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ECOSYSTEMS

FAST AND SLOW VARIABLES IN ECOSYSTEMS

Multiple Scales and the Maintenance of Biodiversity

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ABSTRACT

The problem of multiple scales permeates the study of ecological process and pattern, uniting aspects of space, time, and organizational complexity. In particular, it supports the maintenance of biological diversity, allowing for the magnification of underlying patterns of variation in the physical environment to create many resources from few, through the evolutionary diversification of species' niches and life histories. Specialization to particular stages of a successional gradient facilitates coexistence of multiple types in the presence of uncorrelated local disturbances, such as gap formation, which reinitiate successional sequences. Superimposed upon such successional dynamics are the effects of multiple stable states and multiple successional pathways (Levin 1976), which increase diversity even more. Multiple stable states more generally raise the possibility of sudden flips of systems from one stable configuration to another, and with such changes may come huge changes in the biotic composition. On larger spatial scales and longer time scales, these flips may become correlated, resulting in the transformation of the landscape, or may result in sustained spatiotemporal mosaics of states. Instability at the local level may lead to the maintenance of biodiversity on broader scales. Finally, the ultimate scale mismatch involves that between the dynamics of natural systems and the cultural dynamics of human societies. Our ability to live sustainably in a global commons is dependent upon adjusting normative behavior, and tightening feedback loops more generally, so that individual actions serve the common good.

Key words: multiple scales; biodiversity; competition; cultural norms.

INTRODUCTION

The simplest null model in ecology, the principle of competitive exclusion, tells a story of monotony in featureless environments: In a homogeneous world, with a single resource, there can be at most a single species maintained in steady state (Gause 1934; Levin 1970). Indeed, the great value of this principle is in the elucidation of the manifold ways that it fails to apply in nature. The study of biodiversity is the study of how competitive exclusion is foiled—through the exploitation of heterogeneity and pattern in the environment, and through the evolutionary displacement of the ways species see and utilize the environment.

Pattern and heterogeneity arise from the interplay among processes taking place on diverse scales of space and time. In the rich literature on pattern formation, the most ubiquitous mechanism by which pattern forms involves a balancing of short-range activation and long-range inhibition. Local positive feedback creates heterogeneity, and broader-scale negative feedback stabilizes it. Similar mechanisms underlie the emergence of biological diversity: novel types gain a short-term advantage, when they are rare, through their ability to exploit new niches, only to be reined in through frequency-dependent mechanisms when they become common (Levin 1981). This story is played out within communities over ecological time, and on

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broader scales over evolutionary time, creating the tapestry of biological diversity that fills the biosphere.

The problem of multiple scales takes many forms. Pattern and biodiversity arise through positive feedbacks on short time scales and local spatial scales and are stabilized by negative feedbacks on longer time scales and broader spatial scales. Similarly, individuals of diverse species interact with one another locally, organizing themselves over longer time scales into aggregates whose dynamics emerge from the collective actions of those individuals (Parrish and Hamner 1997; Flierl and others 1999). The study of ungulate herds and fish schools, of forests and grasslands, and of human populations in a global commons all involve an understanding both of how the macroscopic dynamics can be understood in terms of the units that make them up, and of how those collective dynamics may feed back to influence the fates and behaviors of individuals. In this article, I examine a few examples of such interactions across scales, with particular focus on how they influence the maintenance of biodiversity.

MULTIPLE SCALES AND INTERACTING POPULATIONS

Even the most basic notions of population dynamics involve recognition of multiple scales. Populations introduced into new areas typically grow exponentially on a fast time scale, before density dependence restricts growth. The intrinsic rate of natural increase, r, characterizes the fast time scale dynamics, whereas the carrying capacity K determines essential features on longer time scales. Life history theory is largely about the resolution of trade-offs, and the r–K dichotomy is one of the most fundamental of these. In multispecies communities, the situation is more complicated, of course, but the key trade-offs remain. Adaptations such as high dispersal ability and short generation time enable rapid population growth, but at the cost of lowered competitive ability. Species that are doomed to lose in competition on small spatial scales and short temporal scales persist over regional scales and longer time scales by their ability to find new patches of available habitat more effectively than the dominant competitors. The opportunistic dispersers establish temporary beachheads, permitting local growth over short time scales, only to be displaced eventually due to competition. As available sites decrease due to increases in the density of the colonist, its growth rate declines to zero, stabilizing spatiotemporal pattern.

Spatial and temporal pattern, both exogenous and endogenous, creates the opportunity for coexistence through the exploitation of multiple scales and is the *sine qua non* for the generation and maintenance of biodiversity. Evolution not only exploits the diversity of scales but also modifies the ranges of scales that species experience. Through increased dispersal or dormancy, for example, a genotype both alters the environment for others and modifies the way it resolves patterns in space and time.

Competitive hierarchies produce successional seres, leading to the regional coexistence of large numbers of species in essentially homogeneous environments—that is, in environments in which there is no standing pattern in the underlying physico-chemical environment. "Essentially homogeneous" environments are ones in which individual sites may vary from one another at any particular time, due to history, but will exhibit similar statistical features over long enough periods of time. The key is simply that localized disturbance (as caused, for example, simply by the death of a dominant) leads to resource heterogeneity in terms of time since renewal. This heterogeneity in essence makes one resource into many, facilitating coexistence. The effect is most pronounced in an explicitly spatial context but also applies to metapopulations (Levins 1968; Levin and Paine 1974; Hastings 1980; Chesson 1985; Tilman 1994). The key aspect is that the subdivision of the system into islands or patches distinguishes local dynamics from regional dynamics, and short time scales from long.

The island model has a direct analogy in the study of parasite–host systems (Nowak and May 1994). Hosts represent resource islands for parasites, such as viruses, whose evolution involves trade-offs between rapid growth within a host and high dispersal ability among them. The situation is complicated by the fact that rapid growth implies high virus titer, and possibly decreased host survival. The trade-offs between myopic (short-term) benefits and long-time success—that is, between dominance within a host patch and dominance within a host population—can lead to evolution of reduced virulence (Levin and Pimentel 1981) and to the maintenance of a diversity of types (Anderson and May 1982; Dwyer and others 1990). This sort of trade-off is not restricted to host–parasite systems: Chao and Levin (1981) demonstrated experimentally and theoretically (see also Durrett and Levin 1997) the importance of multiple spatial scales in the evolution of bacteriocins, and a variety of theoretical studies have shown how such structuring facilitates the evolution of altruistic behavior or simply the ability to survive in a commons (Levin 1999). In particular (Nowak and May 1992; Durrett and Levin 1994), numerous recent studies have shown the importance of spatial structure and localized interactions for altruistic behavior to emerge, and other work has shown how this can be extended to the evolution of prudent resource use (Kinzig and Harte 1998) or predator attack rates (Klopfer 1997).

MULTIPLE SCALES AND MULTIPLE STEADY STATES

All of the examples given so far involve some local competitive hierarchy, imbedded within a spatial context that allows the emergence of multiple scales of interaction. Even the parasite example involves competition among parasites that occupy distinct positions essentially along an *r*–*K* spectrum. A related example is provided by the fugitive species of Huffaker's predator–prey experiments, which are eliminated locally through exploitation but survive regionally through their capability of finding new refugia for growth. Such interactions can lead not only to the transitory survival of fugitives in a spatiotemporal game (Huffaker 1958; Durrett and Levin 1994), but also to the long-term persistence of the fugitive as the distance between prey (or forest) patches becomes too large to sustain the predator (or fire) that feeds upon it. The prey can survive regionally through its dispersal ability, whereas the predator cannot. Similarly, the prickly pear cactus *Opuntia* in Australia lives in isolated patches that its herbivore enemy, the cactus moth *Cactoblastis cactorum,* cannot find (Ehrlich and Birch 1967).

In many situations, however, the outcome of local interactions is not determinate. Competition is contingent, determined in part by who arrives first, and in part by random factors that determine initial advantage. Founder effects thus influence the outcome of competition. Coexistence of types is still not possible locally, but regional coexistence again may be facilitated by the interplay between colonization and extinction (Levin 1974). Durrett and Levin (1994; see also Gandhi and others 1998) explore the dynamics of such systems through interacting particle models, making clear the importance of multiple scales. In homogeneous and continuous environments, local clusters of competing types form on the fast time scale, and then interact regionally on longer time scales (Figure 1). In the examples considered by Durrett and Levin (1994), slow progression towards monotypic stands still occurs over long time scales; but this effect disappears if the system is open to new propagules, or if there is sufficient nonconvexity in the geometry of the region. In particular, a metapopulation version of their model allows coexistence as different types become established locally through founder effects. The metapopulation structure, in this case, reinforces a separation of scales that can disappear in a continuum, in which correlation lengths are unbounded (Levin 1974, 1979).

The self-organization of developing systems into patches, and the spontaneous emergence of a multiplicity of scales, have both ecological and evolutionary consequences. Pacala and Levin (1997), for example, demonstrate the scale dependence of the measurement of competitive strength, using the forest growth simulator SORTIE. In SORTIE, individual trees are grown on a landscape and, through shading, influence the growth, mortality and reproduction of other trees nearby. If the strength of shading is weak, so that individual trees have little interaction with other trees, there is little competitive displacement. Trees of all types are interspersed with one another, but the total removal of a species from the system at the regional scale has little short-term effect on other species because the effects of shading are so weak. As the strength of local competition (shading) is increased, the situation changes (Figure 2). For slight increases in shading, there is still no spatial segregation of types, but the effects of regional removal are increased. As local competition is increased further, however, strong segregation emerges (Figure 3), with the consequence that regional elimination of a particular species at least initially is hardly felt by the others. Strong competition has created two scales of interaction and a modular structure that facilitates coexistence. The end result is what Connell (1980) called "the ghost of competition past," in that strong historical patterns of competition may lead to ecological or evolutionary displacement. This makes the estimation of strength of competition difficult based on patterns of overlap alone. Low overlap may indeed reflect low contemporary competition, but alternatively may be the result of strong competition in the past.

Thus, spatial segregation has strong evolutionary implications as well as ecological ones. Through character displacement (Lack 1947; Brown and Wilson 1956; Grant and Grant 1989), species may differentiate their niches from one another to minimize the consequences of competition. Even when the displacement is entirely ecological, as in the examples of the last paragraph, the segregation can lead to the specialization of natural enemies upon patches of particular species. In tropical forests, for example, this means that seeds dispersed close to their parents have a particularly dim future, the

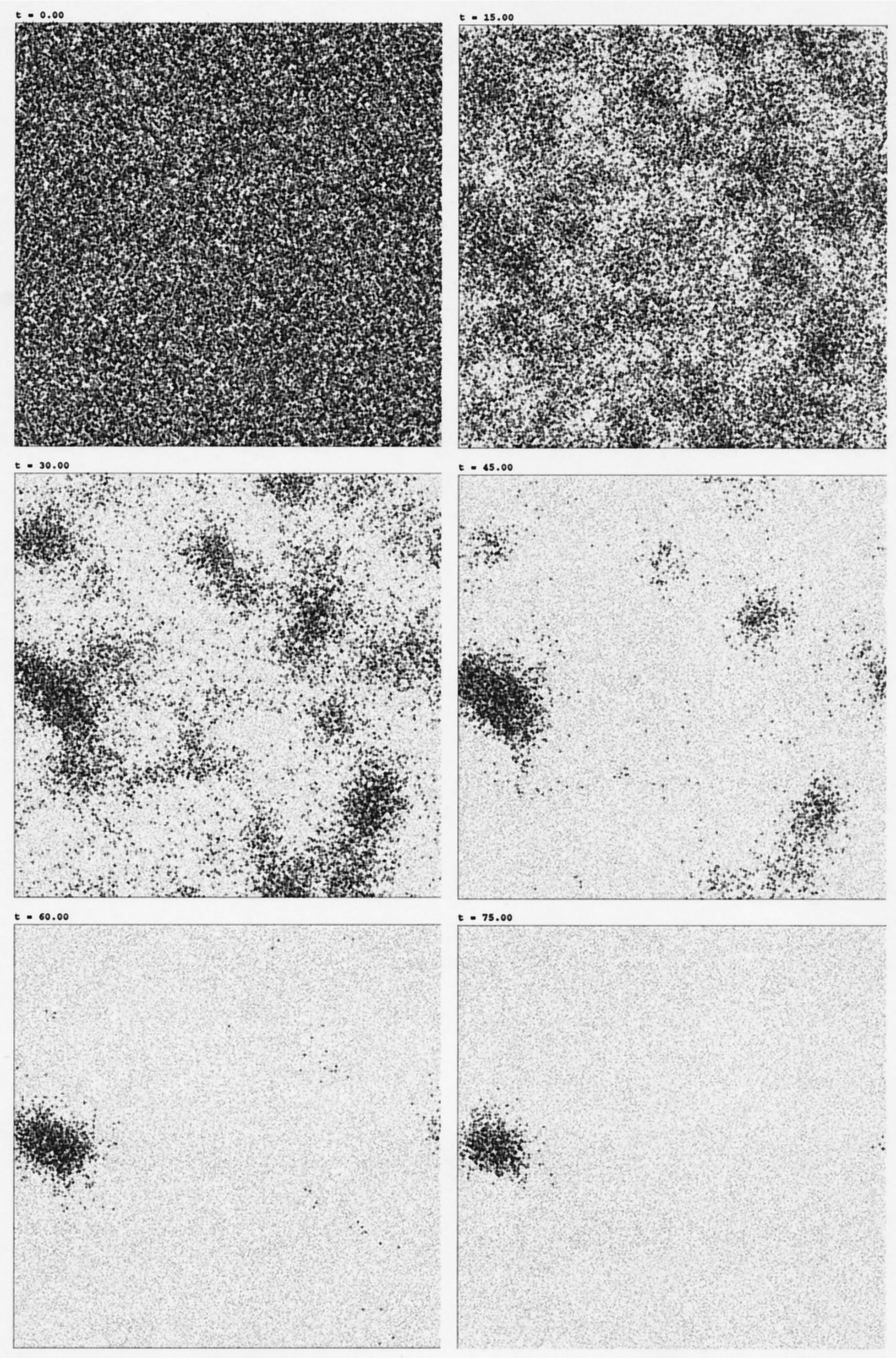

Figure 1. Snapshots from simulation of locally contingent competition, played out on a spatial grid with neighborhood movement at time t = 0, 15, 30, 45, 60, 75. One species' particles are light gray, and the others' are black The run required a million particles on an 128 × 128 grid (from Gandhi and others 1998).

victims of species-specific natural enemies (Janzen 1970; Connell 1971). In general, when ecological segregation occurs, intraspecific competition becomes a stronger evolutionary (and ecological) force than interspecific competition. In the case of the tropical forests, it becomes a mechanism favoring long-distance dispersal. More generally, Pimentel (1963; see also Levin 1972) suggested that such mechanisms facilitate coexistence.

Contingent competition among species presents the simplest example of a system with multiple stable states. More generally, multiple domains of

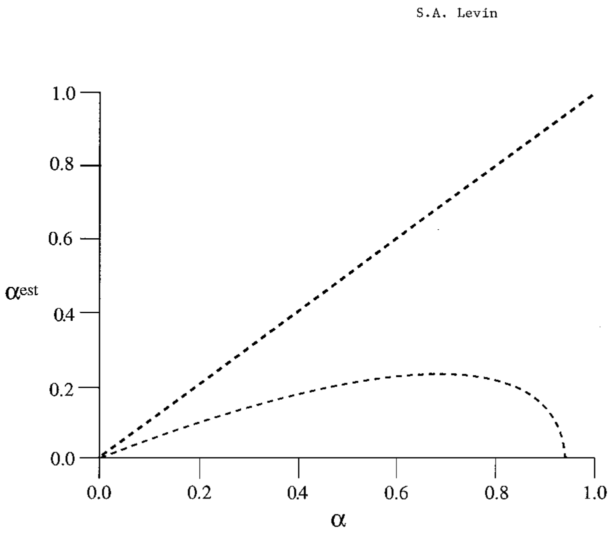

Figure 2. Measured competition coefficient (α^{est}) as a function of local competition coefficient (α). α^{est} is the instantaneous per capita change in density when a competitor is removed, divided by the per capita change when a conspecific is removed. α is a normalized measure of local competition.

attraction may lead to the loss of resiliency of systems, and the potential for flips from one stable state to another (Holling 1973; Levin and others 1998). The spruce-budworm depredations of northern forests provide a textbook example (Ludwig and others 1978), in which slow time-scale dynamics lead to sudden outbreaks of infestation. These are followed by long periods of slow decline in forest quality and budworm density, and then the sudden collapse of the insect population when forest quality declines.

The budworm example illustrates a more general phenomenon. In ecological systems, loss of resiliency can lead to the collapse of fisheries (National Research Council 1998), to the desertification of arable land (Barbier and others 1994), and to the eutrophication of previously clear lakes (Carpenter and others 1999) In the latter example (Scheffer 1990; Carpenter and others 1999), the dynamics of the system suddenly flip between oligotrophy and eutrophy, as a slow variable (phosphorous loading) is increased. Depending on internal loading rates, lowering external loading may or may not lead to the recovery of the lake from its eutrophic condition. Such regime shifts can extend even to global levels. Flips in global climate regimes seem to have occurred in the past over very short time scales (Broecker and others 1985), and general circulation models project that such flips could occur again as levels of global warming and greenhouse gases rise (Manabe and Stouffer 1988). Climate shifts of this magnitude would lead to major changes in biotic composition (Root and Schneider 1995).

Given the obvious importance of such sudden domain shifts, it would be of great value to be able to predict when a system is losing resiliency and is in danger of collapse (Levin and others 1998) and to devise mechanisms to move things away from the brink. In some circumstances, when the cause is extrinsic, as for the eutrophying lakes, that may be feasible; in others, however, one can do little more than argue for precautionary principles (Myers 1993; Arrow and others 2000) and for the maintenance of features such as heterogeneity, redundancy, and modularity that buffer systems against change (Levin 1999).

The flips of lakes when slow variables like external phosphorous loading are increased are analogous to the phase transition one observes, for example, when the temperature of a liquid is increased beyond a critical point. At the critical point itself, the system is correlated on all scales; hence, there is no single correlation length. Bak and Chan (1995) recently have emphasized the importance of another kind of criticality—one that occurs entirely due to internal changes in the organization of a system. This condition, "self-organized criticality," Bak and Chan argue, is an attracting state for self-organizing systems, resulting in a balance between stability and collapse, and a sustained condition of infinite correlation.

Self-organized criticality recognizes two time scales, but only in the trivial sense that logistic growth does. On the fast time scale, the system grows from one with little interaction among components to a self-organized and self-maintaining critical state, in which disturbances propagate throughout the system (following a power-law distribution in intensity), followed by renewal and restoration of the critical state. Holling (1992) has described a similar tendency for systems to go through stages of development and self-organization; but, in his view, those stages include cycles of collapse and recovery that are repeated with fidelity over and over again, much like the budworm system. Bak and Chan's prototypical system is the sandpile, in which all grains of sand are identical and in which there is no modularity in structure. In contrast, in real ecological systems, heterogeneity and modularity play fundamental roles. During relatively benign times, natural selection will erode the variability within populations, homogenizing the population in favor of the most fit types while compromising its ability to withstand environmental change. With loss of heterogeneity comes loss of

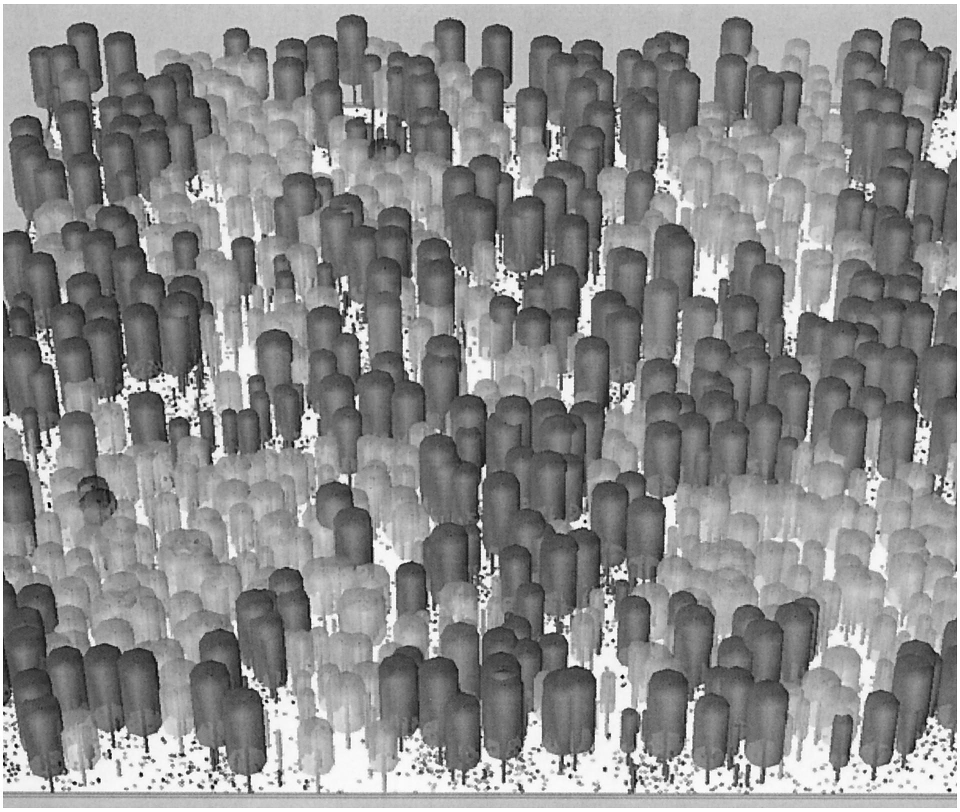

Figure 3. A snapshot of a simulation of the forest growth simulator SORTIE, showing spatial segregation of various species. (Courtesy of my collaborators, Douglas Deutschman and Linda Buttel. Generated at the Cornell Theory Center.)

resiliency, as, for example, for agricultural systems. Selection in nature may favor the maintenance of variation, for example, through mutation or recombination, but only if change is frequent enough that the longer time scale can play a role. Failing that, species will become overspecialized, overly rigid, and candidates for elimination when change does come. There are, of course, parallels in the design of organizations and of management systems and profound lessons for how we manage our natural resources.

The same phenomena may be seen at the community or ecosystem level. For example, forest systems that have been overly protected from fire for long periods of time become homogenized, surrounded by their own litter in the same way we are, and susceptible to catastrophic damage if fire does come. This is, of course, why current forest management practice has changed from the traditional, recognizing the importance of allowing small fires to burn.

THE EVOLUTION OF NORMATIVE BEHAVIOR

The examples discussed above point out the importance of interactions within ecosystems across scales of space, time, and organizational complexity (Levin 1992). Perhaps the central cross-scale challenge of the present, however, is the mismatch between the dynamics of natural systems and the dynamics of human management systems. Although the services ecosystems provide humans are being eroded on regional and global levels, the signals are slow to appear; the result is that it is difficult to convince people of the need to change their behaviors. However, one may feel one's own actions mean little, when the collective actions of billions of people govern the dynamics of the global commons. This is an extreme consequence of a mismatch of scales. The more local the control, the tighter the feedback loops, and the more likely it is that individuals can be motivated to engage in actions in the common good (Levin 1999).

What hope then is there, given these circumstances? Is there any way at all to change patterns of profligate resource use, and to encourage conservation of declining biodiversity? The hopeful answer lies in the fact that people in democracies do vote, despite the fact that they may feel that their own votes will mean little; that they give to charities; and that, in general, they follow the customs and conventions that make societies work. Cultural evolution has developed normative behaviors that tighten feedback loops, promising immediate rewards or punishments (including simply internalized feelings of guilt or well-being) that constrain individual behaviors and build trust among individuals (Skyrms 1996).

Models of the evolution of normative behavior (RT Durrett and SA Levin in preparation) show that cultural norms are sluggish in their dynamics, with much less capacity for individual change than individual behaviors show, because they involve the collective actions of individuals with different agendas. Yet normative behaviors, as well as other fads and customs (Bikhchandi and others 1992), arise locally and can change dramatically over short periods of time. Because cultural change is slow, and feedbacks correspondingly delayed, the emergence of new normative behavior can be maladaptive in the long run for all, locking systems into basins of attraction from which they cannot change. The system of foot-binding in China is illustrative (Mackie 1996; S. Bowles unpublished data), although a more pernicious example is that of caste systems in India (Dasgupta 1995; Levin and others 1998). As Bowles points out, however, such systems may lose their resiliency over time, engendering dramatic changes over very short periods of time (perhaps due to the influx of information, or the increased contact among groups).

The path to the solution of global environmental problems involves changing attitudes, and changing behaviors, of large numbers of individuals. This can be achieved only by recognizing that the large scale dynamics do emerge from individual behaviors, and also that feedback loops must be changed to reinforce behavior in the common good. This means exploring such mechanisms as privatization (with all of its warts) and local control, eliminating perverse subsidies (Myers and Kent 1998) and making individuals realize the selfish benefits of apparently altruistic behavior.

DISCUSSION

The problem of multiple scales permeates the study of ecological process and pattern (Levin 1992, Levin and Pacala 1997), uniting aspects of space, time, and organizational complexity. In particular, it undergirds the maintenance of biological diversity, allowing for the magnification of underlying patterns of variation in the physical environment to create many resources from few, through the evolutionary diversification of species' niches and life histories.

In general, biodiversity is maintained by a combination of forces that favor rare types, thereby conspiring against common ones (Levin 1981). Hierarchical competition, which leads to the monotonous dominance of a single species in stable and homogeneous environments, becomes translated into a mechanism for coexistence of multiple types in the presence of uncorrelated local disturbances, such as gap formation, which reinitiate successional sequences. Species that are doomed locally, on short time scales, survive globally through their ability to find new patches before competitively superior types do, and this mechanism is fundamental to the maintenance of biodiversity in many systems (Watt 1947; Levin and Paine 1974; Tilman 1994). Superimposed upon such successional dynamics are the effects of multiple stable states and multiple successional pathways (Levin 1976), which increase diversity even more.

Multiple stable states more generally raise the possibility of sudden flips of systems from one stable configuration to another, and with such changes may come huge changes in the biotic composition—mass local extinctions and major recolonizations, possibly by new types. Such sudden changes have been described for epidemics and epizootics, for major fisheries, for the conversion of arable land into deserts, and for the flip of lakes from oligotrophy to eutrophy; clearly, flips may lead to either increases or decreases in diversity. On larger spatial scales and longer time scales, these flips may become correlated, resulting in the transformation of the landscape, or may result in sustained mosaics of states that flip back and forth among each other. Instability at the local level may lead to the maintenance of biodiversity on broader scales.

One of the greatest challenges facing humanity involves the distinct scales of environmental change and human response. As we transform our landscapes through a variety of patterns of exploitation, changes emerge in terms of global biodiversity loss and the status of our oceans and atmosphere. Yet, the curse of scale means that these global changes are sometimes slow to make themselves clear, and that humans are even slower to adjust their own behaviors accordingly. The fundamental problem, of course, is that we live in a global commons, in which the scale of the problem overwhelms us in terms of our ability to make a difference. The path to solving this dilemma involves changing patterns of behavior and social norms that influence them; but such norms also typically change only on those longer time scales. Sustainability in the new millennium will depend upon our ability to affect with sufficient dispatch the cultural norms and legal instruments that govern individual behaviors in the global commons.

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