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V. DISEQUILIBRIUM ECOLOGY

Since its foundation as a discipline, ecology has been dominated by an equilibrium view of nature. According to the historian Frank Egerton, the idea of "balance of nature" is present in most "primitive" cosmologies and is inherent in humans' ancestral worldviews. In ancient Greek philosophy, together with the concepts of the "great chain of being" and the "microcosm-macrocosm analogy," the balance of nature remained a fundamental if untested assumption of natural history (1973, 1993).

These assumptions, inherited from an equilibrium worldview, were incorporated without questioning or testing into the most influential ecological theories of the twentieth century, ranging from populations and communities to ecosystems. Examples include the idea of "climax" as the steady-state endpoint of plant succession theory (Clements 1916); W. C. Allee's (1949) notion of balanced animal communities; "the equilibrium theory of island biogeography," which predicts the number of species on oceanic islands as a balance between immigration and extinction (MacArthur and Wilson 1967); and Eugene Odum's (1969) "strategy of ecosystem development," which postulated that all ecological systems progress toward homeostasis. Based on studies on vertebrate and invertebrate social animals, the University of Chicago professors Allee, A. E. Emerson, O. Park, T. Park, and K. P. Schmidt, in their influential book *Principles of Animal Ecology* (1949), concluded that

the community maintains a certain balance, establishes a biotic border, and has a certain unity paralleling the dynamic equilibrium and organization of other living systems. Natural selection operates upon the whole interspecies system, resulting in a slow evolution of adaptive integration and balance. Division of labor, integration, and homeostasis characterize the organism and supraorganismic intraspecies population. The interspecies system has also evolved these characteristics of the organism and may thus be called an ecological supraorganism. (p. 728)

According to these authors, the theory of evolution by natural selection, pioneered by the English naturalist Charles Darwin (1809–1882), provided a mechanism that, through interspecific interactions and evolutionary processes, gave rise to equilibrium at supraorganismic levels, which is analogous to the process of "homeostasis" at the individual level.

Accordingly, twentieth-century ecologists retroactively imparted greater heuristic power to the eighteenth-century notion of the economy of nature as pioneered by the Swedish botanist, zoologist, and

physician Carl Linnaeus (1707–1778). Both Linnaeus and Allee (1949) held that there is an essential analogy between the organs in an animal and the species in a community. In turn, Linnaeus based his *Oeconomia Naturae* notion on the work of seventeenth-century naturalists and theologians and on ancient Greek natural philosophers. The creation myth in Plato's *Timaeus* affirms that the creator made the world as "one visible animal comprehending within itself all other animals of a kindred nature" (30 c-d). Plato's dialogues have had a pervasive influence in European and North American thought, integrating the microcosm-macrocosm analogy with the image of the parts of an animal body as a representation of the different parts of the universe; Plato held that the diversity of species of living beings are the organs of a supraorganismic being and that the universe as a whole is a super superorganismic being.

Such ancient organismic perspectives influenced Linnaeus, who in turn influenced nineteenth-century biologists and thinkers concerned with "organic wholeness" (Jax 1998). In the early twentieth century the German ecologist Karl Friederichs affirmed, "In the same way in that the world is a dynamic system, which actively persists in a delicate state of equilibrium by means of self-regulation, this is also valid for naturally delimited parts of the biosphere (e.g., pond, fen, beach . . .)" (Jax 1998, p. 117).

Friederichs coined the term *holocoen* to refer to "a forest, a lake, a fen"—perceivable habitats that exist as delimited living systems within a nested hierarchy of nature.

Friederichs's view contrasts sharply with that of Arthur Tansley (1935), who understood an ecosystem as an operational distinction made by scientists. Charles Elton (1930) was even more radical in his criticism of the organismic and equilibrium views of nature when he affirmed,

"The balance of nature" does not exist, and perhaps never has existed. The numbers of wild animals are constantly varying to a greater or less extent, and the variations are usually irregular in period and always irregular in amplitude. Each variation in the numbers of one species causes direct and indirect repercussions on the numbers of others, and since many of the latter are themselves independently varying in numbers, the resultant confusion is remarkable. (p. 17)

With the work of Tansley, Elton, and others in the mid-twentieth century, the assumptions of natural equilibrium and balance of nature came under critical scrutiny. H. G. Andrewartha and L. C. Birch (1954) rejected the idea that density-dependent factors (endogenous

factors within the ecological system) alone controlled populations in ecological communities. They emphasized, instead, the importance of allogeneous disturbances (external factors such as volcanic eruptions, flooding and hurricanes) as drivers of population fluctuations.

The alternative tenets of equilibrium vs. disequilibrium ecology have implications not only for the scientific understanding of nonhuman nature but also for the relations that human societies establish with their environments. From the perspective of public understanding, equilibrium views that draw on the traditional metaphor of "the balance of nature" have had profound implications for the broad application of ecological theories to resource-management and conservation issues (Botkin 1990, Wu and Loucks 1995).

RELATED CONCEPTS

Related to the idea of natural equilibrium are the notions of "stability" and "resilience" that have been ubiquitous in community ecology during the twentieth century (Wu and Loucks 1995). Stability is a condition that enables the system to tolerate or resist external perturbation without significant structural and functional change. Resilience is the ability of the ecological system to return to its previous equilibrium state after a disturbance. Both notions have proved to be problematic when empirically tested in diverse aquatic and terrestrial environments (Wu and Loucks 1995).

In the last quarter of the twentieth century, equilibrium-centered theories were gradually supplanted by alternative conceptions stemming from the increasing awareness that frequent disruptive events (or disturbances) on both land and in water lead to the reorganization of ecosystems in often-unexpected directions (Simberloff 1980, Pickett and White 1985). Under this new probabilistic understanding, equilibrium or stable conditions are viewed as special transient cases or as consequences of applying a narrow spatial or temporal gauge in examining large-scale ecosystem dynamics (Wu and Loucks 1995). Nonequilibrium models and empirical studies of fire and pest-outbreak effects on biotic communities, on the other hand, have increasingly demonstrated the existence of multiple equilibriums and have emphasized the role of stochastic and probabilistic processes in ecological systems (Simberloff 1980).

PARADIGM SHIFT: RESULTS AND PROSPECTS

The turn from equilibrium to disequilibrium conceptions of ecological systems since the late 1970s has been considered by many (Simberloff 1980; Pickett et al. 1992, 2007; Wu and Loucks 1995) as a "paradigm shift" in the science of ecology. *Paradigm* here connotes the

constellation of concepts, ideas, and approaches shared by a working community of scientists (Kuhn 1962). This paradigm shift questions, on empirical grounds, the previous tenets of ecological theory (i.e., equilibrium assumptions) and obliges a rethinking of the application of theory to environmental problems such as the design of nature reserves (Pickett et al 1992), the management of wild populations, and the perception of disturbance regimes (Botkin 1990). It also calls into question the traditional view of humans as agents of the destruction and/or restitution of natural "harmony" and "balance" and urges us to reformulate the goals of biological conservation and ecological restoration practices.

According to Pickett and his coauthors (1992), the old equilibrium paradigm of ecology, embodied in the traditional metaphor of "the balance of nature," was replaced in the late twentieth century by a nonequilibrium view, best expressed in the new metaphor "the flux of nature." Such metaphors are essential elements in the understanding of scientific theories and are closely linked to cultural worldviews. Implicit in the old metaphor are (a) the closed character of ecological systems; (b) the predominantly autogenic origin of ecosystem structure and function determined by species and genetic diversity, life histories, biomass accumulation, and other internal biological and physical properties; and (c) the existence of a predictable condition (in the sense of Odum's homeostasis), often called the climax state, that is resistant to occasional external disturbances (Pickett et al. 1992). In turn, the new metaphor, representing the nonequilibrium concept of ecological systems, denotes (a) the open nature of most ecosystems; and (b) their dependence on both exogenous forces (such as fire, climate change, or pollution) and autogenic forces (such as species life histories). A high frequency of disturbances relative to the life spans of the organisms in the local community may drive the system to (c) multiple possible endpoints, theoretically possible stable states notwithstanding. In the nonequilibrium view, a metaequilibrium is possible on a broad spatial scale that examines the collective dynamics of multiple patches in the landscape, although single patches are constantly changing.

The paradigm shift in ecology (from equilibrium to disequilibrium concepts and theories) brings a philosophical turn to the notion of disturbances as destructive or catastrophic forces, usually disrupting the orderly trajectory of ecological systems toward homeostasis. Disturbances are sudden events altering ecosystem or community structure and processes, destroying biomass and releasing resources for the survivors or newcomers (Pickett and White 1985). Ecological studies have demonstrated that "disturbance regimes" can be an intrinsic component of the ecological system under study, depending on the selection of spatial and temporal scales. Under this

perspective apparently destructive forces such as wildfire become necessary for an ecosystem to sustain its characteristic species composition, structure, and productivity (Botkin 1990). Exclusion of fire from such ecosystems through preventive management impoverishes their performance in the long term because of losses of species and changes in structure that drive the system to a state that diverges markedly from its historical patterns. Repeated disturbances such as volcanism and landslides that recur over several millennia maintain the characteristic age structure and species composition of many Andean *Nothofagus* forests in southern South America (Veblen et al. 1996). Hence disturbances can foster conditions (e.g., open patches, resource hot spots) that facilitate the regeneration of species and increase local species richness.

An important corollary of this view of disturbance as a driving force for patch dynamics is the realization that such perturbations can be integrated into the definition of ecosystem insofar as they are seen as products of the interaction between the system's structure and exogenous physical factors. Several examples show how the onset and effect of disturbances can be modulated by species traits and the structure of a community (Pickett and White 1985). For instance, the rates at which trees fall in a forest canopy depend on individual tree longevity and species composition, which in turn influence species diversity and tree regeneration (Johnson and Miyanishi 2007). Species composition and ecosystem structure and processes hinge on a continuous interplay of both endogenous and exogenous forces that lead to multiple possible end points. This perspective challenges the idea that "there is only one point at which balance occurs, and that balance is normally static," thereby affirming Aldo Leopold's (1939) insights into the flux and diversity that inhere in an equilibrium.

SEE ALSO *Ecology: III. Ecosystems; Ecology: VI. Patch Dynamics.*

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VI. PATCH DYNAMICS

The history of the concept of patch dynamics can be traced back to the classic work of A. S. Watt (1947), who described the dynamic mosaic structure of vegetation, with patches constantly dying and regenerating in different areas of the landscape. In a variety of plant communities, including peat lands, grasslands, and forests, Watt analyzed temporal succession of pioneer, building, mature, and degeneration phases. Watt emphasized that