., a species that occurs at temperatures of 10 and 20 °C should also occur at all temperatures between those values). For an entire metacommunity to exhibit coherence, the distributions of a preponderance of species must be associated with the same environmental gradient (Presley et al. 2010). However, the

extent and location of species distributions along the gradient may differ (i.e., although responding to the same gradient, responses to the gradient are not the same), such that coherent metacommunities may evince many different discernible structures. In contrast, if the distributions of a preponderance of species do not respond to the same environmental gradient, coherence is not achieved, and structure is considered to be random (Leibold and Mikkelsen 2002).

The Elements of Metacommunity Structure comprise three attributes of species distributions (i.e., coherence, species range turnover, and range boundary clumping) that combine to discriminate among many nonrandom metacommunity structures (Fig. 15.1: Leibold and Mikkelsen 2002; Presley et al. 2010). EMS is based on an indirect gradient analysis (Ter Braak and Prentice 1988) that uses reciprocal averaging (also called correspondence analysis) to determine the gradient along which sites and species are organized. These gradients are generally called “latent” environmental gradients, because they are not directly measured or explicitly incorporated in the ordination, but are defined by the responses of species to environmental



**Fig. 15.1** A diagrammatic representation (after Presley et al. 2010) of combinations of the three elements of metacommunity structure (ovals) that differentiate among five idealized metacommunity structures and four quasistuctures. Possible results for tests for each element appear in squares: a positive sign (+) indicates results consistent with greater coherence, range turnover, or range boundary clumping than expected by chance, a negative sign (–) indicates results that are consistent with less range turnover or range boundary clumping than expected by chance, and NS indicates results that are indistinguishable from chance expectations. Quasistuctures arise when the range turnover is less than (<) or greater than (>) the mean from the simulations, but not significantly so. (Note: there is no ecological or conceptual basis to expect metacommunities to exhibit less coherence than expected by chance; therefore, this analysis is conducted as a one-tailed test (Presley et al. 2019b))

variation. These latent gradients represent variation in biotic and abiotic environmental factors that are important for defining the distributions of species. Typically, subsequent analyses (e.g., canonical correspondence analysis, variation partitioning, or general linear models) are used to determine the relationship of the latent gradient to variation in important environmental factors that determine the distributions of species (e.g., Presley and Willig 2010; Presley et al. 2009; Presley et al. 2011; Presley et al. 2012; López-González et al. 2012; Dallas and Presley 2014; de la Sancha et al. 2014; Cisneros et al. 2015; Willig et al. 2011; Willig et al. 2021). Importantly, coherence, range turnover, and range boundary clumping are evaluated with respect to particular latent gradients (Presley et al. 2009; Presley et al. 2019b) and are based on incidence (presence versus absence) rather than abundance. This aspect of analysis explicitly recognizes that multiple gradients can structure the same metacommunity and that a different structure can manifest along different gradients (e.g., Presley et al. 2009; López-González et al. 2012). The explicit identification of a gradient along which species are distributed distinguishes the EMS approach from other popular and superficially similar approaches, such as co-occurrence analyses (Stone and Roberts 1990; Presley 2020), which ignore any potential underlying gradient.

Reciprocal averaging is an ordination method that simultaneously optimizes the proximity of species that have similar distributions and the proximity of communities that have similar species compositions (Gauch et al. 1977). Effectively, this ordination allows the entire suite of species distributions (i.e., occurrences at sites in the metacommunity) to define the response gradient (Presley et al. 2009) and is considered to be the best indirect ordination procedure for this purpose. If a preponderance of species in a metacommunity does not respond to the same environmental gradient, the metacommunity is noncoherent and has random structure (Fig. 15.1). Importantly, random structure does not indicate that species occur in communities at random, only that they occur at random with respect to each other (i.e., that their distributions are not defined by the same environmental gradient). In contrast, coherent structures are characterized by species distributions that are molded by a common environmental gradient, with the locations and extents of the distributions of species along the gradient, and the relationships among these distributions defining the structure of the metacommunity (Fig. 15.1). Nested structures are defined by negative range turnover (i.e., less turnover than expected by chance) along the environmental gradient. In these structures, the distributions of species with narrow environmental tolerances or habitat preferences are contained within those of species with wider environmental tolerances or habitat preferences. In contrast, Clementsian, Gleasonian, and evenly spaced structures are defined by positive range turnover (i.e., more range turnover than expected by chance) along the gradient. Quasi-structures have range turnover that is indistinguishable from that expected by chance, but have structures that are otherwise consistent with the conceptual underpinning of Clementsian, evenly spaced, Gleasonian, or nested distributions (Presley et al. 2010). Range boundary clumping is used to distinguish among three types of nestedness as well as among structures with positive range turnover (Leibold and Mikkelsen 2002; Presley et al. 2010). In the case of significantly nested

metacommunities, clumped range boundaries suggest that species are lost (or added) in groups along a gradient (i.e., not randomly with respect to each other). For metacommunities with significant range turnover, positive range boundary clumping corresponds to the existence of compartments (Clementsian structure), negative range boundary clumping corresponds to evenly spaced structures, and range boundary clumping that does not differ from chance is consistent with Gleasonian structure (idiosyncratic range boundary locations along the gradient).

This framework originally contained the concept of a “checkerboard metacommunity structure” associated with the idea of negative coherence (i.e., a metacommunity that is less coherent than expected by chance). Checkerboards originally described geographically interspersed patterns of mutual exclusion by pairs of ecologically similar species (MacArthur et al. 1972; Diamond 1975). Subsequently, this concept was expanded to entire metacommunities by adding the criterion that distributions of each mutually exclusive pair should be independent from other such pairs (Leibold and Mikkelsen 2002). Critically, this definition is nearly identical to that of random metacommunity structure (i.e., noncoherence). The only difference between random and checkerboard metacommunity structures is that each species has one mutually exclusive association in a checkerboard, with all other interspecific associations being random. The dominant mechanism for both of these structures is randomness, and the developed methodology cannot effectively distinguish between random and checkerboard structures (Presley et al. 2019b). Consequently, the idea that checkerboard structures can be detected via analyses of coherence should be abandoned, and analyses of coherence should be implemented as one-tailed tests (Schmera et al. 2018; Presley 2020).

## 15.4 Useful Methods for Understanding Metacommunity Structure and Structuring Mechanisms

Although EMS can identify particular emergent structures based on the distributions of species, complementary or supplementary analyses are required to (1) identify the gradient that structures the metacommunity, (2) determine the number and location of compartments in compartmentalized structures, and (3) evaluate the relative importance of structuring mechanisms. The underlying gradient along which a metacommunity is structured can be identified via relatively simple approaches such as linear or rank correlation analyses, or by more comprehensive approaches such as canonical correspondence analysis (Ter Braak 1986; Ter Braak and Prentice 1988) or generalized linear mixed-effects models (Bates et al. 2015). The number of compartments, as well as the species or sites that comprise each compartment, can be identified via hierarchical partitioning of biodiversity (Jost 2007) and cluster analysis (Legendre and Legendre 2012), respectively. Finally, variation partitioning can discern the relative contributions of local environmental factors and spatial processes to variation among communities in their composition (Cottenie 2005; Peres-Neto et al. 2006; Peres-Neto et al. 2012).

### 15.4.1 *Canonical Correspondence Analysis*

Canonical correspondence analysis (CCA) is a multivariate technique (Ter Braak 1986) and an extension of correspondence analysis (reciprocal averaging) that uses environmental variation among sites to understand variation in community composition. CCA uses linear combinations of the environmental variables to identify ordination axes, such that variation in community composition is directly related to environmental variation. Consequently, the meaning of ordination axes is easy to uncover. Importantly, CCA is an efficient ordination technique when species have bell-shaped response curves to environmental gradients (e.g., Gaussian distributions), making it more appropriate for analyzing data on community composition and environmental variables than is canonical correlation analysis (Ter Braak 1986). The significance of relationships between species composition and environmental factors is determined via Monte Carlo simulations (Ter Braak and Prentice 1988). Because CCA is a marriage of reciprocal averaging and multiple regression, the axes are defined by the same ordination as used in analyses for EMS, resulting in a powerful method for determining associations of environmental factors with meta-community structure (López-González et al. 2012).

### 15.4.2 *Hierarchical Partitioning of Biodiversity*

Understanding the spatial organization of biodiversity is necessary for determining the scales at which mechanisms operate to generate variation in the composition of communities and the abundances of species. More specifically,  $\beta$ -diversity has emerged as an important concept because of its relationships with multifunctionality of ecosystems and the manners in which the hierarchical configuration of biodiversity varies with respect to environmental or geographical gradients (Wilsey et al. 2005; Higgins 2010; Mori et al. 2018; Willig and Presley 2019). Patterns of biodiversity are often scale dependent, highlighting the role of spatial compartmentalization in heterogeneous landscapes (e.g., Scheiner et al. 2000; Jackson and Fahrig 2014). In general, biodiversity may be partitioned into three spatial components: alpha ( $\alpha$ ), beta ( $\beta$ ), and gamma ( $\gamma$ ) partitions.  $\alpha$  estimates mean biodiversity of local sites,  $\beta$  estimates the degree of compositional differentiation among sites, and  $\gamma$  represents the biodiversity for a region regardless of its constituent spatial units. Biodiversity at larger spatial scales ( $\gamma$  components) can be driven by local biodiversity ( $\alpha$  components), if little compositional variation characterizes communities (Gering and Crist 2002), or can be driven by among-site variation ( $\beta$  components), which signals the importance of spatial heterogeneity at landscape or regional scales (Belmaker et al. 2008; Willig and Presley 2019). The contributions of  $\alpha$ - or  $\beta$ -partitions to  $\gamma$ -partitions are largely dependent on the nature of environmental variation within a domain of interest (Freestone and Inouye 2006) and the ways in which different species respond to spatial variation in the environment.



Biodiversity can be partitioned using an additive ( $\gamma = \alpha + \beta$ ) or a multiplicative model ( $\gamma = \alpha \times \beta$ ). Only  $\beta$  differs between these models;  $\alpha$  and  $\gamma$  are the same (Jost 2007). In the additive model,  $\beta$  represents the average number of species in the metacommunity that do not occur at a site ( $\beta = \gamma - \alpha$ ), whereas in the multiplicative model,  $\beta$  represents the number of distinct communities or compartments in the metacommunity ( $\beta = \gamma/\alpha$ ). An advantage of the additive model is that all partitions represent effective numbers of species. This facilitates comparisons of the proportion of regional diversity ( $\gamma$ ) that is a consequence of the diversity of local communities ( $\alpha$ ) versus a consequence of variation among local communities ( $\beta$ ). However, within the context of metacommunity structure, multiplicative  $\beta$  estimates the effective number of distinct communities (i.e., compartments in Clementsian structures) that exist along an environmental gradient, with particular metacommunity structures indicating the form of transition (pattern of species turnover) between compartments (de la Sancha et al. 2014). In addition, cluster analysis can be used to identify which groups of sites or species represent compartments (multiplicative  $\beta$  estimates only the number of compartments, not the number or identity of the sites that compose them).

### 15.4.3 Variation Partitioning

Variation partitioning (also called variance decomposition) can be used to determine the relative importance of sets of environmental factors as well as spatial characteristics in structuring communities (Borcard et al. 1992; Cottenie 2005; Legendre 2007; Legendre et al. 2012). Variation partitioning can be used to evaluate variation among populations (e.g., species abundance) or among communities (e.g., relative abundances of each species in a metacommunity). In addition, partitions can represent single explanatory variables (e.g., temperature, canopy height) or entire suites of variables (e.g., abiotic factors, soil characteristics, percent cover of vegetation types). Variation partitioning identifies unique variation explained by each set of explanatory variables, as well as shared variation explained by combinations of sets of explanatory variables. This method provides considerable flexibility depending on data structure, facilitating the partitioning of explained variation based on two, three, four, or more sets of explanatory variables.

The classical use of variation partitioning to understand relative contributions of mechanisms that structure metacommunities involves use of a set of environmental factors and a set of spatial factors to calculate four components of variation: (1) total variation in species composition accounted for by both environmental and spatial variables, (2) proportion of variation in species composition accounted for by the environmental variables after accounting for effects of spatial variables (unique environment partition), (3) proportion of variation in species composition accounted for by spatial variables after accounting for effects of environmental variables (unique spatial structure), and (4) proportion of variation in species composition

shared by both environmental and spatial variables (i.e., spatial structure in environmental variation). These partitions can be used to evaluate the relative contributions of mechanisms associated with each of four dispersal-mediated mechanistic models (i.e., neutral theory, patch dynamics, species sorting, mass effects) thought to contribute to the structure of metacommunities (Stevens et al. 2007; López-González et al. 2015; Cisneros et al. 2016; Leibold and Chase 2018).

## 15.5 Empirical Gradients

We summarize metacommunity structures as determined by EMS and the mechanisms or processes that structure these metacommunities along a variety of empirical gradients that commonly occur in Neotropical settings, including gradients associated with elevation, landscape structure, and historical biogeography, and do so for gradients representing a broad range of spatial extents (from less than 1 km to more than 2000 km). In addition, we explore the utility of a wide range of complementary methods (e.g., partitioning of biodiversity, variation partitioning, canonical correspondence analysis, cluster analysis, simple correlations or regressions) used to understand how spatial environmental variation structures these Neotropical metacommunities. We do not endeavor to present a comprehensive review of all Neotropical metacommunity research. Rather, we provide an overview of the current understanding of metacommunity structure in the Neotropics associated with a variety of ecological gradients, taxonomic groups, structuring mechanisms, and spatial scales.

### 15.5.1 Elevation

Environmental gradients in montane settings are useful for evaluating processes that mold spatial patterns of species composition (e.g., Terborgh 1971; Terborgh 1985; Presley et al. 2011; Presley et al. 2012; Willig et al. 2011; López-González et al. 2012; Willig and Presley 2016). Along elevational gradients, dramatic variation in environmental characteristics (e.g., solar insolation, temperature, humidity, precipitation, habitat type) occurs over short geographical extents, such that ecological mechanisms, rather than biogeographical or historical mechanisms, mold biological responses. This contrasts greatly with latitudinal gradients, for which considerably greater geographical distances are necessary to produce comparable variation in environmental drivers, making it difficult to disentangle effects associated with ecological mechanisms from those associated with biogeographical processes (Willig and Presley 2013; Willig and Presley 2018). Elevational gradients in biodiversity and species composition continue to be of interest, because effects of climate change are expected to manifest soonest and most strongly at high elevations, especially in tropical environs (Colwell et al. 2008; Malhi et al. 2010). This may be particularly

true to the extent that tropical species have evolved in environments with less intra-annual variability in climatic conditions, leading to narrower niche breadths compared to their extratropical counterparts (Janzen 1967).

Changes in abiotic characteristics (e.g., temperature, precipitation) and floral associations (physiognomy and species composition) are predictable along elevational gradients; however, these changes differ in form. Abiotic characteristics change gradually, but not necessarily linearly, with elevation (Barry 2008), whereas variation in vegetation often exhibits more-or-less discrete boundaries recognized as habitat types or life zones (Martin et al. 2007; Barone et al. 2008). Because habitat specialization and responses to abiotic characteristics are important in defining faunal ranges, the structure of metacommunities along elevational gradients is contingent on which of these mechanisms predominantly determines the distributions of species. If habitat boundaries along an elevational gradient are more-or-less discrete, and many species in a metacommunity have distributions determined by habitat preferences or specializations, multiple species with range boundaries that are coincident with ecotones should result in the clumped range boundaries characteristic of Clementsian structure. Alternatively, if species distributions are primarily determined by responses to abiotic characteristics that change gradually with elevation, species-specific responses to abiotic variation should result in randomly associated range boundaries that are characteristic of Gleasonian structure. Finally, elevational variation in temperature combined with resource abundance and diversity may create physiological constraints associated with energy budgets (Speakman and Thomas 2003), resulting in nested elevational distributions. More specifically, species that are highly constrained by environmental conditions will have distributions that are nested within those of species that can maintain populations along larger portions of the gradient (Presley et al. 2012).

In addition to responses to elevational variation in abiotic factors, resource abundance, and habitat types, interspecific interactions (e.g., competition, predation) may affect metacommunity structure along elevational gradients. These effects are an aspect of processes associated with species sorting, as other species represent part of the environment to which particular species respond (Leibold and Chase 2018). Species sorting requires taxa to perform (i.e., survive and reproduce) differently under different conditions. Within the context of elevational gradients, different habitat types represent the environmental setting and can contribute to the outcome of interspecific interactions such as competition (e.g., species A excludes species B from montane rainforest, but species B excludes species A from cloud forest). Such mutual exclusion may be actively maintained via competitive interactions or may represent habitat associations due to the legacy of historical competition (i.e., the “ghost of competition past”; Connell 1980).

Metacommunity structure along Neotropical elevational gradients has been evaluated for gastropods in northeastern Puerto Rico (Presley et al. 2011; Willig et al. 2011; Willig et al. 2021), for bats, rodents, and passerines in the Peruvian Andes (Presley et al. 2012), and for amphibians, bats, and nonvolant small mammals in Mexico (Ochoa-Ochoa and Whittaker 2014; López-González and Lozano 2015). These metacommunities exhibited a number of structures, including nested

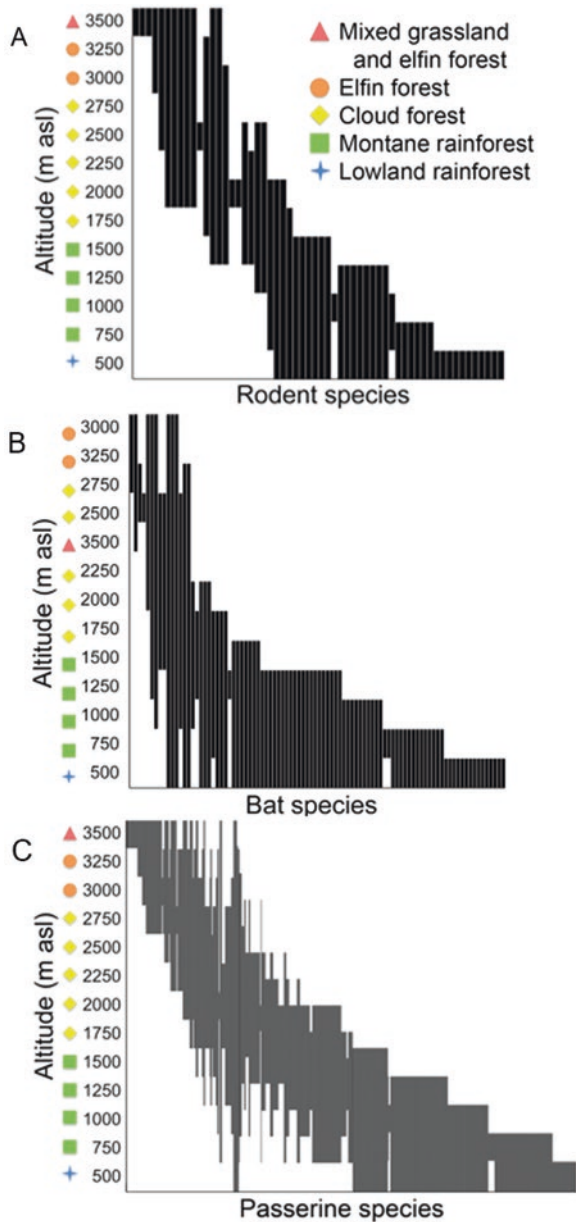
(Peruvian bats), Clementsian (Peruvian rodents, Mexican amphibians, Mexican bats, and Puerto Rican gastropods), quasi-Clementsian (Puerto Rican Gastropods and Peruvian passerines), Gleasonian (Puerto Rican gastropods, Mexican amphibians, and bats of the Mexican Sierra Madre Occidental), and quasi-Gleasonian (Puerto Rican gastropods, Mexican amphibians, and small mammals of the Mexican Sierra Madre Occidental) patterns. Despite this variety of structure, transitions between habitat types (i.e., ecotones) along elevational gradients were important for defining the elevational ranges and elevational range boundaries of species in many metacommunities. In general, Neotropical metacommunities have shown distinctive lowland and upland faunal compartments, with the transition between rainforest and cloud forest often defining the boundary between compositionally distinct communities (Terborgh 1985; Patterson et al. 1998; Willig et al. 2011; Presley et al. 2012).

In Puerto Rico, gastropods were evaluated along paired elevational transects designed to decouple underlying environmental mechanisms (Willig et al. 2011): a palm forest transect was restricted to forest dominated by sierra palm, which occurs along the length of the gradient, whereas a mixed forest transect included montane rainforest, cloud forest, and elfin forest (Willig et al. 2011; Willig et al. 2013). The palm forest metacommunity was quasi-Gleasonian, with structure determined by species-specific responses to elevational variation in abiotic factors (Willig et al. 2011). However, when elevational variation in forest type was superimposed on the gradient of abiotic variation in the mixed-forest transect, gastropods exhibited a Clementsian structure with compartmentalization associated with changes in forest type (Barone et al. 2008; Willig et al. 2013). In the absence of elevational variation in forest type (i.e., along the palm forest transect), gastropod species exhibited broader elevational distributions than in the mixed forest transect. This arose in part because of relaxed energetic constraints, as palm forest sites have greater primary production and concentrations of essential nutrients compared to sites from mixed forest transects at the same elevation (Willig et al. 2011). Importantly, these differences in structure between transects were maintained through time, with sampling a decade later indicating quasi-Clementsian and Gleasonian structure for the mixed forest and palm forest transects, respectively. For gastropods, abiotic variation gave rise to positive turnover along the gradient and variation in forest types contributed to the location of range boundaries, indicating that both biotic and abiotic components of elevational variation structure these metacommunities.

Metacommunity structure was evaluated for trees along the same mixed-forest transect that was used for gastropods (Barone et al. 2008). Trees along this transect exhibited Clementsian structure, with boundary clumping suggesting the locations of three compartments distinguished by ecotones between montane rainforest and cloud forest, as well as between cloud forest and elfin forest. This combination of results for trees and gastropods suggests that the metacommunity structure of plants may play a critical role in affecting metacommunity structure of animals.

Although the same ecotone (e.g., the transition between montane rainforest and cloud forest) can be a catalyst for compositional change in faunas along elevational gradients, the ways in which metacommunities are structured by such ecotones can

**Fig. 15.2** Distributional profiles of each species (black vertical bars) as ordered via reciprocal averaging for (a) rodents, (b) bats, and (c) passerines along an elevational gradient in Peru. Placement of sites (identified by elevation) along the primary axis of correspondence exactly maintained elevational order after reciprocal averaging for rodents and birds, and closely approximated it for bats. (Modified from Presley et al. 2012)



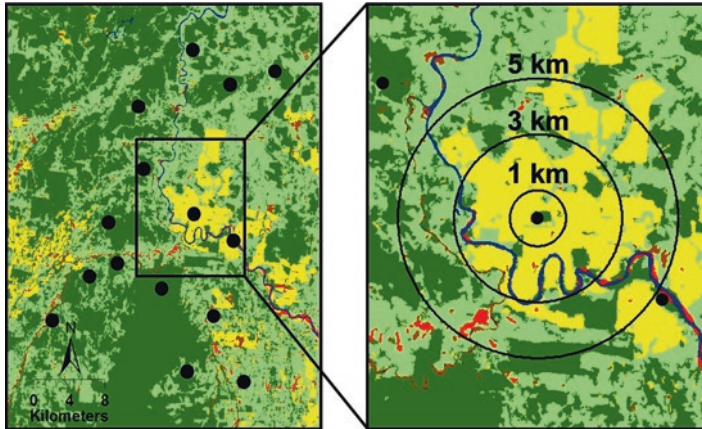
be taxon-specific (Fig. 15.2). The rainforest-cloud forest ecotone in Manu (Peruvian Andes) is an important boundary for compositional change of rodents, bats, and passerines, but different metacommunity structures arose due to autecological differences among faunas (Presley et al. 2012). Rodents have low vagility compared to their volant counterparts (birds and bats), resulting in greater habitat specialization.

Rodents in Manu were specialists of lowland rainforest, montane rainforest, cloud forest, or elfin forest. Even rodents that are habitat generalists only spanned portions of the gradient, generally occupying habitats that were exclusively above or exclusively below the cloud condensation point. Indeed, the cloud condensation point represents a critical biotic feature of the elevational gradient that contributes to the Clementsian structure of the rodent metacommunity (Fig. 15.2a). Bats in the Peruvian Andes generally do not specialize on particular forest types: nearly all bats occur in the lowland rainforest, with species loss occurring with increasing elevation, resulting in a nested structure (Fig. 15.2b). Even so, range boundaries of bats are clumped in the nested structure, with the most dramatic loss of bat species occurring at the ecotone between montane rainforest and cloud forest. The nested structure of bats is a function of direct (colder temperatures) and indirect (reduced resource diversity and abundance) effects of elevational variation in climate (Speakman and Thomas 2003; von Helversen and Winter 2003). Passerines in the Peruvian Andes formed two compartments (Terborgh 1985; Patterson et al. 1998; Presley et al. 2012): one below the cloud condensation point (lowland and montane rainforests) and one above the cloud condensation point (cloud and elfin forests; Fig. 15.2c). However, the transition zone between low- and high-elevation compartments for passerines was relatively broad and indistinct compared to that of rodents (Fig. 15.2). This broad transition zone for birds may arise from the relaxation of environmental constraints during particular seasons, allowing birds to move up or down the gradient for short time periods to track seasonal changes in resources.

### 15.5.2 *Landscape Structure*

The Anthropocene is characterized by pervasive and increasingly dominant effects of human activities on the world's biomes (Monastersky 2015). One of the defining human activities of the Anthropocene is habitat conversion for agricultural, urban, or suburban land uses. Habitat loss and fragmentation have resulted in a considerable loss of biodiversity (Newbold et al. 2015) and altered species distributions (Brown et al. 2016). Consequently, understanding how changing landscapes affect populations, communities, and metacommunities is a grand challenge of the twenty-first Century (National Research Council 2001).

Landscape ecology examines the influence of spatial heterogeneity on ecological systems, and explicitly addresses the importance of landscape composition (i.e., the relative proportions of different land cover types within a focal area) and configuration (the spatial arrangement of land cover types within a focal area) in determining ecological patterns and processes (Presley et al. 2019a). Humans have reshaped over 77% of the terrestrial biosphere (Ellis et al. 2010), resulting in natural (e.g., primary or mature forest) and seminatural (e.g., secondary forest) lands that are embedded within a mosaic of land converted for human use (Fig. 15.3). In general, three anthropogenic landscape-level processes affect the abundance and distribution of species: (1) loss of native vegetation, (2) fragmentation (i.e., formation of



**Fig. 15.3** An example of sites distributed in a heterogeneous landscape that are subject to various forms of land use (left), and an example of multiple focal scales for evaluation of effects of landscape structure on populations, communities, or metacommunities in a focal patch (right). Black dots represent sampling locations, dark green is forest, light green is pasture, yellow is agriculture, blue is water, and red is human settlements

isolated patches of habitat), and (3) matrix quality (i.e., utility of anthropogenically modified habitats to species). Landscape composition reflects the proportion of natural and anthropogenically modified land cover types, whereas landscape configuration measures their spatial arrangement and fragmentation, as well as the connectivity between habitat patches (Fahrig 2003; Tscharntke et al. 2012). Because species perceive their environment at different spatiotemporal scales, landscape dynamics are inherently scale sensitive (Gorresen et al. 2005; Lyra-Jorge et al. 2010). Consequently, a multiscale approach is necessary to ensure that the scale of response to landscape structure is included in experimental designs (Fig. 15.3).

Few studies have evaluated effects of landscape structure on the metacommunity structure of Neotropical biotas. In human-modified landscapes, the a priori assumption is that metacommunities will be nested, with more sensitivity to disturbance forming a gradient in which heavily modified landscapes harbor communities that are perfect subsets of communities from less disturbed landscapes (Meyer and Kalko 2008; Struebig et al. 2008). However, Neotropical metacommunities in disturbed landscapes generally do not exhibit nested subsets. This is true for bats in Costa Rica (Cisneros et al. 2015) or the Amazon (Martins 2016), as well as for small mammals (de la Sancha et al. 2014; Delciellos et al. 2018) or amphibians (Schiesari and Corrêa 2016) in Atlantic Forest. In contrast, nested structure did manifest for bats in Atlantic Forest (Teixeira 2019; Gomes 2020). In Caribbean Lowland Forests of Costa Rica, phyllostomid bats exhibited Gleasonian structure during the dry season and Clementsian structure during the wet season (Cisneros et al. 2015). Distance between forest patches and forest edge density were the most important factors in structuring Costa Rican bat metacommunities during the dry and wet seasons, respectively. Rather than nested distributions along a landscape-modification

gradient, some species (mostly gleaning animalivores of the subfamily Phyllostominae) occurred primarily in less modified, highly forested landscapes, whereas other species (mostly frugivores and nectarivores of the glossophagine and stenodermatine subfamilies) occurred primarily in highly modified landscapes dominated by agricultural land covers (Cisneros et al. 2015).

Small mammals in the highly fragmented Atlantic Forest exhibited Clementsian structure (de la Sancha et al. 2014). Despite the loss of ~90% of the original extent of Atlantic Forest to human activities (Ribeiro et al. 2009), small mammal meta-community structure reflected the presence of multiple centers of endemism (Costa and Leite 2012). These areas of endemism correspond to locations of historical refugia and vicariance events associated with large rivers. The maintenance of historical patterns is particularly noteworthy, because many small mammal species of Atlantic Forest effectively disperse through matrix habitats to other forest fragments and can maintain populations in nonforest habitats as well (Umetsu and Pardini 2007; Umetsu et al. 2008). In a smaller-scale study of small mammals within a single center of endemism in Atlantic Forest, Clementsian structure also manifested, driven primarily by small mammal responses to patch size and to variation in vertical forest structure (Delciellos et al. 2018). In combination, these studies demonstrate that the same metacommunity structure may occur at multiple spatial scales, but with different mechanisms driving structure at each scale.

In a large-scale study of Atlantic Forest, phyllostomid bats exhibited a quasi-Clementsian structure that was associated with spatially structured environmental variation, as well as the habitat loss from human activities (Gomes 2020). However, structure was foraging guild specific: analyses of only herbivores and of only carnivores exhibited Clementsian and nested structures, respectively. Nonetheless, spatially structured environmental variation was the driving force behind each of these structures (nested and Clementsian), showing that the same process can give rise to different metacommunity structures in the same system. In a small-scale study of the effects of fragmentation on metacommunity structure of bats in Atlantic Forest, nested (phyllostomid bats) and quasi-nested (animalivorous bats) structures manifested (Teixeira 2019). For both groups of bats, species found in smaller fragments represented a subset of species occurring in larger fragments or in continuous forest, and metacommunity structure reflected a combination of disturbance tolerance and inter-fragment dispersal ability of species (Teixeira 2019).

Bats in a fragmented landscape in southern Amazonia exhibited noncoherence, failing to respond to a shared environmental gradient, whereas herbivorous bats (frugivores and nectarivores) exhibited quasi-Clementsian structure (Martins 2016). Interestingly, this fragmented landscape was just south of intact, continuous Amazonian forest, with that forest likely harboring source populations for most of the 44 species of bat captured in forest fragments. Consequently, herbivorous species generally formed three groups based on their responses to open habitats and forest fragment sizes: (1) species that preferred large fragments and landscapes near the intact continuous forest (e.g., *Chiroderma trinitatum*, *Vampyressa pusilla*, *Platyrrhinus brachycephalus*); (2) species that preferred small forest fragments with an abundance of forest edges and secondary forest (e.g., *Artibeus concolor*,

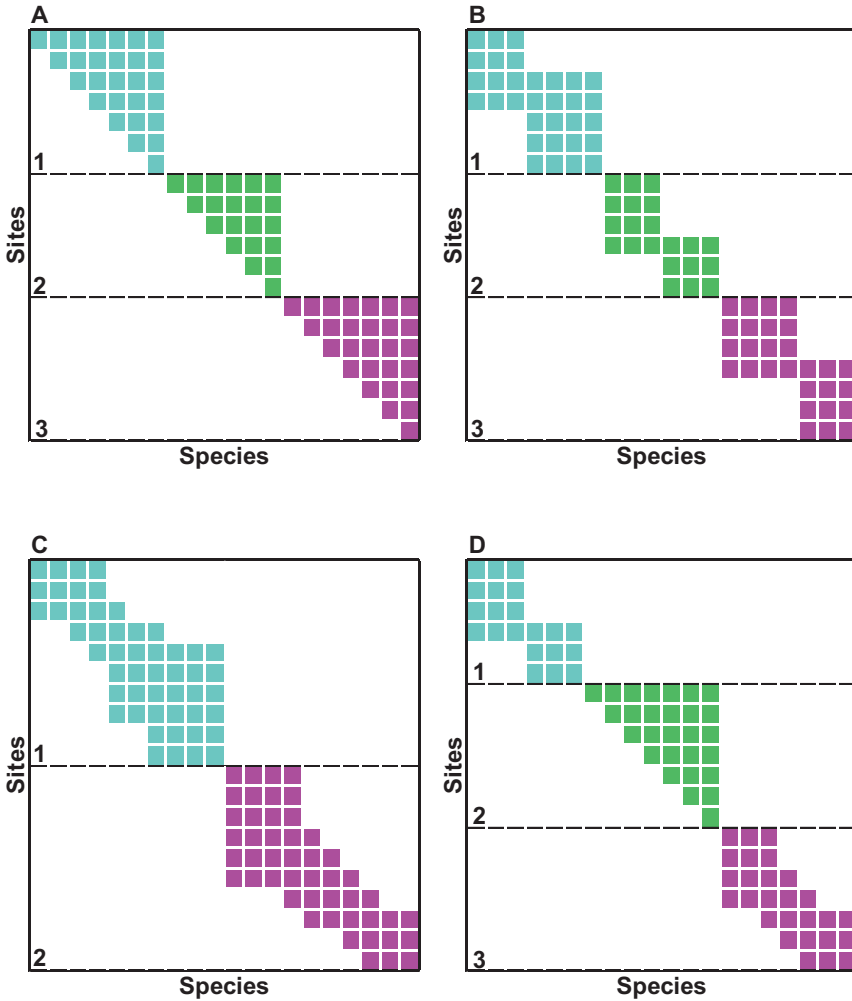


*A. anderseni*, *A. glauca*, *Lichonycteris obscura*, *Platyrrhinus lineatus*), which produce an abundance of fruit and flowers on which these bats feed, and (3) species that were ubiquitous (e.g., *A. lituratus*, *A. planirostris*, *Carollia perspicillata*, *Rhinophylla pumilio*), using all forest fragments regardless of size or location (Martins 2016). However, forest fragments do not only differ in size, they also differ in plant species composition and in physical structure, and this variation in forest physiognomy has differential effects on bat populations (Martins et al. 2017). Gleaning animalivorous phyllostomines are particularly sensitive to vertical forest structure, as they require an open stratum between the understory and canopy to forage effectively (Meyer et al. 2008). These multidimensional and complex responses of bats to this fragmented landscape likely account for the lack of coherence when the entire fauna was considered as a group. This demonstrates that even random metacommunity structure may arise from ecological responses and that autecological knowledge is paramount for understanding the species- or guild-specific responses within a single fauna.

### 15.5.3 Biogeographical Variation

Metacommunity structure can be evaluated at multiple spatial scales as well as in a hierarchical fashion (Presley et al. 2010). The crucial aspects of scale in a metacommunity context are that the definitions of a site (i.e., community) and the extent of the environmental domain are consistent with the theoretical questions addressed in the analysis, as well as with the explanatory factors and mechanisms invoked to account for empirical patterns. For example, to evaluate effect of landscape structure on metacommunity structure of forest fragments (Cisneros et al. 2015; Schiesari and Corrêa 2016; Delciellos et al. 2018), communities are restricted to forest fragments, explanatory variables are characteristics of fragments and the surrounding landscape, and the spatial extent of the metacommunity is confined to one habitat type to ensure that only variation in landscape structure, and not variation in habitat type, affects the composition of communities. In contrast, to evaluate biogeographical attributes on metacommunity structure in an island system (Presley and Willig 2010), communities are defined by islands, explanatory variables are island characteristics, and the spatial extent is a group of islands that represent variation in important biogeographical factors (e.g., area, habitat heterogeneity, distance to source populations). Moreover, focal scale and extent are critical a priori considerations, because metacommunities may evince distinctive structures corresponding to different spatial extents, with different underlying mechanisms associated with each extent (Presley and Willig 2010; López-González et al. 2012; Brasil et al. 2017; Alves-Martins et al. 2019).

Clementsian metacommunity structures that occur at large spatial scales may represent an agglomeration of structures that occur at smaller spatial scales, with distinctive structures associated with each compartment (Fig. 15.4). Because Clementsian metacommunities are defined by compartments (i.e., groups of species



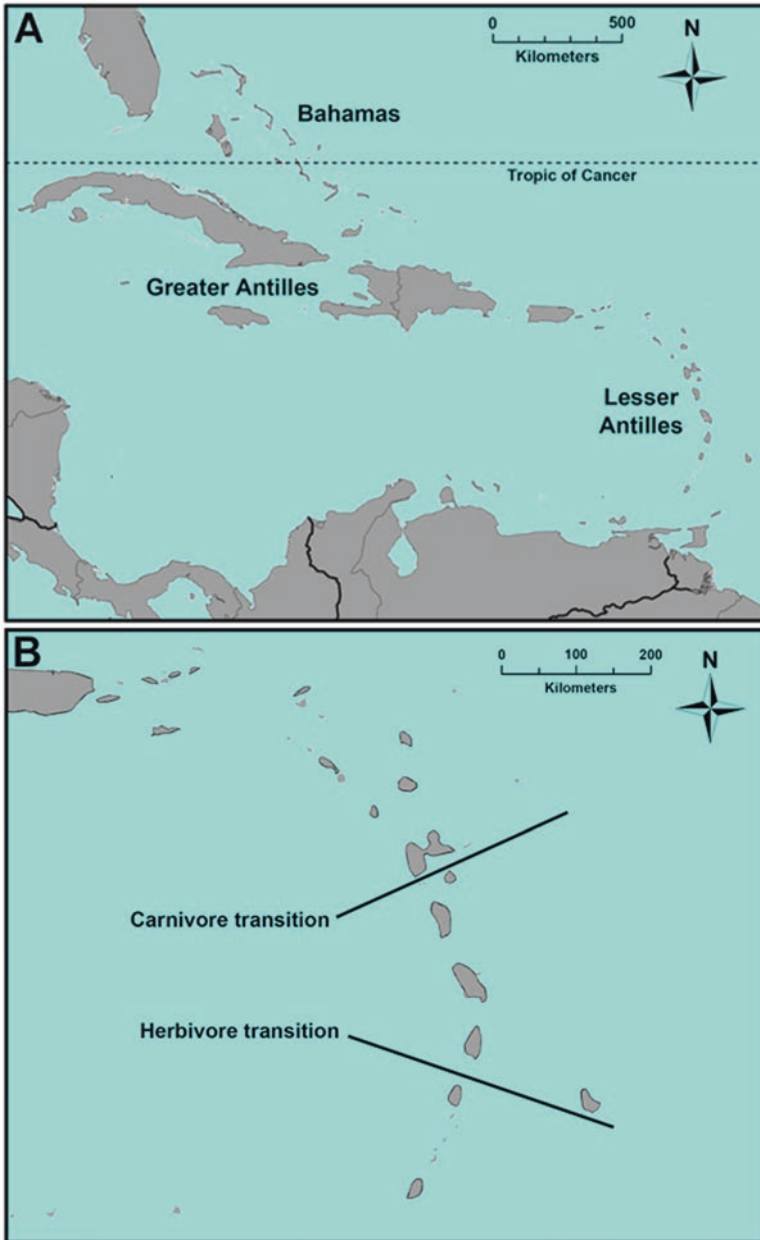
**Fig. 15.4** Four exemplar metacommunities comprising 20 species and 20 sites that evince Clementsian structure (perfect coherence, positive turnover, and clumped range boundaries), but that exhibited different types of structure within compartments. Compartments within each metacommunity are delineated 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. Species in metacommunity (d) exhibit Clementsian (compartment 1), nested (compartment 2), or Gleasonian (compartment 3) structure. (Modified from Presley et al. 2010)

with similar distributions, which typically results in groups of sites with similar species composition; Lewinsohn et al. 2006), identification of compartments provides the basis for multiscale analysis of metacommunity structure. Natural biogeographical divisions are often an ideal basis for identifying compartments, because they generally have distinct species pools (Presley and Willig 2010; López-González et al. 2012; de la Sancha et al. 2014; Brasil et al. 2017; Alves-Martins et al. 2019; González-Trujillo et al. 2020). When easily identifiable biogeographical divisions are not available, cluster analysis (Legendre and Legendre 2012) can be used to identify compartments for analysis at smaller spatial scales. The structure of each compartment in a Clementsian metacommunity, particularly for analyses done at large spatial scales, may be analyzed independently to uncover additional gradients or structures at smaller spatial scales that are embedded within the larger structure.

Caribbean bats exhibited strong Clementsian structure with compartments corresponding to three island groups (the Bahamas, Greater Antilles, and Lesser Antilles; Fig. 15.5a). Each compartment had distinctive bat species composition, and this was true for all bat species, for only herbivorous species, and for only carnivorous species (Presley and Willig 2010). The continental sources of colonization were unique for each island group, contributing to their distinctive assemblages (Koopman 1989). For analyses restricted to only one island group, the structure and number of compartments was related to the number of primary sources of colonization and the geographical relationships of those sources of colonization to islands (Fig. 15.5a), all of which represent biogeographic mechanisms.

The Lesser Antillean bat fauna had two primary sources of colonization (Greater Antilles and northern South America), resulting in Clementsian structure with two compartments for analyses based on only carnivorous bats or on only herbivorous bats. However, the relative influence of each source of colonization was guild specific. Carnivore compartments spanned the northern half of the Lesser Antilles, south to Guadeloupe (bats of Greater Antillean origin), and islands south of Guadeloupe (bats of South American origin), whereas, the transition between herbivore compartments was considerably further south, with the southern compartment restricted to Grenada, St. Vincent, and the Grenadines (Fig. 15.5b). The unique geographical patterns associated with each guild created three distinct bat communities when considering all Lesser Antillean bat species: (1) Grenada, St. Vincent, and the Grenadines, (2) northern islands south to and including Guadeloupe, and (3) islands between and including Marie Galante and St. Lucia (Fig. 15.5b). Because bats are highly vagile, it is likely that most species capable of dispersal from continental sources to newly formed and inhabitable islands colonized those areas during the same geological timeframe. As a result, distinct communities of bats from opposite ends of an archipelago would systematically colonize islands until they met. In this transition area, priority effects (Paine 1977) may allow species to prevent further dispersal of ecologically similar species.

Greater Antillean bats had nested structure, with most (26 of 38) bat species from this island group having evolved on the large islands such as Cuba, Hispaniola, or Jamaica (Baker and Genoways 1978). The ranges of Greater Antillean bats formed nested subsets, with a core group of widespread species that is augmented by



**Fig. 15.5** Maps of (a) the Caribbean Islands, indicating the locations of the Bahamas, Greater Antilles, and Lesser Antilles in relation to continental America, and (b) the Lesser Antilles indicating the different locations of transitions between northern and southern compartments associated with carnivorous and herbivorous bats in their respective Clementsian structures. (Modified from Presley and Willig 2008)

restricted-range species that occur only on the large islands on which they originated as well as on some nearby small islands. The geographical configuration of the Greater Antilles may predispose the creation of nested subsets via speciation and the subsequent dispersal of those species. The greater area represented by larger islands can support more individuals and more habitat types, increasing the number of species that can maintain sustainable populations (Rosenzweig 1995). These factors increase the likelihood that larger islands served as sites of species origination more often than did smaller islands. Finally, larger islands in the Greater Antilles were closer to continental sources of colonization (Florida, Yucatán Peninsula) than were smaller islands. Consequently, populations on larger, western islands replaced continental populations as the primary sources of colonization for smaller, eastern islands of the Greater Antilles. Differential dispersal of species, specialization on locally abundant resources, and size-mediated hierarchical habitat distributions on islands are mechanisms that likely enhanced nestedness for the Greater Antillean bat metacommunity (Presley and Willig 2008).

Mexican bats exhibited Clementsian structure with two compartments associated with a distinct boundary at the tropical-temperate transition zone (López-González et al. 2012). This metacommunity was structured by spatial variation in vegetation and climate, with dry, seasonal, and temperate habitats at one end of the gradient (temperate compartment), and with wet, aseasonal, and tropical habitats at the other end (tropical compartment). This Nearctic-Neotropical dichotomy characterizes much of the Mexican biota (Ortega and Arita 1998). Separate analyses of metacommunity structure for each compartment revealed structures along a heterogeneity gradient associated with topography traversing relatively flat homogeneous regions to topographically heterogeneous regions. Nonetheless, each compartment exhibited distinct structure. The temperate compartment evinced a nested structure, with communities in elevationally heterogeneous sites being species rich, and communities in flat regions being species poor. Widely distributed species were largely temperate in origin and able to persist in deserts, tropical lowlands, and xeric highlands, whereas restricted range species were of tropical origin and occurred only in tropical lowland habitats. In contrast, the tropical compartment exhibited Clementsian structure with a lowland rainforest compartment inhabited by species of tropical origin, and a distinct compartment comprising montane and lowland habitats, including montane rainforests, dry semideciduous forests, wetlands, and tropical scrubland. The second compartment harbored tropical species that occur in a wide range of habitats, as well as species of temperate origin that are euryecious and inhabit tropical highlands.

Amazonian metacommunities comprising damselflies (Zygoptera) or dragonflies (Anisoptera) exhibited Clementsian or quasi-Clementsian structures at large spatial scales that spanned multiple biogeographical regions (Brasil et al. 2017; Alves-Martins et al. 2019). In general, compartments represented areas of endemism: two compartments representing two biogeographical regions (Brasil et al. 2017) or four compartments representing four biogeographical regions (Alves-Martins et al. 2019). Random structures manifested when metacommunities

associated with each compartment (defined by areas of endemism) were analyzed separately, indicating that the distributions of species within biogeographical regions were not structured by a common gradient (Brasil et al. 2017; Alves-Martins et al. 2019). These legacies of biogeographical history persist despite the pervasive impact of human activities as reflected in the water quality of streams, including centuries-long effects associated with a densely populated farming community that has inhabited one region since pre-Colombian times. Streams in each region were classified as negligibly or heavily impacted by human activities (Brasil et al. 2017). The negligibly impacted metacommunity produced the same two-compartment Clementsian structure that was detected when all communities were considered together; however, the heavily impacted metacommunity exhibited a quasi-nested structure, despite including streams from two areas of endemism. This indicates a change in metacommunity structure due to human activities that has erased historical patterns of species distribution. The communities from the region that has hosted farming communities for centuries are nested within those of the region that have only recently been impacted by agricultural activities, presenting evidence of the long-term effects of human activities on the composition and distribution of species.

Between the Amazon and Atlantic Forest are drier habitats (e.g., Cerrado and Caatinga) that isolate these two large wet forests from each other. However, the hilltops in Caatinga and Cerrado often receive greater rainfall and support wet forests, called “brejos de altitude,” which act as high-elevation forest refugia surrounded by open and drier habitats. Metacommunity structure of rodents was studied at small and large spatial scales in this dry zone (Braga 2016). At the smaller scale, rodents in the Brazilian State of Pernambuco exhibited nested structure with clumped species loss. All species occurred in brejos, with a subset of those species occurring in surrounding Caatinga. The species that occurred only in brejos represented remnant populations of species of Atlantic Forest origin. In contrast, at the larger spatial scale, the rodent metacommunity spanning the Brazilian States of Ceará, Pernambuco, and Alagoas exhibited quasi-nested structure with clumped species loss. Again, brejos harbored greater species richness with surrounding drier and open habitats supporting only a subset of the species found on hilltops (Braga 2016). However, the structure in this case revealed three compartments: (1) one at end of the gradient comprising species of Amazonian origin that are restricted to northwestern brejos (in Ceará) as well as species found in the surrounding Caatinga, (2) one at the other end of the gradient comprising species of Atlantic Forest origin that are restricted to southeastern brejos (in Pernambuco and Alagoas) as well as species found in the surrounding Caatinga, and (3) one in the middle of the gradient comprising only species found in lowland xeric habitats of the Caatinga (Braga 2016). This analysis supports the idea that both the Amazon and Atlantic Forests were more expansive in the past, and that brejos represent refugia that support remnant hilltop populations of Amazonian and Atlantic Forest species amidst a xeric habitat that acts as a barrier to dispersal between the two mesic forest types. This observation corresponds to the hypothesis of Mares et al. (1985) for small mammals

of the Caatinga, which posits that species persist by inhabiting climatic interstices, those microhabitats that retain moisture for much of the year.

### ***15.5.4 Other Environmental Gradients***

Metacommunities may be structured along environmental gradients that are not associated with topography, anthropogenically induced changes to landscapes, or historical biogeography. For example, gradients may be associated with heterogeneity in edaphic features, patterns of seasonality, or gradients of disturbance. Moreover, these types of gradients may be spatially structured (Bloch and Klingbeil 2016) or may represent ecological gradients that are spatially interspersed (i.e., not spatially structured) or spatiotemporally dynamic throughout the landscape (Willig et al. 2021). Importantly, multiple gradients may independently or interactively structure metacommunities in complex manners (Presley et al. 2009).

Paraguayan bats exhibited different metacommunity structures along each of two environmental gradients (Presley et al. 2009). Paraguay exhibits strong east-west precipitation and temperature gradients that combine with edaphic heterogeneity to create complex patterns of habitat distribution that range from sand dunes and thorn-scrub forests in the northwest, to seasonally flooded palm savannahs and marshlands near the Paraguay, Paraná, and Pilcomayo Rivers, to tall humid evergreen forests in the east (Hayes 1995). This temperature-precipitation gradient supported two compartments, with insectivorous bats, particularly molossids, dominating communities in dry and flooded habitats, and frugivorous bats dominating communities in evergreen forests (Presley et al. 2009). In contrast, a gradient of edaphic features supported three compartments: one associated with the well-drained western habitats, one associated with seasonally flooded habitats, and one associated with eastern evergreen forests. Although insectivores and frugivores dominated the well-drained and evergreen forest compartments, respectively, the compartment associated with seasonally flooded habitats harbored distinctive communities comprising combinations of insectivores, frugivores, piscivores, and sanguivores. Such complexity is unsurprising, as Paraguay represents a subtropical-temperate nexus within which a number of phytogeographic regions (e.g., Cerrado, Chaco, Interior Atlantic Forest, and Pantanal) interdigitate (Willig et al. 2000).

The tabonuco rainforest in northeastern Puerto Rico is a disturbance-mediated environment that experiences frequent hurricane-induced disturbances (Brokaw et al. 2012). Over the past few decades, this forest has experienced a combination of press (climate change) and pulse (Hurricanes Hugo in 1989, Georges in 1998, and Maria in 2017) disturbances that significantly altered the structure of the forest (Uriarte et al. 2019). Nonetheless, terrestrial gastropods have consistently maintained compartmentalized structures (Clementsian or quasi-Clementsian) despite repeated, severe pulse disturbances and secondary succession occurring in the midst of droughts and increasing temperatures associated with global climate change

(Willig et al. 2021). All gastropods in this metacommunity have geographical ranges that extend beyond the study area; however, species specialize on particular ecological niches in the forests that are differentiated by plant composition and physiognomy related to successional stage after major hurricanes. Consequently, compartments in the metacommunity are dynamic in space and time, with one group of species occurring primarily in mature, closed-canopy habitats and another group of species occurring primarily in early successional habitats. Both groups of species effectively track their preferred microhabitats through space and time to maintain the same ecological compartments and same metacommunity structure (Willig et al. 2021). In contrast to many of the examples presented here, this environmental gradient represents small-scale environmental variation within a single forest type and an annual pattern that has persisted for almost three decades.

Similar to the stable metacommunity structure of Puerto Rican gastropods, the metacommunity structure of semiarid plant communities in the Zapotitlán Valley of Puebla, México, evinced consistent Clementsian structure over a 23-year period (Jiménez et al. 2020). This metacommunity consistently comprised three compartments associated with cardonal (unbranched columnar cacti), tetechera (branched columnar cacti), and shrubland plant formations that occur along a gradient of soil characteristics (e.g., texture, soil class, organic matter). However, the proportion of communities that represent each plant formation changed through time. Although the number of cardonal communities remained unchanged over the past 23 years, 75% of tetechera communities (the most common community type in 1980) were classified as shrubland communities in 2003. This conversion of tetechera to shrubland may represent a natural successional progression, as columnar cacti change soil characteristics, making them more suitable for the shrubs, legumes, and agave that characterize shrublands. Both of these long-term studies (tropical gastropods and semi-arid plants) indicate the importance of supplementary analyses to understand temporal dynamics, even when emergent metacommunity structures do not change through time.

Benthic metacommunities in Todos os Santos Bay (Bahia, Brazil) generally exhibited nested structures along a salinity-contamination gradient (Teixeira Alves et al. 2020). Sites in marine environments supported high species richness; as salinity decreases along the gradient, sites progressively lost species, and were relatively depauperate at freshwater sites. The majority of species in these communities are of marine origin, with tolerance for low salinity and shallow water determining the extent of their incursions into estuarine environments. Although most structures were nested or quasinested, the strongest patterns of nestedness occurred in the estuary with the greatest level of anthropogenic activity and contamination (Teixeira Alves et al. 2020). Some species were intolerant of freshwater itself, whereas other species were intolerant of contamination from the freshwater sources. The combination of low salinity and high contamination resulted in strongly nested patterns, with particularly depauperate communities in proximity to contaminated, freshwater sources. Biogeographical effects may inhibit the ability to detect effects of human activities on metacommunity structure at large spatial scales (e.g., Atlantic Forest Bats and nonvolant small mammals), requiring smaller-scale studies of



communities that share a single species pool to effectively evaluate anthropogenic effects on the distributions of species and emergent metacommunity structures.

In a study of the invertebrates of intertidal habitats of Puerto Rico, the metacommunity exhibited Gleasonian structure (Bloch and Klingbeil 2016). Because coastal habitats in Puerto Rico are human-dominated systems, anthropogenic effects were expected to affect the biodiversity and composition of communities, as well as the structure of the metacommunity. This was not the case. Rather, a gradient of wave exposure, a combination of wave power and wave height, structured the metacommunity, with species evincing idiosyncratic responses to tidal variation. Wave action subjects intertidal organisms to strong hydrodynamic forces that mediate biological interactions and define physical aspects of intertidal habitats. These factors continue to structure Puerto Rican intertidal communities and metacommunities despite increasing anthropogenic activity in these habitats.

### ***15.5.5 Empirical Neotropical Metacommunities: Summary***

Metacommunity approaches have revealed spatial structures associated with many types of environmental gradients in the Neotropics, and have done so from small to large spatial scales and in a hierarchical fashion. Neotropical metacommunities are structured by gradients associated with abiotic variation, edaphic features, habitat type, disturbance, contamination, land use, or by the legacies of historical factors. The flexibility of the EMS approach has been used to generate and test hypotheses associated with a wide range of ecological, biogeographical, evolutionary, and conservation questions by simultaneously evaluating mechanisms that affect spatial patterns at vastly different time scales (e.g., biogeographical history versus modern land use change). Large-scale metacommunity structures are typically associated with historical factors (evolutionary histories, biogeography), whereas smaller-scale patterns arise in response to variation in local factors (e.g., habitat type, disturbance history) or anthropogenic activities (e.g., habitat loss and fragmentation, pollution, and contamination). Finally, ecological differences between taxa have resulted in taxon-specific structure, confirming that the study of multiple metacommunities in the same system may be required to understand the relative influence of historical and contemporary mechanisms.

## **15.6 Future Directions for Metacommunity Research in the Neotropics**

Future research on metacommunities in the Neotropics will no doubt contribute to ecological understanding, because the region (1) includes some of most dramatic and extensive elevational gradients in the world; (2) represents an extensive

latitudinal gradient, spanning nearly 47°, from 23.44° S to 23.44° N Latitude; (3) harbors some of the greatest biological diversity on Earth, strongly contributing to comparative understanding; (4) comprises a broad diversity of terrestrial biomes within which gradients can be studied; (5) is home to a broad variety of freshwater systems, ranging from the Amazon and its tributaries, to the world's largest wetland, the Pantanal; and (6) reflects a complex biogeographical history, including the formation of many island systems, recent connection of North and South American continents, and orogeny of several mountain ranges. This unique combination of complex and extensive environmental gradients combined with high biodiversity makes the Neotropics ideal for conceptual and empirical advancements in metacommunity ecology.

Conducting structured, preplanned, large-scale ecology has always been a challenge, and that challenge remains today. As a consequence, the majority of metacommunity ecology in the Neotropics is born of opportunity rather than design. Two aspects of biodiversity monitoring in the Neotropics can improve our understanding of metacommunity dynamics. First, long-term studies that entail repeated sampling at regular intervals to quantify the extent and nature of changes in metacommunities along gradients subject to combinations of press (e.g., eutrophication, contamination, pollution, climate change) and pulse (e.g., extreme weather events, logging) disturbances are necessary to understand spatiotemporal dynamics. Such studies would benefit from concomitant monitoring of salient abiotic, biotic, or climatic factors so that the nature of latent environmental gradients can be identified with confidence. Second, comparative studies of multiple taxa (e.g., bats, rodents, birds, amphibians, arthropods, trees, fungi) along the same spatial or environmental gradients should be executed to determine which groups are particularly vulnerable to changing environmental conditions, as well as to identify emerging conservation concerns. In addition to new strategies for documenting metacommunities through space and time, development of new approaches for understanding both the spatial structure of metacommunities as well as the processes and mechanisms that give rise to them would benefit metacommunity ecology. Of particular utility would be development of new quantitative methods to objectively identify suites of sites that comprise compartments within Clementsian metacommunities or within nested metacommunities that evince compartmentalized species loss. The three elements of metacommunity structure are all aspects of species distributions; however, the abundances of species vary throughout those distributions. Development of quantitative methods that can characterize metacommunity structure based on considerations of species abundances rather than only their incidence would lend greater insight into spatial structure of metacommunities. Finally, metacommunity ecology would benefit from the incorporation of manipulative studies to facilitate the identification of particular mechanisms that underly the structure of current or future metacommunities.

Metacommunity ecology has made great strides in understanding patterns along environmental gradients, and work in the Neotropics has been crucial to many of these developments. The continued development of methods for characterizing spatial patterns and identifying the local and regional mechanisms that give rise to them

should be leveraged by dedicated long-term research programs (e.g., the Long-Term Ecological Research program of the U.S. National Science Foundation, Pesquisas Ecológicas de Longa Duração of the Brazilian Conselho Nacional de Desenvolvimento Científico e Tecnológico) in Neotropical areas to provide unprecedented opportunity to understand ecological dynamics and its causation at multiple spatial scales. This is particularly urgent as the tempo and mode of human-induced disturbances associated with the Anthropocene will likely have great impact on the structure and functioning of vital ecological systems in the New World tropics, and beyond.

**Acknowledgments** This research was supported by an OPUS grant from the National Science Foundation (DEB-1950643) to MRW and by a grant (DEB-1831952) from the National Science Foundation to the Institute of Tropical Ecosystem Studies, University of Puerto Rico, and the International Institute of Tropical Forestry as part of the Long-Term Ecological Research Program. Support was also provided by the Center for Environmental Sciences and Engineering and Institute of the Environment at the University of Connecticut.

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Randall W. Myster *Editor*

# Neotropical Gradients and Their Analysis

 Springer

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ISBN 978-3-031-22847-6      ISBN 978-3-031-22848-3 (eBook)  
<https://doi.org/10.1007/978-3-031-22848-3>

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