

Chapter 15

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



Steven J. Presley and Michael R. Willig

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

S. J. Presley · M. R. Willig (✉)

Department of Ecology & Evolutionary Biology, University of Connecticut, Storrs, CT, USA

e-mail: steven.presley@uconn.edu; michael.willig@uconn.edu

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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 archetypical 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 archetypal 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 archetypal 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

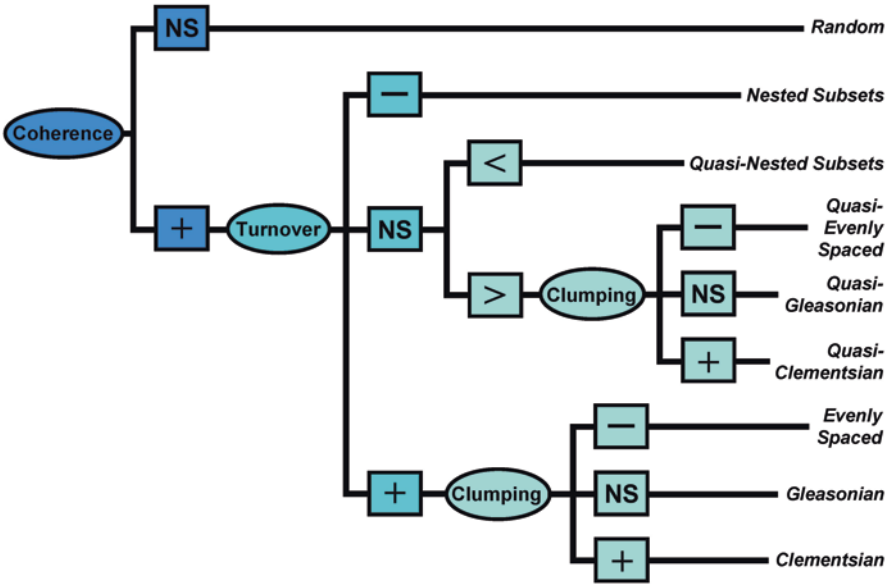


Fig. 15.1 A diagrammatic representation (after Presley et al. 2010) of combinations of the three elements of metacommunity structure (ovals) that differentiate among five idealized metacommunity structures and four quasisttructures. Possible results for tests for each element appear in squares: a positive 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. Quasisttructures 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, β -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 (α), beta (β), and gamma (γ) partitions. α estimates mean biodiversity of local sites, β estimates the degree of compositional differentiation among sites, and γ represents the biodiversity for a region regardless of its constituent spatial units. Biodiversity at larger spatial scales (γ components) can be driven by local biodiversity (α components), if little compositional variation characterizes communities (Gering and Crist 2002), or can be driven by among-site variation (β components), which signals the importance of spatial heterogeneity at landscape or regional scales (Belmaker et al. 2008; Willig and Presley 2019). The contributions of α - or β -partitions to γ -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 β differs between these models; α and γ are the same (Jost 2007). In the additive model, β represents the average number of species in the metacommunity that do not occur at a site ($\beta = \gamma - \alpha$), whereas in the multiplicative model, β 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 (γ) that is a consequence of the diversity of local communities (α) versus a consequence of variation among local communities (β). However, within the context of metacommunity structure, multiplicative β 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 β 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

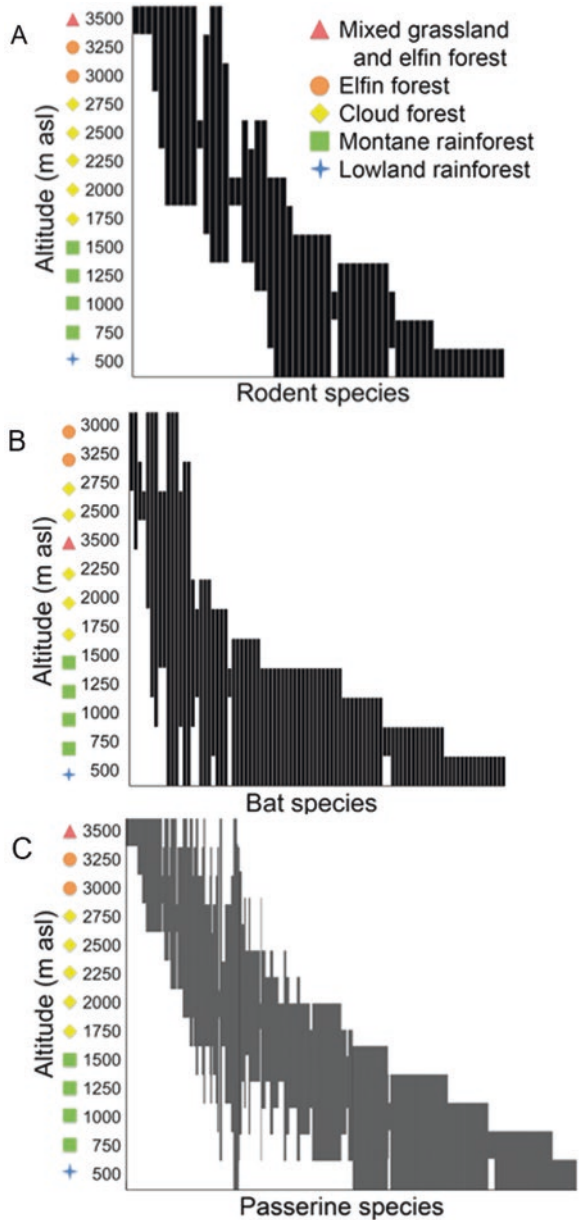
(Peruvian bats), Clementsian (Peruvian rodents, Mexican amphibians, Mexican bats, and Puerto Rican gastropods), quasi-Clementsian (Puerto Rican Gastropods and Peruvian passerines), Gleasonian (Puerto Rican gastropods, Mexican amphibians, and bats of the Mexican Sierra Madre Occidental), and quasi-Gleasonian (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

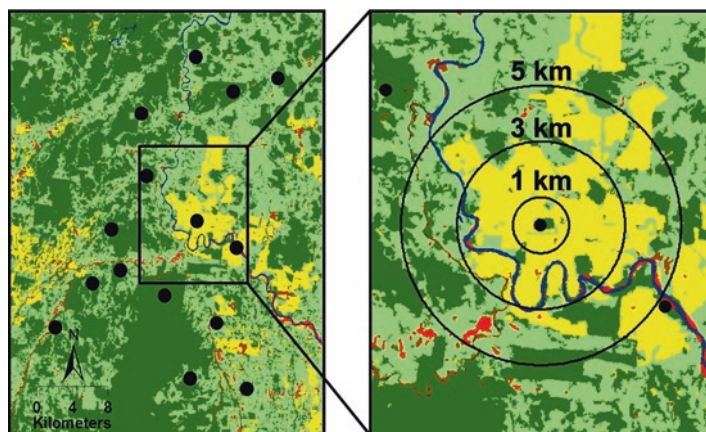


Fig. 15.3 An example of sites distributed in a heterogeneous landscape that are subject to various forms of land use (left), and an example of multiple focal scales for evaluation of effects of landscape structure on populations, communities, or metacommunities in a focal patch (right). Black dots represent 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; Tschamtker 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