

# 8

## Unified Framework I *Interspecific Interactions and Species Diversity in Drylands*

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The goal of this chapter is to delineate how abiotic conditions, regional processes, and species interactions influence species diversity at local scales in drylands. There is a very rich literature that bears on this topic, but here we focus on mechanisms that promote or constrain local diversity and ask how these factors apply to deserts. We ask, “What is different about deserts, relative to other habitats, in their patterns of diversity, temporal variability in productivity, and spatial heterogeneity?” We assess how such differences might modify extant theory, and sketch relevant examples. Compared with other biomes, productivity, population densities, and community biomass are much lower in deserts, and temporal heterogeneity is typically higher. Do these differences imply distinct ecological processes and patterns in deserts? Or, do processes operate in deserts in similar ways as in tropical forests or grasslands? For example, it is often assumed that abiotic factors are more important in deserts. If so, how do abiotic factors modify biotic interactions? How do we integrate physical and biotic interactions? More generally, we ask what should be the main goals and approaches of a research program to understand the role of species

interactions in determining community structure in drylands, as modified by abiotic factors and regional processes.

## What Is Different About Drylands?

### *Relative Diversity of Deserts*

Deserts are traditionally perceived as relatively simple ecosystems harboring low species diversity. Yet increasing evidence suggests that desert communities can be highly diverse and complex. To our knowledge the only systematic analysis of the relative diversity in desert versus nondesert communities was compiled by Polis (1991a). These data suggest that patterns differ widely among taxonomic groups. In some cases, deserts support high diversity, comparable to or even higher than nonarid areas (see Polis 1991b). For example, while avian (Wiens 1991) and anuran (Woodward and Mitchell 1991) diversities are low compared with other biomes, desert annual plants show extremely high species diversity (Inouye 1991). Ants, succulent plants, lizards, scorpions, and tenebrionid beetles also have relatively high diversity in deserts (Polis 1991a–c, Wiens 1991). But, while very high diversity may occur, local diversity varies greatly in space and time (e.g., ants and annual plants: Danin 1977, Inouye 1991, MacKay 1991). We suggest that deserts lie somewhere in the middle of the spectrum of diversity among biomes of the world, rather than at one extreme as often assumed (Polis 1991a–c).

One theme in desert research has been to emphasize clines of diversity along physical and “aridity” gradients. Different patterns may result from the fact that studies compare different taxa, scales, and ecological regions. Studies focusing on trends in species diversity across physical gradients differ in the type of gradient compared. In some cases, precipitation gradients (e.g., birds; MacKay 1991) are studied. Some workers even compare latitudinal clines or a combination of these factors (Ricklefs and Schluter 1993). Thus, conclusions derived as to general patterns of arid-land species diversity may differ depending on the taxon, geographical area, scale (Rosenzweig 1995), and the particular gradient examined. However, in most cases, species richness was not constant across the aridity gradient. In some systems, species richness declines with aridity (e.g., birds), whereas in others, diversity increases (e.g., scorpions).

### *Important Characteristics of Deserts that Affect Diversity*

1. *Low productivity.* By definition drylands differ from other biomes in having low annual precipitation (100–250 mm/year) or net negative evapotranspiration (Polis 1991a). Moreover, desert soils are often nutrient-poor (Anderson and Polis 1999). Low water and nutrient availability translates into very low annual net primary productivity (ANPP averages 5–200 g/m<sup>2</sup>/yr) (Lieth 1978).

2. *Temporal variability.* In addition to being unproductive on average, deserts are also the most variable biome in temperature, precipitation, and productivity (Polis 1991a). Annual variation in precipitation is inversely related to mean precipitation, so interannual variation (unpredictability) in rainfall is higher in arid regions than in biomes with higher annual precipitation (Polis and Yamashita 1991, Polis et al. in press). Annual rainfall may vary by 1–2 orders of magnitude in deserts (e.g., southern California: 34mm–301 mm, Polis and Farley 1980; the Namib: 2.2–134 mm, Seely and Louw 1980; Baja California 0–10 mm in dry years to 150–280 mm in El Niño years, Polis et al. 1997a). Productivity mirrors precipitation during these periods (Seely and Louw 1980, Noy-Meir 1981). For example, the standing biomass in the Namib increased 600–900% (plants and animals respectively) after heavy rains following a 13-year dry period (Seely and Louw 1980). Above-ground ANPP varied by about 20 times between years in the Chihuahuan desert (Ludwig 1986) and 5–43 times on desert islands in the Gulf of California (Polis et al. 1998). Great variation in rainfall drives variation in productivity (Ludwig 1986, 1987) and community structure (see below). Extreme precipitation events (e.g., due to El Niño events) may exert more influence on community composition and ecosystem patterns and processes than do “mean” conditions (Noy-Meir 1973, 1974, Ludwig 1986, Hobbs and Mooney 1995).

Longer term changes in precipitation (at scales from 10 to  $10^6$  years) also occur. For example, American rain-shadow deserts were produced from more mesic areas during orogenic events that built the Andes and Sierra Nevada Mountains. Large parts of the southwestern deserts of North America were under great lakes as little as 10,000–12,000 years ago (Benson and Thompson 1987). Temporal heterogeneity at geological scales could exert strong historical influences. Desert biota probably experience relatively rapid change in patterns of distribution and abundance during wet–dry cycles.

We posit that low mean productivity in deserts may be less important to diversity and species interactions than is high variance in productivity. That is, we speculate that chronic low productivity is more easily accommodated by evolutionary adaptation than is unpredictability in production (Polis 1991a, Wiens 1991). Temporal differences in productivity occur at many different scales and significantly influence communities (Wiens et al. 1986, Giller and Gee 1987, Kotler and Brown 1988, Polis 1991a, Polis et al. 1996). Attempting to elucidate the consequences of temporal variation is one of the most challenging, least resolved, but most important tasks of community ecology.

3. *Spatial heterogeneity.* Deserts have also been postulated to be more spatially heterogeneous than more mesic environments (Crawford 1986). However, unlike temporal heterogeneity, we are not aware of quantitative comparisons of spatial heterogeneity of deserts with other environments except for information on foliage height diversity (Cody 1974). Comprehensive assessments of spatial diversity that include vegetation,

edaphic, and geological characteristics would be a difficult, but important, endeavor.

There seem to be two main lines of reasoning underlying this generalization, both incorporating feedback processes that reinforce heterogeneity over time. First, the paucity of plant cover implies that soil is not well developed. Heterogeneity in the physical nature of the substrate (e.g., rock outcrops, gravel beds, coarse sand, or fine dust) is thus exposed at the surface (rather than buried under soil horizons that may be relatively more uniform in texture, as in more mesic biomes). Surface substrata may differ drastically in water infiltration properties and nutrient storage, and therefore in their potential for plant growth and animal activities. This heterogeneity is reinforced in a positive feedback because of the patterns of run-off of water after rains (Noy-Meir 1981, Yair and Shachak 1987). Run-off sources (e.g., smooth rock, bare soil with a crust) contribute incident water to patches with higher infiltration rate, further increasing soil development in run-on sites (Shachak et al. 1998).

Second, the sparse plant cover in drylands causes strong contrasts between local areas where plants occur, and areas where they do not. The “islands of fertility” around individual plants are due to multiple processes that lead to long-term improvements in soil conditions under plants. By forming wind barriers, plants collect finer soil particles and organic debris and add their own litter, thereby increasing nutrient availability. The presence of relatively impermeable plant crusts (lichens, blue-green algae) on bare soil between shrubs provides further horizontal redistribution of water and other materials; crusts lead to run-off, and shrubs collect run-on water, debris, and seeds. These processes increase water infiltration, which further increases microbial activity and nutrient availability. Besides soil modification, the presence of adult plants modifies animal activities, for example, by concentrating burrows or animal urine and feces under plants. These activities again reinforce the initial heterogeneity that facilitated the plant’s presence.

Thus, “hot spots” of relatively high primary productivity and biological activity juxtaposed to very unproductive interplant areas characterize deserts. Enriched soils and associated plants, in turn, often cascade to exert strong facilitative effects on other organisms. Two general positive effects arise from plants—a trophic effect from their productivity and a refuge effect from their presence in the physical environment. First, plant production travels up the food web to affect secondary productivity and the distribution and abundance of heterotrophs (Noy-Meir 1985, Polis 1999). For example, some desert shrubs support a high diversity of herbivorous insects (Wisdom 1991); in turn, invertebrate predators are attracted to these areas: 26 spider species occur on creosote (*Larrea divaricata*) and more than 25 species on saltbush (*Atriplex canescens*) (Polis and Yamashita 1991). Second, many small animals use plants as refuges from both harsh abiotic conditions and from larger predators. For example, Ayal and Merkl (1994) found that large tenebrionid beetle species were most abundant in habitats with high shrub cover, where they were protected from predatory birds (Groner and Ayal 2001). Ayal et al.

(chapter 2) suggest that this pattern may hold for most detritivores and small herbivores in drylands, and that the structural role of plant cover may outweigh the trophic effect of plants in determining dryland food webs. Kotler (1984) has documented the role of shrubs as patches of refuge from predators.

Other biotic processes likewise increase spatial heterogeneity. For example, many desert plants secrete salt and increase soil salinity around their canopies (Liphshitz and Waisel 1982). Animal activity such as burrowing (ants, termites, isopods) change soil properties by increasing water absorption, and adding nutrients through secretion (Crawford 1986). Abandoned burrows serve as refuges for small animals (Heth 1991). Termites increase local decomposition rate by burying dry plant material in their burrows, whereas ants concentrate seeds of their food plants in their nests (Whitford 1991). The crested porcupine is very effective in increasing spatial heterogeneity in the Negev Desert in Israel as a result of digging activity while feeding on underground storage organs of plants. Its diggings trap both water and organic material, creating better germination sites for many species (Alkon and Olsvig-Whittaker 1989, Boeken et al. 1995). We are uncertain if these biotic facilitations are more or less important in deserts, compared with more mesic systems.

However, it is important to note that some types of spatial heterogeneity are less prominent in deserts. In particular, foliage height diversity in deserts is low. Consequently, whatever effects such architecture exerts on community characteristics (e.g., increasing bird diversity by providing more spatial niches; Cody 1974) must be less important in deserts.

While we have postulated that spatial heterogeneity in soil and geological properties is likely greater in drylands than in more mesic closed-cover plant communities, edaphic conditions and sometimes plant composition in these other communities can also be highly heterogeneous. Nevertheless, we argue that the contrast between sites with no plants at all and some plants—as is found in arid systems—is more dramatic and consequential for the lives of other organisms. As discussed in much of the rest of this chapter, this hypothesized higher spatial heterogeneity in more arid environments could have many important consequences for species interactions, population dynamics, and community structure (chapter 12). With the advent of remote sensing, geostatistics, and other techniques of spatial analysis, comparable data on spatial heterogeneity is beginning to accumulate. For example, geostatistics have been used to describe the magnitude and scale of spatial heterogeneity in old fields (Robertson et al. 1988) and in agricultural fields (Robertson et al. 1993). As more such data are published, it will be possible to test with rigor the hypothesis that spatial heterogeneity is greater in arid environments.

### ***Consequences of Temporal and Spatial Heterogeneity***

One key aspect of heterogeneity is the temporally unpredictable “feast or famine” nature of primary productivity and food availability in deserts

(Polis 1991a, Polis et al. 1998). Under “bad” conditions, precipitation is low or nonexistent and plants grow little, if at all. In “good” periods of adequate to heavy rains, a relatively luxuriant plant growth may occur. Dramatic changes in productivity stimulated Noy-Meir (1973, 1974) to propose his “pulse-reserve hypothesis” as a paradigm for arid areas. Noy-Meir argues that plants and animals grow and establish reserves (e.g., seeds, tubers, tissue, eggs) during good times; these reserves then maintain the population or individual during interim dry periods.

Several basic features of desert organisms may have evolved in response to unpredictable productivity; for example, life history strategies (Polis and Farley 1980, Louw and Seely 1982, Polis 1991a) and opportunistic diets (Noy-Meir 1974, Brown 1986, Polis 1991c). Differences in life history and trophic opportunism exert great influence on interactions such as competition and predation. For example, opportunistic animals exhibit quick functional responses to prey eruptions/fluctuations but probably cannot tightly regulate particular prey species. Crawford (1986) notes that spatial and temporal patchiness of nutritional reserves in deserts, combined with stochastic arrival of moisture, limit the accuracy of predictions about foraging and the impact of consumers.

Spatial patchiness, temporal variation, and aridity clines create a mix of good and bad periods and habitats. Such variation has several consequences at the community level. Perhaps most important, desert systems should be rather dynamic, nonequilibrium communities. “Hide and seek” dynamics in heterogeneous environments allow for local extinctions followed by recolonization (Taylor 1988). Extinctions may be caused by physical disturbances, competitive exclusion, or mortality from predators or pathogens. For example, areas of relatively high productivity (e.g., run-off areas) can serve as refugia in times of severe drought (Noy-Meir 1981). Heterogeneity allows persistence and coexistence among species that are engaged in interactions that could otherwise lead to exclusion (Caswell 1978, Taylor 1988). Resource limitation and competition may only occur during periods of “ecological crunches” (Wiens 1977, 1991). Periods between crunches are marked by little or no competition and relaxed selection. Inferior competitors or prey can escape elimination by being distributed in periods or places that are enemy free. Heterogeneity spreads the risk of extinction and increases population persistence by decreasing overall susceptibility to various mortality factors. These processes, permitted by heterogeneity, promote diversity.

Heterogeneity in production between (micro) habitats may also strengthen demographic and trophic interconnections among habitats. High interpatch variability in productivity likely partitions a species’ population into individuals that live in “source” and “sink” habitats (Pulliam 1988). Source habitats produce a net surplus of individuals. Sink habitats are suboptimal areas where populations are not self-sustaining, but persist due to immigration from sources. Similarly, we expect that marked spatial heterogeneity in productivity creates a landscape where consumer-resource and food web interactions in relatively unproductive habitats are strongly affected by subsidies

from productive patches (Polis et al. 1997b). In general, nutrients, detritus, prey, and predators should move primarily from productive to less productive habitats. We speculate that strong demographic and trophic spatial interconnections might occur commonly in the patchy environment of deserts.

Finally, heterogeneity may slow the speed of evolution and the likelihood that species tightly coevolve. The strength of selection is not constant and gene flow may disrupt locally adaptive changes in gene frequency. A tendency toward trophic generalization suggests that interactions may be relatively less tightly coevolved, leading to the organization of exploiter–victim systems or guilds of potential competitors that are more loosely structured, relative to more homogeneous environments.

## Processes Affecting Species Diversity

### *The Relationship Between Regional and Local Diversity*

Viewed over sufficiently long time scales, all local ecological communities arise via colonization from larger regional and biogeographical species pools, filtered by matches between species autecological requirements and local environments, and interspecific interactions such as predation and mutualism (Zobel 1992, Holt 1993, Belyea and Lancaster 1999). Patterns of species diversity, and in particular the relationship of species richness to local environmental factors such as primary productivity or disturbance rates, ultimately reflect the interplay of multiple factors operating at many spatial and temporal scales (Huston 1999). At a local scale, interspecific interactions such as competition, predation, and mutualism (which directly or indirectly require contacts between individuals) can either enhance or depress species richness. At broad spatial scales, speciation, species migration, and regional extinctions influence the size of the species pool available for colonization into a local focal community (Latham and Ricklefs 1993). For example, the great diversity of tenebrionid beetles in the Namib Desert may be attributed to extensive in situ speciation that occurred in this, the oldest of all extant deserts (Seely 1991). Alternatively, younger or isolated deserts may be depauperate in species diversity because regional pools of desert dwellers may be low or there has been little time for speciation.

Species richness at local sites can be viewed as arising from a series of filters relating species pools at large spatial scales to local communities (Zobel 1992). The first stage in explaining diversity at a particular site is simply the size of the regional species pool. All else equal, sites with larger regional pools are likely to have larger local pools—this “filter” is thus a result of biogeographic and evolutionary (speciation and extinction) processes. These processes are important determinants of local diversity (Ricklefs and Schluter 1993), but beyond the scope of this chapter. Instead, we focus on the filters between a given regional species pool and the local community, including abiotic limitations, facilitation, competition, and consumer–resource interactions.

Cornell and Lawton (1992) argued that if local interactions such as competition are important filters limiting membership in local communities, then one should observe a saturating rather than linear relationship on plots relating local to regional richness. Therefore, the observation that linear relationships seem to be the most common result (e.g., Caley and Schluter 1997) suggests that interspecific interactions may not be prime determinants of patterns in local species richness. This conclusion is controversial (Huston 1999), and it is not our goal here to address the various interpretations of these relationships. Rather, we emphasize that most theory and empirical research on species interactions in community ecology has focused on the role of species interactions in explaining patterns *within* a region with the same species pool, that is, the *scatter* around the lines, rather than with the shape of the lines themselves. Thus, overall linear relationships between local and regional richness *across* different regions does not necessarily imply that interactions have no effect on relative richness among sites *within* a region. Instead, interactions could still strongly influence the extent to which local richness deviates (positively or negatively) from the average expected for a given size of regional pool.

It is useful to start with a null hypothesis, which is that local species interactions do not constrain (or facilitate) community membership; instead, abiotic conditions act as the primary filter. We then go on to explore the roles of positive interspecific interactions, competitive interactions, and consumer–resource interactions in determining community membership.

### ***Abiotic and Demographic Filters***

If one views the regional species pool as analogous to a “continent,” and the focal community as an “island,” the classical dynamic model of island biogeography (MacArthur and Wilson 1967) schematically portrays the interplay of regional and local processes in determining species richness and composition. This classical model views local communities as a balance between colonization of new species from the pool, and extinction of resident species. If species are not interacting, by definition the rate of colonization and extinction for any given species should be independent of local community composition. Factors that enhance colonization or lower extinction rates lead to higher local species richness, whereas factors that diminish colonization or aggravate extinction should push down species richness, relative to the size of the species pool.

The first filter between the regional pool and the local community is the match between a species’ basic niche requirements and local site characteristics. In deserts, compared with more moderate biomes, is there a stronger abiotic filter because of harsh conditions, low resources, or greater temporal heterogeneity, resulting in lower diversity? If so, this could result in either higher extinction rates or lower colonization rates (depending on the life stage at which the lack of match of requirements and site characteristics occurs) and xeric sites having fewer and mesic sites more species than the average



expected, given a certain size regional pool. While this idea of a stronger abiotic filter in extreme environments is old and widespread (e.g., Darwin 1859 for extreme deserts, see Parsons 1996 for more recent discussion), it has also been highly controversial because stronger abiotic filters in more stressful environments are often taken to mean weaker impacts of competition and/or facilitation on community structure. However, this is not necessarily the case. The controversy may result from a confusion between the factors that determine whether a species is present/absent in a habitat ("distribution") versus the factors that determine individual fitness and population dynamics of species ("abundance") that can persist in the habitat. For example, it is possible that more species are eliminated from xeric than from mesic sites by physiological intolerance of prevailing conditions (i.e., that abiotic filters are stronger) but those species that are able to persist compete just as intensely among themselves, as do species that cohabit in mesic conditions. Most existing comparisons of effects of species interactions along favorability or stress gradients test the "abundance" effect rather than the "distribution" effect (see below for review) because they compare competitive intensities among species that naturally co-occur within a habitat, rather than effects of competition on species that do not naturally persist in the habitat. To rigorously test the hypothesis that abiotic filters are stronger in more xeric environments, one would have to transplant to a habitat species that normally do not occur there and monitor their demography in the absence of potential competitors/facilitators/predators.

In addition to complete physiological intolerance, abiotic filters potentially involve several other distinct demographic mechanisms that could control colonization and extinction rates and thus local richness for a given regional pool (table 8.1).

First, because deserts have low productivity, many species are expected to be low in abundance, and/or have low maximal growth rates. All else being equal, these demographic factors tend to lower colonization rates into local communities, and enhance local extinction rates. Consider first the effect of low population size. Because of demographic stochasticity, populations with small absolute sizes experience high extinction risk even in favorable environments (Belovsky 1987). If a species has low average abundance in occupied sites, this both reduces the flux of dispersers available for colonizing empty sites, and weakens the "rescue effect" (Brown and Kodric-Brown 1979) in occupied sites. Now consider the effect of low average growth rates. Episodic disturbances can drive species to troughs of low abundance, during which they risk extinction due to demographic stochasticity. Low growth rates lengthen the time period of increased extinction risk. Moreover, chronic mortality factors are more likely to drive species extinct if there is weak compensation with increased growth rates at low densities (e.g., Holt 1985).

As noted above, compared with many other biomes, deserts have greater coefficients of variation in production, as well as low overall levels of production. To be present in a local community there obviously has to be a match between a species' autecological requirements (i.e., its fundamental niche) and

Table 8.1 Summary of potential effects of low productivity and high temporal and spatial heterogeneity on colonization (C) and extinction (E) rates

Characteristic of Drylands	Processes and Phenomena Affected	Effect on Demography
Low productivity	Low abundance → increased importance of demographic stochasticity	↑ E
	Low abundance → fewer dispersing propagules	↑ E
	Low population growth rate → low rate of recovery from disturbance	↓ C
High temporal variability	Populations at risk under rare “crunch” conditions	↑ E
	Selection for high dispersal rates	↑ C**
	Selection for demographic buffering mechanisms (e.g., seed bank)	↓ E**
High spatial variability	Habitat specialists have fewer suitable patches → more at risk in metapopulation scenario	↑ E
	Greater range of environmental conditions → more sink populations	↑ E
	More potential for habitat selection	↓ E**

*Note:* Increased extinction (↑ E) and/or decreased colonization (↓ C) rates would lead to lower species richness in drylands relative to more mesic conditions.

\*\*Effects in the opposite direction, resulting in higher diversity in drylands.

the local environment. In highly variable environments such as deserts, the match between these may be ephemeral, leading to transient and spatially variable matches between niche requirements and local conditions. This could contribute to a high local extinction rate. Even for species that are generally adapted to dryland environments, because of temporal heterogeneity (e.g., occasional exceptionally long bouts between rainfall pulses) there may be enhanced extinction risks. For instance, for an annual plant species without a seed bank, its long-term growth rate is the geometric mean fitness across long time-series of environmental fluctuations. A single year of very low fitness can doom the plant to local extinction, even in an overall favorable environment.

Finally, as also noted above, for some organisms desert environments may be very patchy. Metapopulation models (see Holt 1997) suggest that habitat specialists may have trouble persisting on scarce habitats, unless they have very low extinction rates, or high colonization rates. If desert environments overall are experienced as highly patchy, this effect could lower local species richness.

Given these demographic considerations alone, one expects a lowering of local species richness, because of increased local extinction and decreased local colonization rates, so that deserts would have lowered slopes in regional–local species richness plots. However, a number of factors may mitigate these demographic effects (table 8.1). For instance, the colonization rate of

empty sites does not vary simply with the abundance of a species in those sites it occupies. Colonization rate is likely to increase with an increasing per-capita propensity to disperse, and with an increasing probability of successfully traversing unsuitable landscapes separating habitable sites. As noted earlier, temporal variability that is often weakly correlated in space is a hallmark of desert ecosystems. Evolutionary theories of dispersal suggest that such patterns of spatiotemporal variability tend to favor increased per-capita rates of dispersal (Holt and Barfield 2001, Ronce et al. 2000). If species in desert systems are characteristically strong dispersers, this should tend to enrich local communities by increasing colonization rates. (Many deserts are famous for nomadic behaviors in consumers.) Because plant biomass is low, passive dispersal propagules carried by the wind may also travel much farther before coming to rest due to physical obstruction. We are unaware of studies that specifically quantify dispersal rates of desert species, compared with other biomes.

Furthermore, many adaptations to desert environments obviously mitigate local extinction risks. For plants, such adaptations include seed banks for annuals, and resource storage structures for perennials. Habitat selection by consumers can permit microhabitats of high or stable fitness to be sought out, reducing the risk of local population extinction. Generalist consumers can benefit from their potential use of a wide range of independently varying resources, which buffer extinction risk.

The ideas sketched above suggest that the relationship between local and regional species richness in desert biomes is influenced by many factors, some of which depress diversity, and others which may enhance diversity. The net effect of these factors is unclear. Needed are long-term population studies in deserts that will permit a comparison of local extinction rates with other biomes.

While we have described these demographic processes under the rubric of abiotic filters, because they could operate in the absence of interspecific interactions, they all could be moderated or intensified by interspecific interactions, as described in the next three sections.

### ***Positive Interactions***

Traditional community theory has emphasized how local interspecific interactions make species persistence and coexistence less likely, thus limiting local species richness. In recent years there has been increasing concern with the potential for positive interspecific interactions to influence communities (Bertness and Callaway 1994). Such positive interactions could lead to increasing colonization or decreasing extinction rates with increasing number of species. Can “diversity beget diversity,” and if so, is this process more important in drylands than other biomes? No general theory exists on this theme, so we here outline some initial tentative steps toward a synthesis of facilitation in desert systems.

Examples of positive interactions in drylands abound (see reviews in Callaway 1995). Here we attempt a rough classification of the many distinct mechanisms that have been described to provide a basis for generalizing about their importance in drylands relative to more mesic environments. As with any classification, the categories are not entirely discrete and our assignments are often ambiguous. Nevertheless, it provides a heuristic value in allowing hypotheses to be developed about classes of mechanisms. The most general distinction is between trophic interactions (those mediated entirely through effects on consumable resources) and nontrophic interactions (not mediated through effects on consumable resources). Nontrophic positive interactions are very similar in definition to ecosystem engineering as defined by Jones et al. (1994, 1997), although they emphasize that engineering can have negative influences as well on some species. We prefer the terminology of nontrophic interactions to emphasize the contrast, and allow further parallel classifications within trophic and nontrophic types of interactions. Within each of these categories, we can further divide mechanisms of positive interactions into direct (no intermediary involved) and indirect (either abundance- or trait-mediated) interactions. Here we focus on two of the possible types of positive interactions: those in which organisms facilitate other organisms in ways other than providing food (nontrophic facilitations, such as habitat amelioration and habitat creation); and those in which organisms indirectly facilitate other organisms by reducing the probability of their becoming food through predation by a third group of organisms (trophic indirect facilitation). Below, we give examples of each of these and review ideas and evidence about how they are expected to vary in xeric relative to mesic environments. The remaining category, trophic direct facilitations, is simply the consumer side of consumer–resource interactions (i.e., the plus side of a  $+/-$  interaction).

For *nontrophic direct facilitations*, the best-documented class of examples in drylands is probably *habitat amelioration*, defined broadly as when organisms improve the physical habitat in terms of resource availability and/or amelioration of stress in some way that benefits other organisms. In plants, this is often more narrowly referred to as “nursing” or the “nurse plant phenomenon” because the facilitator is often an adult, while the facilitatee is often a juvenile (see Callaway 1995, Callaway and Walker 1997 for comprehensive reviews). For example, larger individuals of sessile species can reduce temperatures due to their shading effect—reducing direct negative effects of high temperature and increasing water availability and decreasing water demand (reviewed in Holmgren et al. 1997). Another example is the “island of fertility,” where isolated plants trap organic matter and gradually increase local nutrient supply for other, usually smaller, plants (e.g., Garcia-Moya and McKell 1970). Both of these processes in plants can benefit animals as well. Another class of examples of nontrophic direct facilitation is *habitat creation*, or the creation of new structures by organisms (allogenic ecosystem engineering, *sensu* Jones et al. 1994). These are also well-documented in drylands, for example, increased bird diversity with increased plant structural diversity (Cody 1993) and the favorable germination sites in pits

created by porcupine diggings (Gutterman 1982). *Nontrophic indirect facilitations* would be more complex examples in which these effects propagate through links of other species. For example, a shrub that casts shade might facilitate burrowing activities by rodents, in turn modifying growth conditions for seedlings of other plant species.

Facilitation through habitat amelioration has been argued to be more common in less productive environments (Bertness and Callaway 1994). In demographic terms, that means the presence of organisms should decrease extinction rates or increase colonization rates more strongly in less productive environments. We suggest that facilitation through microhabitat creation is also more common in less productive habitats and that the reason is similar for both mechanisms: in an extremely unfavorable habitat or a site with no suitable habitat at all, even a small improvement in absolute terms makes a large percentage improvement (Bertness and Callaway 1994). A specific model developing this basic argument was presented for nurse plants in drylands by Holmgren et al. (1997). However, Jones et al. (1997) have argued that habitat creation may be more important in environments with extensive plant cover, abundant large animals, and dominant organisms with massive and persistent structures—characteristics of more, rather than less, productive ecosystems. Although previous workers have not always clearly separated effects of habitat creation and habitat amelioration, narrative reviews of facilitation support the idea that nontrophic direct facilitative effects are more common in unproductive environments in plants (Callaway and Walker 1997, Holmgren et al. 1997).

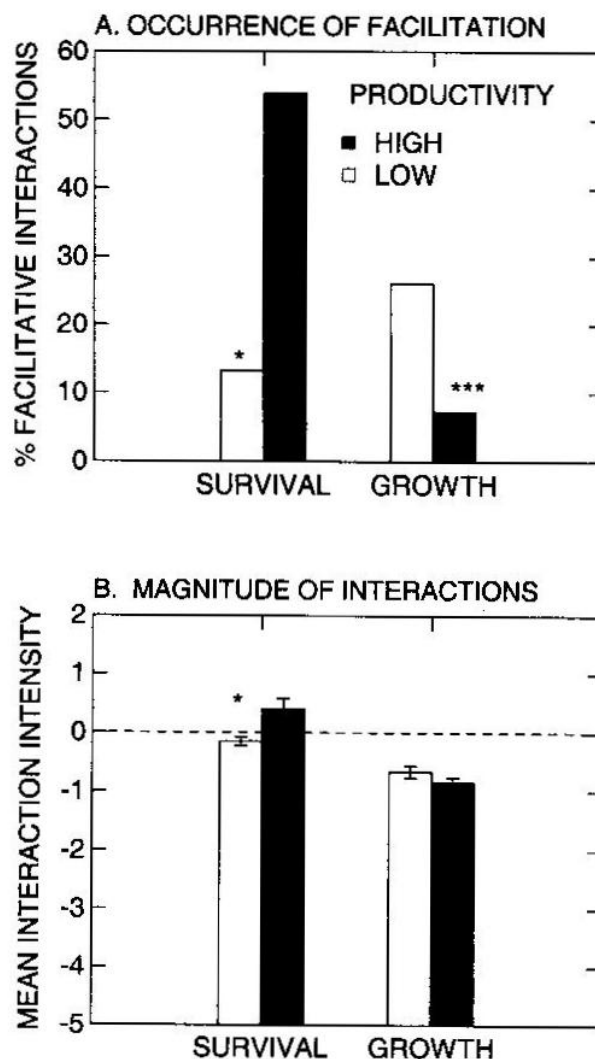
The simplest example of *direct facilitation in trophic interactions* is for a consumer to have a “donor-controlled” relation with its resource population (DeAngelis 1992). This generates the potential for asymmetrical facilitation, given that the consumer clearly requires the resource population to persist, but without reciprocal dependency. This diversity-generating mechanism is usually thought of as operating through chains of specialist consumers, i.e., a greater diversity of resources can support a greater diversity of consumers while keeping degree of resource overlap constant. However, it may be more likely to operate through generalist consumers because of bet-hedging or portfolio effects; if each of various resource populations responds in a species-specific fashion to environmental variability, a generalist consumer may be able to survive in situations where a specialist on any given resource risks extinction. Ritchie (1999) recently observed this effect of trophic generalization on extinction risk for a dryland herbivore (prairie dogs). The higher risk of extinction of trophic specialists should be exaggerated, given chains of trophic specialization (e.g., a specialist herbivore on a single plant species, supporting a specialist parasitoid, supporting in turn a specialist hyperparasitoid; see Holt et al. 1999). The bet-hedging advantage of trophic generalization should be especially important when resource populations are low in average abundance and strongly variable through time. Thus, we expect specialist consumers to be less common in deserts than in other biomes, particularly at higher trophic levels. Diversity at low trophic ranks can

facilitate diversity at higher trophic ranks via the buffering effects of trophic generalization. This advantage of trophic generalization in turn implies that desert food webs are likely to be highly reticulate.

There may also be occasional positive top-down effects upon species richness at low trophic levels. For instance, in situations where competitive exclusion might occur at low trophic ranks (e.g., strong resource competition among rodent species), the scarcity of cover in drylands (chapter 2) could magnify the effect of predators, which in turn can facilitate coexistence (if the more efficient competitor is also more vulnerable to predation, e.g., Kotler 1984).

*Trophic indirect facilitations* include both predator- and competitor-mediated interactions and both trait- and abundance-mediated indirect interactions. In drylands, one documented mechanism is a trait-mediated indirect effect on predator-prey interactions, whereby one group of organisms provides refuges and therefore reduces predation rates on the target organisms. (This can also be regarded as a form of interference, i.e., nontrophic competition from the point of view of the predator). For example, shrubs in drylands often provide refuges from natural enemies for other plants (e.g., Fuentes et al. 1986), for invertebrate prey species (Ayal and Merkl 1994, Groner and Ayal 2001), and for small mammals (Kotler et al. 1993). Two general hypotheses have been proposed about the importance of indirect facilitation involving refuges. Bertness and Callaway (1994) propose that this type of facilitation is most important at high productivity, consistent with Connell's (1975) much earlier argument that natural enemies are more important at high productivity than at low or intermediate productivity. In contrast, Ayal et al. (chapter 2) have proposed that refuges created by vegetation for herbivores or intermediate predators are much more important at low productivity.

A recent quantitative review (meta-analysis) of the results of field removal experiments in plants (Goldberg et al. 1999) compared the frequency and magnitude of positive interactions along productivity gradients. Because it was impossible to extract information on mechanisms of facilitation from most of the studies, the review tested the total summed effects of habitat amelioration, habitat creation, and provision of refuges, even though these different mechanisms are predicted to change in different ways with productivity. Using the same database as Goldberg et al. (1999), we found a higher frequency of facilitative effects on plants in unproductive environments, consistent with the Bertness and Callaway model for habitat amelioration, but only for growth as the measure of plant response (fig. 8.1, top). In addition, despite this more frequent occurrence of positive interactions, the actual magnitude of interactions (degree to which plants were facilitated or inhibited) did not differ significantly for growth responses to neighbors (fig. 8.1, bottom). This suggests that the competitive interactions that do occur at low productivity tend to be stronger than those at higher productivity, that is, that both extremely strong facilitation and extremely strong competition are more likely in unproductive environments. While this is consistent with the higher



**Figure 8.1** A meta-analysis of the effects of neighbors on growth and survival of plants in low versus high productivity environments, using the database from the summary of published experiments reported in Goldberg et al. (1999). Only herbaceous plants with herbaceous neighbors were included. Productivity was estimated by standing crop with values  $< 350 \text{ g/m}^2$  being considered as “low productivity” and  $> 350 \text{ g/m}^2$  as “high productivity.” Interaction intensity was quantified as  $\ln(\text{performance with neighbors}/\text{performance without neighbors})$ ; values  $> 0$  indicate facilitation and  $< 0$  indicate competition. (A) Percentage of all interactions that were positive. (B) Mean interaction intensity  $\pm 1 \text{ SE}$ .  $N = 15, 13$  for survival at low and high productivity and  $n = 115, 123$  for growth at low and high productivity, respectively.

temporal variability expected for low-productivity arid environments, the data in fig. 8.1 cannot be separated for unproductive environments due to aridity versus those due to low nutrient supply within mesic environments. Even more interesting is the observation that facilitation of survival in plants actually shows the reverse pattern: facilitation was significantly more common in more *productive* sites (fig. 8.1, top). In this case, average interaction

intensity was consistent with the frequency data, with significantly more beneficial interactions at higher productivity (fig. 8.1, bottom). Thus, these results for survival are consistent with the Bertness–Callaway prediction about patterns in refuge provision. It is tempting to speculate that the differences between survival and growth responses to neighbors along productivity gradients is consistent with differing demographic consequences of habitat stress (affecting growth) and predation (affecting survival), but more information on the actual mechanisms of facilitation in unproductive (especially xeric) habitats is needed to evaluate these ideas.

## Negative Interactions

Negative interactions between individuals in the same species and between different species in the same trophic level are pervasive in arid ecosystems, as in other communities (Connell 1983, Schoener 1983, Fowler 1986, Gurevitch et al. 1992). By negative interactions, we include all situations where increased population density, individual growth rate, or per-capita population growth rate causes other individuals to decrease activity, individual, or population growth rates. Negative–negative interactions (i.e., competition) occur when negative effects are reciprocal among individuals from different species (e.g., Schoener 1983, Pimm et al. 1985). Negative interactions between species can constrain biodiversity (Rosenzweig 1978, Connell 1980, Schoener 1983, Holt 1984, Sih et al. 1985).

Negative interactions can be divided into trophic and nontrophic interactions. Trophic interactions are both direct (i.e., cannibalism and intraguild predation) and indirect (e.g., exploitation competition for limiting resources). Intraguild predation is widespread in deserts (Polis et al. 1989). Cannibalism is another negative trophic interaction that is widespread across a diversity of taxa, including many desert species (Polis 1980, 1981, 1991c, Polis and Yamashita 1991). Exploitation competition is common among many desert taxa, including plants and granivorous rodents, birds, and ants (e.g., Fowler 1986, Brown and Lieberman 1973, Brown et al. 1979).

Negative nontrophic interactions include a great variety of interference competition mechanisms such as territoriality, dominance hierarchies, chemical fouling, and allelopathy. Interference and allelopathic interactions have been argued to be wide spread among plant communities (Crawley 1986), though the extent to which these interactions affect community dynamics and biodiversity is unknown. Likewise, territoriality occurs in many desert taxa, such as spiders (Riechert 1991), nectivorous hummingbirds (Brown and Kodric-Brown 1979), and granivorous kangaroo rats.

The exact importance of exploitation competition among desert plants is uncertain. A number of conceptual models predict that abiotic factors are more important than biological interactions such as competition at less favorable or “stressful” ends of gradients (Miller 1967, Kruckeberg 1969, Grime 1973, 1977, Rosenzweig and Abramsky 1986, Keddy 1990, and see Connell



1975, Menge and Sutherland 1987 for variants also incorporating predation). In contrast, other models suggest that competition is important regardless of environmental favorability, although the limiting resource may well change among environments (MacArthur 1972, Newman 1973, Tilman 1988). The prevailing thought has been that competitive interactions are rare or weak in arid ecosystems, especially for plants. The reason for this view was that population densities in deserts are often low, and organisms rarely come into contact to interfere or compete for resources. Moreover, the extreme conditions found in deserts often lead to notable morphological and physiological adaptations that may allow the use of a unique niche. Finally, as aridity increases and productivity falls, conditions for species coexistence often narrow. The typical outcome is competitive exclusion rather than coexistence, so the remaining species may exhibit a lack of competition.

Species may need to possess similar adaptations to cope with arid conditions, either due to a shared phylogenetic history or because the range of potential adaptations is more limited in more extreme conditions. This could force species into recurrent competition. As an example, all annuals must be attuned to episodic rainfall pulses, and so may experience transient spikes of competition for water. However, in theory, niche partitioning could allow competitive coexistence in all but the most extreme cases (Chesson 2000).

There is substantial evidence for strong competition due to exploitation of limiting resources in deserts, including habitat selection behavior among coexisting gerbil species in the Negev Desert (Abramsky et al. 1985, 1990, 1991) and their density-dependent activity times (Mitchell et al. 1990), competition for seeds between ants and rodents in the Sonoran Desert (Brown and Davidson 1977, Brown et al. 1979), and competition among perennial plants along a water gradient (Robberecht et al. 1983, Gurevitch 1986, Eissenstat and Caldwell 1988). Competition tends to constrain local diversity, unless there are mechanisms of coexistence (Tilman and Pacala 1993, Chesson 2000).

Early models predicted that the amounts of limiting resources and physical factors set the maximum number of species that can coexist (see references in Armstrong and McGehee 1980). Current models predict the potential coexistence of more than one species on a single resource (Tilman 1990, Grover 1997). However, a general rule is that robust coexistence requires mutual invasibility: two species can coexist when each can invade a community that consists of its competitors at equilibrium, that is, each can increase when rare. This requires two ingredients. First, there must be an axis of environmental heterogeneity. Second, there must be a tradeoff such that each species has a part of the axis where it is superior to its competitors (Brown 1989, Tilman and Pacala 1993), that is, niche differentiation.

Environmental heterogeneity can occur in space, time, and resource attributes. Common niche axes in deserts include habitat differences based on substrate type, sand versus rock (Shmida and Wilson 1985), or vegetation density (wadi bottom vs. hillside), microhabitat (bush vs. open areas; Brown

and Lieberman 1973, Rosenzweig 1973, Kotler 1984), temporal resource variation (Kotler et al. 1993, Ziv et al. 1993), temporal differences in foraging costs due to seasonal activity of predators (Brown 1989), and spatial variation in resource abundance (Brown 1989). Water has a role in most of these.

It is not clear if there are distinctive tradeoffs common in deserts that are rare in other biomes. However, the openness of the desert environment does lead to large spatial heterogeneity in predation risk (Ayal et al., chapter 2), so tradeoffs in competitive abilities in safe habitats and microhabitats versus ability to avoid predators in risky ones clearly contribute to species coexistence (Kotler et al. 1988). Also, extreme variation in precipitation and thus resource availability enhances the importance of tradeoffs in maintenance efficiency (via torpor or life history) to survive between pulses of productivity, versus foraging efficiency to continue to forage profitably even at low resource density. Extreme spatial variability in resource availability promotes tradeoffs in travel and harvest rate versus foraging efficiency (Brown 1989). Tradeoffs of recruitment abilities under different environmental conditions in regards to storage effects may be very important in deserts (Warner and Chesson 1985).

Consider some examples that illustrate these general features of deserts. An example of bush/open microhabitat selection includes the interaction among overwintering sparrows in semiarid grasslands (Pulliam and Mills 1977). Bird species differ in escape abilities, with some bird species being more vulnerable than others away from cover. This can result in coexistence, provided that the most vulnerable species is also the best resource competitor near protective cover. The result is that each species has a microhabitat in which it is superior in competition.

Coexistence on a spatially variable resource occurs between a pair of granivorous rodents in the Sonoran Desert (Brown 1989). Merriam's kangaroo rat (*Dipodomys merriami*) and the roundtailed ground squirrel (*Spermophilus tereticaudus*) coexist in a creosote flat because each can best exploit a different distribution of resource patches. The high travel speed and travel efficiency of the ground squirrel allows it move frequently among patches and to better discover spatially dispersed, rich seed patches; the smaller body size of the kangaroo rat confers a lower overall metabolic cost of foraging and allows it to forage profitably in poorer resource patches than can the ground squirrel.

Coexistence on a temporally variable resource may describe interactions between annual and perennial plants (Shmida and Ellner 1984, Brown 1989). Coexistence is possible between a species superior at maintenance (a species with a low fixed cost of existence that can survive from one peak in resource production to the next) and a foraging efficiency specialist (a species with a low variable cost of foraging that can forage profitable even on relatively depleted resources). Annuals have extremely low costs of existence in their dormant seed stage, while perennials may be able to photosynthesize even when surface moisture is unavailable. Another example may be guilds of pollinators, such as bees, that compete for the daily pulses of nectar (Schaffer et al. 1979).

**Consumer–Resource Interactions (Predators, Pathogens, Parasitoids, Herbivores)**

In strong consumer–resource interactions, one expects a tendency toward instability when the resource itself is a biotic, renewing population. Such instability can lead to population cycles, chaotic dynamics, or localized extinctions. Strong predator–prey interactions certainly exist in desert biomes. However, in contrast to other biomes (e.g., boreal forest), we are unaware of any convincing case of pronounced, regular predator–prey cycles. It is useful to consider some reasons why this pattern (presuming for the sake of argument that it exists) may arise.

Predator–prey cycles tend to be promoted by the conjunction of several factors: (1) high prey productivity (the “paradox of enrichment”); (2) weak direct density-dependence; (3) trophic specialization; (4) temporal and spatial homogeneity. It seems likely that in many desert systems, one or more of these needed ingredients could be lacking. Low productivity systems are ones where by definition resources will be limiting for many species. It thus may be the case that many prey populations in deserts have insufficient basic productivity to sustain predator–prey cycles. As noted above, many consumers have conspicuous interference competition, including cannibalism. Such mechanisms of direct density-dependence dampen consumer responses to changes in prey numbers. There are relatively few detailed food web studies in deserts, but those that have been attempted (e.g., Polis 1991c) reveal that many species are relatively generalized in their diet, and the webs as a whole are highly reticulate. In some circumstances, these factors reduce the likelihood of predator–prey cycles. Finally, spatial heterogeneity at small spatial scales can create refuges, which are broadly stabilizing. Temporal heterogeneity often implies that populations are most limited by “crunch” years of low resource abundance. This weakens the capacity of natural enemies to overexploit their victims during typical years.

McNaughton et al. (1991) have observed that proportionately less primary production goes through herbivory in drylands than in other ecosystems. There are two basic explanations for this, both involving trophic dynamics: (1) a bottom-up explanation emphasizes the role of low overall plant productivity and temporal variability in productivity. Simple resource consumer models (Oksanen et al. 1981) suggest that herbivores persist with difficulty at extremely low productivity and, even if they do persist, it is at low abundances where they consume proportionately less standing crop. This effect is exaggerated by temporal variability in productivity. Strong temporal variation in production leads to consumer populations regulated primarily by food availability in crunch years (Wiens 1977). This implies that in more typical years, there will be fewer herbivores than expected, given ambient production, and therefore total consumption will be proportionately less in highly variable environments in most years (Andrewartha and Birch 1954, 1984). (2) An alternative, top-down explanation is that the low plant cover in drylands

results in greater predation (or at least predation risk) on herbivores and consequently less herbivory (chapters 2 and 4, herein).

We argued above that deserts tend to be dominated by generalist rather than specialist consumers. Numerical and aggregative responses by generalist consumers can put at risk the local persistence of prey populations, particularly of species with low intrinsic growth rates (Holt and Kotler 1987, Holt and Lawton 1994). This observation, taken alone, might suggest that predators will often reduce species richness of their prey in deserts. However, theory suggests that such effects due to apparent competition often decline with decreasing productivity (Holt et al. 1994, Holt 1997). Moreover, given strong temporal variability, the abundance of generalist predators will be set during periods when overall prey abundance is low. Incorporating temporal variability into predator-prey models often reduces average predator abundance (Abrams et al. 1998). For generalist predators with saturating functional responses, in non-“crunch” years a superabundance of prey will be present; alternative prey can then experience indirect mutualism, mediated through the saturated functional response of their shared predator (Holt 1997).

### **A Comment on Desert Food Webs and Diversity**

In the above paragraphs, we have reviewed theory and evidence on pairwise species interactions, emphasizing patterns and processes that are more conspicuous or important in deserts. But all these interactions are of course embedded in species-rich, complex food webs. As noted above, desert food webs often appear to be highly reticulate. In principle, increasing the number of links in food webs can increase the potential for indirect interactions. In practice, the complexity of such linkages can diffuse interactions, making it difficult to discern in empirical studies the net effect of one focal species upon another. The net sign of an interaction is likely to vary as a function of many factors, including the local species composition, habitat heterogeneity, and position along aridity gradients. Rather than review general theory on this topic, or speculate about how this body of theory may or may not bear on desert ecosystems, we simply note that describing and analyzing the dynamics of entire desert food webs is a challenge for future research.

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the current document. In our editing, we have tried to remain faithful to the collaborative and collegial spirit of the initial discussions, as well as to the overall vision that Gary had regarding the nature of desert communities. We have no doubt that the chapter would have evolved considerably beyond its current form had Gary been here to participate in this process.

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