we forget that, though science can census grizzly bears, dusky seaside sparrows, and Siskiyou cypresses, and recommend appropriate habitat protection plans, it cannot make final decisions. That is the job for humans who value one set of goals and outcomes over another." So, in concluding Chapter 21 and completing our book, Grumbine leaves us with a broad theme that runs through the center of these 21 essays. Humans must assume their responsibilities of earth steward, and this can only be done by developing values which, while keeping us at the center of things, make us feel duties to the health and welfare of this planet, which has sustained us through our evolutionary history and is today burdened by the weight of our cultural growth.

Chapter 15

The Shifting Paradigm in Ecology

S. T. A. Pickett and Richard S. Ostfeld

> To the ecological mind, balance of nature has merits and also defects. Its merits are that it conceives of a collective total, that it imputes some utility to all species, and that it implies oscillations when balance is disturbed. Its defects are that there is only one point at which balance occurs and that balance is normally static.
>
> —Aldo Leopold
> *The River of the Mother of God and Other Essays*

This chapter summarizes how the science of ecology has changed over the last few decades, and explores the implications of those changes for natural resource managers. The changes we describe are the most general ones a science can exhibit: changes in its paradigm. A paradigm is the viewpoint a science takes of the world, which consists of the often unspoken background assumptions of the science, and the way the science approaches and answers questions. These two components are often summarized as a world view or belief system, and the exemplars for problem solving. Because a paradigm is so broad in scope, it is an excellent way to encapsulate the more detailed changes in data, techniques, and theories that a science might experience.

We use the synthetic tool of the paradigm to suggest the management implications of some of the vast changes that ecology has undergone. Many of these changes reinforce changes in management strategy already being practiced, while others invite continued evaluation of management goals and techniques.

We first present elements of the classical paradigm in ecology. We then indicate the implications of the classical paradigm for resource management. The failings of the classical strategy are indicated in general terms. The relationship of the classical paradigm and management to the everyday metaphor of "the balance of nature" will be explored. Because the classical paradigm has failed, we outline the new paradigm in ecology, and point out its significance for management. Along the way, we describe a metaphor, the "flux of nature," which is consistent with the new paradigm, and discuss important cautions that managers must practice when employing the new paradigm and its common sense label. The new paradigm calls for new kinds of management, such as process management, ecosystem management, or adaptive management. But it also calls for a firm ecological foundation, and a broad and careful vision in its application.

The Classical Paradigm in Ecology

The classical ecological paradigm comprises six key points that form a network of closely related background assumptions (1). Historically, ecological systems were considered to be primarily closed, self-regulating, and subject to a single stable equilibrium. Furthermore, any changes in communities or ecosystems through time were thought to occur by successions that must always pass through the same phases. Any disturbances that might affect natural systems were considered to be exceptional events, and humans were excluded from the roster of normal ecological factors. What does each of these points mean in real ecological systems? Before giving examples, we must emphasize that the points refer to a whole array of ecological units and entities, including individuals, populations, communities, landscapes, and ecosystems. Throughout this chapter, the term *system* is used to mean any of these units of ecological interest.

Considering ecological systems to be closed means that the important structures and interactions occur within the boundaries set for studying them. Even under this assumption, of course, thermodynamics calls for energetic openness of ecological systems, and ecologists have uniformly recognized external physical constraints or inputs imposed on ecological systems by climate. Thus, assuming ecological systems to be closed is paradigmatic only when applied to the local factors that ecologists invoke to explain the mechanistic workings of their objects of study. For example, the nutrient capital of an ecosystem would be derived from weathering of the local bedrock or parent material; and the organisms involved in important mutualisms would be local residents only.

The paradigmatic assumption that ecological systems are self-regulating follows, in part, from the assumption that systems are closed. If systems are indeed self-contained, then they must be internally regulated if they are to persist. For example, the local cycling of nutrients would govern productivity; within-community interactions would account for species coexistence; internal interactions within populations would regulate the density of the population.

Classically, ecologists focused on single, stable equilibria as the defining points of reference for their systems. But such end points were taken as much more than useful abstract points of reference. They were for a long time considered concrete states that must exist in nature. Such a focus on equilibrium points limits the explanatory mechanisms that can be applied to answer ecological questions. Examples of equilibrium points include the single "climax" state for a community on a coarse scale, the fixed carrying capacity of a population and the saturation number of species fixed by resource partitioning in a community.

When the classical paradigm allowed change in ecological systems, it was by fixed pathways. For example, successions were deterministic in that they required that invading plants appear before later stages; overshoot of a population from its carrying capacity would necessarily decline again to that level, perhaps with orderly fluctuation around that constant; community membership would be reproduced after a perturbation.

Disturbance was thought to be an exceptional occurrence under the classical ecological paradigm. This meant that the primary goal of ecological studies could be the understanding of undisturbed systems. As a result, ecologists emphasized pristine and apparently "natural" systems. Alternatively, they could focus on the return of systems from a disturbed state to the single point of equilibrium. Ecologists largely ignored such systems that were burned or blown down, populations apparently not regulated internally, managed landscapes, and organisms living beyond their usual ranges.

Humans were not considered by ecologists to be part of the classical paradigm because humans violated, either accidentally or intentionally, many of the other assumptions of that paradigm. Humans were often purposely left out of ecology because they introduced multiple states to systems, acted as disturbance agents, transported materials and organisms beyond their usual distributions, acted as external regulators of ecological systems, and prevented orderly, deterministic successions.

Relationship to Resource Management

The classical paradigm has clear parallels in classical management. Not all resource managers have accepted all of these assumptions, however, as there have always been independent and visionary practitioners (2). Indeed, rejection of these assumptions is increasingly seen in the management of natural areas. Laying out the assumptions in their bald form, as we do here, almost immediately illuminates their barrenness.

Systems as Closed

If managers accept this assumption, they would consider any unit of the natural world to be manageable as a separate entity. National parks would be cordoned off, toxic waste sites would be mitigated as isolates, an endangered species could be saved as an entity.

Systems as Self-Regulating

The internal dynamics of natural resource systems would adjust to environmental changes. Such systems could simply be left alone if they were self-regulating. For example, a mammal population would be regulated by internal behavioral and reproductive feedbacks to maintain a relatively stable density through time. Likewise, a species distributed patchily throughout a landscape would maintain its density and distribution by adjusting rates of immigration and emigration among patches. Therefore, the dominant ingredient in management of many systems would be benign neglect.

Equilibrium as a Point

Systems possess a single point at which their composition or function is in equilibrium with the environment. The implication is that ecological systems are at or close to equilibrium. For example, there is a single stable state for vegetation set by a particular climate, soil, elevation, and exposure. Likewise, the "carrying capacity" for a population is a fixed constant. If a single stable point equilibrium is the dominant kind of stability in nature, then managers can simply observe how nature is at any one time, and do whatever is necessary to maintain that state. A second bias about equilibria found in the classical paradigm is that they were the most desirable state of nature (3). These assumptions about equilibria as fixed points link with the previous one to underwrite management by benign neglect.

Succession as Fixed

This assumption suggests that systems subjected to a disturbance will recover their previous state through an obligatory succession. Managers may usefully help the rate of succession along, but the pattern of states through time is fixed, and it inexorably leads to the expected end point, which was often assumed to be the most desirable state of the system. For example, although the post-agricultural succession in tallgrass prairie was long considered to be the necessary sequence of annual weeds, annual grasses, bunch grasses, and climax prairie, that sequence is not often found (4).

Disturbance as Exceptional

If disturbance, the disruption by a sudden event of the structure, resource availability, or environmental controls of a system, is seen as very uncommon or restricted in space, then managers could make and execute their plans without taking it into account. This assumption would lead managers to be unprepared for disturbance when it finally did occur. The assumption could even lead them to attempt to prevent or to compensate inappropriately for the effects of disturbance that should in fact be a part of

the system. For example, the assumption that fire did not belong in presumably equilibrium systems led to its exclusion from management strategies in many systems. A related error is made by those who believe that a large patch of windthrown trees in a moist, broadleaved forest is an unfortunate scar rather than an event that is part of the dynamics of such forests.

Humans Excluded

The assumption that humans are not a component of systems to be managed could lead to management plans that neglected historic or contemporary human influences on a particular system. If such influences were actually important structuring variables in the system, the management strategy would be flawed (5). For example, forgetting the effect of Native Americans on vegetation and animal communities could result in neglecting important ecological controls on systems. Neglecting human effects is unfortunately easy, because many such effects are subtle, or originate at a distance from the site of interest.

In pointing out the general ways in which the assumptions of the classical paradigm could translate into management decisions, we have suggested how they can fail. In idealizing and simplifying the ecological world, the tenets of the classical paradigm have blinded ecologists and managers to critical factors and events that can govern systems. The assumptions have also caused scientists and managers to neglect important dynamical pathways and states, and to disregard important connections among different systems (6).

Balance of Nature and the Classical Paradigm

While it would be unwise to either blame or credit ecology for too much of the practice of natural resource management, at the very least, it is clear that the two areas have shared many of the same assumptions in the past. This situation may reflect the cultural origins of some of the largest assumptions any science makes. Ecology and resource management may both have adopted certain key components of their classical outlooks from the larger society (7). Such a situation is suggested by the pervasiveness and apparently comfortable acceptance of the idea of the "balance of nature."

The balance of nature is a poorly articulated idea that is a cultural metaphor rather than an exact scientific concept. The metaphor implies that natural systems exhibit tight control and adjustment to an equilibrium state. It has extremely deep historical roots (8), is held in high esteem, and often is misused as an apparently unassailable bastion in discussion. Because the idea is not scientific, it is unclear just what its assumptions are, where and when it might apply, what mechanisms might lead to it, and how one might test it.

Yet the balance-of-nature metaphor can stand for some valid scientific ideas. The fundamental truth about the natural world that the idea may relate to is the fact that natural systems persist, and they do so by differential response of various components. The idea also points toward the ecological principle that there are limitations in natural systems. No component of a natural ecological system, at whatever level of organization, grows without limit. Furthermore, the idea also indicates the frequently observed trends of ecological systems toward equilibrium states, given a specified environment and a sufficiently long time. Examples are density-dependent processes (i.e., the tendency of populations to grow when small and shrink when large) and the existence of successional trajectories by which communities tend to approach a stable "climax" state. All these principles are powerful ecological generalizations. But, ecologists themselves have sometimes relied on the venerable, yet vague, metaphor of the balance of nature to represent these principles in a public dialogue about conservation and management. This is inappropriate for two reasons.

First, the balance-of-nature metaphor has serious limitations even as a vessel for valid ecological generalizations. It can lull people into accepting equilibrium points as persistent, and into assuming that trajectories toward presumed equilibrium will necessarily succeed. Second, the metaphor has been closely associated with the classical paradigm in ecology, with its emphasis on equilibrium, containment, regulation, and so on. This is a serious liability now that the basic assumptions of the classical paradigm in ecology have failed. The failure of the classical paradigm is most cogently indicated by how rarely a stable equilibrium point is actually achieved (9). Constraints on equilibrium-seeking tendencies are common and effective, as illustrated by the burgeoning study of natural disturbance (10). The examples of the six assumptions of the classical paradigm we gave earlier in the chapter indicate the pervasive problems with them. We elaborate the failings and replacement paradigm below.

The Flux of Nature and a New Paradigm

The pitfalls of the classical paradigm calls for a new paradigm in ecology. The nonequilibrium paradigm can be connoted in the metaphor, the "flux of nature" (11). The term *flux* highlights variation, fluidity, and change in natural systems, rather than stasis, which is implied by the term *balance*. Although this metaphor does not deny the existence of stable points in nature,

it focuses our attention on the fact that natural systems, which certainly do persist, do so as a result of a variety of fluxes. These include not only the obvious exchanges of energy and matter that are the currencies for trophic relationships of species, but also fluxes that range from the relative migration of various phenotypes and genotypes, through the shifts of dominance within communities, to the movements of patch types in landscapes. Many other kinds of fluxes could be cited. Some may exhibit equilibrium distributions while others may exhibit erratic or steady trajectories.

The new paradigm also must accommodate the contradiction of the six background assumptions of the classical paradigm. Ecological systems are never closed, but rather experience inputs such as light, water, nutrients, pollution, migrating genotypes, and migrating species. Note that the novel emphasis of the modern paradigm is not that ecological systems are self-regulating, but rather experience important limits from external sources. For example, successional rates can be controlled by herbivores from adjacent communities, and populations can rely on mutualists that reside elsewhere. Stable point equilibria are rare, although some systems of sufficient size and duration may exhibit stable frequency distributions of states. For example, a landscape may be a shifting mosaic of patches or community types, and in some cases, the number of young and old communities can remain constant, even though specific spots change as a result of disturbance and succession. Successions are rarely deterministic, but are affected by specific histories, local seed sources, herbivores, predators, and diseases. Disturbance is a common component of ecological systems, even though some sorts of disturbance are not frequent on the scale of human lifetimes. Indeed, many biotic interactions have the same sort of impacts as physical disturbances, like wind and fire, in altering species composition, interaction between species, and availability of resources in systems. And finally, landscapes that have not experienced important human influences have been the exception for hundreds if not thousands of years (12).

These points together constitute the contemporary paradigm in ecology. In a sense, this contradicts the classical paradigm, since it shows that the classical background assumptions are not necessarily true. But although the classical assumptions are not universally true, on certain temporal or spatial scales and under certain conditions, those assumptions may apply. For example, equilibrium states can be a special case under the new paradigm. The new paradigm does not deny the empirical existence or theoretical utility of equilibrium states as special cases or points of reference, but it does not assume that equilibria are the dominant or controlling states in the real world.

So far, we have treated the new paradigm as both a contradiction of the old and an expansion containing the good points of the classical paradigm. To completely appreciate the new paradigm, we must examine several other modern tools for understanding the natural world.

The entities that ecologists study are parts of networks. This, of course, emphasizes the openness of systems, and the potential that regulation resides outside the system of interest. For example, changes in populations other than the one an ecologist is trying to understand may change or constrain its density (13). Interacting populations may be inconspicuous, such as parasitic lung worms relative to their elk hosts. Or the interacting populations can live separately from the focal population for a time. For instance, the butterflies whose larvae attack passion flower vines rely as adults on the flowers of cucumber vines that live in entirely different habitats (14). Changes in number of a prey population may result from asynchronous changes in the dynamics of a predator population that indirectly affects its numbers (15). Similarly, there may be lags between the time a population receives a signal from other populations, and the time when it responds reproductively or behaviorally (16). Finally, internal changes in the population of interest, whether genetic or phenotypic, may affect how that population responds to other populations and physical signals (17). In a sense, for the population level of organization, the general message is that population ecology must in fact be community ecology (18).

In studying networks or communities in ecology, relating change and stability become important tasks. Pimm (19) has defined four kinds of change in networks. Resilience is the rate of recovery to a specified former state. Persistence is the period over which a state exists before a new state is reached. Resistance is the change in a variable following change in interacting variables. For example, an ecological community is resistant if its species composition changes little after the invasion of an exotic species. Finally, variability is the degree of change over time. Variability indicates that fluctuations are accounted for in Pimm's (20) conceptual system.

The new paradigm recognizes that understanding and working with ecological systems depends on their spatial and temporal extent relative to the extent and duration of processes and structures in those systems. *Scale* is the term used to describe the relationships between two measurements such as extent over which a process occurs and spatial extent of a system. Scaling determines what is internal or external to the system. Whether some event is considered a disturbance or not, what is considered normal variation, what is considered self-regulation, and in fact whether the system is in equilibrium, all depend on the scale the system takes. At some scales, events that are considered external disturbances become incorporated into the system. For example, observing biomass of a prairie over a few years detects a fire as a disturbance to the biomass value. In contrast, observing species composition of that same prairie over decades accommodates a regime of fires as a regular part of the system (21). The contemporary paradigm equips us to deal with the structure and function of systems regardless of what scale they are observed on, and whether that scale incorporates all disturbances or regulatory factors within the system. Of course, the lives of both scientists and managers become simpler if we are assigned complete systems that internalize all important factors and exist at scales over which equilibrium can be attained. But neither the natural world nor administrators are usually so kind.

A final spur to adopt the new paradigm is the growing awareness of chaos (22). Chaos technically refers to system behavior that seems totally unpredictable and random, but is driven by strictly necessary (deterministic) relationships without any random elements. Although exactly how chaos might be expressed in ecological systems, and whether our data sets are long or detailed enough to allow that detection are open questions (23), the possibility of chaos in ecology casts further doubt on the utility of the equilibrium paradigm with its focus on linear, deterministic relationships (24).

Opportunities for New Management Strategies

We have already outlined some of the ways traditional management approaches have been limited by the classical ecological paradigm. Assuming systems to be closed and self-regulating, and to possess a stable point equilibrium reached by deterministic successions after rare disturbance events unaffected by humans, has reinforced a particular philosophy of management. Additional kinds of limitations have grown out of this classical paradigm. Management has been limited by its focus on individual components versus management of systems (25).

Here we want to emphasize the organizational implications of the term *system.* A system is any collection of entities linked by functional relationships. Managing an individual entity may neglect important relationships or contexts that are in fact critical to the persistence of the focal entity. Management of commodities, for example, may neglect the remainder of the system, especially inconspicuous or infrequent interactions, on which the commodity depends. Managing an individual population, such as a fishery, is also an example. Modeling specific fisheries as isolated populations has often failed to predict the collapse of the stock. While obvious requirements such as habitat and food may be provided for, the structuring of the population by historical events, or its periodic control by fluctuations in mutualists or consumers may be harder to detect without an explicit system approach. For example, the decline in the black-footed ferret resulted from both a decline in availability of its main prey (prairie dogs) and the introduction of canine distemper resulting from close proximity to humans and their pets. An additional danger of focusing on isolates of systems is that desirable attributes of the entire system may be damaged in the effort to optimize a single entity (26). This has been the case with isolated guilds, such as edge-requiring wildlife, which have been managed to the detriment of more sensitive forest-interior species (27). The increase in white-tailed deer and the brown-headed cowbird are examples of untoward results of management of a single guild or species. Deer inhibit forest regeneration, while the parasitic cowbirds reduce the nesting success of forest interior birds.

The contemporary paradigm suggests that the fluctuations in the natural world are not simply oddities and dismissable excursions from nature's "real" state. Rather, fluctuations in the form of physical disturbances, climate shifts, population cycles, range shifts and the like are significant normal parts of the real world. Management cannot proceed as though such fluctuations did not occur or were not important. Managers must proceed as though fluctuations mattered.

Fortunately, just as we are now in a scientific window of opportunity for developing and applying new management strategies, we may well be in a social window as well. There are enough well-publicized and debated cases of the failure of classical management, or of the failure of policy that did not account for the flux of nature, that the time may be ripe for establishing a new foundation for management. Management within a world of open systems that are subject to internal and externally driven fluxes can be labeled "ecosystem management" or "process management." Whatever it is called, and whether its focus is on some spatial unit or on some dynamic process, management must be able to adapt to natural change.

Fortunately, there is an emerging framework for the accommodation of natural flux, that of adaptive management (28). Under this strategy, the goals of the management plan are articulated using an explicit model of the system that should encompass the components, interactions, and likely fluctuations. Then, appropriate techniques are applied to the system, the results are monitored, and the tactics or even the goals are modified according to what is learned from the response of the system. In other words, management can, like science, be used to test hypotheses. The difference is that in testing management hypotheses, the purpose of the management can be changed if it is found to be unrealistic, ineffective, or counter to the persistence of the system (29).

For example, the management by neglect practiced in many old-growth oak forests has been found to permit those forests to change composition

and structure in undesirable ways. Many are shifting to a predominance of maples with a concomitant decline in understory diversity. One major way in which adaptive management can be useful is in refining the basic model of the system. The failure of a management strategy may indicate that the model of the system is incomplete, perhaps because it does not incorporate some important flux or connection that actually functions in the system. Because conceptual models of systems, whether they be production landscapes or nature reserves, are always tentative, such a strategy is important to adopt widely.

Process Management and Its Constraints

We have said that management for maintaining processes that structure the system of interest is especially appropriate to the new paradigm in ecology. The processes include the relationships to environmental resources and regulators, interactions among populations, and system dynamics or succession over time. However, the concept of "process" should not be taken too narrowly. A narrow meaning might focus solely on biogeochemical flows without concern for the diversity of biological entities that interact with biogeochemical transformations. Ecosystem models are often reduced to such a form, consisting of boxes for the pools of chemicals and arrows showing the chemical transformations within the ecosystem. However, ecosystem scientists recognize the community and population context of the biogeochemical pools and transformations encapsulated in such an abstract model (30).

But we must recognize additional kinds of processes in management. A complete framework for processes of concern in management would include the following: (1) disturbance regimes; (2) movement of materials, energy, and organisms; (3) succession; and (4) species interactions. It may be necessary to prioritize processes and manage to optimize certain ones, depending on the goals. However, even if only one or a few processes are to be optimized, their relationships to other processes must be known in order to avoid management surprises.

A disturbance regime is the spatial and temporal pattern of disturbance in some area. It consists of the agents, intensities, sizes, distributions, and frequencies of disturbances that affect a system. The term *disturbance regime* does not mean that the identity, temporal, or spatial patterns of disturbance are fixed and regular, only that such distributions can be characterized and understood as system attributes. They can be modified and compensated for by management.

Movement of materials and entities is a second focus of process management. The things moving can be either abiotic or biotic. Abiotic fluxes include the familiar ecosystem fluxes of energy and nutrients. In human-modified landscapes, which is beginning to mean most of the Earth, the materials would also include pollutants and plumes of thermally altered air and water, which can interact with natural ecosystems, communities, and populations.

Biotic fluxes include the movement of organisms. The specific processes include natural dispersal, migration, and the transport of exotics. But biotic fluxes also involve larger scales. Shifting mosaics of communities in landscapes is an example of a coarse-scale biotic flux (31).

One of the most universal of ecological processes is succession, the change in community composition or structure through time. Succession must therefore be a concept in the toolkits of all managers (32). It is driven by characteristics of sites determined by natural or human disturbances, by the differential availability of organisms, and by the differential performance of organisms at those sites. Managing a system without information on its successional status or rate is risky, and is likely to produce unexpected results (33).

Species interactions are among the most well-known interactions that must be managed. Although interactions are often labeled by their "net effect" on the populations involved, such that competition is a joint negative effect and mutualism is a joint positive effect, it is important to know just how such interactions proceed. This is because there can be hidden, indirect chains of effects, or interactions mediated by third parties. Thus, competition between two species may be only "apparent" (34), and the outcome driven instead by the stimulatory effects of one of the species in the "competitive pair" on an enemy of the second. Voles and shrews are affected by the same predators, and change in one of the prey species may cause the predator to change its impact on the other prey (35). If just the small mammals are studied, the dynamic would appear as competition. Indirect effects such as apparent competition appear to be legion in natural communities.

How does a process approach to management relate to "ecosystem management"? In reality they can be considered the same thing, because a good management plan will be based on a comprehensive model of an ecosystem. The model will indicate the spatial extent of interest, the inputs and outputs of resources and populations, and the direct and indirect interactions of populations, as well as the interactions between the populations and the physical substrate and fluids in the ecosystem. So ecosystem management must include the processes that occur within that ecosystem and which connect it with others. The phrase *ecosystem management* is valuable because of the spatial implications of the term *ecosystem*. Ecosystem management

reminds us to consider the landscape or regional connections of the situation to be managed (36). And the metaphor, flux of nature, is a reminder that the nature of the system and its context can both change through time, sometimes episodically.

Caveats for Using the Flux of Nature

The metaphor, the flux of nature, is a powerful tool for communicating the new ecological paradigm. It reminds us that the basic substance of nature, the networks of species interacting with one another and exchanging matter and energy with their surroundings, do persist over long periods. But the persistence is the result of dynamism and flux on different scales (37). The assemblages of species change in identity with evolution on the long term, and with natural disturbance and succession on the short term. The assemblages shift in local composition and architecture on the local scale, while the arrangement of patterns in landscapes shift under disturbance regimes and climate change. The richness that evolution has produced is a response to the opportunities produced by disturbance, natural extinction, climate shifts, and the arrival of new immigrants. On a more local scale, even though the time frame may be long for an individual human life, the fall of a mature tree in an old-growth forest generates opportunities for establishment, growth, or reproduction of species that had been excluded from or suppressed on the forest floor. Various animals, microbes, and plants may use the new site, while others avoid it. But over the long term and large areas, the variety of opportunities, resources, and environmental signals is answered by a richness of organisms. That is the beauty of the flux of nature. Most spasms of nature become opportunities, and if the accidents of evolution and history have made organisms available, then they will appear to fill the stage. Subsequent changes in the environment, the species pool, or the nature of interactions may occur. They are all part of the flux of nature, none more intrinsically desirable than another. This is the shifting stage and shifting play that ecologists must understand and managers must deal with.

For all its scientific intrigue and poetic beauty, the flux of nature is a dangerous metaphor. The metaphor and the underlying ecological paradigm may suggest to the thoughtless or the greedy that since flux is a fundamental part of the natural world, any human-caused flux is justifiable. Such an inference is wrong because the flux in the natural world has severe limits.

Knowing what these limits of natural flux are is a critical step in management. In general terms, these limits are functional, historical, and evolutionary. Functional limits are the physiological constraints that organisms operate under. For example, certain molecules cannot be detoxified, leaves must remain open to pollutants if they are to take up CO_2 for photosynthesis, and high temperatures denature proteins. Such limits cannot be overcome due to the mechanics and chemistry of cells and organs. An anthropogenic flux outside those limits is an insult to natural flux.

Historical limits are those that result from the suites of species that have become established through time at a site, the accumulation of resources and organic matter, and the kinds and patterns of disturbances that have operated there over time. For example, if the disturbance regime of a site has not included massive stand-opening events that leave the roots and soil intact, then there are not likely to be species present that can respond rapidly to a novel anthropogenic disturbance of that type.

Evolutionary limits are imposed by the amount of genetic variation available for selection to act on, the intensity of selection, and the time over which selection may have acted. Evolution is also constrained by the physical structures elaborated in the past. If human-induced changes reduce the capacity of lineages to evolve by reducing genetic variation, elevating levels of gene flow, or altering population mating structures, then their effect on the flux of nature will be damaging, perhaps permanently.

Problematic human changes or fluxes are those that are beyond the limits of physiology to tolerate, history to be prepared for, or evolution to react to. Two characteristics of a human-induced flux would suggest that it would be excessive: fast rate and large spatial extent. Natural systems respond to, even exploit flux, if the rates of flux are within the capacity of physiology to adjust, new assemblages to accumulate, and evolution to generate new diversity. Where rates of human-generated flux exceed the natural rates of response, policy makers and managers should be alerted that undesired changes may result. Managers may be in a position to compensate for inappropriate rates of human-caused changes.

The second problem of current human-generated flux is its great spatial extent. Natural flux takes space for the shifting mosaics of landscapes, the sources of genetic novelty, and the refuges from disturbance, predation, and disease. Human-generated flux that subtracts from the area available for natural flux must be carefully evaluated and compensated for.

Conclusion

We have examined the paradigm shift that has been taking place in ecology over the past several decades. The classical paradigm, the equilibrium world view of the discipline, assumed that ecological systems were closed, self-regulating, possessed of single equilibrium points reached by deterministic dynamics, rarely disturbed naturally, and separate from humans. Classical management strategies were cast as though they followed these same assumptions. However, the failures of management reflecting this paradigm became apparent, and along with the accumulation of new data and scales of observation in ecology, contributed to the demise of the classical, or equilibrium, paradigm. With the demise of the equilibrium paradigm, the inappropriateness of the formerly comfortable metaphor of the balance of nature became apparent.

A new ecological paradigm has emerged that recognizes ecological systems to be open, regulated by events arising outside of their boundaries, lacking or prevented from attaining a stable point equilibrium, affected by natural disturbance, and incorporating humans and their effects. A new metaphor of the flux of nature symbolizes the new, or nonequilibrium, paradigm effectively. The new paradigm suggests that the management approaches being developed are much more appropriate to the variability, contingency, and openness of ecological systems. The intimate linkage of opportunity and response that is embedded within the flux of nature takes long times and large spaces to work. Ecosystem management, carried out in an adaptive way in which management plans are viewed as hypotheses based on inclusive models of the systems to be managed, is likely to exploit the contemporary understanding of ecological systems.

Neither process nor ecosystem management should be considered to mean that nutrient or energy flows should be managed without attention to the biodiversity with which they interact. In addition, management for the flux of nature must respect the physiological, historical, and evolutionary limits inherent in natural systems if management is to be successful and sustainable.

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Chapter 16

New Approaches, New Tools: Conservation Biology

Richard L. Knight and T. Luke George

> A thing is right when it tends to preserve the integrity, stability, and beauty of the biotic community. It is not when it tends otherwise.
> —Aldo Leopold
> *A Sand County Almanac*

Aldo Leopold, who is credited with developing the discipline of wildlife management and who articulated the concept of the land ethic, most certainly had sustainable ecosystems in mind when he penned these words. Landscapes that would allow people and wildlife to coexist in harmony were among Leopold's principal motivations for studying and attempting to understand the complexities of the "land organism" (1). A half-century after he penned these words, land managers are revisiting this arena and confronting the difficulties with managing ecosystems sustainably (2). Indeed, one reason for the disarray natural resource disciplines find themselves in today is the widespread public belief that the disciplines do not champion good land stewardship.

Chapters in the first part of this book clearly indicate the traditional approaches and motivations that drove the development of natural resource disciplines. Resources were viewed as inexhaustible and useful only to the degree they could be exploited (3). When resources declined locally, commodity users either moved on or began to develop management approaches that would result in species recovery. Eventually, all of these extractive users and uses of natural resources developed into sciences with accompanying professional organizations and university curricula. Even though university departments and scientific organizations grew and prospered, they still largely focused on teaching and conducting research on wildlife for game, trees for lumber, and grass for cattle.