

THE ROLE OF DISTURBANCE IN NATURAL COMMUNITIES

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INTRODUCTION

Two features characterize all natural communities. First, they are dynamic systems. The densities and age-structures of populations change with time, as do the relative abundances of species; local extinctions are commonplace (37). For many communities, a self-reproducing climax state may only exist as an average condition on a relatively large spatial scale, and even that has yet to be rigorously demonstrated (36). The idea that equilibrium is rarely achieved on the local scale was expressed decades ago by a number of forest ecologists (e.g. 101, 168). One might even argue that continued application of the concept of climax to natural systems is simply an exercise in metaphysics (41). While this view may seem extreme, major climatic shifts often recur at time intervals shorter than that required for a community to reach competitive equilibrium or alter the geographical distributions of species (6, 21, 43, 76, 92). Climatic variation of this kind influences ecological patterns over large areas, sometimes encompassing entire continents. Other agents of temporal change in natural communities operate over a wide range of smaller spatial scales (47, 242).

Second, natural communities are spatially heterogeneous. This statement is true at any scale of resolution (242), but it is especially apparent on what is commonly referred to as the regional scale. (By *region* I mean an area that potentially encompasses more than one colonizable patch.) Across any land or seascape, one observes a mosaic of patches identified by spatial discontinuities in the distributions of populations (153, 159, 161, 231, 239, 240). Closer examination often reveals a smaller-scale patchwork of same-aged individuals (e.g. 85-87, 101, 146, 199, 204, 217-220, 235, 246).

Discrete patch boundaries sometimes reflect species-specific responses to

steep gradients in the physical environment. Such responses account for only a small part of the spatial heterogeneity found in natural communities, however. Even where background physical conditions are relatively uniform across a site, opportunities for recruitment, growth, reproduction, and survival vary spatially, reflecting variation in the intensity of biological interactions, resource availability, and microclimatological conditions. By itself, this spatial and temporal variation in the density of "safe sites" for establishment (*sensu* 83) may only partially explain local differences in the demography of populations. The availability of propagules sometimes limits rates of establishment (84, 94, 215). Since environmental characteristics and population parameters change with time, the mosaic patterns are themselves dynamic.

To interpret and predict the patterns observed in nature accurately, our methods of study must embrace temporal and spatial variability as essential features of population and community dynamics. There is now abundant evidence that in the absence of such variability many species would cease to exist. Inherent in this view is the recognition that traces of history are etched in the structures of many, if not most, natural communities. Often, present-day patterns can only be interpreted if the organisms themselves yield clues (e.g. fire scars) as to the identity and timing of historical events or if the assemblage has been monitored continuously for a long time.

Disturbance is both a major source of temporal and spatial heterogeneity in the structure and dynamics of natural communities and an agent of natural selection in the evolution of life histories. These roles are clearly interdependent. The differential expression of life history attributes under different regimes of disturbance produces much of the spatial and temporal heterogeneity one observes in natural assemblages. On the other hand, the heterogeneity in environmental conditions (both biological and physical) induced by disturbance is probably a key part of the "habitat templet" (194) that selects among life history variants.

This review emphasizes the impact of disturbance on the numerical abundance of populations and on the relative abundance of species in guilds and communities. Disturbance also has an important influence, however, on ecosystem-level processes such as primary and secondary production, biomass accumulation, energetics, and nutrient cycling (e.g. 17, 20, 136, 197, 222, 233). Indeed, too often studies focused at the population or community level overlook potentially significant effects of ecosystem-level processes on population dynamics. In forests, for instance, disturbance sometimes causes a net increase in the amount of soil nitrogen available to early colonizers. It is probably not coincidental that the seeds of a number of pioneer plant species germinate in response to high levels of soil nitrates (9, 157).

Assemblages of both sessile and mobile organisms are subject to disturbance. The effects of disturbance have been much more thoroughly studied in

the former, however, simply because sessile organisms are easier to observe and quantify. Because of this disparity in our understanding of the role of disturbance in the two sorts of assemblages and because of apparent fundamental differences in their responses to disturbance, I have treated mobile organisms in a separate section at the end.

WHAT IS A DISTURBANCE?

Traditionally, disturbances have been viewed as uncommon, irregular events that cause abrupt structural changes in natural communities and move them away from static, near equilibrium conditions (104, 235). This definition has little utility in light of the following observations:

1. Evidence from long-term censuses suggests that few natural populations or communities persist at or near an equilibrium condition on a local scale (37). There is no clear demarcation between assemblages in an equilibrium state and those that are not.

2. The change caused by any force can vary from negligible to extreme, depending on the intensity of the force and the vulnerability of the target organisms. How does one objectively decide what degree of change along this continuum constitutes a disturbance? The response of perennial species to regular seasonal change in the physical environment is a case in point. When temperatures or rainfall oscillate close to their long-term seasonal averages, organisms respond physiologically and/or behaviorally to ameliorate possible negative effects of the change. With more extreme seasonal fluctuations in the physical environment, the limits of effective physiological or behavioral response are exceeded. At first, this may cause reductions in growth and reproduction, but if the stress becomes severe enough, organisms will die. The number killed can vary from one or just a few individuals to entire populations. Thus, the same basic phenomenon can elicit responses ranging from physiological acclimatization to population extinction, depending on the magnitude of the variation. Since lethal and sublethal responses to such changes (e.g. seasonal migrations of birds; see 103) can markedly alter the community structure, the "objective definition of a threshold at which a periodicity becomes a disturbance [is] difficult at best" (104).

Moreover, the levels of environmental fluctuation to which a present-day species responds with effective homeostatic mechanisms probably represented a far greater hazard early in the species' evolutionary history. Differential mortality and/or reproductive success in the past among individuals differing in genotype probably contributed to the evolution of the homeostatic mechanisms. Therefore, an environmental fluctuation that once caused disturbance does so no longer. This dynamic evolutionary relationship between an organism and the environmental stresses it encounters is ongoing and subject to

numerous constraints; no organism can perfectly track fluctuations in its environment. The evolutionary moderation of stress is exhibited in its most extreme form by species that depend on environmental disruption for the completion of their life cycles and the persistence of their populations (227). Allen & Starr (5) argue that at this point the disruptive event ceases to be a disturbance at all.

Given the complexities discussed above, it seems wisest to adopt the view (104) that disturbance lies near one extreme of the continuum of natural perturbations that affect organisms. In the context of this review, a *disturbance* is a discrete, punctuated killing, displacement, or damaging of one or more individuals (or colonies) that directly or indirectly creates an opportunity for new individuals (or colonies) to become established.

AGENTS OF DISTURBANCE

Both physical and biological processes act as agents of disturbance. The former are the kind most often associated with the term disturbance, and their role in natural communities is the primary focus of this review. Examples include fires, ice storms, floods, drought, high winds, landslides, large waves, and desiccation stress. Agents of biological disturbance (45, 235) encompass everything from predation or grazing to nonpredatory behaviors that inadvertently kill or displace other organisms [e.g. digging by mammals and ants in grasslands (114, 163, 179) or by elasmobranchs in marine soft sediments (207, 216)].

The impact of biological agents of disturbance seems generally similar to that of physical agents. Organisms are killed, thereby creating opportunities for recruitment. The timing of biological disturbance, however, is probably subject to a somewhat more complex set of controls. Rates of predation depend on the functional, numerical, and developmental responses of the predator (139). These responses, in turn, are influenced by the physical environment, habitat complexity, presence of alternate prey, availability of prey refuges, and the impact of higher level predators and parasites. For example, the timing of insect outbreaks in forests may be simultaneously influenced by parasitic infection (8), spatial heterogeneity in forest structure (138), and the recent history of physical disturbance (181, 205, 235).

DISTURBANCE IN ASSEMBLAGES OF SESSILE ORGANISMS

A full understanding of the dynamics of populations within habitats subject to disturbance requires knowledge of the regime of disturbance and of the subsequent patterns of recolonization and succession in the disturbed patches. These

patterns are a product of certain characteristics of the original disturbance and the life histories of the species available to reoccupy the disturbed site.

The Regime of Disturbance

How an investigator characterizes a regime of disturbance depends on the particular disruptive force and responses being studied. The most commonly used descriptors (e.g. 35, 62, 86, 192, 223) are listed below:

1. *Areal extent*—the size of the disturbed area
2. *Magnitude*—consists of the following two components:
 - a. *Intensity*—a measure of the strength of the disturbing force (e.g. fire temperature, wind speed, wave velocity)
 - b. *Severity*—a measure of the damage caused by the disturbing force [Both of these terms have often been used interchangeably (e.g. 33, 192). Severity seems to denote better the amount of damage caused by a disturbance.]
3. *Frequency*—the number of disturbances per unit time. Separate terms are used for the average frequency of disturbance at the local and the regional spatial scales:
 - a. *Random point frequency*—the mean number of disturbances per unit time at a random point within a region; this is often expressed as the *recurrence* or *return interval* (i.e. the average time between disturbances)
 - b. *Regional frequency*—the total number of disturbances that occur in a geographical area per unit time
4. *Predictability*—measured by the variance in the mean time between disturbances
5. *Turnover rate* or *rotation period*—the mean time required to disturb the entire area in question

Regimes of disturbance vary considerably along a number of spatial and temporal scales. For example, the well-studied forests of North America exhibit a wide range of variation in both present-day and presettlement disturbance regimes (19). Near one extreme is the mixed mesophytic cove forest of the southern Appalachian mountains (176). Scattered deaths of single trees or at most a few neighboring trees by windthrow, lightning, or glaze storms form the predominant pattern of disturbance. Fire is uncommon. According to one study, treefall gaps range up to 1490 m², but the average gap is only 31 m². For a number of sites, the average percentage of the forest canopy converted to gaps per year ranges from 0.5% to 2.0% (grand average = 1.2%), so that the rotation interval for the canopy layer is 50–200 years. The annual rate at which new gap area is generated by treefall did not vary markedly over time.

The presettlement regimes of disturbance in the conifer and hardwood forests

of the Boundary Waters Canoe Area (BWCA) of northern Minnesota lie near the opposite extreme on the geographical scale of variation. Fire is the primary source of disturbance in all forest types there (85–87). The presettlement fire regime of “near boreal” conifer forests consisted of crown fires and/or severe surface fires with a return interval of 50–100 years. A typical fire in this forest type usually burned a large area, probably 400–4000 ha. Pine forests experienced a regime of moderate surface fires with a return interval of approximately 36 years, as well as an overlying regime of severe surface or crown fires that occurred about once every 180 years. The latter fires burned 40–400 ha of old growth stands. Adjacent enclaves of mixed hardwood forest were burned in 400–4000 ha patches by severe surface and crown fires (where conifers were prevalent) about every 80 years. High intensity surface and crown fires kill most of the trees in a burned stand, and regeneration initiates from dispersed or stored seeds. Extensive fire scar analyses indicate that all present-day stands in BWCA originated after fire. Smaller-scale disturbances such as windthrow were insignificant by comparison. Before the adoption of effective fire suppression procedures, an average of 0.8% of the entire BWCA study area (405,000 ha) burned per year, and the average fire rotation period was about 100 years long (85, 87).

Surprisingly, turnover rates estimated for forests in these two areas are quite comparable, despite the striking dissimilarity in the predominant agent of disturbance. The critical difference is that the Minnesota forests experience infrequent large-scale disturbances whereas the disturbances in the Appalachian cove forests are much more regular in time and smaller in area. In addition, the severity of disturbance caused by intense fires is much greater than that caused by windthrow.

I intentionally chose two rather extreme temperate forest examples to demonstrate the wide range of disturbance regimes that occur within this habitat in different geographical locations in North America. Forests in other regions of the continent—for example, the Harvard Forest Tract in New Hampshire (90)—experience a more balanced mix of disturbance by fire and windthrow.

A knowledge of long-term average climatological conditions is useful in explaining coarse differences in the geographic patterns of disturbance. For example, the average annual pattern of precipitation determines the relative importance of fire versus treefall as agents of disturbance in forest communities (29, 87, 235). Similarly, differences in winter temperatures explain why floating ice commonly scours the rocky intertidal shores of New England and eastern Canada but not those along the Pacific coast of the United States (192, 234).

Local patterns of disturbance cannot be predicted from a knowledge of large-scale climatic variation, however. The regime of disturbance at any one site depends on a multitude of local physical and biological factors. In the

following sections, I briefly describe some of the more common, and better-studied, local physical agents in natural communities.

WIND Wind is an important agent of disturbance in many temperate and tropical forests, where it creates gaps of various sizes in the forest canopy by blowing down large branches or trees (19, 22, 84, 176, 237, 238). Rates of treefall vary substantially over time and across a landscape. In most areas, treefall is seasonal. It occurs most frequently during seasons with strong gusting winds and high rainfall (e.g. 22, 232).

Spatial variation in treefall rates is attributable to a number of factors including differences in topography and soil type. Treefall is more likely to occur where there are high prevailing winds and at sites that lie in the path of hurricanes (22, 232, 236, 238). In some forests, surviving trees at the edges of existing gaps may be more likely to blow down in subsequent storms (22, 84, 237, 238); but in other forests, they are not (176). The risk of windthrow is often greater for trees that grow on steep slopes or in soils where a stable root hold cannot be established—for example, in wet, sandy, and some very fertile soils (22, 84, 176).

As trees grow older and taller, they are more likely to be blown down (22, 176). In part, this is because of the increasing forces a stationary, and relatively inflexible, object like a tree experiences as it grows larger in a moving fluid environment. This is particularly true if the flow sometimes accelerates, as when the wind gusts (224: 94). Other factors also contribute to the increasing risk of blowdown as a tree ages, including the weakening effects of insect attack, lightning strikes, disease, and physiological stress. A heavy load of epiphytes, which often develops on older rain forest trees, may contribute further to the chance that a tree will be blown down in storms (201).

Gap size is related to the manner in which a tree falls (22; G. B. Williamson, unpublished manuscript). As one would expect, gap area is positively correlated with tree size in the most common case where the tree falls laterally owing to wind stress. In contrast, some species of trees die in a standing position and gradually collapse downward. This phenomenon produces smaller gaps, and their size is usually uncorrelated with the size of the tree at the time of death. Limb fall usually creates even smaller gaps.

The very largest gaps are generated by multiple tree falls. Such gaps are created when several trees fall synchronously in “domino” fashion or when a new gap is contiguous or overlaps with an older one. In tropical rain forest, extensive liana connections may increase the rate of multiple synchronous treefall (F. E. Putz, cited in 22).

FIRE The local intensity, frequency, and areal extent of fire in terrestrial plant communities is controlled by complex interrelations among the following six

factors (29, 30, 72, 87, 227): (a) frequency and seasonality of ignition sources, (b) moisture content of the fuel (i.e. the potentially flammable living and dead plant material), (c) the rate of fuel accumulation, (d) structural and chemical characteristics of the fuel, (e) mosaic nature of the landscape, and (f) local weather conditions at the time of the fire. Since all of these factors vary over space and time, there is considerable heterogeneity in local fire regimes and consequently in the effects of fire on vegetation.

Lightning is the most significant natural source of fire (205, 226, 227). Far less common natural sources include spontaneous combustion (221), sparks from falling rocks (89, 135), and volcanic eruptions (219, 220, 227). The frequency of lightning strikes alone, however, rarely explains local patterns of fire occurrence, even where there is little anthropogenic influence on the fire regime. Only about 0.03% of lightning discharges that strike vegetated areas of the world result in wildfires (205). Thus, while it is true that fires must have a source of ignition and that seasonal patterns of thunderstorm activity may influence their timing (87), the other five factors listed above determine, in a proximate sense, the fire regime in a particular area. They determine whether or not ignition will occur, how intense the fire will be, and what area it will cover.

The moisture content of the fuel determines the likelihood of ignition and the ability of the fuel to carry a fire. The amount of moisture is influenced, in turn, by a number of local factors including the aspect of the site, the water retention properties of the underlying soil, and wind conditions (226). In certain geographical regions, there are only brief periods during a "normal" year when fuels are dry enough to ignite and carry a fire. Consequently, the most significant fires (i.e. the most intense, severe, and extensive) burn during periodic droughts that recur at intervals of 10–20 years or longer (66, 85–87, 204, 249). Substantial amounts of fuel accumulate between droughts, so that when fires occur they are exceedingly intense. Similarly, fire only invades semipermanent wetlands such as shrub bogs (29) during droughts. Fires occur much more frequently and regularly in areas that have predictable annual dry seasons as well as occasional droughts [e.g. grasslands and savanna (29, 93, 120, 144, 226), chaparral and forests of the Sierra Nevada Mountains in California (109, 111), and the dry sclerophyll forest of Australia (31)].

The rate of fuel accumulation can influence the frequency and intensity of fires because it determines how much fuel will be available for burning at any given time. Assuming that the likelihood of fire is positively related to the standing mass of fuels, fires should occur most often at sites where fuels accumulate the most quickly, all else being equal. (This assumption is critically evaluated below.) Also, the more fuel that has accumulated since the last burn, the more intense a fire will be.

The rate at which fuels accumulate equals the difference between their rates of production and decomposition (29, 30). Site conditions or characteristics of the vegetation itself that enhance the production of fuels and/or slow their

decomposition result in higher rates of fuel accumulation. Insect and parasite attacks, disease, competition, windthrow, lightning strikes, and senescence convert living vegetation into dead fuels. Since dead plant material is often drier and therefore more flammable than living plant tissue, the likelihood of intense fires is greater in older stands. There are exceptions to this pattern when past fires have killed the vegetation but not consumed it completely. In this case, dead "carry over" fuels may be abundant in the early stages of stand regeneration, creating a high risk of fire even in a young stand (e.g. 66, 86). The rate at which dead fuels decompose is controlled by climatological conditions (i.e. temperature and humidity) and by the characteristics of the vegetation. Sclerophyllous foliage, for example, is decay resistant and decomposes relatively slowly.

Structural characteristics of the fuel influence fire intensity (29, 174). When fuels are distributed in widely separated strata—e.g. in savannas or frequently burned pine woods—relatively low-intensity surface or ground fires are the rule. In shrublands and long unburned coniferous forest, the vertical distribution of fuels is more continuous, and the surface to volume ratio of the vegetation is large. As a consequence, high intensity crown fires are common in these vegetation types.

Fuel flammability is also a function of the chemical composition of the foliage (29, 174, 175). Fuels rich in secondary organic compounds are ignited more easily and burn more intensely. In some plant species, the concentrations of extractable organics vary seasonally and increase with age [e.g. the chaparral shrub *Adenostoma fasciculatum* (158, 175)].

The vegetational mosaic and local topographic features strongly influence the point fire frequency and the areal extent of fires (29, 86, 227). Only a fraction of the fires that burn through the vegetation at a particular point start within the stand that includes that point. Therefore, the point fire frequency depends to a large degree on the rate at which fire encroaches from surrounding areas. This rate is influenced by the ability of neighboring phases of the vegetational mosaic to carry a fire and by the extent and orientation of natural and artificial firebreaks.

Finally, weather conditions at the time of a fire affect its intensity and size (87). Such conditions include the level of precipitation, air temperature and humidity, wind speed, and wind direction, especially with respect to the spatial distribution of fuels and the position and orientation of fire barriers. A fire's impact is also influenced by its rate of spread (30, 93), which depends on both weather conditions and the winds, convection currents, etc., that the fire itself produces. In general, rapidly moving fires consume less fuel and burn at a lower temperature.

In summary, a reciprocal relationship appears to exist between vegetation and fire. The state of the vegetation affects the fire; and the interfire interval regulates the composition, structure, and quantity of living vegetation and dead

fuels. All else being equal, lightning fires are more likely to start in older stands of vegetation and to be more intense than fires that start in younger stands. In many instances, however, this description of fire behavior may be overly simplistic (86). Once a fire starts, it can spread into stands of many different ages. "All else" is rarely equal; the intensity and areal extent of any particular fire may be influenced to a considerable degree by factors other than the characteristics of the accumulated fuel.

WATER MOTION In marine and freshwater environments, moving water exerts forces on sessile organisms, just as wind does in terrestrial environments. In addition, suspended particulate matter (e.g. sediment) or larger objects transported by the moving water (e.g. logs or cobbles) may strike and abrade the substratum over which the water flows. Aquatic organisms may also be killed either by burial under sediments that have been displaced and redeposited by moving water (e.g. 126, 192) or by exposure to air when water motion changes drainage regimes (e.g. coral reef crests; J. H. Connell, personal communication).

Detailed study of the natural regimes of disturbance caused by water motion in freshwater habitats—in streams in particular—is in its fledgling stages (e.g. 88, 113, 131, 131a); little is known about the frequency, areal extent, and intensity of such disturbances. The disruptive influence of moving water has been much more thoroughly studied in marine habitats, particularly along temperate, rocky intertidal shores (e.g. 45, 153, 189, 192) and on tropical coral reefs (e.g. 33–35, 54, 155, 247). Wave action is a major agent of disturbance in these habitats. As with wind and fire, the regime of wave-induced disturbance varies in space and time and is influenced by physical and biological components of the environment. Wave energy is maximal during seasons of high storm activity. Therefore, the disturbance it causes is highly seasonal (35, 45, 54, 153, 189, 192). The frequency of disturbance is also strongly influenced by the physiological and morphological characteristics of the organisms in question and the properties of the substratum to which the organisms are attached.

As a sessile marine organism grows larger in an environment subject to periodically accelerating water motion, i.e. in wave-swept habitats, its risk of being detached or broken by wave stress often increases (50, 117, 192). Older individuals are more likely to suffer injury or death from wave forces if weakening wounds caused by boring organisms, predators, and grazers accumulate with age (35, 192). Epiphytic or epizoid overgrowth can also increase the chance that an organism will be dislodged by wave action (192). The risk of damage or death by a given wave force varies among species that differ in shape, flexibility, or internal structure, among other factors. For example, tree or bush-like corals (e.g. *Acropora* spp.) are more susceptible to wave damage than mound or sheet-like corals (33–35). Similarly, some

aggregations of sessile organisms become more vulnerable to disruption as their individual members increase in size and number. Dense, multilayered beds of the mussel *Mytilus californianus* are less stable and more likely to be torn from the rock surface by wave forces than less dense, single-layered beds (82, 151, 153).

In some aquatic habitats, the stability of the substratum directly determines the rates of disturbance. In streams and on the seashore, strong water motion overturns loose rocks, damaging the attached organisms. The frequency of this kind of disturbance declines with increasing rock size (125, 131, 131a, 150, 189).

The sizes of the areas disturbed by wave action vary considerably (35, 192). Patches cleared in mussel beds during stormy winter months and at more exposed sites are much larger on average than those created during calm summer months or at protected sites (153). Similarly, larger boulders are overturned more often during winter storms and at sites exposed to heavy wave action than at other seasons or sites (189). In both systems, the rate of disturbance differs from one year to the next, reflecting annual variation in the intensity and frequency of storms. Similarly, there was substantial spatial and temporal heterogeneity in the regime of disturbance caused by four hurricanes that struck the reef at Heron Island, Australia (35; J. H. Connell, personal communication). Though such storms are seasonal, their effects are unpredictable from year to year. The underlying causes of the variation in this case are not as clear as in the mussel bed and boulder examples.

PATTERNS OF DISTURBANCE IN ASSEMBLAGES OF SESSILE ORGANISMS
Within any particular habitat, a variety of agents operate independently or in concert to generate the overall regime of physical disturbance to which organisms respond. The heterogeneity of natural disturbance regimes is due, in part, to local variation in the intensity, timing, and spatial distribution of potentially disturbing forces. Often, however, heterogeneity in local patterns of disturbance is better explained by temporal and spatial variation in the "intrinsic vulnerability" (192) of the organisms affected by these forces. Conspecific individuals differing in age and size usually differ in their vulnerability to a particular force. Increasing size and/or age decreases the risk of damage or death from some forces (e.g. of woody vegetation from ground fires; intertidal organisms from desiccation stress; coral colonies from sediment burial) but increases vulnerability to others (e.g. of large, old trees to windthrow; older stands of trees and bushes to crown fires; larger intertidal organisms and branched corals to wave forces).

Vulnerability to a given force is also species- and assemblage-specific. Not uncommonly, the vulnerability of a community to disturbance changes over the course of succession (e.g. 191), owing to differences in the physiology,

morphology, or growth habit of the species characteristic of each seral stage. The risk of disturbance by fire, for example, often changes with the successional age of the vegetation because seral stages differ in fuel characteristics. Such differences can influence the temporal pattern of disturbance. Some terrestrial plant communities appear to exhibit cycles of inflammability that are controlled by the rate of accumulation of combustible plant material (95, 134, 235). There may be similar cycles of disturbance on mussel-dominated shores of the Pacific Northwest coast of the United States. The rate of succession to a community dominated by mussels appears to set a lower limit of 7–8 years on the interval between successive major disturbances of assemblages occupying a particular area of substratum (153).

In many forests, gaps in the canopy are generated primarily by windthrow of isolated individual trees or small groups of neighboring trees. In these cases, gap regeneration is a small-scale, spatially and temporally asynchronous process. There are remarkable, though relatively rare, exceptions to this pattern where large tracts of forest are leveled by wind (e.g. 19, 24a, 56, 168, 170, 232, 237). To my knowledge, however, a large-scale, cyclic pattern of wind-induced tree mortality has only been rigorously demonstrated in some high-altitude balsam fir forests (170, 196, 198).

Such cyclic patterns of disturbance are certainly intriguing and have partially inspired the hypothesis that species have evolved physiological mechanisms and morphologies that promote disturbance and/or determine its characteristics (see below). The phenomenon of regular disturbance controlled by the biotic component of the environment is by no means universal, however. A significant amount of the variability in the impact of a disturbing force may be unrelated to biotic properties. In fact, it has been argued that patterns of local fires in some presettlement forests were largely random with respect to vegetation type and best explained by patterns of lightning ignition and the vagaries of the winds and weather during a fire (86, p. 399). Large-scale disturbances such as mass movements caused by landslides (60, 170, 199, 217–220), earthquakes (68, 219), and volcanic eruptions (219, 220) usually occur at random with respect to the age, successional state, or species composition of the populations and communities they disrupt.

This caution aside, the regime of disturbance in many communities reflects the interplay between the properties of organisms and the characteristics of the physical forces that cause disturbance. Thus, the categories of *endogenous* and *exogenous disturbance* (sensu 19, 20) are difficult, if not impossible to apply (176, 235). It is therefore hard to unambiguously classify a particular successional sequence as *autogenic* or *allogenic* (145).

Present-day disturbance regimes may be very different from the regimes characteristic of communities unaffected by humans. Fire regimes in vegetation surrounding inhabited areas were surely altered when indigenous peoples

began to use fire thousands of years ago as a tool for managing vegetational cover and game animal populations (29, 31, 112, 166, 226). Modern man's influence has been much more pervasive.

While the activities of indigenous peoples and early settlers may have initially increased the frequency of fire, the adoption of effective fire suppression techniques during the last century has sharply reduced its frequency in many vegetation types (e.g. 62, 112, 119, 134, 137, 173, 204, 206). In North America only the unexploited boreal forests of northern Canada and Alaska (87) and forests with extremely long natural fire cycles (66, 172) have remained relatively unaffected by this policy of fire suppression. Where fire cycles have been unnaturally lengthened, large quantities of fuel accumulate and infrequent, unusually intense fires are the result (53, 134). In other habitats, such as swamps where draining has lowered the water table (29), fires are much more frequent now than in presettlement times. These changes in the fire regime have had a marked effect on vegetation patterns (see above citations).

The effects exerted by humans are not limited to disturbance regimes caused by fire. For example, forest logging practices produce much larger clearings than those usually created by windthrow, and the temporal and spatial patterns of harvesting are often quite distinct from natural treefall. Flood control procedures combined with human modification and degradation of watersheds can lead to extreme flooding and sedimentation of abnormally long duration in coastal wetlands. This altered regime of disturbance has much more severe effects on the biota of the floodplains and estuaries than the normal, lower volume discharge of freshwater runoff during the rainy season (147, 250). Human-caused deterioration of riparian watersheds can have similar negative effects on stream communities (214).

The ubiquity of human-caused alterations in natural disturbance regimes significantly complicates evolutionary interpretation of present-day patterns of morphology, physiology, and life history in relation to physical disturbance (e.g. 109). Only in some communities, such as forests, is accurate reconstruction of presettlement regimes of disturbance possible. The same concern applies to human alterations of biotic components of the environment (47, D. Lindberg, J. Estes, K. Warheit, in preparation). Cautious consideration of such effects should precede speculation about the evolutionary mechanisms underlying present-day patterns.

The Repopulation of Disturbed Sites by Sessile Organisms

Propagules of sessile organisms, be they sexually or asexually produced (sensu 143), are rarely able to invade and become established in areas densely occupied by other organisms (22, 35, 36, 46, 74, 77–80, 83, 176, 192, 231, 252). Resident organisms inhibit recruitment from propagules by a variety of

mechanisms. Occupants may consume the dispersed propagules, as in some assemblages of sessile, suspension-feeding invertebrates (35, 190, 192, 246), or the residents may simply have preempted the available space. In other cases, residents modify site conditions in ways that inhibit the germination or metamorphosis of those propagules that do reach the substratum. They may release toxic chemicals (allelopathy) or reduce the supply of essential resources such as food, light, nutrients, and water.

Physical disturbance is one of the major mechanisms that break this inhibition and generate conditions favorable for recruitment, growth, and reproduction. Disturbances not only reduce or eliminate the cover of resident organisms, thereby lessening competition for resources that are present on the site, but in some cases they indirectly replenish some of the depleted nutrients [e.g. nutrient-rich ash produced by fire (17), the accumulation of detritus in pits dug by foraging rays (216), and nutrients leached from rotting treefall debris in forest light gaps (e.g. 22, 222)]. In addition, the disturbance may eliminate toxic chemicals that have accumulated in or on the substratum [e.g. volatilization of allelopathic chemicals by fire (70); see 30 for a recent discussion of the controversial role of allelopathy, and its interaction with fire, in shrublands]. The disturbance may also temporarily reduce the density of predators or parasites of the propagules (70).

The rate and pattern of reestablishment following a disturbance depend on the following elements:

1. The morphological and reproductive traits of species that are present on the site when the disturbance occurs. Such traits determine, in part, the likelihood that these species will survive the event and rapidly reoccupy the site.
2. The reproductive biology of species that were not present on the site when it is disturbed but have occupied it previously or live within dispersal distance of it.
3. Characteristics of the disturbed patch including:
 - a. the intensity and severity of the disturbance that created it,
 - b. its size and shape,
 - c. its location and degree of isolation from sources of colonists,
 - d. the heterogeneity of its internal environment, and
 - e. the time it was created.

Below, under subheadings 3a-e, I briefly discuss the influence of the characteristics of these elements on the recolonization of a disturbed patch. This information is certainly not sufficient to predict the abundance and demography of a species within a particular habitat or even the likelihood that the species will persist there. Such properties of a population depend on the complex interaction of an organism's complete life cycle (including events that occur during disturbance-free periods) with the overall regime of disturbance in the habitat.

INTENSITY AND SEVERITY OF DISTURBANCE The influence of the intensity of disturbance on recolonization has been most thoroughly studied in communities exposed to fire (e.g. 2, 70, 71, 108). Trees and shrubs whose aboveground buds are covered by a thick layer of heat-resistant bark are more likely to survive fires of moderate intensity, even if there is some scorching and defoliation. Hotter fires may kill all aboveground tissues, and only those species that are able to resprout from underground buds associated with rhizomes, roots, root crowns, or lignotubers will survive and regrow vegetatively.

The probability that a plant will survive a fire (even with some bud protection) may decline with increasing age and number of exposures to fire (70, 71). The degree of vegetative regeneration depends on the season in which burning occurs if such regrowth draws on a seasonally fluctuating pool of stored carbohydrates (e.g. 175). There is also the interesting case (100) in which mutualistic ant associates mediate the impact of fire on resprouting swollen-thorn acacia plants. The obligate acacia-ants clear foreign vegetation from around the base and branches of the acacia, thus reducing the chance that the plant will be killed by a fire. If the fire is hot enough to kill aboveground shoots but not the ants, the colony will move into the regenerating sucker and defend it against encroaching vegetation and herbivorous insects.

The mortality of even those species that possess subterranean buds increases with fire intensity (71). This relationship holds especially for underground fires in layers of peat or humus that directly damage tissues below the soil surface and often kill all of the vegetation on a site. Thus, the probability that a site will be repopulated by the vegetative regeneration of surviving residents decreases with the intensity of the disturbance. This same pattern seems to apply to many species of intertidal algae (191, 192) and colonial marine invertebrates (35). On coral reefs, for example, fragments of colonies that are broken loose in storms can establish themselves in clearings and fill the space by asexual reproduction (91). The survival of these asexual propagules is probably inversely related to storm intensity, since heavy wave action breaks fragments into smaller pieces and scours off much of the living tissue; this greatly reduces the number that can successfully colonize disturbed sites (116).

Repopulation of disturbed sites by other kinds of propagules, including those produced by sexual reproduction, can also be influenced by disturbance intensity. Once again, the best examples come from plant communities exposed to fire (e.g. 2, 30, 70, 71, 107–109, 252). The flowering of some plant species characteristic of fire-prone habitats is stimulated by low intensity surface fires. Other species produce seed that is stored in fruits on the plant until fire of a particular intensity triggers their dehiscence [e.g. serotinous pine cones (225–227, 251)]. Still other species release hard-coated seeds that remain dormant on or in the soil until fire, in concert with other environmental factors, stimulates

germination. The cues that stimulate germination and the mechanisms involved vary among species (30). In northern conifer forests, the intensity of the fire is particularly important to patterns of seedling establishment. Hot fires consume the organic layer, including its seed bank, and expose mineral soil that is favorable to the establishment of conifers. Less intense fires leave the organic layer and its seed bank intact; thus, species whose seeds have accumulated in this layer will dominate the regenerating vegetation, and conifer seedlings will be scarce (86).

Plants vary substantially, both within and among species, in the degree to which they respond to fire with vegetative resprouting versus germination from seed (70, 108). Similarly, patterns of serotiny in pines differ markedly among populations and species (132, 156).

A buried seed strategy (20, p. 108) is also employed by some plant species of mesic or wet terrestrial environments in response to disturbances other than fire (11, 13, 22, 25, 39, 40, 78, 79, 83, 84, 130). Large quantities of dormant seed may be stored in the soil. Some of it will have been produced by resident plants—usually early successional species—mature individuals of which no longer occupy the site. The remainder will have been dispersed to the site, in many cases transported by animals (e.g. 20, 25, 40, 84, 130, 211). The creation of a large gap in the vegetation, e.g. by treefall, alters the soil environment and/or the light regime in such a way that seed germination is stimulated (9, 11, 20, 130, 157). Cues for germination vary among species, as does the viability and length of dormancy of their buried seeds. Though an equivalent recolonization mechanism may exist in marine and freshwater communities, its existence has yet to be rigorously demonstrated.

The seeds of other mesic or wet environment plant species do not accumulate in a long-lived seed pool. Instead, they germinate immediately upon dispersal or soon thereafter; germination may be briefly delayed until favorable seasonal climatic conditions develop (25, 67). This pattern is exhibited by some shade-intolerant, early successional species whose light, often wind-dispersed seeds colonize transient or frequently disturbed habitats (e.g. floodplains and river banks). It is particularly characteristic, however, of middle and late successional tree species in temperate and tropical closed-canopy forests (22, 25, 67, 84, 176). Such species produce relatively large seeds that often are dispersed close to the parent tree. The large seed reserve permits germination and establishment in the low light conditions prevalent under a closed canopy and may facilitate root penetration of dense litter on the forest floor. The seedlings are shade tolerant and persist in the understory for varying lengths of time, depending on the species. They grow slowly, if at all, until a gap opens in the canopy over them, permitting a pulse of growth. A suppressed individual rarely can recruit to the canopy layer after a single disturbance. Before it can do so, either the hole in the canopy is closed by lateral expansion of the crowns of

surviving trees on the gap border or the gap becomes so choked with regenerating vegetation that the resources needed to support further growth are used up. Thus, several episodes of low intensity canopy disturbance in the immediate vicinity of the suppressed individual are usually required before it grows into the canopy (176). The disturbance must be severe enough to open a gap, but not so intense that it kills the understory plants. Suppressed individuals are often damaged by falling trees and other debris, but most survive and are able to resprout.

Following an intense disturbance—such as that produced by a landslide (60, 68, 170, 199, 217–220), a volcanic mudflow (49), a long-overtaken boulder on the seashore (191, 192), erosion and redeposition of alluvial sediments on floodplains (63, 141, 200), or a receding glacier (42)—neither resident organisms nor stored dormant propagules survive. All recolonization must come from either propagules dispersed into the open patch from surrounding areas or vegetative ingrowth of neighboring individuals or clones.

PATCH SIZE AND SHAPE The size and shape of a patch indirectly influence its repopulation in several ways. The internal physical and biological environments may vary with patch size. For example, there is an increase in light intensity and its daily duration, in mean soil and air temperature (and their ranges), and in subsurface soil moisture as the size of forest treefall gaps increases (assuming a constant severity of disturbance). The levels of these microclimatological variables are substantially higher in gaps than under a forest canopy (20, 22, 25, 51, 176, 237, 238). Conversely, humidity decreases with gap size; the initial competition for nutrients with surviving trees at the edge of the gap may also. [However, there have been no detailed studies of nutrient dynamics within a single treefall gap (222)]. A number of these patterns have also been observed in disturbed sites in shrublands (30). These size-related differences in the characteristics of the physical environment can influence the germination of seeds, resprouting from buds, and the subsequent survival and growth of seedlings and saplings within a gap.

In aquatic environments, organisms surrounding a clearing can influence the patterns of water flow in and around the open patch and thereby affect the availability of food and the density of settling propagules. These organisms may also consume incoming propagules or otherwise directly interfere with their settlement or recruitment. In intertidal habitats, however, the presence of organisms on the edge of a clearing may moderate the internal microclimate of the patch at low tide when it is exposed to the air. These influences will be more strongly felt in small clearings than in large ones (35, 192).

Small patches have a greater perimeter-to-area ratio than large patches, which has a number of consequences for patterns and rates of recolonization (133). The vegetative ingrowth of clonal organisms or the lateral encroachment

of attached but semimobile solitary organisms will make a proportionately greater contribution than dispersed propagules to the recolonization of small as compared to large clearings if these organisms occur along patch edges. This phenomenon has been demonstrated in beds of intertidal mussels (153, 193, 202) and in subtidal assemblages of colonial invertebrates (35, 106, 154). Numerous factors influence the rate at which a patch of a given size is filled by vegetative ingrowth, including the morphology and rate of expansion of the invading colony, clone, or shifting assemblage of individuals.

Similarly, in some instances the rate of colonization by dispersed propagules varies with patch size. The number of nearby adults per unit patch area is usually greater for small patches than for large ones. This differential may result in a greater density of recruited propagules and therefore more rapid recolonization of small patches. This pattern will only develop when propagules are not dispersed far from their parents and when there is no overriding negative influence on recruitment by organisms that surround the patch. When the size of a clearing is large relative to the dispersal ability of potential colonists, invasion from the edge of the patch may be slow; its closure by recruitment from dispersed propagules may take several generations (94, 195, 230).

In some systems, the abundance of mobile consumer species within disturbed patches and their influence on recolonization varies predictably with the size of the patch. In intertidal mussel beds, for example, small clearings contain higher densities of grazers, particularly limpets, than do large patches (153, 193, 202). This relationship is analogous to the association between rates of vegetative ingrowth and patch size. The surrounding bed of mussels appears to serve as a refuge for small grazers from wave shock, desiccation stress, and possibly predation. These grazers migrate into the open patch from the edge to feed on colonizing algae. Since the length of edge is proportionately greater in small patches, a higher density of grazers accumulates in small clearings than in large ones. As a consequence of this variation in grazing pressure, different assemblages of macroalgae develop in patches of different size (193, 202).

This pattern is likely to occur in any system where natural enemies prefer—or are forced—to live largely within the phase(s) of the community mosaic that surrounds a patch, while their prey occupy the interior of the patch. Bartholomew's (10) demonstration that vertebrates concentrate their grazing and seed predation within a narrow zone along the edge of chaparral stands suggests that their influence on the revegetation of clearings may vary with clearing size in the same way.

Given that the physical and biological environments of patches often vary with patch size, it is not surprising that species are differentially distributed among clearings of various sizes in a number of communities. These include intertidal assemblages (192, 193), subtidal epifaunal assemblages (35, 97,

110), tropical forests (22, 51, 84, 237), temperate forests (20, 57, 176, 243), and old fields (12, 44, 74, 78).

Patch shape also influences the degree to which surrounding organisms affect within-patch dynamics. The more irregularly shaped a clearing of a given area is, the higher the ratio of perimeter length to area and the greater the influence (both positive and negative) organisms in the immediate neighborhood of the patch will have on its recolonization (192). For example, long, narrow gaps in a forest canopy allow less light to penetrate than more circular gaps (22; 149; J. Tomanek, 1960, cited in 176).

THE LOCATION OF THE PATCH AND ITS DEGREE OF ISOLATION FROM SOURCES OF PROPAGULES The proximity of a patch to sources of colonists can greatly influence the mode and rate of colonization (84, 164, 192, 193). For example, colonization by expanding clones is only possible if they occur on or near the borders of the patch. Discrete patches of substratum, such as cobbles on the seashore, are physically isolated from other substrata. When they are denuded by a disturbance, invasion by neighboring clones is impossible, and dispersed propagules must initiate recolonization (35, 192). Patch location is particularly important for species that do not disperse their propagules very far, e.g. many terrestrial and some marine plants (20, 46, 84, 94, 152, 164, 192, 193). In contrast, the larvae of many, but not all (e.g. 69), marine invertebrates spend days, weeks, or months in the plankton before they are competent to settle; consequently they can be dispersed long distances from the parent organism. Recruitment of such species to disturbed patches rarely correlates with the abundance of propagule-releasing adults in the immediate vicinity of the clearing (35, 192, 215).

WITHIN-PATCH ENVIRONMENTAL HETEROGENEITY The environment within a patch cleared by disturbance is seldom, if ever, homogeneous (22, 84, 176). In many cases, this internal heterogeneity influences the process of recolonization. In forest lightgaps, soil conditions and light intensity vary with position in the gap. Fallen dead plant material may significantly alter the local microclimate and distribution of soil nutrients. Conditions along the bole of a fallen tree may be very different from those under and around its crown, and both may differ from conditions near the upturned root mass where mineral soil may be exposed (see references in 176). The association of certain species with particular areas of the forest floor adjacent to a fallen tree suggests a degree of specialization to these microenvironments (149, 176, 210). The decomposing log itself may be a critical germination site for some species (e.g. 66, 218, 220). This local heterogeneity in the conditions for germination and growth can enhance the diversity of vegetation within the gap (e.g. 149, 208).

In marine communities, within-patch heterogeneity in the characteristics of

the substratum may also affect patterns and rates of patch colonization (35, 192). Settlement and/or survival of propagules on hard substrata is sometimes influenced by relatively small-scale differences in surface texture or composition. Larger-scale differences in the rock surface such as cracks and crevices can provide refuges from predators and grazers.

Within-patch heterogeneity in the form of a spatial refuge afforded by a particular substratum can also be important in terrestrial communities. The perennial herb, *Lomatium farinosum*, suffers far lower mortality caused by small mammals in shallow rocky soils than in deeper, less rocky soils (209) because mammals are better able to create runways, dig burrows, and feed on plant roots in deeper soils.

TIME OF PATCH CREATION When an open patch is created by disturbance will indirectly affect colonization if, as is commonly the case, the availability of propagules varies over time. Production of propagules is seasonal for at least some species in most habitats [e.g. tropical rain forest (63, 67, 84, 237), temperate forest (25), temperate intertidal zone (192), temperate subtidal epifauna (150, 203), coral reefs (35), and chaparral (107)]. Yearly variation in the production of propagules is often great (see also 80). Since large patches often remain open to colonization longer than small ones, temporal variation in the availability of propagules may have less of an impact on the long-term development of their assemblages (35). In some systems, the largest patches of open space are only generated in certain seasons, whereas small patches are produced year-round (35, 192). In this case, there should be less variation in the composition of colonists among large patches than among small ones (189), assuming that yearly variation in propagule availability is smaller than seasonal variation.

Temporal variation in the production of propagules may also be less important where propagules are stored for long periods in the soil or on the parent organism. Such storage effectively dampens variation in the number of propagules that are immediately available to recolonize a disturbed site. If the interval between successive disturbances is short, however, there may not be sufficient time to replenish the pool of stored propagules, particularly if this depends on the maturation of individuals that became established since the last disturbance. Under these conditions, few if any stored propagules will be available to repopulate the site, and local extinction may result (70, 251, 253). Therefore, in fire-prone habitats the dynamics of a population that relies on stored propagules for regeneration depends on the interrelation between fire frequency and fire intensity, the rate of propagule production as a function of plant age/size, and the viability of stored propagules. The relationship between inputs to and losses from a pool of dormant propagules is equally important in closed-canopy mesic forests where windthrow is the predominant form of disturbance (25).

The timing of disturbance can have a significant effect on patterns of recolonization even when reproduction is stimulated by the disturbance event itself. For example, patterns of fire-induced flowering and seed production can vary with the time of year the plant is exposed to fire (e.g. 2, 70).

CORRELATIONS AMONG THE CHARACTERISTICS OF A DISTURBANCE REGIME AND COMMUNITY RESPONSE

The characteristics of natural disturbances are often correlated. Disturbances that affect large areas are generally the least frequent and the most severe (i.e. leave the fewest survivors). The above correlation has been observed on coral reefs (35), rocky seashores (192), and in some terrestrial plant communities (235). The simplest explanation for this pattern is that the events that trigger massive earth movements, severe droughts, and large storms occur less frequently than those that produce smaller-scale, less intense disruptive forces. In other cases, this correlation is due to the interacting influences of the biotic and abiotic components of the system on patterns of disturbance. This sort of interaction best describes correlations among characteristics of a fire regime. If ignition is restricted to infrequent periods of severe drought, considerable fuel will have accumulated, and the resulting fire will be intense, killing much of the vegetation over a large area. Alternatively, if dry periods favorable to ignition occur annually, fires will be frequent but usually of low intensity and small areal extent because the short interval between burns will not allow much fuel to accumulate.

One general consequence of this correlation among disturbance characteristics is that there is a fairly continuous relationship between, the predominant mode by which disturbed sites are recolonized and patch size. At one extreme are large clearings with no survivors and no dormant propagules. These areas will initially be recolonized by species producing widely dispersed propagules at the time the patch is opened. Germination or metamorphosis of the propagules soon after dispersal and rapid early growth are advantageous for successful establishment (73). If they are not redisturbed subsequently, such patches often undergo a long period of succession as other species slowly invade and gradually replace earlier colonists. At the other extreme, the smallest disturbances are filled almost exclusively, and relatively quickly, by the vegetative growth of survivors living either within the clearing or on its edge. Little or no successional replacement takes place in this case.

Repopulation of patches whose size and severity of destruction falls between these two extremes occurs by one or more of the following mechanisms: (a) germination or metamorphosis from recently dispersed or stored propagules, (b) growth from a suppressed juvenile state, or (c) regrowth from damaged tissues. The first mechanism predominates in larger patches where conditions are more open and where the disturbance has been severe enough to kill most adults and juveniles. Quite often, mass seeding of such patches in forests

produces extensive even-aged stands (85–87, 101, 141, 146, 199, 204, 217–220).

The latter two mechanisms are more important in smaller patches where some survivors remain and where competition for resources such as light and nutrients is likely to be intense. Here, larger individual size at the outset should be advantageous for procuring the limited resources available. In small light-gaps, for example, suppressed seedlings or saplings usually outcompete individuals that germinate from seed after the gap has opened (25). Similarly, in coral reef communities, attached fragments of corals probably have an advantage over metamorphosing planula larvae in small clearings on coral reefs (35). Because fragments are larger at initial colonization, they can grow to a large size more quickly. At this larger size, they are better able to hold off colonies invading from the edge of the clearing.

It is often impossible to predict *a priori* the relative contribution of each of these mechanisms to the process of recolonization in any particular clearing. This will depend on the environmental setting and the life histories of the particular species involved. Chance events also play a significant role in many cases.

Comments on Evolutionary Responses to Disturbance

Disturbances are clearly an important cause of local heterogeneity in the environmental conditions relevant to the recruitment, growth, survival, and reproduction of organisms. Circumstantial evidence strongly suggests that under the constraints of adaptive compromise, the differential reproductive success of individuals has resulted in specialization to particular phases of the environmental mosaic generated by disturbance (e.g. 11–13, 25, 35, 51, 52, 77–80, 164, 171).

Disturbance causes environmental heterogeneity along two dimensions—the temporal and the spatial. The temporal component derives from asynchrony in patch creation, causing the assemblages of neighboring areas to differ in age. Species may partition this temporal component of heterogeneity by colonizing and/or growing to maturity only during a particular stage of succession (159) or only in patches created at a particular time of year.

The spatial component results from variation in patch characteristics other than age, e.g. size, microclimate, and location. Species may differentially exploit patches that differ in one or more of these characteristics. Levin (124) refers to these temporal and spatial components of disturbance-induced heterogeneity as *phase difference* and *local uniqueness*, respectively. Undoubtedly, most species exploit a combination of these two forms of environmental variation. Despite the specialization described above, many species overlap considerably in the environmental conditions suitable for completion of their life cycles.

Several authors have suggested that organisms are incapable of evolving adaptive responses to disturbances that occur at long intervals relative to their generation time (e.g. 15, 83, 152, 207). As Harper states:

I distinguish (as ends of a continuum) disasters and catastrophes. A disaster recurs frequently enough for there to be reasonable expectation of occurrence within the life cycles of successive generations . . . the selective consequence may be expected to leave relevant genetic and evolutionary memories in succeeding generations. A "catastrophe" occurs sufficiently rarely that few of its selective consequences are relevant to the fitness of succeeding generations. The selective consequence of disasters is therefore likely to be to increase short-term fitness and the consequence of catastrophes is to decrease it (83, p. 627).

I see at least two problems with this idea. The first is largely a matter of semantics. It is unfortunate that Harper chose to assign the specific terms *disaster* and *catastrophe* to opposite ends of the continuum of disturbances. In principle, it seems a poor practice to designate specific categories without providing objective criteria for distinguishing among them. How much "relevant genetic memory" must be passed to future generations for an event to be classified as a disaster and not a catastrophe? While I doubt that Harper intended these terms to be adopted in empirical research, several workers have recently applied these terms to real situations (e.g. 152, 207). Such usage is best discouraged both for the reason just discussed and because these words are so commonly, but ambiguously, used in everyday speech.

The second problem with this view is the tacit assumption that the observed "fit" of an organism to its environment is attributable largely to the optimizing process of natural selection (75). It overlooks the real and lasting influence that a "catastrophe" may exert on the genotypes and phenotypes of succeeding generations, even if its immediate effects are density independent and largely random with respect to genotype. Until we know much more about the relative influences of different evolutionary processes, it is difficult to say whether natural selection by frequent disturbance has a greater evolutionary impact than the population bottlenecks, local extinctions, and founder effects associated with rare catastrophes (228).

A final caveat seems warranted. Hypotheses concerning the adaptive nature of observed patterns of life history, morphology, and behavior are easy to propose. It has often been suggested, or even taken as fact, that certain characteristics have evolved by natural selection in response to recurring physical disturbance. Furthermore, some species that depend on particular kinds of disturbance for completion of their life cycles or whose fitness is otherwise enhanced by such disturbances exhibit morphological or physiological features that seem to increase the likelihood that these disturbances will occur. This correlation has elicited the hypothesis that the latter features, sometimes referred to as "disturbance facilitating," have evolved by natural selection (e.g. 140, 244).

While there is little question that physical disturbance can act as a potent agent of natural selection and may play a part in other evolutionary processes as well one must be careful not to invoke natural selection as an explanation without considering alternatives. For example, many features of plants classically considered to be "fire-adapted," including flammability and the ability to resprout after fire, may have evolved in response to alternative selective forces such as herbivory or drought (29, 30, 70, 71) or by a different evolutionary mechanism altogether (75). "The immediate utility of an organic structure often says nothing at all about the reason for its being" (75:593). Whether "disturbance-dependent" organisms have evolved specific mechanisms that increase the probability of particular kinds and/or patterns of disturbance favorable to their persistence is an interesting, though probably an unanswerable, question.

The Role of Disturbance in Population and Community Dynamics

WITHIN-PATCH DYNAMICS

Demography I have mentioned a variety of factors that influence the reestablishment of populations within a disturbed patch of habitat. Subpopulations inhabiting different regions of a patch may differ in age structure, genetic composition, and life history characteristics (210). The selective effects of intra- and interspecific interaction may vary over small distances within a single patch—e.g. at its edge versus at its center. The evolutionary consequences of such variation have yet to be fully explored.

Interspecific interactions and the patterns of subsequent disturbance strongly influence the absolute and relative abundances of species within a patch, including the probability of continued local persistence.

Species diversity The resources made available by a disturbance are soon exploited by colonists and regenerating survivors, and a successional sequence of species replacements usually ensues (36, 143, 190). In the course of most successions, one or a few competitively dominant and/or long-lived species come to monopolize the resources of the disturbed patch (e. g. 36, 45, 113, 127, 129, 151, 153, 160, 190). In such cases, the time to local extinction of early successional species depends on the characteristics of the patch—for example, its size and degree of isolation (35, 192)—and of the species participating in the succession. When late successional species are able to invade the open patch, dominance will be quickly attained. So, small patches surrounded by adults of these species should be dominated more quickly than larger and/or more isolated patches.

In situations where hierarchical competitive interactions or differential longevities [see the inhibition model of succession in (36)] will probably lead to the monopolization of patch resources, disturbance can maintain within-

patch diversity by one of two mechanisms—compensatory mortality or intermediate disturbance (33, 34). *Compensatory mortality* refers to the situation in which the potential late successional dominant suffers a disproportionately high rate of disturbance-related mortality as compared to other species that it might otherwise exclude from the patch. Selective predation by the starfish *Pisaster* on the competitively dominant mussel *Mytilus californianus* (151) is a classical example of compensatory biological disturbance. Likewise, selective herbivory can maintain high local diversity in plant communities (128). Physical disturbance associated with heavy wave action can act in a similar manner on mussel-dominated intertidal shores (153) and coral reefs (33, 34); spates can have the same influence in stream communities (113).

Physical disturbance that does not cause compensatory mortality may nonetheless maintain within-patch diversity. To do so, a physical disturbance must renew resources, such as space, at a rate sufficient to allow continued recruitment and persistence of species that would otherwise be driven locally extinct. It must not occur so often or with such intensity, however, that many species are eliminated. Therefore, the disturbance must occur with some intermediate frequency and intensity/severity (33, 34), hence the term *intermediate disturbance*. These intermediate scales of disturbance allow species to accumulate within the patch but prevent it from becoming dominated by one or a few of them. The assemblage is maintained in a nonequilibrium state, and assuming that the system is open [i.e. dispersal can freely occur among patches (26)], local coexistence of species is ensured (33, 34, 88, 160, 189). The scales of disturbance that will maintain the highest within-patch diversity in any particular assemblage depend on factors such as the rate of competitive exclusion (96) and the relative rates of recruitment.

The hypotheses of disturbance-mediated coexistence “assume a transitive hierarchical ranking of competitive abilities among the species, with competitive outcomes being consistent and asymmetrical, i.e. one of a pair of competitors always winning over the other” (35). For some assemblages of sessile organisms, this assumption does not seem to hold, however. In some cases, the competitive abilities of species are about equal and the outcome of their interaction is largely stochastic (e.g. 1, 35, 73, 98, 177). The winner in any particular interaction is determined by its order of invasion, its relative size, and the angle of encounter with the competitor, among other factors. In other cases, species are arranged in a relatively intransitive competitive network defined by “the occurrence of a loop in an otherwise hierarchical sequence of interference competitive abilities” (23:223–24). The degree of intransitivity in such a network can vary, depending on the competitive symmetry of its members (35).

Even if there is an overall hierarchy, a high degree of symmetry in competitive interactions among high-ranking species or a competitive network involving such species should reduce the likelihood that within-patch diversity will

decline in the later stages of succession (167). Reciprocal replacement of species, as has been documented in some forest stands (e.g. 248), might also maintain high diversity in the absence of large-scale disturbance. Where such relationships among competitors exist, disturbance might seem unnecessary to maintain within-patch diversity. In the absence of disturbance, however, within-patch diversity in these systems may eventually decline owing to differences in the growth rates and competitive abilities of the species (23) or simply because the populations of some species fluctuate to low densities and go extinct by chance. Even rare disturbances can then be crucial in the long-term maintenance of local species richness (35). If nothing else, such nonhierarchical relationships may slow the rate of competitive exclusion (23, 102, 167) and thus increase the opportunity for mechanisms such as physical disturbance to maintain local diversity.

THE REGIONAL DYNAMICS OF POPULATIONS AND COMMUNITIES

The persistence of populations Most sessile organisms are, to varying degrees, "fugitive species." On a small enough spatial scale, probably no population persists indefinitely (37). The replacement of adults requires dispersal of propagules to sites favorable for recruitment. A population will persist in a given area only if that area provides a sufficient number of safe sites per unit time to guarantee successful recruitment during the adults' lifetimes. The minimum area needed for persistence will vary among species. A species whose offspring can survive and grow under environmental conditions similar to those experienced by the adults usually does not disperse its propagules far, and it potentially can persist in a relatively small area. In contrast, if the offspring require conditions significantly different from those found in the area occupied by the adults, propagules are often dispersed a long distance, and persistence will only occur on a relatively large spatial scale.

As noted earlier, many species depend on disturbance to create conditions favorable for the recruitment, growth, and reproduction of their offspring. The regional dynamics and abundance of such a species will reflect the interplay of its life history and the regime of disturbance. For such a species to persist, disturbances must generate colonizable space within the dispersal range of extant populations and within the period of time it takes for these populations to go extinct (e.g. 152).

Species diversity The species diversity of a region is a function of both the number and relative abundances of species that persist there. The regional abundance of a species can depend on the rate of disturbance (i.e. the area or number of patches cleared per unit time) and its predictability (as just discussed). In addition, regional population dynamics can be influenced by the size distribution of open patches and how synchronously they are produced.

Miller (133) assumes, and Abugov (3) demonstrates theoretically (as have others), that regional diversity peaks at intermediate rates of disturbance. At high mean disturbance rates, early successional species dominate most patches, while at low mean disturbance rates, late successional species do. These studies showed, however, that the distribution of patch sizes and the degree to which disturbances were phased (i.e. how synchronously they occurred) could strongly influence the level of diversity maintained by any given level of disturbance.

Assuming that small patches are usually invaded and dominated more quickly than large ones, Miller (133) concludes that large patches should favor colonizing species (i.e. early successional species) while small patches should favor competitive species (i.e. late successional species). Given these assumptions, he shows that at a low overall disturbance rate, regional diversity will be higher if the mean size of cleared patches is large, thus favoring the continued persistence of colonizing species. When the rate of disturbance is high, regional diversity will be greater when the areas disturbed are small, since this will ensure the continued persistence of competitive species. Alternative ways in which patch size may influence regional dynamics have also been discussed (35, 192).

Abugov (3:289) has examined how the phasing of disturbance might affect regional diversity. He describes *phasing* as follows:

... the disturbance of a patch is unphased if its probability of being cleared during each time interval is independent of whether any other patches are being cleared during the same time interval. Conversely, other patches may be disturbed in phase. Each time a disturbance clears one of these patches it clears them all.

In the simplest case, as phasing increases, so does the proportion of colonizing species in the assemblage. Thus, an increase in the phasing of disturbance will decrease diversity when colonizing species predominate but will increase diversity when competitively dominant species occupy most of the space. More complicated patterns are also possible if one allows for changes in the relative competitive and migratory abilities of the colonizing species. To my knowledge, these theoretical predictions have yet to be tested empirically.

Patch dynamics and landscape pattern Recent research on the role of disturbance in natural communities has increasingly focused on patterns at the regional scale, where the diversifying influence of disturbance is easy to observe. Patchy and locally asynchronous disturbance transforms the land or seascape into a continuously changing mosaic of patches of different sizes and ages (153, 159, 172, 173, 189, 239). The spatial orientation of each of the phases of this mosaic may strongly influence regional dynamics, particularly if the dispersal range of propagules is limited (159, 192). The dynamics of this patchwork of successional stages is beginning to receive theoretical attention (e.g. 153, 184, 185).

Do within-patch, nonequilibrium conditions average to an equilibrium pattern when one considers the mean dynamics of an area containing many such patches? Bormann & Likens (19, 20) refer to this large-scale equilibrium as a "shifting-mosaic steady-state." Many workers would answer the above question affirmatively (e.g. 19, 20, 196, 198, 249); but Romme (172, 173) found strong cyclic, rather than steady-state, dynamics in the vegetation of a 73 km² watershed in Yellowstone National Park. Recent simulation studies (185) indicate that the likelihood of a large-scale steady state is a function of the total landscape area and the size of the individual disturbances. The larger the area affected by a single disturbance, the more extensive the landscape must be to average out its effects. Landscapes that are small in absolute area (including those that have been fragmented by human activity) or that experience typical disturbances covering many thousands of hectares (e.g. 66) are unlikely to be in equilibrium.

DISTURBANCE AND MOBILE ANIMALS

With some notable exceptions, ecologists have largely overlooked the significant role of physical disturbance in the biology of mobile animals. Appreciation of the direct and indirect influences of disturbance on mobile animals has been slow to develop for at least two reasons. First, the direct effects of disturbance on mobile organisms are not as easy to observe and measure as those on sessile organisms. Second, during the last two decades many of the most influential investigators of the ecology of mobile animals—vertebrates in particular—have been proponents of a competition-based equilibrium theory of community organization (104, 241). Once equilibrium is assumed, there is little cause to examine the influence of supposedly rare and inconsequential disturbances.

In recent years, this view has become quite controversial (178). Physical disturbance can be a major cause of local disequilibrium when it kills appreciable numbers of animals, as demonstrated by the following incomplete list of examples: cold temperatures—butterflies (24, 58, 182), coral reef fish (18), stream fish (104, 214); oxygen depletion—lake fishes (213); drought—pond fish (121), stream fish (122), salamanders (99); flooding—desert fish (32); hurricanes—coral reef fish (123); fire—vertebrates (14, 28, 31, 169), soil and litter invertebrates (4, 31, 169); miscellaneous agents—intertidal invertebrates (192).

Severe climatic conditions can indirectly exert a strong negative impact on populations of mobile organisms by eliminating or producing shortages in vital resources. For example, prolonged drought stresses or kills the food plants of butterflies and causes large declines in, or even extinctions of, local populations (59, 182). A similar risk of local extinction is faced by any parasite whose host is subject to physical disturbance (165).

Even when a climatically induced shortage in resources does not cause much mortality, organisms that remain in the area may experience increased intra- and interspecific competition. Highly mobile species may move in search of more benign sites where resources are more plentiful. Increased competition and emigration during harsh climatic periods can reduce local population densities. These effects are well documented in recent long-term experimental and observational studies of lizard (55, 186) and bird (187) assemblages.

As was true for sessile organisms, mobile animals vary considerably in their vulnerability to disturbing forces and in their ability to avoid them. Animal responses to fire are a case in point (4, 14, 31, 118, 169). Highly mobile species can escape harm from all but the most quickly spreading fires by moving just ahead of the advancing flames or by seeking refuge out of the fire's path in patches of unburnt vegetation. If fleeing animals are overtaken, they can survive (as long as the fire is not too intense) by taking refuge in burrows or under rocks. Consequently, low to medium intensity fires often have relatively little direct impact on vertebrate populations. The main effect of such fires is to alter temporarily the spatial distribution and density of these populations. The burned site is frequently reoccupied soon after the fire has passed, though population densities may not return to prefire levels until the appropriate vegetation has regenerated on the site. In contrast, relatively immobile soil and litter invertebrates have no means of escaping an advancing fire; even a low intensity burn can kill large numbers of these organisms. The rate at which the burned area is recolonized by such organisms depends on the species' dispersal abilities and the proximity of source populations in surrounding areas of unburnt vegetation.

Physical disturbances also cause short- and long-term changes in the habitat that can have major indirect effects on populations of mobile species. Some of these changes can be detrimental to mobile animal populations, as the following examples demonstrate. As a result of unusually heavy rains, large quantities of sediment were deposited in a southern California coastal lagoon. These deposits reduced the low tide volume of the lagoon and eliminated much of the previously extensive cover of eel grass. Probably for lack of sufficient habitat—as opposed to direct mortality caused by the sedimentation—the density of water column fishes declined significantly (148). Similar declines in fish populations have been observed on storm-damaged coral reefs (105, 229). Here too, the reduction in fish numbers was due more to storm-induced alterations in the habitat than to any direct mortality caused by storm conditions.

Disturbances can also have indirect positive effects on mobile animal populations. Those that cause some immediate mortality may in the long run produce a net increase in population size and vitality. Fires, for example, may kill some birds and mammals, but they also reduce the populations of parasites that afflict some species (14).

Disturbances from such agents as fire, windthrow, and water motion indirectly affect populations of mobile animals by influencing the composition and structure of sessile assemblages. Sessile organisms provide cover and/or food, thus constituting a major component of the habitat of mobile animals. As this paper has emphasized, physical disturbance transforms sessile assemblages into mosaics of different seral stages. Sessile organisms comprising each of these stages differ in many characteristics critical to the welfare of mobile animals, including structural complexity, species composition, microclimate, and the quantity and quality of the food and shelter available. Although mobile animal species vary in their habitat requirements, many prefer the productive conditions associated with areas undergoing regeneration from recent disturbance. The quantity and palatability of plant foods are often higher in earlier stages of succession (27, 65, 81, 173). Some species of birds forage preferentially for fruits or insects in forest light gaps (180, 211).

Other species exploit the tissues of dead or dying plants as a resource and preferentially colonize recently disturbed sites where this material is abundant. For example, bark beetles and other boring insects are strongly attracted to injured or dead trees (181).

The compositions of insect, bird, and mammal assemblages change with the successional stage of the vegetation (e.g. 7, 16, 28, 61, 64, 115, 142, 173, 181, 183, 188, 206, 245). The population density and species richness of mobile animals often decline in later successional stages, paralleling similar trends in the vegetation. Some species, however, become more abundant as time elapses since the last disturbance. Such patterns reflect species-specific responses to changes in vegetation structure and composition, food availability, and inter-specific interactions that accompany successional shifts in the plant community. Similar changes in mobile animal assemblages occur over the course of succession in sessile communities on rocky seashores (e.g. 48). On the landscape scale, mosaic patterns in sessile assemblages generated by disturbance are likely to have a profound effect on the regional population dynamics of mobile animals (65, 81, 173, 242).

CONCLUSIONS

I have attempted to summarize some of the key themes that run through the vast and rapidly expanding literature on disturbance in natural communities. These include: (a) the factors that determine natural regimes of disturbance, (b) organismal-level responses to disturbance and their evolution, and (c) the influence of disturbance on population and community structure and dynamics at both the local and regional scales.

Although all natural communities probably experience disturbance at some spatial and temporal scale, historically its role in community dynamics has

been largely overlooked, except by some temperate-forest ecologists. There are many reasons for this neglect, but one of the prime causes may be that major disturbances often recur at intervals longer than the duration of an average research project or even than the lifespan of the investigator (146). Thus, the effects of disturbance cannot always be directly observed, which may lead one to conclude that disturbance is unimportant. Even a very long recurrence interval does not necessarily indicate that the impact of disturbance on the community is inconsequential, however. When the affected organisms are long-lived, the "compositional effects of disturbance can persist for centuries or even millennia" (66:216)).

There is a growing realization that disturbance may play as great a role in community dynamics as do biological interactions such as competition and predation, which have received far more empirical and theoretical attention from ecologists. The interplay between disturbance and these biological processes seems to account for a major portion of the organization and spatial patterning of natural communities.

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