

Assembly Rules and Competition in Desert Rodents

James H. Brown,^{1,*} Douglas A. Kelt,^{2,†} and Barry J. Fox^{3,‡}

1. Department of Biology, University of New Mexico, Albuquerque, New Mexico 87131;

2. Department of Wildlife, Fish, and Conservation Biology, University of California, Davis, California 95616;

3. School of Biological Sciences, University of New South Wales, Sydney, New South Wales 2052, Australia

Submitted December 13, 2000; Accepted June 29, 2002

Keywords: assembly rule, coexistence, competition, desert rodents, functional group, null model.

North American desert rodents have long been a model system for the study of community structure and dynamics. Field experiments and nonmanipulative observations have provided consistent evidence that interspecific competition influences spatial patterns and dynamic processes of community organization. Some of the evidence comes from assembly rules, which document how the species that coexist in local communities differ in body size, trophic morphology, functional group, or taxonomy more than would be expected had they been assembled by some random process (Kelt and Brown 1999). One assembly rule proposed by Fox (1987; see also Fox and Brown 1993; Fox 1999; Kelt et al. 1999) is based on functional groups. It hypothesizes that species are assembled in such a way that each functional group tends to be filled before an additional species is added to an existing functional group. Communities that conform to the rule are termed “favored states,” whereas other combinations are termed “unfavored states.” So if the rule is operating, we should observe more favored states than expected by chance.

Although Fox’s assembly rule has been applied to a variety of systems (1999), its application to desert rodent communities has generated controversy. Fox and Brown (1993) showed that there were more favored states than expected by chance in two large data sets: a sample of 115

communities from the Nevada test site (Jorgensen and Hayward 1965) and another sample of 201 communities from sites widely distributed across the southwestern United States (Brown and Kurzius 1987). Stone et al. (1996; also Simberloff et al. 1999) criticized Fox and Brown, claiming that the apparent conformity to the assembly rule was an “artifact” of “the fact that the few widespread species are not treated realistically” (Stone et al. 1996, p. 997). They focused on the southwestern data set and argued that the nonrandom pattern of coexistence was due entirely to the sizes and overlaps of geographic ranges of different species. Kelt and Brown (1999) and Brown et al. (2000) showed that this was not true. They determined the regional species pool for each sample site, composed of just those species whose geographic ranges overlapped the site, and then assembled null communities by drawing the observed number of species at random from these geographically constrained pools. Their analysis showed that the communities obeyed Fox’s assembly rule: the observed assemblages exhibited significantly more favored states than the random draws from the regional pools. Stone et al. (2000) apparently accepted this result, because in this most recent critique they barely referred to the influence of geographic ranges on the patterns of coexistence in the southwestern data set.

Instead, Stone et al. (2000) shifted from the geographical to the regional scale. They focused on the Nevada data set, where the restricted area insured that all of the 115 sample sites were within the geographic ranges of the same species. They also shifted their argument, suggesting that the nonrandom patterns of local coexistence are “an artifact of the fact that the assembly rule treated all species as equally likely to be found on all sites” (Stone et al. 2000, p. 323). They supported this claim by performing two analyses of the Nevada data set.

Critique of the Analyses

Stone et al. (2000) began by comparing the observed frequency of occurrence of certain species across sites with the expected frequency. They generated the expected frequency by randomly drawing species from the pool with equal probability, just as we had done in our analyses. In

* Corresponding author; e-mail: jhbrown@unm.edu.

† E-mail: dakelt@ucdavis.edu.

‡ E-mail: b.fox@unsw.edu.au.

their table 1, they reported results for four of the nine species, noting that *Ammospermophilus leucurus*, *Dipodomys merriami*, and *Perognathus longimembris* inhabited significantly more sites than expected by chance, whereas *Peromyscus crinitus* inhabited significantly fewer. Based on this result, Stone et al. (2000, p. 323) asked “why Fox invented the concept of favored states when a simple test of observed versus expected sites occupied would have sufficed to give exactly the same result.”

The answer is simple. Our question was not simply whether the frequencies of occurrence in individual species deviate from some null hypothesis. It was whether the frequencies of co-occurrence of species deviate from randomness in a particular way; specifically, on whether the species are members of the same or different functional groups. In their 1996 article, Stone et al. noticed that species differed conspicuously in the sizes of their geographic ranges, and they inferred—incorrectly, and without performing the critical analysis—that this was sufficient to account for the nonrandom assembly with respect to functional group. In their 2000 article, Stone et al. showed that some species occurred at disproportionately many or few sites, and again they inferred that this was sufficient to account for the nonrandom community assembly with respect to functional group. And once again they did not perform the critical analysis. Their first analysis (their table 1) completely ignored both functional group membership and patterns of co-occurrence.

The second analysis performed by Stone et al. (2000) attempts to incorporate the differential occurrences of species across sites in a test of Fox’s assembly rule. It uses the technique, introduced in their 1996 article, of leaving the matrix of species by sample sites unchanged, randomly permuting functional group assignments among species, and calculating the number of favored and unfavored states in these simulated null communities. We (Brown et al. 2000) criticized this test for its low statistical power because of large variances in expected number of favored states. Stone et al. (2000, p. 326) replied that “so long as probability statements are in terms of percentage tails, standard deviations, and confidence intervals (as were those of Stone et al. 1996), the existence of large variance does not automatically make a test weak.” They (Stone et al. 2000, p. 326) justified their method of permuting functional group assignments by claiming that their test “has power in this context. All we need to show is that the test can discriminate model communities with competition internally built in.” To do this, they created communities according to an assembly rule in which “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.”

We did not, however, base our test on this particular “competition scheme.” We can imagine several different ways that competition could operate to result in Fox’s assembly rule. For example, there might be some probability, significantly higher than random, that every species that is added is a member of an underrepresented functional group. This might be an even weaker scheme than the one used by Stone et al. (2000), but it is still sufficient to result in significantly more favored states than expected by chance. Stone et al.’s (2000) technique may indeed be able to detect some theoretical nonrandom assembly process, but this hardly proves it has sufficient power to detect the actual processes that have produced the observed assembly rule.

The issue is not an analysis of power within the framework of Stone et al.’s (2000) test. The issue is a comparison of the relative powers of Stone et al.’s (2000) and our tests to determine which one has the greater capacity to detect the kinds and magnitudes of nonrandom organization observed in real desert rodent communities. Our test strongly rejects the null hypothesis of random assembly, whereas theirs does not. As reported in table 4 of Stone et al. (1996), the observed number of favored states was 93. Their null communities had a mean expected number of favored states of 64.19 and a standard deviation (SD) of 22.59. Since 95% of the observations would be expected to fall within ± 2 SD, nearly all of the communities (110 of the 115) would have to be favored states to reject the null at the conventional $P < .05$. By contrast, we (Brown et al. 2000, table 1) applied our randomization test to several different treatments of the Nevada data set, and in all cases the standard deviations were small and the null was rejected at $P < .0005$. Our test clearly has greater power to detect the kinds of nonrandom organization that are found in desert rodent communities.

The bottom line is that the two parties in this debate have erected and tested different null hypotheses. Stone et al. (1996, 2000) insist on conducting null tests in which the frequencies of occurrence of species across sample sites is the same in randomly assembled communities as in real communities. They do this by randomly reassigning species to functional groups. Their method of permuting the matrix of species occurrence by sample site insures that both the column and row totals are held constant. There is nothing inherently wrong with this, but it removes any influence of competition on the association between functional group and the frequencies of species occurrences and co-occurrences in the real communities. Stone et al. (2000) regard the occurrence of different species at different numbers of sites simply as an “artifact” that has no relationship to how competition might operate differen-

tially within and between functional groups. They remove this “artifact” by randomly reassigning species to different functional groups.

In contrast, our null models assume that any species in the regional pool, regardless of functional group membership, has an equal probability of occurring at any site and of coexisting with any other species. Our Monte Carlo methods insure that the numbers of species at each sample site (column totals), but not the numbers of sites inhabited by each species (row totals), are the same for the randomly assembled as for the real communities. So our tests are sensitive to effects of competition on the composition of the regional species pool and to the way that frequencies of occurrence and coexistence of species are associated with functional group membership. As pointed out earlier in this debate (Kelt and Brown 1999), there are different ways to erect and test null models of community assembly. The alternative methods are not necessarily right or wrong, realistic or artificial.

Stone et al. (2000) regard as “artifact” a nearly universal phenomenon in ecology: the wide variation among taxonomically related, ecologically similar species in the number of local sites where they occur and the number of species with which they coexist (e.g., Brown 1984; Brown and Kurzius 1987). All species would be expected to occupy equal numbers of sites only if overall competitive abilities were nearly equal and there were trade-offs such that those species excluded from some sites were able in turn to exclude other species from an equal number of sites. There is no evidence that competitive ability is equalized across species in this way. If it were, it would produce a different kind of nonrandom pattern of community assembly, one that has not been reported in more than two decades of intensive research on desert rodents. So we agree that the numbers of sites in Nevada occupied by certain species deviated significantly from the number expected if each species had equal probability of occupying all sites. This would be expected because of competition. If species differ in competitive ability, it follows that superior competitors should occupy many sites, be abundant in these local communities, and frequently (but not always) exclude inferior competitors (which should be less abundant in those communities where they do coexist). This is just the pattern that is observed (Brown 1984; Ernest and Brown 2001). Rather than regarding it as an “artifact,” we incorporated it explicitly into our null test.

Concluding Remarks

The assembly rule at issue here is only one piece of a large interrelated fabric of evidence for the influence of interspecific competition on the abundance, distribution, and community organization of North American desert ro-

dents. Quantitative comparative analyses of the placement of geographic ranges of rodent species and of the species composition of hundreds of local communities have identified several additional deterministic assembly rules. As predicted by competition hypotheses, species that are more similar in body size, functional group, and taxonomic relatedness not only coexist less frequently in local communities but also overlap less in their geographic ranges (Bowers and Brown 1982; Kelt and Brown 1999). Complementary evidence comes from our long-term manipulative experiments of the local community near Portal, Arizona. For example, if competition can determine boundaries of geographic ranges, it might be expected to affect colonization and extinction at local scales. Indeed, other granivorous rodent species had higher colonization rates, lower extinction rates, or both on experimental plots where competing kangaroo rats had been removed than on control plots where kangaroo rats were present (Valone and Brown 1995). This is only one of many studies documenting the severalfold increase of other seed-eating rodents, but not insectivorous or folivorous species, when seed-eating kangaroo rats were excluded (Brown 1998; Kelt and Brown 1999). There is compelling evidence that competition affects local abundance, limits local distribution, and restricts membership in local communities to a subset of the regional species pool (see also Valone and Brown 1995; Brown et al. 2001a; Ernest and Brown 2001).

Stone et al. (2000, p. 326) conclude that “ecological communities are complex entities, and, in spite of decades of research, much remains to be understood about North American desert rodent communities,” and they profess to be “baffled by the complexity of nature.” We agree that there are still many poorly understood complexities (Brown et al. 2001b), but we do know a great deal about competition and community organization in these model organisms.

Acknowledgments

We thank the National Science Foundation (most recently grants DEB-9707406 to J.H.B. and DEB-9873708 to D.A.K.) and the Australian Research Council (grant A19700994 to B.J.F.) for long-term support of our research. We thank R. K. Colwell, D. Schluter, an anonymous reviewer, and several students for helpful discussions and suggestions.

Literature Cited

- Bowers, M. A., and J. H. Brown. 1982. Body size and coexistence in desert rodents: chance or community structure? *Ecology* 63:391–400.
- Brown, J. H. 1984. On the relationship between abundance

- and distribution of species. *American Naturalist* 124: 255–279.
- . 1998. The granivory experiments at Portal. Pages 185–203 *in* W. L. Resetarits, Jr., and J. Bernardo, eds. *Experimental ecology: issues and perspectives*. Oxford University Press, Oxford.
- Brown, J. H., and M. Kurzius. 1987. Composition of desert rodent faunas: combinations of coexisting species. *Annales Zoologici Fennici* 24:227–237.
- Brown, J. H., B. J. Fox, and D. A. Kelt. 2000. Assembly rules: desert rodent communities are structured at scales from local to continental. *American Naturalist* 156: 314–321.
- Brown, J. H., T. G. Whitham, S. K. M. Ernest, and C. A. Gehring. 2001a. Complex species interactions and the dynamics of ecological systems: long-term experiments. *Science* (Washington, D.C.) 293:643–650.
- Brown, J. H., S. K. M. Ernest, J. M. Parody, and J. P. Haskell. 2001b. Regulation of diversity: maintenance of species richness in changing environments. *Oecologia* (Berlin) 126:321–332.
- Ernest, S. K. M., and J. H. Brown. 2001. Delayed compensation for missing keystone species by colonization. *Science* (Washington, D.C.) 292:101–104.
- Fox, B. J. 1987. Species assembly and the evolution of community structure. *Evolutionary Ecology* 1:201–213.
- . 1999. The genesis and development of guild assembly rules. Pages 23–57 *in* E. Weiher and P. A. Keddy, eds. *The search for assembly rules in ecological communities*. Cambridge University Press, Cambridge.
- Fox, B. J., and J. H. Brown. 1993. Assembly rules for functional groups in North American desert rodent communities. *Oikos* 67:358–370.
- Jorgensen, C. D., and C. L. Hayward. 1965. Mammals of the Nevada test site. *Brigham Young University Science Bulletin Biological Series* 6:1–81.
- Kelt, D. A., and J. H. Brown. 1999. Community structure and assembly rules: confronting conceptual and statistical issues with data on desert rodents. Pages 75–107 *in* E. Weiher and P. A. Keddy, eds. *The search for assembly rules in ecological communities*. Cambridge University Press, Cambridge.
- Kelt, D. A., J. H. Brown, K. Rogovin, and G. Shenbrot. 1999. Patterns in the structure of Asian and North American desert small mammal communities. *Journal of Biogeography* 26:825–842.
- Simberloff, D., L. Stone, and T. Dayan. 1999. Ruling out an assembly rule: the method of favored states. Pages 58–74 *in* E. Weiher and P. A. Keddy, eds. *The search for assembly rules in ecological communities*. Cambridge University Press, Cambridge.
- Stone, L., T. Dayan, and D. Simberloff. 1996. Community-wide assembly patterns unmasked: the importance of species' differing geographic ranges. *American Naturalist* 148:997–1015.
- . 2000. On desert rodents, favored states, and unresolved issues: scaling up and down regional assemblages and local communities. *American Naturalist* 156: 322–328.
- Valone, T. J., and J. H. Brown. 1995. Effects of competition, colonization, and extinction on rodent species diversity. *Science* (Washington, D.C.) 267:880–883.