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Elements of metacommunity structure of Paraguayan bats: multiple gradients require analysis of multiple ordination axes

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Abstract Techniques to evaluate elements of metacommunity structure (EMS; coherence, species turnover and range boundary clumping) have been available for several years. Such approaches are capable of determining which idealized pattern of species distribution best describes distributions in a metacommunity. Nonetheless, this approach rarely is employed and such aspects of metacommunity structure remain poorly understood. We expanded an extant method to better investigate metacommunity structure for systems that respond to multiple environmental gradients. We used data obtained from 26 sites throughout Paraguay as a model system to demonstrate application of this methodology. Using presence–absence data for bats, we evaluated coherence, species turnover and boundary clumping to distinguish among six idealized patterns of species distribution. Analyses were conducted for all bats as well as for each of three feeding ensembles (aerial insectivores, frugivores and molossid insectivores). For each group of bats, analyses were conducted separately for primary and secondary axes of ordination as defined by reciprocal averaging. The Paraguayan bat metacommunity evinced Clementsian distributions for primary and secondary ordination axes. Patterns of species distribution for aerial insectivores were dependent on ordination axis, showing Gleasonian distributions when ordinated according to the primary axis and Clementsian distributions when ordinated according to the secondary axis. Distribution patterns for frugivores and molossid insectivores were best described as random. Analysis of metacommunities using multiple ordination axes can provide a more complete picture of environmental variables that mold patterns of species distribution. Moreover, analysis of EMS along defined gradients (e.g., latitude, elevation and depth) or based on alternative ordination techniques may complement insights based on reciprocal averaging because the fundamental questions addressed in analyses are contingent on the ordination technique that is employed.

Keywords Biogeography · Boundary clumping · Coherence · Reciprocal averaging · Species composition

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Introduction

The recent maturation of metacommunity concepts (Leibold and Miller 2004; Leibold et al. 2004; Holyoak et al. 2005) has focused on spatially mediated models (i.e., mass effects, neutral model, patch dynamics and species sorting) and their underlying mechanisms (e.g., dispersal, biotic interactions or responses to abiotic environmental characteristics). Indeed, many innovative analytical approaches

(e.g., Hoagland and Collins 1997; Hofer et al. 1999; Leibold and Mikkelson 2002; Hausdorf and Hennig 2007) have been developed recently that allow researchers to explore, identify and evaluate numerous aspects of metacommunity structure; however, these approaches largely are under utilized by ecologists. One such approach, analysis of elements of metacommunity structure (EMS; i.e., coherence, species turnover and range boundary clumping), specifically was developed to determine the pattern of best fit for species distributions within a metacommunity (Leibold and Mikkelson 2002). This methodology is a powerful tool that simultaneously tests multiple idealized patterns of species distribution, including checkerboard, nested, Clementsian, Gleasonian, evenly spaced and random distributions, to determine which one best fits the data. Species turnover and range boundary clumping are the primary characteristics that distinguish most idealized patterns (Leibold and Mikkelson 2002). More specifically, nested distributions exhibit less turnover than expected by chance, whereas Clementsian, Gleasonian and evenly spaced distributions exhibit more turnover than expected by chance. The latter group of patterns may be differentiated by the distribution of species boundaries: Clementsian distributions have clumped boundaries, Gleasonian distributions have randomly spaced boundaries and evenly spaced distributions have hyperdispersed boundaries. Within the context of analyses of EMS, a metacommunity is defined as "a set of ecological communities at different sites (potentially but not necessarily linked by dispersal), whereas a community is a group of species at a given site" (Leibold and Mikkelson 2002). The spatial extent of a site may differ among metacommunity studies; however, the crucial aspect of scale in a metacommunity context is that the definition of a site is consistent with the theoretical questions addressed in the analysis as well as the explanatory variables and mechanisms invoked to explain patterns.

Use of reciprocal averaging to arrange the data matrix prior to analysis is an asset of the techniques used to analyze EMS (Leibold and Mikkelson 2002). Reciprocal averaging is the best indirect ordination procedure to discern sample variation in response to environmental gradients (Gauch et al. 1977; Pielou 1984). More specifically, reciprocal averaging allows composition of communities and occurrence of species to define the gradient that is important to metacommunity structure and ordinates communities and species along that gradient. Other analytical approaches (e.g., canonical correspondence analysis or multiple regression) may suffer from assumptions about which variables (e.g., temperature, latitude or elevation) define species distributions or the nature (e.g., linear or curvilinear) of such relationships. By allowing the metacommunity to define the gradient of ordination, such problems that may weaken the ability of analyses to detect patterns

are avoided. In addition, species may respond to environmental variables at multiple scales. Whereas other methodologies impose a particular scale for analysis, reciprocal averaging allows species to ordinate at multiple scales simultaneously, eliminating this problem. Consequently, when subjected to reciprocal averaging, a metacommunity may ordinate along a gradient that integrates multiple environmental characteristics that are important to species distributions.

Despite the utility of the EMS approach, few studies have endeavored to apply it to empirical data sets. To our knowledge, only five investigations (Kusch et al. 2005; Zimmerman 2006; Bloch et al. 2007; Burns 2007; Werner et al. 2007) have applied the entire EMS analysis to determine the best fit pattern for species distributions; moreover, in all but one case (Kusch et al. 2005) EMS analyses were tangential to the focus of the research and results of the analyses were not discussed. Considering the rapid increase in metacommunity research, the general lack of use of this powerful approach is unfortunate.

Leibold and Mikkelson (2002) restricted analyses of EMS to ordinations based on the primary ordination axis of reciprocal averaging. However, often in ordination analyses (e.g., principal component analysis) multiple axes represent biologically meaningful gradients. Indeed, reciprocal averaging "will in some cases reveal a second direction of sample variation in its second axis" (Gauch et al. 1977). In previous research (López-González 1998, 2004; Stevens et al. 2007), analyses resulted in two axes that explained a significant amount of variation in Paraguayan bat species composition, with each axis representing distinct environmental gradients (i.e., temperature/precipitation gradient and soil moisture related to edaphic features) to which bat composition responded; although, such responses were mediated through associations of vegetation. Biome associations (Willig et al. 2000; López-González 2004) and fit with spatially mediated models (Stevens et al. 2007) have been investigated previously for Paraguayan bats; however, patterns of species distribution for these bats remain unknown. Moreover, prior research has focused on the entire bat assemblage; analyses restricted to particular ensembles that evaluate distinct patterns related to the functional ecology of each group are lacking. We hypothesized that metacommunities may exhibit patterns of species distribution along multiple ordination axes and that distribution patterns on each axis may represent distinct, ecologically meaningful responses to the environment. Because Paraguayan bat composition responds to multiple environmental gradients (López-González 2004; Stevens et al. 2007), we used this metacommunity to explore EMS along multiple ordination axes. More specifically, we expanded the methodology of Leibold and Mikkelson (2002) to conduct analyses for matrices ordinated based on

the second ordination axis as well as for matrices ordinated based on the first ordination axis.

Materials and methods

Study area

Paraguay is a small (406,752 km) landlocked country located at the subtropical–temperate interface in central South America (Fig. 1). Despite its small size, Paraguay has strong gradients in mean annual temperature (21–26°C) and mean annual precipitation (400–1,800 mm), being warmer and drier in the northwest and progressively cooler with increased rainfall toward the south and east (Fariña Sánchez 1973). In concert with strong climatological gradients, edaphic features have created distinct phytogeographic zones (Hayes 1995). Annual rainfall in the Alto Chaco is low (~400 mm) and soils facilitate percolation of water; therefore, the Alto Chaco is characterized by xerophytic thorn–scrub forest. In contrast, much of the Matogrosense and Bajo Chaco as well as parts of eastern Paraguay (Ñeembucú) adjacent to the Paraguay and Paraná rivers are inundated seasonally or permanently; such areas support palm savannas and marshlands. In contrast, eastern Paraguay is more humid and physiographically diverse. Ñeembucú is edaphically similar to Bajo Chaco and contains similar habitats that interdigitate with tall, humid forests that are characteristic of the nearby Central Paraguay region. Campos Cerrados is a savanna-like formation dominated by a mosaic of xerophytic woodlands and grasslands over rolling terrain. The Central Paraguay region is diverse, including lowlands along the banks of the Paraguay River and tall humid forests in the hilly terrain to the east. The Alto Paraná is separated from Central Paraguay by a series of low mountain ranges and is characterized by fast flowing rivers and tall humid forests. Eastern Paraguay experienced extensive deforestation during the last half of the 20th century (Ríos and Zardini 1989; Keel et al. 1993), such that <20% of the original forest remains (Huang et al. 2007).

Bat assemblage data

Bat species composition was characterized at 26 sites distributed throughout the country (Fig. 1), which span environmental gradients representing precipitation, temperature and edaphic characteristics. Bat species composition at each site was estimated by identifying all bats captured within a 50-km^2 quadrat. Bat species composition within quadrats was assembled from a faunal survey undertaken from July 1995 to June 1997 and supplemented by an exhaustive search of museums for additional specimens (López-González 1998, 2005). Bats were collected using
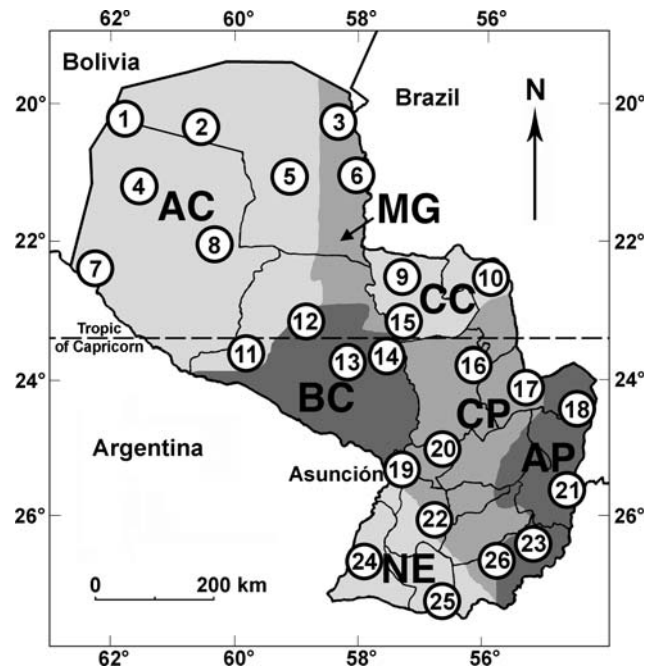

Fig. 1 Location of 26 assemblages (*circled numbers*) of Paraguayan bats used for analyses. Biogeographic regions in Paraguay: Matogrosense (*MG*), Alto Chaco (*AC*), Bajo Chaco (*BC*), Campos Cerrados (*CC*), Central Paraguay (*CP*), Alto Paraná (*AP*), Ñeembucú (*NE*). *Black lines within a country* indicate boundaries of Departamentos

mist nets erected at ground level in all available habitats. Nets were monitored from dusk until 0100 hours, and often from dusk until dawn. Effort, typically, was greater than 100 net nights per site. On occasion, specimens also were obtained from roosts (e.g., buildings or culverts). Additional details about the collection of bats, species lists and museum records are available elsewhere (López-González 1998, 2004, 2005; Willig et al. 2000; Stevens et al. 2004). We followed the taxonomic treatment of Simmons (2005) for bat nomenclature.

Paraguayan bats belong to many trophic guilds. The relative importance of environmental characteristics may be contingent on guild affiliation (Stevens et al. 2003; Stevens 2004). We assigned each species to one of seven broad foraging guilds based on published recommendations (Wilson 1973), and guild assignments were used to conduct ensemble-level analyses. An ensemble (sensu Fauth et al. 1996) is defined as a taxonomically restricted group of species belonging to the same trophic guild. Analyses were conducted for all Paraguayan bats (i.e., the Paraguayan bat metacommunity) as well as for each of three ensembles (i.e., aerial insectivore, frugivore and molossid insectivore meta-ensembles) that exhibited sufficient richness and incidence to provide biologically meaningful results. Analyses of the metacommunity were based on 5,012 individuals from 26 sites, representing 48 species; analyses of the aerial insectivore meta-ensemble were based on 993 individuals

from 25 sites, representing 15 species; analyses of the frugivore meta-ensemble were based on 1,393 individuals from 18 sites, representing nine species; and analyses of the molossid meta-ensemble were based on 1,010 individuals from 25 sites, representing 15 species.

Statistical analyses

To evaluate EMS (coherence, species turnover and range boundary clumping) related to the distribution of species, we employed methodologies described by Leibold and Mikkelson (2002). Analyses required only a site by species incidence matrix. Matrices were ordinated via reciprocal averaging (i.e., simple correspondence analysis), which maximizes the degree to which sites (i.e., communities) with the most similar species compositions are adjacent in the matrix and species that have comparable distributions are adjacent in the matrix. The primary axis represents the best possible ordering of sites and species to maximize the correspondence between species scores and site scores. The second and higher axes also maximize the correspondence between species scores and site scores, but are constrained to be uncorrelated to previous axes (i.e., axes are orthogonal; Gauch 1982). Because axes extracted via reciprocal averaging are orthogonal, and because secondary axes have the potential to represent biologically meaningful information (Gauch et al. 1977), analyses of EMS based on secondary (and higher) axes may provide insights into species distributions beyond that obtained on the first axis. As a result of the orthogonal nature of the axes, one can employ the same procedures to compute and determine the significance of empirical values of EMS metrics (i.e., embedded absences, number of replacements and Morisita's index) for any number of axes (though it is likely that axes beyond the second one rarely would yield ecologically meaningful insight), with the only necessary change being the assignment of the desired axis of ordination for the empirical and randomly generated matrices.

Coherence was evaluated by counting the number of embedded absences in the ordinated matrix and comparing the empirical value to a null distribution. In the original methodology for EMS, two null model approaches were presented that represent ends of a gradient from liberal to conservative (Leibold and Mikkelson 2002). The first null model (Random 0) assumes equiprobable occurrence throughout the matrix; null models such as Random 0 that have no structure whatsoever are highly prone to type I errors (Gotelli 2000). The second null model (Random 4) fixes both row and column totals to equal observed values and is highly prone to type II errors (Gotelli and Graves 1996). The fixing of row and column totals can incorporate too much biology into the null model, which generally will include the mechanism of interest, thereby, preventing the

analysis from detecting any pattern but random. To avoid statistical pitfalls associated with these two null models, we chose a null model that fixed row totals (species richness of sites) to equal empirical values but assigned an equiprobable chance of occurrence to each species (equiprobable column totals). This null model has more desirable type I and type II error rates than does Random 0 or Random 4 (Gotelli and Graves 1996; Gotelli 2000). In addition, it incorporates an appropriate amount of biological realism for studying the spatial distribution of Paraguayan bats. In our study, observed species richness was contingent on site characteristics, which differed in habitat quality and sampling effort (hence fixed row totals). Although the number and identity of sites at which Paraguayan bats occur are determined by biotic and abiotic factors, bats are sufficiently vagile as to be capable of occurring at each site (hence equiprobable column totals). To our knowledge, this is the first study of EMS that has selected a null model based on biological knowledge of the metacommunity instead of using one of the null models that were originally selected for demonstration purposes (Leibold and Mikkelson 2002).

To assess coherence, the empirical data matrix was ordinated according to the selected axis (i.e., primary or secondary) using reciprocal averaging and the number of embedded absences in the ordinated matrix was counted. We then generated 1,000 random matrices, ordinated each randomly generated matrix using the selected ordination axis (primary or secondary, whichever was used to ordinate the empirical matrix), and counted the number of embedded absences in each of the random, ordinated matrices. The mean and SD of the embedded absences were estimated from the 1,000 random matrices, and a z-test was used to assess statistical significance of the observed number of embedded absences. A metacommunity or meta-ensemble was considered to be significantly coherent if the probability of obtaining a random number of embedded absences that was less than the observed number of embedded absences was ≤ 0.05. Significant coherence indicates that species presences are not random, but occur in response to environmental variation represented by the ordinated matrix (Leibold and Mikkelson 2002) and are consistent with nested, Gleasonian, Clementsian, or evenly spaced distributions. Non-coherent matrices indicate that species presences occur at random with respect to the axis of ordination, or that species responses are idiosyncratic with respect to environmental variation. Significantly negative coherence (i.e., more embedded absences than expected by chance) is indicative of checkerboard distributions.

If a metacommunity or meta-ensemble exhibited significant coherence, we evaluated species turnover and range boundary clumping. Analyses of turnover and boundary clumping may be performed from two perspectives (Leibold

and Mikkelson 2002): the range perspective is defined by species range turnover and range boundary clumping, and the community perspective is defined by community turnover and community boundary clumping. Herein, all analyses were conducted from the range perspective. Species turnover was measured as the number of times one species replaced another between two sites (i.e., number of replacements). The observed number of replacements was compared to a distribution of randomly generated values based on a null model that randomly shifted entire ranges of species (Leibold and Mikkelson 2002). Significantly low species turnover was consistent with nested subsets; significantly high species turnover was consistent with the remaining distribution patterns. Boundary clumping was evaluated with Morisita's index (Morisita 1971) to distinguish among Clementsian, Gleasonian, and evenly spaced distributions. The expected value of Morisita's index is 1.0; values not significantly different than 1.0 indicate randomly distributed boundaries and are consistent with Gleasonian distributions. Results significantly >1.0 indicate clumped boundaries and are consistent with Clementsian distributions. Results significantly <1.0 indicate hyper-dispersed boundaries and are consistent with evenly spaced distributions. For all analyses, we used an α-level of 0.05 to determine significance.

Rankings and scores for each ordination axis were obtained from the simple correspondence analysis option of Minitab 15.1.1.0. Analyses of coherence, turnover and boundary clumping were conducted with algorithms written in Matlab 6, Release 12 (script files for Matlab are available from the authors upon request or may be downloaded at http://www.tarleton.edu/~higgins/EMS.htm). To determine if site scores for each ordination axis were correlated significantly with the predominant climatological gradients (temperature and precipitation) in Paraguay, Pearson product moment correlations and Spearman rank correlations were conducted with an α-level of 0.05. Data for mean annual precipitation and mean annual temperature were taken from maps (Comisión Nacional de Desarrollo Regional Integrado del Chaco 1986). Correlations were conducted using the R programming environment (R Development Core Team 2005).

Results

Results for all bats were similar regardless of whether the metacommunity was ordinated on the primary or secondary axis. For analyses based on the primary axis, the metacommunity exhibited positive coherence, positive species turnover and positive boundary clumping (Table 1); all of which were consistent with a Clementsian distribution (Leibold and Mikkelson 2002). For analyses based on the secondary axis, the metacommunity exhibited positive coherence, random species turnover and positive boundary clumping. These results also were most consistent with a Clementsian distribution, although the fit with the model was not as strong as for the primary axis. For the primary axis, sites were ordered from west to east (Figs. 2, 3), corresponding to gradients of temperature and precipitation. Pearson product moment and Spearman rank correlations indicated that environmental parameters and primary axis scores were significantly correlated (Table 2). The only significant correlation between secondary axis scores and

Table 1 Results of analyses of coherence, species turnover and boundary clumping for the bat metacommunity of Paraguay

	Coherence					Species turnover				Boundary clumping		
	Percent inertia	Abs	P	Mean	SD	Rep	P	Mean	SD	Morisita's index	P	Best fit pattern for distributions
Primary axis												
All bats	14.5	**482**	**<0.001**	**671**	**25.6**	**20,914**	**0.028**	**15,558**	**2,439.5**	**1.251**	**0.012**	Clementsian
Aerials	17.9	**113**	**0.004**	**142**	**11.2**	1,016	0.214	704	251.3	1.394	0.112	Gleasonian
Frugivores	27.7	37	0.581	36	4.9							Random
Molossids	16.4	**115**	**0.022**	**139**	**12.0**	1,746	0.372	1,398	390.0	0.727	0.816	Random
Secondary axis												
All bats	9.8	**622**	**0.002**	**694**	**24.4**	10,957	0.819	11,398	1,922.5	**1.304**	**0.005**	Clementsian
Aerials	15.1	**114**	**<0.001**	**158**	**10.3**	**1,031**	**0.006**	**524**	**184.6**	**2.706**	**<0.001**	Clementsian
Frugivores	19.3	36	0.081	43	5.0							Random
Molossids	15.7	133	**0.042**	**152**	**11.1**	1,313	0.533	1,548	377.2	0.727	0.816	Random

Analyses were performed for all bats as well as for each of three foraging guilds. For each group of bats, analyses were performed separately on matrices ranked based on the first ordination axis extracted via reciprocal averaging and based on the second ordination axis extracted via reciprocal averaging

Abs No. of embedded absences, *Rep* number of replacements

Significant results (*P* ≤ 0.05) are in *bold*

Fig. 2 Maps illustrating the ranking of sites based on the primary axis derived via reciprocal averaging for each of the 26 sites for all bats as well as for analyses restricted to aerial insectivores (A), frugivores (F) and molossid insectivores (M). If a group was not represented at a particular site, that site was omitted from analysis and had no rank. Sites with the same species composition had equal ranks. For other abbreviations, see Fig. 1
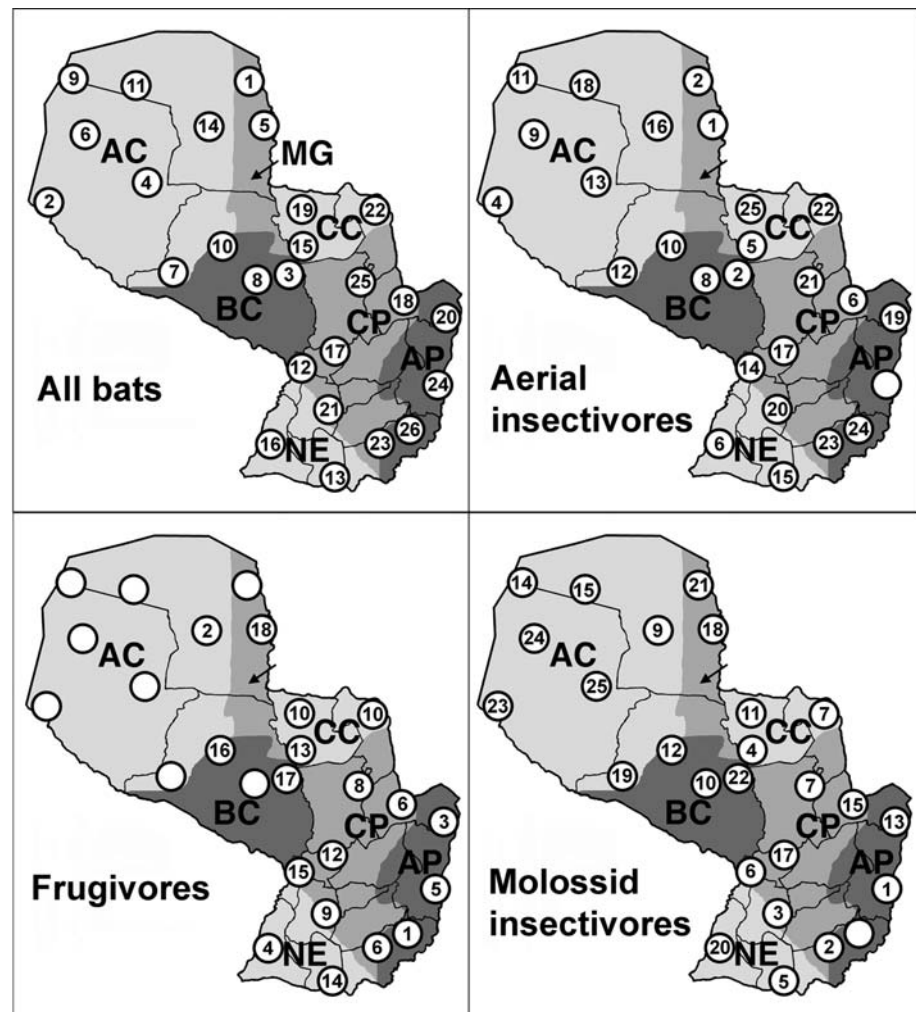
environmental variables was the Spearman rank correlation with precipitation. The separation that manifested on this axis reflected variation in edaphic features; sites (3, 6 and 14) from permanently inundated areas had positive scores >0.5 and sites (1, 4, 5, 7, 8 and 11) from regions with dry soils that facilitate percolation of water and that have little rainfall had negative scores <−0.3 (Fig. 3). Most frugivores, nectarivores and gleaning animalivores had positive values on the primary axis, whereas the majority of aerial insectivores, molossids, piscivores and sanguinivores had negative values (Fig. 4). In general, this pattern reflected species presences associated with gradients of temperature and rainfall, with herbivores and omnivores predominating in the cooler, wetter regions and species with animal-based diets predominating in warmer, drier climes.

Results for analyses restricted to aerial insectivores were contingent on the ordination axis. When ordinated according to the primary axis, the aerial insectivore meta-ensemble exhibited positive coherence, random species turnover and positive but not significant boundary clumping. The pattern most consistent with these results is Gleasonian.

When ordinated according to the secondary axis, the aerial insectivore meta-ensemble exhibited positive coherence, species turnover and boundary clumping; all consistent with Clementsian distributions. Similar to patterns for analyses based on all species, the primary axis based on the aerial insectivore meta-ensemble ordered sites along gradients of temperature and precipitation (Figs. 2, 3); both were correlated significantly with component scores for this axis (Table 2). Aerial insectivores were ordered on the primary axis from species occurring primarily in eastern Paraguay to ubiquitous species to species occurring primarily in western Paraguay; however, no discernable delineation among distributions occurred on this axis (i.e., a Gleasonian pattern). In contrast, on the secondary axis, distinct groupings of species manifested (i.e., a Clementsian pattern). Aerial insectivores that primarily occurred in the chaco and flooded habitats (*Histiotus macrotus* and *Lasiurus ega*) had negative values near −1.0; relatively ubiquitous species had values between −0.20 and 0.20 (*Myotis albescens*, *Myotis nigricans*, *Myotis riparius*, *Myotis simus*, *Eptesicus furinalis*, *Lasiurus blossevillii* and

Fig. 3 Scores for each site for the primary and secondary axes of ordination derived via reciprocal averaging for analyses that included all bats as well as for analyses restricted to A, F and M. *Vectors* represent Spearman rank correlation coefficients between mean annual temperature or mean annual precipitation and site scores for each axis. For abbreviations, see Figs. 1 and 2
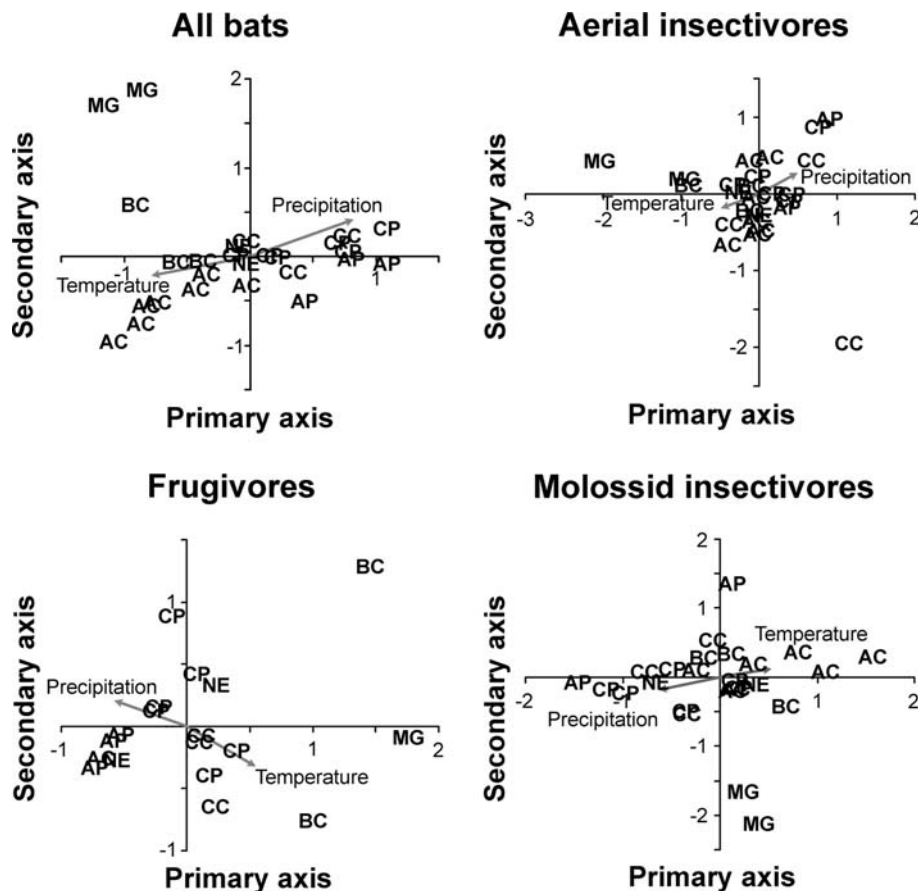

Table 2 Pearson product moment (*r*) correlations, Spearman rank (*ρ*) correlations, and associated *P*-values for correlations between mean annual temperature and mean annual precipitation and the scores for components 1 and 2 (i.e., primary and secondary axes) for sites extracted via reciprocal averaging

Taxon	Pearson product moment correlations				Spearman rank correlations			
	Temperature		Precipitation		Temperature		Precipitation	
	r	*P*-value	*r*	*P*-value	*ρ*	*P*-value	*ρ*	*P*-value
All bats								
Component 1 scores	**−0.795**	**<0.001**	**0.782**	**<0.001**	**−0.792**	**<0.001**	**0.835**	**<0.001**
Component 2 scores	0.172	0.402	0.239	0.239	−0.226	0.267	**0.429**	**0.029**
Aerial insectivores								
Component 1 scores	**−0.546**	**0.005**	0.356	0.081	**−0.474**	**0.017**	**0.512**	**0.009**
Component 2 scores	−0.263	0.204	0.208	0.318	−0.198	0.343	0.283	0.170
Frugivores								
Component 1 scores	**0.554**	**0.017**	**−0.529**	**0.024**	**0.539**	**0.021**	**−0.567**	**0.014**
Component 2 scores	−0.241	0.335	0.186	0.461	−0.330	0.181	0.208	0.407
Molossid insectivores								
Component 1 scores	**0.555**	**0.004**	**−0.642**	**<0.001**	**0.533**	**0.006**	**−0.613**	**0.001**
Component 2 scores	−0.278	0.178	0.061	0.772	0.125	0.552	−0.177	0.398

Significant results (*P* ≤ 0.05) are in *bold*

Noctilio albiventris); species that occurred primarily in eastern Paraguay had scores between 0.85 and 1.15 (*Eptesicus brasiliensis*, *Eptesicus diminutus* and *Lasiurus cinereus*); species that occurred only in Campos Cerrados (*Natalus stramineus*, −3.41) or Alto Paraguay (*Myotis ruber*, 1.70) had extreme score values (Fig. 4).

For primary and secondary axes, the frugivore meta-ensemble did not exhibit significant coherence (Table 1), indicating that occurrences of frugivores were not strongly associated with environmental gradients as defined by the primary axis of ordination. However, it is possible that the relatively small matrix size as well as the high degree of fill

Fig. 4 Scores for each species for the primary and secondary axes of ordination derived via reciprocal averaging for analyses that included all bats [A, gleaning animalivore (*G*), F, M, nectarivore (*N*), piscivore (*P*), sanguinivore (*S*)] as well as for analyses restricted to A, F and M. For other abbreviations, see Figs. 1 and 2
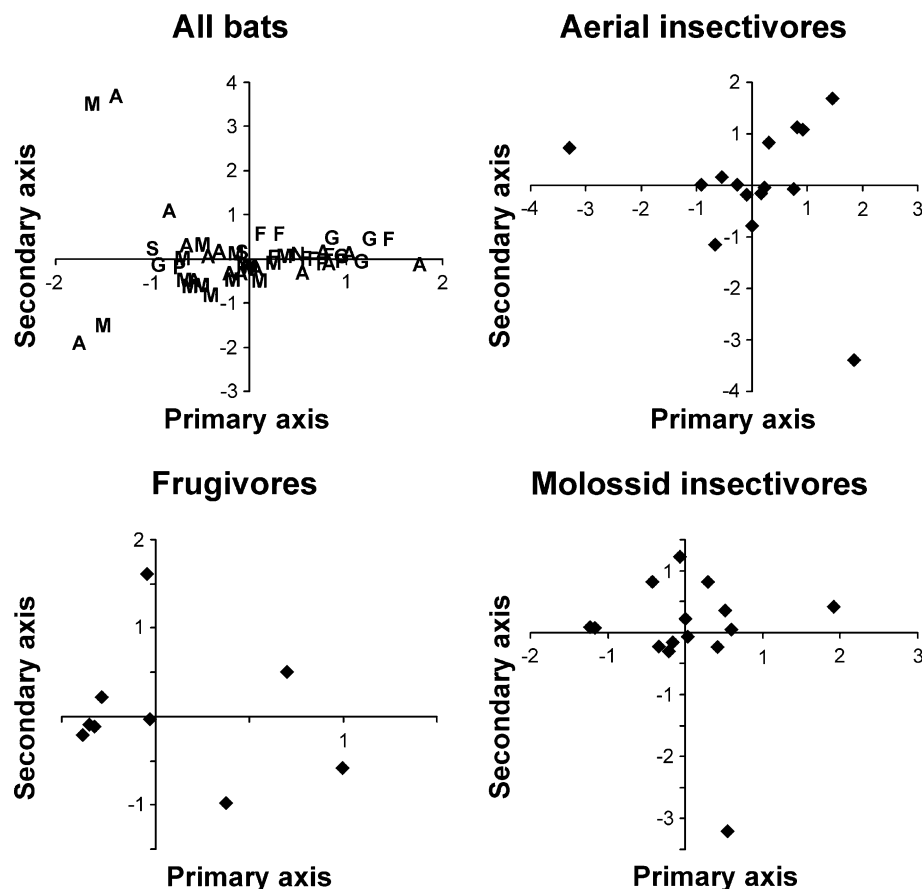
of this matrix made detecting significant coherence difficult. Similar to results for other ensembles, sites were ordered on the primary axis according to their geographic location along gradients of temperature and precipitation (Fig. 3). *Artibeus jamaicensis* and *Platyrrhinus lineatus* were the frugivores responsible for distinguishing between groups of sites in eastern Paraguay; these species occurred in sites of Central Paraguay and the Campos Cerrados, but did not occur in Alto Paraná sites.

For analyses restricted to molossid insectivores, the meta-ensemble exhibited positive coherence for each ordination axis (Table 1); however, results for species turnover and boundary clumping were not significantly different from random for either axis. Consequently, random species distributions best described molossid insectivores for each axis. Despite the fact that species distributions were randomly distributed on the primary axis, site order was consistent with temperature and precipitation gradients (Fig. 3) and temperature and precipitation were significantly correlated with scores from the primary axis (Table 2). Positive coherence and significant correlations between site scores and environmental characters indicated that occurrences of molossids were not random, but were influenced by environmental factors, whereas random patterns of turnover and boundary clumping indicated that responses of molossid

species were idiosyncratic. Species with restricted distributions had unique and extreme values on one axis; *Promops nasutus* (component 1 score = 1.91) was restricted to the Alto Chaco, *Eumops auripendulus* (component 1 score = −1.23) and *Molossops abrasus* (component 1 score = −1.20) occurred in flooded habitats and along rivers and *Molossus currentium* (component 2 score = −3.20) was restricted to the Matogrosense (Fig. 4).

Discussion

In general, analyses of EMS have been effective at distinguishing among random, nested, Clementsian and Gleasonian distributions; however, among the published examples (Leibold and Mikkelson 2002; Kusch et al. 2005; Zimmerman 2006; Bloch et al. 2007; Burns 2007; Werner et al. 2007; analyses herein) no patterns were consistent with checkerboards or evenly spaced distributions. From a theoretical perspective, it is unclear how a checkerboard distribution of ranges, which originally was conceived for pairs of species, might manifest at the community level. Because sites were ordinated to minimize the number of embedded absences at the metacommunity level, rearrangement of checkerboards would produce a pattern better described by

an alternative model. For example, if the boundaries between mutually exclusive pairs, which are the basis for checkerboards, are randomly distributed, Gleasonian distributions (or random distributions if the metacommunity is not coherent) would be the pattern of best fit. Similarly, if the boundaries between mutually exclusive pairs are coincident, Clementsian distributions would be the pattern of best fit. From a practical perspective, it may be extremely difficult for this approach to detect a community-wide pattern of checkerboard distributions. Although no metacommunity has evinced the characteristics (positive coherence, positive species turnover and negative boundary clumping) that describe evenly spaced gradients, there is no theoretical or methodological reason to expect that these cannot be detected.

Multiple ordination axes

If communities occur along an explicit spatial gradient (e.g., elevation, longitude or latitude), ordering them along that gradient may be preferred to other ordinations. In contrast, if sites and species are ordered along latent environmental gradients based on distributions of species among sites [i.e., the metacommunity is allowed to define the gradient(s) of response], multiple ecologically meaningful ordinations may be possible, with each ordination capable of representing a distinct pattern of species distributions along distinct gradients.

As is often misinterpreted by ecologists (e.g., Heino 2005; Hausdorf and Hennig 2007), eigenvalues associated with reciprocal averaging do not indicate the amount of variation accounted for by the axis, as is true for other ordination techniques. Rather, these values are equivalent to the correlation coefficient between site and species scores for the axis, indicate the degree of correspondence achieved by the ordination, and are termed the inertia of the axis (Gauch et al. 1977; Gauch 1982). Although ordinations are constructed based on sample variation, reciprocal averaging does not attempt to represent multidimensional data as faithfully as possible in low-dimensional space (i.e., maximize the amount of variation accounted for by each axis), nor does it produce coefficients to describe linear combinations of variables that best account for sample variation. Instead, sample variation is used to order sites to maximize correspondence. As such these axes are more appropriately called "axes of correspondence" than "axes of variation". Inertia for each axis generally is presented as percent of total inertia (sum of inertia values for all possible axes). Because multiple ordinations of a matrix may have similar inertia (though these values necessarily decrease with each successive axis), and because the number of axes may be great (i.e., smaller of two values, number of sites − 1 or number of species − 1), it is not uncommon for percent

inertia of a primary axis to be relatively low, though a few times greater than average axis inertia. For reasons outlined above, individual inertia values are not particularly informative; however, comparison of inertia values from different axes derived from the same matrix allows one to evaluate the relative correspondence achieved by ordinations on each axis. For analyses of Paraguayan bats, inertia for primary axes ranged from 2.3 to 3.6 times greater than average inertia for all possible axes, whereas inertia for secondary axes ranged from 1.5 to 2.5 times greater than average. Indeed, correspondence achieved by the secondary axis was nearly as great as for the primary axis for analyses of aerial insectivore and molossid insectivore meta-ensembles (Table 1), which may indicate that each ordination represented information of similar ecological relevance for those meta-ensembles and that analyses based on each ordination may provide insights into EMS.

The best fit pattern of species distributions for Paraguayan bats (all species or particular ensembles) as well as the degree of consistency with a specific idealized pattern was contingent on the ordination axis used for analysis (Table 1). Consequently, expansion of analyses of EMS to multiple ordination axes may improve the identification of environmental gradients that mold patterns of species distribution as well as the understanding of mechanisms responsible for patterns of species distribution along those gradients. This is particularly true if a metacommunity, such as Paraguayan bats, is known to respond to multiple environmental gradients (López-González 2004; Stevens et al. 2007). A common criticism of interpretations of ecological data based on multiple axes extracted via reciprocal averaging or similar methods (e.g., principal components analysis) is that they can produce "arch" or "horseshoe" effects, which represent quadratic distortions of the first axis and do not reflect any real feature of the data (e.g., Gauch 1982; Pielou 1984). In cases of such distortion, secondary patterns in the data may be found on the third axis. No such distortion appears in our data (Figs. 3, 4), suggesting that ordinations on secondary axes in this metacommunity are independent of those on primary axes and that patterns associated with each axis likely are associated with independent responses to the environment. Most exemplary of the need to evaluate multiple axes were the results for the aerial insectivores, which exhibited Gleasonian distributions on the primary axis, but strong Clementsian distributions on the secondary axis. The distribution of aerial insectivores on the primary axis was random with respect to species turnover and boundary clumping, although species did exhibit coherence (i.e., species responded to gradients of temperature and precipitation and occurrences themselves were not random). In contrast, aerial insectivores evinced a strong Clementsian pattern (i.e., highly significant and positive coherence, species turnover and boundary

clumping) on the secondary axis. The Clementsian pattern of distributions on the secondary axis (Table 1; Fig. 4) arose as a result of habitat specialization of some species. Although no distinct clusters of species existed along the temperature/precipitation gradient (i.e., primary axis), habitat specialists formed unique groups on the secondary axis.

Paraguayan bat metacommunity

Regardless of species group (metacommunity or meta-ensemble), the primary axis was correlated significantly with temperature and precipitation (Table 2), indicating that these variables are of primary importance in determining the occurrence of bats via the types of habitat and the associated resources available for bats as a result of particular combinations of these variables. In analyses of all bats, the secondary axis ordinated sites based on edaphic features; however, such distinction was not apparent for ensemble-level analyses. The Paraguayan bat metacommunity displayed Clementsian distributions regardless of axis; although a Clementsian pattern was a better fit to distributions on the primary axis than on the secondary axis. A Clementsian pattern is consistent with biogeographic work on Paraguayan mammals (Myers 1982; López-González 2004). The Paraguay River is coincident with a phytogeographic boundary associated with differences in drainage capability on each side of the river. Environs east of the river support tall, evergreen, tropical forests, in which many fruit-bearing plants occur on which frugivorous bats rely (Myers 1982; Hayes 1995; Willig et al. 2000). In contrast, lands west of the river are seasonally inundated or support xeric thorn scrub; habitats that do not support fruit-bearing plants on which bats feed. Consequently, distributions of bats with considerable frugivorous or nectarivorous components to their diets largely are restricted to areas east of the river, with only occasional transients captured in the west (López-González 1998, 2005). Alternatively, molossids are more species-rich and abundant in drier habitats throughout Central and South America (Mares et al. 1981; Dolan 1989; Redford and Eisenberg 1992; Anderson 1997; López-González 1998, 2005; Willig et al. 2000), including areas west of the Paraguay River. As a result, the synergism of edaphic features and rainfall creates a sharp boundary with distinct bat assemblages on each side of the river. Despite the fact that many vespertilionids are found throughout Paraguay, the dichotomy between frugivores and molossids was sufficient to create Clementsian distributions for the entire metacommunity.

Two biological factors may contribute to the lack of significant coherence for frugivores in Paraguay. First, the size of the area in Paraguay that supports species-rich ensembles of frugivorous bats is small; consequently, the variation required for sites to order along a gradient may not be present. Second, these analyses were based only on presence/absence data. For highly vagile animals, it may be that incorporation of relative abundances is required to detect a gradient of environmental variation over a relatively small geographic area such as eastern Paraguay. Four frugivores (*Artibeus jamaicensis*, *Artibeus lituratus*, *Platyrrhinus lineatus* and *Sturnira lilium*) had occurrences of transients in western Paraguay. It was possible that these occurrences in habitats that do not support frugivore populations contributed to the random pattern of frugivore distributions; consequently, analyses of frugivores restricted to eastern sites were conducted. Results were not qualitatively different (i.e., non-coherence) from those that included all sites, indicating that species distributions of the frugivore meta-ensemble were random in eastern Paraguay. Alternatively, it is possible that a lack of coherence for the frugivore meta-ensemble results from a lack of statistical power. The ability to detect significant differences in null model tests such as those used in analyses of coherence and turnover are affected by matrix size, with power increasing with matrix rank. Of the analyses herein, those of frugivores were based on the smallest matrix (18 sites and nine species), which would make these analyses the most susceptible to insufficient power. Nonetheless, this matrix was larger than a number of matrices for which significance was detected for coherence, turnover, and boundary clumping (Kusch et al. 2005; Leibold and Mikkelson 2002; Presley and Willig unpublished). It appears that this matrix is sufficiently large that a finding of significance is possible, though such a finding may be less likely than for similarly structured larger matrices. In addition, it is possible that the relatively high degree of fill in the frugivore matrix (60%) combined with the size of the matrix reduces the null space defined by the null model to such a degree that power in the associated analyses was low.

Molossids are reported to have patchy distributions throughout their geographic ranges (Dolan 1989); however, recent work (C. López-González, unpublished data) suggests that molossid populations track resources in space and time, and that their location in a particular place and time may be contingent on resource availability and dietary requirements of the bats. Molossids may be able to employ this unique strategy because they are highly vagile and migrate long distances (e.g., Norberg and Rayner 1987), which enhances their ability to take advantage of ephemeral resources and small patches of suitable habitat within their geographic distribution. Considering their migratory ability, idiosyncratic tendencies, and ability to respond quickly to changes in resource abundances, the random distribution of molossid ranges in Paraguay is not a surprising result.

Results of the ordination of sites via reciprocal averaging were consistent with results of previous assemblage-level analyses that incorporated biome associations (Willig et al.

2000) or habitat variables (López-González 2004; Stevens et al. 2007); bat assemblages are not distinct for each biome. Rather, sites formed four groups, corresponding to eastern Paraguay, flooded habitats, Matogrosense and Alto Chaco (Fig. 3). Although sites for each analysis were ordered in a manner consistent with the temperature/precipitation gradient, at the ensemble-level distinct clusters of sites (whether associated with a particular biome or not) typically did not emerge (Fig. 3). One exception was for analyses based on frugivores, in which sites formed three distinct clusters, but clusters were not coincident with particular biomes.

Pitfalls of analysis of EMS

In addition to the range perspective presented here, Leibold and Mikkelson (2002) suggested that analyses of turnover and boundary clumping are appropriate to conduct from the community perspective as well. Nonetheless, it is unclear if analyses from a community perspective are ecologically relevant or interpretable within the context of idealized patterns of species distribution. For example, from the range perspective, species turnover as a result of the replacement of one species with another along a gradient is consistent with the concepts of species turnover (i.e., beta diversity) and the ecological importance of such patterns is a subject of long and rigorous study (e.g., Peet 1974; Leibold et al. 1997; Veech et al. 2002; Chalcraft et al. 2004). Similarly, if the boundaries of species are coincident, evenly spaced, or randomly spaced, such patterns may be explained by multiple mechanisms based on biotic interactions or species-level responses to abiotic variables; the biological implications of such patterns are readily apparent. In contrast, it is unclear how to interpret community turnover or community boundary clumping within a metacommunity context. For example, if community boundaries are clumped it means that a single species represents the boundary of the environmental gradient for a number of sites. Such a species represents the most environmentally tolerant species to occur at each site, but it is unclear what interpretation could be applied to that fact within the context of models of species distribution, or how such observations could be interpreted to represent Clementsian distributions. Alternatively, a single site from the range perspective can represent an environmental boundary or ecotone at which range boundaries of species are clumped, which could result from multiple biogeographic or ecological mechanisms and is consistent with Clements (1916) original conception of patterns of range distributions.

If one accepts that analysis of patterns of species distributions from each perspective (range or community) is justified, additional complications emerge when the pattern of best fit is contingent on perspective. For example, predators

of sticklebacks evinced Gleasonian distributions from the range perspective, whereas nestedness was the pattern of best fit from the community perspective (Zimmerman 2006). In this case, the Gleasonian distributions from the range perspective, which likely represent the proper analysis of species distributions, were ignored and nested subsets were assumed to describe the predator metacommunity. This decision was made despite the author's observation that distinct groups of predators "represented a mixture of small and large predators that did not co-occur with each other". The described pattern as well as the ordinated metacommunity (Table 4 in Zimmerman 2006) were not consistent with nested subsets, but with positive species turnover and Gleasonian distributions. The reasons and criteria for the author's decision were not given. Moreover, problems can emerge if authors are not careful with terminology. For example, in an exhaustive analysis of a lepidopteran metacommunity (Kusch et al. 2005), the perspective (range or community) of analysis was not specified. The terms "community patterns" and "community boundaries" were used in Table 3 (Kusch et al. 2005), which implied a community perspective was used in analysis, but the authors stated that they followed the methods of Leibold and Mikkelson (2002), which were conducted from a range perspective. Obviously, these inconsistencies make the analyses difficult to interpret. As a result of these complications, unless a specific hypothesis requires use of the community perspective, we recommend analyses of EMS for metacommunities be restricted to the range perspective.

In addition to ordination of a metacommunity using reciprocal averaging, analysis of EMS based on alternative ordinations may be appropriate depending on the question of interest. For example, there is some discussion (Leibold and Mikkelson 2002; Hylander et al. 2005) about the proper ordination method for analysis of nestedness. We contend that each ordination addresses a different question that is contingent on the basis of ordination, and that the answers to each question may be ecologically valid. For example, traditional analyses of nestedness (Wright and Reeves 1992; Wright et al. 1998; Jonsson 2001) ordinate matrices based on richness of sites and incidence of species and evaluate if the degree of nestedness in the metacommunity is greater than expected by chance regardless of any particular environmental gradient. In contrast, analysis of EMS addresses the pattern of species distribution only along a specific gradient (that resulting from ordination via reciprocal averaging). Consequently, results based on EMS and traditional approaches to evaluate nestedness may be inconsistent, but not at odds as it is possible for a metacommunity to be nested without being nested along a specific gradient.

Although EMS may distinguish among idealized patterns of species distribution, results commonly do not coincide

perfectly with a particular model; nonetheless, there is always a pattern of best fit. In such cases, the correspondence between an idealized pattern and that of the metacommunity may not be strong and the investigator is required to be more discerning when interpreting results. For example, best fit patterns for lepidopteran distributions (Kusch et al. 2005) were reported as "not detected" for three analyses for which random distributions was the best fit pattern. In each of these analyses, two of three results (random turnover and random boundary clumping) were consistent with randomly placed distributions; consequently, that was the pattern of best fit. Moreover, because the only test not consistent with the best fit model, the test for coherence that uses Random 0, is prone to type I errors (Gotelli and Graves 1996; Leibold and Mikkelson 2002), a conclusion of random distributions was justified.

Analytical approaches that select the pattern of best fit among several options are powerful tools that can simultaneously test multiple hypotheses. Improved understanding of the application of analyses of coherence, species range turnover and species boundary clumping could enhance identification of patterns of species distributions and understanding of mechanisms that effect changes in species composition in geographic space. If EMS are studied for a wide-range of taxa and locations, general associations may emerge between particular idealized patterns of distribution and specific taxa, ecological contexts or biogeographic situations.

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