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Author(s): Seth R. Reice

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# Nonequilibrium Determinants of Biological Community Structure

*Biological communities are always recovering from the last disturbance. Disturbance and heterogeneity, not equilibrium, generate biodiversity*

Seth R. Reice

Not far from my home in the Piedmont region of North Carolina, the diversity of life is evident in New Hope Creek. More than 160 macroinvertebrates, most of them insects, thrive in the stream. Nearby Botany Pond, however, has only 15 species of macroinvertebrates. This pattern is far from unique; in fact, it is repeated among clean streams and ponds worldwide. Neighboring biological systems often include members of overlapping families and genera, but they tend to have distinctly different community structures.

This curious finding provokes questions: Why should neighboring systems be so dissimilar? What determines the differences in structure among similar communities?

The answers to these questions are at the heart of a long-standing debate in ecology—a debate that recently has taken a new turn. The model that has guided policies on ecosystem management and biodiversity issues may have ignored important aspects of community dynamics. Human efforts to stabilize ecosystems have resulted in the loss of biodiversity, when the opposite result was the goal. It is time

to look at the response of biological communities to disturbance in a different way.

Historically, the question of what determines community structure has been approached from two directions. One group of theorists has supported environmental processes as determinants of community structure. In the view of H. Gleason, writing in the 1920s, and H. G. Andrewartha and L. C. Birch, in a 1954 book, a community's composition is determined by its environment, which sets the range of possibilities for colonization, reproduction, growth and survival. The presence or absence of a given taxonomic group results from random colonization processes and variability in the environment.

This view has not, however, been dominant in this century. Another paradigm, equilibrium theory, has dominated both ecological thought and public policy. This view has its origins in the writings of Charles Elton, who in 1927 emphasized the role of interspecific (between-species) interactions to explain why only a subset of the species that could colonize an area actually coexist there. His theory of limited membership argued that biotic interactions—competition and predation—determine the community structure we observe.

Equilibrium theory asserts that systems are at equilibrium—in a steady state, with overall species composition and relative abundances stable through time—as a result of biotic interactions among its members. Such systems return to their original structure after perturbation.

Equilibrium models presume a constant environment, excluding the signif-

icance of disturbance or any other environmental fluctuations. In such a worldview, it is a simple step to conclude that biotic interactions are the key determinants of community structure. R. H. MacArthur and E. O. Wilson's *The Theory of Island Biogeography* epitomizes this view. Under equilibrium conditions, the community is the direct result of the competitive and predator-prey relationships among species. Predator-mediated coexistence and spatial heterogeneity are important in maintaining high species diversity, but they still fall within the equilibrium.

The predictions of interspecific-interaction models, however, often do not appear to hold in nature. Indications of the shortcomings of equilibrium theories include the coexistence of quite similar species and the frequent lack of demonstrable effects both of suspected competitors on each other and of predators on their prey distributions. Such contradictions have been identified in a variety of ecosystems: Peter Sales's study of coral reef fishes, Joe Connell's work on tropical rain forest trees and coral reefs, Bob Peet's examinations of chalk grasslands and pine savannas, and my own work on benthic invertebrates in streams have all led to a new view of community dynamics.

**Figure 1. Nonequilibrium theories of biological community structure counter the long-held notion that equilibrium in an ecosystem maximizes biodiversity. Instead, such theories emphasize environmental disturbance and spatial heterogeneity as factors that encourage colonization and species diversity. Here, in Yellowstone National Park, a surge of botanical diversity is obvious only months after the famous fires of 1988. (Photograph by Renee Lynn, Photo Researchers Inc.)**

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*Seth R. Reice is an associate professor of biology and chairman of the curriculum in ecology at the University of North Carolina at Chapel Hill. Growing up in New York City in no way impeded his development as an ecologist; he soon received his Ph.D. in zoology from Michigan State University. His particular area of research interest is in disturbance ecology as applied to stream communities and other systems. He also is interested in conservation and sustainable development, particularly in Latin America. Address: CB# 3275, Wilson Hall, University of North Carolina at Chapel Hill, Chapel Hill, NC 27599-3275.*



		disturbance		
terrestrial ecosystems		type	frequency	predictability
freshwater ecosystems	deciduous forest	fire windstorm insect defoliation	1 / 40–200 years 1 / 10–25 years rare	none
	coniferous forest	fire windstorm insect defoliation	1 / 40–200 years 1 / 10–25 years rare	moderate none none
	rain forest	windstorm fire storms	frequent 1 / 200–500 years 1 / 50–100 years	none none none
	chaparral	fire	1 / 15–25 years	high
	grasslands	fire	1 / 5–10 years	moderate
	desert	frost	1 / 50–200 years	none
	swamp	fire	1 / 10–25 years	none
	river	spring snowmelt storm floods drying up freezing	annual 0–15 / year 0–2 / year 0–2 / year	high none moderate to high high
marine ecosystems	lake	storms freezing	0–4 / year 0–1 / year	none high
	pond	freezing drying up	0–1 / year 0–2 / year	high low to high
	intertidal	hurricanes, tornadoes log damage	1 / 20 years annual	low low
	pelagic zone	storms	aperiodic	low
	deep sea benthos	carcasses storms	aperiodic aperiodic	low low

**Figure 2.** Frequency and predictability of disturbances affect characteristics of the biological community. For example, the number of years between disturbances is roughly proportionate to, and nearly always shorter than, the life span of the dominant species in the system. Biota adapt readily to predictable disturbances, such as spring snowmelt, but many more individuals are lost when disturbance is erratic.

To explain these apparent anomalies, nonequilibrium theories of community structure have recently been proposed. These include concepts such as disturbance theory, patch dynamics and supply-side ecology, which I shall discuss in detail later. In essence, nonequilibrium theories attribute the high diversity of species and the coexistence of similar species that we observe to processes of disturbance and recruitment.

I shall argue that community structure is primarily determined in a non-equilibrium fashion by the interactions of the heterogeneity of the physical-chemical environment, disturbance and recruitment. Homogeneity in natural systems is clearly illusory. Although I acknowledge that biotic interactions are certainly important in communities that are at or near equilibrium, I contend that equilibrium is an unusual state for natural ecosystems. In systems where the interval between disturbances is long relative to the generation time of the dominant species, biotic interactions may well have an important role. However, I suggest that the normal state of communities and ecosystems is to be recovering from the last disturbance. Natural systems are so frequently disturbed that equilibrium is rarely achieved.

Furthermore, it appears that disturbance not only creates patches (the environmental mosaic) but also is a product of the patches themselves. The underlying physical-chemical environment determines the frequency and magnitude of a disturbance, influences the time course of recovery and ultimately determines the community structure. The interaction between disturbance and patchiness in virtually all systems is the underlying basis for the control of community structure. Stochastic (random) recruitment in a heterogeneously disturbed, patchy environment results in high overall species diversity. These interdependent variables are the nonequilibrium determinants of community structure.

#### All Environments Are Heterogeneous

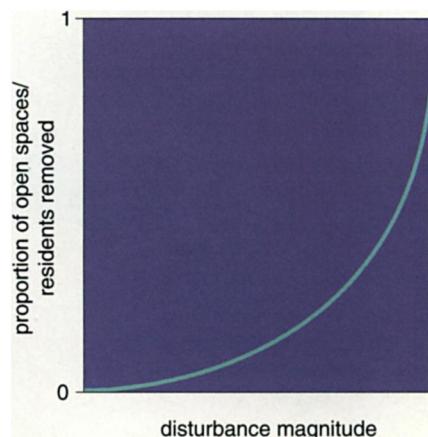
All environments in all ecosystems are patchy in space and variable in time. The environmental patchiness is based on physical and chemical gradients that are ubiquitous. In terrestrial ecosystems we encounter variations in elevation, slope, temperature and moisture, and a host of chemical gradients in the soil. In aquatic ecosystems

we encounter variations in depth, temperature, current velocity, substrate particle size, salinity, pH, dissolved oxygen, nutrients and heavy metals. The limnologist and longtime *American Scientist* columnist G. Evelyn Hutchinson argued that even the pelagic (open-water) zones of lakes, which superficially appear homogeneously mixed, are patchy systems.

In spite of this obvious spatial heterogeneity and complexity, many ecological modelers assume the existence of a homogeneous environment. We would all agree that a superior experimental study manipulates or controls only a few environmental variables out of the thousands that are the parameters of the niche of every species. It is not surprising, then, that we tend to minimize the effects of environmental heterogeneity on community structure. We are simply overwhelmed by the complexity of the environment.

Spatial heterogeneity is frequently invoked as a mechanism for maintaining diversity. A heterogeneous environment allows species to subdivide resources. Thus the problem of diversity becomes the traditional issue of limiting similarity (dating back to Elton). In 1984, A. Shmida and Stephen Ellner (of North Carolina State University) modeled the coexistence of equivalent species in a spatially heterogeneous environment. They showed that dispersal from optimal microsites can support marginal populations in suboptimal microsites. This mechanism is important in all patchy environments whenever disturbances occur.

Ecologists acknowledge the importance of temporal variability. Tropical scientists, for example, are well aware of the seasonality of rainfall. Arctic and near-arctic ecologists, on the other hand, emphasize seasonal fluctuations in temperature. Temperate-zone ecologists deal with both. Even so, it is rare that temporal variability is seen as having an important role in structuring the community. Shmida and Ellner argue that temporal environmental variation can permit the coexistence of trophically equivalent species. Under one set of environmental conditions, one competitor is more fit; when things change, another species is favored. Coexistence results from fluctuations in the environment. This mechanism also has its greatest impact in disturbed systems. Fluctuations in the environment generate what John Weins in 1977 called



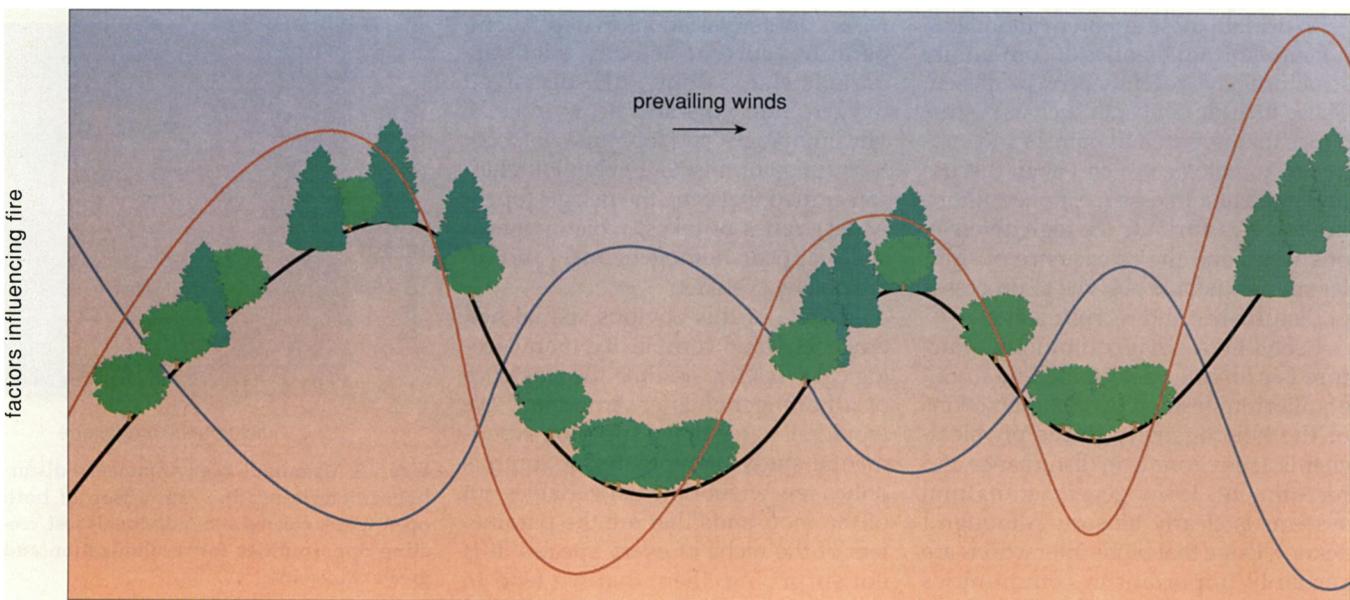
**Figure 3. Magnitude of environmental disturbance determines the proportion of both open spaces created and individuals lost, creating opportunities for recolonization and greater diversity.**

"environmental crunches," which affect the relative importance of competition in communities through time. When resources are scarce, competition becomes much more important.

#### Disturbance versus Equilibrium

Ecologists have recently begun to understand the implications of disturbance for community structure. The theoretical basis for the role of disturbance in community organization has been articulated by many ecologists. I shall use the definition of Steward Pickett and Peter White, who wrote: "A disturbance is any relatively discrete event in time that disrupts ecosystem, community or population structure, and changes resources, availability of substratum, or the physical environment." This description defines disturbance as a physical event, not as the biotic outcome of the event. I view a disturbance as a physical force such as a fire, flood or tornado that damages natural systems and removes organisms. The first impact of a disturbance is always to remove organisms.

Disturbance is scale dependent. If the area studied is large enough or the period of observation long enough, all disturbances are predictable and "normal." At smaller scales or shorter durations, disturbances appear completely random. Vincent Resh and his colleagues have argued that if a disturbance is predictable, the biota can and will adapt to it; a disturbance that is unpredictable will have a greater impact. The absence of predictable disturbances (for example, spring snowmelt floods or the arrival of snow in the winter) often has a greater impact than their presence.



**Figure 4.** Susceptibility of a forest system to fire (red) is determined by the characteristics of the system itself. Its altitude, orientation to prevailing winds, the moisture content of the wood (blue) and the abundance of the fuel all affect the ability of fire to take hold and spread. Thus the system may influence both the likelihood and the severity of disturbance.

Contrast disturbance with predation. Predation is an important agent for the removal of prey individuals. It is not, however, a disturbance. Predation is intrinsic to the life of the prey species, which can and does adapt to it.

Enrichment events often constitute disturbances, although they appear not to fit the definition presented above. Fertilization often leads to the loss of species diversity by favoring particular species' growth and reproduction at the expense of others. The enrichment event can be viewed as the indirect cause of the disturbance. For example, a dam burst on a farm manure pond near Raleigh, North Carolina, and flooded the Neuse River with a million gallons of liquid pig manure. This material had a high concentration of organic matter, with high biochemical oxygen demand (BOD). The influx of the manure slurry was actually the indirect cause of the disturbance. The disturbance was the loss of dissolved oxygen, which killed thousands of fish.

The enrichment of lakes and streams that results from ordinary agricultural runoff is one step further removed from the disturbance. The nutrients in the runoff stimulate algal blooms, often shifting the community composition from green to blue-green algae. The BOD from the decay of the algae can alter community structure by selectively killing off organisms that have greater needs for dissolved oxygen. Again, it is the loss of dissolved oxygen that is the actual disturbance.

Disturbance typically is not a population process; it causes restructuring of the whole ecosystem (for example, following a fire or flood), wherein the habitat is altered or rearranged and, as a result, organisms are removed. Disturbance is a reinitializing step in the successional development of a community. Different disturbances remove different species to different degrees. Therefore, the particular response of the community is likely to be a unique successional sequence.

It is important to understand that community structure is made up of both species richness (the number of species) and evenness (the distribution of individuals among the species). (We ecologists combine these parameters into diversity indices, such as the Shannon-Weaver Diversity Index.) The effects of disturbance on richness and evenness can be quite different. In my experiments on disturbance in stream benthic communities (bottom dwellers), for example, species richness was rarely affected, because whole species were rarely eliminated or added. There are often, however, major shifts in relative dominance, which can dramatically affect evenness.

The Intermediate Disturbance Hypothesis (IDH) was presented by Joe Connell in 1978 to explain the high species diversity in tropical rain forests and coral reefs. The IDH presumes a competitive hierarchy of species. When disturbances are infrequent or small,

superior competitors eliminate inferior competitors, reducing the species richness of the system. The model also presumes that the superior competitors are efficient occupiers of space (they are resident species).

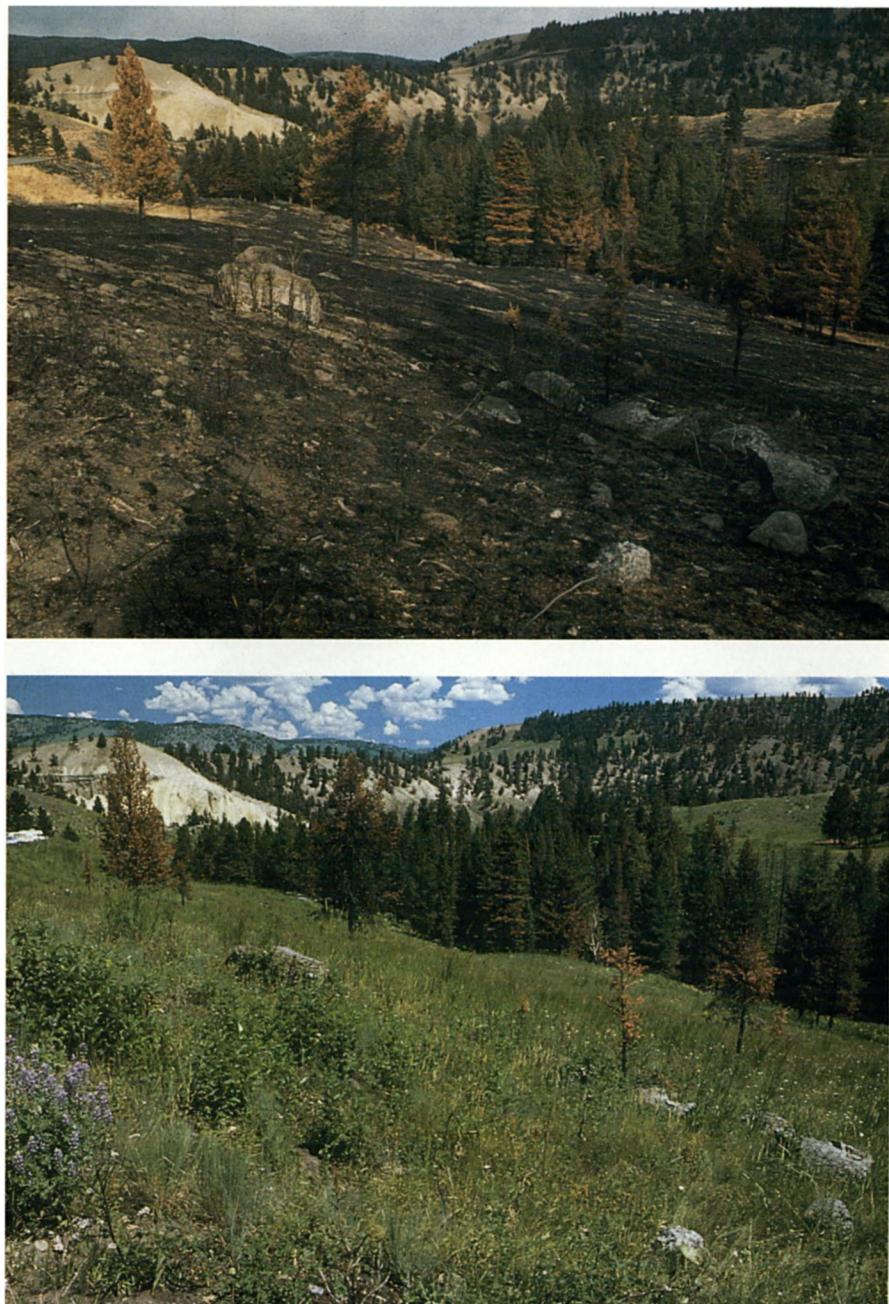
Under a frequent or intense disturbance regime, by contrast, the dominant competitors are reduced or eliminated, and colonizing species (assumed to be inferior competitors) dominate the system. The absence of the resident species reduces species richness. Finally, under a disturbance regime that is intermediate in frequency, magnitude and intensity, some resident species persist in the system along with colonizing species, which exploit the disturbed areas. Thus intermediate disturbance leads to maximum species richness.

Michael Huston's 1979 "dynamic equilibrium" model showed that community structure can result from the trade-offs between population growth rates, rates of competitive exclusion and the frequency of population reductions. Huston demonstrated that if disturbance recurred at intervals shorter than the time necessary for competitive exclusion to take place, poorer competitors would persist in the system, increasing species richness. He wrote: "Diversity is determined not so much by the relative competitive abilities of the competing species as by the influence of the environment on the net outcome of their interactions."

It is my view that disturbance is the major source of these population reductions and is the key factor in determining community structure. Many systems are disturbed frequently enough to prevent equilibrium conditions from ever being established. And in a heterogeneous environment, when disturbance routinely recurs more quickly than equilibrium can be attained, high diversity is the result.

Nonequilibrium dynamics can best explain the temporal and spatial patchiness that characterizes nearly all communities. Disturbances are common and important in virtually all ecosystems (Figure 2). In terrestrial ecosystems, fire and windstorms are most important. Neither is predictable, and both can destroy plants and animals. Nevertheless, many terrestrial species are adapted to their disturbance regimes. In fact, many species require fire to flower or set seed. In chaparral vegetation, Norm Christensen and Cornelius Muller have shown that life histories are linked to the periodic disturbance of fire. As debris builds up during non-burn periods, the susceptibility to fire increases. The reproduction of these plants is keyed to fire, as the seeds will not germinate without it. This is true for serotinous pines, such as jack pine (*Pinus banksiana*) and pond pine (*Pinus serotina*). In the Australian bush, eucalyptus forests are fire adapted and fire maintained. This is not limited to a particular species but applies to the dominant genus of the entire continent. In Tasmania, Jackson showed that fire sets the boundaries and controls succession from rain forests to eucalyptus or moist sclerophyll (hard-foliage) forests. On poor soils, fire frequencies of more than once every 300 years will result in the transition from rain forest to moist sclerophyll forest. With fire frequencies of less than 1 per 500 years, the transition is to a diverse rain-forest system. This suggests that 1 per 500 years may be an intermediate disturbance frequency for these trees.

The role of disturbance in stream communities has been analyzed by myself, Resh and his colleagues, and J. David Yount and Gerald Niemi of the University of Minnesota. Benthic invertebrates in flowing waters that flood frequently have morphological features that allow them to cling to the substrate (for example, mayfly nymphs have claws). Others live in the bound-

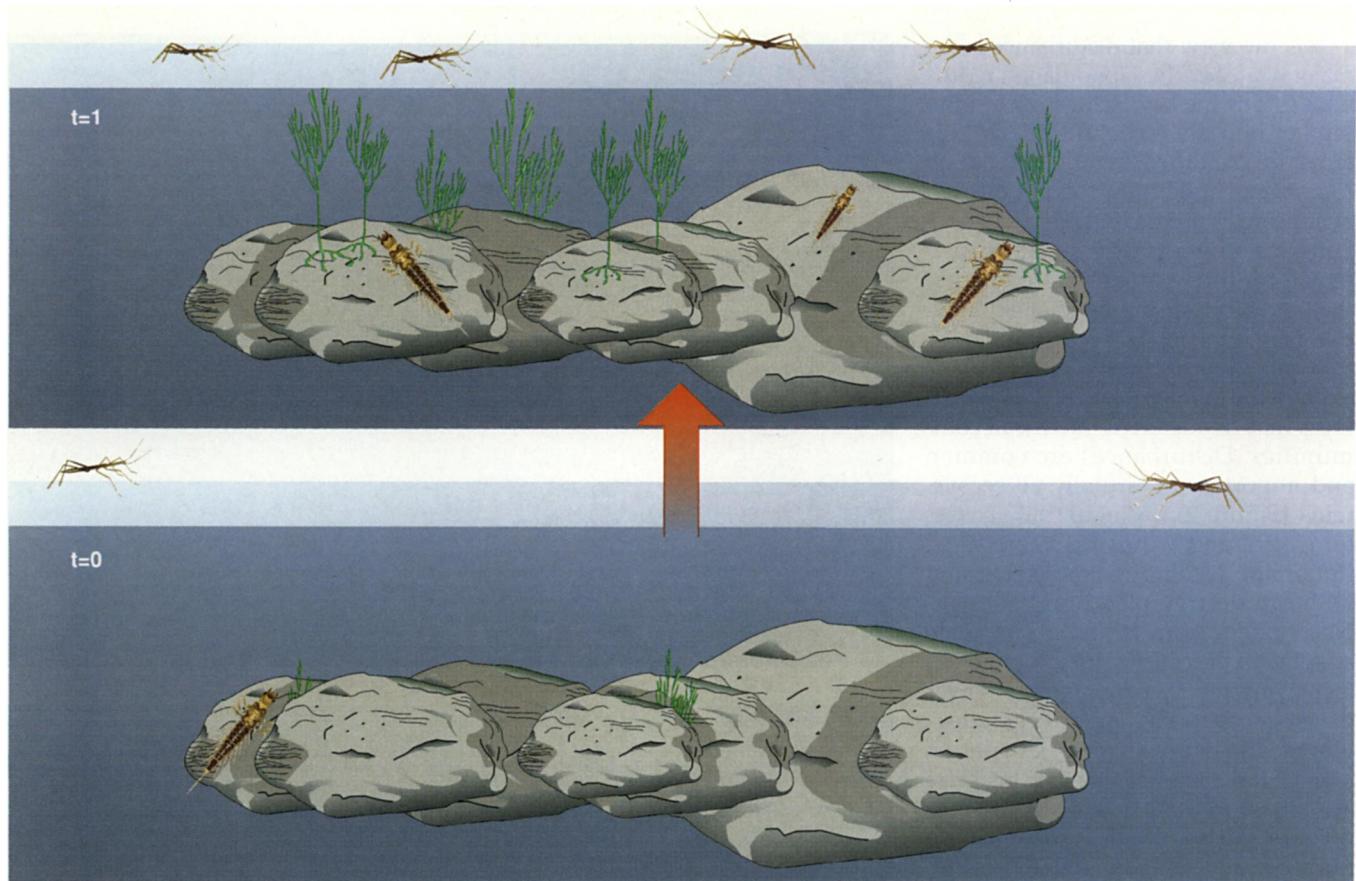


**Figure 5. Photographs of the same location in Yellowstone National Park taken immediately after the 1988 fire (top, November 4, 1988) and the next summer (above, July 26, 1989) show how disturbances are patchy in their distribution and how quickly systems respond to disturbance with a variety of new life. (Photographs by Jim Peaco, Yellowstone National Park.)**

ary layer and filter above it (for example, black flies [*Simuliidae*] have collecting fans that project into the flow so their bodies are protected from the full force of the current). *Simuliidae* are excellent colonizers of newly opened space. Adaptations of species to disturbance regimes are common in many other systems.

Not only are all ecosystem types disturbed, but most also are disturbed frequently relative to the life history of the dominant species. The return

interval of disturbance is roughly proportionate to the life span of the dominant organisms (the space holders) in different systems (Figure 2). Forest trees can live hundreds of years, and the frequency of fire or windstorm disturbances is much shorter than that. Stream insects live up to four years, and fishes even longer. The flood cycle is typically annual or shorter. The return interval of disturbance may be a critical determinant of life-history characteristics such as the

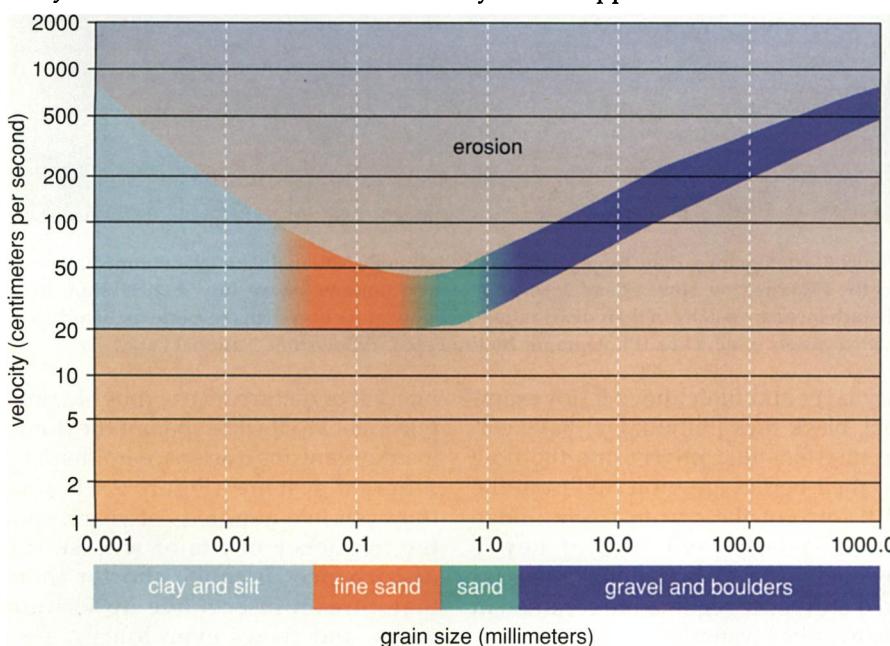


**Figure 6.** Recolonization takes place by only three mechanisms. Biota (typically plants) may regrow from surviving individuals; organisms that walk or crawl may migrate from adjacent patches; or individuals that swim, float or fly may be recruited from outside the proximate system.

generation time and the intrinsic rate of natural increase. The common condition for most communities is to be recovering from the last disturbance. Only when the return interval for the

next disturbance is long, relative to the life span of the resident species, can something approaching equilibrium be attained. I argue that this nearly never happens.

**Disturbance Means Loss of Individuals**  
The initial impact of a physical disturbance in a community is to remove individuals, who may be either killed or displaced. Disturbance is the major mechanism of density-independent population reductions. The removal of individuals creates opportunities for new species to colonize, changing the community structure. Colonization by individuals of pre-existing species can transform the age structure of populations and change their interactions with the community. Whether fire or flood, the result of disturbance is that individuals and populations are lost from the system. As a result of the losses, new physical and niche space is created. The creation of opportunities for recolonization is the vehicle for generating high species diversity. Greater magnitude disturbances remove more individuals and create more open space (Figure 3).



**Figure 7.** Grain size influences the water velocity at which material in a streambed begins to move. Adhesive properties cause the smallest particles, clays and silts (*left*), to respond at a wide range of threshold velocities. Thus consolidated clays and silts have as much resistance to disruption by moving water as boulders, whereas unconsolidated small particles move as readily as sand grains.

**Three Mechanisms of Recolonization**  
There are only three mechanisms by which a species can recolonize newly available niche space after disturbance: regrowth, migration or recruitment. Regrowth is repopulation by survivors

of the disturbance. Trees can regrow from stump sprouts, and surviving coral polyps can regenerate an entire reef. Migration is recolonization from adjacent patches within the system. Mayflies can crawl from one stone to another, and crabgrass can spread into tilled gardens. Recruitment is recolonization by individuals from outside the proximate system. This includes windblown seeds in a forest, or egg laying or drift by stream insects. The germination of seeds from a seed pool is viewed as recruitment.

The relative importance of these three mechanisms varies widely among systems and taxa. Some systems, such as the rocky intertidal ecosystem, are dominated by recruitment. Migration is less important in others (temperate forest trees, for example), where regrowth and recruitment have important roles. Regrowth in sexually reproducing animals is rare, but migration is common. Regrowth is strictly fixed: Only survivors of disturbances can regrow, and they replace themselves.

Migration blends random and fixed processes. Immigrants are a random sample but only of the residents of the neighboring patches (a limited subset of potential colonists). Migration results from crowding. In nature recruitment is largely random: Open space is colonized by a random sample of potential occupants.

Disturbance *per se* does not determine diversity. It creates opportunities for colonization of vacated spaces by new species. If regrowth dominates, there is no change. Disturbance leads to change in community structure only if there is an ample supply of recruits to the community.

### Patchiness and Disturbance

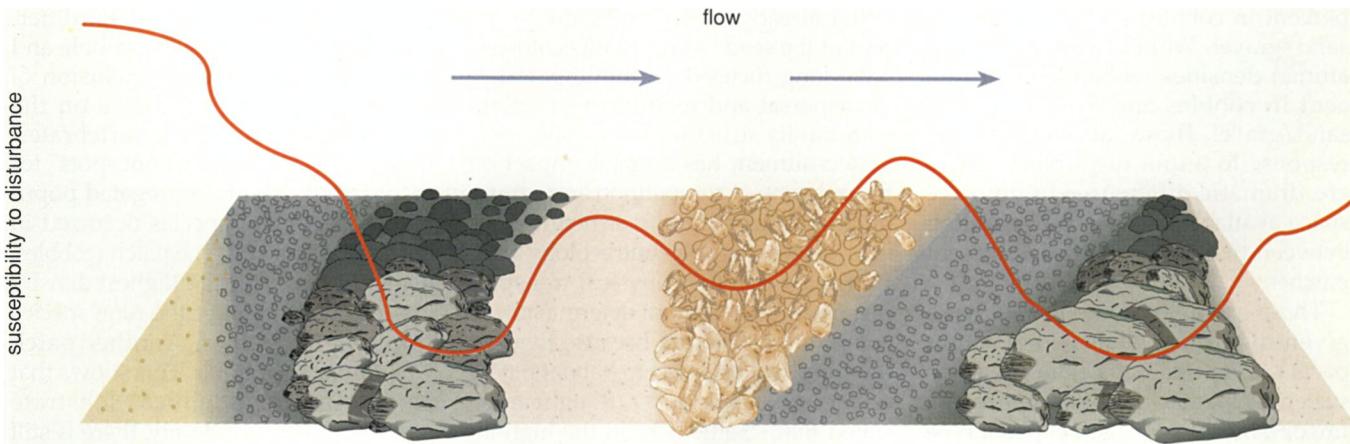
Most of the literature focuses on disturbance as the agent causing or maintaining the mosaic of species distribution. A tornado or fire destroys one patch of trees but not another. A flood scours one riffle, opening some patches, and transports other animals into it. It is easy to see that disturbance is a source of environmental patchiness. A complementary perspective is that the patches influence the disturbances. Patches can mitigate or intensify a disturbance event. Various patches have differential susceptibility to a unit disturbance (one of uniform strength or magnitude across the range of patches). The result of the disturbance is to enhance the patchiness, in that one patch sustains far greater population losses than another. As a result, different patches will be differentially open to recolonization. Two examples will illustrate this idea.

Fire susceptibility in forests depends on many variables, but the two main factors are fuel quality and fuel quantity. Soil moisture influences fuel quality, because wet wood does not burn well. Furthermore, decomposition on the forest floor is more rapid where the soil is wetter. So soil moisture affects the fuel quantity as well. Wind is critical, too. It can create fire danger by blowing down trees and drying the wood, and it can also help spread flames. Fire vulnerability is greatest on the mountaintops and lowest on the moist valley floors. The risk of fire is not uniform across the forest (Figure 4). In the Yellowstone National Park fire of 1988, whole forest stands were burned to the ground while others were barely singed. Mark Harman, Susan Bratton and Peter White

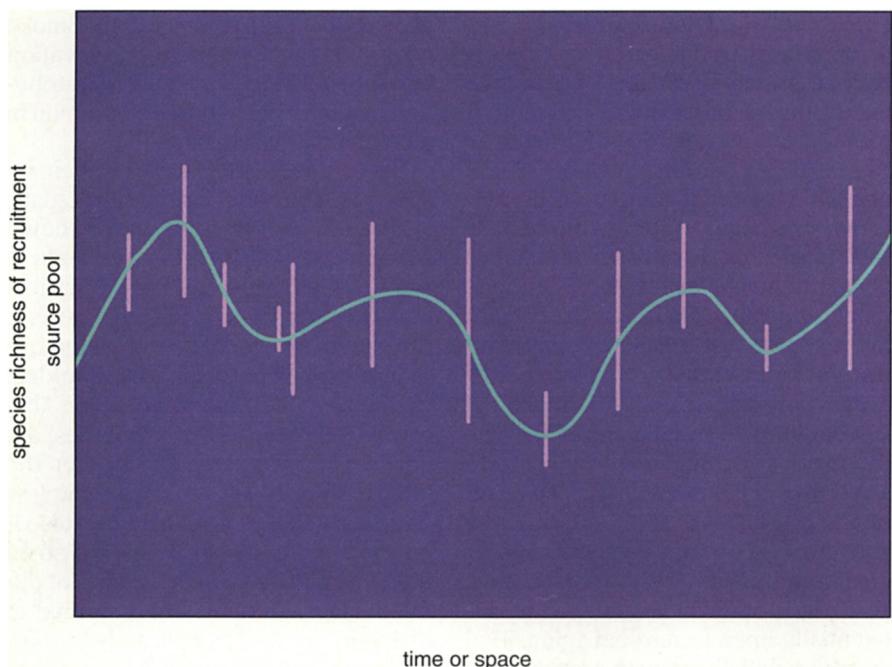
showed that fire frequency in the Smoky Mountains is dependent on elevation and soil moisture. Variability in distribution and intensity of burns is common in all terrestrial systems.

Stream beds are patchy in their responses to floods. Sedimentologists, such as R. W. Newbury, have shown that particles of different sizes begin to move at various ranges of critical stream velocities. In Figure 7 we see that sand moves at lower velocities than all other particle sizes. Boulders (because of their mass) and clays (because of their adhesive properties) are hardest to mobilize. The higher the critical velocity for a particle, the less frequently will that velocity be exceeded. Sediments in streams are distributed in a patchy fashion. Patches of different size sediments are disturbed at different frequencies, based on their critical velocities (Figure 8). Sands are disturbed most frequently; they move even in small spates. But only major storms generate the velocities necessary to disturb the clays or boulders. Shifting sediments can be a significant disturbance to the benthic community. Invertebrates, fish eggs and algae can be dislodged, buried or crushed, resulting in injury or death. Consequently, space is opened up, creating opportunities for recolonization. So the frequency of disturbance to the biota is a result of the physical patchiness of the environment.

The relation between sediment particle size, frequency of disturbance and community structure has not yet been thoroughly investigated. The resilience of community structure in a stream with a particular sediment type should



**Figure 8.** Stream bottoms are rarely composed of only one grain size. More typically they contain grains ranging from clay to boulders, materials that have great differences in susceptibility to disturbance. In flood conditions, biota located in sandy areas are much more likely to be disturbed than those that inhabit boulders.



**Figure 9.** Richness of the recruitment pool—the individuals available from outside to replenish a system depleted by a disturbance—varies significantly in time and space. Thus the conditions in neighboring or even remote systems may influence the diversity of recruitment after a disturbance in another system.

be directly related to the frequency of disturbance in that sediment type. A higher frequency of disturbance should produce communities with higher rates of recovery. My students and I imposed unit tumbling disturbances on patches of cobbles and patches of sand mixed with gravel. We assessed sediment-specific recovery in terms of changes in species richness and population sizes in disturbed and undisturbed patches of both sediment sizes. Following a disturbance, species richness was reduced 24 percent in cobbles, and 40 percent in sand/gravel. Total animal densities were reduced 48 percent in cobbles and 79 percent in sand/gravel. Within two weeks these animal densities rebounded 240 percent in cobbles and 510 percent in sand/gravel. These data show that, in response to a unit disturbance, there are dramatic differences in both the space available and the recolonization between two distinct stream sediment patches.

These examples demonstrate that a given disturbance has different impacts on various patches in the same system. Whether the disturbance is a fire or a flood, each distinct patch type in each system has a unique response. This results in differential loss rates of organisms from the different patch types, intensifying the patchiness of the

system. The result of the disturbance is to create a mosaic of open spaces in the system and a range of opportunities for recolonization. Such varied disturbance regimes have direct consequences for the structure of biotic communities in all ecosystems.

**Recruitment Varies in Space and Time**  
In streams colonists drift, crawl or swim into available places. Egg laying supplies recruits in lakes, streams and terrestrial systems. In marine systems (the rocky intertidal zone, for example) pelagic larvae settle. In terrestrial plant systems the recruits are seeds that are either already in the seed bank or are part of the seed "rain." Plant ecologists have long focused on the importance of dispersal and recruitment to plant community structure.

Recruitment has a major impact on the outcome of competition and, consequently, on community structure. This idea, dubbed supply-side ecology by R. Lewin, asserts that physical transport processes are important determinants of community structure because they set the supply of colonists to habitat patches. Steven Gaines and J. Roughgarden stated that, "Settlement in the high intertidal community ... appears to play as important a role as postsettlement processes such as predation and competition." They also show that a tacit as-

sumption of high settlement rate underlies the Intermediate Disturbance Hypothesis. They suggest that without high recruitment, diversity may decrease with disturbance.

Shmida and Ellner showed how recruitment promotes the coexistence of even very similar species. The abundance of recruits reaching a site can offset the effect of competition. As individuals of the poorer competitor are killed, they are replaced by more individuals of that species. With a big supply of recruits of the weaker competitor, competitively dominant and inferior species can coexist indefinitely.

What determines the identity and variety of the new recruits? At any point in space and time, the pool of potential recruits is highly variable (Figure 9). This is a venerable concept, illustrated by Louis Pasteur's experiment in which he exposed a series of identical sterile flasks of "sugared yeast water" to air. He found different bacterial and fungal "species" in the identical flasks. A century later, Ruth Patrick exposed identical glass slides in a stream and found that they were colonized by a wide and unpredictable array of diatoms. Studies of seed rain and the seed pool show temporally and spatially variable arrays of potential recruits. In Figure 10, the recruits available to colonize an opening at a given instant are shown as random subsets of the source pool. Those individuals and species from the source pool who happen to be in the right place at the right time become the recruits to that newly available patch.

I compared the stream macrobenthic community structure in patches of clean cobbles and pebbles, half with fish-excluding mesh tops. Large differences were found between cobble and pebble patches, but the exclusion of fish had only minor effects on the abundance of benthic invertebrates. Particular patches were "hot spots" for recruitment. Highly aggregated populations of several species occurred in individual patches. One patch (cobbles, fish excluded) had the highest density observed for seven of the nine species common in cobbles. Another patch was similarly popular. This shows that among initially identical substrate patches, set out randomly, there is still differential recruitment, leading to diverse communities.

When openings in the habitat are created, who settles in is unpredictable.

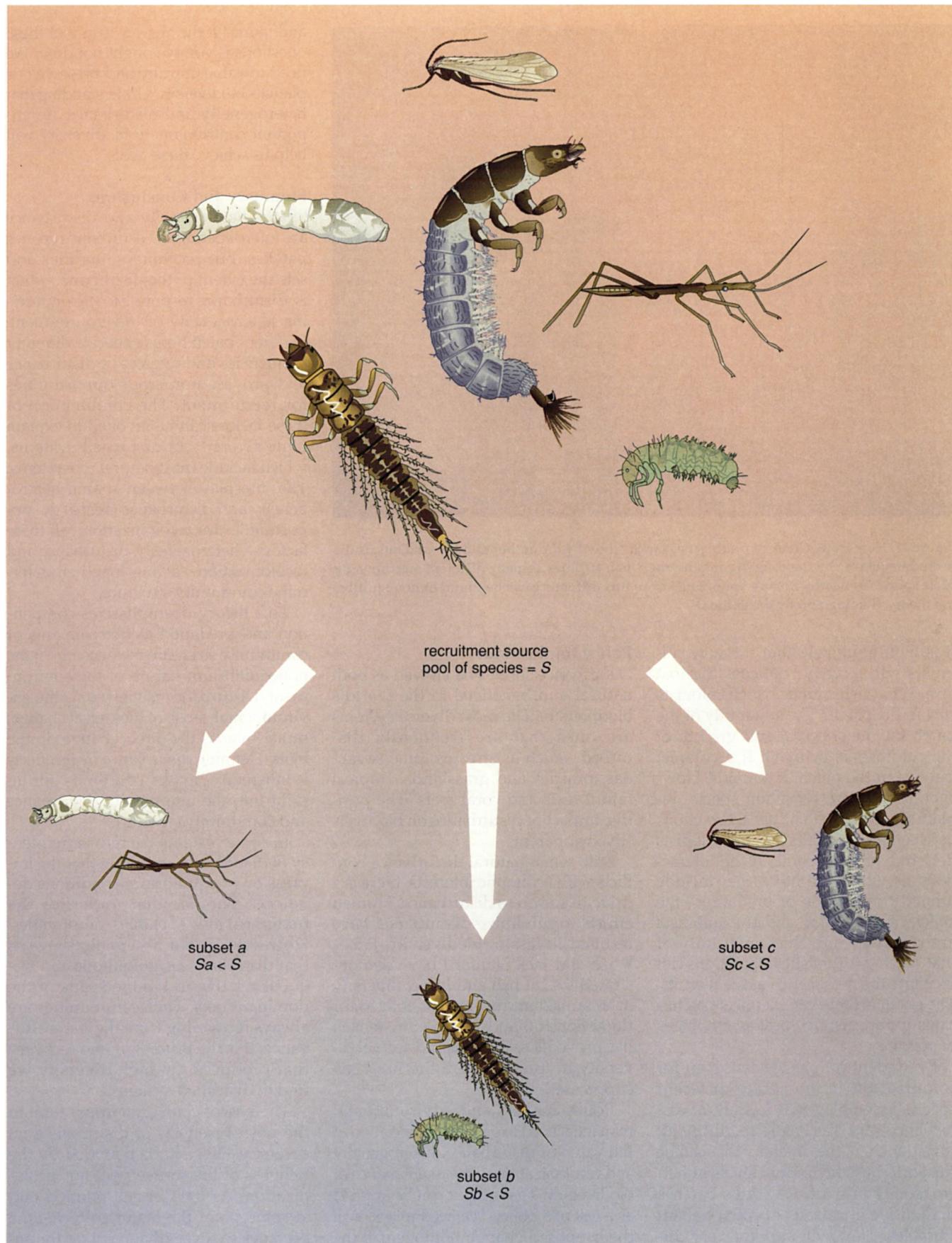


Figure 10. Nearby patches opened by disturbance may develop distinctly different communities because only a portion—not necessarily the same portion—of the recruitment pool reaches each patch. Each patch's community consists of a random subset of the populations available for recruitment.



**Figure 11.** New Hope Creek, the subject of much study by the author and his students, is disturbed frequently by flooding. It contains more than 10 times as many different macroinvertebrate species as nearby Botany Pond. The key to this difference can be found in nonequilibrium theory. (Photograph by the author.)

It is highly unlikely that the new colonists will exactly replicate the lost taxa. What determines which colonists stay in the patch? The suitability of the patch for the survival and growth of the colonists is primary. If a colonist can live in the patch, it remains. However, if there are surviving species remaining in the patch, the interactions between the residents and the colonists determine the outcome. If the interactions are weakly negative (they include limited competition or predation), the species can coexist, and the colonists are recruited into the community of that patch. Mutualistic interactions can facilitate the persistence of the recruits. The result is that even identical patches can support distinct local assemblages of species.

Even identical patches left open for colonization can generate different species assemblages as a result of disturbance and stochastic recruitment; consider, then, the diversity that can be supported by the normal levels of heterogeneity in nature. Various patches may differ in dozens of microhabitat variables. They will support very different communities because of the adaptations of particular colonists to distinct microhabitats.

### Policy Implications

Disturbance should be viewed as both natural and beneficial to the world's biodiversity. The most diverse systems are ones that are frequently disturbed—such as streams, pine savannas, prairies and grasslands, tropical rain forests and coral reefs. The positive impact of disturbance on biodiversity is apparent.

Still, when natural disturbance conflicts with economic interests, there is a drive to suppress disturbance. Human efforts to minimize disturbance have resulted in loss of biodiversity. James Ward and Jack Stanford have demonstrated loss of fish and insect diversity in streams dammed or channelized for flood control, and Norm Christensen has proved loss of plant and animal diversity in forests where fire has been suppressed.

Policy makers and environmental managers need to gain an appreciation of the value of disturbance, heterogeneity and recolonization to the maintenance of biodiversity. That insight can be applied as a test of a policy. We need to ask: Will the proposed change homogenize the system? Will it reduce the frequency or magnitude of disturbance? Or will it cut off routes of recolonization by the flora

and fauna? If the answer to any of these questions is yes, we ought not do it. We need to value, nurture and preserve our planet's biodiversity. Understanding that heterogeneity and disturbance are important contributors to biodiversity will help us achieve these goals.

### Summary and Conclusions

Spatial heterogeneity and disturbance are interdependent. Disturbance creates patches, but patchiness modifies and sets the extent of the disturbance—that is, disturbance responds to the underlying heterogeneity of the environment. Different patch types generate different frequencies and degrees of disturbance and provide numerous opportunities for recruitment. The combination of these factors can be invoked to explain high diversity in disturbed systems, which include most natural ecosystems. The interplay between spatial heterogeneity and disturbance creates the opportunities for recolonization. All these factors—heterogeneity, disturbance and recolonization—acting together, determine community structure.

This theory deemphasizes competition and predation as determinants of community structure by focusing on the nonequilibrium nature of the environment. Disturbance is viewed as the environmental cause of biological change, rather than as the direct changes in the biota. Defining disturbance by its effects is inherently circular and limits our insight into the interplay of disturbance and community structure.

In some systems the return frequency of disturbance is so long that the impression of equilibrium conditions develops. This is what underlies the traditional idea of climax communities. However, careful observation reveals that disturbance is ubiquitous and frequent relative to the life spans of the dominant taxa. Thus communities are always recovering from the last disturbance. It is the process of that recovery that produces the high diversity we find in disturbed systems.

There is, of course, an upper limit to the positive effects of disturbance on diversity. Diversity is bounded by the richness of the source pool for recolonization. As Joe Connell pointed out, at some point the disturbance regime becomes so severe that it makes the environment uninhabitable except for the hardiest colonizing species.

So, now to answer the original ques-

tion I posed about New Hope Creek and Botany Pond. Why are the bottom dwellers of the stream so much more diverse than those of the pond? It is because streams are both more patchy and more frequently disturbed. The opportunities created by the disturbances permit the recruitment of taxa into the various patches. Thus stream communities maintain a far more diverse fauna than do the less heterogeneous and less disturbed pond communities. This result holds when one compares naturally disturbed to undisturbed systems of all types.

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ARTHUR CONAN DOYLE, M.D., OBSERVES A PASSERBY WHO HAS TOBACCO STAINS ON HIS FINGERS, PAINT ON HIS TROUSERS AND PLASTER ON HIS JACKET, AND QUICKLY DEDUCES THE MAN IS A SLOB

