

## On Desert Rodents, Favored States, and Unresolved Issues: Scaling Up and Down Regional Assemblages and Local Communities

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Fox (1987, p. 201) suggested a new assembly rule for ecological communities: "There is a much higher probability that each species entering a community will be drawn from a different genus (or other taxonomically related group of species with similar diets) until each group is represented, before the rule repeats." The rule was inspired by a desire to mimic the workings of interspecific competition between similar species. The only input required is an a priori knowledge of how the species are divided into functional groups (Fox 1989, 1999). Finding rules that govern the composition of complex ecological communities is a formidable task, so a rule that requires us to know so little about the species in question is attractive indeed. It means ecologists need not identify habitat preferences, relative abundances, relative dispersal abilities, geographic ranges, and so forth; all species in a functional group are taken as equivalents. In the quest for general rules governing community composition ("assembly rules"), this has the makings of a breakthrough.

Desert rodents of southwestern North America are an excellent group on which to test this model because they have been studied intensively and because experimental research shows that at least some species compete (reviewed by Brown and Harney 1993). Fox and Brown (1993) tested this model with two data sets (Nevada Test Site and Chihuahuan Desert) and found these desert rodent communities accorded with Fox's (1987) rule, with "favored states" found significantly more frequently than would be expected if different species colonized independently.

However, when reanalyzing the same data, we (Stone

et al. 1996) could not reject a hypothesis that species join local communities independently. This suggested, as did the research in Wilson (1995), that the Fox and Brown (1993) result is probably an artifact of the fact that the assembly rule treated all species as equally likely to be found on all sites. Moreover, the excess of the observed number of favored states over that expected can probably be explained by the fact that the few widespread species are not treated realistically. We also proposed randomly permuting the functional group assignments of the species in the pool as a test.

Brown, Fox, and Kelt take issue with our analyses. They invoke the Narcissus effect, suggesting that, among these desert rodents, there is evidence that competition influences biogeographic and evolutionary processes that structure the regional pool of species. They state that "at issue here is how this geographic information should be incorporated into analyses of assembly rules and how the analyses should be interpreted. We show that it is important to consider the influence of competition on the geographic distribution of species and the composition of regional species pools, as well as on the coexistence of species in local communities" (Brown et al. 2000, in this issue, p. 000).

The new analyses by Brown et al. are a step in the right direction. They now draw random local communities from the actual regional species pools, and, in the Nevada Test Site, they draw them from species that use specific habitat types. However, the random draws still do not account for the number of sites each species occupies. And our functional group randomization test is null to the Narcissus effect as far as biogeography goes. As we argue below, Brown et al. fail to impugn the results of that test.

In their analyses, all species are equally likely to colonize any site. In practice, failing to incorporate observed disparities in numbers of sites occupied is not a trivial omission. To see this, consider Brown et al.'s analysis of the Nevada Test Site, where the widespread species include *Ammospermophilus leucurus*, *Dipodomys merriami*, and *Perognathus longimembris*. These species occupied 71, 80, and 89 sites, respectively, of the 115 possible sites. *Peromyscus crinitus*, on the other hand, exemplifies poorly rep-

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resented species, appearing on only 23 sites. We examined 2,000 of the Brown et al. model communities and found that in none of them did the widespread species occupy as many sites as they occupied at the Nevada Test Site (table 1). In the same 2,000 model communities, the poorly represented species such as *P. crinitus* always occupied more sites than in the Nevada data. The average number of sites where a species was found differed by several standard deviations from the observed. With null model communities differing so from the observed data, it is little wonder that Brown et al. reject the null hypothesis—the null models are unable to reflect basic characteristics of the observed communities. In a case like this, one wonders why Fox invented the concept of favored states when a simple test of the observed versus expected sites occupied would have sufficed to achieve exactly the same results. And in any case, it is this signal, that is, the inadequate representation of the sites colonized, that is ultimately driving the statistical quirks they report for the favored state index.

Aspects of Brown et al.'s approach could be useful if there were indeed sufficient evidence that competition heavily influences biogeographic and evolutionary processes that structure the regional pool of species from which local communities are assembled, and, most importantly, that it dictates the frequency of species occurrences in local communities. Here, we investigate the evidence cited by Brown, Fox, and Kelt that competition affects the geographic ranges of species, the structure of regional assemblages, and the fact that some species occupy many sites while others occupy few sites. Finally, we return to the randomization test, rejected by Brown et al., and show that it readily detects competition.

### Does Competition Affect Geographic Ranges of Species?

Brown, Fox, and Kelt argue that rodents of southwestern North American deserts exhibit a pronounced Narcissus effect. The Narcissus effect (Colwell and Winkler 1984, p.

352) is an underestimation of the role of competition that stems from sampling a postcompetition species pool. They argued that the species most vulnerable to competition, which they see as closely similar sympatric species, may already have been eliminated from a region. The manifestation of the Narcissus effect that Brown et al. claim is that geographic ranges of the southwestern desert rodents are already determined at least partially by competition. Thus, randomly drawing species from any species pool to colonize sites, and then looking to see whether similar species (in this case, species in the same functional groups) tend not to co-occur, will inevitably underestimate the effect of competition.

In Stone et al. (1996, p. 1004), we pointed to possible influences on range limits: “differing dispersal abilities [by which we meant ability to cross barriers], different tolerances of physical factors, and differential susceptibility to extinction (Brown and Gibson 1983; Patterson and Brown 1991). Another reason could be differing competitive ability.” However, Brown et al. present no evidence that the geographic ranges of these species are heavily influenced by competition. To support their claim, they cite (p. 000) Brown and Gibson (1983), Brown and Bowers (1984), Brown (1987), Brown and Lomolino (1998), and Kelt and Brown (1999). Brown and Bowers (1984) and Brown (1987) do not discuss nonoverlapping geographic ranges. Brown and Gibson (1983) and Brown and Lomolino (1998) are successive editions of one book, and the sections on how competition might affect geographic ranges are very similar. This section cites three major forces that sometimes determine range limits: physical factors, disturbance, and interactions with other organisms. The subsection on species interactions, in turn, has sub-subsections on competition, predation, and mutualism. The sub-subsection on competition lists one relevant example, five species of *Dipodomys* with nonoverlapping ranges in the Southwest, of which two have completely disjunct ranges and three are parapatric with at least one other species. The authors concede this is a circumstantial case and say,

**Table 1:** Sites occupied for three widespread species and poorly represented species (names in text)

	<i>Ammospermophilus leucurus</i>	<i>Dipodomys merriami</i>	<i>Perognathus longimembris</i>	<i>Peromyscus crinitus</i>
SO	71	80	89	23
<SO>	52.2	52.1	51.9	53.2
SD	5.0	5.1	5.1	5.2
Range	37–67	35–69	35–70	38–70

Note: Observed data are from Jorgensen and Hayward (1965). Statistics of the Brown et al. (2000, in this issue) model are mean sites occupied, standard deviation, and range of sites occupied in 2,000 model communities. SO = sites occupied.

“Although such cases strongly suggest that competition limits species distributions by preventing coexistence, they are subject to alternative explanations, and often there is no direct evidence of competitive interactions occurring on the boundaries” (Brown and Lomolino 1998, p. 83). Kelt and Brown (1999) address nonoverlapping ranges once (p. 92), suggesting that allopatric speciation might account for some nonoverlapping ranges but that a “proper phylogenetic analysis” would be required to understand its role. For the *Dipodomys* species, they tentatively rule it out as an important factor because the five species appear to be less closely related to one another than to other kangaroo rats.

The sum total of the evidence presented is meager. In general, as pointed out by Brown and Gibson (1983) and Brown and Lomolino (1998), many different factors can determine geographic range limits, of which biotic interactions, including competition, are but one. For one subset of these rodents—the five large kangaroo rats—the contiguous ranges of three species are suggestive, but there is no direct evidence that they are determined by competition. In addition to physical factors, disturbances, and biotic interactions, other factors are important in setting range limits. Brown (1987), discussing the Southwest rodents, points to a historical legacy—dispersal barriers—as key to differences between the eastern and western Great Basin.

#### Does Competition Affect the Composition of Regional Biotas?

Brown et al. (2000, in this issue, p. 000) argue that “comparative geographic studies of many assemblages have repeatedly shown that the communities exhibit deterministic structure.” The key issue is, Do these studies indeed demonstrate that regional assemblages exhibit deterministic, competitively determined structure at regional scales? They refer us to several authors whose studies dealt with patterns of community structure. Among those are Fox and Brown (1993), whose analyses are at the heart of this debate. A close look reveals that the majority of studies cited by Brown et al. dealt with patterns of local coexistence but not regional patterns, which is the scale of interest for us here. The relevant ones follow.

Brown and Kurzius (1987) found that local faunas typically comprise two to five species, often significantly fewer than would be expected if all species with overlapping geographic ranges co-occurred, a pattern they saw as compatible with competitive exclusion. Patterson and Brown (1991) found nested subset patterns among local assemblages. This finding is significant for understanding the relationship between regional and local species assem-

blages but does not address the role of competition in structuring regional species pools.

Morton et al. (1994) compared desert rodent communities in numerous local sites from North America and Australia and found that many species occurred at small proportions of the sites within their geographic ranges: “The presence of most of the species at only a small proportion of the sites within their geographic ranges suggests highly specific habitat requirements and tolerances, or perhaps stochastic colonizations and local disappearances through time. Likewise, the fact that communities consisted of many different species, and the presence of many different specific combinations, suggest that species occurred primarily in response to the presence of locally favorable habitat rather than to highly structured interspecific interactions” (Morton et al. 1994, pp. 520–521). Morton et al. do not mean to imply that interspecific interactions play no part in defining the composition of communities, but again, even if they do, this study can demonstrate it only at a local scale.

Kelt et al. (1996) searched for convergence in community organization using trapping data for local coexistence from multiple sites in North and South America, Australia, Israel, and Greater Eurasia. Similarities between deserts included low alpha diversity, high beta diversity, and local coexistence of 20%–30% of the species in the regional pool. These results, interesting in themselves, do not enable us to explain the composition of large-scale geographic assemblages. In fact, Kelt et al. (1996, p. 753) state that local richness of desert small mammal communities is relatively independent of regional richness and may be a general characteristic of small mammal communities: “If so, this argues against local richness being a relatively linear function of regional enrichment (e.g., Ricklefs 1987; Ricklefs and Schluter 1993). Instead it implies greater regulation of local species diversity and composition by local ecological processes, e.g. competition, predation, etc.” Kelt et al. do state that this is not meant to imply local community composition is not affected by regional and historical factors. They consequently discuss various forces affecting regional assemblages (phylogeny, history, age, topography, precipitation) but not competition.

The only studies of those cited by Brown, Fox, and Kelt (2000, in this issue) that deal with competitively determined structure in regional biotas are those that focus on sizes. Dayan and Simberloff (1994) studied size structuring of trophic apparatuses in heteromyid rodents. They found a regular pattern of overdispersed means of incisor widths among species within a regional pool and suggested that this trait coevolved in response to the presence of other species in a large number of possible species combinations. Dayan and Simberloff (1994) argued that coevolution is

not likely to occur in small local assemblages but on a larger geographical scale. If species too similar to those already in the regional species pool were unable to join it, this would suggest that the composition of regional biotas was affected by competition. However, while coevolution was found, Dayan and Simberloff (1994) lacked appropriate data to test whether regional species pools were also affected by size sorting (see discussion in Dayan and Simberloff 1998).

So, in fact, only Bowers and Brown (1982; see also Brown and Bowers 1984) provide evidence for forces affecting both local and regional species composition. They found that species of similar body mass co-occur less frequently than expected on the basis of chance in both local assemblages and regional faunas. Regionally, they looked at overlap of ranges of all pairs of species whose ranges are within 200 km of one another. They compared observed overlap (if any) with expected overlap. They divided pairs into those differing in body weight by  $>1.5$  or  $<1.5$  and found significantly less overlap compared to expected for species pairs that differed in body mass by  $<1.5$ . This result suggests a role for competition in determining actual geographic range overlap.

Brown and Harney (1993) review evidence for the influence of interspecific competition on local community composition and suggest that competition can also operate at larger spatial scales. "For example, competitive exclusion may limit the geographic ranges of species, and this in turn will affect the composition of the regional species pools from which local communities are assembled" (Brown and Harney 1993, p. 633). And this remains the key point in this exchange: whether there is evidence that local competition feeds upward to influence the structure and composition of regional biotas, and the frequency of species occurrences in local assemblages. On the basis of the above studies we conclude that, while this process may certainly operate, this possibility is supported by only one study (Bowers and Brown 1982).

Does the fact that some species are common and occur in many local assemblages, while others are rare and occur in few, reflect the workings of interspecific competition? A basic tenet of the favored states model is that species within a guild are equivalent and interchangeable. It is surprising that, while Brown et al. use this model, they point out that different species differ dramatically in traits directly relevant to their chances of dispersal and colonization. "Previous publications have emphasized that some desert rodent species have wide geographic ranges, occur in many local communities, and tend to be abundant whereas others have highly restricted ranges, occur in many fewer local communities, and tend to be rare" (Brown et al. 2000, in this issue, p. 000). We found that an approach that focuses only at the level of functional

groups, treating species as if they were interchangeable, seems destined to find nonrandom local community patterns (see also above). The nonrandomness merely mirrors the fact that species are not interchangeable, if only for the same reasons that Brown et al. outline (above). For example, for the southwestern data set of Brown and Kurzius (1987), a full 316 of 623 occurrences recorded in the Nevada Test Site data are of four species, and the other 307 occurrences represent the remaining 24 species.

Brown and Kurzius (1987) note that

some pairs or groups of species coexist frequently. These tend to be ... both geographically widespread and locally abundant (see Brown 1984, fig. 9, for an example for desert rodents). Most of the spatial variation in guild composition can be attributed to the presence and absence of species with restricted ranges and low abundances ... most species are rare. The majority of species have restricted geographic ranges (Willis 1922) and low population densities within local sites (Williams 1964, Preston 1962)... Because they are apparently restricted to a narrow range of environments where their specialized requirements are met, rare species characterize habitats more precisely than abundant, widespread species with broader tolerances. (p. 234)

Brown and Harney (1993), reviewing the desert rodent literature, point out that *Dipodomys merriami* was the most common species in the Chihuahuan Desert study site and the only species captured in every month. Other species, "apparently because of their much narrower tolerances and requirements, have smaller geographic ranges and lower population densities. These species ... tend to occur in fewer local habitat patches and in a smaller proportion of the sites within their geographic ranges" and "also tend to be more ephemeral even in habitats where they normally occur" (Brown and Harney 1993, p. 630).

So at issue here is whether these narrower tolerances and requirements are competitively determined. This question is crucial because local desert rodent community assembly may be affected by species' abilities to immigrate and to colonize from other localities (e.g., Schroder 1987; Kelt et al. 1996). Differing abilities of species to disperse and to colonize local sites must be related to the number of patches they occupy and to their relative abundances (see discussion in Bowers 1988). So the realism in testing the method of favored states hinges on this issue. It cannot be ignored. At this point we conclude that the published literature does not show that interspecific competition dictates this pattern rather than the other forces.

Thus, the claim by Brown et al. of a "strong" or "pronounced" Narcissus effect for this fauna is simply a hypothesis. The use of the Fox and Brown (1993) assembly rule cannot demonstrate a Narcissus effect, as claimed by Brown et al. (2000, in this issue).

### The Randomization of Functional Groups

To alleviate any concern that the Narcissus effect is built into procedures that force different species to occupy different numbers of sites, we devised a test that, with respect to geography, is null to the Narcissus effect—we simply randomly permuted the species' functional group assignments. All species stay in their observed sites. Brown et al. (2000, in this issue) argued against this test on the grounds that, because the variance of the null distribution is large, the statistical test is inevitably weak. This statement is simply incorrect. So long as probability statements are in terms of percentage tails, standard deviations, and confidence limits (as were those Stone et al. 1996), the existence of large variance does not automatically make a test weak. The relative power of various statistical tests, including this one and the Brown et al. Monte Carlo procedure that they claim is more powerful, would have to be determined by a full power analysis.

Nevertheless, it is simple to resolve the argument by demonstrating that the randomization advocated in Stone et al. (1996) has power in this context. All we need to show is that the test can discriminate model communities with competition internally built in. We have accomplished this by following to the letter the method of generating communities used in Brown et al. and hence, on this one occasion, have not made allowance for differences in numbers of species occurrences. First, the local habitat pools of all 115 sites were determined from the observed Nevada data. The computer model then simulated colonization of local sites by drawing species at random from appropriate pools. However, to incorporate competition into the model communities, the computer program attempted, wherever possible, to prevent species from the first functional group from colonizing sites on which that group was already present. This corresponds to the competition scheme envisaged by Fox and Brown (1993), except it is weaker, in that competition occurs only in one functional group rather than all of them.

In an ensemble of 2,000 such random competition matrices, the mean number of favored states (FS) was calculated as  $\langle FS \rangle = 88.65$  with  $SD = 3.80$ . Note that the Nevada matrix itself had  $FS = 92$ , within 1 SD of the mean and thus did not significantly differ from the competition matrices, at least in terms of number of favored states.

We then applied the randomization test (i.e., where functional group assignments were shuffled) to two data sets: the actual Nevada community and a typical model competition matrix. The results are presented in table 2. As reported in Stone et al. (1996), the number of favored states in the observed Nevada community was not significantly unusual. Some 11% of the randomized matrices had higher numbers of favored states than the observed

Table 2: Effectiveness of the functional group-randomization test

	FS observed	$\langle FS \rangle$	SD	Proportion of matrices with $FS \geq FS$ observed (%)
Observed matrix	92	62.07	22.51	11.00
Competition matrix	90	62.67	12.91	.55

Note: Observed Nevada Test Site matrix was not significantly different from expected, whereas the simulated competition matrix was, at  $P < .0055$ .  $FS =$  favored states.

FS (92). We thus cannot reject the null hypothesis that species join local communities independently.

Nevertheless, the randomization test readily detected the competition process in the model competition communities. For example, beginning with an arbitrarily chosen model competition matrix with  $FS = 90$ , only 11 randomizations of the 2,000 (i.e., 0.55%) attempted had more favored states than the initial matrix. The randomization test thus leads us to reject the null hypothesis that species colonize independently. To ensure that the competition matrix analyzed above was not pathological, the test was repeated on an ensemble of 2,000 model competition communities generated by the same method. Each model matrix was subject to the above randomization test. We found that all but 60 matrices (3%) in the ensemble were significantly unusual ( $P < .05$ ).

### Concluding Remarks

Ecological communities are complex entities, and, in spite of decades of research, much remains to be understood about North American desert rodent communities. Reichman (1991, p. 312) stresses: "Only a handful of the more than 30 species of heteromyid rodents in North America have been studied in relation to their contributions to the communities in which they live." It is also noteworthy that some of the compelling experimental studies showing interspecific competition were carried out between rodents of different functional groups. They focused on the interaction between species in one functional group (bipedal heteromyids) and species of two other functional groups (quadrupedal heteromyids and quadrupedal omnivores; Munger and Brown 1981; Lemen and Freeman 1983; Brown and Munger 1985). That is certainly not to say that intrafunctional group competition is unimportant, only that clearly interfunctional group competition is also important and must further complicate analyses of community assembly. While it is hard to find any other system so intensively studied, it is perhaps not surprising that we are still often baffled by the complexity of nature.

Ecologists are united by the wish to understand the forces affecting the composition and structure of ecological communities. Understanding higher levels of organization in nature is an enormous intellectual challenge. Our role is to formulate hypotheses and to test them critically. We hope this exchange is another step in the development of ecology as a rigorous science.

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