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NOTHING ENDURES BUT CHANGE: ECOLOGY'S NEWLY EMERGING PARADIGM

JOHN KRICHER *

“Nothing endures but change.”
Heraclitus, c 540-480 B.C.

(From a sign in an decrepit building in the ghost town of Bodie, California.)

Abstract - The study of history, human or otherwise, is really the study of change, the processes by which change is effected, and the effects of change. Change is normal in ecosystems. Measurement of change is scale dependent in both time and space. In nature, change occurs relatively continuously, though at varying rates and multiple spatial scales. The balance of nature, a philosophical construct that dates back to largely incorrect assumptions, is an artifact of scale as it relates to human intuitive perception. It is not real. The paradigm now accepted by most ecologists is that periodic disturbance at multiple scales is the most important determining factor in structuring ecosystems. The history of bird and mammal populations of eastern forests strongly supports this newly emerging paradigm.

There is a seeming constancy as well as an obvious complexity about any animal or plant species. American robins (*Turdus migratorius*) will look, sound, and act like American robins throughout a human lifetime. Audubon observed American robins that were not phenotypically distinct from those alive today. Such constancy initially made creationism seem logical and organic evolution implausible. The Darwinian Revolution, arguably the most important paradigm change in biology, if not in all of Western philosophy, reversed the focus from species stasis to gradual, mechanistically generated mutability, with the resultant evolution of often radical new forms from previously existing forms. One of Darwin's major arguments in attempting to persuade his readers of the truth of evolution was that the process is too slow to be easily detected within human lifespans (Dar-

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win 1859). In other words, the normal time scale of evolution generally exceeds the units of time that are intuitively meaningful to humans: minutes, hours, days, years, decades. Thus organic evolution, though perhaps obvious in the fossil record, is far from obvious in everyday human experience. As a process it is non-intuitive, and thus the apparent stasis of species is largely illusionary. It is a matter of time scale, somewhat like watching an hour hand on a clock: it does not appear to move when watched constantly but only "moves" when examined at appropriate intervals.

Ecosystems are perceptually like species in that they too exhibit characteristic form (physiognomy), impressive complexity, and apparent constancy. An oak-hickory forest, a northern hardwoods forest, and a spruce-fir forest each have distinct and easily recognizable characteristics that make it possible for virtually anyone to distinguish among them (Kricher 1988). Provided it is not cut down or otherwise radically disturbed, a tract of forest will persist well beyond any human lifetime: it will appear to be stable. And there is yet another similarity in how humans perceive ecosystems and species. Both concepts seem intricately balanced, interactive units of nature. The complexity and adaptiveness of species was apparent to ancient Greek philosophers, some of whom attempted to derive naturalistic rather than deistic origins for species. Nonetheless, the Greek view, articulated clearly by Plato, was that species are essentialistic, fixed parts of a living, harmonious cosmos. Once created (and Plato was a polytheist), species do not significantly change. Neither Plato nor Aristotle was an evolutionist (Mayr 1982). Given the view that each species is intricately and immutably crafted (by whatever force), it is not much of an intellectual jump to assume that natural assemblages of species, namely ecological communities, are fundamentally balanced, which was, indeed, the Greek view of nature. The concept of balance of nature, a view in which species are highly and, in many cases, precisely interdependent, thus derives at least in part from an erroneous notion of the very nature of species. Therefore, the belief that all of nature is somehow balanced is also largely artificial.

It may be fairly asked just what is meant by a balance of nature? In the naive sense, it implies total interdependency, the notion that species are like dominoes arranged in such a manner that if one falls, others, maybe many others, inevitably follow. This view of nature is sometimes expressed in questions such as "What is the purpose of mosquitoes?," the implication being that such creatures have an innate mission to fulfill in the order that is nature. Ecologically, the notion of balance of nature is more apt to be expressed as the belief that ecosystems eventually attain equilibrium, becoming self-reproducing and re-

sistant to invasion by other species, because niche space is rather precisely allocated among the constituent species, so that competition among species is minimized or non-existent. Further, a balance of nature can be envisioned as a kind of normal "set point," a species composition to which disturbed ecosystems return in the process of "recovery" following perturbation.

Eastern forests, as well as many other ecosystems, have been cited in various writings as examples of the balance of nature. Thoreau saw order in the way in which abandoned New England pastures would gradually revert back to forests (Worster 1977), though he recognized the individualistic nature of each response to disturbance (David Foster, pers. comm.). Years later, Frederic Clements (1928) would discuss this same process, ecological succession, as an example of how ecosystems can be viewed as "supraorganisms," in which successional changes are sufficiently orderly to be analogous to life cycle changes in organisms. According to this view, successional change climaxed in a mature, stable (balanced) ecosystem typical of the climatic region. Later still, Eugene Odum (1969), in one of the most influential papers in modern ecology, would envisage ecological succession as a natural "strategy" of nature to restore complexity and stability (and implied balance) to ecosystems.

Well-meaning conservationists continue today to argue against ill conceived assaults on ecosystems as interfering with the balance of nature. Arguments are occasionally heard in which it is said that "nature knows best," and should be left to its own devices. Such a view is obviously based upon the presumption of a natural balance. But if there is no natural balance, such arguments need to be reformulated.

The concept that there is, indeed, a natural balance of nature has been viewed somewhat differently throughout history, but is nonetheless very deeply ingrained in human thinking (Egerton 1973). And it persists. One current school of thought perceives Earth as a self-regulatory system in which the organisms, particularly microbes, maintain equilibrium by correcting perturbations in large-scale biogeochemical cycles. The Gaia hypothesis (Lovelock 1979) is a contemporary iteration, on a global scale, of balance such that the entire planet can be perceived as a self-regulatory superorganism.

The history of eastern forests is, however, not one of stasis but one of change. Some examples, at differing time and spatial scales, will make the point.

First, at the risk of stating the obvious, there was no eastern forest for most of the 4.5 billion year history of the planet. The evolution of flowering plants and of the various species of birds and mammals that live among them, of oaks and pines, of jays and wood-warblers, at

most encompasses less than two percent of the total history of Earth. Any hectare of land that now supports an oak-hickory forest once was barren and lifeless. It required many millions of years before it became populated by tree-sized horsetails and primitive conifers, among which lived early dinosaurs. Only in the last years of the Mesozoic Era and throughout the Cenozoic Era, a time span of at most 80 million years, have modern conifers and broad-leaved, flowering trees and shrubs been present (though not in their current species assemblages).

And the means by which multitudes of evolutionary changes have been effected is far from orderly. The Mesozoic Era is now widely believed to have ended abruptly following an impact by a large asteroid. The Cenozoic Era has seen Earth's climate becoming increasingly temperate and less equitable, with relatively recent periods of major glacial advance. During the height of glaciation, up to two miles (3.22 km) of ice sat atop land that now supports northern hardwood forest. Forests extant after the most recent glacial advance were fragmented, their component species displaced southward to various ice free refugia. When the ice retreated, the forest did not migrate back as a unit, but rather individual species moved northward at different rates (Delcourt and Delcourt 1988). Such factors as dispersal mechanisms, seed size, and, most importantly, climatic characteristics all influenced the rate at which each plant species expanded northward following glacial retreat. The present composition of eastern forests is modern in origin, dating back only to the few thousand years of the present interglacial period, and continuing to change up to and since the time of European settlement. It is also largely coincidental, with species assemblages representing various combinations of those species with sufficient dispersal powers, physiological hardiness, and adequate competitive abilities to persist together, a view of the ecological plant community originally put forth by Henry Gleason (1926) and referred to as the "individualistic plant community."

Animal communities, like plant communities, demonstrate individualistic assembly at various temporal and spatial scales. Beavers (*Castor canadensis*), porcupines (*Erethizon dorsatum*), and bobcats (*Lynx rufus*) all presently cohabit large tracts of northern hardwood and boreal forest. But beavers apparently first evolved in Europe about 35 million years ago, arriving in North America only about 15-20 million years ago (Savage and Long 1986). Some beaver species, now extinct, did not even inhabit forests. The porcupine, presently a common rodent throughout much of northeastern forests, originated in South America, moving northward along with species such as sloths, armadillos, and opossums during the great faunal interchange that

occurred between North and South America when glaciation exposed the Isthmus of Panama (Kricher 1997). Felids, like beavers, appear to have evolved in Europe about 24 million years ago and first arrived in North America around 18 million years ago. Examined on a long-term time scale, the various species that today form natural associations are really accidents of history.

Such processes continue today. Currently the following largely unrelated bird species are expanding their ranges northward, and, in Massachusetts, each has undergone significant population increases in the last 30 years: turkey vulture (*Cathartes aura*), red-bellied woodpecker (*Melanerpes carolinus*), acadian flycatcher (*Empidonax vireescens*), tufted titmouse (*Parus bicolor*), Carolina wren (*Thyothorus ludovicianus*), blue-gray gnatcatcher (*Polioptila caerulea*), worm-eating warbler (*Helminthos vermivorus*), northern cardinal (*Cardinalis cardinalis*), and orchard oriole (*Icterus spurius*) (Veit and Petersen 1993). A few mammalian species, such as Virginia opossum (*Didelphis virginiana*), are also undergoing significant range expansion northward. It is not clear exactly what causal factor is most responsible for allowing these southern species to expand their ranges dramatically (gradual climatic warming is often suggested), but what is clear is that each seems able to move into ecosystems it has not previously occupied. The rapid population growth of such species as European starling (*Sturnus vulgaris*), house sparrow (*Passer domesticus*), and house finch (*Carpodacus mexicanus*), none of which is native to the Northeast, also supports the notion that ecosystems are not so naturally balanced as to close out opportunities for invader species. Indeed, the ease with which some species colonize is notable.

The contrary is also true. The loss during this century of the American chestnut (*Castanea dentata*) as a numerically dominant tree species throughout eastern North America resulted in a negligible ecological effect on the forest as a whole. The most numerous bird species ever to occur in Northeastern forests was the passenger pigeon (*Ectopistes migratorius*). The species was almost certainly an important disperser of oaks and hickories, but it is now totally extinct (see below) and there is no evidence that its loss has resulted in any significant reduction in mast crop producers throughout its former range.

Smaller temporal and spatial scales are also illustrative of the fact that nature is dynamic, not static. If a habitat, any habitat, is left entirely alone, protected, with nothing done to it, it will nonetheless eventually exhibit change. Change is inevitable because eventually some form of natural disturbance will occur.

Natural disturbance is becoming increasingly recognized by ecologists as the primary factor that maintains ecological communities in

what is essentially a permanent state of nonequilibrium. Because disturbances, both temporally and spatially, tend to overlap, the overall view of community change has been termed hierarchical patch dynamics (Wu and Loucks 1995). Even such complex and species-rich ecosystems as lowland tropical rainforests owe much of their vast biodiversity to multiscale, periodic disturbance (Kricher 1997). A disturbance may be small scale, such as a single treefall caused by a lightning strike, moderate scale, such as a localized blowdown of a group of trees, or large scale, such as a widespread fire or the effects of a major hurricane. Such disturbances create habitats suitable for groups of a species that are not adapted to closed forests. In the Northeast, the presence of successional species such as most goldenrods (*Solidago* spp.), asters (*Aster* spp.), sumac (*Rhus* spp.), eastern red cedar (*Juniperus virginiana*), field sparrows (*Spizella pusilla*), prairie warblers (*Dendroica discolor*), and brown thrashers (*Toxostoma rufum*) is the evolutionary and ecological result of relatively frequent disturbances providing a continued presence of open, non-forested areas (see Marks [1983] regarding origins of eastern successional plant species). These species, though undoubtedly less abundant when the region was densely forested, can be viewed as native to the region, just as closed-forest species such as sugar maples (*Acer saccharum*), eastern hemlocks (*Tsuga canadensis*), and wood thrushes (*Hylocichla mustelina*) have been.

The Pleistocene arrival of *Homo sapiens* had a profound effect on North American ecosystems. Because culture provides humans with the ability to greatly alter nature, and because such alterations often result in extreme change to ecosystems, it is understandable that humans view themselves as having disturbed nature's natural balance. Particularly in Western culture, humans perceive themselves as largely apart from nature (White 1967), a dualism that isolates humans from nature as well as often puts them at odds with nature. Even Native Americans, a group of people often collectively identified as having a deep seated cultural kinship with nature, exerted significant and often negative effects on natural ecosystems (Cronon 1983). Indeed, evidence exists that the immigration of people into North America soon produced a devastating effect on the so-called Pleistocene megafauna, the ground sloths, mammoths, etc., resulting in a massive wave of extinctions (Mosimann and Martin 1975).

In general, it is believed that the overall abundance of eastern forest wildlife dramatically declined as populations of European settlers took increasing control over the landscape. Various early estimates of animal abundance suggest vast concentrations of wildlife (Matthiessen 1959, Cronon 1983). However, it is difficult to make accurate compari-

sons of largely anecdotal data taken by a select few observers with such modern coordinated databases as the Breeding Bird Survey. For example, both John James Audubon and Thomas Nuttall each believed the bay-breasted warbler (*Dendroica castanea*) to be extremely rare, and Audubon doubted that it bred in the United States, writing that it "must spend the summer in some of the most remote north-western districts, so that I have not been able to discover its principal abode." (Audubon 1841, p. 34). Audubon was also moved to comment on the extreme rarity of the chestnut-sided warbler (*Dendroica cantanea*), a species he encountered but once (Audubon 1841). Given that both Audubon and Nuttall worked without binoculars, it is certainly possible that they may have somehow overlooked these species. But given their obvious observational skills with numerous other species, this seems unlikely. More likely is that the bay-breasted and chestnut-sided warblers were really rare and both have greatly increased in population only during the present century.

No one doubts that humans have been responsible for several large-scale perturbations affecting eastern forest bird and mammal communities. The result is that forests today are markedly different from those present at the time of European colonization. The most significant of the many ecosystem alterations occurred in the 18th and 19th centuries as European settlers cleared forest for pasture, agriculture, and human habitation. Forest-dwelling species were faced with a significant decline in available habitat. The one bird species that probably suffered the most from forest clearance might well have been the passenger pigeon, once estimated as perhaps the most abundant bird species on Earth. The extinction of the passenger pigeon, often assumed to have been caused by excessive hunting pressure, was probably more the result of extreme habitat loss from forest clearance (Bucher 1992). Grassland and successional species were able to expand their ranges throughout the eastern states as forest species presumably became collectively less abundant. Species such as eastern meadowlark (*Sturnella magna*) and grasshopper sparrow (*Ammodramus savannarum*) undoubtedly benefited from forest clearance, just as populations of these species have recently suffered from habitat loss partly caused by regeneration of forest throughout the present century. Indeed, ecological succession of field to young woodlot is considered a significant factor in the recent decline of golden-winged warbler (*Vermivora chrysoptera*), which inhabits early successional habitats, and its replacement by the similar blue-winged warbler (*V. pinus*), which can inhabit a wider range of disturbed areas, including late successional deciduous forests (Veit and Petersen 1993).

Predator species such as mountain lion (*Felis concolor*) and gray

wolf (*Canis lupus*) were rapidly extirpated from eastern regions. In 1717 gray wolves remained sufficiently common on Cape Cod, Massachusetts that it was proposed to build a fence between Sandwich and Wareham to exclude wolves and make the outer Cape a livestock sanctuary (Matthiessen 1959). Species such as the fisher (*Martes pennanti*) were much reduced by fur trapping. In general, the collective effect of such activities was to significantly deplete top carnivores from eastern forest ecosystems, a characteristic that persists today, though some species such as red (*Vulpes fulva*) and gray (*Urocyon cinereoargenteus*) foxes, raccoons (*Procyon lotor*), and coyotes (*Canis latrans*) appear to be thriving, and other species, such as the fisher, are rebounding at least in parts of their ranges. White-tailed deer (*Odocoileus virginianus*) populations, often problematically abundant today, owe much of their present abundance to the absence of large predators.

Human actions continue to alter the animal communities of eastern forests. Avian predators such as the accipiter hawks (*Accipiter* spp.), peregrine falcon (*Falco peregrinus*), and soaring hawks (*Buteo* spp.) have increased with protection and conservation awareness and, in the case of the peregrine, captive propagation. Wild turkey (*Meleagris gallopavo*) populations have been successfully reestablished throughout much of their former eastern range. But at the same time, habitat fragmentation largely due to increasing human populations in suburbia poses threats for some species such as wood thrushes while others, such as blue jays (*Cyanocitta cristata*) and common grackles (*Quiscalus quiscula*) seemingly benefit.

Eastern forest ecosystems continue to change; some species decline, while others advance. As a result of research over the past several decades, ecologists have come to understand the reality of ecosystem dynamics, and have largely abandoned the notion that nature exists in some sort of meaningful natural balance (Botkin 1990, Pickett et al. 1992, Pickett and Ostfeld 1995, Wu and Loucks 1995). Given this reality, what effect should it have on informing decisions regarding land use and conservation of species?

It is essential to understand that human stewardship of ecosystems is now mandatory. Because of the magnitude of effects resulting from human potential and action in altering landscapes, nature, such as it is, must now be managed. Nature will not automatically restore some sort of idyllic "natural" balance as long as humans do not interfere. On the contrary, humans must proactively manage ecosystems based on such carefully considered goals as selective conservation of threatened species, maximization of local and regional biodiversity, maintenance of watersheds and soil systems, and other essential functions provided by natural ecosystems (Daily 1997). In the next millennium, the balance of nature is what humanity will make it to be.

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