Community structure, abundance, and morphology

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The role of interspecific competition in structuring communities has been a highly debated issue for the last two decades. The nonrandom nature of morphological patterns within communities has been at the center of this controversy. Null models addressing community-wide dispersions in morphology have produced equivocal results and may be based on assumptions that are too restrictive (e.g., competitive exclusion or displacement). If morphological distinctiveness allows species to escape competitive pressures and exhibit higher densities, then a positive relationship should exist between morphological dissimilarity and abundance. We develop a suite of models that evaluates patterns in abundance that are associated with the morphological proximity of a species to other competitors. We evaluated the relationship between morphological distance and abundance from a variety of morphological perspectives, from those representing strictly diffuse interactions to those representing only interactions between a species and its nearest neighbor in morphological space. These models were sufficiently powerful to detect positive associations between abundance and morphological differences in a nocturnal desert rodent guild for which the effects of competition on structure are well established. Models such as these may be more useful than traditional models evaluating morphological dispersions for many reasons. They do not require that communities reach equilibrium before competitive interactions give rise to deterministic structure. They do not suffer from limitations of potentially inaccurate faunal pools or from phylogenetic constraints. Lastly, they may be used as a diagnostic tool in comparative studies to determine the degree to which competitive interactions structure communities.

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Theory and empirical evidence suggest that interspecific competition can play an important role in structuring natural communities (Cody and Diamond 1975, Strong et al. 1984, Diamond and Case 1986, Kikkawa and Anderson 1986). Nonetheless, the influence of competition on community structure remains one of the most controversial issues in ecology (Strong et al. 1984). In particular, patterns in the morphology of co-occurring species have been a popular means to characterize community organization (Mares 1976, Bowers and Brown 1982, Willig 1982, 1986, Case and Sidell 1983, Moulton and Pimm 1983, 1986a, b, 1987, Schoener 1984, Brown and Bowers 1985, Moulton 1985, Diamond and Case 1986, Willig and Moulton 1989, Dayan and Simberloff 1994, Stevens and Willig 1999). An important assumption of this approach, consistent with competition theory, is that the ability to detect, handle, and process food is dependent on morphology. Substantial evidence indicates that this assumption is generally true (Brown and Lieberman 1973, Hespenheide 1973, Bonaccorso 1975, Smartt 1978, Freeman 1979, 1984, 1988, Findley and Wilson 1982, Findley and Black 1983, Dayan and Simberloff 1994, Stevens and Willig 1999). Accordingly, if the morphologies of two

or more species are not sufficiently distinct, then the resources that they consume likely will be similar, and interspecific competition will ensue. With enough time and intensity, competitive interactions should manifest as character displacement or competitive exclusion (Gause 1934, Brown and Wilson 1956, Hardin 1960, Case and Sidell 1983). In either case, competition should give rise to hyperdispersion of morphologies within ecological communities.

Prior to the 1980s, hyperdispersed morphologies were interpreted as strong evidence of competitively induced community structure (Simberloff and Boeklen 1981). However, null models have demonstrated that many patterns in morphology originally believed to be the result of interspecific competition can be generated by chance (Connor and Simberloff 1979, Strong et al. 1979, Ricklefs and Travis 1980, Grant and Schluter 1984). As a result, evidence is equivocal regarding the nature of mechanisms leading to morphological patterns within communities. Indeed, such competitively induced community structure is not as common as once believed (Strong et al. 1979, Simberloff and Boeklen 1981, Willig and Moulton 1989, Lossos 1992, Roughgarden 1995), and consequently, some have abandoned the notion that competition theory provides substantial insight into the structure of natural communities (Strong et al. 1984).

Species experiencing more competitive pressure should exhibit lower abundance (Volterra 1926, Lotka 1932). This provides another means to detect deterministic structure. If morphological similarity is a viable surrogate for ecological similarity, then those species that are morphologically dissimilar from other species in a community should experience the least competitive pressure and exhibit the highest abundance. This phenomenon is known as density compensation (Crowell 1962, Root 1973, Hawkins and McMahon 1989). Thus, a positive relationship should exist between the abundance and the morphological distance of a species with respect to potential competitors; the strength of this relationship should be greater than that produced by stochastic processes.

Herein, we develop a suite of models that evaluates whether competitive effects, based on ecological similarity, give rise to density compensation. Our models evaluate the degree to which an association between abundance and the ecomorphological distance of a species is positive and nonrandom within communities. We then apply these models to a system in which the effects of competition are well understood (nocturnal desert granivores), and demonstrate that this approach can detect non-random patterns in situations where competition has been documented to structure communities.

The model

Analyses are predicated on the assumption that morphological attributes of species are good predictors of ecological attributes, and a species with high ecomorphological similarity to one or more potential competitors should suffer reduced density as a result of competition. As a consequence, a quantitative relationship should exist between the position of a species in ecomorphological space and its density. Moreover, we assume that competitive interactions that lead to structure are most intense within functional subsets of the community (e.g., feeding guilds, sensu Root 1967) and that these subsets represent the appropriate foci for evaluating competitively induced community organization.

Simulation analyses were performed to determine if associations between morphological dissimilarity and abundance of species were non-random. Log-transformed morphological measurements were used to calculate Euclidean distance among species (Digby and Kempton 1987). Correlation coefficients were used to describe the degree of association between morphological distance and abundance. Parametric correlation coefficients are ideal descriptors of association when variates are bi-normally distributed and covariance is linear (Sokal and Rohlf 1995). Nonetheless, such assumptions of linearity and normality may not be most appropriate to studies involving numerous communities; we have no a priori reason to believe that abundance, morphological distance, and their association adhere to these assumptions. Thus, we calculated both parametric (Pearson product-moment) and distribution-free (Spearman rank) correlation coefficients to describe the magnitude of the association between abundance and morphological distance. Traditional tests of significance assume that variates follow a specified distribution. For example, hypothesis tests for both Pearson product-moment and Spearman rank (when $N < 30$) correlation analyses assume that random variates adhere to a t-distribution (Sokal and Rohlf 1995). If actual variates do not follow this distribution, traditional hypothesis tests may be inaccurate (Noreen 1989). Simulation analyses are not subject to these biases. By randomizing actual data to yield a distribution to which the observed statistics are compared, such assumptions are not necessary and their violations cannot jeopardize the accuracy of significance levels (Noreen 1989).

To evaluate deterministic structure, we compared the correlation coefficient describing the degree of association between morphological distance and abundance from an actual guild to those of simulated guilds. To produce random guilds, we preserved the integrity of the morphological relationships among species and randomized abundances. A correlation co-

efficient was then calculated between randomized abundances and actual morphological distances. Ten thousand iterations of this process yielded a probability density function. The correlation coefficient from the actual guild was then compared to the probability density function of simulated correlation coefficients. Many factors influence the abundance of species (Andrewartha and Birch 1954, 1988, Begon et al. 1990). As such, strong positive correlations between morphological distance and abundance caused by competition may be diminished by autecological or other synecological processes (e.g., mutualism, predation). Consequently, caution should be employed to prevent falsely rejecting competition as an important influence on community structure. To minimize the possibility of such a Type I statistical error, we consider significance as $p \leq 0.10$.
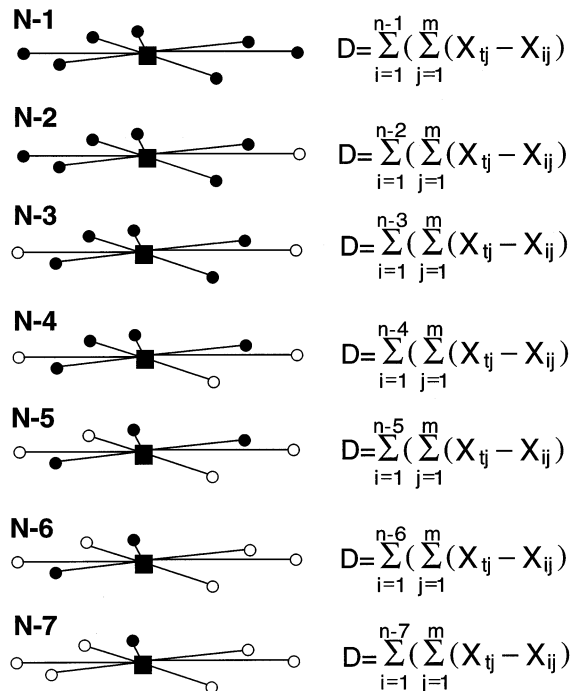
N-1

$$D = \sum_{i=1}^{n-1} (\sum_{j=1}^{m} (X_{tj} - X_{ij}))$$

N-2

$$D = \sum_{i=1}^{n-2} (\sum_{j=1}^{m} (X_{tj} - X_{ij}))$$

N-3

$$D = \sum_{i=1}^{n-3} (\sum_{j=1}^{m} (X_{tj} - X_{ij}))$$

N-4

$$D = \sum_{i=1}^{n-4} (\sum_{j=1}^{m} (X_{tj} - X_{ij}))$$

N-5

$$D = \sum_{i=1}^{n-5} (\sum_{j=1}^{m} (X_{tj} - X_{ij}))$$

N-6

$$D = \sum_{i=1}^{n-6} (\sum_{j=1}^{m} (X_{tj} - X_{ij}))$$

N-7

$$D = \sum_{i=1}^{n-7} (\sum_{j=1}^{m} (X_{tj} - X_{ij}))$$

Fig. 1. Seven competitive scenarios based on considerations of morphology and abundance. In calculations of distance (D) for focal species based on a suite of ecomorphological characters (X), i represents other species in the guild from most distant (1) to least distant (N-1), and j represents any of m different ecomorphological characters. In the first scenario (N-1), the abundance of the focal species (square) is a function of its ecomorphological relationships with all neighbors (black dots); Euclidean distances (D) include all species in the feeding guild (N-1). In the second scenario (N-2), the morphological relationship between the focal species and its most distant neighbor (open circle) has no influence on the abundance of the focal species; all but the most morphologically distant neighbor is included in calculations of Euclidean distance. In subsequent scenarios (N-3 to N-7) decreasing suites of species are used in calculations of Euclidean distance. In the last scenario (N-7), only the focal species and its nearest neighbor determine morphological distance.

Competitive scenarios

Community structure can be produced via a spectrum of interspecific interactions, ranging from pairwise effects, to those based on all possible interactions among guild members. Ecomorphological dissimilarity can be measured from a variety of perspectives as well. In general, if diffuse competition is important in structuring communities, then the morphological distance of each species to all others in a feeding guild primarily determines the density of each species. In contrast, if the primary factor affecting community structure is strong interaction only between species with relatively similar ecologies, then the density of a species should be most related to its ecomorphological distance to nearest neighbors.

We exhaustively evaluated seven competitive scenarios (Fig. 1) along the spectrum of possibilities for a Sonoran Desert nocturnal rodent granivore guild (Brown 1989). In the first scenario, the abundance of a species is the product of its morphological relationships with all other (N is the total number of species) species in the feeding guild. The Euclidean distance (D) for each species represents the ecomorphological (Findley 1976, Mares 1976, Findley and Wilson 1982) distance of a species with respect to all other guild members. Remaining scenarios represented a descending series in which furthest morphological neighbors were excluded consecutively from analyses. Thus, the N-2 scenario represented the morphological distance of each species from its six closest neighbors and the N-3 scenario represented the morphological distance of each species to its five closest neighbors. This continued until the N-7 scenario, which represented the morphological distance of each species with respect to its nearest neighbor.

Community organization

We evaluated the efficacy of this model using the granivore guild of nocturnal rodents from the Sonoran Desert, east of Tucson, Arizona, USA (Brown 1989). Although communities have explicit textbook definitions, they are often methodologically difficult to circumscribe. We chose this community because the sampled area was a well-defined system (creosote flat) that contained all microhabitats necessary for the focal group of species. Moreover, considerable effort must be spent to ensure accurate relative abundances. Brown's (1989) bi-monthly census protocol was conducted for two years and suitably meets this criterion. Finally, it was desirable to assess if this model could detect patterns of abundance in a community whose organization has been demonstrated to be mediated by interspecific competition. Brown (1989) for this community, as well

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Table 1. Community structure (relative abundance and ecomorphological distance) of the nocturnal granivore guild in the Sonoran Desert based on seven competitive scenarios, from most diffuse (*N*-1) to nearest neighbor (*N*-7).

Species	Relative abundance	Sum of morphological distances						
		N-1	*N*-2	*N*-3	*N*-4	*N*-5	*N*-6	*N*-7
Perognathus amplus	26.96	3.043	2.363	1.808	1.338	0.893	0.510	0.184
Chaetodipus baileyi	0.10	2.643	2.000	1.445	0.978	0.517	0.271	0.113
C. penicillatus	0.10	2.636	2.169	1.719	1.281	0.865	0.481	0.154
Dipodomys merriami	71.80	4.258	3.529	2.848	2.188	1.537	0.894	0.384
Peromyscus eremicus	0.10	2.319	1.659	1.188	0.750	0.352	0.200	0.087
P. maniculatus	0.29	2.271	1.620	1.175	0.759	0.386	0.228	0.087
P. merriami	0.10	2.445	1.935	1.474	1.075	0.703	0.338	0.154
Mus musculus	0.57	2.466	1.737	1.287	0.905	0.539	0.293	0.142

as others (Brown and Lieberman 1973, Brown 1984, Lemen and Freeman 1987) working on desert rodents, suggest that this is true.

We utilized a suite of log-transformed cranial and body characteristics (length of body, length of foot, length of ear, greatest length of skull, greatest width of skull, length of maxillary toothrow, and interorbital width) to estimate the position (size and shape) of each species in ecomorphological space. Morphological measurements were obtained for at least four male and four female individuals of the same subspecies as found in the actual community, either from Hoffmeister (1986) or from specimens deposited in The Museum, Texas Tech University.

Results

Variation in relative abundance and ecomorphological distance of species was considerable, spanning almost two orders of magnitude for relative density and approximately five-fold for morphology (Table 1). Simulation analyses indicated a nonrandom, positive association between ecomorphological distances of species and their abundances (Fig. 2). Species that were more ecomorphologically distant from other guild members exhibited higher abundances. Moreover, this pattern of significance was detected for all seven competitive scenarios. In general, when using parametric correlation coefficients, the relationship was strongest when competitive scenarios represented diffuse competition or competition between more nearer neighbors, and weakest for intermediate scenarios. Non-parametric correlations coefficients were less powerful at detecting significance but exhibited a pattern similar to that of parametric coefficients.

Discussion

Previous research has documented that this guild of nocturnal granivores is structured by competition (Brown 1989). Our model was sufficiently powerful to

corroborate this condition and detect competitive effects under all competitive scenarios. Consequently, it holds promise as a quantitative tool for detecting competitive effects that may not manifest as morphological hyperdispersions at the community level.

Patterns of abundance

Evaluating patterns of abundance has definite advantages because one need not assume that populations or communities are at equilibrium. Accordingly, it is not necessary to demonstrate competitive exclusion or character displacement to confirm deterministic structure. Models evaluating displacement and exclusion require morphological hyperdispersion to detect deterministic structure, yet this may be unrealistic. Competitive interactions are strongest when environments approach saturation and support species at carrying capacity (Volterra 1926, Lotka 1932, Andrewartha and Birch 1954, 1988, Chesson 1988). Moreover, to produce detectable morphological patterns in a community, competitive interactions must be intensive enough to cause extinction or morphological shifts, extensive throughout the entire community (affect all species), and must supersede other interactions (Moulton and Pimm 1986a). Consequently, predictable environments that persist for long periods of time should harbor communities which manifest hyperdispersions. Nonetheless, the precise environmental context that promotes strong competitive interactions may not be characteristic of many systems. A variety of environmental perturbations or disturbances prevent populations from reaching equilibria (Andrewartha and Birch 1954, 1988, Sale 1977, Simberloff 1984). If communities are not at equilibrium, morphologically similar species may still coexist. Thus, failure to detect hyperdispersion in morphology may be controvertible evidence at best. As long as species are not at such a state of disequilibrium that no density-dependent effects occur, the magnitude of competitive interactions may be expressed through abundance. In fact, the strength of the relationship between abundance and morphological distance may be

a good indicator of a community's proximity to equilibrium.

Another serious methodological problem that is overcome by models of abundance is the treatment of transient species. The presence of transient species in communities may occur as a consequence of source or sink phenomena operating across the landscape, or by the ability of some species to track fluctuating resources and enter the community when they are high. When resources becomes scarce, however, competition becomes more intense and these species usually are unable to persist. Most morphological models give either equal status to both permanent and transient members of a community, or exclude transient members from analy-

ses. Both methodologies probably are not ideal and certainly do not take into account the dynamic demographic nature of species. Abundance models can include transitory species and can adjust for density dependence by assigning them different status (i.e., their relative abundances measures their importance in the community). If abundance data derive from regular sampling during appropriate and meaningful time periods (e.g., sampling in all seasons throughout an entire year) a transient species with the same number of individuals as a permanent species at one point in time will have lower relative abundance because it will appear only during a fraction of the study. Thus, abundance data may be much more sensitive than
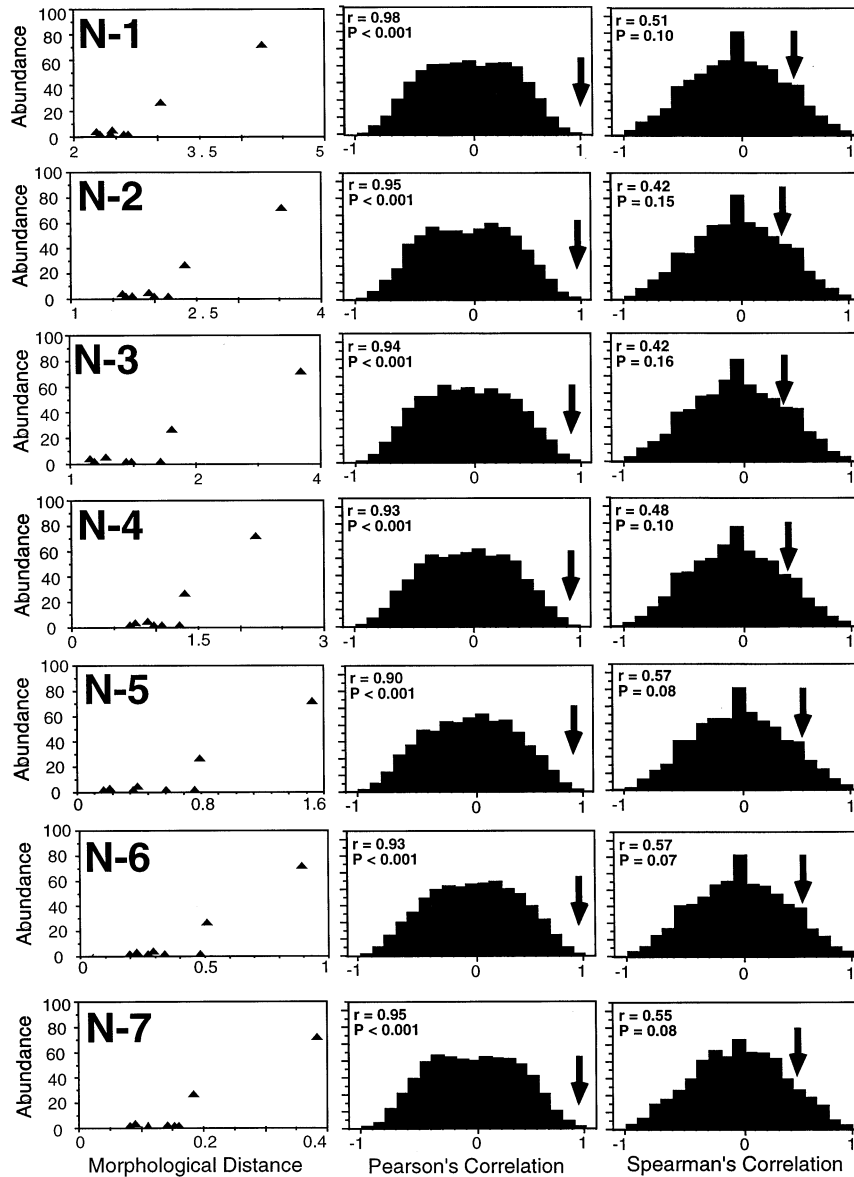
Fig. 2. Results of simulation analyses that evaluate each of seven competitive scenarios for deterministic structure. Left column depicts the relationship between abundance and morphological distance based on each of the competitive scenarios. Middle and right columns represent frequency distributions describing simulation results for Pearson-product moment and Spearman Rank correlation coefficients, respectively. In histograms, the Y-axis ranges from 0–1500, r represents the magnitude and direction of the association, the arrow represents the position of the actual correlation coefficient with respect to the simulated distribution, and P represents the probability that the observed correlation coefficient is no greater than what would be expected, coming from a distribution of random coefficients, given the constraints of the model.

presence-absence data to temporal changes in community structure.

Patterns in abundance may be sensitive to heterogeneity in resource levels, and thus be a more sensitive measures of competitively induced community organization. For example, many rodent communities, like the one used to corroborate our model, exhibit large among-year fluctuations in abundance of constituent species while experiencing little to no change in species composition (Beatley 1969, 1971, M'Closkey pers. comm.). Additionally, many systems are characterized by high levels of spatial heterogeneity, which also are accompanied by large variations in abundance, with little or no change in species composition across a landscape (M'Closkey 1978, 1981). In both situations (temporal heterogeneity and spatial heterogeneity), assemblages may exhibit a canonical population density across a gradient of heterogeneity. Consequently, only those species that exhibit positive population densities persist at the community level. Morphological models cannot evaluate heterogeneity unless it causes changes in species composition. Conversely, models of abundance may be more sensitive, and hence, more ideally suited for evaluating the relative degree to which competitive interactions provide structure along any environmental gradient because they can be used to make comparisons when changes in structure occur solely due to changes in abundances without concomitant changes in composition. Moreover, by using models such as these as descriptive tools, comparisons can be made across landscapes or years to better determine the circumstances that give rise to competitively induced structure.

Diffuse competition

Density compensation occurred under all competitive scenarios, and was strongest under scenarios reflecting all or most species in the feeding guild. Our results indicate that effects due to diffuse competition (N-1) may be just as important in the structure of feeding guilds as those caused by interactions between nearest neighbors. Competitive effects that are diffuse throughout a guild can occur in one of two ways. First, species may overlap ecologically to such a degree on a single resource axis, that any one species shares resources and competes with all others. Second, overlap may occur on more than one niche axis and the identities of species that overlap are different for each axis. For example, if species only compete for seeds, and partitioning is based on size, then species should compete most intensely with their nearest neighbors on a single eco-morphological axis. Nonetheless, many desert granivores also consume insects. If partitioning with regard to insects is not mirrored on the morphological size axis, then additional morphological dimensions may be necessary to account for ecological differences. Thus, competitive interactions transpire between nearest neighbors with regard to each morphological niche axis, but because positions of species on independent axes are not identical, each species full complement of nearest neighbors is greater than two. If species coexistence is based on multiple resource axes, as in some lizard communities, then multiple morphological axes are required to capture the salient features of community organization (Pianka et al. 1979). Our results suggest that diffuse interactions potentially based on multiple resource axes structure the nocturnal granivore guild in the Sonoran desert.

Phylogenetic constraints

Models that evaluate compensatory adjustments in community structure which occur in ecological time may be more useful for detecting deterministic structure than are models evaluating patterns resulting from size assortment or adjustment. Many models identify deterministic structure through hyperdispersed morphological patterns (Ricklefs and Travis 1980, Simberloff and Boeklen 1981, Moulton and Pimm 1986a). However, species in a community may never exhibit a dispersion in morphology that minimizes competitive interactions in that community. Many factors other than coexistence at the community level determine the morphology of each species. Bounds may be placed on morphology by phylogenetic, developmental, or physiological constraints (Stini 1979, Strauss 1987, Norberg 1990, Raff 1996). Secondly, gene flow from other communities may maintain a locally maladapted state (Camin and Ehrlich 1958, Endler 1977, Dhondt et al. 1990, Blondel et al. 1992, Riechert 1993). Lastly, the morphologies of species in a local community may be the product of interactions that transpire across the entire geographic range of a species (Ricklefs and Miles 1994), as well as those related to processes that maximize performance at a particular location. Indeed, populations within communities may exhibit only limited morphological lability with which to minimize local competitive interactions. For this reason, models evaluating constant size ratios or morphological hyperdispersions may require unrealistically stringent requirements to demonstrate nonrandom structure. In contrast, historical effects do not limit the power of models evaluating patterns of abundance. Despite attendant morphological patterns that derive from historical phenomena, species that are similar in morphological space should be similar in ecological space and experience higher degrees of competition. In turn, these species should exhibit lower abundance relative to other community members. Phylogenetic and biogeographic phenomena may very well structure the morphologies within a

community; however, they likely have little direct influence on patterns of abundance, per se.

Our models possess substantial advantages because all necessary data (measures of morphology and abundance) are often available. In contrast, many models evaluating morphological patterns suffer serious methodological limitations because they require delineation of source pools that comprise species with a reasonable potential to take part in community assembly and assortment (Graves and Gotelli 1983, Gotelli and Graves 1996). Species pools often are formed using information regarding species distributions; if a species is distributed in or around a community, it is included in the faunal pool. Certainly, most if not all information regarding species distributions is incomplete (Patterson 1994, Willig and Gannon 1997), and estimates of colonization potential are indirect or unsubstantiated. Moreover, distributional information often is not at the same grain as is community information. In other words, a species may bear the potential to occur in a community because that location is encompassed within the bounds of its geographic distribution; however, that species may not have the ability to persist there given any of a number of reasons that are not competitively based. One thing is certain: determination of appropriate faunal pools and assignment of colonization potentials represent a considerable methodological problem which has little likelihood of solution (Graves and Gotelli 1983, Colwell and Winkler 1984, Gotelli and Graves 1996, Willig and Moulton 1989, Stevens and Willig 1999).

In summary, we have presented a family of models that evaluates the degree to which communities are structured based on the relationship between morphological distance among species and their abundances. These models are effective and are not complicated by assumptions that competition gives rise to morphological adjustments or competitive exclusion. Moreover, abundance models overcome limitations related to phylogenetic and biogeographic artifacts. These models provide insight as to the complexity of ecological interactions. Lastly, abundance models may be used to compare structure at sites along environmental gradients to more precisely determine those conditions that give rise to deterministic structure.

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