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REVIEW

Complex Species Interactions and the Dynamics of Ecological Systems: Long-Term Experiments

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Studies that combine experimental manipulations with long-term data collection reveal elaborate interactions among species that affect the structure and dynamics of ecosystems. Research programs in U.S. desert shrubland and pinyon-juniper woodland have shown that (i) complex dynamics of species populations reflect interactions with other organisms and fluctuating climate; (ii) genotype \times environment interactions affect responses of species to environmental change; (iii) herbivore-resistance traits of dominant plant species and impacts of "keystone" animal species cascade through the system to affect many organisms and ecosystem processes; and (iv) some environmental perturbations can cause wholesale reorganization of ecosystems because they exceed the ecological tolerances of dominant or keystone species, whereas other changes may be buffered because of the compensatory dynamics of complementary species.

Throughout the 20th century, most theoretical and empirical research attempted to understand the structure and dynamics of populations, communities, and ecosystems by identifying the components and studying their relations in isolation from the complicating influences of larger systems. This research strategy was suc-

cessful in elucidating fundamental ecological processes: responses to stresses of extreme abiotic conditions; limiting resources of food, water, and inorganic nutrients; and the biotic interactions of competition, mutualism, predation, parasitism, and disease. It was less successful in revealing the complex patterns of

temporal and spatial variation in the abundance, distribution, and diversity of species or the complicated roles of species in ecosystems. By the 1980s, it was becoming apparent that more holistic, synthetic approaches were needed (1–4). To understand realistically complex ecological systems, it is necessary to study how the components affect and are affected by the larger, more complicated systems in which they are embedded.

Especially valuable insights have come from decades-long studies that combine experimental manipulations of selected species

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or functional groups of organisms with monitoring of critical environmental variables. These studies have revealed both unexpected complexity and emergent simplicity. They have crossed the boundaries between the traditional specialized subdisciplines of ecology and demonstrated linkages between different kinds of organisms and different levels of organization. In particular, they have shown how the dynamics and interactions of species populations link the biology of individual organisms to the biogeochemical processes of ecosystems (5, 6).

Here we draw on two studies of arid ecosystems to show the unique kinds of results and insights that have come from keeping controlled experimental manipulations in place for a long period. In 1977, Brown and colleagues initiated experiments in the Chihuahuan Desert near Portal, Arizona (7). The manipulations involved removal of selected species or functional groups of species of seed-eating rodents or ants from large (50 m by 50 m), replicated plots of desert shrub habitat (Fig. 1). These

treatments have been imposed continuously, and rodents, ants, plants, and weather have been monitored with standardized techniques. In 1982, Whitham and collaborators initiated experiments in pinyon-juniper woodland at Sunset Crater, near Flagstaff, Arizona. Volcanic eruptions that ended ~800 years ago covered 2000 km² in lava, cinders, and ash (8). Pinyon pine (*Pinus edulis*) has recently colonized these hot, dry, nutrient-poor soils, where it suffers from abiotic stress and chronic pest attack (Fig. 2). Pinyon pine is a dominant tree species with an extensive paleoecological record indicating high sensitivity to changes in climate (9). Long-term removal of insect herbivores and mitigation of abiotic stress revealed how these factors affected not only pinyon but also its interactions with microbes, insects, birds, and mammals and with biogeochemical processes.

These two studies had several features in common. They continuously removed particular species or functional groups of organisms in controlled experiments. They also simultaneously monitored multiple variables that pro-

vided information on relations between species and the abiotic environment, interactions among species, and effects of species that ramify through intervening links to affect other components of the ecosystems. The combination of experimentation and monitoring was crucial, because the controlled experiments were embedded in temporally and spatially varying environments. Some of the most interesting findings come from the response to the joint perturbations of intentional experiments and uncontrolled variation in climate and other factors. These results could not have been obtained from either short-term experiments or longterm monitoring without experimental manipulation.

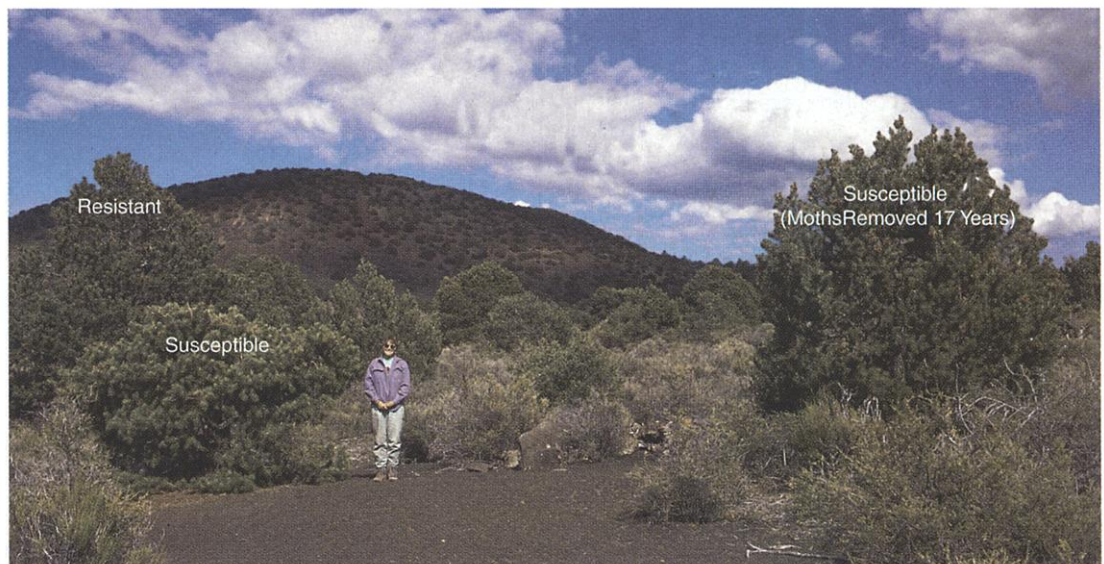
Complex Dynamics

The experiments at Portal were designed to evaluate conflicting ideas about resource limitation and competition. Theoretical studies, laboratory experiments, and short-term field manipulations indicated that population dynamics and species composition could be governed by resource supply and interspecific competition (10–14). However, some investigators questioned the extent to which these processes influenced the dynamics of ecological assemblages under realistic conditions in the field (15, 16). Studies of desert rodents had suggested that resource limitation and competition play a major role in determining abundance, distribution, and species diversity. Short-term observations had found that populations increased after seasons of exceptionally heavy precipitation and plant production and decreased during the intervening droughts (17–19). Other evidence

Fig. 1. Chihuahuan Desert shrub ecosystem at the Portal study site. In the foreground is a mound of the banner-tail kangaroo rat (*Dipodomys spectabilis*), which is a keystone species in this ecosystem. Many species of plants, fungi, arthropods, and vertebrates rely on the disturbance, shelter, or stored food provided by the mounds, and these species declined or disappeared from the study site when the banner-tail kangaroo rats declined to local extinction in the early 1990s. [Photo by J. H. Brown]



Fig. 2. At the Sunset Crater study site, the effects of the stem-boring moth, *Dioryctria albovittella*, on resistant and susceptible pinyons, *Pinus edulis*, have been observationally and experimentally studied with three groups of trees since 1983. These groups are naturally resistant trees, susceptible trees, and susceptible trees that have had moths removed every year. Although similar in age, they exhibit pronounced differences in performance. All three groups of trees grow intermixed at an elevation of ~2000 m. Moth-resistant trees exhibit an upright and conical growth form, whereas loss of terminal shoots because of moth attack causes susceptible trees to develop as compact, flat-topped shrubs. At the initiation of the moth removal experiment, half of the susceptible trees were selected for spraying once each year with the systemic insecticide Cygon. At the onset of the experiment, the tree designated as "Susceptible (Moths Removed)" was of similar size to the nearby



tree marked as "Susceptible." Once moths were removed, there has been a steady and pronounced release effect on plant growth so that "Susceptible (Moths Removed)" trees now resemble "Resistant" trees. Foreground shows typical open spaces and black cinder soil. [Photo by T. G. Whitham]

suggested that coexisting species compete for limited food resources (20, 21).

Twenty-five years of data from Portal did not reveal the simple relation between precipitation, food supply, and rodent populations that we had expected on the basis of previous studies (Fig. 3). Sometimes the rodents increased during droughts and failed to increase after exceptionally rainy periods. At least three factors appeared to account for the complex dynamics: (i) plant growth and seed production were affected as much by the temporal pattern as by the overall quantity of precipitation within a season; (ii) predation, seed storage from previous seasons, and other factors mediated the response of rodent populations to fluctuations in food supply; and (iii) extreme rainfall events caused extensive rodent mortality, introducing a nonlinear component into the relation between precipitation and rodent populations (22–26).

Responses of rodents to experimental manipulation of interspecific competition were also unexpectedly complex (Fig. 4). On plots where three species of kangaroo rats (genus *Dipodomys*, the dominant seed-eating rodents) were removed, numbers of other seed-eating rodents more than doubled (7, 27, 28). This demonstrated the existence of competition. Furthermore, because populations of other seed-eating rodents were consistently higher on kangaroo rat removal plots than on control plots where kangaroo rats were present, competition was obviously not restricted to infrequent periods of resource scarcity. On the other hand, the response of rodents to reduced competition from kangaroo rats was highly variable. It included not only increases in populations of species that were already present on the study site but also colonization of kangaroo rat removal plots by species that had dispersed to the study site from surrounding habitats (29, 30). Our decades-long study revealed complex dynamics of rodent populations in response to variation in resource supply and competition that had not been detected in short-term observational or experimental studies.

Our data also documented ecological response to climate change. The initiation of the Portal study coincided with a two-decade period when winter precipitation across the desert region of southwestern North America was well above the century-long average (31). At the study site, this caused major changes in the ecosystem. Cool-season-active woody shrubs that have the C_3 photosynthetic pathway increased threefold, with a corresponding decrease in warm-season-active C_4 perennial grasses. Many animal populations were also affected, either directly by the climate change or indirectly through its effects on plants. Previously dominant species of rodents, ants, and other taxa decreased markedly and in some cases went locally extinct. Other species benefited from the changes and either increased or

colonized. However, even though the same regime of increased winter precipitation occurred throughout a wide region of southwestern

North America, many other ecosystems, some only a few kilometers from the Portal site, were relatively unaffected. This is further evidence of

Fig. 3. The relation between precipitation and rodent population dynamics at the Portal site. (A) Precipitation during the winter (white bars) and summer (black bars) seasons from 1980 to 2000. (B) Fluctuations in the abundance of desert rodents on unmanipulated control plots from 1997 to 2000, showing banner-tail kangaroo rat (*D. spectabilis*), which was the second most abundant species at the start of the study but declined in the 1980s and went extinct in 1995 (white circles); Merriam's kangaroo rat (*D. merriami*), which was on average the most abundant rodent species throughout the study (black circles); and total abundance of all rodent species (black squares). There was no consistent positive relation between precipitation and rodent abundance; instead, (i) rodent populations were high but precipitation was low in the 1990s and (ii) exceptionally heavy rainfall events (vertical lines), in fall 1983 and summer 1999, caused drastic declines in the kangaroo rat populations.

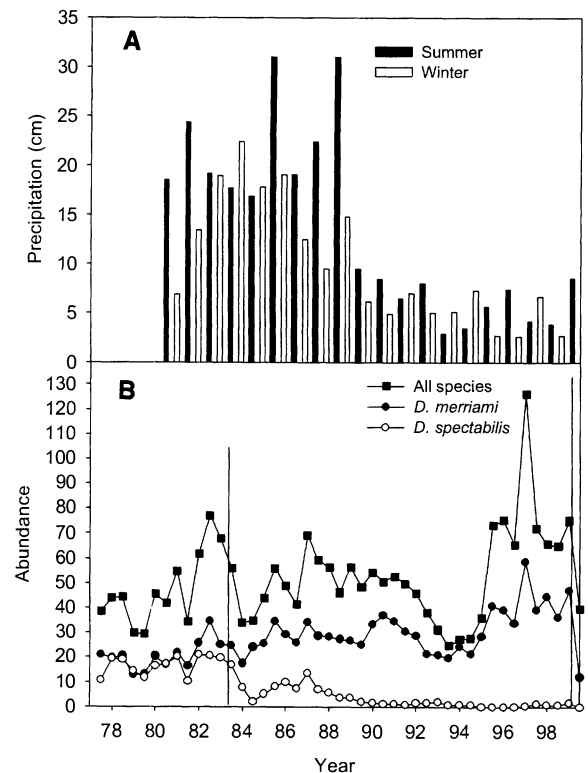
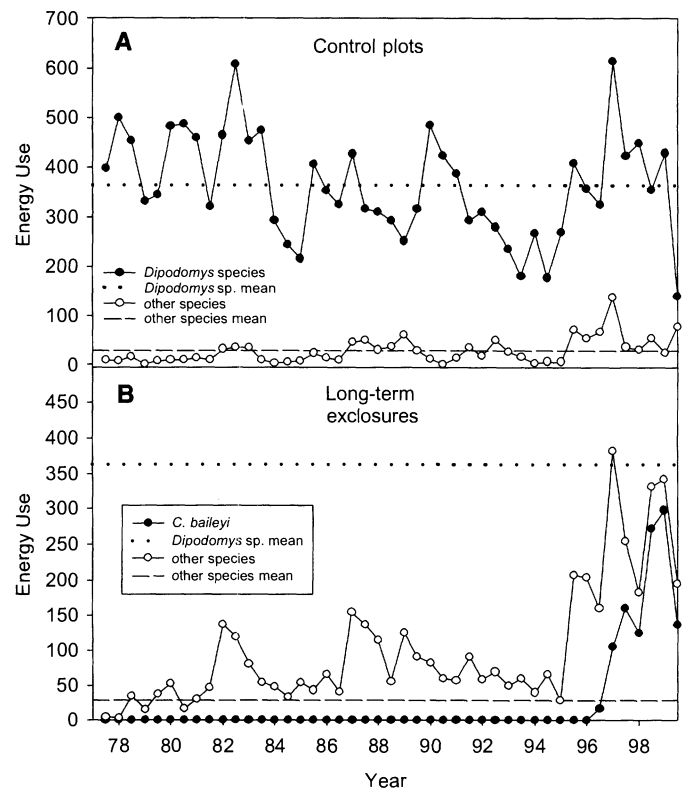


Fig. 4. Response of other seed-eating rodents to experimental removal of kangaroo rats at the Portal site. (A) Energy use of kangaroo rats (black circles) and other rodents (white circles) on control plots, with average abundances over the entire period indicated by the dotted and dashed lines, respectively. (B) Abundance of all other rodents (white circles) on experimental plots from which kangaroo rats had been removed, with the abundance of Bailey's pocket mouse (*Chaetodipus baileyi*) shown separately (black circles); for reference, the dotted and dashed lines again show the average abundances of kangaroo rats and other rodents on the control plots (as above). The other rodents were on average substantially more abundant on kangaroo rat removal plots than on control plots where kangaroo rats were present, but the extent of competitive compensation was initially and increased over time, especially after Bailey's pocket mouse colonized the site in 1995.



the complex responses of species and ecosystems to environmental change.

In the Sunset Crater ecosystem, complex

dynamics emerged from the interactions of abiotic stress with a dominant tree, keystone herbivores, and diverse organisms from microbes

Table 1. Levels of herbivory on moth-resistant, moth-susceptible and moth removal trees and the impact of that herbivory on cone production, cone harvest by birds, and levels of ectomycorrhizal colonization. Moth herbivory has been monitored annually on the 150-year-old trees since 1982. The younger trees represent a long-term experiment in which moths have been removed from a group of susceptible trees since 1983.

| Tree type | Moth herbivory (mean % shoot mortality)* | Cone production (mean number)† | Avian cone harvest (estimated %)‡ | Ectomycorrhizal colonization (mean %)§ |
|-------------------------------------|--|-----------------------------------|---|--|
| Resistant (150-year-old trees) | 8.6 | 2441.1 | 100.0 | 37.2 |
| Susceptible (150-year-old trees) | 24.1 | 172.3 | 38.1 | 25.4 |
| Resistant (60-year-old trees) | 2.3 | 165.1 | 37.5 | 50.5 |
| Susceptible (60-year-old trees) | 16.4 | 13.2 | 19.2 | 34.0 |
| Moth removal (60-year-old trees) | 1.3 | 146.7 | 36.1 | 55.1 |

*Data for the 150-year-old trees represent mean values of shoot mortality for 20 resistant and 20 susceptible trees for the 9-year period from 1982 to 1990. Data for the 60-year-old trees were taken after 7 years of moth removal (44).
†Data collected on the trees described above during the mast cone production year of 1994. ‡Avian cone harvest was estimated on the basis of an equation generated from data on the relation between cone crop size and cone harvest rate by birds at Sunset Crater (39). §Data represent the average of spring and fall samples from each group and were taken in 1989–90 (44).

to vertebrates. The volcanic ash and cinder soils of Sunset Crater are a harsher environment than the sandy-loam soils of adjacent woodlands, and the pinyon pines that colonized these cinders have encountered abiotic stresses for which they are only marginally adapted. After a 100-year record drought in 1996, the mortality rate of mature trees growing in cinder soils exceeded 40% in some stands (32). Comparisons of adjacent trees in which one lived and the other died showed that mortality was associated with greater variation in growth rates, a measure of environmental sensitivity. These differences in mortality rates of trees with different growth characteristics show how climatic change might select for drought-tolerant genotypes. Such selection is one mechanism that would tend to buffer a species population and maintain ecosystem homeostasis in the face of environmental change. Perturbations that decimate pinyon cause declines or extinctions of many dependent species. This occurred in the 1950s, when prolonged drought caused massive mortality and shifts in the distribution of pinyon-juniper woodlands (9, 33). So, long-term studies of species at the margins of their ecological tolerances can serve as barometers of global change and reveal how natural and anthropogenic perturbations affect population, community, and ecosystem-level processes.

Changes in climate or other abiotic conditions can have nonlinear effects because they are amplified by species interactions. In the region surrounding the volcanic field where more favorable sandy-loam soils predominate, insect outbreaks on pinyon pine have been relatively minor. At Sunset Crater, however, pinyons growing on the stressful cinder soils have been attacked by stem-boring moths (*Dioryctria albovittella*). During 18 years of study, 80% of mature trees were susceptible to moths and suffered chronic shoot mortality year after year (34, 35) (Table 1). Because moths destroyed the terminal shoots, they turned trees into shrubs. Loss of terminal shoots also caused the loss of nearly all female cone-bearing shoots, resulting in trees with male-only function. In contrast, the remaining 20% of the pinyons suffered little moth damage, had normal architecture, and produced nearly all of the mature cones and seeds. Figure 2 shows how resistant and susceptible trees differed in general appearance. Because moths attack the growing shoots, the resulting architecture of susceptible trees reflects the accumulated herbivory of a lifetime (Fig. 5). To confirm that the moth was in fact responsible for these differences in architecture and reproduction, we experimentally removed moths from susceptible trees since 1983. Figure 2 shows the resulting release from herbivory. The architecture of susceptible trees with moths removed came to resemble that of resistant trees. Changes in allocation to reproduction occurred slowly, but over 17 years of moth removal the cone crops

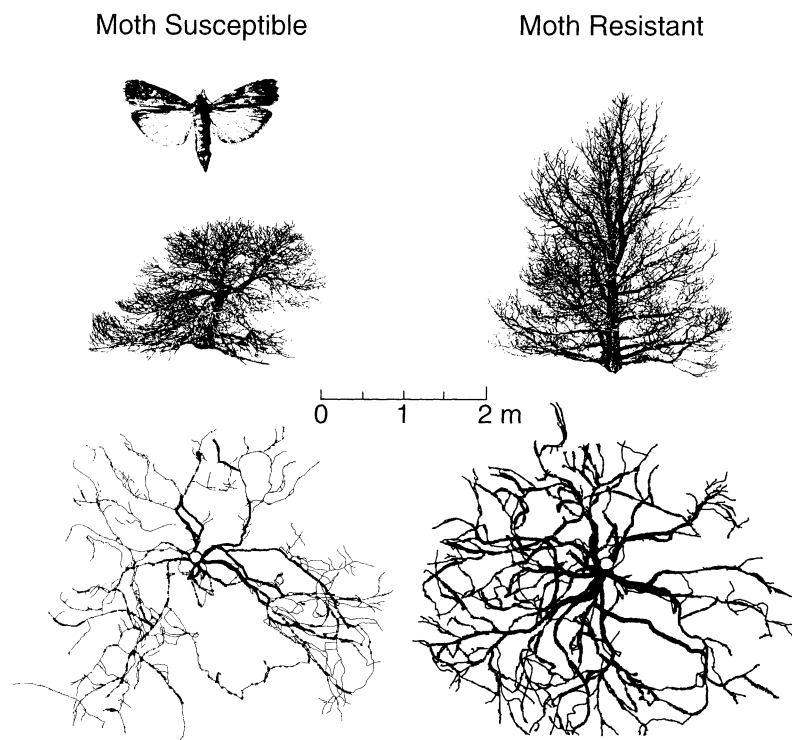


Fig. 5. Moth-susceptible and -resistant pinyons (*Pinus edulis*) at Sunset Crater have very different above- and below-ground architectures (branches and roots are shown to the same scale, but not the moth). These high-contrast photos are from two trees that vary in their resistance to moth attack (average annual shoot mortality of the susceptible tree was 30.3%, compared with only 1.9% for the resistant tree). The needles from both trees were removed to reveal branch architecture. The cinder substrate of a ~4-m-diameter circle centered on the trunk was blown away to reveal coarse root architecture. The differences between the two trees show how a lifetime of moth herbivory can accumulate to affect the growth of a dominant tree species. The susceptible tree is 91 years old and 1.68 m tall, whereas the resistant tree is 2.67 m tall and 63 years old. [Photos by T. G. Whitham]

of the once-susceptible trees increased to equal (Table 1) and eventually to exceed cone crops of resistant trees. This last finding, which could only have come from such a decades-long experiment, suggests that there is an energetic cost to being resistant.

Why are some trees resistant and some susceptible? Cobb *et al.* (35) showed that the susceptible pinyons growing in cinder soils invested about two-thirds less into resin defenses than resistant trees. Furthermore, these two groups of trees were genetically distinct, differing substantially in both allelic frequencies and heterozygosity (36). Because the trees at Sunset Crater represent the descendents of recent colonists, it seems likely that both susceptible and resistant genotypes grow on nearby sandy-loam sites. There, under relatively benign growing conditions, even susceptible genotypes suffer little moth attack. In the stressful cinder soils at Sunset Crater, however, the susceptible genotypes are expressed—an example of a genotype \times environment interaction, differential expression of a heritable trait depending on environmental conditions. In support of this hypothesis, we found that when abiotic stresses of susceptible trees were alleviated experimentally by supplying supplemental water and nutrients, the resin defenses of susceptible trees tripled and they suffered substantially less moth attack (35). Such plant genotype \times environment interactions are well documented in relatively simple agricultural systems, but their consequences for other ecosystems are poorly understood.

Diverse and Cascading Interactions

The two-decade experimental studies at Sunset Crater demonstrated an extended network of strong interactions among diverse taxa and trophic levels. Indirect interactions among distantly related taxa were as strong, if not stronger, than direct interactions. These interactions included interspecific exploitative competition among insects, birds, and mammals for pinyon seeds and complex relations among insect herbivores and mycorrhizal fungi.

The impact of moth herbivory on female cone production described above reverberated to affect birds and mammals that relied on pinyon seeds for food. Some of these birds and mammals scatter-hoard seeds, thereby dispersing some of them to favorable sites for germination (37, 38). During the 1994 mast year, 150-year-old moth-resistant trees averaged 2441 cones per tree, whereas moth-susceptible trees averaged only 172 cones (Table 1). Observational and experimental studies showed that avian seed dispersers such as Clark's nutcrackers (*Nucifraga columbiana*) and pinyon jays (*Gymnorhinus cyanocephalus*) responded to such differences in cone production, selectively foraging from trees with larger numbers of cones (39). Table 1 illustrates the predicted differences in seed harvest by birds on resistant

and susceptible trees on the basis of the relation between the number of cones produced by individual trees and the observed harvest rate (39). Estimated seed harvest was three times greater for 150-year-old resistant trees than for susceptible trees of the same age (Table 1). Although overall harvest rates on 60-year-old trees were lower because of smaller size and lower cone production, there were similar differences between resistant and susceptible trees (Table 1).

Moth herbivory had greater negative effects on the harvest rates of birds than mammals (40), resulting in differential seed dispersal. The ratio of mammal to bird harvest increased linearly with increasing moth damage, so that seeds that survived moth herbivory were as much as 350 times more likely to be harvested by mammals than by birds. Seeds harvested by birds and mammals had different fates. For example, pinyon jays commonly dispersed seeds several meters to 5 km and sometimes as much as 10 km (41). In contrast, small mammals dispersed seeds a maximum of about 40 m (37). Thus, the moth not only severely reduced seed production by damaging the cone-bearing shoots of susceptible trees, it also had important indirect effects on the behavior of seed consumers, the dispersal of seeds, and likely the recruitment of seedlings.

Other ramifying impacts of abiotic stress and herbivory affected the crucial belowground mutualism between pinyon roots and ectomycorrhizal fungi. Figure 5 shows the root systems of moth-susceptible and moth-resistant trees, highlighting the reduction in coarse root biomass that resulted from chronic moth herbivory. Susceptible trees also showed similar reductions in colonization of fine roots by ectomycorrhizal fungi. These fungi obtain carbon from photosynthesis of the host plant, and in return they enhance nutrient and water uptake and provide protection from pathogens (42). For example, the shoot biomass of pinyon seedlings was positively linearly correlated with the abundance of ectomycorrhizae in both cinder and sandy-loam soils (43). However, in response to insect herbivory, less photosynthate was available to support these fungi, and moth-susceptible trees had substantially fewer ectomycorrhizae than moth-resistant trees (Table 1). When moths were experimentally removed from susceptible trees, the ectomycorrhizae rebounded to levels comparable to those of resistant trees, demonstrating that moth herbivory was responsible for the declines (44) (Table 1).

Moth herbivory also caused shifts in ectomycorrhizal fungal composition. Although resistant and susceptible trees had a similar average number of fungal species, two-thirds of the fungal species associated with susceptible trees were members of the subphylum Ascomycotina, whereas the majority of the fungi associated with moth-resistant trees were members of the subphylum Basidiomycotina (45). Although

the effects of these different fungi on pinyon pine are unknown, taxa of ectomycorrhizal fungi are known to vary in drought tolerance (46), ability to use organic nutrient sources (47), and energetic cost to the host plant, all of which may affect their roles as mutualists. Because the effects of mycorrhizal fungi on their host plants can vary between mutualism and parasitism (48), such marked shifts in fungal composition may have important impacts not only on the host trees but also on ecosystem carbon and nutrient dynamics.

The above examples illustrate how a genotype \times environment interaction affects a dominant tree species and how the resistance and susceptibility traits of pinyon cascade through the ecosystem to affect diverse organisms from different trophic levels (49, 50). Similar relations were observed in other plant and herbivore species at Sunset Crater. For example, young pinyon pines were heavily attacked by the needle-feeding scale insect (*Matsucoccus acalyptus*) (51). Before the 1996 drought, scales were largely restricted to pinyons growing in stressful cinder soils (48). At Sunset Crater, pinyons varied in their susceptibility to the scale, and susceptible trees that experienced chronic attack had an altered architecture and fewer ectomycorrhizae than resistant trees (51–53). Similarly, female trees of the codominant tree, one-seed juniper (*Juniperus monosperma*), suffered threefold higher levels of parasitism by a xylem-tapping mistletoe (*Phoradendron juniperinum*) at Sunset Crater than at a nearby sandy-loam site (54). So, an important insight is that extreme environmental conditions can cause seemingly insignificant organisms to become keystone species that have unexpectedly large effects on the ecosystem. On sandy-loam soils, the moth (*D. albobittella*) and the scale (*M. acalyptus*) are just two of many herbivores that cause negligible damage to pinyon. In the stressful environment of Sunset Crater, however, these species emerge as keystone species that have large, cascading impacts on diverse organisms and ecosystem processes.

Data from Portal also provide insights into the linkages between episodic abiotic events, keystone species, and cascading interactions. One of the extreme rainfall events referred to above was Hurricane Octave, which flooded the site with 129 mm of precipitation, nearly half the annual average, during a few days in October 1983. This led to marked declines in several rodent and ant species that store seeds in large underground granaries. One of these was the banner-tail kangaroo rat (*Dipodomys spectabilis*), which subsequently went extinct on the study site and was greatly reduced in the surrounding habitat (55) (Fig. 1). The banner-tail kangaroo rat is a keystone species (7). Its large burrow mounds provide areas of disturbed, nutrient-enriched soil that contribute to overall

plant species diversity by supporting several disturbance-requiring species (56). With the successional changes on the abandoned rodent mounds, these specialized plants decreased greatly in abundance and became much more restricted in distribution. The mounds also provide habitat for specialized fungi that infest the seed stores and for many kinds of arthropods, reptiles, and other vertebrates (57, 58). All of these species undoubtedly declined, but decreases in Mojave rattlesnakes (*Crotalus scutulatus*) and burrowing owls (*Athene cunicularia*) were especially marked and well documented (31). Horned lizards (*Phrynosoma cornutum* and *P. modestum*) decreased markedly after the declines in their harvester-ant prey. These events illustrate the networks of interactions that link the fates of many other organisms to a few keystone species and link the keystone species to abiotic conditions, such as weather and climate.

Compensatory Species Dynamics and Ecosystem Homeostasis

The long-term studies at Portal and Sunset Crater provide different, but complementary, perspectives on the responses of ecosystems to environmental change and on the roles of species interactions in these dynamics. The Chihuahuan Desert at Portal has been perturbed both by climatic changes and by experimental removal of species, some of which are keystones. In response to these perturbations, the ecosystem reorganized, but it did not collapse. Some of changes tended to be compensatory or homeostatic.

The shift in winter precipitation regime and the extreme rainfall events described above caused major changes in rodent species composition on the study site: Some species went locally extinct, others colonized, and many others increased or decreased in abundance. Yet, total rodent abundance, biomass, and energy use and overall species diversity remained relatively invariant; these system-level variables fluctuated somewhat over the seasons and years, but, unlike abundances of several species, they showed no consistent long-term trends. Analysis of species dynamics revealed that the variations in energy use were compensatory. When environmental changes disfavored some species so that they decreased in abundance or went extinct, the total energy use by all rodents remained relatively constant because other species increased in abundance or colonized (59). The colonizations and extinctions were offsetting, so that the total number of species remained nearly constant despite major changes in the identity of species (59, 60).

Our experimental perturbations elicited similar compensatory responses. Removal of kangaroo rats from experimental plots led not only to increases in the populations of other rodents that were already present but also to

decreased extinction rates for those species and, most importantly, increased colonization rates for new species. Overall rodent species diversity did not differ between kangaroo rat removal and control plots (29). For many years, however, the rodents that were able to colonize and persist on the manipulated plots were not able to compensate in energy use for the missing kangaroo rats. This changed in the late 1990s when a new species, Bailey's pocket mouse (*Chaetodipus baileyi*), colonized and single-handedly provided almost complete compensation (28). The phenomenon of compensation was not confined to rodents. Experimental removal of rodents or ants from plots caused major changes in species composition of winter annual plants. The changes were compensatory, however, so that overall abundance and species diversity remained virtually unchanged (60).

The Sunset Crater study provides a complementary perspective on the extent to which ecosystems have homeostatic properties. Different species and functional groups varied in their response to the spatial gradient from low-stress sandy-loam soils to high-stress cinder soils. For example, ectomycorrhizal fungi showed a major shift in taxonomic composition and a doubling in abundance at cinder sites, but overall species richness remained similar (43, 61). The greater abundance was related to the increased investment of many plants in their ectomycorrhizal mutualists when soil moisture and nutrients were most limited. Similarly, the taxonomic composition of rhizosphere bacteria differed markedly between sandy-loam and cinder soils, whereas patterns of abundance and taxonomic richness were less variable (62, 63). In contrast, the transition from sandy-loam to cinder soils caused a marked decrease in the arthropods associated with pinyon. The 298 species of herbivores, predators, and parasites decreased in species richness by 33% and in abundance by 92% (64). So, the interaction of environmental stress and herbivory had very different impacts on different kinds of organisms. For soil microbes, species composition shifted markedly, but species richness remained equivalent, suggesting some degree of compensation. However, arthropods decreased substantially in abundance and species richness, suggesting greater sensitivity to abiotic and biotic stresses and very little capacity for homeostasis. Such opposite responses may be due to the fundamentally different ecological roles of these organisms. Ectomycorrhizal fungi and some root-associated bacteria form mutualisms with plants (65, 66). Because of this tight association, the microbes may be more buffered from environmental stresses than free-living arthropods, many of which are plant pests.

The ability of ecosystems to exhibit compensatory responses is also likely to depend on the overall number and magnitude of perturbations and the environmental setting in

which they occur. For example, field experiments showed that under benign growing conditions, simulated moth herbivory at realistic levels (i.e., 25% shoot mortality) had no detectable effect on ectomycorrhizal mutualists. But the same level of simulated herbivory on insect-resistant trees growing in the stressful cinder soils caused a proportional decline in ectomycorrhizal abundance (67). Trees at Sunset Crater continually endure high environmental stress and chronic pest attack. An additional perturbation, such as the record 100-year drought of 1996, caused high mortality, altering the structure and dynamics of the ecosystem. Even though nearby sites with sandy-loam soils experienced the same drought, because of the more favorable conditions, pinyons and the ecosystem as a whole were buffered and resilient. This is similar to the situation at Portal, where the shift in winter precipitation regime, beginning in the late 1970s, caused major changes in precipitation, and a shift from C_3 woody shrubs to C_4 perennial grasses. However, this marked change occurred only within a narrow range of transitional habitat. Although they experienced the same climate change, shrublands at slightly lower elevations and grasslands at slightly higher elevations were virtually unaffected (31). So, environmental perturbations can be either buffered or amplified depending on characteristics of local ecosystems, such as the magnitude of the changes and their effects on dominant or keystone species. Perturbations are likely to have greater impacts when the dominant or keystone species are near the limits of their distributions and already under stress.

General Implications

Long-term studies offer a unique perspective on the roles of species in ecosystems, especially on the response of ecosystems to environmental change. On the one hand, all species are embedded in continually changing local and regional ecosystems and all ecosystems are embedded in a continually changing global environment. The responses of species to these changes and the effects of species on other species and on their ecosystems are often complex, nonlinear, and difficult to predict on the basis of ecological theory or short-term empirical studies. Small changes can be amplified to have large impacts on species composition, networks of interactions, and pathways of energy and material flow. Conversely, perturbations can be dampened, so that these ecosystem characteristics remain relatively unchanged.

The complex dynamics are due in large part to dominant and keystone species, which have strong direct and indirect interactions with many other species. Pinyon is such a species—anything that impacts pinyon is likely to cascade to transform the entire ecosystem. Some

keystone species, such as the moth *Dioryctria albovittella*, are cryptic. Their potential to alter the ecosystem depends on subtle interactions, which may occur only under restrictive conditions, such as times of climate change or in chronically stressful marginal habitats. Extinction of native species or colonization of alien ones can also have cascading effects that reconfigure the network of interactions and alter ecosystem processes.

An important question, then, is when are perturbations amplified and when are they dampened? Our results suggest that compensatory dynamics are especially likely when multiple species have overlapping or complementary ecological relations. Some ecologists have suggested that species may be so similar as to be ecologically "redundant" (68–71). Our decades-long studies suggest a different perspective. Some species do indeed have very similar ecological relations, but these interactions are different enough so that the species are by no means identical or redundant. The species respond differently to natural or human-caused perturbations. When some decrease or go extinct, others increase or colonize to take advantage of the altered conditions. Also important are the adaptive dynamics of species: their proclivities to shift habitat and resource use in response to changing availability, to increase in population and disperse across the landscape until limited by available resources, and to evolve by natural selection to better exploit environmental conditions. Such adaptive responses depend on genetic variation and can be facilitated by the kind of genotype x environment interaction reported above.

Of course, such compensation or homeostasis can only occur within certain limits. If the perturbation is too large relative to the compensatory capacities of species and functional groups, the ecosystem will reorganize, but the original properties may not be preserved. Homeostatic capacity will be reduced when the system is stressed, so that the dominant and other keystone species are already near their ecological limits. If the perturbation causes extinction or even large declines in native species, especially if those species are dominants or keystones, the result may be the wholesale reorganization of the ecosystem with major changes in species composition and ecosystem processes. Such drastic changes may not occur, however, if the system is open to colonization and surrounding areas contain a pool of species, some of which are able to tolerate the altered conditions, compensate for the missing species, and have a homeostatic influence. This is one reason why isolated ecosystems, such as islands and biological reserves surrounded by low-diversity, human-modified habitats, are so sensitive to environmental change.

The simple, linear, pair-wise perspective on species interactions that dominated 20th-century

ecology is inadequate to deal with the complexity of natural ecosystems. A new perspective is emerging. Systems of interacting species exhibit a wide range of phenomena. Some features, such as the dynamics of many single-species populations in spatially and temporally varying environments, are seemingly idiosyncratic and extremely difficult to predict. At the same time, however, networks of interacting species appear to generate emergent patterns and processes. These very general, relatively invariant properties hint at homeostatic mechanisms that confer resilience to certain kinds of perturbations. Earth has always experienced environmental changes of varying severity, from tectonic upheavals to shifts in climate. Currently, however, many ecosystems are being subjected to new kinds and unprecedented magnitudes of perturbations because of human activity. To preserve wild places with minimal human impacts, to staunch the loss of biodiversity through extinction of native species and spread of exotic ones, to produce food, water, and other "renewable natural resources" for human use, and to dispose of human-generated wastes and products with minimal deleterious environmental impacts, it is important to understand how ecosystems function. Long-term experimental studies of species interactions will continue to play a critical role.

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72. Both projects have been supported by grants from NSF's Long-Term Research in Environmental Biology (LTREB). J.H.B. and S.K.M.E. thank all the many

people who worked on the Portal project. The most recent NSF grant is DEB-9707406. S.K.M.E. was also supported by NSF grant DGE-9553623. T.G.W. and C.A.G. thank the many individuals who contributed to the Pinyon Ecology Research Group at Sunset Crater, including N. Cobb, S. Mopper, K. Christensen, G. Koch, T. Theimer, P. Keim, S. Hart, J. Mitton, C. Kuske, K. Ogle, B. Hungate, B. Wade, T. Lane, S. Chapman, A. Classen, T. Trotter, R. Swaty,

K. Charters, M. Van Ert, R. van Ommeren, K. Haskins, J. Ruel, and M. Caouette. The work has been funded by NSF, the U.S. Department of Agriculture, and/or the U.S. Department of Energy since 1985. Current grants include NSF DEB-9615313, DEB-9816001, DEB-9909109, DEB-0083623, DEB-0075563 and DEB-0087091, and DUE-0088626. D. Boone and R. Redsteer assisted with the illustrations.

REVIEW

Long-Term Studies of Vegetation Dynamics

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By integrating a wide range of experimental, comparative, and theoretical approaches, ecologists are starting to gain a detailed understanding of the long-term dynamics of vegetation. We explore how patterns of variation in demographic traits among species have provided insight into the processes that structure plant communities. We find a common set of mechanisms, derived from ecological and evolutionary principles, that underlie the main forces shaping systems as diverse as annual plant communities and tropical forests. Trait variation between species maintains diversity and has important implications for ecosystem processes. Hence, greater understanding of how Earth's vegetation functions will likely require integration of ecosystem science with ideas from plant evolutionary, population, and community ecology.

The past decade has seen the emergence of a new synthesis in plant ecology that draws together a variety of once disparate approaches in studies of vegetation dynamics. Questions about the determinants of plant life histories, species composition, diversity, productivity, and stability—previously considered separate areas of inquiry—have become increasingly closely integrated. Findings from long-term experimental and observational studies, combined with comparative and theoretical work, have helped synthesize the questions and approaches of evolutionary ecology, population ecology, and ecosystem ecology. The link has come from the realization that many of the same environmental constraints and organismal tradeoffs that shape the evolution of plant morphologies, life histories, and physiologies also influence the dynamics of interspecific interactions and the mechanisms of coexistence that control community and ecosystem functioning (1–3). We provide a brief tour of the developments in vegetation science, highlighting areas where known patterns of variation in demographic rates between species have provided insights into the structure, dynamics, and functioning of plant communities.

Successional Dynamics

Successional dynamics are highly predictable and have been described in numerous systems (4–8). Early-successional plant species typically have a series of correlated traits, including high fecundity, long dispersal, rapid growth when resources are abundant, and slow growth and low survivorship when resources are scarce. Late-successional species usually have the opposite traits, including relatively low fecundity, short dispersal, slow growth, and an ability to grow, survive, and compete under resource-poor conditions (5, 6). These attributes define MacArthur's classical *r*- and *K*-selection continuum (9) and underpin most explanations of secondary successional diversity.

In the absence of disturbance, late-successional species eventually competitively exclude early-successional species, because they reduce resources beneath the levels required by the early-successional species. Early-successional species persist as a result of two processes. High fecundity and long dispersal allow these species to colonize recently disturbed sites before the dominant competitors arrive. In addition, rapid growth under resource-rich conditions allows them temporarily to outperform late-successional species, even if both arrive simultaneously in a recently disturbed site. We refer to the first mechanism as the competition-colonization tradeoff (10) and the second as the successional niche (11).

Given that colonist species persist in recently disturbed sites, it is not surprising that they have morphologies and allocation strategies that maximize resource capture in conditions of

high light and nutrients. This means that both competition-colonization and the successional niche mechanism operate in parallel in many systems. These two mechanisms are undoubtedly important in many secondary successions, although their roles in maintaining diversity within stable communities are less clear. However, we suspect that in productive habitats, where disturbances are of small spatial extent, the niche mechanism will be more important than competition-colonization. This is because the competitive dominants are abundant and are therefore likely to colonize virtually all disturbances.

The Dynamics of Annual Plant Communities, Grasslands, and Prairies

Understanding of the processes that structure communities of annual and short-lived perennial plants has developed rapidly in the past decade. Progress has resulted from a move away from viewing species in isolation, where details of the ecology are seen as paramount, to a synthetic approach emphasizing the role of tradeoffs (12–16). One pivotal character in this new synthesis is seed size. This character has a profound effect on fecundity, establishment success, seedling survival, seedling growth rate, competitive ability, and persistence in the seed bank. Within floras and local communities, seed size generally follows a log-normal distribution, with many small seeded species and few large seeded ones (16, 17). The underlying processes driving this pattern are not well understood, but its widespread existence suggests that many plant species are colonization-limited, in agreement with experimental evidence (18), and so smaller seed sizes—resulting in increased fecundity and hence improved colonization ability—have a selective advantage.

Seed size is linked with fecundity via the seed size–number tradeoff: For a plant species with constant reproductive allocation, fecundity is inversely proportional to seed size. This unbreakable constraint means that small changes in seed size result in large changes in fecundity, whereas small changes in reproductive allocation have less effect. The magnitude of the variation in per capita fecundity within communities is enormous.

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