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Morphological assembly mechanisms in Neotropical bat assemblages and ensembles within a landscape

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Abstract Empirical studies on bat assemblages have shown that richness is not appreciably influenced by local processes such as ecological interactions. However, most of these studies have been done in large areas that include high heterogeneity, and they analyse all bat species within such areas, and thus they may be not reflecting local but supra-community conditions. We followed an ecomorphological approach to assess how bat assemblages of species from the families Phyllostomidae and Mormoopidae, and ensembles of frugivorous bats, are assembled in local habitats within a single landscape. We measured the volume of the space defined by wing morphology and quantified the average distance between species within such a volume. Then, we related these measures to local richness. Such relationships were contrasted against relationships with random assemblages to test for statistical differences. At the ensemble level of organization, we found that the frugivorous bat morphological assembly mechanism is different from random patterns, and it corresponds to the volume-increasing model. On the other hand, bat assembly mechanisms may be ubiquitous at the assemblage level, because groups of species coexisting in a local habitat and delimited only by phylogeny include more than one ecological group with no potential to interact. Assembling processes are crucial to an understanding of species diversity in local communities, and ecomorphological analyses are very promising tools that may help in their study.

Keywords Chiroptera · Community niche · Coexistence · Null models · Packing

Introduction

The relative contribution of local versus regional processes in determining the species diversity and structure of local assemblages is a currently debated question, and may be the key to understanding patterns of composition and diversity in ecological communities (Cornell and Lawton 1992; Ricklefs and Schluter 1993; Lawton 1999; Gaston 2000; Whittaker et al. 2001; Ricklefs 2004). Local processes, such as competition, predation, mutualism, environmental variability, resource productivity, and resource diversity, are manifested at ecological scales, whereas regional processes, such as differences in age, rates of speciation and immigration, and history of extinction, occur at historical, biogeographical scales (Ricklefs and Schluter 1993). The mechanisms leading to changes in the diversity of local communities are critical to an understanding of the regulation of local richness as a balance between local interactions and regional processes (Ricklefs 2004).

Analyses of bat assemblages have tried to distinguish their structuring processes, showing that they do not differ from random subsets of the regional pool. These results suggest that ecological processes, such as competitive exclusion, have only a marginal contribution in building bat assemblages (Willig and Moulton 1989; Arita 1997) or are not consistent over different biogeographical areas and feeding guilds (Stevens and Willig 1999). However, these studies have considered assemblages in large areas that include high heterogeneity in environmental conditions (regional or gamma diversity), and thus they may be not accurately reflecting co-occurring groups of species at a particular habitat and time (local or alpha diversity).

In this paper, we examine the assembly mechanisms of bat assemblages and ensembles using an ecomorphological approach. Ecomorphology analyses morphological

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traits of individuals to infer their ecological characteristics, assuming that the concurrent effects of ecological requirements and evolutionary histories have determined the size and shape of living organisms (Wainwright and Reilly 1994). Ecomorphology has been extensively used in the study of bat assemblages, as the direct relationships between ecology and morphology has been clearly demonstrated for Chiroptera (Findley and Wilson 1982; Norberg 1994; Swartz et al. 2003). Here we describe the ecomorphological patterns of bat assemblages and ensembles in local habitats within an ecological landscape, with different levels of species richness. We follow Fauth et al. (1996) in using the term “assemblage” to describe a set of species delimited by phylogeny that coexist in a local habitat, and the term “ensemble” to describe a set of species within an assemblage that belong to a common functional group. At the level of assemblages, because of the inclusion of species that rarely or never interact, ecological processes are expected to have only a very weak effect, producing no detectable morphological patterns. In contrast, at the ensemble level of organization, ecological interactions are expected to have a stronger effect, producing a significant signal on the morphological patterns of the species sets.

In theory, when increasing in number of species, local communities can change in two basic directions (Ricklefs and Schluter 1993; Ricklefs and Miles 1994): (1) by packing new species into the niche space already occupied by original species (the “species packing mechanism”), or (2) by increasing the volume of the niche space to accommodate the new species (the “volume-increasing mechanism”). If species packing and niche volume are measured using morphological traits, in the first case the morphological distance among species should decrease, while the volume should remain constant. In the second case, volume should increase, while the average morphological distance can change or not depending on the arrangement of new species outside the original volume (Fig. 1). For example, the average distance among species can decrease, even with an increase of the niche volume, if new species are arranged outside the original space, but at short morphological distances among them and to the original species (Fig. 1e, f). An example of this mechanism may arise when a biogeographical constraint, such as a barrier, prevents the dispersion of a complete functional group with limited dispersal ability. When the barrier ceases to function, the whole functional group can invade the existing assemblage, thus increasing its niche volume but decreasing the average distance among species. A fourth alternative model would be one in which the volume decreases while species richness increases, but this cannot occur because even if new species pack very closely to each other into the niche space already occupied by present species, the original species would have to constrain their niche for this to occur.

Ricklefs and Schluter (1993) and Ricklefs and Miles (1994) have stated, as an empirical rule based on results for vertebrate assemblages, that the volume-increasing

mechanism is a more common process in natural communities. This generalization suggests that assemblages, regardless of the number of species in their regional pool, experience strong ecological processes that ultimately determine their species richness and assemblage structure. This contradicts available information regarding the structuring of Neotropical bat assemblages, for which neutral processes have been proposed as determinants of richness and structure (Willig and Moulton 1989; Arita 1997). In this paper we analyse this apparent contradiction by testing possible assembly mechanisms of local bat assemblages and ensembles belonging to a single regional pool.

Materials and methods

Study site and bat captures

The study area is located in central Veracruz, Mexico, between 19°17' and 19°22' N latitude, and 96°43' and

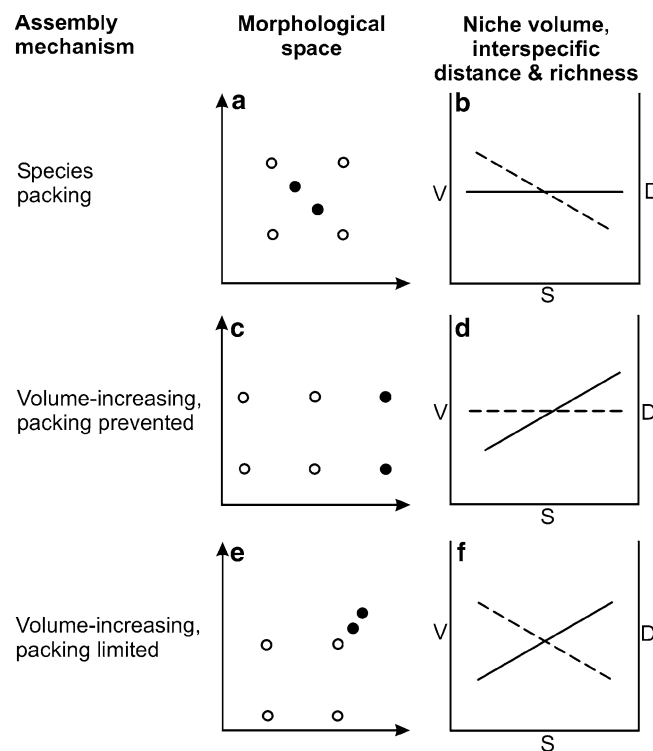


Fig. 1 Three theoretical models for species distribution in morphological space and the relationship between species richness (S) and niche volume (V , solid line) and interspecific distance (D , dashed line). **a** When new species (filled circle) pack into the space defined by resident species (open circle), **b** an increase in species richness is not related to niche volume and species packing causes a decrease in the interspecific distance. **c** When packing is prevented and new species occupy positions out of the morphological space of resident species, **d** richness is positively related to niche volume, and has no effect on interspecific distance. Finally, **e** when packing is limited and guilds are added close to (but out of) the morphological space of resident species, **f** richness is positively related to niche volume and negatively to interspecific distance

96°49' W longitude. Elevation ranges from 350 to 700 m a.s.l. Plateaus, deep ravines with high slopes, as well as valleys and limestone hills, characterize the landscape. Mean annual temperature is 22°C and mean annual rainfall is 1,500 mm. The area covers approximately 42 km² and comprises tropical subdeciduous forest, deciduous forest, riparian vegetation, palm stands, secondary vegetation, mango plantations and corn fields. Fourteen sampling sites were distributed throughout these seven habitats. At each sampling site, bat surveys were conducted every 2 months from July 1995 to June 1997, except on full-moon nights to avoid capture bias due to lunar phobia (Morrison 1978). In each survey, the order in which sites were sampled was set at random. Bats were captured with standard mist nets (38 mm mesh, 2.5 m high and 12 m wide) set at ground level. Nets were opened at dusk for 1–3 h, for 1 night at each sampling site. Nets were monitored every 30 min and individual bats were identified to species with field keys (Medellín et al. 1997). Bats were marked with plastic collars and released at the site of capture. As this sampling procedure underestimates the presence of bats of the families Vespertilionidae and Molossidae that are able to detect the nets or that rarely fly at ground level (Bonaccorso 1979; Aldridge and Rautenbach 1987; Rautenbach et al. 1996; Fenton and Griffin 1997; Kalko 1997), we limited our analysis to families Phyllostomidae and Mormoopidae. Sampling effort was standardized per habitat, and the completeness of each habitat inventory was analysed (Moreno and Halfpeter 2000). A detailed description of the study area and sampling effort is given in Moreno and Halfpeter (2000, 2001).

Morphological measures

Ecomorphological analysis of bat assemblages has been based on different traits, including wing, skull and brain morphology (Findley and Wilson 1982). Wing morphology has deserved special attention because of the clear relationship between wing size and shape with ecological and behavioural traits of bat species (Findley et al. 1972; Findley and Wilson 1982; Findley and Black 1983; Schum 1984; McKenzie and Rolfe 1986; Aldridge and Rautenbach 1987; Norberg and Rayner 1987; Crome and Richards 1988; Willig and Moulton 1989; Fullard et al. 1991; Norberg 1994; Heller and Volleth 1995; Arita and Fenton 1997; Stevens and Willig 1999).

Three main descriptors of wing morphology have been proposed (Findley and Wilson 1982; Norberg and Rayner 1987; Findley 1993; Norberg 1994; Arita and Fenton 1997): (1) aspect ratio (wing length/wing width) is a general shape measure; (2) wing loading (weight/wing area) is a measure of the pressure needed to sustain flight; (3) wing tip index [tip area ratio/(tip length ratio–tip area ratio)] measures the shape of the wing tip. Basically, bats with wide, short and rounded wings (with low wing loading, low aspect ratio and high wing tip index) exhibit great agility, high manoeuvrability and

fly slowly among vegetation, thus preferring dense canopy habitats (Neuweiler 1989). In contrast, bats with narrow, long and pointed wings (high wing loading, high aspect ratio and low wing tip index) fly fast but exhibit limited agility and manoeuvrability, thus prefer to fly in open habitats.

For each individual, we computed body weight (w , in Newtons) as body mass (in kilograms) $\times$ gravitational acceleration (9.81 ms^{-2}). We also measured the forearm length (arm-wing length: l_{aw}) and the length of the third digit (hand-wing length: l_{hw}), and obtained a wing tracing by placing the ventral side of each bat on paper, extending the right wing to its maximum, and drawing around this half of the body. From wing tracings we measured wingspan length (B) and areas of different parts of the wing (hand-wing area, S_{hw} ; arm-wing area, S_{aw}) by cutting around each part of the drawing and passing the paper pieces through a leaf area meter. Total wing area (S) is the sum of S_{hw} and S_{aw} . These data allowed us to compute the main descriptors of wing morphology: aspect ratio: $AR = B^2/S$, wing loading: $WL = w/S$, and wing tip index: $I = T_s/(T_l - T_s)$, where $T_l = l_{hw}/l_{aw}$ and $T_s = S_{hw}/S_{aw}$, according to Norberg and Rayner (1987).

Data analysis

In a preliminary analysis, for those species with adequate sample sizes, we tested for differences in each wing morphology descriptor between sexes using ANOVA, and found significant sexual variability only for the wing loading value of one species (*Sturnira ludovici*, $P < 0.05$). Thus, we decided to use average values of wing descriptors for each species, regardless of sex. Because of the comparative purposes of the study, we used a single value for each variable for each species, averaging the values of individuals.

First, we performed a logarithmic transformation of wing descriptors to equalize the variances of the measurements (Ricklefs and Travis 1980). The log-transformed variables were then normalized by calculating their Z values: $Z = (x - \bar{x})/s$, where x is the value of the variable for each species, $\bar{x}$ is the mean value of the variable and s is its SD. Analyses are based on the position of each member of an assemblage or ensemble in a three-dimensional morphological space, the axes of which are the normalized values of the three variables: wing loading, aspect ratio and wing tip index (Fig. 2).

We tested the generalization about species diversity proposed by Ricklefs and Schluter (1993) and Ricklefs and Miles (1994), by computing mean interspecific distance within the morphological space occupied by the assemblage, and the dimension or volume of such morphological space. To perform this, we followed two approaches: the first one was to calculate the average nearest-neighbour distance (NND), based on Euclidean distances between pairs of species in an assemblage, as a measure of interspecific distance (Ricklefs and Travis 1980).

Volume of the morphological space was calculated with the formula:

$$V = 4/3\pi(2SD_{WL})(2SD_{AR})(2SD_I) \\ = 32/3\pi SD_{WL}SD_{AR}SD_I,$$

where V is the volume of the morphological space, SD_{WL} is the SD of wing loading, SD_{AR} is the SD of

aspect ratio, and SD_I is the SD of wing tip index. We modified the formula proposed by Ricklefs and Travis (1980) to measure the morphological volume as a sphere including 95% of observed values. Both interspecific distance and volume of each assemblage were calculated with Visual Basic programs.

In the second approach, we constructed the minimum-spanning tree (MST) for each assemblage based on Euclidean distances in the space formed by the three morphological variables (Moulton and Pimm 1986; Willig and Moulton 1989; Arita 1997). The MST is the shortest series of $n-1$ segments connecting the n species in an assemblage. The mean length of the connecting segments was calculated as a measure of interspecific distance, and the total length of the MST was used to quantify the volume of the morphological space. To construct the MSTs, we computed the amalgamation schedule of single linkage Euclidean distances for each assemblage with PCORD (McCunne and Mefford 1999), and using custom programs written in Visual Basic.

We decided to use both NND and MST approaches because some key references on morphological niche structure have used either NNDs (Ricklefs and Travis 1980; Ricklefs and Miles 1994) or MSTs (Moulton and Pimm 1986; Willig and Moulton 1989; Arita 1997; Stevens and Willig 1999), with contrasting results. In general, analyses based on NNDs support the idea that strong ecological processes determine species richness and assemblage structure, whereas those using MSTs tend to support the idea that neutral processes determine richness and structure in assemblages. We are not aware of any study using both approaches applied to the same data base.

Relationships between species richness and interspecific distance, and between species richness and volume of the morphological space, were tested with Pearson product-moment correlations, for both the NND and the MST approaches. Additionally, we tested if those relationships differed from random patterns, by comparing our results against custom-designed null models written in Visual Basic. The models generated 5,000 simulations of random sets of species based on two pools: the species pool of the ensembles of frugivores, and the species pool of all the Phyllostomid and Mormoopid assemblages. Each simulation computed seven random assemblages or ensembles according to the number of species for the seven real sets of species: eight, eight, eight, nine, 11, 11, and 12 species for ensembles and 11, 13, 13, 14, 15, 15, and 18 species for assemblages. In the generated ensembles and assemblages, each species was randomly and independently selected among the others, without replacement. We wrote Visual Basic programs for computing interspecific distance and volume in the morphological space, according to the NND and the MST approaches. Then, we computed Pearson correlations between these morphological variables and species richness for each simulation. The frequency distribution of the 5,000 correlation coefficients obtained

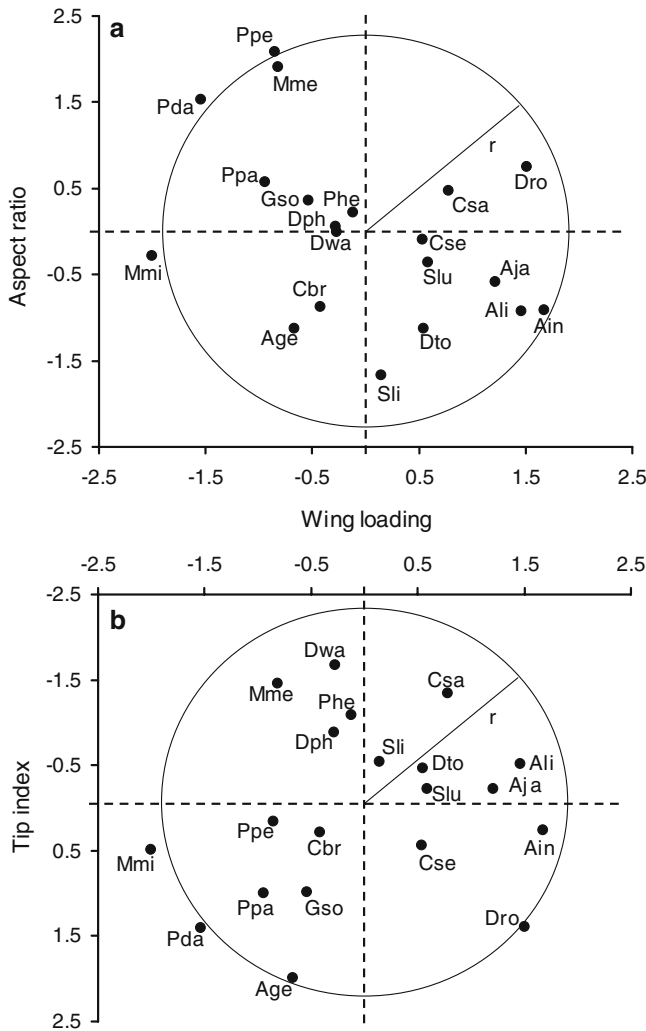


Fig. 2 The bat assemblage of Jalcomulco, Veracruz, Mexico in a morphological space determined by **a** wing loading and aspect ratio and **b** wing loading and tip index. Variables are normalized to have mean = 0 and variance = 1. Circles encompass 95% of observations (assuming normally distributed variables). Species are represented as points on two projections of the three-dimensional (3-D) space; to visualize the 3-D position of species, imagine folding the figure along the wing-loading axis so the aspect-ratio variable pops out on a third dimension perpendicular to the figure's plane. Species included are: *Anoura geoffroyi* (Age), *Artibeus intermedius* (Ain), *Artibeus jamaicensis* (Aja), *Artibeus lituratus* (Ali), *Carollia brevicauda* (Cbr), *Chiroderma salvini* (Csa), *Centurio senex* (Cse), *Dermanura phaeotis* (Dph), *Dermanura tolteca* (Dto), *Dermanura watsoni* (Dwa), *Desmodus rotundus* (Dro), *Glossophaga soricina* (Gso), *Mormoops megalophylla* (Mme), *Micronycteris microtis* (Mmi), *Platirrhinus helleri* (Phe), *Pteronotus davyi* (Pda), *Pteronotus parnellii* (Ppa), *Pteronotus personatus* (Ppe), *Sturnira lilium* (Sli), *Sturnira ludovici* (Slu)

was used to find P -values of the correlation coefficients found between richness and morphological variables for real assemblages and ensembles (see Fig. 3 as an example of this procedure). If natural assemblages and ensembles were randomly assembled, we would expect non-significant P values (>0.05). In contrast, significant P -values (<0.05) could be interpreted as biologically meaningful deviations from random, suggesting the effect of ecological interactions.

Results

We obtained wing morphological measures of 173 individuals of 20 Phyllostomid and Mormoopid species; 118 individuals of 12 frugivorous species, and 55 individuals of eight species from other guilds (five insectivorous, two polinivorous and one vampire species). Data on species composition in each habitat are shown on Table 1, and more information regarding their abundance can be found in Moreno and Halffter (2001).

For frugivores, as species richness increases in the bat ensembles, interspecific morphological distance

decreases (Fig. 4a, b; $r = -0.777$, $P = 0.0378$, $df = 6$ and $r = -0.902$, $P = 0.0024$, $df = 6$). Conversely, as bat species richness increases the volume of the morphological space defined by the 12 frugivorous species increases (Fig. 4c, d; $r = 0.908$, $P = 0.003$, $df = 6$ and $r = 0.988$, $P < 0.001$, $df = 6$). Both the NND and the MST approaches showed consistent correlations significantly different from randomly built ensembles ($P < 0.05$; Table 2). These patterns of bat frugivorous ensembles correspond to the assembly model of limited packing (Fig. 1e, f).

For the assemblages of Phyllostomid and Mormoopid bats, interspecific distance is not significantly correlated with species richness ($r = 0.15$, $P = 0.76$, $df = 6$ for the NND and $r = 0.026$, $P = 0.95$, $df = 6$ for the MST approach; Fig. 5a, b). On the other hand, volume of the morphological space is significantly correlated with species richness of Phyllostomid and Mormoopid assemblages only for the MST approach [$r = 0.289$, $P = 0.55$, $df = 6$ for the NND approach (Fig. 5c); $r = 0.93$, $P < 0.001$, $df = 6$ for the MST approach (Fig. 5d)]. Given the distribution of the points and the sign of correlation coefficients, it seems that bat assemblages follow the assembly model in which species packing is prevented (Fig. 1c, d). However, as expected because of the inclusion of species that are unlikely to ever interact competitively, all these results for all the Phyllostomid and Mormoopid bats species assemblages were not statistically different from those for random assemblages ($P > 0.09$, Table 2).

Discussion

Our results reveal that chance may determine bat assembly mechanisms if we base our analyses on groups of species coexisting in a local habitat and delimited only by phylogeny (assemblages). This is because these assemblages include more than one functional group with species having low probabilities of interacting. However, at the ensemble level of organization, and at the scale of local habitat (alpha diversity), we found that the morphological assembly mechanism of frugivorous bats differs from random, thus corresponding to the volume-increasing model.

The observation that real assemblages of all the Phyllostomid and Mormoopid species are not different from random assemblages supports the idea that species richness and structure of Neotropical bat assemblages are determined by neutral processes (Willig and Moulton 1989; Arita 1997). This general pattern is probably due to the wide variety of organizational and spatial levels involving groups of coexisting bat species that have been used in bat community ecology. Many of these studies deal with levels of organization above the community (supra-community), thus including confounding effects, such as habitat diversity, beta diversity, island area and distance to faunal pools (Willig 1986). So, using assemblages of combined functional groups to assess the effects

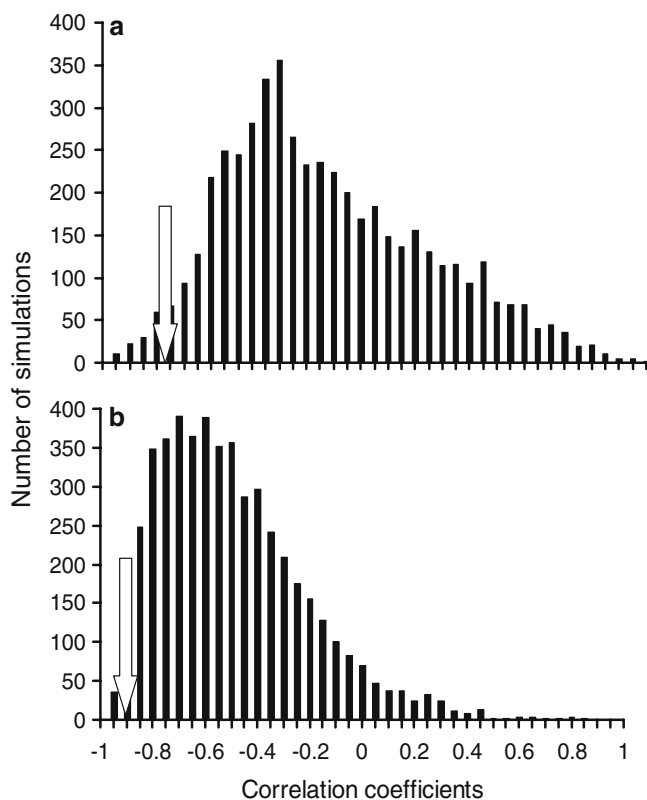


Fig. 3 Frequency distributions of 5,000 correlation coefficients between species richness and interspecific distance for randomly assembled frugivorous ensembles. Interspecific distance for simulations was measured following **a** the nearest neighbour distance approach (NND) and **b** the minimum spanning trees (MST) approach. Arrows show the correlation coefficients obtained from real ensembles (**a** -0.777 , **b** -0.902) which correspond to a P -value of 0.029 for **a** and 0.037 for **b**

Table 1 Presence (1) or absence (0) of bat species^a (Chiroptera: Phyllostomidae and Mormoopidae) recorded in seven habitat types within a Neotropical landscape in Central Veracruz, Mexico

	Tropical subdeciduous forest	Tropical deciduous forest	Mango plantation	Cornfield	Secondary vegetation	Palm stand	Riparian vegetation
Phyllostomidae							
<i>Chiroderma salvini</i> Dobson 1878	1	0	1	1	1	1	1
<i>Platyrrhinus helleri</i> (Peters 1866)	1	1	1	0	1	0	0
<i>Carollia brevicauda</i> Schinz 1821	1	1	1	1	1	0	1
<i>Artibeus jamaicensis</i> Leach 1821	1	1	1	1	1	1	1
<i>Artibeus intermedius</i> J. A. Allen 1897	1	1	1	1	1	1	1
<i>Artibeus lituratus</i> (Olfers 1818)	1	1	1	1	1	1	1
<i>Centurio senex</i> Gray 1842	1	0	0	0	1	1	0
<i>Dermanura phaeotis</i> Miller 1902	1	1	1	0	1	1	1
<i>Dermanura tolteca</i> (Saussure 1860)	1	0	1	1	1	1	1
<i>Dermanura watsoni</i> (Thomas 1901)	1	0	1	0	0	0	0
<i>Sturnira lilium</i> (E. Geoffroy 1810)	1	1	1	1	1	1	0
<i>Sturnira ludovici</i> Anthony 1924	1	1	1	1	1	1	1
<i>Anoura geoffroyi</i> Gray 1838	1	0	0	0	0	0	0
<i>Glossophaga soricina</i> (Pallas 1766)	1	1	1	1	1	1	1
<i>Desmodus rotundus</i> (E. Geoffroy 1810)	1	0	1	1	1	1	0
<i>Micronycteris microtis</i> (Gray 1842)	1	1	1	0	0	0	0
Mormoopidae							
<i>Mormoops megalophylla</i> (Peters 1864)	1	0	0	1	1	1	1
<i>Pteronotus davyi</i> Gray 1838	0	0	0	1	0	0	1
<i>Pteronotus parnelli</i> (Gray 1843)	1	1	1	1	1	1	1
<i>Pteronotus personatus</i> (Wagner 1843)	0	0	0	1	0	0	1

^aThe first 12 species are the frugivorous ones

of ecological interactions on assembly mechanisms is not advisable, even less so if the data on species composition come from large areas (gamma level), which may include high environmental heterogeneity (Stevens and Willig 1999). To elucidate clear patterns in community assembly mechanisms, studies should be focused on the ensemble level of organization and at the alpha scale, where in situ ecological processes affect both the taxo-

nom composition and ecomorphological structure (Willig 1986).

For the ensembles of frugivorous bats we detected the potential occurrence of ecological interactions, by fulfilling the criteria proposed by Huston (1999) to avoid potential serious problems in searching for local processes. First, we included organisms of the same functional type (only frugivorous bats), so they can be considered potential competitors. Second, we defined as local ensembles groups of species that inhabit seven vegetation types within a landscape, which are areas small enough that, at least theoretically, coexisting individuals of the various species can interact competitively. These small areas may be considered as homogeneous in environmental conditions (elevation, soils, microclimate, disturbance history) so they really reflect

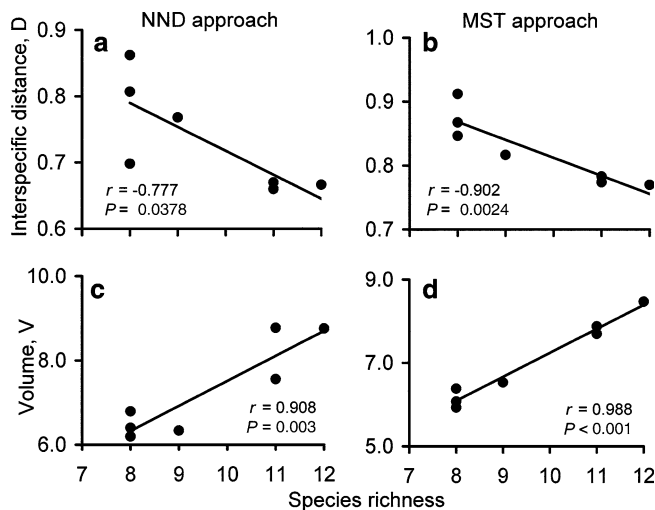


Fig. 4 Relationship between species richness and **a, b** interspecific distance and **c, d** niche volume of the ensemble (guild) of frugivorous bats from seven communities following the **a, c** NND approach and the **b, d** MST approach. Pearson correlation coefficients ($n=7$) are provided with their P -values. For abbreviations, see Fig. 3

Table 2 Probability values based on the frequency distributions of correlations coefficients from 5,000 simulations of null models. Two approaches were followed: one based on the nearest neighbour distance (NND) and the other on the minimum spanning trees (MST)

	NND	MST
Ensembles (guilds) of frugivorous bats		
Interspecific distance	0.029	0.037
Volume of morphological space	0.017	0.009
Assemblages of Phyllostomid and Mormoopid bats		
Interspecific distance	0.169	0.098
Volume of morphological space	0.398	0.157

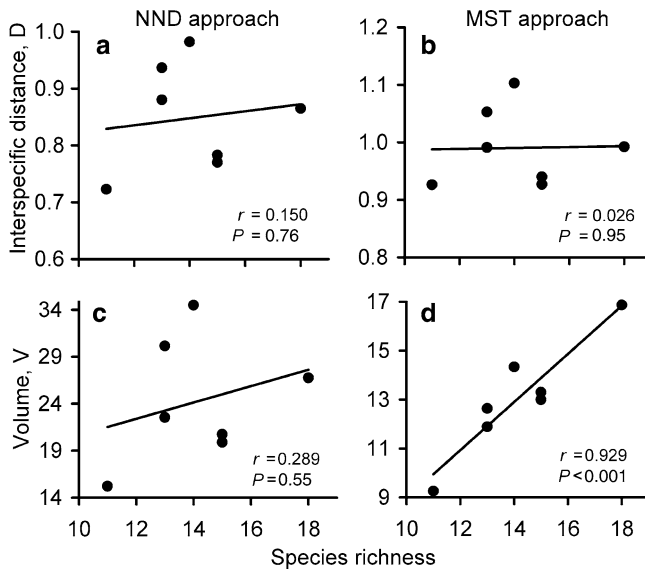


Fig. 5 Relationship between species richness and **a, b** interspecific distance and **c, d** niche volume of assemblages of Phyllostomid and Mormoopid bats from seven communities following the NND and the MST approaches. Pearson correlation coefficients ($n = 7$) are provided with their P -values. For abbreviations, see Fig. 3

local conditions (i.e. alpha diversity; Moreno and Halffter 2001). And third, we include conditions in which competitive equilibrium may be approached, at least within natural habitats, where natural or anthropogenic disturbances are not so frequent to theoretically prevent competitive equilibrium from occurring.

Under these conditions, for the ensembles of frugivorous bats, the volume-increasing mechanism with a limited species packing occurs, so these ensembles may be experiencing ecological processes that ultimately determine their species richness and structure. This conclusion is in agreement with the pattern observed for other vertebrate communities (Ricklefs and Schluter 1993 and Ricklefs and Miles 1994).

As we show in this paper, ecomorphological analyses can be a very powerful tool in understanding community assembly and organization, especially in those groups, such as bats, for which niche and other ecological attributes are very difficult to measure directly. A pluralistic approach is always better than relying on a single technique, and methodological problems emphasize the importance of supporting the results of studies on community assembly, resistance to invasion, competitive exclusion, resource limitation, niche shifting, and convergence in guild structure. In this way, ecomorphological analyses may contribute enormously to community ecology studies.

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