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Density compensation in New World bat communities

Richard D. Stevens and Michael R. Willig

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Understanding the role of competitive interactions in shaping the structure of communities has been one the most unrelenting challenges to ecology. Traditionally, competitive interactions were assumed to be the most important agent of deterministic structure, with overdispersed morphological patterns based on body size and trophic status as their hallmark. However, models of community organization based solely on morphology have yielded only equivocal results for many taxa. Fortunately, morphological patterns may not be the only indications of competitively induced deterministic structure. Herein, we explore the degree to which the structure of five feeding guilds (aerial insectivores, frugivores, gleaning animalivores, molossid insectivores, and nectarivores) from 15 New World bat communities reflects density compensation. Nonrandom associations between abundance and morphological distance were detected in five communities, in three feeding guilds, and with respect to four competitive scenarios. Nonetheless, patterns consistent with the hypothesis of density compensation were neither pervasive nor consistent in New World bat communities. Competitively induced community structure may exist under only narrow temporal and environmental conditions, and may not be characteristic of organization in most situations.

R. D. Stevens and M. R. Willig, Dept of Biological Sciences and The Museum, Texas Tech Univ., Lubbock, TX 79409-3131, USA (cmrds@ttacs.ttu.edu) (MRW also at: National Center for Ecological Analysis and Synthesis, Univ. of California, 735 State St., Suite 300, Santa Barbara, CA 93101-3351, USA).

Identifying a single mechanism that accounts for the structure of natural communities dominated empirical and theoretical ecology for more than a quarter of a century. Although predation (Hairston et al. 1960, Paine 1966, Lubchenco 1978, Brown et al. 1988), disturbance (Sousa 1984, Petraitis et al. 1989), environmental variability or heterogeneity (Hutchinson 1941, 1961, May 1974), and chance (Connor and Simberloff 1978, 1979, Strong et al. 1979, Simberloff and Boeklen 1981) each have been championed, most studies have explored competition as the mechanism structuring communities (Diamond 1975, Bowers and Brown 1982, Tilman 1982, Moulton and Pimm 1986). Contemporary theory suggests that competitive interactions should maintain regularities in community structure by either preventing the invasion and persistence of species, or by directing natural selection and favoring phenotypic attributes that reduce niche overlap (Hutchinson 1959, MacArthur and Levins 1967, Cody and Diamond 1975, Case and Sidell 1983). Under equilibrial conditions, a limit exists as to how similar species can be and still coexist in the same community (MacArthur and Levins 1967, Abrams 1983). Nonetheless, to effectively structure communities so as to be detectable in quantitative analyses, competitive interactions must affect most species, be the most influential mechanisms in operation, and must be intensive enough to cause extinction or phenotypic shifts (Moulton and Pimm 1986).

The evolution of morphology through natural selection suggests that much of the morphological variation among species should be adaptive with respect to ecological function. Consequently, morphology has been a popular means to represent and estimate the ecological attributes of species and characterize the organization of communities. Characters, especially after log-transformations, are amenable to powerful statistical analy-

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ses because they tend to be distributed normally and have homogeneous variances (Ricklefs and Travis 1980). They are quantified much more easily than are direct ecological measures such as reproductive power (Brown et al. 1996), population pressure (Maurer 1999), environmental stress (Palmer and Strobeck 1986, Clarke 1995), or ecological overlap (MacArthur and Levins 1967, Schoener 1974). Moreover, morphological attributes correlate well with many ecological characteristics such as resource utilization, home range size, population density, mobility, and reproductive output (Peters 1983, Blackburn et al. 1993, Fa and Purvis 1997). Importantly, morphological characters integrate or reflect influences of ecological processes that are experienced at different periods or seasons during the lifetime of the organism (Ricklefs and Travis 1980). Finally, strong relationships exist between the size and shape of species, and the resources they consume (Brown and Lieberman 1973, Hespenheide 1973, Bonaccorso 1975, Smartt 1978, Freeman 1981, 1984, 1988, 1992, Findley and Wilson 1982, Findley and Black 1983, Dayan and Simberloff 1994, Pavey and Burwell 1997, Stevens and Willig 1999). Clearly, evaluating the morphological structure of communities has many advantages over alternative ecological approaches. Many morphological models of community organization are based on the assumption that a community at equilibrium comprises only a subset of the regional species pool, and that this subset is determined by an ecological filter (Ricklefs and Travis 1980, Moulton and Pimm 1986, Willig and Moulton 1989, Ricklefs and Schluter 1993, Gotelli and Graves 1996, Stevens and Willig 1999). The filter occurs because of a limit to ecological similarity. Species that are too morphologically similar should consume resources that are also similar, and interspecific competition will ensue. Given enough time and sufficient intensity, competitive interactions should give rise to morphological hyperdispersion within communities. Thus, species in a community should either diverge morphologically (character displacement) until hyperdispersion is reached, or be eliminated by competitive exclusion (local extinction).

Ecologists have explored hyperdispersed morphological patterns in many taxa. Recent studies focusing on bat communities indicate that hyperdispersion does exist in some situations, but it is not pervasive (Stevens and Willig 1999). Consequently, the role of competitive interactions in determining bat community structure remains uncertain. Hyperdispersed morphological patterns are not the only way that competitive interactions contribute to community structure. Competition may not be strong enough to drive species to local extinction, but it may instead result in a reduction in the population sizes of competitors. If this is true, then abundances should be correlated negatively with degree of ecological similarity. This aspect of competition theory is known as density compensation (Root 1973, Hawkins and MacMahon 1989, Stevens and Willig 2000). Recently, a community model of density compensation was introduced that uses morphological similarity as a surrogate of ecological similarity, and evaluates the degree to which the relationship between morphology and abundance is nonrandom (Stevens and Willig 2000). Herein, we apply this model to five feeding guilds from 15 sites to explore if density compensation in bat communities is pervasive throughout the New World.

Methods

The model

Analyses are predicated on three assumptions. First, morphological measures are good descriptors of ecological attributes. This is true for many taxa in general (Brown and Lieberman 1973, Hespenheide 1973, Smartt 1978, Dayan and Simberloff 1994), and for bats in particular (Bonaccorso 1975, Freeman 1981, 1984, 1988, 1992, Findley and Wilson 1982, Findley and Black 1983, Stevens and Willig 1999). Second, species with high ecomorphological similarity to one or more potential competitor should suffer reduced density as a result of interspecific competition. Finally, those competitive interactions that structure communities transpire within groups of species (i.e., guilds or ensembles) that consume similar resources in a similar manner. Although analyses are aimed to evaluate if density compensation characterizes bat community organization, failing to subdivide species into groups that reflect differences in resource use may confound results (Willig 1986, Stevens and Willig 1999). Thus, analyses were restricted to each feeding guild separately.

Distance in morphological space was estimated as Euclidean distance based on log-transformed morphological measurements (Digby and Kempton 1987). As a consequence of competitive effects, a quantitative relationship should exist between the proximity of species in ecomorphological space and density. Few studies have explored if density compensation exists within communities. Moreover, even less is known regarding the form of the relationship between morphological distance and abundance. We were most interested in the general form of this relationship (abundance increases as dissimilarity increases). Consequently, we characterized abundance from the perspectives of relative frequency and rank abundance, and examined its relationship with ecomorphological distance based on Pearson Product-Moment and Spearman Rank correlation coefficients, respectively. Like many mobile organisms, it is difficult to assess the abundance of bats with great accuracy based on contemporary sampling techniques (Jones 1965, Kunz and Kurta 1988). Our analyses provide added flexibility because they include rank

tests of association. Where absolute measures of abundance are suspect or where guilds differ dramatically in their catchability (Patterson et al. 1996), species need only be ranked *within* feeding guilds from most abundant to least abundant.

To determine if density compensation occurred in a feeding guild, we compared the correlation coefficients from each actual guild to a distribution of correlations produced by a stochastic process. While preserving the integrity of the morphological relationships among species, abundances were assigned at random. A correlation coefficient was then calculated between randomized abundance and actual morphological distance of members within the simulated guild. One thousand iterations of this process yielded a probability density function for subsequent hypothesis tests. The correlation coefficient from the actual guild was compared to the probability density function of simulated correlation coefficients. If the coefficient for the actual guild occurred within the upper decile of the distribution, we concluded a nonrandom positive association between morphology and abundance in the actual guild ($\alpha = 0.10$). Many phenomena other than guild-wide competitive interactions can influence the abundance of species. Accordingly, positive associations between abundances and morphological distance, consistent with competition theory, may be obscured partially by species experiencing autecological influences (i.e., differential response to resources or disturbance) or by a plethora of other interactions (i.e., predation, mutualism) occurring at the community level. To safeguard against these possibilities and wrongfully failing to reject the null hypothesis, we set alpha at 0.10. A full description of this model and its power to detect competitive effects in a well-studied desert rodent community appear in Stevens and Willig (2000).

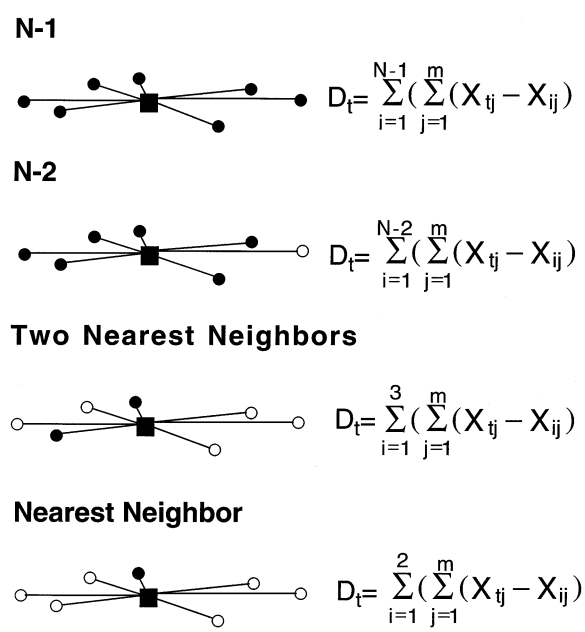

Fig. 1. Four competitive scenarios based on morphology and abundance. In the first scenario (N-1), the abundance of the focal species (square) is a function of its relationship with all of its neighbors (circles); Euclidean distances (D_t) include all species in the feeding guild. In the second scenario (N-2), the morphological relationship between the focal species and its most distant neighbor are so weak as to have no influence on the abundance of the focal species; all but the most morphologically distant neighbor is included in calculations of Euclidean distance. In the third scenario (two nearest neighbors), only the two nearest neighbors influence the abundance of the focal species and only those species are included in the calculation of Euclidean distance. In the last scenario (nearest neighbor), only the closest morphological neighbor to a focal species is included in the calculation of Euclidean distance. N is the number of species in a local feeding guild, m is the number of characters on which ecomorphological distance is based (7) in this study, and t identifies a particular focal species.

Competitive scenarios

Community structure can be produced via a spectrum of interspecific interactions, ranging from pairwise effects, to those based on all possible interactions. Ecomorphological dissimilarity can be measured from a variety of perspectives as well, corresponding to the ways competition could structure communities. If diffuse competition pervades a feeding guild, then the abundance of a species will be the product of its morphological proximity to all other species. This should be true when all guild members are fairly general in dietary requirements and consume resources that in at least some way overlap with those of ecomorphological neighbors. In contrast, interactions between a species and its most ecologically similar neighbors may be the primary factor acting on community structure, and the morphological relationships between a species and its nearest neighbors should most affect abundance. This should be true when species possess fairly narrow dietary requirements and resource overlap involves few species in a feeding guild.

We evaluated four competitive scenarios along the spectrum of possibilities (Fig. 1). In the first scenario ($N - 1$) the abundance of a given species is the consequence of its morphological relationships with all other species in the feeding guild. It evaluates diffuse competitive interactions. In the second scenario ($N - 2$), interactions between a focal species and its most morphologically distinct neighbor may be so weak as to have no effect on abundance. Therefore, simulations were conducted in which the Euclidean distance included all species in the feeding guild except the most morphologically different neighbor ($N - 2$ of the species in the feeding guild). In the third and fourth scenarios, the abundance of species is not the product of diffuse competition but is a consequence of interactions with morphologically similar neighbors, hence

Table 1. Sources of data used to evaluate ecomorphological structure of bat communities. Letters refer to feeding guilds (A, aerial insectivore; F, frugivore; G, gleaning animalivore; M, molossid insectivore; N, nectarivore; P, piscivore; S, sanguinivore); when in lower case, a feeding guild was present in the community, but could not be analyzed for methodological reasons.

Community	Country	Feeding guilds	Reference
Iowa	United States	A	Kunz 1973
California	United States	A, g, m	Suprenant 1977
Chiapas	Mexico	a, F, G, M, n, p, s	Medellin 1993
Guanacaste-1	Costa Rica	A, F, G, M, N, p	LaVal and Fitch 1977
Guanacaste-2	Costa Rica	A, F, G, n, p, s	Fleming et al. 1972
Puntarenas	Costa Rica	A, F, g, N	LaVal and Fitch 1977
Heredia	Costa Rica	A, F, G, N, s	LaVal and Fitch 1977
Sherman	Panama	A, F, G, n, m, p, s	Fleming et al. 1972
Rodman	Panama	A, F, G, m, n, s	Fleming et al. 1972
Barro Colorado Island (BCI)	Panama	a, F, G, m, n, p, s	Bonaccorso 1975
Zabelitas	Colombia	a, F, G, N, s	Thomas 1972
Pance	Colombia	a, F, m, n	Thomas 1972
Jenaro Herrera	Peru	A, f, G, M, N, s	Ascorra and Gorchov in litt. Ascorra et al. 1993 Gorchov et al. 1995
Edaphic Cerrado of Ceara	Brazil	A, F, G, M, n, p, s	Willig 1982
Caatinga of Pernambuco	Brazil	A, F, G, M, N, p, s	Willig 1982

only the two nearest neighbors of a focal species or the nearest neighbor of a focal species were included in calculations of Euclidean distance in those scenarios, respectively.

Communities

Fifteen New World bat communities were evaluated for evidence of density compensation (Table 1, Fig. 2). Taxonomy of species followed Koopman (1993). A number of criteria (Stevens and Willig 1999) limited the number of communities selected for analyses. First, sampling must have been conducted in a well-delimited local area that likely represented an *actual* community of species that, because of their spatial proximity, exhibit the potential to interact. Faunas of geopolitically bounded areas were not acceptable because it was difficult to be reasonably sure that only one community was sampled. Second, sampling must have been for at least one year. This minimized the failure to detect rare species. Lastly, data must have been the product of sampling in all seasons that bats were active. If density compensation occurs, it may manifest through the absence of species during portions of the year when resources are rare. By considering abundance throughout all seasons, density compensation can be evaluated from an annual perspective.

Each community was categorized into seven feeding guilds (sensu Root 1967): aerial insectivores, frugivores, gleaning animalivores, molossid insectivores, nectarivores, piscivores, and sanguinivores. Assignment of species to guilds was based on designations from the original description of the community or from other published dietary information (e.g., Wilson 1975, Gardner 1977). We examined only five guilds (aerial insectivores, frugivores, gleaning animalivores, molossid insectivores, nectarivores). The piscivore and sanguinivore guilds were not included in analyses because at least three species are necessary for correlation analysis. Piscivores never met this criterion; sanguinivores did, but at only one location.

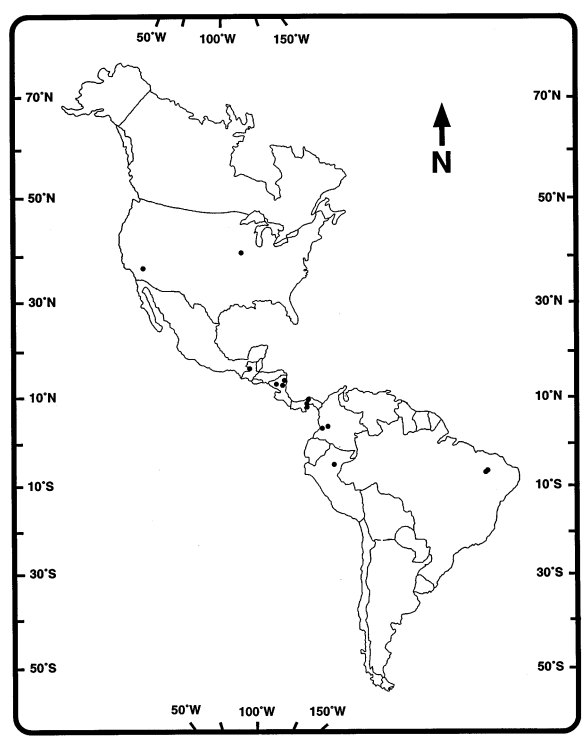

Fig. 2. Location of the 15 bat communities used to evaluate density compensation.

Morphological structure

Seven ecomorphological attributes characterized the size and shape of each species. These were forearm length, greatest length of skull, condylobasal length, width across the postorbital constriction, breadth of the braincase, length of the maxillary toothrow, and breadth across the upper molars (see Stevens 1996). These morphological characters reflect important trophic characteristics of mainland New World bats (Stevens and Willig 1999). In all cases, morphological measurements were obtained from museum specimens. In most cases, the mean of each morphological character was based on eight individuals, usually four males and four females. Often times individuals collected from the same community were located in museum collections and used in analyses. When original investigators did not collect vouchers, specimens from nearby locations were used. In most cases, specimens for each community were from the same phytogeographic area within 700 km of the actual community. In all cases, specimens were from the same subspecies as those found in the actual community.

Common logarithms of each character were used in analyses following Ricklefs and Travis (1980). Log transformations often enhance normality and homoscedasticity (Ricklefs and Travis 1980, Sokal and Rohlf 1995). Moreover, log transformations reduce the disparity in size among morphological characters of a species, thereby reducing the propensity for differences in large characters to disguise differences in small characters and linearize allometric relationships among characters.

Results

Total species richness, regardless of guild, ranged from eight in the Iowa community to 58 in the community at Jenero Herrera. Similarly, the number of guilds per community ranged from one in Iowa, to seven in the Chiapas, Sherman, Barro Colorado Island, edaphic Cerrado, and Caatingas communities (Table 1). As total species richness increased, the number of guilds within a community increased as well (Spearman rank correlation analysis, $r = 0.52$, $n = 15$, $p = 0.023$). Considerable variation among communities also characterized the species richness of particular guilds: aerial insectivores (4–15 species), frugivores (6–19 species), gleaning animalivores (7–18 species), molossid insectivores (3–7 species), and nectarivores (4–11 species). Nonetheless, the likelihood of significant deterministic structure was unrelated to the number of species within a guild or to the number of species within the community from which the guild was obtained (Appendix 1).

Density compensation was detected in five communities (Appendix 1 – Guanacaste-1, Sherman, Barro Colorado Island, Jenaro Herrera, and edaphic Cerrado) and in three feeding guilds (Appendix 1 – aerial insectivores, frugivores, gleaning animalivores). Statistically significant positive correlations between abundance and morphological distance ranged from $r = 0.44$ to $r = 0.978$ and were detected by both parametric and rank statistics. Nonetheless, no community was characterized strongly by deterministic structure in all its constituent feeding guilds, and no feeding guild was deterministically structured at all locations. Obvious patterns as to which communities or feeding guilds consistently exhibit deterministic structure were unclear.

Despite a lack of statistical concordance, the possibility exists that when results are combined, either across all locations for a particular feeding guild, or across all feeding guilds in a particular community, overall deterministic structure may be revealed (Sokal and Rohlf 1995). We conducted a meta-analysis based on Fisher's test of combined probabilities (Sokal and Rohlf 1995) to evaluate this possibility. Although results were not consistent across morphological scenarios, three communities (Guanacaste-1, Sherman, and edaphic Cerrado) and one feeding guild (gleaning animalivores) exhibited structure that generally was deterministic based on at least one metric (Table 1).

Density compensation was detected under all competitive scenarios (Table 2). However, when nonrandom abundances occur within feeding guilds, they rarely occurred in all four competitive scenarios. Often, density compensation was detectable when only nearest neighbors were utilized for the determination of competitive pressure.

Discussion

The role of competitive interactions in structuring communities has been questioned critically. Consequently, the importance of competition theory and its implications to understanding community organization remain suspect (Strong et al. 1984). At the heart of the controversy are questions concerning the random nature and ubiquity of morphological patterns. Many morphological patterns have been shown to lack statistical validity (Simberloff and Boeklen 1981), that is, they are indistinguishable from patterns generated by stochastic processes. Moreover, a preponderance of reported morphological patterns pertain to vertebrate communities and may not fairly represent the structure of other communities (Strong 1984). Although morphological patterns are well-documented in bat communities (Findley 1976, Fleming 1986, McKenzie and Rolfe 1986, Willig 1986), hyperdispersions are not a consistent attribute of their structure (Willig and Moulton 1989, Stevens and Willig 1999).

Table 2. Results of Fisher's test assessing overall deterministic structure of communities and feeding guilds by combining probabilities from all communities and guilds, respectively. Probability levels based on Pearson Product-Moment (P_p) and Spearman Rank (P_s) correlations are reported for each competitive scenario. Acronyms for feeding guilds are: AEINS, aerial insectivore; FRUGI, frugivore; GLEAN, gleaning animalivore; MOLOS, molossid insectivore; NECTA, nectarivore. Four competitive scenarios (N-1, N-2, two nearest neighbors, and nearest neighbor) are defined in text. Bold values indicate overall deterministic structure at $p \leq 0.10$.

Ecological unit	Competitive scenarios							
	N-1		N-2		Two nearest neighbors		Nearest neighbor	
	p_p	p_s	p_p	p_s	p_p	p_s	p_p	p_s
Communities								
Iowa	0.184	0.287	0.176	0.290	0.265	0.348	0.267	'0.503
California	0.118	0.365	0.131	0.331	0.115	0.436	0.767	0.815
Chiapas	0.228	0.246	0.315	0.411	0.510	0.504	0.603	0.649
Guanacaste-1	0.315	**0.019**	0.325	**0.029**	0.441	0.182	0.506	0.379
Guanacaste-2	0.623	0.506	0.610	0.598	0.598	0.411	0.774	0.811
Puntarenas	0.941	0.837	0.955	0.915	0.979	0.979	0.990	0.937
Heredia	0.968	0.970	0.960	0.937	0.971	0.991	0.929	0.938
Sherman	**0.051**	0.242	**0.016**	**0.069**	**0.035**	0.388	**0.021**	0.127
Rodman	0.485	0.626	0.411	0.428	0.381	0.289	0.404	0.379
BCI	0.357	0.251	0.356	0.262	0.928	0.802	0.893	0.812
Zabelitas	0.440	0.366	0.469	0.469	0.793	0.864	0.437	0.743
Pance	0.712	0.832	0.697	0.855	0.836	0.945	0.833	0.846
Jenaro Herrera	0.947	0.998	0.895	0.995	0.951	0.634	0.981	0.940
Edaphic Cerrado	0.507	0.667	0.126	0.244	0.114	0.333	0.365	**0.034**
Caatingas	0.966	0.765	0.965	0.873	0.941	0.891	0.883	0.820
Feeding guilds								
AEINS	0.269	0.465	0.160	0.368	0.235	0.622	0.528	0.612
FRUGI	0.454	0.162	0.419	0.207	0.917	0.802	0.968	0.914
GLEAN	0.847	0.848	0.475	0.468	0.447	0.281	0.359	**0.056**
MOLOS	0.799	0.889	0.839	0.964	0.836	0.922	0.805	0.951
NECTA	0.971	0.953	0.988	0.985	0.990	0.999	0.993	0.998

Density compensation also is not a pervasive attribute of the structure of bat communities or feeding guilds. Nonetheless, it is an additional approach for characterizing the influence of interspecific competition on community organization. Community ecologists have been hasty to discount the validity of competition theory based on rejections of single predictions. Although we have by no means exhaustively evaluated all of the possible ways that competition can structure bat communities, two plausible scenarios have been eliminated (this study, Stevens and Willig 2000), and consequently suggest that competitive interactions are not a general structuring mechanism. Indeed, competitive interactions are not sufficiently strong to cause nonrandom patterns in morphology or abundance.

Conditions for community-level effects

Interspecific competition is a density-dependent phenomenon (Begon et al. 1990), but its ability to structure communities is predicated on a narrow range of conditions. For example, environmental characteristics must be such that density-dependent phenomena manifest at the community level. For one species to influence the population density of another, at least one must be approaching carrying capacity. Ultimately, competitive interactions must be strong and sufficiently pervasive to cause the competitive exclusion and character displacement that result in morphological hyperdispersion (Moulton and Pimm 1986). Clearly, many factors may cause populations to be disequilibrial, resulting in a more random appearing structure.

Particular species-specific attributes may permit some taxa to beguile the effects of density dependence. For example, the volant nature of bats allows them more plasticity regarding responses to resource levels and competitive interactions; a number of bat species exhibit only temporary residence in communities only when sufficient resources exist (Bonaccorso 1975, Cockrum 1991, Wilkinson and Fleming 1996, Ceballos et al. 1997). Mobile organisms simply may leave a community when resources are low and thereby escape strong competitive effects. Later, these species may easily and rapidly re-colonize when systems regain sufficient resource levels. Thus, high mobility may contribute to disequilibrial conditions, narrow the range of conditions that support deterministic structure, and essentially exorcise the "ghost of competition past". Moreover, defection by only one or a small subset of species likely will diminish the integrity of the community sufficiently to result in more random appearing structure.

Competitive interactions are not the only constraints on the abundance of species. Other biotic factors, such as mutualism, predation, and parasitism, along with environmental factors such as productivity and climatic variability, influence abundance as well (Andrewartha and Birch 1954, 1988, Begon et al. 1990). These factors may modulate abundances to such an extent that sufficient background noise exists to obfuscate the effects of competitive interactions. Moreover, when environments are variable, life history attributes may restrict the operation of density-dependent phenomena. Bats are long lived for animals of their size, and have low fecundity and high survivorship (Keen and Hitchcock 1980, Tuttle and Stevenson 1982, Fleming 1988, Findley 1993). Such characteristics reduce resilience to perturbations or variation in resource levels (Pimm 1991). Thus, bats probably are not capable of the rapid population growth that would be necessary to track resources when they are variable. If resources were relatively more variable than a population's ability to respond to that variability (via change in population size), then species populations may never reach their maxima and the potentially strong density-dependent effects of interactions such as competition may never give rise to deterministic structure at the local level. To this end, bats may need persistently stable environments to experience the types of competitive interactions that induce deterministic structure. In light of the impressive amount of environmental heterogeneity that characterizes even tropical areas, it should be of no surprise that only a few of the communities that we evaluated exhibited deterministic structure.

Lastly, data characterizing New World bat communities come from locations that span approximately 50 degrees of latitude. These communities not only represent a number of biomes, but undoubtedly lie along extensive gradients of temperature, precipitation, and productivity. Variability in the degree of deterministic structure may reflect the efficacy of competitive interactions to structure communities along any or all of these environmental gradients.

Summary

We evaluated five feeding guilds from 15 bat communities distributed throughout the New World for non-random patterns between abundance and ecomorphology. Although deterministic structure was detected in three feeding guilds and in five communities, it was not a pervasive phenomenon. The unique life history attributes of bats, combined with high levels of environmental heterogeneity and variability likely prevent competitive interactions from inducing deterministic structure in a ubiquitous fashion.

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Appendix 1. Results from simulation analyses evaluating nonrandom patterns in the association between abundance and ecomorphological distance in each of 15 bat communities. R represents species richness of each ecological unit. Four competitive scenarios (N-1, N-2, two nearest neighbor, and nearest neighbor) are defined in text. r_p and r_s represent Pearson-product moment and Spearman-rank correlation coefficients, respectively. p_p and p_s represent the probability that particular Pearson-product moment and Spearman-rank correlation coefficients, respectively, come from a simulated distribution in which $r = 0$. Bold values indicate deterministic guild structure at $p \leq 0.10$. Guild acronyms are defined in Table 2.

Community	Competitive scenarios																
		N-1				N-2				Two nearest neighbors				Nearest neighbor			
	R	r_p	p_p	r_s	p_s	r_p	p_p	r_s	p_s	r_p	p_p	r_s	p_s	r_p	p_p	r_s	p_s
Iowa	8																
AEINS	8	0.367	0.184	0.228	0.287	0.385	0.176	0.228	0.290	0.249	0.265	0.156	0.348	0.263	0.267	−0.006	0.503
California	10																
AEINS	8	0.471	0.118	0.167	0.365	0.464	0.131	0.191	0.331	0.481	0.115	0.071	0.436	−0.292	0.767	−0.362	0.815
Chiapas	50																
FRUGI	13	0.226	0.227	0.154	0.302	0.216	0.233	0.113	0.360	−0.217	0.754	−0.118	0.648	−0.142	0.662	−0.032	0.553
GLEAN	14	−0.181	0.732	0.081	0.397	−0.204	0.756	0.081	0.393	−0.348	0.891	−0.113	0.645	−0.359	0.897	0.130	0.670
MOLOS	3	0.950	0.103	1.000	0.161	0.866	0.166	0.866	0.335	0.950	0.107	1.000	0.168	0.866	0.173	0.866	0.330
Guanacaste-1	36																
AEINS	12	**0.474**	**0.045**	**0.736**	**0.002**	**0.490**	**0.041**	**0.753**	**0.001**	**0.465**	**0.067**	**0.641**	**0.012**	**0.428**	**0.084**	**0.534**	**0.043**
FRUGI	6	−0.164	0.620	0.174	0.362	−0.203	0.637	−0.087	0.591	−0.221	0.653	−0.087	0.592	−0.147	0.596	0.044	0.469
GLEAN	9	0.311	0.233	0.409	0.142	0.351	0.192	0.443	0.114	0.319	0.230	0.298	0.216	0.205	0.329	0.151	0.344
MOLOS	4	−0.651	0.820	−0.200	0.630	−0.734	0.860	−0.400	0.791	−0.734	0.871	−0.400	0.784	−0.416	0.700	−0.211	0.673
NECTA	4	−0.158	0.576	0.400	0.375	−0.528	0.765	−0.600	0.833	−0.528	0.769	−0.600	0.837	−0.674	0.840	−0.894	1.000
Guanacaste−2	27																
AEINS	8	−0.372	0.822	−0.419	0.850	−0.365	0.819	−0.419	0.851	−0.390	0.829	0.419	0.854	−0.428	0.856	0.249	0.738
FRUGI	8	0.147	0.354	0.407	0.144	0.169	0.348	0.323	0.208	0.257	0.279	0.503	0.101	−0.266	0.738	−0.006	0.497
GLEAN	7	0.113	0.382	−0.073	0.578	0.145	0.371	0.085	0.570	0.059	0.436	−0.024	0.550	0.192	0.308	−0.124	0.614
Puntarenas	24																
AEINS	9	−0.171	0.637	−0.009	0.508	−0.221	0.699	−0.230	0.727	−0.364	0.825	−0.426	0.876	−0.382	0.846	−0.410	0.873
FRUGI	8	−0.344	0.800	−0.238	0.730	−0.334	0.797	−0.238	0.733	−0.351	0.805	−0.286	0.774	−0.469	0.874	−0.243	0.724
NECTA	6	−0.446	0.814	−0.200	0.675	−0.450	0.820	−0.200	0.674	−0.522	0.849	−0.429	0.826	−0.549	0.871	−0.120	0.643
Heredia	57																
AEINS	15	−0.090	0.615	−0.110	0.658	−0.107	0.638	−0.131	0.682	−0.136	0.668	−0.084	0.617	−0.087	0.617	0.125	0.324
FRUGI	15	−0.234	0.803	−0.047	0.572	−0.246	0.807	−0.052	0.582	−0.170	0.726	−0.330	0.885	0.004	0.492	−0.295	0.866
GLEAN	18	−0.267	0.854	−0.351	0.924	−0.253	0.837	−0.316	0.896	−0.340	0.918	−0.312	0.897	−0.340	0.919	−0.277	0.869
NECTA	6	−0.339	0.726	−0.638	0.909	−0.247	0.653	−0.174	0.640	−0.308	0.715	−0.667	0.930	−0.380	0.769	−0.731	0.940

Appendix 1. (Continued)

Community	Competitive scenarios																
		N-1				N-2				Two nearest neighbors				Nearest neighbor			
	R	r_p	p_p	r_s	p_s	r_p	p_p	r_s	p_s	r_p	p_p	r_s	p_s	r_p	p_p	r_s	p_s
Sherman	32																
AEINS	6	**0.858**	**0.011**	0.464	0.180	**0.939**	**0.003**	**0.754**	**0.052**	**0.909**	0.004	0.493	0.146	**0.884**	**0.007**	0.493	0.175
FRUGI	14	0.207	0.242	0.258	0.188	0.221	0.219	0.326	0.128	−0.150	0.695	−0.024	0.537	−0.064	0.593	−0.051	0.562
GLEAN	8	−0.286	0.750	−0.049	0.557	−0.233	0.701	0.049	0.433	0.140	0.373	−0.025	0.541	0.445	0.133	**0.575**	**0.071**
Rodman	28																
AEINS	4	−0.569	0.790	−0.633	0.838	−0.523	0.764	−0.633	0.834	−0.523	0.765	−0.633	0.836	−0.488	0.743	−0.389	0.746
FRUGI	12	0.310	0.168	0.314	0.157	0.325	0.149	0.388	0.110	0.280	0.192	0.300	0.173	−0.037	0.558	0.224	0.233
GLEAN	8	0.018	0.489	−0.406	0.854	0.094	0.414	−0.063	0.557	0.265	0.280	0.381	0.175	0.488	0.110	0.291	0.234
BCI	36																
FRUGI	12	0.366	0.120	**0.455**	**0.073**	0.369	0.121	**0.448**	**0.081**	−0.165	0.698	0.007	0.492	−0.111	0.640	0.011	0.496
GLEAN	11	−0.465	0.928	−0.498	0.939	−0.458	0.921	−0.402	0.896	−0.464	0.924	−0.411	0.898	−0.418	0.899	−0.437	0.913
Zabelitas	35																
FRUGI	19	0.167	0.245	0.211	0.199	0.173	0.243	0.179	0.232	−0.035	0.550	−0.126	0.703	−0.031	0.540	0.084	0.636
GLEAN	6	0.144	0.394	0.091	0.400	0.144	0.387	−0.030	0.546	−0.088	0.571	−0.030	0.538	0.463	0.174	0.000	0.511
NECTA	5	−0.081	0.556	0.100	0.479	−0.229	0.646	0.100	0.479	−0.244	0.667	−0.300	0.742	−0.100	0.564	0.000	0.533
Pance	16																
FRUGI	12	−0.170	0.712	−0.301	0.832	−0.167	0.697	−0.329	0.855	−0.300	0.836	−0.483	0.945	−0.307	0.833	−0.316	0.846
Jenaro Herrera	58																
AEINS	11	−0.345	0.842	−0.474	0.933	−0.341	0.832	−0.460	0.924	−0.431	0.903	−0.515	0.944	−0.456	0.924	−0.528	0.953
GLEAN	15	0.115	0.365	−0.215	0.782	0.135	0.331	−0.109	0.657	0.113	0.365	**0.415**	**0.059**	−0.085	0.607	0.177	0.268
MOLOS	3	−0.971	0.931	−1.000	1.000	−0.655	0.731	−0.866	1.000	−0.971	0.927	−1.000	1.000	−0.655	0.734	−0.866	1.000
NECTA	4	−0.740	0.869	−0.600	0.833	−0.689	0.841	−0.600	0.834	−0.689	0.846	−0.600	0.838	−0.805	0.900	−0.738	0.917
Edaphic Cerrado	25																
AEINS	7	−0.402	0.819	−0.198	0.671	−0.358	0.790	−0.198	0.669	−0.094	0.580	−0.126	0.609	−0.240	0.702	−0.073	0.569
FRUGI	7	0.162	0.367	0.321	0.254	0.165	0.373	0.250	0.302	0.153	0.378	0.036	0.484	0.023	0.482	−0.147	0.649
GLEAN	4	0.746	0.122	0.316	0.383	**0.978**	**0.009**	**0.949**	**0.043**	**0.978**	**0.010**	**0.949**	**0.043**	**0.901**	**0.057**	**0.943**	**0.000**
MOLOS	3	−0.637	0.718	−0.500	0.835	−0.490	0.663	0.000	0.665	−0.637	0.724	−0.500	0.828	−0.490	0.663	0.000	0.669
Caatingas	34																
AEINS	5	−0.563	0.842	−0.718	0.937	−0.593	0.858	−0.718	0.934	−0.735	0.922	−0.667	0.892	−0.517	0.819	−0.890	0.968
FRUGI	7	−0.097	0.575	0.179	0.362	−0.008	0.509	0.214	0.331	0.132	0.397	0.214	0.316	0.269	0.280	0.275	0.271
GLEAN	9	−0.191	0.700	0.268	0.240	−0.169	0.670	0.268	0.246	−0.120	0.607	0.100	0.362	−0.114	0.616	0.284	0.205
MOLOS	7	−0.402	0.805	−0.655	0.950	−0.431	0.834	−0.655	0.945	−0.545	0.902	−0.746	0.966	−0.367	0.795	−0.692	0.955
NECTA	3	−0.390	0.623	−0.500	0.830	−0.553	0.696	−0.867	1.000	−0.390	0.629	−0.500	0.833	−0.553	0.689	−0.866	1.000