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1

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J. Baird Callicott and Robert Frodeman
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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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Ricardo Rozzi
Juan J. Armesto
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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

there are frequent departures from unidirectional, ordered sequences and that the spatial mosaic of patches can be interpreted in terms of their temporal relations: "The community consists of patches, each of limited area, and differentiated by floristic composition, age of dominant species and by habitat" (Watt 1947, p. 16). This view of the community as a dynamic mosaic of patches differing in a succession of ages has become known as "the pattern and process hypothesis," which emphasizes the relations between structure and function (Wu and Loucks 1995). The term *patch* refers to a discrete unit of space differing in nature and appearance from the surrounding landscape (Wiens 1976). Patches may be identified at different spatial scales, from an island surrounded by ocean or a tract of forest surrounded by pastures to a tree-fall gap in the forest canopy to an aggregate of barnacles on a rock of the intertidal zone. In landscape ecology (Forman and Godron 1986) patches are the basic functional units of the landscape. Usually the area of habitat surrounding a recognizable patch type is termed the ecological "matrix," although a matrix may itself comprise different patches (Pickett et al. 2000).

Patches differ in area, shape, structure, species composition, duration, structural complexity, and boundary characteristics. Some patches may be sharply bounded (e.g., a lake, a remnant woodlot within a cultivated area); in other cases boundaries may be diffuse (e.g., the transition from steppe to forest). Patches may differ greatly from the species composition and abundance in the surrounding matrix, or the differences may be subtle. Patch shapes may be regular, approaching Euclidian geometric figures such as a circle or square, or they may be irregularly shaped, which demand the use of fractal geometry.

MECHANISMS OF PATCH FORMATION

Patches are originated by a variety of physical and biological mechanisms, including patch creation and habitat fragmentation by humans. Physical mechanisms of patch origination in unmanipulated landscapes include disturbances such as lightning-caused fires, tree windfalls, hurricanes, droughts, floods, landslides, volcanic eruptions, earthquakes, and climate change. There is a striking example of remnant patches caused by climate change along the Pacific margin of southern South America, where fog-dependent rain-forest patches on the summits of the coastal hills of semiarid Chile (annual rainfall below 150 millimeters) became segregated from their main temperate latitudinal range by more than 1,000 kilometers because of incremental aridization during the Quaternary (Núñez-Avila and Armesto 2006). On a smaller scale, the north-facing and south-facing slopes—sometimes separated by just a few meters—of the coastal and Andean mountains of central Chile also exhibit contrasting patches characterized by differences of temperature, solar radiation, and humidity. This physical microheterogeneity, in turn, generates sharp differences in plant composition, flowering periods, pollinator ensembles, and genetic differentiation among populations of the same species (Armesto and Martínez 1978; Rozzi et al. 1997).

Biological mechanisms of patch origination include animal effects (e.g., burrowing activities, building of dams, defoliation of trees, trampling, and wallowing) plant effects (e.g, allelopathy, accumulation of organic matter, shading effects), resource distribution (e.g., soil types, large fruit crops, nutrients under bird perches), aggregation patterns (e.g., marine mammal congregations, limited seed dispersal, vegetative propagation), and migratory routes and dispersal patterns (e.g., bipolar distribution of plant species found in subarctic and subantarctic regions because of seed dispersal by migratory birds and similar climatic conditions). Human creation of patches include historical land use change, such as the creation of bodies of waters through the building of dams or open land by the clear-cutting of forests; introduction of exotic animal and plant species involving monocultures for husbandry or crops; gardening and planting seeds in cultivated patches such as the "islands" of palms planted in Amazonian savannas by indigenous peoples; and the creation of barriers to dispersal of animals and plants, such as those imposed by highways, channels, fences, or the application of pesticides or herbicides.

PATCHINESS

Patch mosaics of a given landscape can be described in terms of patch composition (patch types and their relative abundances), the spatial configuration of patches, and the connectivity among patches. Connectivity can be a function of both the nature of boundaries (the transition between patches and the surrounding matrix) and the permeability of the matrix to the transit of organisms moving between patches. Patch connectivity is a critical yardstick for biodiversity conservation and is thus an important source of information for conservation policy at the landscape scale because of the negative effects of isolation on mating probabilities (Sieving et al. 2000; Díaz et al. 2006), population sizes and gene flow, and the facilitation or impeding of the movement of exotic invasive species or pests (Fahrig 2003).

The descriptive parameters and scale of patchiness are both organism-dependent because different species have varying capacities for filtering heterogeneity in a given environment (Wiens 1976). Accordingly, patchiness varies

for organisms with different degrees of mobility (e.g., immobile plants vs. mobile animals), physiological tolerance of environmental stress (e.g., mammals vs. frogs, because the latter have higher skin permeability, making them more dependent on moisture), life-history characteristics (e.g., bamboo species with single mass flowering events vs. oak trees with annually recurrent flowering events), and perception mechanisms (e.g., bumble bees that can see ultraviolet wavelengths but not red colors vs. hummingbirds than cannot see ultraviolet wavelengths but can see red, a flower color for which they have a preference). In many cases it will be necessary for ecologists and conservation policy makers to adjust the scale of observations to the heterogeneity perceived by the target organism and the ecological processes under study or under adaptive management.

Patchiness can change as a consequence of patch dynamics. Patch dynamics are the result of the simultaneous operation of various physical, biological, and human patch-generating mechanisms (Pickett et al. 2000). How do patches and ecological systems persist in the presence of destabilizing forces? In the traditional ecological view of disturbances, a clearly exogenous factor occurs at a single time—creates a "patch" with abrupt or clearly defined boundaries—and increases the resources available for new growth through decreased biological use, increased decomposition, or both (Pickett and White 1985). Nevertheless, disturbances can be caused not only by exogenous factors (originating from outside the ecosystem) but also by endogenous factors (originating from within the ecosystem) such as synchronous aging of cohorts of trees or insect outbreaks. In practice exogenous and endogenous factors interact. For example, insect infestation of trees increases vulnerability to windfall, and, in turn, windfall might facilitate insect infestation.

The term *disturbance regime* is used to characterize the spatial scale and temporal patterns of exogenous and endogenous disturbances and the subsequent response and recovery of ecosystems. Patchiness within a landscape reflects the types of disturbance and their frequencies and magnitudes; landscape elements of topography, substrate conditions and organisms, and resource base available to organisms; and life histories and assimilative capacities of species present or potentially available to colonize a disturbed site (Forman and Godron 1986). Disturbances vary in magnitude, depending on the intensity and severity of the disrupting event. The eruption of Mount St. Helens in 1980, the Yellowstone fires of 1988, and Hurricane Hugo in 1989 are examples of intensive and large scale disturbances that captured public attention (Turner et al. 1997). Both large- and small-scale disturbances operate simultaneously and generate, within a landscape, mosaics with patches of varying size, species composition, and age structure (Pickett and Thompson 1978). For example, in forest ecosystems small-scale disturbances such as falling trees usually favor shade-tolerant plant species, whereas larger-scale disturbances such as landslides favor shade-intolerant plant species.

In ecological systems stability has been characterized mainly through four properties (Wu and Loucks 1995):

1. resistance (capacity of a system to resist an external perturbation),
2. resilience (rapidity with which a system returns to a previous equilibrium after a perturbation),
3. persistence (ability of a system to remain within defined limits despite perturbations),
4. and invariability or constancy (uniformity of system properties over a given period).

Resistance and resilience presuppose an equilibrium from which the ecosystem may depart or to which it may return. Persistence and invariability, however, do not necessarily imply equilibrium. Nonequilibrium models emphasize openness, transient dynamics, and stochastic processes of ecosystems. In 1987 ecologist Zev Naveh contrasted the static notion of homeostasis (maintenance of a static structure), by introducing the concept of homeorhesis (Wu and Loucks 1995, p. 444). Under a homeorhetic perspective, resilience can be understood in nonequilibrial terms: After a perturbation systems may return to their original trajectory or rate of change rather that to equilibrium.

Patches can vary at different temporal and spatial scales in the same landscape (Wu and Loucks 1995) because of disturbance, species interactions, and propagation modes. Consequently, understanding and modeling patch dynamics in a given landscape and making decisions about resource management and conservation policy require a recognition of the diverse causes and mechanisms of patchiness in various spatial and temporal scales.

ANTHROPOGENIC PATCHINESS

Spatial patterns and temporal heterogeneity created by humans are often qualitatively and quantitatively different from unmanipulated ecological heterogeneity. Landscapes are rarely homogeneous, but human monopolization of the landscape for urban settlement, farming, or forestry can greatly reduce heterogeneity and alter ecosystem and landscape patchiness. The drivers of ecological change will produce new configurations and compositions of patches that will affect organisms over a spectrum of scales, generating novel spatial patterns and trajectories of change. Landscape contexts can strongly influence local ecosystems; the consideration by environmental policy makers of spatial and temporal heterogeneity, which are constantly

changing as the products of natural and anthropogenic patch dynamics, is necessary to support biodiversity, maintain ecological and evolutionary processes, and provide multiple ecosystem services to humans (Kolasa and Pickett 1991). The role of patchiness and patch dynamics in ecological and evolutionary processes has led to the development of metapopulation theory which examines the dispersal and isolation of individuals between patches in heterogeneous landscapes. This theory is relevant to the persistence of species in fragmented habitat patches created by human land use.

The ubiquity and persistence of the spatial legacies of past disturbances underscore the importance of the historical dimensions of natural and anthropogenic patch dynamics. Knowing that landscapes are dynamic mosaics composed of various kinds of interdependent patches, humans can no longer manage a park or reserve as a homogeneous unit (Biggs et al. 2003). Moreover, the spatial patchiness of a given landscape, whether natural or anthropogenic, must be maintained in order to conserve biodiversity. This approach has been called the "minimum dynamic area" concept (Pickett and Thompson 1978).

CONCLUSION

Patch-dynamic concepts offer a contemporary unifying framework for ecology, evolution, and conservation practices under a nonequilibrium view that appreciates the spatiotemporal variability of "shifting mosaics" (Wu and Loucks 1995). The patch-dynamic perspective has largely supplanted traditional succession theory (Clements 1916), which assumed an orderly, repetitive, and deterministic sequence of change tending toward equilibrium. Alternatively, vegetation dynamics can be represented by a hierarchical patch-dynamics theory (Pickett et al. 1987) that accepts multiple end points starting from the same initial condition (but varies with stochastic and probabilistic events) (Simberloff 1980) and does not require the assumption of a stable "climax" stage.

SEE ALSO *Ecology: V. Disequilibrium Ecology.*

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