Geographical ecology of Paraguayan bats: spatial integration and metacommunity structure of interacting assemblages

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Summary

1. We examined the relative contributions of regional spatial characteristics and local environmental conditions in determining Paraguayan bat species composition.

2. We used a suite of full and partial redundancy analyses to estimate four additive partitions of variance in bat species composition: (a) unexplained variation, (b) that explained purely by spatial characteristics, (c) that explained purely by local environmental conditions and (d) that explained jointly by space and environment. The spatial component to bat species composition was greater than the environmental component and both pure spatial and pure environmental characteristics accounted for significant amounts of variation in bat species composition.

3. Results from variance decomposition suggest that the mass effects model describes metacommunity structure of Paraguayan bats better than species sorting or neutral models. Such mass effects may potentially be general for bats and could explain the inability of purely local factors to fully account for bat community organization. Mass effects also have substantial conservation implications because rescue effects may enhance the persistence of mobile species in fragmented landscapes with relatively few protected sites.

Key-words: bat assemblage, chiroptera, community structure, metacommunity, variance decomposition.

Introduction

Community ecology has witnessed the rapid development of a new paradigm that unites both local and regional processes to understand more clearly the spatial structure of groups of communities within regions (Leibold & Miller 2004; Leibold *et al*. 2004; Holyoak, Holt & Leibold 2005). Indeed, the metacommunity concept has revolutionized community ecology by integrating within-community phenomena such as biotic interactions and environmental tolerances with larger-scale spatial phenomena such as dispersal, spatially structured biotic interactions and habitat fragmentation. Moreover, the conceptual underpinnings of the metacommunity approach have broad applicability not only to communities, but to sets of coexisting species that are geographically, taxonomically or functionally restricted such as assemblages, guilds, local guilds and ensembles (Fauth *et al*. 1996).

A powerful approach to explore metacommunity structure explicitly incorporates effects due to local environmental characteristics and effects of spatial contagia such as dispersal, disturbance or spatially structured biotic interactions (Cottenie *et al*. 2003). A number of types of spatially mediated metacommunity structure have been modelled and described (Leibold *et al*. 2004). Caswell (1976), Bell (2000) and Hubbell (2001) described neutral models of metacommunity structure that reflect purely spatial processes. In such models, species are assumed to be equivalent in interactions with themselves and their environment and differences among communities reflect purely

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spatial processes of migration combined with ecological drift. Models of species-sorting describe deterministic spatial variation among communities (Tilman 1982; Chase & Leibold 2003) resulting from the effects of local abiotic features on population growth and interspecific interactions. Species exhibit strong partitioning based on environmental characteristics, but dispersal is low and cannot facilitate the persistence of species outside their optimal habitat or niche. Mass-effects models describe spatial integration among communities resulting from high amounts of dispersal in combination with differences among species regarding their response to environmental characteristics (Holt 1993; Amarasekare & Nisbet 2001; Mouquet & Loreau 2002). High rates of dispersal of species into suboptimal habitats allow for the integration of communities regardless of species responses to environmental heterogeneity. Leibold *et al*. (2004) summarize the main differences among these models as

a continuum characterizing opposing dispersal and species–environment interactions. At one extreme, the neutral model describes structure mediated only by dispersal. Alternatively, metacommunity structure could reflect strong species sorting in response to environmental characteristics. Between these extremes, mass effects prevail.

Much of the effort to develop the metacommunity concept and ultimately models of metacommunity structure has been either theoretical or experimental, with much less empirical work describing the degree to which metacommunities exhibit such structure in nature (Leibold & Miller 2004; Leibold *et al*. 2004). Much of this empirical work has focused on invertebrates (Gonzalez 2005; Kolasa & Romanuk 2005; Miller & Kneitel 2005; van Nouhuys & Hanski 2005), in particular aquatic invertebrates (Cottenie *et al*. 2001, 2003; Cottenie & De Meester 2003, 2004; Cottenie 2005) living in relatively bounded lake communities. Thus, these studies have focused primarily on groups possessing limited mobility and have demonstrated primarily strong species sorting that overwhelms effects of migration.

Bats offer an exceptional opportunity to explore determinants of spatial variation in species composition and metacommunity structure. Bats are highly mobile, suggesting that sites within regions may be highly integrated via dispersal (Willig & Moulton 1989; Stevens & Willig 1999; Bernard & Fenton 2003; Fenton 2003). Moreover, species composition of bats may be related to environmental characteristics (Willig *et al*. 2000; López-González 2004; Stoner 2005), habitat degradation (Fenton *et al*. 1992; Medellín, Equihua & Amin 2000; Estrada & Coates-Estrada 2002; Clarke, Pio & Racey 2005), architecture of habitat fragmentation (Gorresen & Willig 2004; Gorresen, Willig & Strauss 2005) or resource availability (Aguirre *et al*. 2003; Giannini & Kalko 2004). Herein, we examine metacommunity structure of 26 Paraguayan bat assemblages. Specifically, we examine the relative contributions of habitat characteristics and spatial characteristics in an attempt to determine the degree to which local and regional processes structure the Paraguayan bat metacommunity.

Materials and methods

STUDY SITE

Paraguay is a small (406 752 km^2) landlocked country that occurs between Argentina, Brazil and Bolivia (Fig. 1). The country is bisected by the Tropic of Capricorn and therefore occurs at the temperate–tropical interface. Climate is subtropical and continental being characterized by hot, wet summers and cool, dry winters. Temperature and precipitation vary gradually along a gradient from warmer and drier in the north-west to cooler and wetter in the south-east. Mean annual temperature ranges from 21 °C to 26 °C and precipitation ranges from 400 mm to 1800 mm (Fariña Sánchez
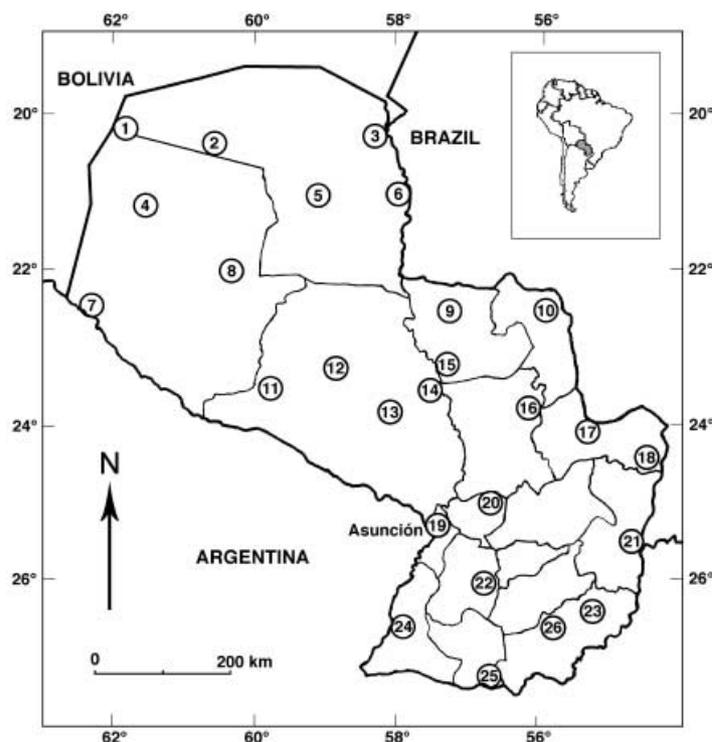

Fig. 1. Geographic position of 26 sites sampled. Each point indicates the centre of a 50 × 50 km^2; names refer to geographical landmarks within the squares, as follows: 1, Boquerón, Parque Cue; 2, Alto Paraguay, Parque Nacional Defensores del Chaco, Cerro León; 3, Alto Paraguay, Bahía Negra; 4, Boquerón, Parque Nacional Teniente Agripino Enciso; 5, Alto Paraguay, Laguna Placenta; 6, Alto Paraguay, Fuerte Olimpo; 7, Boquerón, Base Naval Pedro P. Peña; 8, Boquerón, Mariscal Estigarribia; 9, Concepción, Parque Nacional Serranía San Luis; 10, Amambay, Parque Nacional Cerro Cora; 11, Presidente Hayes, Fortín General Díaz; 12, Presidente Hayes, Rio Verde-Juan de Zalazar; 13, Presidente Hayes, Estancia La Victoria; 14, Presidente Hayes, Estancia Loma Pora; 15, Concepción, R. L. Petit; 16, San Pedro, Yaguarete Forests; 17, Canindeyu, Reserva Natural del Bosque Mbaracayu; 18, Canindeyu, Reserva Privada Itabo; 19, Central, Asunción; 20, Cordillera, Estancia Sombrero; 21, Alto Parana, Itaipu Binacional; 22, Paraguari, Parque Nacional Ybycui; 23, Itapua, Mayor J. Otaño; 24, Ñeembucú, Estancia Yacare; 25, Misiones, Yabebyry Ayolas; 26, Itapua, Parque Nacional San Rafael.

1973). Seven different phytogeographical zones are recognized for Paraguay (Hayes 1995). Topography is relatively flat, with only a few rolling hills in the eastern portion of the country (Gorham 1973). Moreover, soil types change along these gradients with well-drained soils in the Alto Chaco, poorly drained soils in the Matogrosense, Bajo Chaco and Ñeembucú, and rich, well-drained soils in the Campos Cerrados, Central Paraguay and Alto Paraná phytogeographical regions.

BAT SPECIES COMPOSITION

Bat species composition was characterized at 26 sites distributed throughout the country (Fig. 1). Sites 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 centred at the site. Bat species composition within quadrats was assembled from a faunal survey that occurred between 1995 and 1997 and additional museum specimens (López-González 1998). Effort at each site associated with the faunal survey consisted of capturing bats in mist-nets set in all obvious habitats. Nets were monitored from dusk until 0100. Often, nets were monitored until dawn. On average bat species composition of sites was based on more than 100 net nights of effort. Our database comprised a total of 5012 individuals representing 48 species and five families of bats. Further information on Paraguayan bat communities in general and sampling protocols for these sites in particular can be found in Myers (1982), López-González (1998, 2004), Willig *et al.* (2000), Gorresen & Willig (2004), Steven, Willig & Gamarra de Fox (2004) and Gorresen, Willig & Strauss (2005).

We conducted a variance decomposition to determine the relative effects of habitat and spatial characteristics on variation in species composition using the methods of Borcard, Legendre & Drapeau (1992), Cottenie *et al.* (2003) and Cottenie (2005). These methods provide considerable flexibility depending on data structure. Specifically, our analyses began with two spatial variables consisting of the *x* and *y* geographical coordinates of each site, four environmental variables describing variation in elevation, precipitation, temperature and evapotranspiration (a surrogate for net primary productivity) and percentage cover of 17 different vegetation types (found in López-González 2004). Preliminary analyses indicated that the environmental variables did not account for substantive amounts of variation in bat species composition over and beyond the vegetation variables. Therefore we eliminated the environmental variables to improve power of our analyses. To reduce the number of independent variables, we conducted principal components analysis on the 17 vegetation attributes. We used the first two principal components (PCs), which accounted for most of the variation among sites in terms of vegetation attributes. This also balanced the number of environmental and

spatial variables giving equal weight to each class of variable in the analysis.

The two spatial and two environmental variables were entered into a series of full and partial redundancy analyses to obtain four components of variance: (1) total variation in bat species composition accounted for by both the spatial and environmental variables, (2) proportion of variation in bat species composition accounted for by the environmental variables after accounting for the spatial variables (pure environment structure), (3) proportion of variation in bat species composition accounted for by spatial variables after accounting for environmental variables (pure spatial structure) and (4) proportion of variation in bat species composition shared by both environmental and spatial variables (i.e. spatial autocorrelation).

To determine the total variation in bat species composition accounted for by spatial and environmental variables, we conducted a redundancy analysis whereby bat species composition was the dependent matrix and spatial and environmental variables composed the independent matrix. To determine the pure spatial component, or that variation accounted for by the spatial variables after removing spatial autocorrelation, we conducted a partial redundancy analysis. In this analysis, bat species composition was the dependent matrix, spatial variables represented the independent matrix and environmental PCs were used as a covariate matrix. To determine the pure environmental component, or that variation accounted for by the environmental PCs after removing spatial autocorrelation, we conducted another partial redundancy analysis. In this analysis bat species composition was the dependent matrix, environmental PCs were the independent matrix and spatial variables were used as a covariate matrix. Finally, the amount of variation accounted for by the interaction between space and environment (spatial autocorrelation) was determined by subtracting pure spatial variation and pure environmental variation from the total explained variation. Such an approach decomposes spatial variation in species composition into independent components due to species responses to (a) environmental characteristics, (b) spatial characteristics and (c) spatially structured environmental characteristics (i.e. spatial autocorrelation).

DISTINGUISHING BETWEEN MODELS OF METACOMMUNITY STRUCTURE

Four models of dispersal-mediated metacommunity structure have been described: mass effects, species sorting, neutral and patch dynamics models. These models can be distinguished based on the relative importance of local and regional processes (Table 1, based on Holyoak, Holt & Leibold 2005).

Species sorting models assume that species are highly responsive to environmental characteristics associated with sites within a metacommunity and that

Table 1. (a) Classification of different models of metacommunity dynamics based on differences in dispersal and species responses to environmental heterogeneity (after Holyoak, Holt & Leibold 2005). (b) The identification of three models based on significance or lack thereof of different variance components. E and S stand for the amount of variation in species composition of bats accounted for by the environmental and spatial descriptors, respectively. E/S refers to the amount of variation accounted for by environment after removing variation shared with space. S/E refers to the amount of variation accounted for by space after removing variation shared with environment

| | | Dispersal sufficient for persistence | | |
		No	Yes	
(a) Species respond to	No	–	Neutral	
environmental variation	Yes	Species sorting	Mass effects	
(b) Model	E	S	E/S	S/E
Neutral	NS	***	NS	***
Species sorting	***	NS	***	NS
Mass effects	***	***	***	***

dispersal is insufficient to affect the persistence of species in particular patches (Tilman 1982; Chase & Leibold 2003). In such a scenario, environmental characteristics and not dispersal should determine spatial variation in species composition. Accordingly, in the variance decomposition we employ, if metacommunity structure is the product of species sorting, spatial characteristics should not be strong and should not account for significant variation in bat species composition. In contrast, environmental variation should be strong and should account for a significant amount of variation in bat species composition over and beyond that of spatial autocorrelation; only the pure habitat variance partition should be significant.

Under a scenario of mass effects [mass effects + species sorting perspective of Cottenie (2005)], species are responsive to environmental characteristics associated with sites, but dispersal allows species to persist in less suitable patches via source–sink dynamics (Holt 1993; Mouquet & Loreau 2002). In such a scenario both environmental and spatial characteristics should be strong and account for variation in bat species composition over and beyond the effects of spatial autocorrelation. In the variance decomposition, both pure habitat and pure spatial partitions should be significant, with the relative sizes of these partitions reflecting the relative degree to which spatial and species–environment interactions contribute to metacommunity structure.

The neutral model (Caswell 1976; Bell 2000; Hubbell 2001) makes predictions of metacommunity structure given that all species are 'ecologically equivalent' and do not differ greatly in rates important to metacommunity dynamics such as dispersal, competitive abilities, birth and death. As such, species should not exhibit strong associations with habitat characteristics, and the structure of spatial variation among sites in the metacommunity should be determined solely by spatial processes. Consequently, spatial variation should account uniquely for variation in bat species composition and significance of only the pure spatial component indicates agreement with predictions of the neutral model. The patch dynamics model (Levins & Culver

1971; Yu, Wilson & Pierce 2001) is similar to the neutral model in the importance of spatial processes in determining structure of the metacommunity. The main difference is that a temporally dynamic trade-off between dispersal and competitive ability causes differences among sites in terms of species composition. Because we do not have a time–series of samples at each site, these two models cannot be distinguished with these data. None the less, both patch dynamics and neutral models predict that only spatial processes are important to the structure of the metacommunity, and as such these two models can be considered in the same vein when contrasted against mass effects and species sorting models (Cottenie 2005).

We predict that for bats in general, and for the Paraguayan metacommunity in particular, dispersal-mediated metacommunity structure will exist, and that mass effects will describe this structure most effectively. Bats can exhibit strong habitat affinities (Stoner 2001; Aguirre 2002; Adams *et al.* 2003; Clarke, Pio & Racey 2005) and do so in Paraguay (López-González 2004). Moreover, because of their volant nature, bats have proven dispersal capabilities (Wilkinson & Fleming 1996; Petit & Mayer 1999; Kurta & Murray 2002; Carstens *et al.* 2004), sometimes spanning continental scale distances (McCracken, McCracken & Vawter 1994; Cryan *et al.* 2004). Taken together, both habitat characteristics and spatial characteristics should act in concert to affect bat assemblage structure.

Results

Principal components analysis identified two salient environmental gradients summarizing the 17 habitat variables (Fig. 2). PC's had eigenvalues > 1·0 and together they accounted for approximately 66% of variation in habitat characteristics among sites. In each case a readily identifiable gradient underlies the derived variable. The first PC represents an east–west axis with sites from eastern Paraguay having negative values and sites from western Paraguay having positive values. This axis reflects the vegetation changes across the country ranging from dry chaco in the north-west to
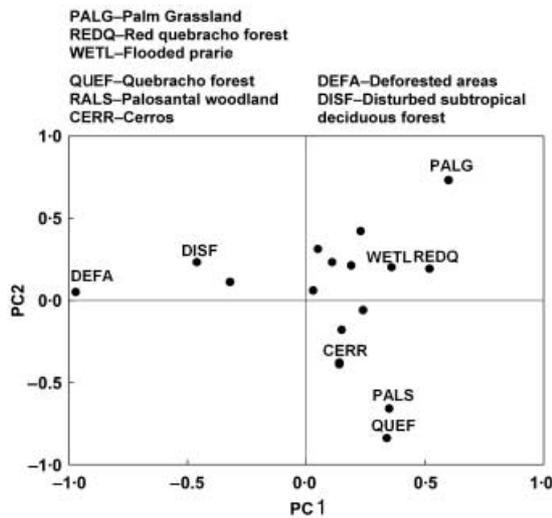
Fig. 2. Correlations of original habitat variables with the first two principal components. Acronyms define variables that were correlated significantly with at least one principal component.

semideciduous broadleaf subtropical forest in the east. The second PC reflects vegetation and soil characteristics that vary from well-drained habitats at low values to seasonally inundated habitats at high values.

In the full redundancy analysis, the four explanatory variables (PC1, PC2, *x*-coordinate, *y*-coordinate) accounted for approximately 50% of the variation in bat species composition among sites and this result was highly significant ($P < 0.001$). Spatial and habitat characteristics alone accounted for 40% and 32% of the variation among sites regarding bat species composition, respectively (Fig. 3). Both spatial and habitat characteristics accounted for significant amounts of variation

Variance Decomposition		
Component	Percent Variation	P-Value
[S+E]	0·499	< 0·001
[E]	0·315	< 0·001
[S]	0·401	< 0·001
[E∣S]	0·099	0·011
[S∣E]	0·184	< 0·001
[S∩E]	0·216	NA

Fig. 3. Results from full and partial redundancy analysis decomposing variation in bat species composition into additive components. Proportion of variation accounted for habitat variables after accounting for spatial variables (E∣S), proportion of variation accounted for spatial variables after accounting for habitat variables (S∣E), and variation accounted for by both spatial and habitat variables (S∩E) sum to form variation accounted for by the model (S + E). (E) and (S) refer to amount of variation accounted for by habitat and spatial variables, respectively, without taking into account their correlated effects.

in bat species composition even after controlling for the effect of the other type of variable. Spatial characteristics accounted for 18% of the variation ($P < 0.001$) in species composition after removing variation shared with habitat characteristics. Habitat characteristics accounted for 10% ($P = 0.011$) of the variation in species composition after removing variation shared with spatial characteristics. Finally, spatially structured habitat characteristics (interaction term) accounted for approximately 22% of the variation in bat species composition among sites. Spatial and environmental effects when considered alone accounted for substantive variation in species composition. Both effects still accounted for appreciable variation after controlling for the other type of variable. Strong variation in both the pure space and pure habitat components, as suggested by the magnitude as well as statistical significance of variance components, indicates that mass effects [also known as the mass effects + species sorting perspective of Cottenie (2005)] probably determine the structure of this metacommunity.

Discussion

Paraguayan bat assemblages demonstrate considerable structure at the regional level. Our suite of analyses suggests that both habitat characteristics and spatial processes contribute to this structure. Moreover, variance decomposition suggests that the mass effects model describes most clearly the structure of this metacommunity. In other words, spatial heterogeneity in bat species composition results from significant habitat affinities that are regulated by the integration of sites via dispersal.

IMPLICATIONS OF MASS EFFECTS

Our results suggest that metacommunity structure of Paraguayan bats results from the integration of local processes and dispersal. Indeed, variance decomposition indicates that spatial processes accounted for more unique variation than do environmental characteristics and suggests that mass effects are important in determining the distribution and abundance of bats in this metacommunity. Paraguayan bats exhibit substantive environmental relationships (Gorresen & Willig 2004; López-González 2004; this study) that probably enhance the persistence of particular species at some sites as well as diminish or even prevent occurrence at other sites. None the less, source–sink dynamics probably mediate such environmental effects. The high mobility of bats probably provides subsidies from more productive to less productive habitats, thereby integrating distant sites and generating spatial processes.

A recent meta-analysis evaluating the ubiquity of dispersal-mediated metacommunity structure as well as the relative frequency of different types of structure indicates that the greatest proportion of metacommunities (44% of 158) were influenced to only a minor degree by

spatial processes and could be characterized by the species sorting model (Cottenie 2005). The type of structure characterizing Paraguayan bats, explained more clearly by the mass effects model, accounted for approximately 29% of evaluated metacommunities. It is logical that highly mobile organisms will conform typically to a mass effects model and that the degree of mobility will influence which type of model best describes structure for a particular taxon.

Typically, bats exhibit significant habitat associations. This is true in Paraguay (Gorresen & Willig 2004; López-González 2004) as well as in general (Krusic *et al*. 1996; Walsh & Harris 1996; Ellison, Everette & Bogan 2005; Russo *et al*. 2005). None the less, the amount of variation in bat species composition accounted for by environmental characteristics is typically only moderate (40%, Paraguay, López-González 2004; 67·4%, Mexico, Wang *et al*. 2003; 26·1%, Switzerland, Jaberg & Guisan 2001) and probably reflects generality of habitat use or diversity of environments included in analyses. All species evaluated here probably have the dispersal potential to occur at all sites in Paraguay. Moreover, bats probably take advantage of their high mobility and track resources through time at the landscape scale (Fleming 1988; Cryan 2003; Richter & Cumming 2006), thereby spatially integrating communities through dispersal. Such mobility has major implications to our understanding of community organization. Previous studies of New World bats have demonstrated that purely local phenomena, in particular biotic interactions, do not provide consistent structure, at least as defined by theoretical predictions of species sorting or deterministic abundance patterns (Arita 1997; Stevens & Willig 1999, 2000). The relatively high species richness of most feeding guilds characterizing New World bats suggests ample potential for competitive interactions. None the less, high mobility, in particular mass effects that allow species to occur in suboptimal habitats, may reduce competitive exclusion and enhance the likelihood of species coexistence. Indeed, regional perspectives integrating the effects of spatial processes on local interactions may be required to understand more comprehensively the factors that structure local bat communities.

CONSERVATION CONSIDERATIONS

Spatial processes have considerable conservation implications. Perhaps the most important is that bat assemblages are connected by dispersal. The mass effects described by our analyses suggest that rescue-effects (Brown & Kodric Brown 1977) may play an important role in conserving bat species composition within communities. This is important, particularly in Paraguay, because a high rate of deforestation has occurred over the last century (Universidad Nacional de Asunción 1991, 1994). Dispersal-integrated sites may be a promising conservation option for vagile species (e.g. birds and bats). Analyses of sites in Paraguay (Yahnke 1998; Andelman & Willig 2002) and those involving reserve siting in general often point out inadequacies of contemporary reserve systems but do not take such integration into account. As such, they represent worst-case scenarios based on assumptions of a lack of rescue effects, no positive or negative biotic interactions, and the inability of species to adapt to less than ideal environmental characteristics. None the less, the conservation implications of metacommunity dynamics are profound, because they suggest that the innate characteristics of species, in particular their dispersal abilities, offer an effective conservation tool. Moreover, these innate characteristics may be even more effective than the limited and often politically precarious conservation strategies implemented by mankind.

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