Assembly rules for functional groups of North American shrews: effects of geographic range and habitat partitioning

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We examined the representation of shrew species within assemblages at 197 sites in the southern Appalachian Mountains, USA. Assemblages were classified according to representation of functional groups, including fossorial, small epigeal, and large epigeal. Average ($\pm$SD) species richness was 2.9 ± 1.0 and assemblages averaged 0.8 species in the fossorial and large epigeal groups and 1.3 species in the small epigeal group. Compliance with Fox's assembly rule was evaluated by dividing sites into those likely under the rule (favored) and those unlikely under the rule. The number of favored sites was compared to expected numbers of favored sites under three null models of community development, which variously incorporated observed characteristics of species in the regional pool. Number of favored sites (175 [89%]) exceeded the number found in each of 25,000 sets of assemblages simulated ($P < 0.00004$) using algorithms that incorporated the observed species richness of each site and the observed incidences of each species. However, the number of favored sites did not differ ($P = 0.1054$) from the number expected when patterns of allopatry and sympatry were preserved in the null model. Thus, the tendency for the equitable representation of functional groups in shrew assemblages was primarily due to the pattern of allopatry among similar species, and we believe that the striking compliance of these sites with Fox's assembly rule is largely due to structure within the regional species pool, rather than extant competitive interactions.

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Shrews (Insectivora: Soricidae) exist in diverse local assemblages, often including five or more congenerics (Sheftel 1989, Kirkland 1991). Understanding the mechanisms of coexistence in shrews has been elusive because of the difficulties involved in the live-study of these taxa. Therefore, ecologists have used circumstantial evidence, such as morphology (Malmquist 1985), habitat selection (Michielsen 1966, Hawes 1977), and diet (Butterfield et al. 1981, Churchfield 1984), to infer the degree to which shrews interact. These studies suggest that habitat preferences, diet, and vertical foraging mode are important factors allowing coexistence of syntopic species and that these factors are strongly influenced by body size. Nevertheless, shrews often exhibit strong interspecific overlap in these areas. For example, Churchfield and Sheftel (1994) found that dietary overlap was $\geq 50\%$ between pairs of shrews of similar size in the Siberian taiga.

Fox and Kirkland (1992) applied an assembly rule developed for Australian mammals (Fox 1987) to shrews

of northeastern North America and concluded that shrews of similar size are less frequently syntopic than expected by chance. Fox's (1987) assembly rule is that "there is a much higher probability that each species entering a community will be drawn from a different functional group ... until each group is represented, before the cycle repeats" (Fox 1987). Assemblages that follow Fox's (1987) assembly rule have a relatively even representation of functional groups, suggesting that competition among animals within a group is important in determining community structure. When local assemblages of small mammals have been classified according to the representation of trophic guilds, the tendency for an equitable representation of guilds has become apparent for Australian mammals (Fox 1987), rodents of southwestern North America (Fox and Brown 1993), and rodents of southern Chile (Kelt et al. 1995).

There has been much debate regarding the appropriate method of determining null expectations in these studies (Fox and Brown 1995, Wilson 1995a, b, Stone et al. 1996, Fox 1999, Simberloff et al. 1999, Brown et al. 2000, 2002, Stone et al. 2000). The dispute has focused on whether observed patterns of incidence and geographical ranges (patterns of allopatry and sympatry) should be represented in the null model. Fox and Brown (1995), Fox (1999) and Brown et al. (2000, 2002) argued that competition may influence patterns of incidence and placement of geographic ranges, which in turn influence local assemblages. Therefore, it is appropriate to exclude these factors from null models of community development; models that include these factors would suffer from the Narcissus effect (Colwell and Winkler 1984). Conversely, Wilson (1995a), Simberloff et al. (1999) and Stone et al. (2000) contend that patterns of incidence and geographic ranges should be represented in null models because, otherwise, rejections of the null model are an artifact of the fact that species differ in their frequencies of occurrence and have geographic ranges of different sizes and locations. Patterns of incidence and placement of geographical ranges are not necessarily a function of competition within assemblages (Stone et al. 2000).

We examined a data-set of shrew assemblages from 197 sites in the southern Appalachian region in the southeastern United States and determined the number of assemblages complying with Fox's (1987) assembly rule (favored assemblages). By comparing our results with the number of favored assemblages expected under three alternative null models of community development, we were able to better understand the influences of species' incidences, pattern of allopatry and sympatry, and local interactions on the structure of shrew assemblages in this region.

Methods

Species pool and data-set

The shrew species pool at the southern terminus of the Appalachian Mountains represents a confluence of temperate and austral species. Temperate species – including *Sorex cinereus*, *S. dispar, S. fumeus*, *S. hoyi*, *S. palustris* and *Blarina brevicauda* – have geographical ranges that extend into the southeast only along the mountain range, often at relatively high elevations. Austral species, including *S. longirostris* and *B. carolinensis*, have distributions that extend northward into the foothills and lower elevations of the mountain range. Finally, *Cryptotis parva* has a widespread distribution in eastern North America that is both temperate and austral. All nine members of this species pool were represented in the data-set used in the present study.

We used a data-set collected by the Georgia Museum of Natural History and described, along with data from other sites, in Laerm et al. (1999) and Ford et al. (in press). We chose this particular sub-set of the larger data-set because these sites were all sampled with the same trapping protocol and were all located near the southern terminus of the Appalachian Mountain Range. The sample included 197 sites in forests of the Blue Ridge, Ridge and Valley, Cumberland Plateau and Piedmont Physiographic Provinces of the southern Appalachian Mountains in Alabama, Georgia, North Carolina, and South Carolina (34°30′–35°11′ N, 82°17′–86°10′ W). Each site was sampled with 20 pitfall traps operated for an average ($\pm$SD) of 1102 ± 604 trap nights, 1993–1998. We found no evidence that perceived species richness and sample effort were related (Hoeffding dependence coefficient $D < 0.0001$, $P = 0.3562$, $N = 197$), suggesting that variability in trapping effort did not affect the representation of species in our data-set. Pitfall traps are passive devices that produce relatively unbiased samples of local shrew assemblages (Williams and Braun 1983). Complete field procedure is available in Laerm et al. (1999).

We devised four functional groups for shrews in this species pool (Table 1). Because there is evidence to suggest that shrews consume prey according to their body size and vertical placement at the soil–litter interface (Pernetta 1976, Churchfield 1993, Rychlik and Jancewicz 2002), we constructed functional groups primarily based on these factors. Our first group included the relatively fossorial species in the genus *Blarina* (*B. brevicauda* and *B. carolinensis*). These species have morphological characters typical of fossorial mammals (e.g. sleek pelage) and a diet consisting almost entirely of sub-terranean invertebrates (George et al. 1986, McCay 2001). *Sorex palustris* is the only semi-aquatic shrew found in this region and aquatic invertebrates make up a large portion of its diet (Beneski and

Table 1. Assigned functional group and incidence of shrews in the southern Appalachian region, USA. Proportion of sites occupied was based only on data from within the species' geographical range.

Species	Functional group	Proportion of sites occupied in range	
		Study area	Blue Ridge
Blarina brevicauda	Fossorial	0.84	0.91
B. carolinensis	Fossorial	0.71	NA
Sorex cinereus	Small epigeal	0.69	0.69
S. hoyi	Small epigeal	0.60	0.65
S. longirostris	Small epigeal	0.26	0.14
S. dispar	Large epigeal	0.03	0.03
S. fumeus	Large epigeal	0.81	0.92
Cryptotis parva	Large epigeal	0.04	0.02
S. palustris	Semi-aquatic	0.02	0.02

Stinson 1987). Because its food habits markedly differ from other shrews in the region, we omitted this species from simulation analyses.

The remaining shrews share epigeal foraging habits, concentrated at the soil–litter interface, and were placed into two size categories following Kirkland (1991), Fox and Kirkland (1992), and our unpublished mass and length data. The species pool included 3 small epigeal shrews (*Sorex cinereus*, *S. hoyi* and *S. longirostris*) and 3 large epigeal shrews (*S. dispar*, *S. fumeus* and *Cryptotis parva*). Despite similar food habits, epigeal species ecologically differed in other ways. Notably, *S. dispar* demonstrates a stronger association with emergent rock and talus than other shrews in our species pool (Kirkland 1981). However, this species has been captured in a variety of other habitats (Healy and Brooks 1988, Ford et al. in press) and has a diet similar to other epigeal shrews. The role of interspecific competition in motivating habitat selection by *S. dispar*, and the habitat selection demonstrated by other shrews, is unclear. Thus, we disregarded ecological differences not related to foraging habits in defining functional groups.

Method of favored states and null models

We determined whether each assemblage followed Fox's (1987) assembly rule. Sites at which the species richness of functional groups differed by ≤ 1 species followed the rule and were considered favored sites (Fox 1987). The observed number of favored sites was compared to three null distributions of numbers of favored sites. Each null distribution was estimated by calculating the number of favored sites in each of 25,000 simulated sets of 197 sites.

Our first algorithm for simulating communities was based on the neutral model of Fox (1987), which had been previously applied to shrew assemblages of the northeastern United States (Fox and Kirkland 1992). This method retained the observed pattern in species richness (e.g. 18 sites with 1 species, 50 sites with 2 species, and so on), and species were sampled from the pool without replacement. The chance that a species would enter a local assemblage varied according to the portion of the sample area included within the species' range (Fox and Brown 1993). For example, if the range of a species encompassed one-half of our sites, it had one half the chance of entry of a species whose range included the entire sample area. Range boundaries were determined based on published species accounts, the present data-set, and biogeographic boundaries. Otherwise, members of the species pool had an equal chance of entry into assemblages (Fox and Kirkland 1992).

Our second algorithm for simulation of null communities was based on the method of random interchanges and involved randomization of the empirical presence–absence matrix such that row and column totals were conserved (Roberts and Stone 1990). These constraints preserved the observed pattern in species richness and the observed pattern of incidences. Species in the simulated set of sites were present at the same number of sites as in the observed community. The method of random interchanges was implemented by randomly exchanging sub-matrices of the forms

$$\begin{bmatrix} 0 & 1 \\ 1 & 0 \end{bmatrix} \quad \text{and} \quad \begin{bmatrix} 1 & 0 \\ 0 & 1 \end{bmatrix}.$$

Sub-matrices were located by jumping into the matrix at random cells. If the selected cell was part of a sub-matrix of the form described above, it was exchanged. If not, a new random location was chosen. Rows and columns were randomly sorted prior to each sub-matrix exchange. During each simulation run, we performed J sub-matrix exchanges, where J was a random integer chosen from a distribution uniform on the interval $[0.95 \times 3200, 1.05 \times 3200]$. The midpoint of this interval (3200) was chosen so that the probability that a given cell within the matrix would be left untransformed was < 0.001 (Roberts and Stone 1990).

Our final algorithm was based on the group-randomization test of Stone et al. (1996). In this method, the original presence–absence matrix was not changed. However, each species in the community was randomly assigned to a functional group. Thus, *B. brevicauda* was

equally likely to be assigned to fossorial, small-epigeal, and large-epigeal functional groups. Assignments were constrained so that the total number of species within each guild was the same as the observed. Numbers of favored sites were then calculated given these random group assignments. Because this method used the empirical presence–absence matrix, it preserved patterns of incidence and also patterns of allopatry and sympatry. For example, *S. cinereus* and *S. longirostris* never syntopically occurred at our sites and, therefore, never occurred together in the assemblages simulated using this method.

Species incidence in the Blue Ridge province

To better understand how species incidence affects community structure, we compared the observed pattern of species incidence to a null binomial model that assumes random species assortment (Cody 1994). The binomial $P(k; n,p) = n!/k!(n-k)! \, p^k(1-p)^{n-k}$ was used to calculate the probability that each species would occur at k out of n possible sites. The model assumes that each species might be expected to occur at each site with probability (p) estimated as the average local species richness divided by the total species pool. Species that occupied a greater number of sites than expected by chance were termed core species (Cody 1994). Because this model does not account for differences in geographic ranges, we restricted this analysis to 119 sites in the Blue Ridge physiographic province, which is inhabited by eight shrews (our species pool without *B. carolinensis*) with ranges that likely encompass all of our sites within the area.

Results

Mean ($\pm$SD) species richness was 2.9 ± 1.0, with an average of 0.8 fossorial, 1.3 small epigeal, and 0.8 large epigeal shrews at each site (Table 2). Sites commonly included one fossorial shrew (82% of sites) and one large epigeal shrew (74%). There were approximately equal numbers of sites with one (45%) and two (42%) small epigeal shrews. Of our 197 sites, 175 (89%) complied with Fox's (1987) assembly rule.

Table 2. Number of sites in the southern Appalachian Mountains, USA with 0, 1, or 2 species representing three functional groups and mean ($\pm$SD) number of species representing each functional group across all sites (N = 197).

Functional group	0	1	2	Mean$\pm$SD
Fossorial	35	162	0	0.82 ± 0.38
Small epigeal	27	88	82	1.28 ± 0.69
Large epigeal	46	146	5	0.79 ± 0.47

Method of favored states

The distribution of number of favored sites in communities produced with Fox's (1987) neutral model (F_n) was highly normal with mode, median, and mean approximately 119 (Fig. 1, Table 3). No set of assemblages simulated using the neutral model had ≥ 175 favored sites (P $[F_n \geq F_{obs}] < 0.00004$). Distribution of the number of favored sites based on the method of random interchanges (F_i) was highly non-normal with four dissimilar peaks (Fig. 1). Although the mode of this distribution was 154, no simulated set of assemblages had ≥ 175 favored sites (P $[F_i \geq F_{obs}] < 0.00004$). The distribution of number of favored sites in communities based on random group assignment (F_g) was non-normal and very erratic due to the limited number of possible random states. Approximately 10% of randomly generated sets of sites had ≥ 175 favored assemblages (P $[F_g \geq F_{obs}] = 0.1054$).

Pattern of incidences

Species varied widely with respect to how frequently they were encountered at our sites (Table 1). Based on a binomial model assuming random species assortment, it was unlikely that any species would be found at > 50% of our study sites in the Blue Ridge (Fig. 2). Four of the eight species in this region were, nevertheless, captured at > 50% of sites and may be termed core species. Core shrews were *Blarina brevicauda* (fossorial shrew), *Sorex fumeus* (large epigeal shrew), and *S. hoyi* and *S. cinereus* (small epigeal shrews). *Sorex longirostris*, an austral species in the small epigeal group, was found at a relatively low number (14%) of sites. The remaining shrews, including *Cryptotis parva*, *S. dispar* and *S. palustris*, were markedly restricted within the region, and the latter two are uncommon in most North American habitats. When considering the entire study area, the pattern in the Blue Ridge largely held (Table 1). However, *B. carolinensis*, which is not found in the Blue Ridge, might be considered a core species within its range. Also, *S. longirostris* and *C. parva* become more widespread outside the Blue Ridge.

Pattern of allopatry and sympatry within functional groups

Our fossorial shrews, *B. brevicauda* and *B. carolinensis*, were never captured together and are believed to be completely allopatric within our study region (George et al. 1986). Similarly, *S. cinereus* and *S. longirostris* were never syntopic. The ranges of these small epigeal shrews broadly overlap in the southern Appalachians; however, here they strongly separate along an elevation gradient and among forest types (Ford et al. 2001). Also within
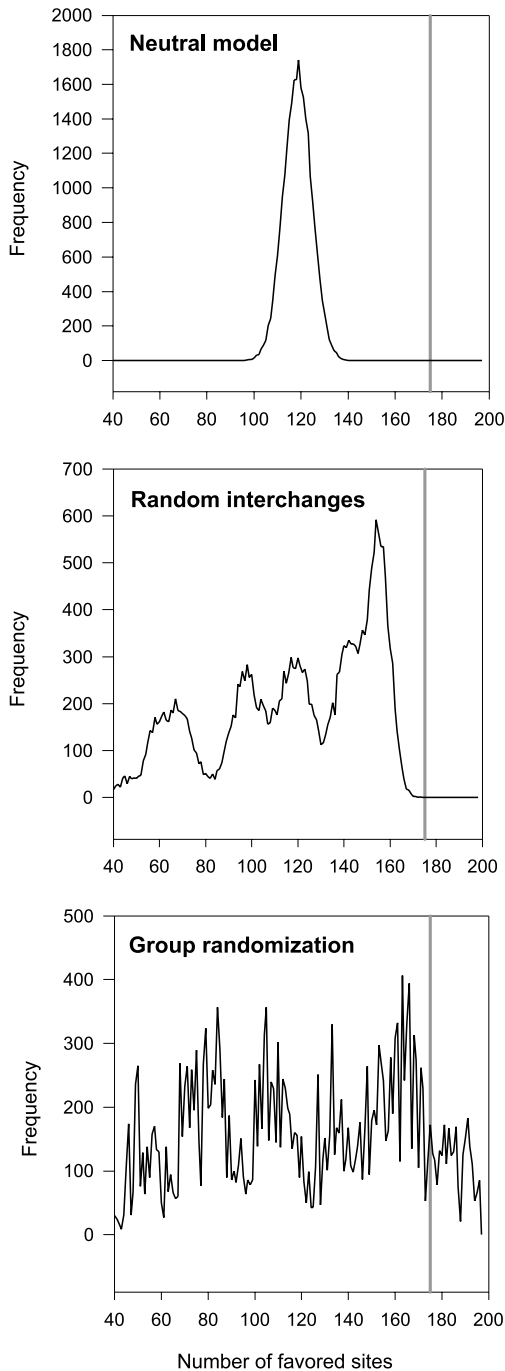
Fig. 1. Distributions of the number of favored assemblages (Fox 1987) expected within a sample of 197 shrew assemblages in the southern Appalachian Mountains under three models of community development. Vertical gray line indicates the observed number of favored assemblages (175).

the small epigeal group, *S. cinereus* and *S. hoyi* frequently occurred together (55 of 82 possible sites), and *S. hoyi* and *S. longirostris* frequently occurred together (27 of 51 possible sites). Within the large

epigeal group, *S. dispar* and *C. parva* were very uncommon in this region, captured at only 3 and 7 sites, respectively, in the present data-set. Therefore, evaluation of patterns of co-occurrence was not possible within this group. Nevertheless, the fact that one large epigeal species was very widespread and the other two were very infrequent (Table 1) dictated that many sites would be occupied by a single large epigeal shrew.

Discussion

When shrew species were divided into groups based on size and foraging mode, almost 90% of 197 sites in the southern Appalachians supported assemblages consistent with Fox's assembly rule. Similarly, Fox and Kirkland (1992) found that 31 of 43 sites (72%) in the upper mid-Atlantic region of North America followed this rule when shrew species were allocated to functional groups based on size. Shrew assemblages in eastern North America, therefore, seem to be characterized by an equitable number of species in groups with divergent foraging strategies and morphologies. Our simulation analyses, however, point to the importance of structure in the regional species pool and patterns of allopatry, rather than modern competitive interactions, in producing this pattern. Species that were similar in terms of diet and body size were less likely to have overlapping geographic ranges than dissimilar species.

A large portion of our sites (82%) was inhabited by one fossorial species; whereas, no sites were inhabited by both fossorial species. *Blarina brevicauda* and *B. carolinensis* are widespread and common species with allopatric ranges in the southern Appalachian region (Table 1, George et al. 1986, McCay 2001). Although areas of sympatry currently exist (Tate et al. 1980) and have existed in the past (Graham and Semken 1976), these species are and probably have been largely separated in space. The majority (87%) of sites in the southern Appalachians was characterized as having either 1 or 2 small epigeal shrews; no sites included three small epigeal shrews. This was due to the strict allopatry between *S. cinereus* and *S. longirostris* that exists in this region (Ford et al. 2001). A large portion (74%) of our sites included one large epigeal shrew. Because this functional group included one very widespread species (*S. fumeus*) and two infrequent species (*S. dispar* and *C. parva*), this pattern was almost certain.

Data obtained in this sampling effort (Laerm et al. 1999, Ford et al. in press) and by others suggest that shrews of similar size and foraging mode spatially separate themselves according to elevation, soil moisture, forest type, and along other ecological gradients. For example, *S. palustris* occurs almost exclusively in riparian habitats and consumes aquatic invertebrates (Beneski and Stinson 1987), reducing potential competi-

Table 3. Properties of null distributions of the number of favored assemblages (Fox 1987) expected within a sample of 197 shrew assemblages in the southern Appalachian Mountains, USA under three models of community development. Neutral-model simulations followed Fox (1987) with geographical constraints after Fox and Brown (1993). Method of random interchanges followed Roberts and Stone (1990), and the group-randomization method followed Stone et al. (1996).

Method	Mode	Median	Mean	SD	Range	$\%F \geq F_{obs}$
Neutral model	119	119	118.5	6.0	95–141	< 0.004
Random interchanges	154	123	118.9	33.1	31–173	< 0.004
Group randomization	163	119	121.0	42.1	38–196	10.54

tion with large epigeal shrews. *Sorex dispar* selects for rocky outcroppings and talus slopes; whereas, *S. fumeus* typically occurs in areas with well-developed soils (Kirkland 1981, Owen 1984). *Sorex longirostris* occurs at lower elevations than *S. cinereus* in the southern Appalachians (Pagels and Handley 1989, Ford et al. 2001), and there is some evidence that *S. hoyi* selects for relatively xeric environments in regions where *S. cinereus* also is found (Laerm et al. 1999). This ecotypic selection, as reflected in the pattern of allopatry among these species, contributed to the observed equitable representation of species within functional groups in this study.

Variability in species' distributions at small spatial scales can be drastic (Brown et al. 1995) and is often not included in descriptions of a species' geographic range (Gaston 1991). These patterns of ecotypic selection make it difficult to accurately determine the appropriate species pool from which site colonization may occur. The distinction is an important one in the search for assembly rules operating in communities because separation that occurs over evolutionary time typically is not included in definitions of assembly rules (Wilson 1999). Also, patterns of ecotypic selection should not necessarily be attributed to competition in the past, but also may be due to physical tolerances and other historical factors (Connell 1980).

We agree with Simberloff et al. (1999) who argued that detailed knowledge of each species within a region is prerequisite to understanding the mechanisms by which they form assemblages. However, it is unclear to us whether detailed ecological and behavioral data can be incorporated into models of community formation without restricting study to the post-competition species pool (i.e. Narcissus effect). For example, we do not know whether the pattern of ecotypic partitioning between *S. cinereus* and *S. longirostris* is maintained by competition or differing environmental tolerances. If we restrict the species pool for sites at high elevations to include *S. cinereus* but not *S. longirostris*, then we have assumed that differing environmental tolerances underlie the pattern. Subsequent failure to reject null expectations would suggest, perhaps erroneously, that competition was not important in shaping these assemblages.

Detailed field studies of live soricids, such as those conducted by Hawes (1977) and Churchfield (1984), are necessary to understand the extent to which shrews compete in varying environments. Although the field study of small endotherms is difficult, it remains the best way to understand interspecific interactions among shrews.
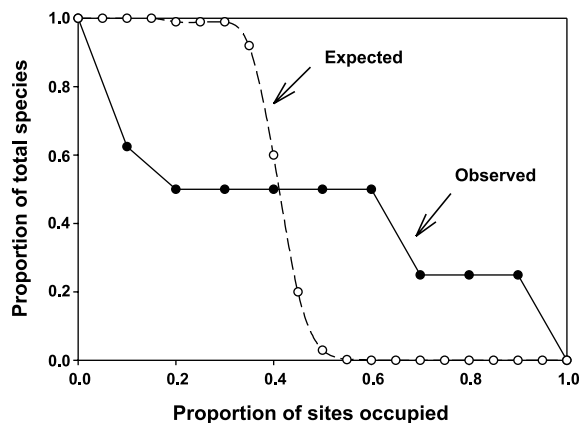
Fig. 2. Cumulative proportion of shrew species as a function of the proportion of sites occupied by those species (incidence) in the Blue Ridge province of the southern Appalachian Mountains. Null expectation based on the binomial model of Cody (1994), which assumes random species assortment.

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