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Composition of desert rodent faunas: combinations of coexisting species

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To assess spatial variation in the composition of local biotas, we analyzed data on the distribution of 29 species of granivorous desert rodents among 202 sites in the southwestern United States. Throughout its geographic range, each species occurred with many other species as a member of many different combinations. The number of species with which each species coexisted was positively correlated with the number of sites at which it was found and with its area of geographic range. Most species were found at less than 30% of the sites within their geographic ranges. Nevertheless, they cooccurred locally with more than half of the species with overlapping geographic ranges. Although most local assemblages consisted of only two to five species, 124 different combinations were observed.

These results have several implications: 1) Species distributions are highly individualistic, 2) composition of local biotas is highly variable, 3) rodents (especially rare species) respond to environmental change on a small spatial scale, 4) single, local samples of assemblages may not be representative of communities of larger regions, and 5) opportunities for coevolution between pairs of continental species are limited.

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1. Introduction

A longstanding debate about the nature of ecological communities dates back at least to the early part of this century. Clements (1916) espoused the view that interdependent species occur together repeatedly to form highly integrated communities. In contrast, Gleason (1917, 1926) viewed communities as facultative assemblages of species, each distributed according to its unique requirements. Recent discussions have continued this debate. Ideas and data suggesting alternative, stable communities and close coevolution among coexisting species (e.g. MacArthur 1972; Diamond 1975, 1986; Roughgarden 1979; Grant 1986) supported the Clementsian view. Empirical studies demonstrating independent distributions of species in space and time (e.g. Whittaker 1956, 1960; Cole 1982, Huntley & Birks 1983) have supported the Gleasonian concept. The last decade has also seen a different, but related, debate about the extent to which communities exhibit deterministic composition or are random assemblages of species (e.g., see Strong et al. 1984, Diamond & Case 1986, and included references). It might seem logical to associate the Gleasonian concept with random assemblages, but as we shall see, species that exhibit a great deal of independence in their distributions can nevertheless show highly nonrandom patterns of coexistence.

The number and identity of species that coexist are determined by the interaction of proximal ecological factors and larger scale biogeographic and evolutionary events. Insights into how these diverse factors influence the distribution of species must come, at least in part, from analyses of geographic variation in the composition of local biotas. Several questions are particularly relevant: What are the patterns of variation among sites in the number and identity of coexisting species, and how do these patterns reflect the interacting processes that have determined the composition of contemporary communities? With what combinations of other species does a particular species occur over its geographic range, and how do these differences in associated species reflect the influence of environmental variation on abundance and distribution?

Table 1: Occurrence of 29 species of granivorous rodents at 202 sites (site number: species numbers). Species are listed by number at the end of the table. Site locations, habitats, and numbers are listed by source in Table 2.

1: 2, 4, 13, 17, 18, 19, 21, 25
2: 2, 17, 18, 19, 21, 25
3: 2, 12, 18, 19, 25
4: 2, 14, 18, 19, 25
5: 2, 12, 17, 18, 19, 21, 24
6: 2, 12, 17, 18, 19, 21, 25
7: 2, 12, 14, 17, 18, 19, 25
8: 18, 19, 21
9: 5, 18, 19
10: 2, 18
11: 18
12: 18
13: 18
14: 2, 17, 25
15: 17, 21, 25
16: 2, 14, 17, 25
17: 4, 17, 21, 25, 28
18: 4, 13, 16, 17, 21, 25
19: 18
20: 18, 19
21: 6, 23
22: 18, 19
23: 3, 5, 18, 19
24: 6
25: 5, 19, 25
26: 2, 5, 18, 19, 25
27: 6, 23
28: 5, 15, 19, 21, 23, 25
29: 1, 5, 15, 17, 19, 21, 23, 25
30: 6, 23, 26
31: 17, 25
32: 5, 19, 25
33: 5, 11, 15, 19, 21, 22, 25, 29
34: 1, 5, 15, 17, 19, 21, 25
35: 5, 19, 23, 25
36: 3, 5, 10, 19
37: 2, 9, 13, 14, 16, 17, 19, 21, 25
38: 17, 25
39: 6, 23
40: 5, 19
41: 10, 19, 23, 25
42: 19, 21, 25
43: 2, 14, 17, 19
44: 2, 4, 17, 21, 25
45: 5, 19, 21, 25
46: 2, 8, 19, 24
47: 3, 10, 19
48: 3, 19
49: 3, 5, 19
50: 5, 19
51: 3, 10
52: 3, 10
53: 10, 19
54: 3, 19
55: 3, 10
56: 18, 19
57: 3, 19
58: 1, 5, 6, 17, 19, 23, 25
59: 1, 10, 19, 23, 25
60: 1
61: 1, 5, 11
62: 1, 11
63: 1, 20, 22
64: 1
65: 1, 11, 15
66: 1, 5, 15, 19
67: 1, 19
68: 1, 19
69: 5, 15, 19, 25
70: 5, 19, 23
71: 5, 19, 23
72: 5, 17, 19, 23, 25
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77: 4, 25
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127: 1, 5, 19, 23
128: 1
129: 1, 19, 21, 26, 29
130: 1
131: 1, 25, 29
132: 1
133: 1, 5, 7, 23
134: 5, 7, 23, 25
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137: 1, 29
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140: 1, 21, 22, 23
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177: 9, 19
178: 19, 21
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182: 5, 19
183: 19
184: 5, 19
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187: 3, 5, 19
188: 10, 23
189: 10, 23
190: 10, 19, 23
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192: 5, 10, 23
193: 5, 19
194: 5, 19
195: 5, 10, 19
196: 3, 5, 6, 10, 19
197: 5, 19, 23, 24
198: 6, 10, 15, 19
199: 3, 5, 10, 19
200: 5, 19
201: 4, 17, 25
202: 4, 17, 25

1. *Perognathus flavus*
2. *Pg. longimembris*
3. *Pg. amplus*
4. *Pg. parvus*
5. *Chaetodipus penicillatus*
6. *C. intermedius*
7. *C. nelsoni*
8. *C. fallax*
9. *C. formosus*
10. *C. baileyi*
11. *C. hispidus*
12. *Microdipodops pallidus*
13. *M. megacephalus*
14. *Dipodomys microps*
15. *D. spectabilis*
16. *D. panamintinus*
17. *D. ordii*
18. *D. deserti*
19. *D. merriami*
20. *Reithrodontomys montanus*
21. *R. megalotis*
22. *R. fulvescens*
23. *Peromyscus eremicus*
24. *Pm. crinitus*
25. *Pm. maniculatus*
26. *Pm. boylii*
27. *Pm. pectoralis*
28. *Pm. truei*
29. *Pm. leucopus*

Table 2. Literature reports of rodent censuses used in data analyses: sources, location, habitat type, and site numbers. (Site numbers are referred to in Table 1.)

- Brown 1973
  - Great Basin Desert, sand dune (1–7, 14–18)
  - Mojave Desert, sand dune (8–10)
  - Sonoran Desert, sand dune (11–13)
- Brown 1975
  - Sonoran Desert, desert shrub (19–30)
  - Great Basin Desert, sand dune (31)
- Brown unpublished
  - Chihuahuan Desert, desert shrub (39–42, 45)
  - Great Basin Desert, desert shrub (38, 43–44)
- Brown et al. 1979
  - Sonoran Desert, desert shrub (36)
- Chew & Butterworth 1964
  - Mojave Desert, desert shrub (150)
- Chew & Chew 1970
  - Chihuahan Desert, desert shrub (59)
- Denyes 1956
  - Chihuahuan Desert, desert shrub (123–127, 132–134, 141–142); desert grassland (128–131, 136–140, 143)
- Feldhamer 1979
  - Great Basin Desert, desert shrub (120–121) desert grassland (122)
- Hafner 1977
  - Mojave Desert, desert shrub (144–149)
- Hallett 1982
  - Chihuahuan Desert, desert shrub (58)
- Hardy 1945
  - Mojave Desert, desert shrub (165–179)
- Harney unpublished
  - Mojave Desert, desert shrub (197, 200)
  - Sonoran Desert, desert shrub (198–199)
  - Great Basin Desert, dune (201–202)
- Jorgensen & Hayward 1965
  - Mojave Desert, desert shrub (109–116)
- Kingsley 1981
  - Mojave Desert, desert shrub (86–101)
  - Great Basin Desert, desert shrub (102–108)
- Larsen 1978
  - Great Basin Desert, shrub-steppe (74–85)
- Nichols et al. 1975
  - Great Basin Desert, desert shrub (117–119)
- O'Farrell 1974
  - Great Basin Desert, desert shrub (37)
- Petryszyn unpublished
  - Sonoran Desert, desert shrub (135, 158, 196)
- Rickard 1960
  - Great Basin, desert shrub (151–154, 160–164); desert grassland (155–157, 159)
- Rosenzweig et al. 1975
  - Chihuahuan Desert, desert shrub (32–33)
- Rosenzweig & Winakur 1969
  - Sonoran Desert, desert shrub (47–57)
  - Chihuahuan Desert, desert grassland (60–73)
- Steenburgh & Warren 1977
  - Sonoran Desert, desert shrub (180–195)
- Thompson 1982
  - Mojave Desert, desert shrub (46)
- Whitford 1976
  - Chihuahuan Desert, desert shrub (34–35)

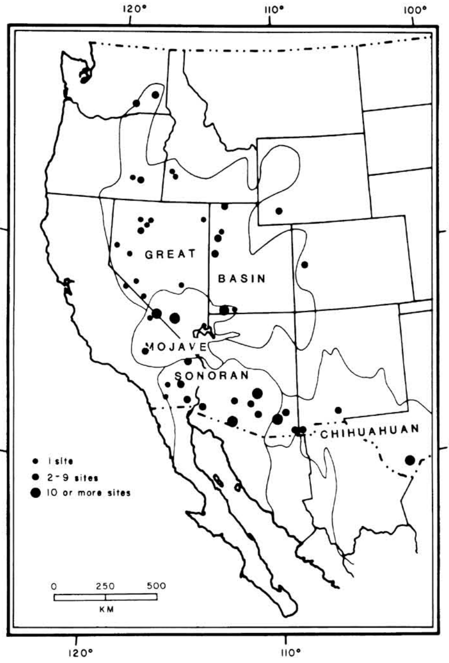


Fig. 1. Geographic distribution of rodent census sites used in the present study.

We have begun to investigate these questions by analyzing geographic variation in the composition of an ecologically and taxonomically constrained biota. We assembled data on the combinations of granivorous rodent species that occurred together at 202 local sites distributed throughout the arid region of the southwestern United States. Our analyses show extensive spatial variation in the composition of these rodent biotas — a large number of different species combinations, yet an average of only four species per site. Our data suggest a highly individualistic or Gleasonian view of community organization which has important implications for such disciplines as coevolution, paleontology, and biogeography, as well as ecology.

2. Methods

The basic data set is a presence-absence matrix of rodent species occurrences at sample sites (Table 1). We assembled data from the literature on rodent censuses within small habitat patches at 202 sites (Table 2). These sites are distributed primarily among the four North American deserts (Great Basin, Mojave, Sonoran, Chihuahuan), but include a few peripheral areas (Fig. 1). Only census data with a minimum of 100 trapnights in small, relatively uniform patches of desert shrub, desert grassland, or other xeric habitat were included. In long-

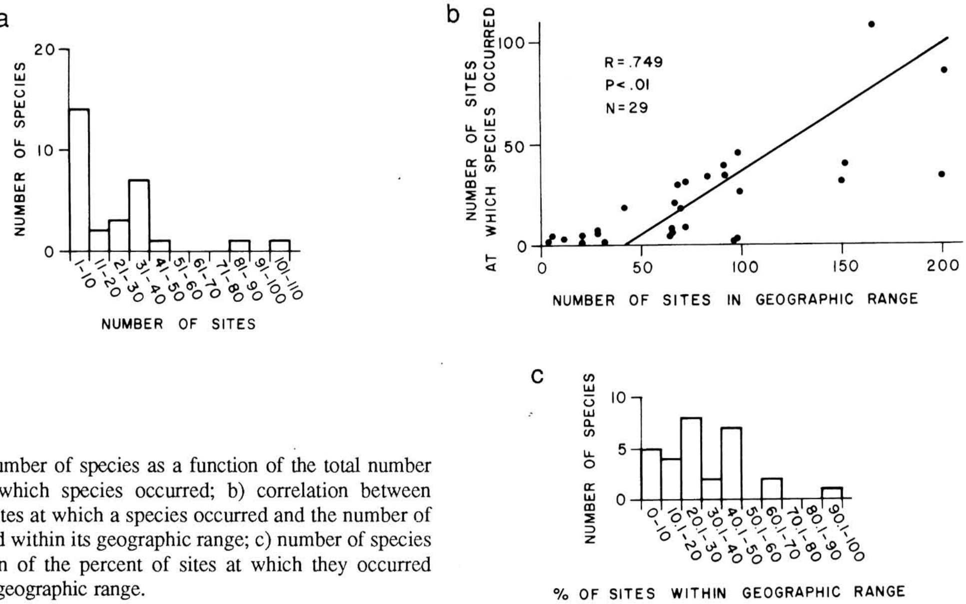


Fig. 2. a) Number of species as a function of the total number of sites at which species occurred; b) correlation between number of sites at which a species occurred and the number of sites sampled within its geographic range; c) number of species as a function of the percent of sites at which they occurred within their geographic range.

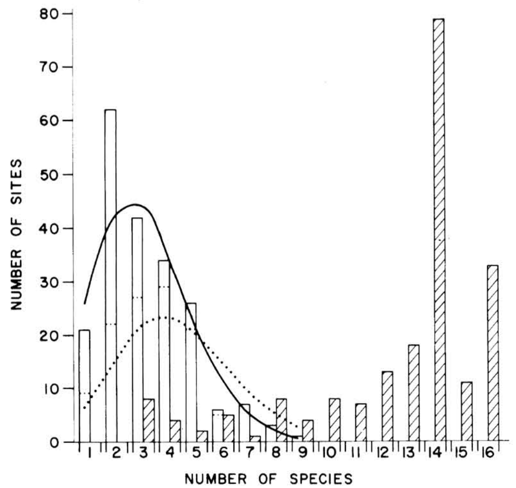


Fig. 3. Number of sites as a function of the number of species per site (open histogram) and of the number of species whose geographic ranges overlap each site (hatched histogram). Horizontal dotted lines on open histogram represent the number of sites that have different combinations of that number of species. Solid curve is a Poisson distribution of the number of sites inhabited by different numbers of species, expected on the basis of random distribution of species among sites. Dotted curve is a Poisson distribution of the number of sites that have different combinations of species, expected on the basis of random distribution of different combinations among sites.

term censusing studies, only data from the first year (May through August) were used. We confined analyses to 29 species of rodents that feed largely or entirely on seeds. For analyses involving the geographic ranges of species, we used range maps in Hall (1981). Analytical methods are described in detail in the presentation of results; statistical analyses generally follow Sokal & Rohlf (1981).

3. Results

3.1. Distribution of species among sites

Collectively, the 202 sites supported many different species and assemblages of granivorous rodents. Most of the rodent species were restricted to a small proportion of sample sites, even within their geographic ranges. Almost half of all species (48.3%) occurred at ten or fewer sites (Fig. 2a). The occurrence of species at sites was highly correlated ($r = 0.749$, $P < 0.01$) with the number of sites within a species' geographic range (Fig. 2b). Yet the majority of species (58.6%) occurred at fewer than 30% of the sites within their geographic ranges and only three species occurred at more than 60% of those sites (Fig. 2c). The number of sites at which a species occurred was positively correlated with both the total number of species with which it cooccurred and the total number of sites in the species' geographic range (multiple $r = 0.847$, $P < 0.001$). We used a G-test to

Fig. 4. Frequency distributions of sites as a function of the number of coexisting species per site for four species. The number of different combinations is noted by the hatched portion of each histogram.

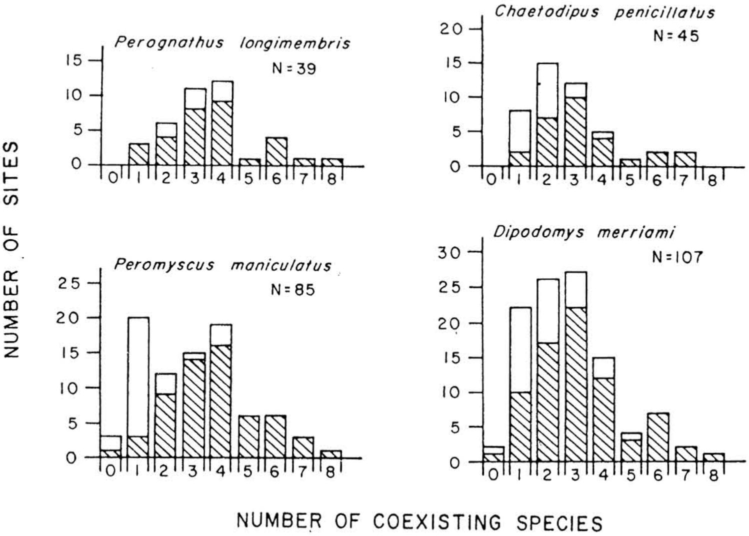
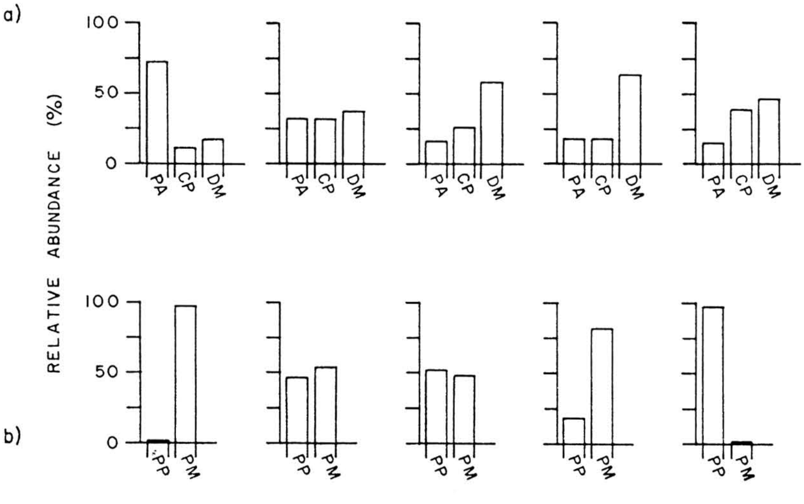


Fig. 5. Relative abundance of species at sites with same species combination: a) of three species, *Perognathus amplus* = PA, *Chaetodipus penicillatus* = CP, *Dipodomys merriami* = DM; and b) of two species, *Perognathus parvus* = PP, *Peromyscus maniculatus* = PM.



determine how close a fit could be predicted by these two variables alone; the results ($G = 184$, $P < 0.001$) implied that they were not sufficient predictors of the number of sites of occurrence.

3.2. Distribution of species among sites with respect to other species

More than 80% of the sites were inhabited by combinations of two to five species; 11.4% of the sites had only a single species, and 8.4% had six or more species (Fig. 3, open histogram). When this distribution is compared with the number of species that have geographic ranges that overlap the sites (Fig. 3, hatched histogram), it is apparent that the actually occurring combinations were comprised of far fewer species (e.g., 79 sites could have been occupied by combinations of 14 species). It is evident that some criteria other than geographic range effect the patterns of coexistence and distribution of species among sites. The frequency distribution of the number of species per site was compared to a Poisson distribution (Fig. 3, solid curve) using a *G*-test. Although the distribution appears similar to the Poisson, it is statistically significantly different ($G =$

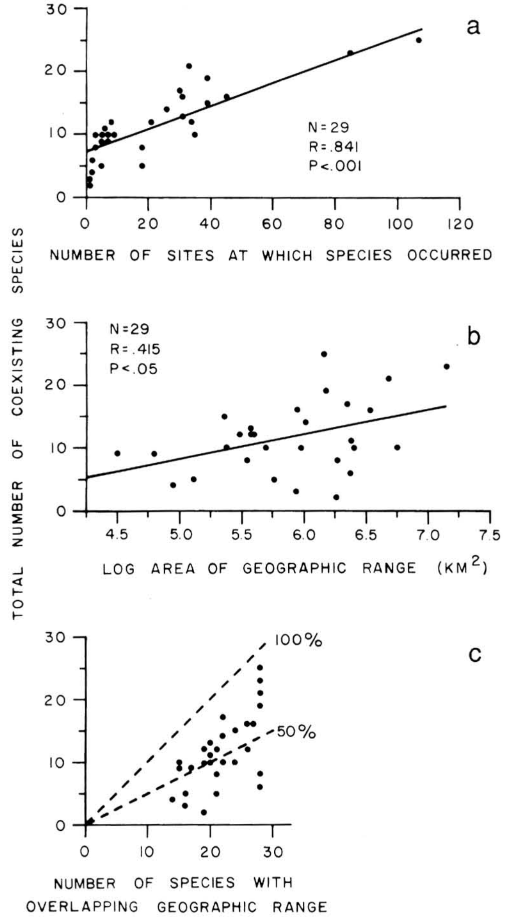


Fig. 6. Relationship between the total number of species with which a species coexisted and a) the number of sites at which that species occurred, b) the area of its geographic range (log scale), and c) the number of species that had overlapping geographic ranges (note that most species cooccurred with more than 50% of the species with overlapping ranges).

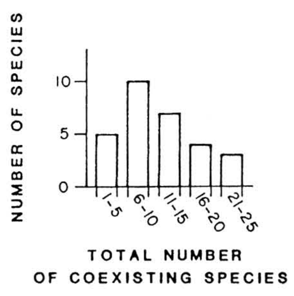


Fig. 7. Number of species as a function of the total number of species with which they coexisted.

20.2, $P < 0.001$). The discrepancy between the two distributions appears to be due to the much larger number of two-species communities observed than expected based on the Poisson.

Because sites with few species were more likely to have redundant combinations of species, the frequency distribution of different combinations observed (Fig. 3, dotted lines on open histogram) peaks at four-, rather than two-species combinations. The distribution of the number of species in different combinations was also compared to a Poisson distribution (Fig. 3, dotted curve) and found to be significantly different ($G = 20.5$, $P < 0.001$). There were more few-species (2–4) combinations and fewer multi-species (> 6) combinations observed than expected. Individual species show similar patterns (for example, Fig. 4), occurring most frequently in local association with two to four other species and in different combinations with three or four other species.

Yet it should be noted that even sites with the same combination of species showed marked differences in the relative abundances of those species (for example, Fig. 5a and b). Thus using presence-absence data underestimates the differences among sites and the individualistic nature of species cooccurrences.

The total number of species with which a species coexisted was highly correlated with the number of sites at which it was recorded ($r = 0.841$, $P < 0.01$) and with its area of geographic range ($r = 0.415$, $P < 0.05$) (Fig. 6a and b). Species cooccurred locally with a large proportion of the species with which their geographic ranges overlapped (Fig. 6c). Of the 29 species, 62.1% occurred locally with more than 50% of species with overlapping geographic ranges. This is probably an underestimate of species' cooccurrences due to sampling limitations. Almost 50% of species cooccurred with more than ten other species (Fig. 7).

3.3. Combinations of coexisting species

A large number of different combinations of species was observed. At 202 sample sites, 124 different combinations were recorded, 90 (72.6%) of which were observed only once (Fig. 8). The most frequent combination (of two species, *Perognathus parvus* and *Peromyscus maniculatus*) occurred at 14 sites.

Most species occurred with many different combinations of other species. Of the 29 species, 14 (48.3%) occurred in more than 10 different combina-

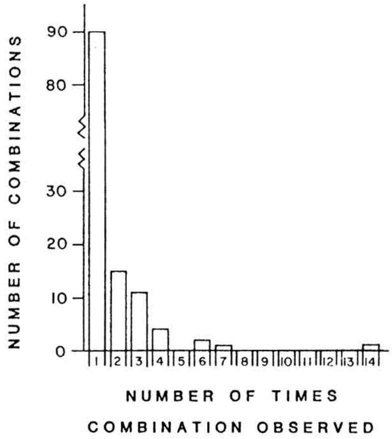


Fig. 8. Frequency distribution of the number of combinations of species as a function of the number of times each combination was observed. A total of 124 different combinations were observed.

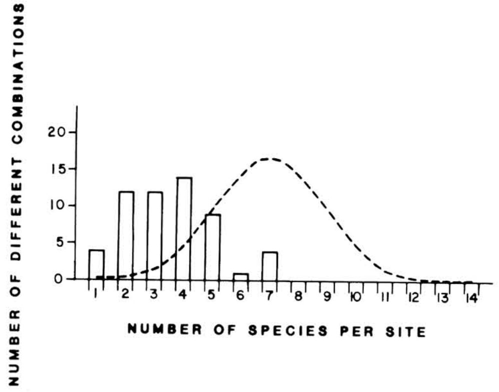


Fig. 10. Frequency distribution of the number of species of different combinations as a function of the number of species per site (histogram) at the 79 sites where the geographic ranges of 14 species overlap. The dashed line represents the expected number of different combinations (given 79 sites and 14 species) based on the null hypothesis that any different combination is equally likely.

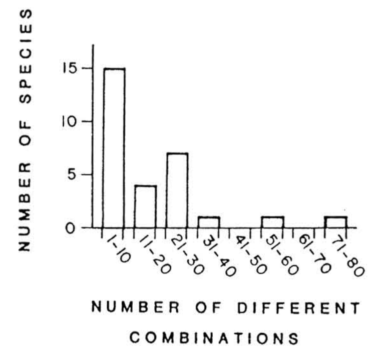


Fig. 9. Frequency distribution of the number of species as a function of the number of different combinations in which they occurred.

tions, and two occurred in more than 50 combinations (Fig. 9). As expected, the total number of different combinations in which a species was recorded was highly correlated with the number of species with which it actually occurred (*r* = 0.877, *P* < 0.01). However, it was poorly correlated with the log area of geographic range of the species (*r* = 0.342, *P* > 0.05).

For 79 sites where the geographic ranges of 14 species overlapped, we calculated the frequency distribution of different combinations as a function of the number of coexisting species per combination (Fig. 10, bar graph). Fifty-six different combinations of one to seven species were found, and communities consisting of two to five species occurred most frequently. This distribution was contrasted with the theoretically possible distribution of different combinations of 14 species (Fig. 10, curve), in which the most frequent number of combinations consisted of seven species. In our sample of 79 sites, far more single-, two-, three-, and four-species combinations were found than would be expected on the basis of chance, assuming that any possible combination was equally likely (*G* = 59, *P* <0 .001).

4. Discussion

The results of our analyses provide a perspective that cannot be obtained from focused observational or experimental studies of individual local communities. Knowledge of the extent of spatial and temporal variation in the composition of biotas should contribute to understanding the variables and mechanisms that influence community organization.

Perhaps the most important implication of the patterns revealed by our analyses is that they support an individualistic or Gleasonian (Gleason 1917, 1926; see also Shreve 1914, Hutchinson 1958, Brown 1984) concept of the spatial distribution of individual species and assemblages of species. Although our data directly demonstrate only the extremely patchy distribution of individual species and the enormous variation in the species composition of local rodent assemblages, in combination with other information on this well-studied guild they suggest some of the processes that determine community organization and cause it to vary in space. Although each of the sites contained a few hectares of relatively homogeneous desert shrub habitat, the sites differed from each other not only in geography, but also in climate, geology, physiography, vegetation, and fauna. The fact that most of the species occurred at only a small proportion of the sites within their geographic ranges, suggests that each species had highly specific requirements and tolerances, and that only a small proportion of local habitat patches provided suitable conditions for survival and reproduction. The fact that local assemblages were comprised of many different species and combinations of species implies that the composition of these assemblages reflected primarily the ability of local patches to meet the individualistic requirements of different species rather than highly structured interactions between particular combinations of species. The large number of different combinations together with the observation that most of the species coexisted locally with the majority of species with which their geographic ranges overlapped is evidence that these continental assemblages of rodents were not organized into a small number of alternative stable communities as suggested by MacArthur (1972), Diamond (1975), and others.

The uniqueness of local assemblages emphasizes the need for caution in generalizing about species interactions from one or a few local studies. However, we emphasize that our results are not necessarily incompatible with the view that community organization is determined by a common set of processes, that include competition, predation, and interactions with the physical environment. Indeed, despite the variation in species composition, it is possible to detect nonrandom patterns of species richness and coexistence that apparently reflect the operation of such deterministic processes. Desert rodent assemblages are non-random in at least two ways. First, local faunas are typically comprised of two to five species. This is significantly fewer than would be expected if species with overlapping geographic ranges associated at random (Fig. 10). Second, it has been shown elsewhere that closely related species of similar body size coexist locally less frequently than expected on the basis of chance (Bowers & Brown 1982, Brown & Harney in press). Both of these patterns are consistent with the interpretation that interspecific competition limits the distribution of some species. The infrequent coexistence of similar species may be attributed to competitive exclusion, which also may account for the small size of local faunas.

The use of presence-absence data and the failure to consider abundance within a site emphasizes the importance of rare species. This raises concerns about sampling. The number of species recorded would be expected to increase, but at a continually decreasing rate, as the sampling effort increases. So long as this positive relationship obtains, limited sampling from local sites will be biased against rare species and inaccurately reflect the composition of assemblages. However, the number of rodent species recorded was not a function of sampling intensity; the correlation between number of species captured and number of trapnights at a site was not significant (r = 0.135, $P > 0.05$). There was a significant positive relationship between the number of species and the number of individuals captured at a site (r = 0.324, $P < 0.01$), but this probably reflects the relationship between productivity and granivorous rodent species diversity (Brown 1973, 1975) rather than an artifact of sampling. We do not claim that the samples that we have analyzed include all the rare and ephemeral species that may occur at some sites, but we believe that much more intensive sampling regimes should reveal patterns qualitatively similar to those reported above. This is supported by the fact that even when different sites are inhabited by the same combination of species, the relative abundances of these species are often very different (Fig. 5). Thus presence-absence data underestimate, rather than overestimate, spatial variation in community organization.

Although in this study we did not incorporate information on the abundance of species within sites, the composition of rodent faunas appears to reflect the positive relationship between the abundance and distribution of species (Hanski 1982, Brown 1984). Some pairs or groups of species coexist frequently. These tend to be forms that are 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.

Although these rare species are ignored or deemphasized in many studies of community ecology (e.g., for desert rodents, Brown 1973, 1975), they are potentially important for several reasons. First, 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). In the present study the majority of species were restricted to a small proportion of the census sites. Second, because most species are rare, a knowledge of their ecology is essential to understanding the large-scale processes that influence their evolution and determine their geographic distributions. Local ecological conditions are the proximal factors that constitute both the selective pressures that cause evolutionary change and the geographic barriers to dispersal that limit distribution. Third, the distribution of rare species potentially provides valuable information about spatial variation in habitat, resources, and interspecific relationships. 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.

A major question raised by this study is how representative are the "study areas" of community ecologists? This is significant because it affects the extent to which it may be valid to extrapolate from the results of local studies. Our analyses reveal extensive spatial variation in the composition of desert rodent guilds, even among superficially similar habitats within a restricted geographic region. Any complete understanding of the patterns and processes in continental communities must account for this variation.

The spatially varying composition of assemblages affects the kinds of interactions and hence the possibilities for coevolution among species. There has been much speculation about the extent to which pairs of species have coevolved to reduce the intensity of competition. Individualistic distributions mean that species have limited opportunities for coevolution in continental biotas. It is hard to imagine strong, consistent selective pressures for coevolution between any pair of species, when each of these species encounters the other at only a limited number of sites and encounters different species that would select for different attributes at other sites (even within the same local region). Thus, our analysis points out yet another reason why it may be misleading to try to understand the ecology and evolution of assemblages of many species in terms of pairwise interspecific interactions.

The spatial variation among local assemblages also has important implications for paleontology. What spatial area and time frame are sampled by a fossil deposit? When a deposit represents the accumulation of remains from a large area or a long period of time, it may contain many more species than actually coexisted locally. On the other hand, when a fossil deposit provides an accurate representation of a local community, it will not reflect the diversity of assemblages that occurred in larger geographic areas.

There have been numerous attempts to subdivide continents into biogeographic provinces, i.e., regions with similar biotas. These regions are presumed to represent the influence of climate and geomorphology, and the history of isolation and migration. Although we recognize that local biotas can be clustered into objective biogeographic regions (that reflect some combination of contemporary ecological conditions and historical barriers to dispersal), such constructs should be interpreted cautiously. The individualistic patterns that we have documented imply that each species responds differently to biotic and abiotic characteristics of the environment. Consequently, the clusters of similar species distributions are to some extent artificial constructs, based on contemporary or historical factors that may have affected only a small proportion of the biota. This problem will be particularly severe within regions, such as the interiors of many continents, where gradients of ecological change are gradual and major barriers to dispersal are absent.

Despite the difficulty of defining biogeographic regions that reflect the common influence of contemporary or historical factors on the biota as a whole, the composition of local biotas can be used to characterize the response of different kinds of organisms to spatial variation in the environment. Beta diversity, the change in species composition from site to site, especially within local gradients of rapid environmental change, has been quantified in several studies (Whittaker 1972, 1977; Cody 1975; Wilson & Shmida 1984). We have deliberately avoided presenting our data in terms of beta diversity, because of problems in interpreting this measure of species turnover among sites. Nevertheless, quantitative comparison of the change in species composition as a function of the distance between sites should provide a useful measure of the spatial scale or grain to which different taxa respond to variation in the landscape. It would be interesting to repeat the kind of analysis we have performed here on other groups — such as insects, which might be predicted to use the environment on a finer scale and hence to show even more variation in faunal composition among sites, and birds, which might be less affected by barriers to dispersal and hence show less variation than rodents.

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