

# 10. Diversity and niche structure in desert communities

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## Introduction

Do deserts generally tend to support communities that are either more or less diverse than communities in wetter areas? To what extent do desert communities possess characteristic patterns of resource partitioning and community structure? Are there general answers to these questions, or do they differ among various plant and animal taxa? Here I explore these questions, first briefly from a theoretical standpoint and then I examine the meager existing empirical evidence.

## Some theoretical considerations

### *Species diversity*

Diversity has been quantified in a wide variety of different ways (see, for example, Simpson, 1949; MacArthur & MacArthur, 1961; Pielou, 1969; MacArthur, 1972; Hill, 1973 and Peet, 1974). The two basic components of species diversity are simply the total number of species actually present and the degree to which they are equally important. Relative importance has been measured in a number of ways, ranging from abundances to biomass to the energetic importance within the community. In birds and lizards, at least, estimates of species diversity computed with various diversity indices are strongly correlated with the much simpler measure of the actual number of species present, termed species richness or species density (Tramer, 1969; Longuet-Higgins, 1971; Pianka, 1975).

MacArthur (1972) pointed out that species diversity in resource-limited, competitive communities is a simple function of three variables: (1) diversity of available resources or the overall size of the niche space, or hypervolume, (2) diversity of utilization of these resources by an average species or mean niche breadth, and (3) the extent to which resources are shared or the amount of niche overlap. All else being equal, community species diversity clearly should increase with increased diversity of available resources and increased niche overlap; conversely, as average niche breadth is enlarged, diversity must decrease unless there are concomitant changes in resource diversity and/or tolerable niche overlap. MacArthur also points out the importance of resource dimensionality or the number of different ways in which competition is avoided; again, all else remaining

## *Component processes*

equal, an increased number of niche dimensions allows maintenance of a greater number of species. Increased niche dimensionality also results in a greater potential number of neighbors in niche space and hence a heightened potential for diffuse competition.

### *Optimal foraging tactics and niche breadth*

A fairly substantial body of theory on optimal foraging predicts that niche breadth should generally increase as resource availability decreases (see for example, Emlen, 1966, 1968; MacArthur & Pianka, 1966; Schoener, 1971; MacArthur, 1972; Charnov, 1973). The reasoning behind this conclusion is that, in an environment with a scant food supply, a consumer cannot afford to bypass substandard potential prey items because mean search time per prey item encountered is long (expectation of prey encounter is low). Under this situation, a broad niche maximizes returns per unit expenditure and generalization is favored. In a food-rich environment, however, search time per item is low and a consumer encounters numerous potential prey items; under such circumstances, inferior prey types can be bypassed because expectation of finding a superior item is high. Hence rich food supplies should favor selective foraging and narrow niche breadths.

Deserts are less productive than other ecosystems owing to low water supply and should therefore support fewer potential prey items per unit area. A probable consequence of such a low prey density is that an average consumer will have a broad niche, which in turn should result in reduced species diversity in desert communities.

### *Spatial heterogeneity and environmental variability*

Spatially complex habitats support richer communities than structurally simpler areas because there are more ways of exploiting the former. Many deserts, especially the more diverse ones such as the Sonoran desert, support a structurally complex vegetation which provides animals with ample opportunities for niche segregation involving differential use of microhabitats.

Deserts frequently have very variable precipitation regimes. Environmental variability can both enhance and limit diversity. To the extent that different species can adapt to particular subsets of conditions, temporal or seasonal heterogeneity can promote diversity (Hutchinson, 1961). Continually changing interactions between species may also facilitate persistence of a variety of species, provided that each enjoys a competitive advantage during some time period. By promoting a diversity of plant life forms, climatic variability can act to increase spatial heterogeneity and

animal species diversity. Under some circumstances, however, members of a community may be unable to partition resources temporally. If an individual organism must be able to tolerate a variety of conditions in order to persist, environmental variability promotes generalization, broad niches, and hence lower species diversity.

*Taxon-specific adaptations and historical events*

Some anatomical and physiological traits confer an advantage upon particular taxa in appropriate environments. For example, lizards tend to be more diverse in deserts than elsewhere, probably partially as a result of their poikilothermy and consequent ability to capitalize on scant and variable amounts of primary productivity by becoming inactive and retreating underground during harsh periods. Thus lizards are in some senses 'predapted' for performance in hot and arid environments. Indeed, competition between lizards and birds may favor lizards under desert conditions (Pianka, 1967, 1973). Such complementary interactions between taxa can obscure trends in community structure and diversity when taxonomic subsets of the community are treated as a unit of study.

Accidents of history also profoundly shape community composition and, indirectly, species diversity. For example, Australian desert lizards have usurped some of the ecological roles played by snakes and mammals in deserts on other continents (Pianka, 1969*a*, 1973); moreover, the mammalian and snake faunas of the Australian deserts appear to be somewhat impoverished.

**Empirical aspects**

*Plants*

Plant species diversity generally varies independently of overall productivity (Whittaker, 1972). Data from the Great Smoky Mountains (Fig. 10.1) show that shrub diversity is highest on the more xeric ridges and peaks, while trees reach their highest diversity in more mesic canyons, draws, and ravines. In the same region, summer herbs attain high diversities under two disparate environmental conditions, namely in mesic low altitude cove forests and at high altitudes on xeric open slopes (Fig. 10.1).

Whittaker (1972) also points out that the Sonoran desert, with its bimodal annual march of precipitation, supports an exceedingly diverse array of plant communities in spite of its aridity and unpredictability. On Sonoran desert mountain slopes, species diversities of both perennials and annuals are higher than in most eastern forests. Perennials have adopted a wide range of plant life forms, apparently alternative ways of coping with unpredictable water availability. Annuals are very irregular in both

Component processes

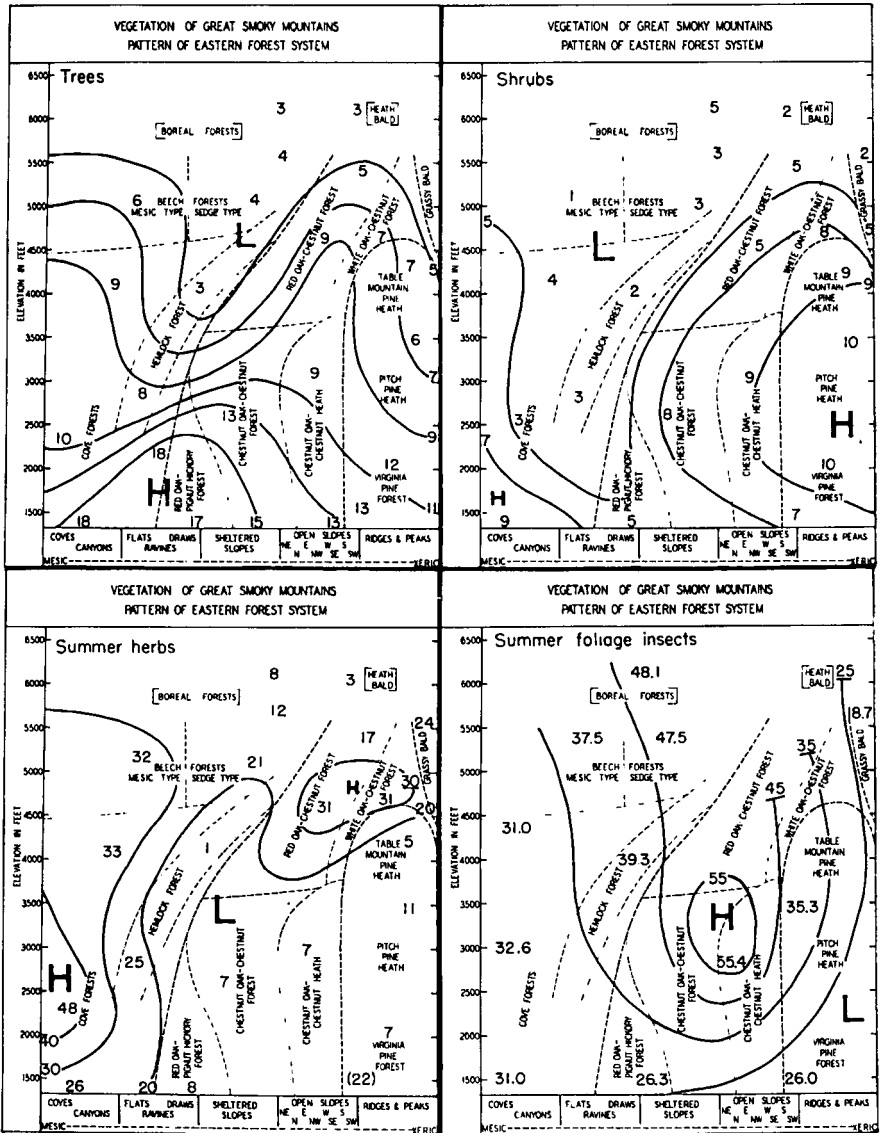


Fig. 10.1. Species diversity of trees, shrubs, summer herbs, and summer foliage insects in the Great Smoky Mountains. Diversity of each group of organisms is plotted along a xeric to mesic continuum against elevation. Diversity of the different groups vary with altitude and water availability, but high and low diversity situations differ markedly among groups. Contours outline number of trees, shrubs and summer herb species in 0.1 ha quadrats and alpha indexes for sweep samples of summer foliage insects. (From Whittaker, 1972.)

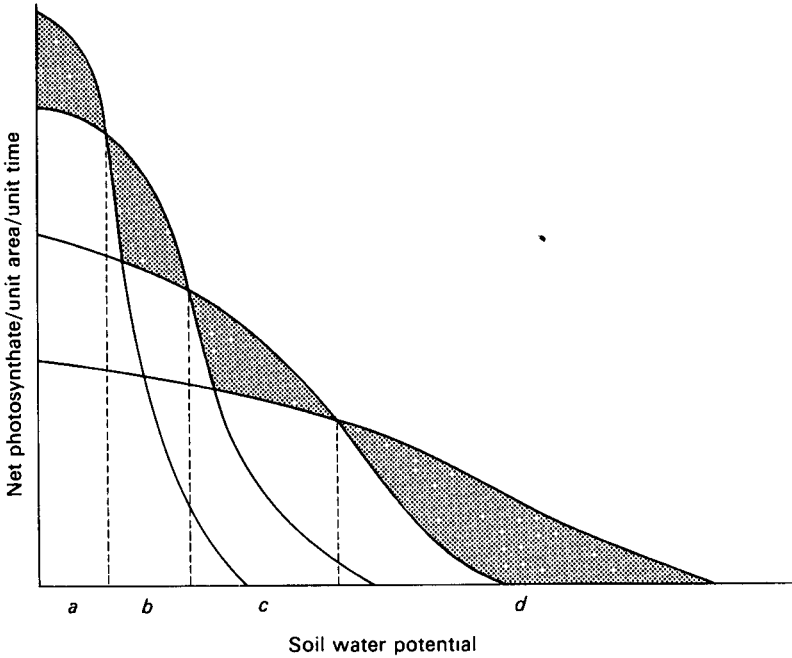


Fig. 10.2. Hypothetical relationship between net photosynthate per unit of leaf surface area per unit time and soil water potential for different types of leaves. The most mesophytic leaf type performs best under conditions of high soil water availability, marked *a* (low soil water potential), while the most xerophytic leaf type shown performs best over the range of conditions marked *d* (low water availability). Intermediate leaf types are more efficient photosynthesizers under intermediate conditions of water availability (marked with *b* and *c* in the figure). Shaded zones represent the soil water potential conditions under which the various leaf types are superior. (Adapted from Orians & Solbrig, 1977.)

their temporal and spatial patterns of appearance; many species of annual plants have evolved specific germination requirements and respond differentially to winter and summer rainfall. The bimodal annual pattern of rainfall clearly has allowed diversification of annual plant species, with a conspicuous dichotomy between summer annuals and winter annuals (Shreve, 1964). Certain plant communities in the Sonoran desert, however, are of very low plant species diversity, such as the almost 'pure' stands of creosote bush *Larrea divaricata* (Shreve, 1964; McCleary, 1968). Extreme aridity clearly must result in very low productivity and plant species diversity.

The high diversity of plant life forms on Sonoran desert slopes is probably a reflection of a variety of leaf tactics which have evolved in response to the great spatial and temporal variability of water availability in the Sonoran desert (Orians & Solbrig, 1976). Using cost-benefit

## Component processes

arguments, these authors contrast a continuum of leaf types, ranging from the relatively inexpensive deciduous 'mesophytic' leaf to the most costly evergreen 'xerophytic' leaf. Mesophytic leaves photosynthesize and transpire at a rapid rate, and hence require high water-availability (low 'soil water potential'). In contrast, xerophytic leaves cannot photosynthesize as rapidly when abundant water is available, but they are also able to extract water from relatively dry soil. Orians & Solbrig argue that each plant leaf tactic has an advantage at either different times or in different places (along washes, etc.), promoting plant life form diversity. During wet periods, plants with mesophytic leaves photosynthesize rapidly, but, under drought conditions they must drop their leaves and become dormant. During such dry periods, however, the slower photosynthesizers with xerophytic leaves are still able to function by virtue of their ability to extract water from dry soils. Of course, all degrees of intermediate leaf tactics exist, each of which may enjoy a competitive advantage under particular conditions of water availability (Fig. 10.2). Orians & Solbrig argue that the net annual profit per unit of leaf surface area determines the winning phenotype; moreover, even a relatively brief wet season may suffice to give mesophytic leaves a higher annual profit, thus accounting for the prevalence of high transpiration leaves along desert washes.

Lowe, Morello, Cross & Goldstein (1972) and Lowe *et al.* (1973) have correlated plant species diversity in the Sonoran and Monte deserts with various measures of soil texture (Fig. 10.3).

## Insects

Sweep samples of summer foliage insects in the Great Smoky Mountains showed maximal insect species diversities at intermediate elevations in habitats intermediate along the xeric to mesic continuum (Fig. 10.1). Janzen & Schoener (1968) took sweep samples of insects from the understorey of tropical forests along a moisture gradient during the dry season in Costa Rica. The absolute number of species increased with increasing moisture, as did insect species diversity, although somewhat more erratically.

Otte & Joern (1978) have studied species density and food-niche breadths of grasshoppers on numerous sites in deserts and along several desert-grassland ecoclines (Otte, personal communication). The number of grasshopper species is generally higher in more productive grasslands than it is in deserts (Otte & Joern, 1978).

Within deserts, the number of species of grasshoppers increases with the number of plant species (Fig. 10.4). In the Sonoran desert, both plant species numbers and grasshopper species density increase from low *Larrea* spp. flats towards higher slopes. Otte & Joern (1978) do not

Diversity and niche structure

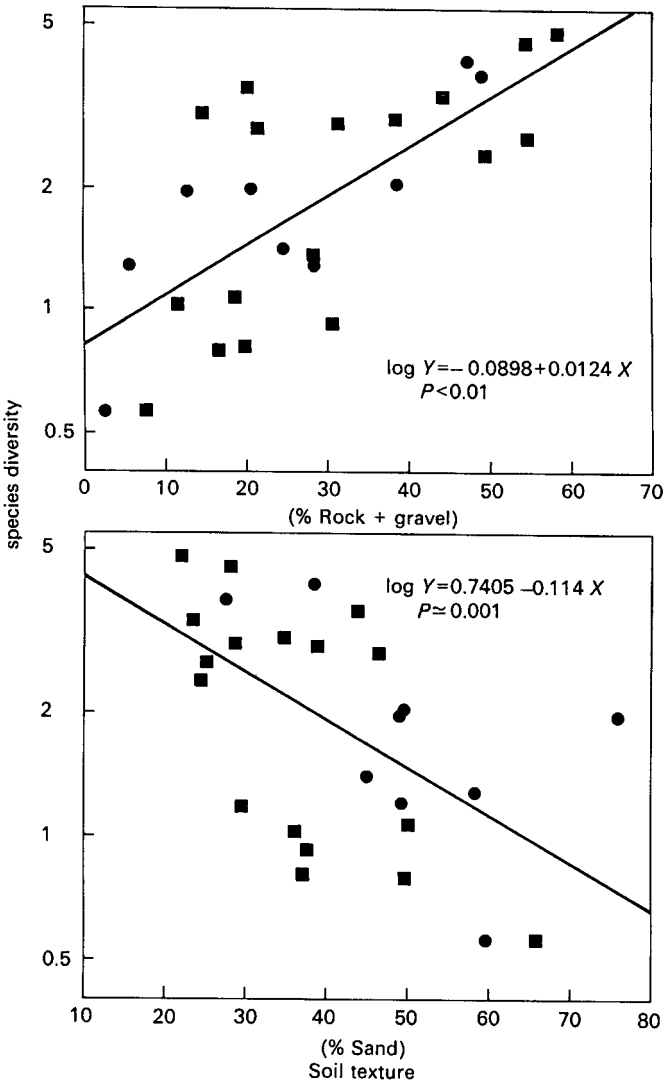


Fig. 10.3. Two plots of plant species diversity against two measures of soil texture for desert sites in Arizona (squares) and Argentina (dots). (From Lowe *et al.*, 1972, 1973.)

consider competition for food to be a major factor determining grasshopper species richness, but they place much greater emphasis upon the available predator escape tactics. Thus, more diverse plant communities support a greater variety of grasshopper species because they offer grasshoppers a wider variety of ways of camouflaging themselves from potential predators. Otte & Joern consider it highly likely that grasshopper

## Component processes .

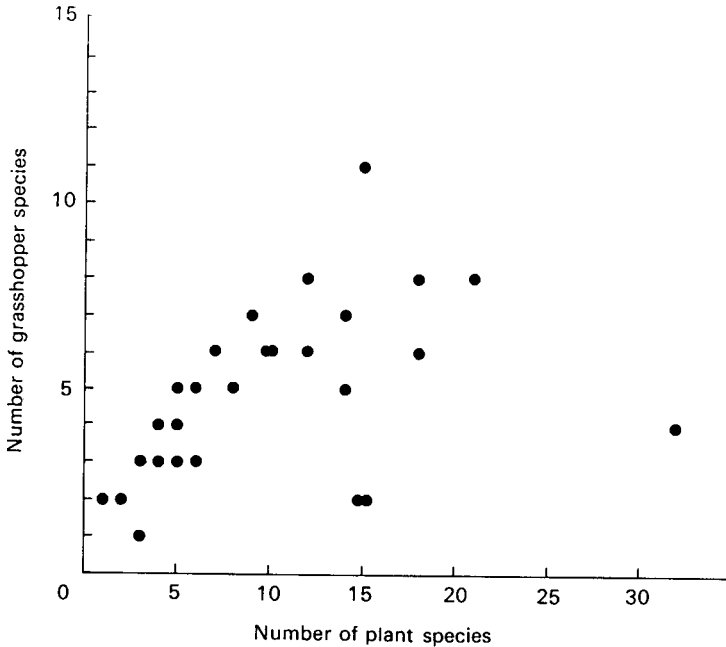


Fig. 10.4. Number of grasshopper species plotted against the number of plant species along an elevational gradient in the Sonoran desert of Arizona. (From Otte & Joern, 1978.)

communities are responding to increased structural complexity of the vegetation, rather than to plant species diversity, *per se*. Indeed, some plant species support more than one species of grasshopper, with different grasshopper species mimicking different parts of the plant (leaves, stems, etc.).

Somewhat surprisingly, grasshopper diets tend to be more restricted in deserts than in grasslands, with the result that average food niche breadth is narrower in deserts (Otte & Joern, 1978). Otte & Joern suggest that the high incidence of monophagy in deserts could be related both to high predictability of certain food plants in space and time and to decreased nutrient accessibility due to chemical and/or structural antiherbivore protective devices of woody perennials. However, they point out the great difficulty in determining whether the observed dietary specialization of desert grasshoppers is due primarily to crypsis-related factors or to adaptation to specific food plant secondary substances. Moreover, Otte & Joern note that predator escape tactics and foraging behavior are intricately interrelated and confounded; they state that no species of desert grasshopper forages away from foliage upon which it gains protection from potential predators.

In old fields in Michigan, species diversity of homopterans is strongly correlated with both plant species diversity and plant structural diversity



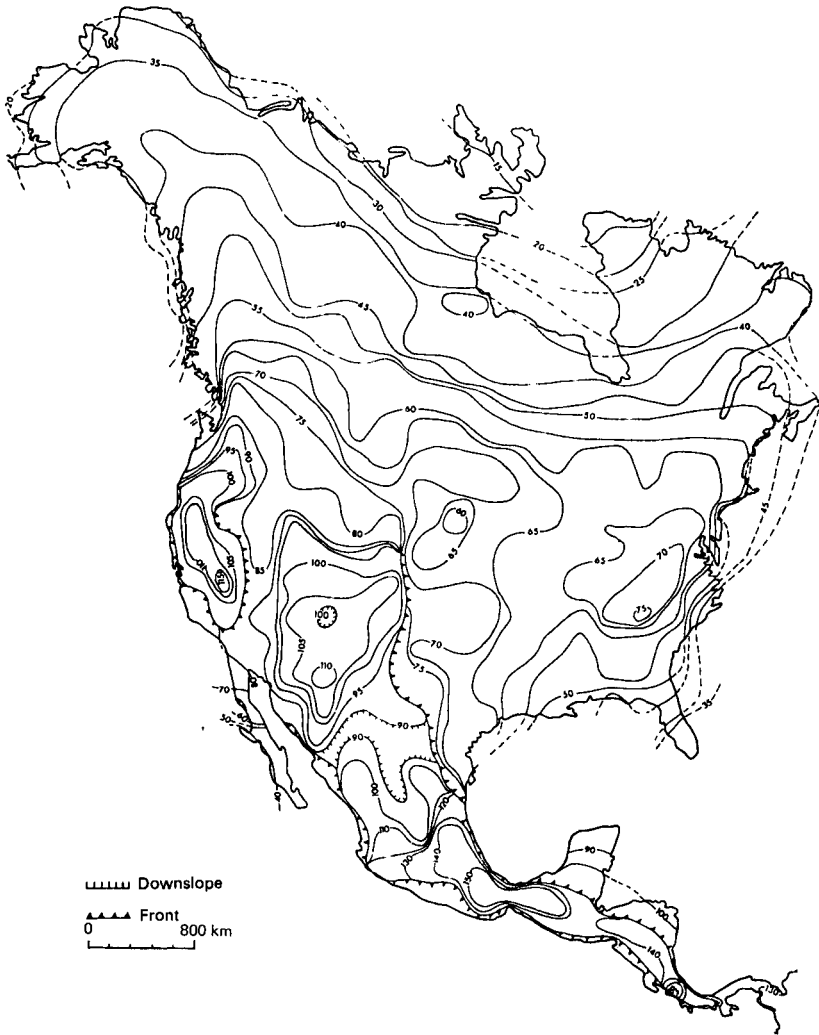


Fig. 10.5. Isopleths of the number of mammal species occurring in quadrates 240 km on a side over North America. (From Simpson, 1964.)

(Murdoch, Evans & Peterson, 1972), which are highly correlated themselves.

### *Mammals*

Simpson (1964) plotted isopleths of mammal species density for the North American continent (Fig. 10.5). This map is based on numbers of species known to occur in large quadrats 240 km on a side; in topographically

### *Component processes*

diverse regions, animals from several habitats are added together so that the figure includes both the between-habitat component of diversity as well as the within-habitat component. Nevertheless, desert areas in western North America are not conspicuously impoverished in numbers of mammal species. Indeed, mammal species density appears to be high in this area, perhaps largely because of the great topographic relief of the area and a consequent high between-habitat component of diversity. Simpson concludes that the observed pattern of mammal species density does not indicate a positive correlation with annual precipitation (and hence productivity), but rather suggests an *inverse* relationship. Indeed, there is a highly significant inverse correlation ( $r = -0.59$ ,  $P < 0.001$ ) between average annual precipitation and mammal species density in Simpson's quadrats within the continental US (Pianka, 1978). Within the state of Texas, the number of species of small mammals reaches maximal values in the far western trans Pecos area, which houses the Chihuahuan desert and is the driest and least productive part of the state (Rogers, 1976).

A number of fairly detailed studies of community structure and resource partitioning have been made on desert rodents (Rosenzweig & Winakur, 1969; Rosenzweig & Sterner, 1970; Brown, 1973, 1975; Brown & Lieberman, 1973). Rosenzweig & Winakur (1969) found little correlation between rodent species diversity and plant species diversity, but they did not attempt to evaluate the effects of precipitation or productivity upon rodent diversity. Rather, to account for observed patterns of rodent diversity, they constructed an index of habitat complexity that includes both various edaphic factors and aspects of vegetation structure.

Working with many of the same species of rodents on other study areas, Brown (1973, 1975) found that rodent species density was strongly correlated with both average annual precipitation and with the predictable amount of annual rainfall, as measured by the mean precipitation minus the standard deviation (Fig. 10.6). Hence, in these desert habitats the number of mammal species increases with increasing precipitation, even though on a more global scale (see Fig. 10.5 and above) mammal species richness decreases as precipitation increases.

Since local species density measures primarily the within-habitat component of diversity whereas total species density on a more global scale includes both the within-habitat and the between-habitat components, these contrasting results suggest that between-habitat turnover in mammal species must be greater in arid regions than in more mesic areas. (Note, however, that these patterns could merely reflect the extent to which average annual precipitation is inversely correlated with topographic relief and the resulting greater diversity of habitats per unit area.)

Larger species of heteromyid rodents husk seeds faster than smaller

## Diversity and niche structure

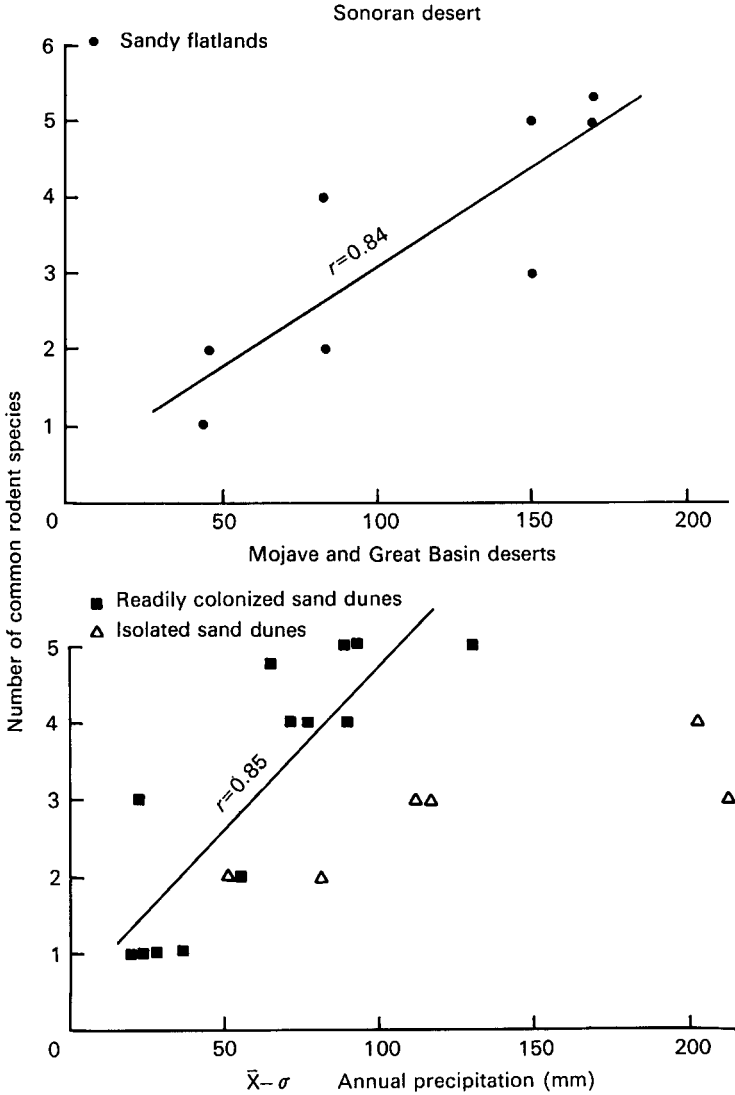


Fig. 10.6. Two plots of number of rodent species against the difference between the mean and the standard deviation in annual precipitation, which is a measure of the annual amount of predictable precipitation and productivity. (From Brown, 1975.)

ones, but smaller animals probably extract more energy per unit expenditure and should therefore have a competitive advantage in seed-husking ability (Rosenzweig & Sterner, 1970). These authors also indicate that seed selection is of dubious significance among coexisting heteromyids. Brown & Lieberman (1973) and Brown (1975), however, demonstrate that dif-

## *Component processes*

ferent species of seed-eating desert rodents clearly partition seed resources by differentially harvesting seeds of various sizes and in different locations. Larger species tend to harvest more large seeds and various species forage at differing characteristic distances from desert shrubs. More productive habitats support a higher number of rodent species and niche overlap is greater. Brown & Lieberman (1973) interpret their results as demonstrating that species with similar resource utilization patterns can coexist in productive habitats thus promoting high diversity. They argue that ecologically similar species are excluded in less productive areas leading to lower diversity. Brown (1975) states that these rodents utilize an exceptionally wide range of seed sizes where, for historical reasons (biogeographic barriers), they occur in the absence of close competitors.

Actual evapotranspiration is strongly correlated with net above-ground primary productivity (Rosenzweig, 1968*a*). Using a partial correlation analysis to examine factors influencing body size of mammalian carnivores, Rosenzweig (1968*b*) found that actual evapotranspiration was a good predictor of body size in areas of low productivity such as deserts and tundra; moreover, these correlations persisted when the effects of latitude were held constant by partial correlation. Rosenzweig interpreted these results as indicating that body size of carnivorous mammals is limited by prey availability.

## *Birds*

Cook (1969) analyzed species density of North American birds using 245 km square quadrats and found that the latitudinal gradient in bird species density is more pronounced than in mammals. Within the continental United States, bird species density is inversely correlated with long-term mean annual precipitation ( $r = -0.64$ ,  $P < 0.001$ ) and average annual actual evapotranspiration ( $r = -0.58$ ,  $P < 0.001$ ), which themselves are strongly correlated ( $r = 0.88$ ) (Pianka, 1978). Thus birds follow the mammalian pattern.

In many (probably most) bird communities, bird species diversity is strongly correlated with foliage height diversity (MacArthur & MacArthur, 1961; Recher, 1969; Cody, 1970; Pianka & Huey, 1971). However, both MacArthur (1964) and Tomoff (1974) point out that species diversity of breeding birds in the succulent-rich Sonoran desert correlates rather poorly with foliage height diversity; Tomoff (1974) argues that particular plant life forms, especially various cacti, strongly influence bird species present at a particular site because of their importance as nest sites.

Cody (1974) studied the niche relationships and species diversity of eleven bird communities, including two on desert areas (Mojave and Sonoran deserts). Among the sites he studied, the two desert areas

## *Diversity and niche structure*

supported an intermediate number of bird species (12 and 16, compared to a range of 5–20 on other areas). Bird species diversity on the desert sites was also intermediate (2.03 and 2.66, compared to a mean on non-desert areas of 2.03 with a range of 1.34–2.71). Within North America (8 sites), his two desert areas had low productivities (as measured by estimated actual evapotranspiration values of 177 and 291) when compared to six non-desert sites (mean is 353, range 275–473). Variance in rainfall during the breeding season was low on the desert sites (0.154 and 0.541; mean of non-desert areas is 0.913, range 0.099–2.036).

Habitat niche breadths increase with climatic predictability and tend to be slightly broader in desert birds than in non-desert species (see Fig. 29 in Cody, 1974). Cody found high niche overlap in bird communities on areas of high climatic predictability (low rainfall variability) including both desert communities and several non-desert ones. Habitat overlap tended to be lower in non-desert communities with less predictable climates. Cody's results do not suggest any fundamental differences between avian community structure in desert versus non-desert areas.

Independently-evolved desert avifaunas may differ in community structure; comparison of the niche structure and community organization of desert birds in Australia with the Kalahari desert of southern Africa shows some fundamental differences (Pianka & Huey, 1971). Compared with the Australian deserts, the Kalahari supports proportionately more species of ground carnivores, fewer arboreal species, but about the same number of ground herbivore species (Table 10.1). Lein (1972) has also noted some trophic differences between avifaunas of the different faunal regions, and emphasized the paucity of ground-feeding insectivorous birds in the Australian biogeographic region. Cody (1973, 1974) makes a case for convergence in both ecology and diversity between avifaunas of chaparral and matorral habitats in Chile and California, both areas with mediterranean-type climates.

### *Amphibians and reptiles, especially lizards*

Kiester (1971) constructed species density maps for amphibians and reptiles in the continental US. As might be anticipated, amphibian species density is low in dry areas and correlates relatively well with average annual precipitation (see also Terentev, 1963, for a similar result from the Soviet Union). Species densities of both amphibians and reptiles show marked latitudinal gradients (Kiester, 1971). Within the continental United States, reptile species density is positively correlated with sunfall (Fig. 10.7) and *inversely* correlated with bird species density (Fig. 10.8) (Pianka, 1978). Moreover, reptile species density is positively correlated with long-term mean annual precipitation ( $r = 0.33$ ) and average annual actual

Table 10.1. The numbers of species of birds (N) in each of four niche categories are listed for nine Kalahari study areas and for eight structurally similar areas in the Western Australian desert. Percentages are given in parentheses. The two right-hand columns give the overall percentage of carnivorous and arboreal species

N	Ground herbivores	Ground carnivores	Arboreal herbivores	Arboreal carnivores	Percentage carnivorous	Percentage arboreal
			Kalahari			
15	4.0 (27)	7.0 (47)	0.0 (0)	4.0 (27)	(73.2)	(26.7)
16	5.5 (34)	6.5 (41)	0.0 (0)	4.0 (25)	(65.6)	(25.0)
16	5.5 (34)	4.5 (28)	0.0 (0)	6.0 (38)	(65.6)	(37.5)
16	5.5 (34)	5.5 (34)	0.0 (0)	5.0 (31)	(65.6)	(31.2)
19	5.5 (29)	6.0 (32)	0.0 (0)	7.5 (40)	(71.0)	(39.4)
21	6.5 (31)	6.5 (31)	1.0 (5)	7.0 (33)	(64.3)	(38.1)
29	6.8 (23)	8.7 (30)	1.8 (6)	11.7 (40)	(70.7)	(46.6)
33	8.3 (25)	9.7 (29)	0.3 (1)	14.7 (45)	(74.2)	(45.4)
40	7.3 (18)	11.7 (29)	2.8 (7)	18.2 (46)	(75.0)	(52.4)
Means	6.1 (28)	7.3 (34)	0.7 (2)	8.7 (36)	(69.5)	(38.0)
			Australia			
15	6.2 (41)	3.8 (25)	0.0 (0)	5.0 (33)	(58.6)	(33.3)
16	4.2 (26)	2.8 (18)	0.0 (0)	9.0 (56) <sup>(1)</sup>	(73.8) <sup>(1)</sup>	(56.2) <sup>(1)</sup>
28	7.3 (26)	5.7 (20)	2.3 (8)	12.7 (45)	(65.6)	(53.4)
28	7.0 (25)	5.5 (20)	2.3 (8)	13.2 (47)	(66.8)	(55.3)
30	8.2 (27)	4.8 (16)	2.0 (7)	15.0 (50)	(66.3)	(56.6)
31	9.2 (30)	5.8 (19)	2.8 (9)	13.2 (43)	(61.2)	(51.9)
31	7.8 (25)	4.7 (15)	3.0 (10)	15.5 (50)	(65.1)	(59.6)
33	9.2 (28)	5.3 (16)	3.3 (10)	15.2 (46)	(62.2)	(56.0)
Means	7.4 (29)	4.8 (18)	2.0 (7)	12.4 (46)	(64.9)	(52.7)

<sup>(1)</sup> Probably an overestimate.

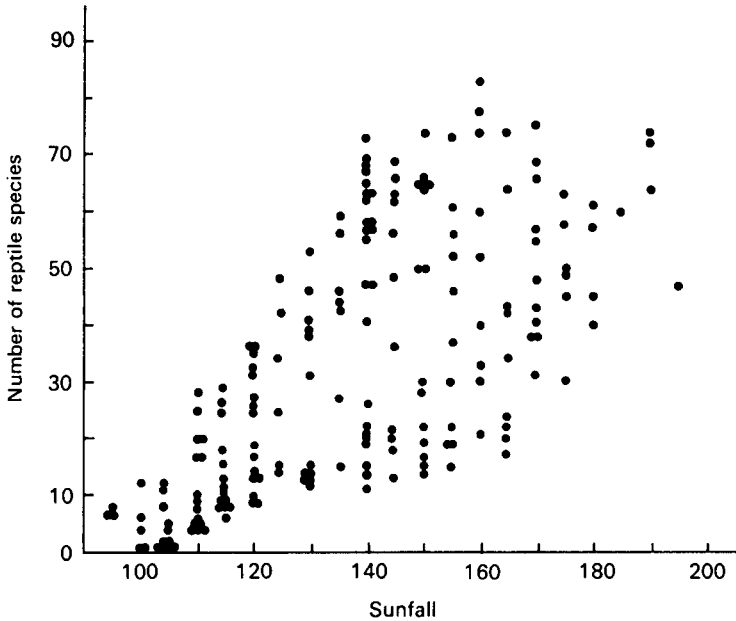


Fig. 10.7. Number of reptile species plotted against sunfall in kilocalories per square meter per year for 193 quadrates in the continental United States ( $r=0.66$ ,  $P<0.001$ ). (From Pianka, 1978.)

evapotranspiration ( $r=0.45$ ), in contrast to the numbers of species of mammals and birds, both of which are inversely correlated with average annual precipitation and actual evapotranspiration (see above and Pianka, 1978). The correlations between reptile species density and annual precipitation and actual evapotranspiration are greatly improved by partial correlation holding constant the effects of sunfall on reptile species density ( $r_{xy.z} = 0.76$  and  $0.73$ , respectively). Evidently, physical factors regulating reptile diversity differ from those influencing avian and mammalian diversity (for a more detailed analysis see Schall & Pianka, 1978).

Over the last decade I have studied the niche relations and species diversity of desert lizards in some detail (see, for example, Pianka, 1966, 1967, 1969 *a*, 1969 *b*, 1971, 1973, 1974, 1975). Some 32 desert study sites at similar latitudes on three continents (North America, southern Africa, and Western Australia) support from 4 to 40 sympatric species of lizards. Below I limit discussion to numbers of lizard species because species diversity is very strongly correlated with species density ( $r=0.84$ ,  $P<0.001$ ); hence similar results would emerge from analysis of species diversity.

Although the study sites on the three continents have evolved independently of one another, presumably in response to similar selective

Component processes

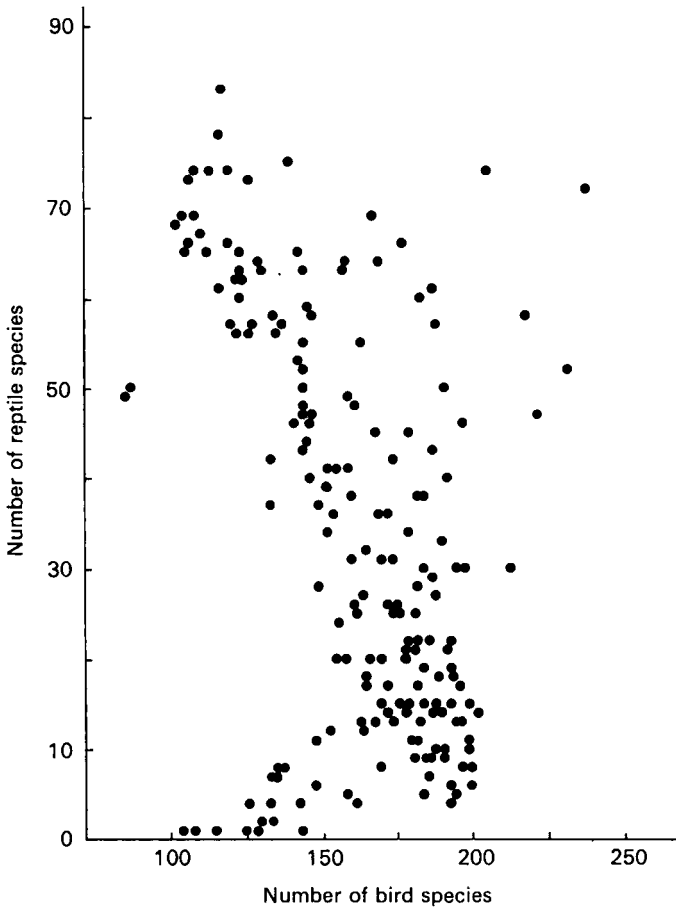


Fig. 10.8. Plot of number of reptile species versus number of bird species for the continental United States. The weak inverse correlation is statistically significant ( $r = -0.397$ ,  $P < 0.01$ ). (From Pianka, 1978.)

pressures, there are striking differences between continents in the diversity, composition, and structure of their lizard communities (Pianka, 1973, 1975). Different sites within North America support between 4 and 11 sympatric species of lizards (Pianka, 1966, 1967, 1975). In the Kalahari desert of southern Africa, from 11 to 18 lizard species occur together on any given study area (Pianka, 1971). The richest known saurofaunas occur in the Great Victoria desert of Western Australia, where as many as 18–40 lizard species are found in sympatry (Pianka, 1969a, 1969b, 1973, 1975).

Lizard species density is significantly correlated with both long-term mean annual precipitation ( $r = 0.42$ ,  $P < 0.05$ ) and the standard deviation in annual precipitation ( $r = 0.68$ ,  $P < 0.001$ ). The latter correlation remains



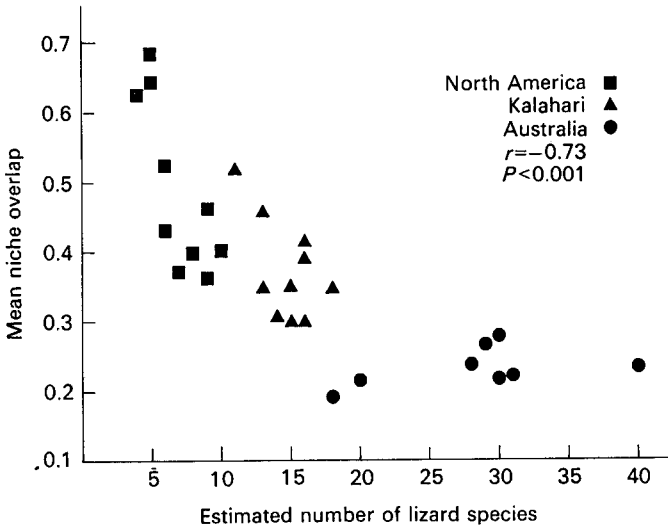


Fig. 10.9. Average niche overlap plotted against the number of lizard species on twenty-eight desert study areas on three continents. (From Pianka, 1974.)

significant ( $r = 0.54$ ,  $P < 0.01$ ) after partial correlation is used to hold constant the effects of long-term mean precipitation (however, the former correlation between lizard species density and long-term mean precipitation disappears when the standard deviation in precipitation is held constant by partial correlation).

Detailed analyses of the niche relationships of desert lizards in these saurofaunas (Pianka, 1973, 1974, 1975) show that average niche breadth does not vary markedly or consistently with numbers of species; however, niche overlap decreases as lizard species density increases (Fig. 10.9). Hence the number of coexisting lizard species in diverse lizard faunas is not facilitated by increased overlap, but rather reduced niche overlap contributes negatively to diversity. Niche overlap also varies inversely with standard deviation in annual precipitation (Pianka, 1974, 1975), but this correlation vanishes when the number of lizard species is held constant by partial correlation.

The relative importance of various niche dimensions in separating niches differs among continents. Food is a major dimension separating niches of North American lizards, whereas in the Kalahari, niche separation is slight on the trophic dimension and differences in microhabitat and time of activity are considerable. All three niche dimensions separate niches rather more equally in Australia. Resource diversity appears to be the major factor promoting differences in lizard species density within and between continents (Pianka, 1973, 1975).

Various historical phenomena have pronounced effects upon the struc-

## Component processes

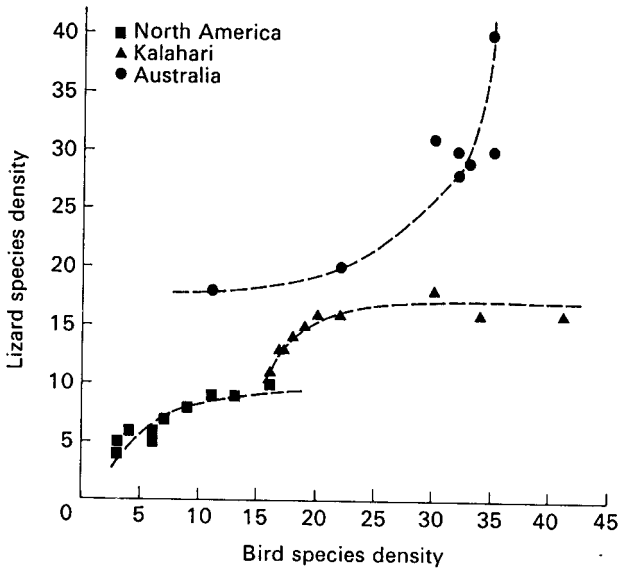


Fig. 10.10. Number of lizard species plotted against the number of bird species on twenty-eight desert study areas. Lizards increase faster than birds in Australia, whereas the reverse is true in North America and the Kalahari, where there appears to be a distinct upper limit on the number of lizard species. (From Pianka, 1975.)

ture of independently-evolved desert communities; historical differences in the interactions between taxa can profoundly influence the niche relationships of component species. Some such interactions between taxa are quite evident while others can be exceedingly subtle. Part of the difference between the Kalahari and Australian deserts in numbers of lizard species can be attributed to differences in their avifaunas (Table 10.1). Thus, the reduced numbers of species of ground-foraging carnivorous birds in Australia may be a factor allowing increased lizard species density on that continent (Fig. 10.10). A more complete analysis of community structure that included both lizards and birds might be very revealing. As indicated above, Australian desert lizards have also usurped some of the ecological roles played by other taxa on other continents, including mammals, snakes, and perhaps some predatory arthropods (Pianka, 1969a, 1973, 1975). However, these mammal-like and snake-like lizard species contribute at most only a few species to the saurofauna of any particular area. Thus there are many more species of 'lizard-like' lizards in the Australian deserts. The influence of some historical differences remains obscure: for example, termites constitute some 40% of the diet by volume of Kalahari lizards, whereas they represent only about 16% of the total food eaten by lizards in North America and Australia (Pianka, 1973).

## Conclusions

While the above very brief review of various empirical studies on just five major taxa is far from exhaustive, it clearly suggests major differences among these organismic groups in the factors influencing their niche structure and diversity. Moreover, reciprocal niche relations and interactions between taxa can play subtle, but sometimes profound, roles in shaping community structure. Whittaker (1975) emphasizes that different environmental factors influence diversity in different plant and animal groups; he concludes that species diversity of communities is an interesting property to observe and attempt to interpret, but that diversity is seldom really very predictable.

Few, if any, generalizations about diversity and niche structure in desert communities seem possible at present, but future studies on community structure and function could ultimately produce some general principles of community organization that might allow some such generalizations about desert communities.

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