

Pages 252-261 in: S. T. A. Pickett, R. S. Ostfeld, M. Shachak, & G. E. Likens (eds.) 1997. **20** Ecological Basis of Conservation: Heterogeneity, Ecosystems, and Biodiversity. Chapman & Hall, New York.

## Ecosystem Processes and the New Conservation Theory

John J. Ewel

### Summary

Heterogeneity and ecosystem processes are closely linked, and together they have implications for conservation. At the scale of communities, life form and temporal patterns may exert stronger control over some ecosystem processes (such as fluxes of energy and materials) than do species. Where conservation involves restoration, every effort should be made to include the original community's full complement of life forms, phenologies, and seasonality of fire occurrence and water flows.

The natural heterogeneity of substrates, and the variation in ecosystem processes that this entails, is sometimes masked by a single species that spreads over vast areas. Where dominance by a single species has been facilitated by the actions of people and domesticated ungulates, recuperation of the former diversity in ecosystem processes can only be achieved by restoration of biotic diversity. On the other hand, where single-species dominance is a natural phenomenon, both pattern and process are likely to be relatively homogeneous: the imposition of heterogeneity (and diversity) under these circumstances may be an artificial conservation strategy.

Notwithstanding the many conservation benefits of moderate disturbance and the heterogeneity this creates, there are two circumstances when it can work against the steward. One of these occurs when opportunities for regeneration permit invasions by nonindigenous species. The second involves nutrient loss from exposed soil, a process that is most marked in large patches and in wet climates. Heterogeneity in moderate doses serves conservation well, but in excess it can imperil conservation of natural resources.

### Introduction

Conservation efforts tend to be directed toward three objectives: preservation of species and their attendant genetic variation; protection (or, where needed, restoration) of ecosystem patterns that reflect a landscape's biological and environmental diversity; and maintenance of the processes that occur within ecosystems. The first two are straightforward—conserve species and conserve communities. The third is most often regarded as a no-cost benefit that logically results from the first two: save the species and save the communities, and the services provided by the ecosystem will be forthcoming.

It is the conservation of species and complexes of populations that have been especially well served by recognition of the roles of heterogeneity—gaps, patches, periodic disturbance, episodic devastation, and the like. The reasoning is straightforward and well known, and it has been rigorously tested in many systems: (1) patchiness in pattern creates heterogeneity in resource availability, (2) heterogeneity in resource availability provides an array of opportunities for colonization and survival, and (3) the existence of multiple opportunities fosters diversity, thereby accomplishing the principal objective of conservation biology.

Heterogeneity is not merely a series of tree-fall gaps in vast expanses of old-growth forest, or logs and boulders strewn across stream beds. It occurs at many scales, ranging from the differential nutritional value of leaves on a tree to mosaics of land and sea in archipelagos. This heterogeneity is reflected in ecosystem processes, both those that manifest themselves off-site, such as fluxes of materials and energy, and those, such as the reciprocal influences of organisms and environment, that occur at smaller scales.

### Heterogeneity and Ecosystem Processes

Beneath the broad umbrella of global patterns, it is at the community level where conservation biologists tend to practice their trade. This is because communities are assemblages of populations (the main level of interest), and preservation of the parts is dictated by maintenance of the whole. At the community level, heterogeneity manifests itself in four ways: species composition, physiognomy, seasonality, and substrate. Each of these has different implications for ecosystem processes.

#### Species Composition

There are many familiar and well-documented examples of the impacts of species on ecosystem processes: *mor* profiles develop in the soil beneath conifers, *mull*

beneath broad-leaved trees; browsing ungulates tip the balance between woodland and savanna; nitrogen-fixing species hasten succession; and sizes of predatory fishes and their prey affect the structure of benthic vegetation. Perhaps even more remarkable is the fact that disappearances of some species have had effects that were far less dramatic than one might have guessed beforehand: the forests of the Appalachians still process energy and protect soil, despite the loss of the chestnut; the world's oceans still churn, driving global weather, despite the collapse of sea turtle and whale populations; and swamps of the Caribbean and southeastern United States support detrital food chains and slow the seaward flux of phosphorus, despite the loss of parakeets and parrots.

Is there any difference between heterogeneous mixes of species and simpler communities, with respect to ecosystem processes? The answer depends on what is meant by ecosystem processes. If the term refers to fluxes of energy and materials, then the answer is that the mix of species may not matter very much: a species-depauperate forest on a remote tropical island can afford as much protection against soil erosion as does a hyper-diverse continental rain forest. If, on the other hand, ecosystem processes refers to the internal workings of the system—trophic interactions, symbioses, pollination, within-system recycling—then the makeup of the community exerts a tremendous influence, and processes within diverse communities are invariably more complex than those in simple communities.

What about differences between equally heterogeneous communities of markedly different composition? Here John Harper's analogy with timepieces is apropos: spring-and-gear-driven watches bear no internal resemblance to today's electronic resonators, yet each accurately conveys the hour. One ecological example comes from experiments in which ecosystem processes were compared between species-rich tropical successional communities and communities constructed of an equally rich but different mix of species (Ewel [1986a] and references cited therein). The two proved similar with respect to herbivory, nutrient retention, exploitation of soil by roots, primary productivity, abundance of insects by feeding guild, and nematode abundance and species composition. There were differences, to be sure, but the surprise finding throughout was the remarkable ability of one unique combination of species to duplicate the functional attributes of another.

Would two such strikingly different ecosystems have similar impacts on the surrounding landscape? Perhaps not. To invoke Harper's watch once again, the mechanical model requires periodic repair, whereas the other mandates a constant throughput of heavy metals. By the same token, species composition determines, in large part, the hospitability of a forest to migratory birds. There may be many species combinations that lead to similar internal workings, but substitution at the species level could dramatically affect interactions between systems. This has never been tested experimentally.

### Physiognomy

The physical structure of an ecosystem is a function of its species composition. Nevertheless, when viewed from even a modest distance, the detailed attributes of individual species disappear, whereas a characteristic, overall appearance of the community remains. In the case of forests, this physiognomic signature is a combination of plant architecture and size. The greater the diversity and range of architectural models, and the greater the range of age classes within species, the more complex the physiognomy. Thus, physiognomy is dictated in large part by two kinds of diversity—life forms and age classes.

Different life forms influence ecosystem processes in many ways (Ewel and Bigelow, 1996). Shrubs tend to access different nutrient supplies than trees, epiphytes intercept and redistribute water, fallen palm fronds crush seedlings and create moist microhabitat for amphibians, vines bind tree crowns, and so forth. Some life forms routinely affect off-site ecosystem processes. Flammable grasses and resin-rich shrubs, for example, lead to volatilization and redistribution of nitrogen, sulfur, and carbon across the landscape; replacement of sedge-dominated marsh (much of Florida's Everglades, for example) by closed-canopy forest changes both the magnitude and the seasonality of water throughflow. A conservation program that adds or removes a species may have only modest impact on an ecosystem's workings, but one that affects the combination of life forms is almost certain to affect ecosystem processes. Thus, from the perspective of ecosystem function, a first and foremost conservation guideline might be to preserve (or restore) the life-form composition.

Age and size tend to be correlated in higher plant species (with plenty of exceptions, such as perennial grasses). Gram for gram, young plants sequester mineral nutrients and carbon faster than do older plants. The amounts stored in the biomass of communities composed of old individuals tend to be higher than the amounts in communities or patches dominated by young plants, but the net rate of accrual is higher in the latter. Thus, when conservation objectives call for capture and immobilization (creation of significant carbon sinks, for example), the plan should call for youth; when retention of materials previously amassed is called for (retention of cations, for example), then a forest dominated by large, old trees will do the job best.

### Seasonality

Plant growth, and the change in vegetation physiognomy that accompanies it, is not the only temporal change of significance to ecosystem processes. The pulse of seasons is accompanied by acceleration and deceleration of ecosystem processes, some of which are driven by changes in solar radiation, others by rainfall, and still others by temperature.

These abiotic causes tend to manifest themselves most conspicuously through their influence on plant phenology. Some relationships between phenology and biotic processes such as food choices of herbivores are reasonably well documented, even in parts of the tropics once regarded as relatively aseasonal (van Shaik et al., 1993). Examples of the influence of plant phenology on processes usually thought of as primarily abiotic, such as nutrient leaching, are not as common. In one recent example from the humid tropics comparing simple communities dominated by one or two life forms (trees alone or trees plus large, perennial monocots), my coworkers and I found that rainstorms in the short dry season had very different effects on the two communities. The trees lost their leaves with the onset of drought, and when a downpour came it was accompanied by significant leaching beneath the trees-only stands. Where the trees were underplanted with monocots, however, leaching losses were minuscule. The difference in the two was undoubtedly related to uptake: the leaf-free trees did not capture soil nutrients mobilized by the rainwater, whereas uptake by the monocots, which are evergreen, continued.

A less subtle example, one that is common today throughout the world's grasslands, concerns season of burning. Lightning ignitions were once most common at the onset of the rainy season, when vegetation was still dry and the year's first convection storms appeared. Human-mediated ignitions, in contrast, are concentrated at two very different seasons: most wildfires tend to occur in the midst of the dry season, when ignition is effortless, whereas most prescribed burns are done in the cool season, when wind patterns are most predictable and fire temperatures are moderate. Neither of these mimics the environment in which grassland species presumably evolved. The outcome is an inevitable shift in dominance, and in some cases it may lead to extinction.

Not all seasonal pulses in ecosystem processes are due to plants. The droppings of migratory passerines may be inconsequential, but the redistribution of biogeochemical wealth by nesting seabirds is clearly significant. Thus, seabird conservation is certain to have impacts that extend well beyond the species targeted for protection.

A comprehensive conservation approach must pay due attention to temporal changes in ecosystems, such as phenology of components, the timing of pulses (fire and oscillations of water flows, for example), and migrations, both local and long range. One that neglects the seasonal march of ecosystem processes jeopardizes the sustainability of the resource.

### Substrate

The growing medium is often dictated by geology, and it exerts undeniable influence on species' distributions. One alga is found on silt bottom, another on

fallen logs; this tree grows in swamps, that one in well-drained sands; and this herb tolerates high concentrations of nickel, whereas its neighbor does not. Nevertheless, species distributions can, under some circumstances, transcend boundaries imposed by substrate, and management actions can have important implications for this process.

One example is *Imperata cylindrica*, a grass that, thanks to logging, agriculture, and fire, now dominates a broad range of once-forested soil types throughout the southeast-Asian tropics. It is flammable, well dispersed, and effective at holding sites against incursions by woody colonists. A return to dominance by a greater diversity of species, species whose more specialized habitat requirements reflect the heterogeneity of the soils, probably requires fire prevention and establishment of larger-stature plants that can out-compete the grass.

A second example, counter to the first, concerns the *Gilbertiodendron*-dominated forests in west-central tropical Africa (Hart, 1990). This leguminous tree, like *Imperata*, dominates vegetation across a broad range of soil types, but there is no strong evidence that its distribution reflects a widespread episode of past destruction or an overriding environmental factor, such as recurring fire. Clearly, there are other species well suited to the various soils on which it occurs. Why, then, the widespread dominance by such a habitat generalist? No one knows for sure. One possible explanation is that *Gilbertiodendron* is exemplary of Connell and Slatyer's (1977) inhibition model of succession whereby, in the absence of local disturbance, long-lived organisms achieve dominance. Perhaps the rest of the world is subjected to more frequent disturbance than is this part of Africa, which is free of wind storms, geologically stable (and very old), and not routinely subjected to fires. Does this pose a dilemma for conservation biologists? The imposition of disturbance would add heterogeneity, and plant species that specialize on particular soils might dominate some patches of landscape, thereby increasing overall diversity. On the other hand, the natural trend in these forests has been toward decreased diversity—the right-hand side of the diversity-disturbance parabola (Connell, 1978).

The interaction between substrates and species is not unilateral, for just as substrates can dictate species' distributions, species can exert marked effects on substrates (Stone, 1975). When they do, they influence ecosystem processes through their impacts on soil. Yellow poplar, for example, leads to calcium enrichment (Kalisz, 1986); leaf-cutting ants, beetles, and gophers churn soil, affecting both its physical and its chemical properties (Alvarado et al., 1981; Kalisz and Stone, 1984); and the development of successional communities everywhere is hastened and sometimes redirected by nitrogen-fixing trees and shrubs, both natives and aliens (Reiners, 1981; Vitousek and Walker, 1989). In ways like these and many others a potentially homogeneous substrate is made heterogeneous by organisms.

## Dangers of Heterogeneity to Conservation

The same chain of reasoning that makes heterogeneity such a popular ally can, in some circumstances, work against the cause of conservation. When patches permit colonization by unwanted species, or when they facilitate irreversible depletion of nutrients (e.g., Walker et al., 1981), then they are to be avoided.

### *Patches Attract Problems*

Modest disturbance does free resources, facilitating regeneration of species having a broad array of life-history traits. When the potential colonists include vast numbers of nonindigenous species, however, creation of opportunities for colonization is not in the best interests of conservation. Consider the case of the Hawaiian Islands, at 3500 km from the nearest donor continent the most remote archipelago on Earth. Here the native flora is outnumbered by human-introduced aliens, many of which are more effective than the native species at taking advantage of newly available sites for regeneration. This leads to shifts of dominance away from communities composed primarily of native species toward communities dominated by nonindigenous species.

What can conservation biologists do to impede the shift from native to alien vegetation? The most common strategy, and one whose importance cannot be denied, is to attack the aliens, thereby reducing the threat they pose to native ecosystems. The disadvantages of this approach are twofold. First, in places like Hawaii that already support hundreds of nonindigenous species, the battle can never be won. If the threat of invasion by one species is contained, another stands ready to take its place. Because native systems cannot be sustained without immense human subsidy, conservationists must commit to eternal warfare on exotics—a depressing prospect.

The second disadvantage to this approach is that it often attacks the symptoms rather than the disease. Some invasions by alien species are facilitated by changes in the environment, as when dense populations of nonindigenous earthworms attract introduced pigs, which dramatically modify the opportunities for plant regeneration by churning the surface soil and by preferentially dispersing alien plants, or when water is channeled and shunted from the land, creating hydrologic conditions that differ greatly from those under which the native biota evolved (e.g., Ewel, 1986b). In such cases the aliens may be better adapted to the newly created environmental conditions, and it is almost inevitable that they will triumph in head-to-head competition with natives. The best option under these circumstances may be to attempt to restore the initial environmental conditions: elimination of (alien) earthworms may be an essential precursor to the elimination of (alien) pigs, which may in turn be required before (alien) guavas can be controlled, just as restoration of surface flow may be needed before native plants can prosper throughout the Everglades once again.

Suppose that aliens are already present in such diversity and profusion that they cannot be excluded, or that conservation biologists resist adopting the engineering mindset needed to restore abiotic conditions? There are two options. One is to guard against opportunity for colonization in the native communities. This is extremely difficult because most agents of disturbance and heterogeneity such as wind storms, senescence, and landslides are uncontrollable. Nevertheless, some positive actions can be implemented. One example is prevention of human-created gaps created by harvests of single trees from closed-canopy forests; such small-scale harvesting is commonly regarded as ecologically innocuous, yet in some cases, it can pave the way for invading species. Another action, on a larger scale, is consolidation of land holdings, thereby reducing the ratio of edge to area and reducing the threat of invasion.

The second option is to live with nonindigenous species. That is not to say that such a decision should be reached only by relaxation of effort, by giving up the fight, as it were. Rather, we may have to tolerate some aliens in some situations. Those we accept should be ones that offer the least threat to native biological diversity and exert the least dramatic change on ecosystem processes. By accommodating aliens, we may be able to conserve most diversity at the species level and still retain ecosystem services such as gas exchange, fixation of carbon and nitrogen, and soil protection. It is diversity at the community level, that is, loss of community types, that is sacrificed by such accommodation.

### *Patches Leak*

To sustain biological richness, the abiotic features of the ecosystem must be retained, and in the case of terrestrial ecosystems the most vulnerable abiotic factor is soil fertility. To jeopardize soil nutrient status is to tinker with the pendulum of plant competition and influence the forage quality of plant parts. Furthermore, undesirable losses of nutrients from terrestrial ecosystems do not disappear; they often show up as equally undesirable nutrient enrichment of aquatic systems.

Especially in warm, humid climates, where leaching is reduced by transpiration, the presence of actively growing vegetation can mean the difference between net retention and loss of nutrients. Recovery, of greenery if not species composition, is faster in wet climates than in dry, so gaps in a rain forest are inevitably shorter-lived than gaps in a semiarid woodland. In wet climates, it is the sustained excess of rainfall over evapotranspiration that drives nutrient loss from the soil (Bruijnzeel, 1989), a process that can be more accentuated in gaps than under vegetation (Parker, 1985). In semiarid regions, on the other hand, it is episodic deluges—freak storms or the rainy seasons triggered by El Niño-southern oscillation—that accentuate losses from vegetation-free gaps.

Even within the same bioclimate zone, not all patches leak equally; nutrient loss tends to increase with two factors, patch size and duration. Size and duration

of vegetation-free patches influence rates of nutrient loss in parallel ways (Fig. 20.1). In small patches, or in short-lived patches, nutrient loss is probably very small. For small patches, this is because the patch is underlain by living roots from surrounding plants, which continue to take up nutrients, whereas for short-lived patches it is because soil organic matter, both living and nonliving, has the capacity to absorb a substantial fraction of the nutrients normally freed by gap formation. Large patches and long-lived patches, on the other hand, incur much greater rates of loss: large gaps because their core area exceeds the reach of roots from surrounding vegetation, old gaps because organic matter decomposes, and the inputs required to sustain soil heterotrophs are gone.

If the step-model functions depicted in Figure 20.1 are approximately correct, then rates of nutrient loss per unit area are likely to be parallel, if not equivalent. Nevertheless, the total losses (amount per area or per time, in the case of patch size and duration, respectively) will differ because patch area increases as the square of the radius (if circular). Thus, big holes in terrestrial communities pose proportionally greater threats to soil fertility than do those that are long-lasting.

What are the messages for conservation biology? First, losses of soil fertility are often far more subtle than erosion, and nutrient accrual that took place over millennia can be lost in a very short time, especially in regions of high rainfall. The best defense against such loss is vigorous, healthy vegetation. There is a critical size of gap—probably a size that is unique to each combination of soil, vegetation, and climate—below which nutrient losses are likely to be negligibly small. The mound of the gopher and the single-tree windthrow, for example, will not jeopardize soil quality in grassland and forest regeneration, respectively. Likewise, short spurts of soil exposure are unlikely to lead to significant nutrient loss. The breakdown of soil as a living system takes place on scales of months

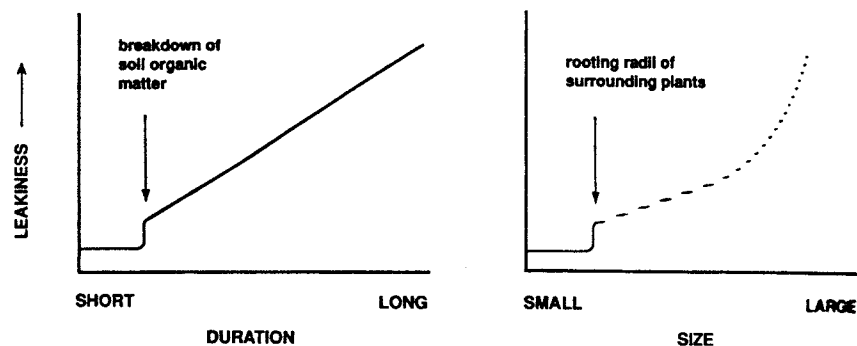


Figure 20.1. Hypothesized impacts of gap duration [left] and size [right] on nutrient loss. Losses are extremely small under both short-lived and small gaps; they increase faster as a function of size than as a function of duration because of the exponential relationship between radius and area.

to years, not days or weeks, and most soils, even without plants, have substantial nutrient-retention capability. The dangers to site quality—and to conservation—are accentuated with increasing precipitation, likelihood of episodic rains, patch size, and patch duration. The first two are beyond our control, but they can be used to identify zones and seasons of high risk. The latter two can be manipulated, and it behooves all conservation biologists to keep the abiotic side of ecosystem processes firmly in mind as we implement stewardship and restoration actions.

### Acknowledgments

The ideas in this chapter were developed in part as a result of research supported by National Science Foundation grant DEB 9318403. I thank S. Tartowski and S. T. A. Pickett for reviews.