

THE RESPONSE OF ANIMALS TO DISTURBANCE AND THEIR ROLES IN PATCH GENERATION

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INTRODUCTION

Natural and anthropogenic disturbances play critical roles in molding the structure and function of many terrestrial ecosystems. Because the definition of disturbance encompasses a variety of meanings, it allows considerable latitude in classifying phenomena as sources of disturbance. In general, disturbance may be considered "any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate availability, or the physical environment" (White and Pickett, 1985). Other notions of disturbance include events that remove a community from its "normal" state, processes that result in mortality or loss of biomass (e.g., Huston, 1994), processes that prevent the attainment of equilibria (e.g., Krebs, 1994), or events that open sites for regeneration (e.g., Harper, 1977). The variety of events that have been considered as disturbances in natural systems is reflected in a list compiled by White and Pickett (1985) which includes (1) climatic events such as hurricanes and windstorms, ice storms and freezes, or rainstorms and flash floods; (2) large-scale geological events such as earthquakes and volcanic eruptions; (3) alterations in climatic conditions such as droughts; and (4) biotic processes such as tree-falls, insect outbreaks, disease, predation, and burrowing or building by animals.

We use the definition of disturbance provided by White and Pickett (1985), but limit its application for both practical and conceptual reasons. First, we exclude the effects of trophic interactions (i.e., positive effects obtained by a consumer and negative effects suffered by the consumed as a consequence of feeding). Although trophic interactions have important effects on the structural and functional attributes of populations,

and ecosystems (see Schowalter and Lowman, Chapter 9, this volume), appropriate conceptual contexts for examining these relationships already exist, and the benefit to the theory of disturbance of including them as examples of disturbances is unclear. Massive outbreaks or epidemics may represent an exception to this disclaimer, but even then, it is difficult to distinguish the population size or impact of the consumer necessary to distinguish cascading trophic effects from catastrophic effects. Second, we do not consider long-term alterations in climate as disturbances. We might consider a freeze to be a disturbance, but we would consider global warming as outside the domain of disturbance theory. The difference between these two kinds of events is not purely semantic. We believe that it is useful to limit the term disturbance to include "relatively discrete events in time" that may recur continually, but to exclude long-term changes or fluctuations that are continuous in nature.

Disturbances may be characterized by their frequency (mean number of events per time period), intensity (physical force of the event per unit area per unit time), and extent (area disturbed) within a domain of interest (White and Pickett, 1985). Typically, the domain of interest is an ecosystem within which population, community, or process characteristics are examined. The intensity of a particular event (e.g., landslide) may be great at a local scale, but less when considered at the level of the domain of interest. Elements of disturbance regimes may be visualized as potentially occupying regions of space defined by each of three orthogonal axes (Waide and Lugo, 1992). Some disturbances are rare, high-intensity events that alter broad portions of the landscape

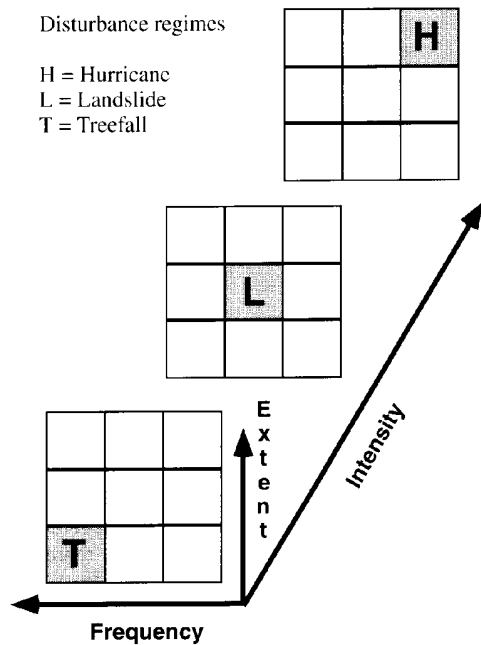


Fig. 27.1. Diagrammatic representation of disturbance regimes as defined by their frequency, intensity, and extent. These three attributes may be correlated in natural systems.

(e.g., hurricanes, fires, floods), whereas others may be frequent, low-intensity events that affect smaller portions of the landscape (e.g., tree-falls, small animal disturbances). Between these extremes are infrequent, moderately intense disturbances that affect areas of intermediate extent (e.g., landslides). Perusal of the literature suggests that natural disturbances are not homogeneously distributed in this three-dimensional space (Fig. 27.1). Frequency may be inversely related to intensity and extent, whereas intensity and extent may exhibit a positive association. Nonetheless, these associations may be a biased reflection of the interests of investigators, as much as an accurate reflection of the distribution of disturbance attributes in nature.

Most work that has examined the response of terrestrial animals to disturbance has focused on the two extreme types: broad, intense, and infrequent disturbances caused by atmospheric or geological processes, or narrow, less intense, and frequent disturbances with a biotic origin. Similarly, the taxonomic and geographic focus of research has not been homogeneous (e.g., mostly vertebrates). Moreover, the response of animals to disturbance primarily has considered static features

of populations (e.g., density or distribution) or communities (e.g., richness or composition), rather than dynamics or interactions (e.g., rates of immigration, emigration, mortality, and natality for populations; strengths of competition or predation for communities). By necessity, our exposition reflects these limitations.

For heuristic and historical purposes, we distinguish three effects of natural disturbances on animals: (1) direct effects; (2) indirect effects derived from an altered physical environment; and (3) indirect effects that result from an altered biological environment (Fig. 27.2). The direct effects are immediate and occur as a result of mortality associated with the disturbance, or the spatial redistribution of individuals occurring during the disturbance. Indirect effects that derive from the altered physical environment become manifest shortly after the initial disturbance, and likely occur because of altered mortality or the behavioral response of mobile species to a currently inhospitable physical environment. In practice, it may be difficult or impossible to distinguish between direct and indirect effects, because of the logistic delays usually associated with sampling an area immediately after a disturbance.

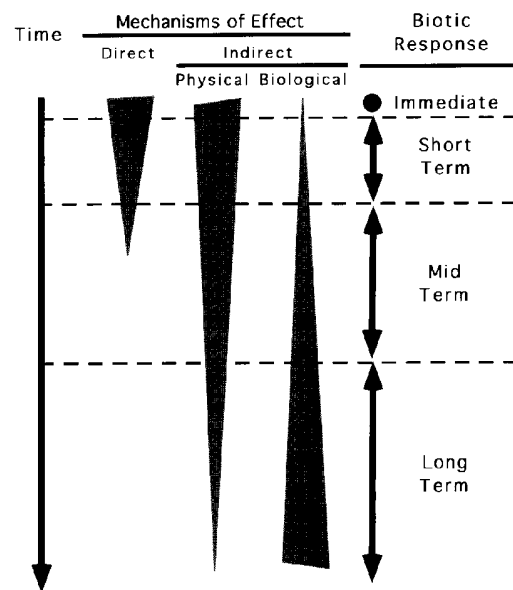


Fig. 27.2. Diagrammatic representation of the relative time periods during which direct, indirect physical, and indirect biological mechanisms associated with disturbance affect animal responses. The absolute times associated with the temporal axis will differ among disturbances (e.g., tree-falls versus fires versus hurricanes).

This is especially important when considering mobile organisms (i.e., animals) whose positions in geographic space are not static (as in plants). Finally, the changes in population and community attributes of the biota that derive from the first two types of effects alter the frequency and strength of both intraspecific and interspecific interactions, thereby impinging on the natality, mortality, emigration, and immigration of the remaining species. This is the beginning of a cascading sequence of events, which, combined with the effects of dispersal into the area, results in trajectories of recovery during succession. The interplay of these three determines the response of animal populations and communities at any time after a disturbance.

MAJOR DISTURBANCES

In this chapter, we consider two broad categories of disturbance based on the factors responsible for initiating the disturbance. Abiogenic disturbances are those primarily caused by changes in the physical environment (e.g., hurricanes, fires, floods, earthquakes) as a consequence of climatological or geological processes, whereas biogenic disturbances primarily are initiated by the actions of species (rodent burrows, animal carcasses). The intensity of abiogenic events such as wind storms (e.g., wind velocity) and fires (e.g., temperature) can be measured independently of the consequences of these events (i.e., severity *sensu* White and Pickett, 1985) on the biota. In most cases, one may expect the severity of a disturbance to be correlated with the intensity of the event that caused it. However, it is inherently difficult to define the intensity of biogenic disturbances independent of their consequences.

We do not intend to provide a comprehensive review of the literature concerning the response of animals to all types of disturbance. Instead, we consider the effects of disturbances on animals by focusing on illustrative examples that include destructive, climatic events such as hurricanes and fires, as well as patch-generating phenomena such as tree-falls. Moreover, we consider a variety of animal activities as agents of disturbance, and illustrate their effects on plants and animals. Finally, we present a case study of the effects of animal disturbances on the structure and function of a sand shinnery oak (*Quercus havardii*) ecosystem in western Texas.

Hurricanes, typhoons and cyclones in tropical forests

These infrequent, high-intensity storms affect large regions of the tropics and subtropics. Their impact on the structure and function of ecological systems has been particularly well documented in regions bordering the Caribbean (Walker et al., 1991, 1996; Wiley and Wunderle, 1993). Indeed, they are considered to be among the most important features that mold the biotic complexion of these ecosystems. Direct effects as a consequence of wind and rain (Kennedy, 1970; Walker et al., 1991) cause appreciable mortality in plants, but mortality of animals is rarely documented in the literature (e.g., Waide, 1991a; Will, 1991; Willig and Camilo, 1991). Nonetheless, anecdotal evidence and extrapolation suggest that rain, wind, and flooding can cause mortality to animals during cyclonic wind storms (Wiley and Wunderle, 1993). Storm-induced tree defoliation opens the canopy and alters the microclimatic attributes of the forest with regard to temperature and humidity. Similarly, the felling of trees and massive input of debris (leaf litter, branch falls) caused by hurricanes alter the distribution of biomass, as well as the vertical and horizontal structure of the forest. Finally, destruction of food supplies (e.g., fruits and flowers) and refugia (e.g., nest or roosting sites) can enhance post-hurricane mortality for an extended period after the initial impact (Jeggo and Taynton, 1980).

Because of severe structural damage and attendant human misery (Saffir, 1991; Sparks, 1991), direct effects of tropical storms on populations or communities of animals are rarely documented, and it is quite difficult to distinguish them from indirect effects subsequently caused by alterations in the physical environment or by modifications in biotic interactions. As a consequence, we use the terminology of Waide (1991b) to categorize the initial responses of animals to tropical storms (immediate, 1–3 months; short-term, 4–6 months; mid-term, 7–18 months), with responses beyond 18 months considered to be long-term consequences.

Immediate responses

Effects of Hurricane Hugo (1989) on animal populations within 3 months of impact were quite variable in Puerto Rico, depending on taxon. For example, despite reductions in density associated with the direct effects of Hurricane Hugo, total spider densities were substantially higher 3 months after the hurricane

(90 833 individuals ha^{-1}) compared to before the hurricane (Pfeiffer, 1996). Most of this increase in density was attributed to the orb-weaver, *Leucauge regnyi*. Nonetheless, responses to Hurricane Hugo were species-specific, and some taxa (e.g., the pholcid, *Modisimus signatus*) decreased in abundance. Density responses were related to habitat use; taxa that attach webs to undersides and margins of live leaves decreased in abundance, whereas species that built webs in furled dead leaves suspended from fallen branches and twigs increased in abundance (Pfeiffer, 1996). Although detailed quantitative studies of many insect species are not available prior to Hurricane Hugo (Garrison and Willig, 1996), Torres (1992) reported conspicuous increases in the abundance of a number of insects in the Luquillo Forest within 90 days of impact by Hurricane Hugo. Diptera, especially fruit flies (Drosophilidae), increased within one month of the hurricane's impact. This increase was linked to inputs of decaying fruit on the forest floor as a consequence of wind and rain associated with Hurricane Hugo. Similarly, bark beetles (Scolytidae) and pin-hole borers (Platypodidae) increased in density, as a consequence of increased quantities of decaying tree trunks and branches. Among birds, frugivores (*Columba squamosa*, *Euphonia musica*, *Geothlypis montana*) and nectarivores (*Anthracothorax viridis*, *Chlorostilbon maugaeus*, *Coereba flaveola*) clearly decreased as a consequence of Hurricane Hugo, whereas insectivores (e.g., *Todus mexicanus*) and omnivores (e.g., *Margarops fuscatus*, *Melanerpes portoricensis*, *Neospingus speculiferus*, *Turdus plumbeus*) increased in abundance (Waide, 1991a, 1996; Wunderle, 1995). Although lizards (*Anolis* spp.) did not exhibit differences in density three months after hurricane impact, their spatial (vertical) distribution was altered significantly (Reagan, 1991, 1996). Moreover, susceptibility to the effects of hurricanes may be age-dependent; for example, the density of adult frogs (*Eleutherodactylus coqui*) was unaffected, while the density of juveniles decreased in the aftermath of Hurricane Hugo (Woolbright, 1991, 1996; Stewart and Woolbright, 1996).

Like the Caribbean Basin, islands in the Indian and Pacific Oceans are subject to cyclonic storms and typhoons at relatively frequent intervals (Bani, 1992; Craig and Syron, 1992; Robertson, 1992; Elmqvist et al., 1994). In the aftermath of cyclones, substantial reductions in densities of flying foxes (Pteropodidae) have been reported at a number of sites, including Rodrigues Island (Carroll, 1984), Mauritius (Cheke

and Dahl, 1981), Guam (Wiles, 1987) and Samoa (Craig and Syron, 1992; Craig et al., 1994). Speculation suggests that some individuals are killed directly or blown far out to sea (Craig and Syron, 1992). Most data indicate that death derives from reduced health or vigor caused by diminished food supplies and increased exposure to rain, wind, and heat, as well as from enhanced predation by domestic animals (e.g., cats, dogs, and pigs) and human hunters (Stinson et al., 1992). These same indirect effects may induce bat movements to areas less devastated by the disturbance; because pteropodids are strong fliers, this includes other islands as well as protected habitats within islands (Pierson et al., 1996).

Short-term responses

The heterogeneity of response to hurricanes becomes greater when one focuses on the short term (4–6 months), and expands the geographic basis for comparison. In Puerto Rico, frugivorous and nectarivorous birds still exhibited little recovery from Hurricane Hugo, whereas insectivorous and omnivorous birds had returned to pre-hurricane densities (Waide, 1991a; Wunderle, 1995). In sharp contrast, Yih et al. (1989) reported the virtual absence of birds in Nicaraguan lowland forest 4 months after the impact of Hurricane Joan. In response to Hurricane Gilbert in Jamaica, frugivorous and nectarivorous birds decreased in montane areas, but increased in the lowlands; no consistent responses in density were observed with regard to insectivorous and omnivorous species of birds (Wunderle et al., 1992). On the Yucatan Peninsula of Mexico, frugivorous, nectarivorous, insectivorous, and omnivorous birds had not yet, in 1990, recovered to levels prior to the impact of Hurricane Gilbert; in fact, many species of frugivores and nectarivores were rare or absent (Lynch, 1991). Although Puerto Rican lizards exceeded pre-hurricane levels within 4–6 months of disturbance (Reagan, 1991), frogs continued to exhibit the same age-specific response (see above) as detected in earlier surveys (Woolbright, 1991) – namely, that juveniles were affected but not the adults.

A detailed study of two species of tree-roosting flying foxes (*Pteropus samoensis* and *P. tonganus*) on islands in the South Pacific before and after two consecutive cyclones (Ofa in 1990 and Val in 1991) provides considerable insight into the way in which large frugivorous bats respond to disturbance (Pierson et al., 1996). Prior to the impact of Cyclone Val in the Tafua Rain Forest Reserve (~5000 ha), average

density estimates of *P. tonganus* indicated about 1400 individuals in the reserve. Four months later, density estimates averaged only four individuals. In addition to such marked reductions (>99%) in density, *P. tonganus* became more diurnal and was observed feeding alone rather than in groups, often in areas of human habitation or dominated by agriculture. Similarly, in Falealupo Rain Forest Reserve (also ~5000 ha), a colony of several hundred *P. tonganus* was reduced to no more than five individuals within four months of Cyclone Ofa. In contrast, *P. samoensis* persisted in pre-cyclone roost sites, albeit in somewhat lower numbers, and continued to forage diurnally within forested areas. In response to the reduction in native fruits 4 months after Cyclone Ofa, *P. samoensis* consumed petioles of an unidentified vine that proliferated on defoliated trees, leaves of an epiphytic orchid (*Eria robusta*), and bracts of a storm-resistant liana (*Freycinetia reineckeri*) that survived the storm. Facultative folivory on the part of this species buffers it from the otherwise devastating effects of resource depletion, and is an important survival strategy in response to altered landscapes and tree phenology (Pierson et al., 1996).

Mid-term responses

Outbreaks of many species of Lepidoptera occurred in the aftermath of Hurricane Hugo (Torres, 1992). Peak lepidopteran densities, 7–9 months after the hurricane, were associated with the invasion of early-successional plants and increased proportional abundance of herbaceous plants and vines. After 12–18 months, vertebrates (birds, lizards, and frogs) differed from invertebrates in the degree to which they had recovered from the impact of Hurricane Hugo in Puerto Rico. Most of the populations of vertebrates (birds, lizards, juvenile frogs) partially or fully recovered, and some (adult frogs) appreciably exceeded pre-hurricane levels. In contrast, walking sticks or phasmids (e.g., *Agamemnon iphimedia*, *Lamponius portoricensis*), snails (*Caracolis caracolla*, *Nenia tridens*, *Polydotes acutangula*), and a slug (*Gaeotis nigrolineata*) showed severe reductions in density and altered spatial distributions one year after Hurricane Hugo (Willig and Camilo, 1991). Nonetheless, the hurricane did not affect the size-distribution of *C. caracolla* to an appreciable extent; hurricane effects were independent of size or age for this common snail.

Similarly, the response of bats to Hurricane Hugo differed in a species-specific fashion (Gannon and

Willig, 1994; Willig and Gannon, 1996). One year after the hurricane, *Artibeus jamaicensis*, a frugivore, showed a severe reduction in density; *Stenoderma rufum*, another frugivore, exhibited moderately reduced density; *Monophyllus redmani*, a nectarivore, exhibited a slight increase in density. More detailed demographic data for *S. rufum* suggested a 50% reduction in the proportion of reproductively active females, as well as a 60% reduction in the proportion of juveniles in the population. In addition, the home range and foraging range of *S. rufum* were smaller one year after the hurricane, compared to a two-year-period before it.

After 11 months of recovery from Cyclone Ofa, mean population density of *Pteropus tonganus* was only 2% of pre-cyclone numbers in Tafua Rain Forest Reserve (Pierson et al., 1996). In the Falealupo Rain Forest Reserve, bat numbers increased to less than 10% of pre-cyclone numbers (Pierson et al., 1996). High juvenile mortality after the storm (virtually 100%), combined with slow recovery by a highly damaged, preferred food source (*Syzygium inophylloides*), likely contributed to the slow recovery of the bat population.

Long-term responses

Documentation of the long-term responses of animals to hurricanes is rare. The most extensive and intensive data exist for snails, slugs, frogs, and bats in the Luquillo Experimental Forest of Puerto Rico. These studies form the basis for the exposition that follows.

Although initially their densities were much reduced after the hurricane, the most common species of snails (*Caracolis caracolla*, *Nenia tridens*, *Polydotes acutangula*) and slugs (*Gaeotis nigrolineata*), greatly exceeded their pre-hurricane densities (two- to seven-fold increases) as a consequence of five years of secondary succession in areas drastically affected by Hurricane Hugo (Bisley Watersheds) (Secrest et al., 1996; Willig et al., 1998). Large inputs of litter after the hurricane, followed by rapid development of the understory and its subsequent diminution as a consequence of canopy closure, provided increased quantities of food and substrate for these species.

In areas less drastically affected by Hurricane Hugo (El Verde), pre-hurricane surveys of gastropods were not conducted, but an extensive monitoring of attributes at population and community level provides the necessary data to assess long-term responses to hurricanes (Secrest et al., 1996; Willig et al., 1998). Demographic responses (1991 to 1995) to disturbance differed among the more common species. For example, two snail

species (*Alcaldia striata* and *Cepolis squamosa*) showed asymptotic declines in density, two species (*Nenta tridens* and *Platysuccinea portoricensis*) exhibited increases in density, one species (*P. acutangula*) declined for 2.5 years and then increased for 2.5 years, and one slug species (*Gaeotis nigrolineata*) increased for 2.5 years and then decreased for 2.5 years. Complex patterns at the community level emerge as a consequence of these fluctuations, even after controlling for differences in historical land-use. In general, species richness, evenness, and diversity declined in response to Hurricane Hugo in areas with appreciable or moderate anthropogenic disturbance in the past. In contrast, areas with little anthropogenic disturbance did not exhibit obvious or consistent trends with regard to indices of diversity. Unfortunately, previous land-use history and susceptibility to disturbance from Hurricane Hugo were confounded spatially, making interpretations of effects difficult.

Population density of *Eleutherodactylus coqui*, the most common frog in the tabonuco forest of Puerto Rico (tabonuco, *Dacryodes excelsa*, is the dominant hardwood tree) increased after Hurricane Hugo for 2.5 years, but then decreased during the subsequent 2.5 years almost to the levels before the hurricane (Stewart and Woolbright, 1996; Woolbright, 1996). The population increase was related to increases in the number of retreat sites provided by forest-floor debris from the hurricane, as well as to decreases in the abundance of predators. The subsequent decrease in frog population size was associated with the degradation of woody debris and the resurgence of predator populations.

After five years of recovery from Hurricane Hugo, the two common frugivorous bats attained numbers much greater than those prior to the hurricane (Willig and Gannon, 1996; Gannon and Willig, 1998). In particular, *Artibeus jamaicensis* was almost seven times as abundant, and *Stenoderma rufum* was approximately twice as abundant. Moreover, the proportion of reproductively active female *S. rufum* returned to pre-hurricane levels of approximately 60%.

Less than two years after the impact of Cyclone Ufa, another major cyclonic storm (Val) struck the islands of Samoa (Pierson et al., 1996). This disturbance again impinged on the Tafua Rain Forest Reserve, and within 1.5 months the population of *P. tonganus* had decreased to 5% of their pre-cyclone (but post-Ufa) numbers. After 8.5 months of secondary succession, densities were even lower less than

0.1% of pre-cyclone numbers. By mid-January, 1993 (slightly less than 3 years after Ufa and 14 months after Val), mean population had increased to about 24 individuals in the reserve. Because the population had not recovered from the severe reduction after Cyclone Ufa, it did not confront the same degree of resource depletion per capita after Cyclone Val. Fewer nutritionally compromised bats were observed, and levels of predation by humans and domesticated animals were less, at least in part because of the implementation of conservation education programs to reduce hunting pressure, especially on American Samoa (Daschbach, 1990).

In summary, the direct effects of hurricanes on terrestrial animals are poorly documented and anecdotal in nature for the most part. Nonetheless, it is clear that in some instances (reviewed by Wiley and Wunderle, 1993), rain, wind, and flooding can enhance mortality and lead to emigration, while altering migratory patterns and changing geographic distributions. Indirect effects are associated with changes in abundance of food supplies, alteration in the quality and quantity of nesting or roosting sites, changes in exposure to predation, modification of the three-dimensional structure of vegetation, altered microclimate, and interactions with human activity. Animals respond with dietary shifts, altered use of habitat and microhabitat, and modified demographic patterns (i.e., natality, mortality, emigration, and immigration). Historical contingencies (history of previous disturbance and land-use) also affect the response of animals to contemporary disturbances.

Grassland fires

Because fires have been a consistent disturbance in grasslands over their history (Anderson, 1990), they should have important effects on population and community structure of both plants and animals. Warren et al. (1987) identified three distinct phases associated with fire disturbance. The combustion phase is the period over which the fire passes through an area. The shock phase is the period between the end of the combustion phase and the initiation of plant regrowth. The recovery phase is the period between the initiation of plant growth and the eventual recovery of animal populations.

Fire has a variety of short-term and long-term effects on animal populations and communities. First, fires affect animals directly by causing mortality or

emigration during the combustion phase (reviewed by Lyon et al., 1978; Warren et al., 1987). Second, fires affect animal populations indirectly by altering the characteristics of the physical environment. This effect should be the strongest during the shock phase. Finally, fire affects animals indirectly by altering the biotic components of the community during the recovery phase.

Direct effects

Because grassland fires can be produced experimentally, it is possible to examine the direct effects of fire that occur during the combustion phase. Fire directly affects animals at this time. It may either kill the animals or cause them to emigrate from a burned area in an attempt to survive the fire [nonetheless, some species are attracted to fires and may move into a region after fires have been started (Lyon et al., 1978)]. The effect of emigration on eventual population and community structure depends on the rate at which species recolonize following fires. The rate of recolonization may be determined by the size of the fire, or the extent to which the fire alters the physical and abiotic environment. For example, mobile animals, such as birds, may be able to recolonize rapidly following a fire if environmental conditions are appropriate. Many species of ground-nesting birds were observed to lay eggs in a recently burned field, although most nests were built in regions of the field that were not damaged by the burning (Kruse and Piehl, 1985).

Fire directly causes mortality because (1) animals are consumed by the fire, (2) temperatures generated by fires (e.g., Gibson et al., 1990) are lethal (Howard et al., 1959), or (3) individuals suffocate because of reduced concentrations of atmospheric oxygen (Chew et al., 1958). The level of mortality depends on fire intensity and timing, as well as on characteristics of the species. Indirect sources of mortality also occur during the combustion phase. For example, Komarek (1970) and Gillon (1972) observed that predation rates increase during a fire because predators are attracted to the large numbers of escaping arthropods.

Animals survive high temperatures associated with grass fires (Gibson et al., 1990) either by fleeing the approaching fire or by remaining in a protected location. Thus, the survival of mobile animals should be greater than the survival of less mobile animals. For example, Warren et al. (1987) noted that orthopterans that are poor fliers, such as crickets (Gryllidae),

cockroaches (Blattidae), and mantids (Mantidae), experience high mortality during fires, whereas short-horned grasshoppers (Acrididae) were able to escape the fire because of good flying ability. In addition, parasites may be able to survive a fire by being carried away by their hosts. For example, Stoddard (1946) observed that even the most intense fires were unable to eliminate ticks, presumably because of the survival of individuals attached to vertebrate hosts that escaped the fire.

Animals that have immobile life stages may be especially susceptible to being killed by fire. For example, eggs of species that nest on the ground or lay their eggs on vegetation, litter, or the soil surface may be exposed to increased risks of mortality. Fire destroyed all nests of upland bird species such as ring-necked pheasants (*Phasianus colchicus*) and northern bobwhite (*Colinus virginianus*) in Nebraska (Erwin and Stasiak, 1979). However, fire is not necessarily fatal to ground-nesting birds. Kruse and Piehl (1985) observed that 69% of clutches of ground-nesting birds survived a fire in a North Dakota grassland. Nonetheless, most of the nests that survived were in areas that did not experience fire. Certain arthropods may be particularly susceptible to fire during the egg stage. For example, fire has been used as a mechanism to control mite species with aestivating eggs (Newman, 1936; Wallace, 1961) and to reduce the density of leaf hoppers that lay eggs on grass (Osborn, 1893; Osborn and Ball, 1897). Some gall-forming insects are highly susceptible to fire as well. Fay and Samenus (1993) observed that all galls of the cynipid wasp *Antistrophus silphii* were destroyed by an experimental fire on Konza Prairie in Kansas (U.S.A.). However, the large woody galls produced by some Australian Coccinoidea may be adaptations to fire in eucalyptus forests (Koteja, 1986).

Animals of low vagility must avoid fire-dependent mortality by minimizing *in situ* effects. Burrowing is one of the most effective means to do so, because temperature decreases rapidly as depth beneath the soil surface increases (Ahlgren and Ahlgren, 1960; Cooper, 1961; McFayden, 1968). For example, surface-dwelling spiders experience high mortality due to fires, whereas spiders that live in burrows have much lower mortality (Riechert and Reeder, 1972). Burrowing species such as ants also survive initial effects of fire (Warren et al., 1987). In contrast to large mammals that flee to avoid the effects of fire (Lyon et al., 1978), most species of small mammals rely on burrowing to survive fires (Kaufman et al., 1990). In fact, the

survival of small mammals that nest below ground (e.g., the deer mouse, *Peromyscus maniculatus*) was much higher than that of species (e.g., the harvest mouse, *Reithrodontomys megalotis*) that nested above ground (Erwin and Stasiak, 1979; Kaufman et al., 1983, 1988). In general, fire should not have a large direct effect on mortality of the soil macro- and micro-faunas because they are insulated from the direct effects of fire (James, 1982; Seastedt, 1984).

Animal species differ in their susceptibility to fire at different life stages. As a consequence, the timing of fires can have important effects on mortality rates. Some species avoid fire by producing fire-resistant stages or by living in locations where they are safe. For example, grasshopper species that overwinter in the egg stage are unaffected by spring fires, whereas species that overwinter as nymphs experience extremely high mortality (Warren et al., 1987). Many attempts to use fire as a means of pest control have shown that the timing of the fire influences the level of mortality experienced by pest populations (Warren et al., 1987).

Animals may reduce their susceptibility to fire by selecting macrohabitats or microhabitats that have a lower probability of burning or experience less intense fires. Fay and Samenus (1993) suggested that cynipid gall wasps choose to lay eggs in large clumps of their host plant rather than on isolated individuals, because these large clumps are less likely to be destroyed by fire.

Indirect effects

The destruction of litter and vegetation by fire results in an immediate change in the physical and biotic characteristics of the environment. Thus, animal species are affected indirectly by fires during the shock and recovery phases. Fire reduces plant biomass and reduces the extent of the leaf-litter layer, thereby increasing the penetration of light to the soil surface. Increased light penetration results in an increase in soil temperature and a decrease in the soil moisture content (Daubenmire, 1968; Hulbert, 1969; Owensby and Smith, 1973). Whether these environmental changes have positive or negative effects is species-specific.

Physical effects: Indirect responses to changes in the physical environment may be especially common during the shock phase. Some species living in the soil are affected by changes in the physical environment that follow fires. Decreases in populations of soil microarthropods following fires have been attributed to increases in soil temperature and decreases in soil

moisture content (Buffington, 1967; van Amburgh et al., 1981; Seastedt, 1984). The small size and high surface-to-volume ratio of microarthropods may make them especially sensitive to these changes. Alterations of environmental conditions may be favorable for some species. For example, grasshopper nymphs emerged earlier than usual following fires, because increased soil temperatures increased developmental rates (Warren et al., 1987).

Litter acts as a food source for detritivores. Thus, populations of detritivores should decrease as a consequence of emigration or mortality immediately after a fire. For example, densities of detritivorous macroinvertebrates in burned areas of Konza Prairie in Kansas were ~50% of those in unburned areas (Seastedt et al., 1985). Similarly, winter burning decreased the summer density of millipedes (Diplopoda) in an Illinois prairie (Rice, 1932).

In addition, the densities of species that rely on litter for cover should decrease following fires. Tester and Marshall (1961) attributed decreases in grasshopper abundance following fires to a reduction in cover. Clark and Kaufman (1990) suggested that prairie voles (*Microtus ochrogaster*) emigrated from burned areas because the reduction of litter did not allow them to construct runways or nests. Conversely, species that prefer more open conditions may respond positively to the removal of litter. For example, Kaufman et al. (1988) and Clark and Kaufman (1990) suggested that deer mice immigrated into burned areas in response to the open vegetation structure and sparse litter cover.

Changes in physical characteristics also may limit immigration into disturbed areas following a fire. For example, immigration of spiders following a fire that killed most of the residents was limited to those species that are capable of tolerating decreased moisture availability and the reduced availability of support structures needed for web construction (Riechert and Reeder, 1972).

Biological effects: The eventual recovery of animal communities following fire is affected strongly by interactions within the biotic component of the environment. Because plants affect the physical environment, act as a source of cover, or act as a source of food, the recovery of animal communities is predicated on the recovery of the plant community. Similarly, the recovery of certain animal species may be affected by the recovery of other animal species that act as their prey or their predators. Because plant

community response depends on the season of the fire (Owensby and Anderson, 1967; Bragg, 1982; Towne and Owensby, 1984; Hulbert, 1985), the response of many animal species is dependent on when the prairie burns. Moreover, the plant community may recover relatively slowly following fire, and as a result, the recovery phase for animal species may be protracted.

Fires in grasslands affect the phenology, species composition, and productivity of the plant community. Fire tends to increase the proportion of warm-season grasses while decreasing the proportion of cool-season grasses and forbs (Gibson, 1989). In general, burning increases the subsequent production of foliage, rhizomes, and roots of prairie grasses (Hadley and Kieckhefer, 1963; Kucera and Dahlman, 1968). Consequently, population sizes of herbivorous species that either survive the fire or immigrate into burned regions should increase following fires. Numerous studies have documented such an increase in populations of phytophagous hemipterans and homopterans following fires (reviewed by Warren et al., 1987), although this pattern was not ubiquitous. In addition, lepidopteran densities increased following fire (Warren et al., 1987), as did dipterans with herbivorous larvae (van Amburgh et al., 1981).

Evans (1984, 1988a,b) studied the response of grasshopper communities to fire on Konza Prairie, and demonstrated how the response of animals depends on fire history. His studies documented the response of grasshoppers to spring fires set on sites that differed in fire history (unburned, burned every year, burned every other year, or burned once every four years). Fire-induced mortality of grasshoppers was low because most of the individuals, regardless of species, were present as eggs in the soil, which provided protection from elevated temperatures and reduced concentrations of atmospheric oxygen (Knutson and Campbell, 1976). Thus, interspecific differences in response to fire were due to differences in post-hatching survival, emigration, or reproductive rates.

Differences in fire history affected plant-community composition and diversity which in turn affected the grasshopper community. Forbs were less abundant in annually burned regions than in less-frequently or unburned regions (Gibson and Hulbert, 1987; Evans, 1988a). Plant species richness and diversity increased with decreasing fire frequency (Abrams and Hulbert, 1987; Gibson and Hulbert, 1987). These differences were mirrored in the composition of the grasshopper community, in that forb feeders became relatively less

common as fire frequency increased, and grasshopper species richness or diversity was correlated positively with plant richness or diversity.

Population sizes of root-feeding arthropods should be higher following burns because of higher root production. Scarabid beetle larvae and cicada nymphs were more abundant in burned than in unburned prairie (Seastedt, 1984; Seastedt et al., 1985). However, densities of some root-feeding homopterans were not affected by burning (Seastedt and Reddy, 1991). Populations of earthworms were higher in burned than in unburned areas (James, 1982), suggesting that these organisms also responded positively to the increased production of roots following fires.

Populations of carnivorous species whose prey populations increase following a fire should increase as well. The density of predaceous damselflies, dragonflies, and wasps increased following fire (Hurst, 1971; van Amburgh et al., 1981). Few studies have monitored simultaneously the fire response of predators and their prey.

In summary, animals may escape the direct effects of fire by fleeing or seeking refuge in protected locations. Animals that live or nest below ground tend to suffer fewer direct effects than do animals that live or nest on the surface. Disturbances may indirectly affect animals by causing alterations of the physical environment. Species that feed on or live in the leaf litter may suffer negative effects following the removal of litter by fire, and soil arthropods are affected negatively by the increase in soil temperature and decrease in soil moisture content that occurs following the removal of vegetation and litter. The ultimate recovery of animals following disturbance is influenced strongly by changes in the biotic community. Populations of above- and below-ground herbivores may increase following fires as a result of increased production of roots and above-ground vegetation.

Forest tree-falls

In many forest ecosystems, tree-falls are important agents of landscape heterogeneity (Brokaw and Scheiner, 1989; Poulson and Platt, 1989; Spies and Franklin, 1989; Veblen, 1989). Depending on their size and shape, tree-falls open space in the canopy, redistribute biomass to the forest floor, and alter microclimatic conditions. As a consequence, many forests are a melange of patches that differ because they are in different stages of secondary succession

(Brokaw, 1985; Runkle, 1985; Veblen, 1985). This has led Lieberman et al. (1989) to advocate abandonment of the treatment of forests as a mosaic of two states – gap and non-gap – in favor of a gradient approach based on a continuum of forest geometries. In either case, spatial heterogeneity should be reflected in the distribution and activities of animals as well as plants; consequently, it has been hypothesized that patch-generating phenomena are a diversity-enhancing mechanism in many ecological systems (e.g., Denslow, 1985; Pickett and White, 1985).

Birds

Tree-fall gaps affect the abundance and diversity of tropical birds in Panama (Schemske and Brokaw, 1981). Some species clearly prefer gaps (e.g., *Cyanocopsa cyanooides*, *Cyphorhinus phaeocephalus*, *Dysithamnus puncticeps*, *Hylophylax naeviooides*, *Threnetes ruckeri*), whereas others prefer the forest matrix (e.g., *Gymnopithys leucaspis*, *Pipra mentalis*, *Platyrinchus coronatus*). Moreover, 19 additional species of birds, most of them rare or uncommon, were captured exclusively in forest gaps. The vast majority of gap specialists were insectivores, and none were frugivores. As a consequence of these species- or guild-specific differences in abundance, distinct bird assemblages were documented for gaps versus the forest matrix.

Nectarivorous birds in a Costa Rican cloud forest responded to the distinctive characteristics of tree-fall gaps as well (Feinsinger et al., 1988). Species richness as well as total density in tree-falls was higher than in mature forest, consistent with the greater density of flowers there. Nonetheless, true gap specialists were not detected for the nectarivore guild. The frequent appearance, low intensity, and rapid recovery of gaps were considered to be driving conditions that allow the accommodation of generalist species to a heterogeneous landscape and diminish selective pressures that favor gap specialists.

Similarly, differences at the population and community levels were detected between tree-fall gaps and surrounding matrix in the tabonuco forest of Puerto Rico (Wunderle et al., 1987). Four of 17 species were captured more frequently in gaps than in forest (*Chlorostilbon maugaeus*, *Coereba flaveola*, *Dendroica caerulescens*, *Loxigilla portoricensis*), but only one of them (*D. caerulescens*) was not captured in mature forest as well. The distinctive species composition of gaps and forest is more a product of differences in

bird density than differences in presence or absence of species, *per se*. In fact, it was argued that the small size and rarity of gaps in tabonuco forest were characteristics selecting against the production of gap specialists. Those species found more frequently in gaps than in mature forest were canopy species that follow the border of the canopy into and out of gaps. Moreover, differential responses by birds to gaps and forest matrix are context-dependent (Wunderle, 1995). Although new gaps and surrounding forest were statistically distinguishable based on foliage profiles one year after the passage of Hurricane Hugo, no significant differences existed between their avifaunas at that time. Most birds may not respond directly to the differences in foliage profiles between gaps and forest matrix; rather, differential habitat use is based on the existence of distinctive food resources, and these are not sufficiently different between habitats after one year of secondary succession. Wunderle (1995) hypothesized that, because of the slow rate of canopy closure in tabonuco forest after a hurricane, many years may pass before gaps and forest matrix are sufficiently distinctive in vegetative structure and resource profile to support distinctive bird assemblages.

Birds in upland deciduous forest of Illinois (U.S.A.) responded differentially to gaps compared to surrounding forest (Blake and Hoppes, 1986), and did so in a season-dependent fashion. In general, more individuals and greater species richness were recorded in gaps compared to forest understory in spring and fall. Nonetheless, total species richness in gaps was not different from that in forest sites. However, a large number of species exhibited significant preferences for gap habitats, including *Carduelis tristis*, *Catharus ustulatus*, *Dendroica fusca*, *D. magnolia*, *Dumetella carolinensis*, *Empidonax flaviventris*, *Regulus calendula*, *R. satrapa*, *Seiurus aurocapillus*, *S. noveboracensis*, *Setophaga ruticilla*, *Vireo olivaceus*, *Wilsonia canadensis* and *Zonotrichia albicollis*. Most gap species were birds that foraged on the ground or in lower vegetation, and most were not following the border of the canopy into or out of gaps. Most feeding guilds (e.g., flycatchers, ground insectivores, foliage insectivores, granivore-omnivores, and frugivores) were represented by more individuals in gaps than in forest understory. No guild preferred the forest understory, and only one guild (bark foragers) occurred equally in gaps and in forest.

Mammals

Rain-forest bats in Australia strongly differentiate

between forest matrix and moderate-sized (0.03–0.07 ha) gaps produced by felling (Crome and Richards, 1988). Four bat species (*Eptesicus sagittula*, *Hipposideros ater*, *Nyctophilus gouldi*, *Rhinolopus megalophyllus*) were recorded exclusively in forest matrix, whereas five species (*Chaerophon jobensis*, *Chalinolobus nigrogriseus*, *Mormopterus beccarii*, *M. planiceps*, *Scotorepens halstoni*) were recorded exclusively in gaps. Only three species (*Eptesicus pumilus*, *Hipposideros diadema*, and an unknown taxon, possibly *Emballonura nigrescens* or a close relative) were “gap-incorporators” – in other words, they were detected in both gap and closed-canopy situations. Importantly, gap-incorporators accounted for little of the activity in either habitat (8% in gaps, 27% in closed canopy). This is markedly different from the situation for birds in tropical or temperate ecosystems, where most species are gap incorporators (Schemske and Brokaw, 1981; Blake and Hoppes, 1986; Wunderle et al., 1987; Feinsinger et al., 1988). Moreover, these three groups of bats exhibited distinct morphologies related to considerations of aerodynamic capability (e.g., aspect ratio and wing loading). Gap specialists are fast flyers with high aspect ratio and wing loading, canopy specialists are slower and more maneuverable (low aspect ratio and wing loading), gap-incorporators are intermediate in morphology.

Invertebrates

Because of their small size and reduced mobility compared to volant vertebrates, one might expect invertebrates to respond more strongly to the dichotomy between gap and forest matrix. Although insects exhibit numerous adaptations to disturbance (Schowalter, 1985), few studies have addressed, in a quantitative fashion, the responses of invertebrates, at population or community level, to gaps created by tree-falls.

A comparison of gastropod density in tree-fall gaps to density in adjacent areas of undisturbed understory has been undertaken in the tabonuco forest of Puerto Rico [unpublished observations by Alvarez (1991) and Alvarez and Willig (1993)]. Only three species were exclusively captured in gaps (*Cepolis squamosa*, *Oleacina playa*, *Vaginulus occidentalis*), and each of them was quite rare (approximately 0.1% of the total captures). Five species evinced sufficiently high density to allow statistical evaluation of disturbance effects. Three species (*Austroselenites alticola*, *Megalomastoma croceum*, *Subulina octana*) did not differ in density between gap and undisturbed understory. In

contrast, the density of *Nenia tridens* was higher in gaps than in understory, while the density of *Caracollus caracolla* was higher in undisturbed understory than in the gaps. The higher abundance of *N. tridens* in gaps was attributed to increased availability of substrate (dead wood) and food (fungi and algae). The preference of *C. caracolla* for undisturbed areas of the understory may be related to abiotic factors and physiological limitations (microclimatic conditions reducing evaporative water loss). One of the snail species (*C. squamosa*), exclusively detected in gaps during pre-hurricane surveys, became a common member of the snail community within one year of the hurricane's impact (Willig et al., 1998). As the canopy closed during secondary succession, quantities of dead and decaying branches decreased; concomitantly, abundance of *C. squamosa* decreased from approximately 190 individuals ha⁻¹ in 1991, to less than 50 individuals ha⁻¹ in 1995 (Willig et al., 1998).

At the community level, a number of important differences exist between gaps and forest understory. Snail species diversity in quadrats of 8 m² in Puerto Rico was significantly higher in undisturbed understory than in tree-fall gaps (Alvarez, 1991; Alvarez and Willig, 1993). Moreover, differences in snail species composition between gaps and understory were consistent, regardless of season. Compositional differences were reflected in the greater turnover of species between gap and undisturbed forest, than between sites within gaps or between sites within forest understory.

In summary, few data are available to document the direct effects of tree-falls on populations or communities of animals. Indirect effects include alteration of microclimatic conditions, especially temperature and humidity, addition of biomass to the forest floor, which increases structural complexity and the quantity of dead and decaying material, and recruitment of early-successional plants. The response of animal species depends upon their trophic position, physiological capabilities, mobility, and interactions with other members of the biota.

ANIMALS: UBIQUITOUS AGENTS OF DISTURBANCE

Animals are agents of disturbances through their usual activities including movement, feeding, building, digging, burrowing, elimination, and death. Animal-generated disturbances generally occur more fre-

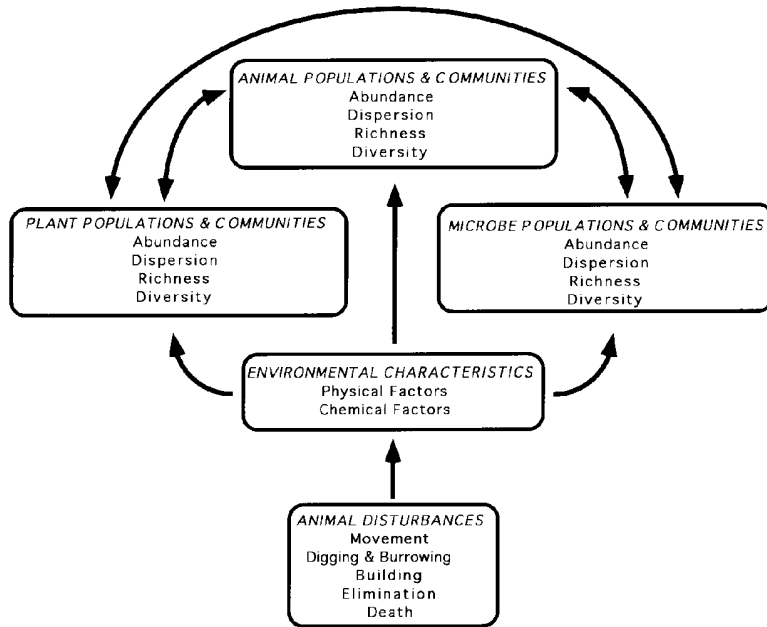


Fig. 27.3. Conceptual model illustrating the mechanisms whereby the direct effects of animal disturbance on environmental conditions indirectly affect the biota.

quently, but are smaller in extent and smaller in magnitude than are abiotogenic disturbances generated by climatological or geological events. However, animal-generated disturbances can have profound direct and indirect effects (Schowalter and Lowman, Chapter 9; Oesterheld et al., Chapter 11; MacMahon, Chapter 12; Bradbury, Chapter 24; this volume) on the structure of plant, animal, and microbial communities (Fig. 27.3). In general, the importance of animal-generated disturbances comes not from their direct effects as destructive events, but rather from the indirect effects that arise as a result of their alteration of the environment. An important effect of many animal-generated disturbances is the creation of novel habitats that often harbor their own unique combinations of species.

Movement

The physical forces that derive from locomotion by animals can act as a disturbance, either by causing mortality or by altering environmental conditions (Harper, 1977). For example, trampling by grazing animals can reduce the depth of leaf litter (Johnston,

1961; Johnston et al., 1971; Langlands and Bennett, 1973; Leege et al., 1981; Naeth et al., 1991; Holland, 1994), increase proportion of bare ground (Langlands and Bennett, 1973; Bassett, 1980; Williams, 1992), or compress the soil (Johnston et al., 1971; Langlands and Bennett, 1973; Gibson, 1988). Even the coiling behavior of rattlesnakes can alter the distribution of leaf litter on the soil surface (McGinley, pers. observ.).

The effects of animal movement depend on a number of characteristics, including the mass of the animal, as well as the number of animals and the frequency with which they move through an area. These likely depend on the social and spacing system of a species. For example, the effects of movement of colonial animals are more concentrated than are the effects of solitary animals. Moreover, the effect of movement may depend on the activity with which it is associated. If animals are traveling to and from foraging or mating areas, their activities usually are concentrated on trails, where the repeated passage of animals effects the removal of vegetation. However, if animals are traversing a habitat in search of food, the effects of movement are more dispersed throughout the area.

Trampling may indirectly alter abiotic soil char-

acteristics. The fragmentation and reduction of leaf litter increases the amount of insolation reaching the soil surface and consequently results in an increase in soil temperature (Weaver and Rowland, 1952; Johnston et al., 1971; Langlands and Bennett, 1973; Knapp and Seastedt, 1986) and a decrease in soil moisture content (Johnston et al., 1971; Langlands and Bennett, 1973; Knapp and Seastedt, 1986). Trampling by cattle can increase rates of litter decomposition, which in turn affects rates of loss of nutrients due to leaching (Knapp and Seastedt, 1986). Furthermore, trampling compacts the soil (Johnston et al., 1971; Langlands and Bennett, 1973; Gibson, 1988), which can reduce the amount of nutrients lost through leaching (Langlands and Bennett, 1973; Knapp and Seastedt, 1986). The relatively ubiquitous effect of activity by cattle likely homogenizes many aspects of the environment (Rusch, 1992).

Digging and burrowing

Many species search for food by digging, or dig burrows to provide protection, nesting sites, and secure food caches. In fact, the burrowing activity of soil micro- and macrofauna is essential for the formation and maintenance of soil characteristics (Killham, 1994). Clearly, soil animals play an important role in decomposition. Burrowing animals, especially earthworms, are responsible for mixing organic matter throughout the soil profile (Killham, 1994), thereby affecting the spatial distribution of plants and microbes.

The direct effects of digging and burrowing by larger animals include the death of plants by burial, and the exposure of the soil surface creating bare spaces. The effects of digging and burrowing may be concentrated when associated with colonial species such as prairie dogs (*Cynomys* spp.), or dispersed across a habitat for more solitary species such as pocket gophers (*Geomys* spp.), kangaroo rats (*Dipodomys* spp.), and badgers (*Taxidea taxus*).

In general, digging activity generates heterogeneity in environmental conditions such as soil depth (Kershaw, 1959) and nutrient content (e.g., Gibson, 1988; Moorhead et al., 1988; Reader and Buck, 1991; Dhillon et al., 1994; McGinley et al., 1994). In addition, digging affects the distribution, abundance, and composition of soil microbial communities (Allen et al., 1992; Friese and Allen, 1993; Dhillon et al., 1994; McGinley et al., 1994) and opens sites for plant regeneration. The effects of animal-generated

disturbance on plant communities have been well documented (e.g., Platt, 1975; Hobbs and Mooney, 1985; Huntly and Inouye, 1988; Moorhead et al., 1988; Peart, 1989; Coffin and Lauenroth, 1990; Mun and Whitford, 1990; Dean and Milton, 1991; Reader and Buck, 1991). Interestingly, the production of mounds may also have direct effects on animal populations. For example, grasshopper abundance was correlated with the density of gopher mounds, because the mounds were used as oviposition sites by the grasshoppers (Huntly and Inouye, 1988).

In addition, animal burrows represent novel habitats. The burrows of prairie dogs are used by a number of other species of animals (Hoogland, 1995). For example, the abundance and spatial distribution of the burrowing owl (*Speotyto cunicularia*) depends on the availability of preexisting burrows of rodents or badgers (Best, 1969; Green and Anthony, 1989). Heteromyid rodents often store food in large subterranean burrow systems (Voorhies and Taylor, 1922; Reichman et al., 1985). The warm temperature and high humidity in the burrows of the banner-tailed kangaroo rat (*Dipodomys spectabilis*) allow the development of a diverse and distinctive fungal community compared to that found outside the burrow (Reichman et al., 1985).

Building

Many birds construct nests (Welty, 1982); some mammals such as beavers (Grinnell et al., 1937), muskrats (Errington, 1963), and woodrats (Linsdale and Tevis Jr, 1951; Rainey, 1956; Finley, 1958) build houses; and some insects such as termites, wasps, and ants build mounds or nests (Borror et al., 1989). The collection of materials for house building by mammals such as beavers and woodrats directly alters the distribution of woody biomass in the ecosystem. Not only does house building concentrate wood at the house site, but because selectivity varies as a function of distance (McGinley, 1984), it also results in an unequal distribution of stick sizes across the landscape. This redistribution of woody biomass can alter patterns of nutrient cycling. The concentration of wood in houses produces "islands of fertility" which affect the subsequent growth of woody and herbaceous plants (Zak et al., 1994). Moreover, woodrat houses are inhabited by a variety of species, including snakes, lizards, toads, and small mammals (Fitch and Rainey, 1956).

The building of dams by beavers results in larger

effects than would be predicted by their size, activity, or abundance (Naiman et al., 1994). Beaver dams alter stream characteristics, alter nutrient flow, modify riparian zones, and create wetland habitat (Naiman et al., 1986, 1994; Naiman, 1988; Smith et al., 1991). Such alterations affect the use of habitat by terrestrial animals, as well as altering population sizes and community composition of terrestrial insects with aquatic larvae (Clifford et al., 1993).

Some termites build large mounds (Howse, 1970; Lee and Wood, 1971). Nutrients in the soil of termite mounds are unavailable for use by plants. For example, mounds in a savanna in the Northern Territory, Australia, held 2% of the total soil, 9% of the total organic carbon, 5% of the total nitrogen, and 11% of the total calcium in the system (Lee and Wood, 1971). The redistribution of nutrients by termites can affect patterns of vegetation, and large termite mounds can support distinct vegetation (Lee and Wood, 1971). The mounds of some species of termites contain fungal gardens which provide sites for a unique fungal community (Bakshi, 1962; Howse, 1970).

Waste products

The disposal of waste products by animals (i.e., elimination and defecation) has important direct and indirect effects. Fecal deposition by cattle may directly affect plants by acting as a cause of mortality or a barrier to the establishment of seedlings, and indirectly by influencing abiotic soil characteristics (Harper, 1977). For example, the deposition of dung by cattle can add nutrients such as nitrogen, phosphorus, potassium, calcium, magnesium, and a number of trace elements to the soil (Petersen et al., 1956b; Underwood, 1956; Barrow, 1967; Weeda, 1967; MacDiarmid and Watkin, 1972). As a result, nutrient content directly beneath cattle feces is different than that of adjacent soils. The deposition of feces by smaller herbivores, such as rabbits, also influences soil fertility. For example, the feces of jackrabbits (*Lepus californicus*) annually represent up to 4% of the standing crop of nitrogen in the Chihuahuan Desert (Shoemaker et al., 1973; Gist and Sferra, 1978).

Defecation generates spatial and temporal heterogeneity in environmental characteristics. Because of patterns of cattle activity, feces are not distributed uniformly across the landscape (Petersen et al., 1956a). Moreover, differences in rates of release of nutrients from decomposition, and nutrient-specific differences

in lability in the soil, can generate variation in nutrient content over time. For example, nitrogen and potassium under cattle dung attain a peak in concentration soon after deposition, and decrease rapidly (Weeda, 1967; MacDiarmid and Watkin, 1972), so that their effects are short-lived. In contrast, phosphorous and calcium in the soil generally increase more slowly and remain elevated for extended periods of time (Weeda, 1967; MacDiarmid and Watkin, 1972).

The addition of nutrients through feces affects plant growth and community composition. In pastures, addition of cow dung increased productivity of adjacent plants (Weeda 1967; MacDiarmid and Watkin, 1972). Moreover, the alteration of nutrient content results in changes in species composition of plant communities (Norman and Green, 1958; Weeda, 1967; MacDiarmid and Watkin, 1971). The addition of dung from smaller herbivores may affect plant growth as well. Watt (1981) suggested that the growth and survival of several species were affected by decomposition of rabbit dung.

The addition of feces to the environment provides a novel habitat for colonization by decomposers. From that perspective, the community dynamics during dung decomposition has been well studied (e.g., Valiela, 1969; Hanski and Koskela, 1977; Doube, 1987). In general, feces represent an ephemeral resource that is variable in space and time (Doube, 1987). Fecal communities were similar to, but only a subset of, communities found in decomposing carcasses (Doube, 1987; and see below). Interestingly, the dung community is well adapted to the characteristics of the feces of the native fauna. For example, when cattle were introduced to Australia, their dung was decomposed poorly by the native fauna. As a consequence, dung beetles were introduced to break down feces of these exotic mammalian herbivores (Waterhouse, 1974; Doube, 1987).

When defecation is localized, the accumulation of feces can form the basis of unique ecosystems. Such communities are found in caves in the accumulations of guano produced by bats (e.g., Martin, 1977; Benarh and Kunz, 1981; Culver, 1982; Conn and Marshall, 1991; Whitaker et al., 1991) or crickets (Poulson and Kanc, 1981; Poulson et al., 1995). The input of guano and other detritus provides the base of the food chain for these communities, described at length in Volume 30 of this Series. The amount and quality of guano differs between sites and varies over time in response to differences in climate (Poulson et al., 1995), or the diet

and physiological state (e.g., maternity colonies versus hibernacula) of the bats (Studier et al., 1994). Such communities contain disparate feeding guilds including fungivores (e.g., acarins, psocopterans), detritivores (e.g., coleopterans, dipterans), predators (e.g., acarins, coleopterans, hemipterans), and ectoparasites (e.g., hemipterans, siphonopterans; Benarth and Kunz, 1981; Whitaker et al., 1991; Trajano and Gnaspini-Netto, 1994). Moreover, many of the microclimatic attributes (temperature, humidity, ammonia concentration) of these cave ecosystems are a consequence of the processing of guano by the resident biota.

Death

The decomposition of animal carcasses alters environmental conditions in a manner that affects surrounding vegetation and soil fauna for an extended period of time. According to Bornemissza (1958), plants beneath a carcass may be killed, but the growth of plants in a zone surrounding the carcass increase. In addition, Bornemissza found that the decaying carcass interacted with leaf litter to form a crust that inhibited plant regeneration for over a year. By-products from the decomposition of carrion reduced the density of the usual soil fauna. For example, the densities of Collembola and Acari were reduced beneath a carcass during particular periods of decomposition, and some species were eliminated completely for a period of over a year.

Carcasses provide novel habitats for organisms in the detrital circuit. The succession of animal species that inhabit decaying carcasses has been well documented (Putman, 1978a; Beaver, 1984; Schoenly and Reid, 1987). Putman (1978b) examined the flow of energy and nutrients from a carcass during decomposition. In fact, patterns of carrion succession are so predictable that they have been used by forensic scientists to estimate the time of death (e.g., Catts and Goff, 1992; Goff, 1993). Decomposing carcasses contain diverse communities including primary consumers such as fly larvae and dung beetles, and higher-level consumers, such as predatory beetles (reviewed by Doube, 1987). Guilds of primary consumers include species that consume moist flesh (e.g., sarcophagid fly larvae), dry flesh (e.g., phorid flies), skin (e.g., dermestid beetles), and dung (e.g., scarabaeid dung beetles), whereas guilds of secondary consumers include both predators and parasitoids. These taxa and feeding guilds would not otherwise occur within the terrestrial community.

A CASE STUDY: THE SAND SHINNER OAK ECOSYSTEM

The effects of animals on the sand shinner oak ecosystem of western Texas provide an illustrative example of biogenic disturbances (Fig. 27.4). Sand shinner oak (*Quercus havardii*) is a low-growing (<1 m tall), clonal species that is dominant on sandy soils in the Southern High Plains (Dhillion et al., 1994). The plant community consists of an almost continuous cover of oak (>85%) with an understory of predominantly herbaceous, prairie species (Dhillion et al., 1994; Holland, 1994). Because of the abiotic factors that characterize this ecosystem (i.e., sandy soils, low rainfall, and cold winter temperatures; Dhillion et al., 1994), disturbances produced by animals may be especially important. The oak is deciduous and rates of decomposition are low, so the soil is covered by a layer of leaf litter which appears to limit plant regeneration (Dhillion et al., 1994; and unpublished observations of McGinley and Jeffery). The sandy soil is home to a number of species of burrowing animals such as pocket gophers (*Geomys bursarius*), cottontail rabbits (*Sylvilagus audubonii*), heteromyid rodents (e.g., *Dipodomys ordii* and *Perognathus flavescens*), and several species of ants (e.g., *Crematogaster punctulata*, *Pheidole dentata*, *Pogonomyrmex barbatus*), whose digging or mound-building activities produce soil disturbances that open sites in the leaf litter through the removal or burial of litter (Dhillion et al., 1994). Grazing by cattle is a common agricultural practice in this region, so the sand shinner oak ecosystem is disturbed by the activity of cattle as well.

Dhillion et al. (1994) reported that soil disturbances produced by animals created variation in abiotic and biotic characteristics of soils. For example, soil associated with active mounds of cottontail rabbits had higher nitrogen and magnesium contents, higher organic matter concentrations, and higher densities of fungi and bacteria than did soils from adjacent non-mound areas. Soil nutrient content, organic matter content, moisture, pH, and the potential for mycorrhizal infection differed among soils associated with mounds built by the three species of ants mentioned (McGinley et al., 1994). The addition of feces by cattle and rabbits increased nutrient and organic matter, and altered the microbial content of soil (unpublished observations of McGinley and Purdom). Experiments that mimicked animal disturbance through the removal of leaf litter were sufficient to alter the nutrient

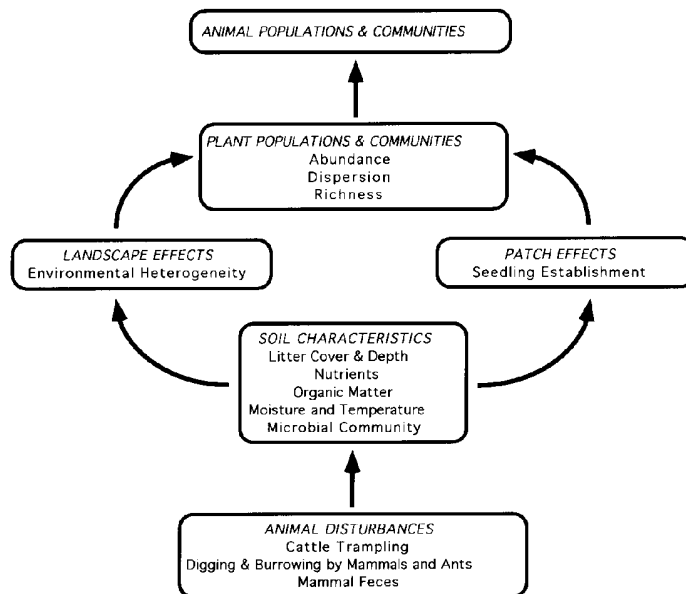


Fig. 27.4. Conceptual model illustrating the mechanisms through which animal disturbances affect populations and communities of plants and animals in the sand shinnery oak ecosystem of western Texas. Effects of animal disturbance on soil characteristics appear at landscape or patch scales, which together affect plant populations and communities.

content of soils for at least three years (unpublished observations of McGinley and Jeffery). Thus, the activity of animals acted as an important source of environmental heterogeneity, and the effects of animal disturbance persisted for long periods of time.

Environmental heterogeneity created by animal disturbance affected seedling establishment. Seedlings of the perennial grasses, sand dropseed (*Sporobolus cryptandrus*) and Lehman's lovegrass (*Eragrostis lehmanniana*), survived better in greenhouse studies when grown in soil collected from gopher or harvester-ant mounds than when grown in soil collected from rabbit mounds (unpublished observations of McGinley et al.). Environmental heterogeneity also affected seedling growth rates. For example, seedlings of the perennial grass, little bluestem (*Schizachyrium scoparium*), grown in the greenhouse in soil collected from mounds of *Pogonomyrmex barbatus* were twice as large as seedlings grown in soil collected from mounds of *Crematogaster punctulata* and *Pheidole dentata*. This difference likely occurred because soils from *Pogonomyrmex* mounds contained more nitrogen than did soils from mounds of the other two species (McGinley et al., 1994).

Not all species responded to animal-generated environmental variation in the same manner. In greenhouse studies, seedlings of little bluestem, unlike those of sand dropseed and Lehman's lovegrass, survived equally well in soil collected from harvester-ant, gopher, or rabbit mounds. Seedlings of blue grama (*Bouteloua gracilis*) and little bluestem were larger when grown in soil collected beneath rabbit feces than when grown in typical soil, whereas the growth rate of seedlings of sand lovegrass (*Eragrostis trichodes*) was not affected by the deposition of rabbit feces (unpublished observations of McGinley and Purdom). Thus, animal disturbance affected different species in different ways.

An important effect of animal-generated soil disturbances in this community was to open sites for plant regeneration (Dhillion et al., 1994). Seventy-one percent of seedlings were associated with disturbed sites even though bare ground constituted only 19% of the total area (Dhillion et al., 1994). Moreover, herbaceous plant density was positively correlated with the number of disturbances in ungrazed areas (unpublished observations of McGinley). Thus, animal disturbance played an important role in determining the

abundance of herbaceous plants in sand shinnery oak communities.

Animal disturbance also affected patterns of plant dispersion. Animal disturbances were distributed in a patchy fashion (Holland, 1994); because animal disturbance influences plant establishment, patterns of herbaceous plant dispersion should match patterns of disturbance. As expected, there were similarities in the spatial dispersion of *Euphorbia fendleri*, a species that can only establish in bare ground (unpublished observations of McGinley and Jeffery) and the spatial distributions of animal disturbances (Holland, 1994).

Environmental heterogeneity associated with animal-generated disturbances of soil was sufficiently large to alter plant-microbe interactions (McGinley et al., 1994). For example, infection by mycorrhizal fungi enhanced the growth of seedlings of little bluestem when grown in the greenhouse in soil from ant mounds (*P. dentata* and *C. punctulata*) with low nitrogen content. However, mycorrhizal infection decreased the growth of seedlings of little bluestem in soil from ant mounds (*P. barbatus*) with high nitrogen content. Environmental heterogeneity produced by animal disturbance shifted the mycorrhiza-plant interaction from mutualism to parasitism.

Cattle activity influenced patterns of abiotic characteristics as well as patterns of herbaceous plant dispersion, abundance, and diversity in sand shinnery oak ecosystems (Holland, 1994). The activity of cattle reduced litter depth and increased the cover of bare ground. The concentration of soil nutrients other than nitrogen (i.e., calcium, magnesium, phosphorus, and sodium) was lower in grazed regions than in ungrazed regions. In addition, variation in the content of most soil nutrients (calcium, magnesium, phosphorus, and sodium; but not nitrogen) was higher in grazed than in ungrazed areas. This, combined with the fact that dispersions of herbaceous plants were more clumped in the ungrazed region than in the grazed region, suggests that cattle activity had a homogenizing effect in this environment.

The greater proportion of bare ground and shallower depth of litter caused by the activity of cattle offered increased opportunities for seedling establishment in grazed regions. The density of herbaceous plants was almost twice as high in grazed as in ungrazed regions (Holland, 1994). Because species richness in a quadrat of 4 m² is highly correlated with the number of individual plants in that area, quadrats in grazed areas contained approximately twice as many species as did

quadrats in ungrazed areas. Thus, disturbance by cattle increased species richness at a local scale.

Animal-induced changes in the physical environment, as well as modifications of the spatial dispersion, abundance, composition, and diversity of the plant community, may have indirect effects on animal populations and communities. Population sizes of herbivores may be predicted to respond positively to increased abundance of herbaceous plants associated with grazing. Grasshoppers (e.g., *Arphia conspersa*, *Brachystola magna*, *Dactyloctenium aegyptium*, *Melanoplus* spp. and *Schistocerca alutacea*) were common herbivores in the sand shinnery oak ecosystem, and their densities were higher in grazed than in ungrazed regions of this community (M.A. McGinley, pers. observ.). In contrast, the activity of cattle did not affect differences between grazed and ungrazed regions in the abundance or dispersion of ant or gopher mounds (Holland, 1994).

The consequences of disturbance on the abiotic environment and structure of the plant community lingered for some time. The effects of litter removal (experimental treatments differed in the amount and pattern of litter removal) were still evident three years after the initial disturbance (unpublished observations of McGinley et al.). Plots in which all litter was removed, subsequently had more bare ground and shallower leaf litter even after three seasons of leaf fall. In addition, soil nutrient content differed between plots where all litter was removed and plots that were continuously covered by litter. Moreover, seedlings of sand dropseed were larger when grown in the greenhouse in soil collected in plots that had been continuously covered with litter than when grown in soil from plots where litter was removed. These differences in seedling growth led to differences in the size distributions of adult plants in the field. Plants grown in undisturbed plots in the field were larger than plants growing in plots where litter was removed. Moreover, abundances and species richness of herbaceous plants were higher in plots where litter had been experimentally removed three years earlier compared to those which were undisturbed.

In summary, the effects of any single animal-generated disturbance was small and localized. Nonetheless, their cumulative effects were large because they were frequent, pervasive, and potentially long-lasting in this community. A common effect of animal disturbance was the opening of sites for herbaceous plant regeneration by removal and burial of the leaf litter. In addition, animal disturbance acted as a source

Table 27.1
Generalizations concerning the characteristics of animals which influence their responses to direct and indirect effects of disturbances

Characteristic	Description
Mobility	organisms of low mobility are more likely to suffer high mortality because of their inability to avoid the deleterious effects of a disturbance by seeking refugia <i>in situ</i> or fleeing to other areas; similarly, rates of establishment should be higher for mobile species (high colonization rate) with appropriate phenotypic attributes to prosper in a post-disturbance environment
Habitat/microhabitat	subterranean organisms as well as organisms that inhabit protected locations (e.g., caves) should experience lower direct mortality than do surface-dwelling animals; associations between habitat affinity and indirect responses depend upon the peculiarities of the disturbance and specific habitat requirements of the species
Life history	different life stages (e.g., pupae versus adult) may be more or less vulnerable to direct effects of disturbance, depending on the particulars of the disturbance and the phenotypes of the life stages; in addition, organismal response to disturbance may be dependent on the timing of the disturbance with respect to the phenology and ontogeny of the species
Body size	smaller animals (higher surface to volume ratios) should be more vulnerable to alterations in temperature and humidity as a consequence of disturbance; on the other hand, small size may allow species to exploit microhabitats that provide protection from the altered abiotic environment; smaller species may also recover more rapidly because of their higher reproductive rates and shorter generation times
Trophic position	responses of animals to direct effects of a disturbance are independent of trophic status; the response of a species to changes in the biotic environment should depend on how direct and indirect effects have altered its food supply, as well as the population sizes of its competitors and predators

of environmental heterogeneity, which can potentially influence seedling growth and survival. Thus, animal disturbance had strong effects on patterns of plant dispersion, abundance, and diversity suggesting that a thorough knowledge of disturbance history and the mechanisms through which disturbances affect seedling establishment is necessary to understand patterns of community structure in this ecosystem.

CONCLUSIONS

Disturbances affect animals directly or indirectly through modifications of the physical or biological environment. Direct effects occur as a consequence of mortality or emigration; however, they are rarely documented. Although disturbances can act as sources of mortality, many species can avoid mortality by fleeing the area or escaping detrimental effects *in situ*. The ability of animal species to survive disturbance is influenced by the timing, magnitude, and intensity of the disturbance, as well as by the phenotype and life-history characteristics of the animal (Table 27.1).

Disturbances alter the physical environment; in terrestrial systems, this involves the removal or redistribution of vegetation. As a consequence, patches of various sizes experience increased exposure to sunlight, which results in an increase in temperature

and a decrease in humidity. These indirect effects are most frequently cited as causes of short-term responses to disturbance. Indeed, small, less mobile, or heterothermic organisms may be especially susceptible to changes in the physical environment.

Animal populations and communities change in response to alterations in the plant, animal, and microbial communities that follow a disturbance. Although initial responses are species-specific, much of the variation in trajectories of recovery is related to trophic position or guild affiliation. Despite the intensity of many disturbances, some animal populations and communities return to initial conditions relatively rapidly (Zimmerman et al., 1996).

Animals are important agents of disturbance, mostly as a consequence of the manner in which their activities alter the physical environment and create novel habitats. Compared to many abiogenic disturbances, the effects of individual animal-generated disturbances are small, but because they occur frequently they have major cumulative effects on the abiotic environment, as well as on microbial, plant, and animal communities. In rare circumstances (e.g., beaver dams), animal activity drastically alters the structure and function of communities and ecosystems, or represents the defining characteristic of the ecosystem (e.g., guano communities in caves).

One of us (MRW) was once asked after a presentation concerning the role of animals in a forested ecosystem, "What would the forest be like if it contained no animals?" The somewhat startled response was "It would not be a forest at all, just as if the system contained no trees. It is critical to see the forest beyond the trees!" Clearly this statement represents more of a belief than a fact at this point in time. Indeed, the challenge to animal ecology in particular, and systems ecology in general, is to document the situations in which animals are important agents of ecosystem structure and function, and to identify the mechanisms of the interactions and attributes of system under the regulation of animal activities.

FUTURE DIRECTIONS

Progress in understanding the complex nature of disturbance as it affects populations and communities of animals requires a multifaceted approach that differs in essence from those characterizing most past studies. In particular, we recommend approaches which integrate experimental manipulations, comparative approaches, and long-term perspectives. In addition, research assessing dynamic processes (e.g., rates of emigration, immigration, natality, mortality, and species turnover) rather than static attributes (e.g., density, diversity) should provide greater insight to mechanisms of response to disturbance.

Manipulative experiments in the field are valuable tools for addressing questions in ecology (Hairston, 1989); however, this approach has been used less in studying disturbance than in other areas of ecology. The lack of an experimental approach to disturbance ecology is not surprising, given the difficulty of producing effects analogous to those of intense abiotic disturbances such as hurricanes and landslides. However, when it has been feasible to experimentally create disturbances (e.g., controlled burns, artificial tree-falls or gaps, experimental animal exclusions), it has been possible to dissect direct and indirect effects of disturbance in detail. Because of differences in the spatial and temporal scale necessary to study disturbances effectively, the experimental approach has been applied much more often to study the response of plants than the response of animals. Nonetheless, manipulative experiments are powerful tools for field ecologists examining the responses of animals to disturbance because they allow researchers

to (1) control the timing, intensity, and extent of disturbance, (2) document pre-disturbance conditions, (3) distinguish between the relative importance of direct responses and indirect responses, and (4) disentangle the effects of confounding factors associated with particular disturbance events (e.g., distinguish the effects of opening the canopy from those of redistributing biomass to the forest floor).

Most studies concerning the response of animal populations and communities to disturbances have focused on events whose timing, location, or extent are beyond the control of the investigator. As a consequence, researchers usually have inadequate background information about environmental conditions, or population and community structure prior to the disturbance. Pseudoreplication is a pervasive problem. However, researchers conducting long-term studies have been well poised to take advantage of opportunities presented by rare disturbance events (see Walker et al., 1991, 1996) because they have considerable information about salient environmental features before the disturbance. Thus, long-term ecological studies are essential for understanding responses of animal populations and communities to disturbances that cannot be manipulated experimentally.

Comparative approaches offer considerable insight to understanding the manner in which disturbances affect populations and communities. Comparisons that contrast taxonomic groups (e.g., birds versus bats) or functional groups (e.g., frugivores versus insectivores) are particularly promising. In addition, understanding the context-dependent nature of disturbance is critical (e.g., contrasting the effects of tree-falls when rare and dispersed, to the effects when common and in close proximity to each other).

Finally, human activities may be classified in the same manner as those of other animals (transport, construction, waste disposal, etc.). Human populations continue to grow at alarming rates, with attendant environmental assaults on virtually all terrestrial (and aquatic) ecosystems. It is all too clear that ecology in the next millennium will become the study of disturbed ground. Clear understanding of the effects of animal-generated disturbance on natural ecosystems may provide insight to understanding the impact of anthropogenic disturbance as well.

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