Species composition and morphological structure of the bat fauna of Yucatan, Mexico

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Summary

1. The relationship between regional and local assemblages of species can be analysed by comparing the composition of species and their morphological structure.

2. I made such a comparison using data of the bat fauna of Yucatan, Mexico and of a regional pool of species. Null models were constructed to test for differences in composition in terms of taxonomic affiliation and of feeding and roosting habits. Additionally, dispersal ability and species-to-genus ratios were compared. Morphological structure was analysed using nearest-neighbour distances and minimum spanning trees were constructed on a morphological plane determined by the first two principal components of external and skull measurements.

3. No significant differences were detected in the comparisons of species composition, except in the case of dispersal ability. The Yucatan bat fauna was a random subsample of the pool in terms of taxonomy, diet and roosting habits. However, species with a higher dispersal ability were better represented in the Yucatan fauna than expected by chance.

4. No clear pattern could be detected in the comparisons of morphological structure. Nearest-neighbour analyses and minimum spanning trees showed only unclear and inconclusive results.

5. The bat fauna of Yucatan is apparently formed by those species from the pool that possess a higher dispersal ability. The forces that determine the composition and structure of this fauna are probably regional in nature, and the search for structuring factors at the local level might be a futile endeavour.

Key-words: bats, community structure, local and regional processes, Mexico, null models.

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Introduction

As stated by Elton (1927), whether communities have 'limited membership' or are mere assemblages of species that happen to co-occur is one of the primary questions in community ecology (Roughgarden 1989). For several years, researchers have tried to answer this question regarding communities of neotropical bats (Findley 1993). The study of assemblages of neotropical bats has in some sense mirrored the development of ideas in community ecology.

Early studies of bat communities were based on the premise of local ecological interactions, mainly competition, as structuring forces and on Hutchinson's (1959) empirical rule of a regular spacing of species along a size gradient (Tamsitt 1967; MacNab 1971; Fleming, Hooper & Wilson 1972). Despite the failure of most studies to find regular patterns, many researchers continued to think of neotropical bat communities as structured assemblages organized by competition (Bonaccorso 1979; Humphrey, Bonaccorso & Zinn 1983).

Simberloff and collaborators (e.g. Connor & Simberloff 1979; Strong, Szyska & Simberloff 1979; Simberloff & Boecklen 1981) proposed the use of null models to challenge most ideas of the MacArthurian perception of communities, and called attention to alternative factors (including random effects) that can affect ecological assemblages. Soon after, similar studies based on morphological analyses found no evidence for competition in neotropical bat communities (Willig & Moulton 1989).

Current research in community ecology focuses on the relative contribution of local and regional forces in shaping assemblages of species (Ricklefs 1987; Cornell & Lawton 1992; Ricklefs & Schluter 1993). Inter-

est has been centred on the effect of regional and historical factors in determining species richness at the local level. The effect of regional processes on other components of ecological diversity, such as relative abundance of species and structure and function of communities, has received less attention, although results suggest that this line of research can be very illuminating in searching for the answer to Elton's limited membership question. This approach has been used to suggest that the morphological structure of neotropical and palaeotropical communities of insectivorous bats is determined primarily by evolutionary history, rather than by present day processes (Heller & Volleth 1995).

This paper presents the results of a comparison of a local community with a regional pool of neotropical bats. The comparisons included null-model analyses of patterns of species composition and of morphological structure in these assemblages. The results are discussed under the light of the current controversy on the relative role of local and regional processes in structuring ecological communities.

Materials and methods

DEFINITION OF THE FAUNA AND THE SOURCE POOL

The study fauna is defined here as the set of bat species that are found in the state of Yucatan, which occupies the north-western portion of the peninsula of the same name in Mexico. The political borders of the state roughly coincide with the limits between evergreen and tropical deciduous forests (Rzedowski 1978). A lesser mountain range, the Sierrita de Ticul (< 200 m in altitude), marks the southern limit of the state and is the only mountain range in the otherwise flat northern part of the peninsula. Because of these features, the state of Yucatan is treated here as a separate entity from the rest of the peninsula.

The bat fauna of Yucatan can be considered a local assemblage as most species reported from the state can be found in any single locality. For example, 29 of the 31 Yucatan bat species have been observed in the vicinity of Tekax, in the Sierrita de Ticul (Jones, Smith & Genoways 1973; Arroyo-Cabrales & Alvarez 1990; Arita & Vargas 1995), and one of the missing species, *Saccopteryx bilineata* (Temminck 1838), is very likely to occur there. As among-locality variation in species composition is negligible in this case, the Yucatan fauna is treated here as a single local assemblage.

The Yucatan bat fauna consists of 31 species in seven families (Table 1). The list is based on the species reported by Ramírez-Pulido *et al.* (1986) and a recent record of *Centurio senex* (Bowles, Heideman & Erickson 1990). Species reported from Yucatan on the basis of erroneously identified specimens, such as *Rhynchonycteris naso* (Wied-Neuwied 1820), *Micronycteris*

schmidtorum Sanborn 1935, *Myotis nigricans* (Schinz 1921) and *Tadarida brasiliensis* (E. Geoffroy 1824), were excluded (see Jones *et al.* 1973; LaVal 1973; Hall 1981). Also excluded were *Macrotus waterhousii* Gray 1843 and *Plecotus mexicanus* (G. M. Allen 1916) because their presence in Yucatan is doubtful (Gaumer 1917; Anderson & Nelson 1965; Jones *et al.* 1973; Koopman 1974).

In studies dealing with archipelagos, source pools have been constructed from the faunas of the mainland adjacent to the islands (Grant 1966; Simberloff 1970; Graves & Gotelli 1983) or using the combined fauna of the archipelago itself (Connor & Simberloff 1979; Gotelli & Abele 1982). For a study of continental faunas of neotropical bats, Willig & Moulton (1989) created nested source pools based on the whole fauna of South America. As discussed by Graves & Gotelli (1983), none of these approaches is completely objective. Habitat and topographic differences between islands and the source area are frequently ignored, and the geological and climatological history of the region is rarely considered. Further complications are differences in habitat preference and dispersal ability of the potential colonizing species.

The source pool is defined here as the set of bat species found in the lowlands (altitude < 1000 m) of the Gulf and Caribbean versants of south-eastern Mexico, Belize and Guatemala, areas that constitute the base of the Yucatan Peninsula. Alternative sources, including the state of Florida (bat fauna from Hall 1981); north-eastern Mexico, including the states of Tamaulipas, San Luis Potosí and Nuevo León (Wilson *et al.* 1985); the northern extreme of South America (Eisenberg 1989); and the Greater Antilles, including Cuba, Jamaica, Puerto Rico and Hispaniola (Koopman 1990), were discarded in preliminary analyses because they showed much less similarity to Yucatan than the chosen source. The bat fauna of Yucatan is a subset of the source pool, and the same subspecies occur in both regions. A review of the literature revealed the presence of 85 bat species in the source pool.

The natural vegetation of the state of Yucatan is tropical deciduous and thorn forests, whereas the southern part of the peninsula additionally harbours other more humid habitats (Rzedowski 1978). To correct the original source pool for habitat preferences among species, 16 of the original 85 species were deleted because they are not known to occur in dry areas elsewhere in the neotropics, based on Koopman (1978), Ceballos & Miranda (1986), Eisenberg (1989), Willig (1983) and Wilson (1983). The remaining 69 species, representing eight families, formed the source pool controlling for habitat use, and will be referred to as 'the pool' hereafter.

TESTS FOR COMPOSITION OF THE FAUNA

One type of null-model test in ecological communities is the search for unusual patterns of species compo-

Table 1. List of bat species recorded from Yucatan

Emballonuridae
Peropteryx macrotis (Wagner 1843)
Saccopteryx bilineata (Temminck 1838)
Noctilionidae
Noctilio leporinus (Linnaeus 1758)
Mormoopidae
Mormoops megalophylla (Peters 1864)
Pteronotus davyi Gray 1838
Pteronotus parnellii (Gray 1843)
Phyllostomidae
Phyllostominae
Chrotopterus auritus (Peters 1856)
Micronycteris megalotis (Gray 1842)
Mimon bennettii (Gray 1838)
Glossophaginae
Glossophaga soricina (Pallas 1766)
Carolliinae
Carollia perspicillata (Linnaeus 1758)
Stenodermatinae
Artibeus jamaicensis Leach 1821
Artibeus lituratus (Olfers 1818)
Artibeus phaeotis (Miller 1902)

Centurio senex Gray 1842
Sturnira lilium (E. Geoffroy 1810)
Desmodontinae
Desmodus rotundus (E. Geoffroy 1810)
Diphylla ecaudata Spix 1823
Natalidae
Natalus stramineus Gray 1838
Vespertilionidae
Eptesicus furinalis (d'Orbigny 1847)
Lasiurus blossevillii (Lesson & Garnot 1826)
Lasiurus ega (Gervais 1856)
Lasiurus intermedius H. Allen 1862
Myotis keaysi J. A. Allen 1914
Rhogeessa aeneus Goodwin 1958
Molossidae
Eumops bonariensis (Peters 1874)
Eumops glaucinus (Wagner 1843)
Molossus ater E. Geoffroy 1805
Molossus sinaloae J. A. Allen 1906
Nyctinomops laticaudatus (E. Geoffroy 1905)
Promops centralis Thomas 1915

sition. Species in the study area are classified into categories defined by some criterion (taxonomic, ecological, behavioural) and the frequency distribution of species among the categories in the derived fauna(s) is then compared against the null distribution obtained by randomly sampling from the pool. If significant differences are found, the possible forces that would have produced such deviations can then be considered (Harvey *et al.* 1983).

The structure of the bat fauna of Yucatan was compared with that of the pool using four classification criteria: taxonomy, diet, roosting preferences and distributional range. Additionally, the species-to-genus ratio in the source pool and the Yucatan fauna were compared to examine further the structure of the bat fauna.

To do the comparisons based on taxonomy, diet and roosting habits, sampling without replacement from the pool was simulated using the hypergeometric frequency distribution (Hastings & Peacock 1975; Graves & Gotelli 1983). Species in the pool were divided into families and, for the diverse family Phyllostomidae, into subfamilies (Table 1). For feeding habits, the broad categories used in other studies of neotropical bats (Table 2; Fleming *et al.* 1972; Wilson 1973; LaVal & Fitch 1977; Bonaccorso 1979; Willig 1983; Willig & Moulton 1989) were maintained because the foraging habits of many species are not known in detail, so a finer classification was not feasible. Frugivores included for example *Artibeus* spp. and *Carollia perspicillata*, which feed mainly on fruits although they also consume some insects and, less commonly, nectar and pollen. The category of foliage gleaners included species such as *Micronycteris megalotis* and *Chrotopterus auritus*, which capture insects or vertebrates from a substrate. In contrast, aerial

insectivores, such as *Myotis keaysi* and *Natalus stramineus*, capture flying insects on the wing, frequently manoeuvring near dense vegetation. Fast-flying insectivores members of the family Molossidae also capture flying insects, but they do so by pursuing their prey at high speed in open spaces. The diet of nectarivores is based on nectar and pollen, although the sole member

Table 2. Expected and observed values for the number of species in taxa and feeding categories of bats of Yucatan. Probabilities are two-tailed exact probabilities of deviations > observed, calculated using the hypergeometric distribution. Expected number of species was based on the proportions in the source pool

	Species in Yucatan	Expected	P
Taxa			
Emballonuridae	2	2·25	1·00
Noctilionidae	1	0·45	0·45
Mormoopidae	3	1·80	0·32
Phyllostominae	3	6·29	0·07
Glossophaginae	1	1·80	0·62
Carollinae	1	0·90	0·20
Stenodermatinae	5	4·94	1·00
Desmodontinae	2	1·35	0·58
Natalidae	1	0·45	0·45
Vespertilionidae	6	5·84	1·00
Molossidae	6	4·94	0·53
Feeding categories			
Frugivores	6	5·84	1·00
Gleaners	3	6·29	0·07
Aerial insectivores	12	10·33	0·45
Fast-flying insectivores	6	4·94	0·53
Nectarivores	1	1·80	0·62
Vampires	2	1·35	0·58
Piscivores	1	0·45	0·45

of this group in Yucatan (*Glossphaga soricina*) is actually an omnivorous species. The two species of vampire bats that occur in Yucatan (*Desmodus rotundus* and *Diphylla ecaudata*) feed exclusively on vertebrate blood. Finally, *Noctilio leporinus*, the only piscivorous species in Yucatan, feeds almost exclusively on small fish, which it captures from the surface of water using its elongated claws.

The classification of Mexican bats in terms of cave use proposed by Arita (1993b) was used to test for roosting preferences. Species in the pool were allotted either to the category of cave bats (species that use caves as the main or alternative diurnal roosting sites) or non-cave bats (species that do not use caves or that use caves occasionally). Using a BASIC program based on the formulae provided by Graves & Gotelli (1983), exact probabilities were computed for the deviation of the Yucatan fauna from distributions created by random sampling from the pool.

To quantify the area of distributional range for each species in the pool, its presence or absence in eight discrete zoogeographical areas of the neotropics was recorded: (i) the Pacific versant in western Mexico (Ceballos & Miranda 1986); (ii) the Gulf of Mexico versant in north-eastern Mexico (Hall 1981; Ramírez-Pulido *et al.* 1986); (iii) the West Indies (Koopman 1990); (iv) the northern Neotropics (Eisenberg 1989); (v) the Amazon basin; (vi) eastern Brazil; (vii) the Pacific versant of South America; (viii) the Patagonia (these last four areas as defined by Koopman 1983). For each area in which a species was present, one point was added, so a given species could have any value from 0 (endemic to the Yucatan peninsula and its pool) to 8 units (present in all areas). The use of this scale provides a better resolution than the binary classification (widespread vs. restricted species) that has been used in other studies. For species in the pool, the frequency distribution of the number of occupied geographical areas was approximately normal, allowing the null hypothesis that the Yucatan fauna does not differ in terms of dispersal ability of its constituent species, to be tested by using the statistical distribution of the mean of samples from finite populations (Freund & Walpole 1987).

Several studies have shown that communities with lower species richness tend to have fewer species per genus (S/G) than richer assemblages (Järvinen 1982; Harvey *et al.* 1983). It can be shown statistically, however, that communities with few species have lower S/G ratios simply because of their smaller sample size compared with that of more complete communities. In fact, real assemblages tend to have higher S/G ratios than expected on the basis of adequate sampling models (Simberloff 1970; Gotelli & Abele 1982; Järvinen 1982). A BASIC program was developed to calculate the expected value and the variance for the S/G ratio of the Yucatan fauna, using rarefaction formulae based on the hypergeometric distribution (Heck, van Belle & Simberloff 1975; Simberloff 1978).

MORPHOLOGICAL COMPARISONS

In what is known as the ecomorphological approach, morphological traits of organisms are used to infer ecological features of the species (Karr & James 1975; Wainwright & Reilly 1994). This approach has been used extensively for studying the structure of bat communites, as the correlation between ecology and morphology is well established for chiropteran species (Findley & Wilson 1982; Findley 1993; Norberg 1994). The bat fauna of Yucatan was analysed using the ecomorphological approach by comparing the distribution of the species of Yucatan in morphospace with that of the source pool to provide a test for the null hypothesis that the derived fauna is a random subsample of the pool.

Museum skins and skulls deposited in the collection of the National University of Mexico (UNAM) were examined, including specimens for all bat species in the pool. Five external and five skull measurements were recorded for each specimen. Length of the forearm is a measure of overall size. Wing tip length, including the lengths of the metacarpal and the phalanges of the third digit, and length of the fifth digit correlate with wing span and wing width, respectively. Length of the tibia measures the size of the uropatagium in those species that have one. Length of the ear is an indicator of auditory and echolocation capabilities in bats (Fenton 1972; Arita 1990). The greatest length of the skull, depth of the brain case, and mastoid breadth quantify the size of the skull in the three dimensions, whereas length of maxillary tooth row and width at the level of the last molars measure the size of the trophic apparatus. All variables except length of ear were measured directly from museum specimens; length of the ear was recorded from the collectors' tags. Adult specimens both from the pool area and from Yucatan were measured. For most species reported from Yucatan, the sample included at least five males and five females from each area. For a few very rare species, such as *Phyllostomus stenops*, only one or few specimens were available from the area of study.

Preliminary analyses showed little sexual or geographic variation in size as detected by univariate and multivariate analyses of variance (ANOVA and MANOVA). Differences between sexes or between the study fauna and the pool were significant in only a small proportion of cases with sufficient sample sizes (five of 52 for sex differences, four of 18 for geographic variation). Given these results, averages were used for each species, regardless of sex or locality.

Univariate analyses

Several parameters were used to measure the regularity of the distribution of species along a morphological gradient to compare the Yucatan assemblage with the pool (Simberloff & Boecklen 1981;

Pleasants 1990, 1994; Arita 1993a). For an assemblage of *n* species arranged along a logarithmic size gradient, let x_i be the log value of the size of the *i*th species, so x_1 corresponds to the smallest and x_n to the largest species. Define d_i to be equal to $x_{i+1} - x_i$, the distance between adjacent species. The parameter Var (Poole & Rathcke 1979) is the variance of the values of *d*:

$$\text{Var} = (n-2)^{-1} \sum_{i=1}^{n-1} (\bar{d} - d_i)^2.$$

Min is the minimum value of *d*, that is the magnitude of the shortest segment of the morphological line.

If distances are arranged in increasing order of magnitude and they are renamed so g_1 becomes the shortest and g_{n-1} the longest distance, the *G* parameters of Simberloff & Boecklen (1981) can be defined as follows: $G_{r,s} = g_r/g_s$ *(the ratio of the rth smallest to the sth smallest segments of the morphological line).* Simberloff & Boecklen (1981) proposed the use of three of these ratios ($G_{1,n}$, $G_{2,n}$ and $G_{1,n-1}$) to test Hutchinson's (1959) hypothesis of size-ratio constancy. Pleasants (1990) has argued deficiencies in the *G* parameters, but Arita (1993a) has shown otherwise, and the efficiency of these parameters in detecting character displacement has been demonstrated in recent papers (Dayan *et al.* 1989, 1990).

A preliminary analysis was performed to search for unusual morphological dispersion in the pool. If the pool itself is organized in any manner, detecting an additional structure in a sample can be a misleading exercise (Colwell & Winkler 1984). Tests were made in four of the feeding categories (frugivores, gleaners, aerial insectivores and fast-flying insectivores) for one external (forearm length) and one skull (length of the tooth row) variable. Species were arranged by their size and the morphological distances were calculated, using a logarithmic scale, for contiguous species. By means of a BASIC program, parameters of dispersion (Var and Min) were computed and the values were compared against hypothetical faunas generated by sampling from a random uniform distribution. For each feeding category, 1000 simulations were run.

A similar test was performed for two of the most speciose genera in the pool: *Artibeus*, with four species, and *Myotis*, with six species. The tests using these two genera were performed to have a better resolution in the question of a possible pattern of unusual morphological dispersion. Traditionally, such tests are designed to study closely related species, normally belonging to the same genus (Hutchinson 1959; Dayan *et al.* 1989, 1990).

Unusual dispersion was tested in four of the feeding categories of Yucatan bats (frugivores, gleaners, aerial insectivores and fast-flying insectivores). Sample sizes were insufficient for the piscivorous (*n* = 1), vampire (*n* = 2) and nectarivorous (*n* = 1) groups. For each category, morphological gradients were created for each of the 10 log-transformed variables defined above. Then, using a BASIC program, the parameters

for dispersion (Var, Min and the *G* parameters) were computed and the values were compared against a frequency distribution of hypothetical communities generated by randomly sampling the pool. For the gleaner and the fast-flying insectivore groups, the program generated all possible assemblages of the same number of species as in the Yucatan fauna (364 possible combinations of three-species assemblages from a pool of 14 gleaner species; 462 possible combinations of six-species communities from a pool of 11 molossids). For frugivores and aerial insectivores, 1000 random assemblages were created. (For frugivores, there were 1716 possible combinations of six species from a pool of 13; for aerial insectivores, with a pool of 23 species, $> 1.35 \times 10^6$ assemblages of 12 species were possible.) The null hypothesis is that species in the real communities are not particularly segregated along the morphological line. One-tailed probabilities were estimated by comparing the observed values of the five parameters against the distribution obtained from the hypothetical assemblages generated from the pool.

Multivariate tests

The multivariate analysis of structure in ecological communities is a direct extension of the univariate case. The procedure involves the study of the relative position of the different species in an *n*-dimensional morphospace that is assumed to mirror the multidimensional niche space (Karr & James 1975; Findley 1976; Ricklefs & Travis 1980; Ricklefs, Cochran & Pianka 1981; Findley & Black 1983; Moulton & Pimm 1986; Willig & Moulton 1989; Ricklefs & Miles 1994). Using skull and external measurements, multivariate analyses for each of the feeding groups were performed. Principal-components analysis of the log-transformed data was used to reduce the dimensionality of the morphospace. Because they accounted for most ($> 90\%$) of the variance of the original variables, only the first two components were retained in all cases. Principal components were extracted from the correlation matrix and Euclidean distances were computed for each of the $n(n-1)/2$ pairs of species in the plane of the first two principal components.

Mean neighbour distances and variances were used to quantify the spacing of the elements of the assemblages. In previous studies, only the nearest-neighbour distances were normally used. However, a complete series of means and variances for the different orders of nearest-neighbours, as defined by Manly (1991), were calculated for the bats of Yucatan. For an assemblage of *n* species, q_i (*i* = 1 to *n* −1) is defined as the mean distance from points to their *i*th nearest neighbour. The first-order mean distance (q_1) is equal to the nearest-neighbour distance used in previous studies to quantify species packing in the community (Findley 1976; Ricklefs & Travis 1980; Travis & Ricklefs 1983).

As defined here, q_1 tests for patterns of competitive

exclusion. An unusually high value for this parameter would indicate a lowered frequency of pairs of very similar species in the derived fauna, suggesting the effect of exclusion of competing species. Parameters for higher orders test for patterns of segregation among more distant species. High values for these parameters would show displacement among species with less similarity, indicating the effect of a more diffuse competition. Similarly, the variance of the distances for the different neighbour orders can be used to quantify the evenness of the distances between species, therefore testing the idea of a displacement among species in the morphospace.

For each feeding category, the $n-1$ q parameters and their variances were computed and their value compared against the frequency distribution compiled from 1000 randomly generated communities from the pool. Under the competition hypothesis, q-values should be significantly higher and variances should be significantly lower than expected by chance. One-tailed probabilities were used for testing the null hypothesis of no segregation.

In an additional battery of tests, a series of parameters that are analogous to those used in the univariate analyses were computed. First, a minimum spanning tree in the plane of the first two principal components was constructed for each feeding category. The minimum spanning tree is the series of $n-1$ segments connecting all species in the community that has the minimum extension. The length of this tree has been used to quantify the dispersion of species in the morphospace (Moulton & Pimm 1986; Willig & Moulton 1989). Using the lengths of the segments in the trees as the lengths of the morphological lines in the univariate cases, the same variables (Var, Min and the G parameters) were calculated. Although similar, these parameters are not exactly equivalent in the univariate and the multivariate cases. In the univariate analyses the segments are arrayed along a line, whereas in the multivariate case they are arranged in multidimensional space (in the present study, on a plane).

An additional parameter, Mean, which is the mean distance between pairs of species along the minimum spanning tree, was used. In contrast with the univariate case, in which its value is determined by the position of only two species (Arita 1993a), Mean is a valid parameter in the multivariate case. Mean measures the dispersion of the species because it is directly proportional to the total length of the minimum spanning tree.

Results

TESTS FOR COMPOSITION OF THE FAUNA

There was almost no deviation of the proportion of species in the different taxonomic groups from the expected values. In fact, most taxa were represented

by the number of species that would be expected in a random draw from the source pool (Table 2). In the present study, the traditional classification of Phyllostomidae in six subfamilies was used (Smith 1972; Hill & Smith 1984). Baker, Hood & Honeycutt (1989) have proposed a new arrangement that summarizes recent information on the phylogeny of this diverse family. The results were not affected if the new classification was used, because the major groups remain intact in the new arrangement, changing only their hierarchy from subfamilies to tribes. The only taxonomic group that would yield different results is the Phyllostominae, which Baker *et al.* (1989) and van den Bussche & Baker (1992) have split into four subfamilies. The subfamily Vampyrinae in the new classification would be represented in Yucatan by one species out of three from the pool, whereas the tribe Phyllostomini would be represented by one of the eight species in the pool. In both cases the deviation from the expected number of species is not significant ($P > 0.05$).

Similarly, there was little deviation from expected values in the observed number of species grouped by feeding categories (Table 2). All groups were represented in the Yucatan fauna proportionally to their frequency in the pool.

Of the 69 species in the pool, 31 (45%) roost in caves. In Yucatan, 17 out of 31 use caves regularly (55%; Arita & Vargas 1995). The expected number of Yucatan cave species based on a random draw from the pool is 14·78. The hypergeometric probability of drawing 17 or more cave species from the pool in a sample of 31 is $P = 0.197$. Thus, the apparent over-representation of cave species in the Yucatan fauna is not statistically significant, and no difference can be claimed.

The mean number of zoogeographical units in which a species from the pool occurred was 4·26, with a variance of 3·65. The observed mean for the Yucatan fauna was 5·35 units with a sample variance of 2·92 (Fig. 1). The probability of observing a mean > 5.35 for a sample of $n = 31$ is very low ($z = 4.26$, $P < 0.001$). The null hypothesis was clearly rejected; species with larger areas of distribution were over-represented in the bat fauna of Yucatan.

Analysis of the species-to-genus ratio provided no evidence of any deviation from random sampling from the source pool. The expected number of genera in a 31-species sample from a pool of 69 species in 44 genera is 24·52. The observed value for the Yucatan fauna was 24 genera (probability of a deviation $>$ observed is $P > 0.05$).

MORPHOLOGICAL COMPARISONS

Preliminary analyses

Almost no evidence of any unsual morphological pattern was found in the preliminary analysis of the pool.
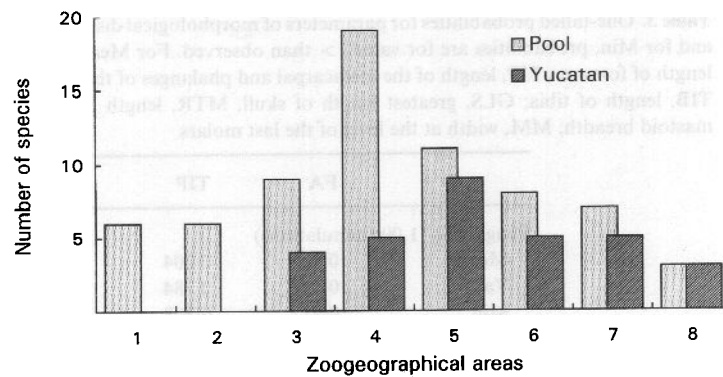
Fig. 1. Frequency distribution of the area of distributional range for bat species in the pool and the Yucatan fauna. Zoogeographical areas are defined in the text. The mean for the Yucatan fauna differed from the expected value ($P < 0.001$).

In all cases (frugivores $n = 13$; gleaners $n = 14$; aerial insectivores $n = 23$; fast-flying insectivores $n = 11$) results were not significant ($P > 0.05$) for both forearm length and length of tooth row. In the analysis of the genus *Myotis* ($n = 6$), a similar result was obtained; no significant pattern was found for forearm length or for length of the tooth row. For *Artibeus*, only the analysis for forearm length using the Min parameter was significant ($P = 0.03$).

Univariate analyses

The results revealed little evidence for segregation of bat species along univariate morphological gradients. In the guild of frugivores, for example, there was no significant deviation from expected for any of the parameters in any of the variables (in all cases $P > 0.05$; Table 3. Similarly, for the group of gleaners, none of the external variables indicated any tendency to morphological segregation (all cases $P > 0.05$). Only two parameters suggested segregation for maxillary tooth row and for mastoid breadth ($P < 0.05$).

In the category of aerial insectivores, only one of the 10 variables (mastoid breadth) showed an indication of a regular arrangement of species. For this variable, parameters Min and $G_{1,(n-1)}$ deviated significantly ($P < 0.05$) from their expected values, but the other parameters did not. Among fast-flying insectivores, one variable (width at the level of the last molars) showed an isolated significant deviation ($P < 0.05$ for $G_{2,n}$), and the parameters for another (greatest length of skull) were significantly ($P < 0.05$) different from that expected.

Multivariate tests

As with the univariate analyses, multivariate tests showed little evidence of any structure in the fauna of bats of Yucatan. Mean Euclidean distances in the plane of the first two principal components revealed no significant pattern in the guilds of gleaners, aerial insectivores and fast-flying insectivores (Fig. 2). All values were within the 95% confidence interval deter-

mined by random sampling from the pool. In the aerial insectivore group, the mean Euclidean distances for the first three orders were very close to the upper 5% limit, suggesting a tendency of similar species not to coexist in the Yucatan fauna, but the pattern was statistically not significant. In the guild of frugivores, q-values tended to be higher than expected, with three of them (q_2, q_3 and q_4) being significantly so (one-tailed $P < 0.05$; Fig. 2). In the case of the variance of the distances, all values for all guilds for all neighbour orders were within the expected values with a 95% confidence.

The analysis of the minimum spanning trees yielded similar results, and demonstrated no tendency for overdispersion or segregation. None of the values for any of the parameters was significantly different from expected in any of the cases (Fig. 3 and Table 4).

Discussion

SPECIES COMPOSITION

The results of comparisons based on species composition indicate that the study fauna is a random subsample of the pool in terms of taxonomic composition, feeding strategies and roosting preferences. Dispersal ability, measured by the size of distributional range, is the only characteristic that differentiates the fauna of Yucatan from its source.

This result dismisses the significance of some patterns of the Yucatan fauna that would seem to be striking. For example, Phyllostomines are represented by 14 species in the pool and by only three in the Yucatan fauna. Even in this case, however, the deviation from expected was not statistically significant ($P > 0.05$). In a similar case, only one of the six species of the genus *Myotis* that exist in the pool was present in Yucatan (*M. keaysi*), and the peninsular fauna harboured only one nectar-feeding bat (*G. soricina*). Other tropical areas of Mexico normally contain several species of *Myotis* and many nectarivorous species (for example, the tiny state of Colima in western Mexico contains six *Myotis* species and five Glos-

Table 3. One-tailed probabilities for parameters of morphological displacement for the bat fauna of Yucatan. For G parameters and for Min, probabilities are for values > than observed. For Mean and Var, probabilities are for values < observed. FA, length of forearm; TIP, length of the metacarpal and phalanges of the third digit; D5, length of fifth digit; EAR, length of ear; TIB, length of tibia; GLS, greatest length of skull; MTR, length of maxillary toothrow; DBC, depth of brain case; MB, mastoid breadth; MM, width at the level of the last molars

	FA	TIP	D5	EAR	TIB
Frugivores (1,000 simulations)					
Mean	0·323	0·204	0·421	0·190	0·536
Var	0·707	0·784	0·698	0·701	0·701
Min	0·417	0·808	0·533	0·279	1·000
G_1,	0·423	0·874	0·669	0·442	0·924
$G_{2,n}$	0·499	0·974	0·885	0·425	0·636
$G1_{,(n-1)}$	0·532	0·980	0·700	0·665	0·923

	GLS	MTR	DBC	MB	MM
Mean	0·186	0·162	0·294	0·306	0·217
Var	0·568	0·724	0·199	0·525	0·672
Min	0·055	0·237	0·050	0·152	0·664
$G_{1,n}$	0·172	0·308	0·050	0·199	0·847
$G_{2,n}$	0·434	0·349	0·223	0·382	0·427
$G1_{,(n-1)}$	0·105	0·248	0·074	0·330	0·815

	FA	TIP	D5	EAR	TIB
Gleaners (364 simulations)					
Mean	0·115	0·225	0·115	0·173	0·173
Var	0·396	0·453	0·459	0·901	0·148
Min	0·107	0·159	0·085	0·506	0·071
$G_{1,n}$	0·236	0·286	0·256	0·731	0·107
$G_{2,n}$	1·000	1·000	1·000	1·000	1·000
$G_{1,(n-1)}$	1·000	1·000	1·000	1·000	1·000

	GLS	MTR	DBC	MB	MM
Mean	0·288	0·412	0·258	0·157	0·187
Var	0·113	0·036*	0·146	0·071	0·665
Min	0·110	0·110	0·052	0·036*	0·245
$G_{1,n}$	0·077	0·019*	0·096	0·038*	0·459
$G_{2,n}$	1·000	1·000	1·000	1·000	1·000
$G_{1,(n-1)}$	1·000	1·000	1·000	1·000	1·000

	FA	TIP	D5	EAR	TIB
Aerial insectivores (1,000 simulations)					
Mean	0·518	0·787	0·550	0·394	0·260
Var	0·388	0·276	0·825	0·383	0·488
Min	0·596	0·077	0·095	1·000	0·550
$G_{1,n}$	0·584	0·061	0·166	0·848	0·467
$G_{2,n}$	0·747	0·225	0·433	0·703	0·622
$G_{1,(n-1)}$	0·475	0·052	0·166	0·940	0·629

	GLS	MTR	DBC	MB	MM
Mean	0·483	0·405	0·460	0·403	0·589
Var	0·690	0·683	0·397	0·450	0·124
Min	0·374	1·000	0·087	0·030*	0·074
$G_{1,n}$	0·433	0·902	0·074	0·058	0·072
$G_{2,n}$	0·544	0·546	0·197	0·117	0·162
$G_{1,(n-1)}$	0·526	0·939	0·237	0·033*	0·046

	FA	TIP	D5	EAR	TIB
Fast-flying insectivores (462 simulations)					
Mean	0·695	0·771	0·550	0·394	0·260
Var	0·106	0·219	0·058	0·574	0·178
Min	0·448	0·275	0·394	0·818	0·546
$G_{1,n}$	0·442	0·063	0·126	0·818	0·379
$G_{2,n}$	0·212	0·167	0·188	0·885	0·221
$G_{1,(n-1)}$	0·537	0·188	0·247	0·818	0·348

Table 3. (Continued)

	GLS	MTR	DBC	MB	MM
Mean	0·576	0·619	0·500	0·413	0·424
Var	0·002**	0·102	0·751	0·379	0·162
Min	0·028*	0·275	0·545	0·249	0·621
$G_{1,n}$	0·002**	0·091	0·788	0·234	0·413
$G_{2,n}$	0·004**	0·165	0·483	0·396	0·043*
$G_{1,(n-1)}$	0·012*	0·126	0·695	0·214	0·448

* $P < 0.05$, ** $P < 0.01$.

sophaginae in a fauna of 47 bats; Ramírez-P. et al. 1986). Rarefaction demonstrated that the patterns in the Yucatan fauna are not as unexpected as they seem to be. In fact, the hypergeometric probability of getting one or no *Myotis* in random 31-species samples from the pool is $P = 0.15$.

Feeding categories coincide closely with the taxonomic arrangement of neotropical bats. For example, molossids are in their own feeding group, the gleaners are in the subfamily Phyllostominae, and all frugivores are classified in the subfamilies Carollinae and Stenodermatinae. Comparative studies of neotropical bat faunas face the unavoidable mixing of ecological effects and phylogenetic inertia (Felsenstein 1985; Harvey & Pagel 1991; Brooks & McLennan 1991). Not surprisingly, the analysis using feeding groups yielded similar results to the one performed with taxonomic groups.

The karst landscape of Yucatan, a flat terrain punctuated by numerous caves, would lead one to expect cave bats to occur in a higher proportion than in the source pool, where caves are less abundant. The cave bat fauna of Yucatan is indeed rich and abundant, with individual sites harbouring as many as 12 different species (Arita & Vargas 1995). However, the apparent overrepresentation of cave species in the Yucatan bat fauna (17 of 31 species) is not statistically significant.

The area of distributional range is the only feature that discriminates species from the pool that occur in Yucatan. If one assumes, as Graves & Gotelli (1983) have done, that area of distributional range is a measure of dispersal capability, the results presented here would indicate that colonization ability is the key factor determining the particular combination of species that constitute the study fauna. However, that could also be a subtle indication of other forces structuring the fauna. Widespread species might have larger distributional ranges because they are superior competitors, capable of excluding other species in impoverished areas. Conversely, species with small distributional ranges would be poor competitors, restricted to rich areas in which competition might be less strong. Similarly, there is a positive correlation between area of distribution and local abundance for neotropical bats (Arita 1993c), suggesting that the bat fauna of Yucatan might be formed by proportional

sampling from the pool, with species that are more abundant having higher probabilities of being present in the study fauna.

Graves & Gotelli (1983) and Järvinen & Haila (1984) have obtained comparable results with avifaunas. Species of neotropical birds with the largest distributional ranges are more likely to be found in land-bridge islands than restricted species (Graves & Gotelli 1983). Similarly, 33% of the absences of bird species in the Finnish island of Ulversö can be accounted for by initial rarity in the source pool. In the short term, that percentage is as high as 75% (Järvinen & Haila 1984). In these avifaunas and in the Yucatan bat fauna, initial rarity and dispersal ability seem to be the key features that allow species to occur in the study sites.

MORPHOLOGICAL COMPARISONS

Preliminary analyses performed on the pool found no organized pattern in this fauna. Because the major purpose of this study was not to examine the pool fauna, the results of these preliminary analyses were used only to validate the comparison of the local and regional faunas. If a clear pattern of organization is found for the pool, then the following analyses would be invalid, because the power of the tests to show a more organized pattern would be impaired by the structured nature of the pool itself. For the Yucatan bat fauna, however, it seemed safe to perform the comparisons with the pool.

The idea of an almost random construction of the Yucatan bat fauna is supported by the lack of evidence of segregation provided by the morphological tests. Most analyses yielded ambiguous results that allowed no definite conclusion about the morphological structure (if any exists) of the Yucatan bat fauna.

In the guild of frugivores, for example, both univariate analyses and the analysis of the minimum spanning trees showed almost no evidence for unusual patterns. Only one variable (depth of brain case), for which the Min and $G_{1,n}$ parameters detected some segregation among the species ($P = 0.05$), indicated some degree of separation. Dayan et al. (1989, 1990) have shown that, for a given group of species, segregation can occur in a measurement, whereas others may show a great deal of overlap. They found that
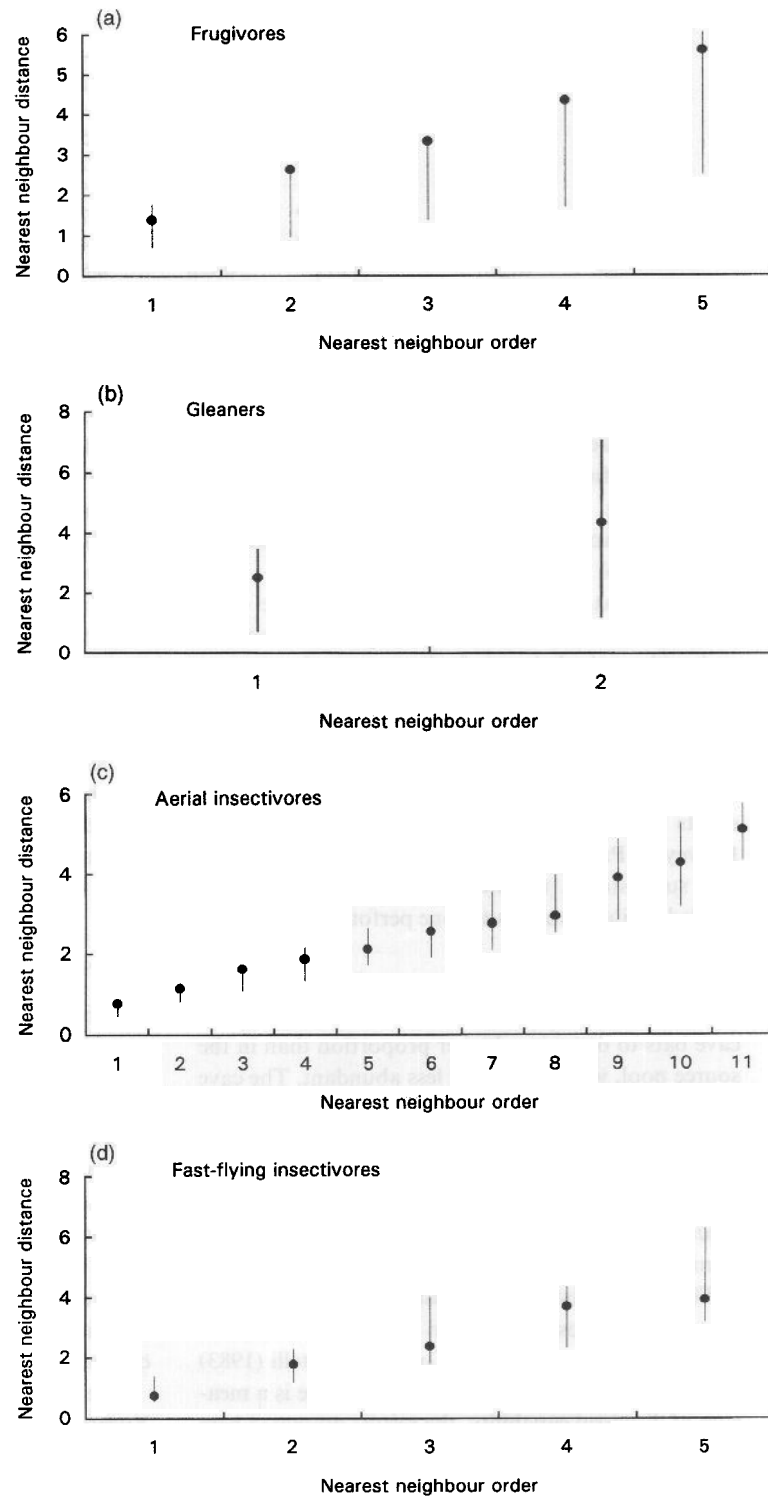
Fig. 2. Mean nearest-neighbour Euclidean distances in four guilds of bats. Points show values for the Yucatan fauna. Lines are upper and lower 5% limits for expected values obtained from the pool.

segregation in size occurs in carnivores principally along the line of the diameter of the upper canines, a variable directly associated with the trophic apparatus of carnivorous animals. In the case of the frugivorous bats of Yucatan, a segregation along the line of the depth of the brain case has no such direct interpretation. Besides, the pattern was not shown for the variables associated with the trophic structures.

In the multivariate analyses for frugivores, the values of the q parameters suggested, but failed to clearly demonstrate, the exclusion of pairs of very similar species. In this particular case the analysis showed a more subtle segregation of species on the morphological plane. That q_1 was not significantly higher than expected means that pairs of very similar species do coexist in the Yucatan fauna. Significant

(a) Frugivores

(b) Gleaners

(c) Aerial insectivores

(d) Fast-flying insectivores
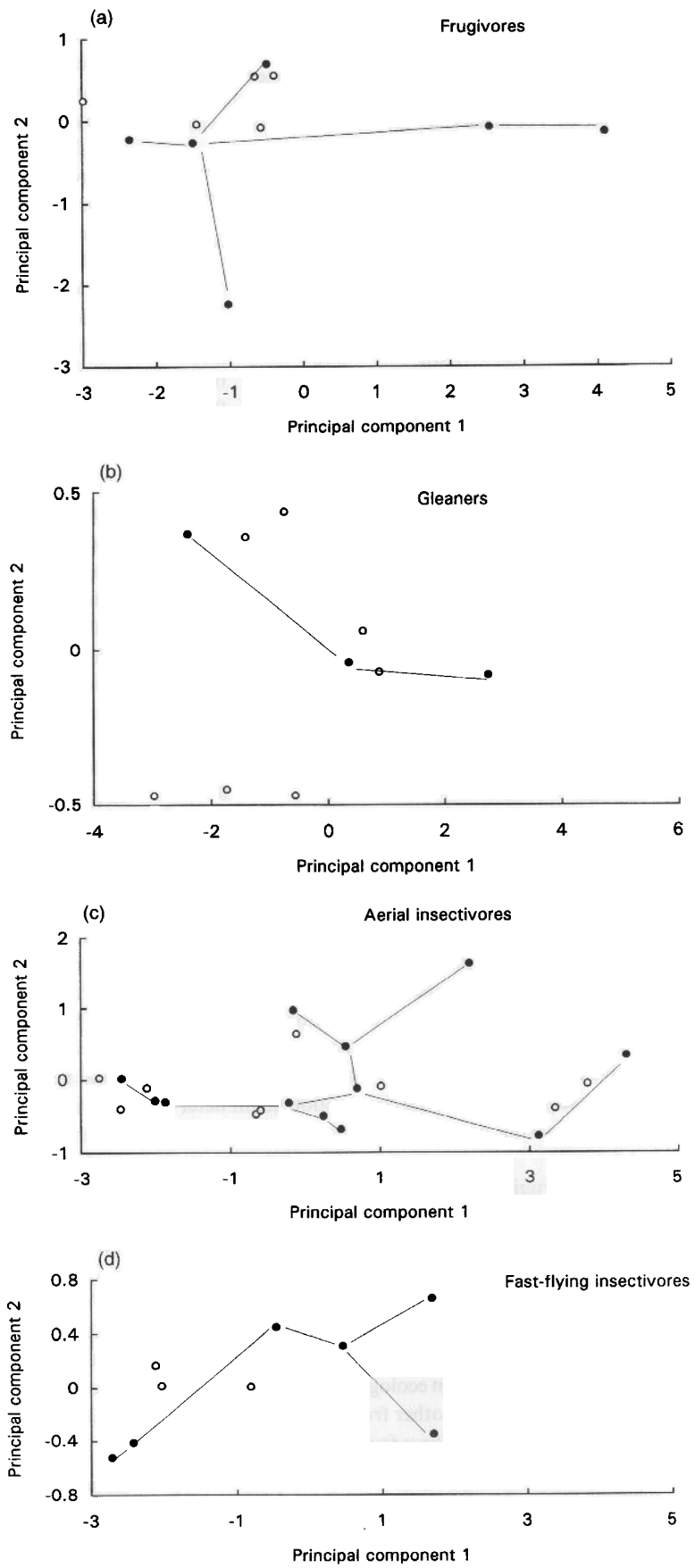
Fig. 3. Projection of bat species of four feeding groups on the plane of the first two principal components for skull variables. Lines are minimum spanning trees connecting Yucatan species. Open circles are species from the pool not found in Yucatan.

that shows the bat fauna of Yucatan as a random subsample of the pool in terms of species composition

That almost no unusual pattern can be shown for the bats of Yucatan when compared with random assemblages from the pool does not mean that the study fauna lacks order altogether. One could argue that some pattern might be already present in the pool, and that the Yucatan fauna simply cannot be more organized than its source (see similar arguments in Colwell & Winkler 1984). If this is true, any attempt to show a more conspicuous pattern in the Yucatan fauna would be a futile exercise.

In any case, the results of this study suggest that local processes, and particularly competition, have a minor contribution to the structuring of the Yucatan bat fauna. It appears that regional processes have a more determinant effect on the composition and structure of bat assemblages in Yucatan. Dispersal ability seems to be the key characteristic of Yucatan bats; thus, historical events of colonization, and not local processes, probably hold the key to the understanding of this and other neotropical bat communities.

Acknowledgements

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