Title
Concepts in historical ecology: The view from evolutionary ecology

Author
Winterhalder, Bruce

Publication Date
1994

Chapter 2

Concepts in Historical Ecology

The View from Evolutionary Ecology

BRUCE WINTERHALDER

Our charge in this volume is to identify or, more boldly, to create concepts to guide an endeavor we call "historical ecology." Some things seem to me critical in such an undertaking. First, we must know what we mean by the term; clear definition will be essential. Second, we must be aware that concepts have a particular role in scientific analysis. They are important but they are not theory or methods, even though these three aspects of scientific investigation are always entangled. Third, although it will be important to enlist concepts supportive of this endeavor, we also must identify and try to understand how existing, sometimes implicit ideas may impede or thwart it. Finally, our deliberations occur in a context of heightened concern about the health of the environment. We have assumed practical as well as scholarly obligations to think in ways that entail pragmatic and ethical issues of remedy. This imposes urgency and groundedness on our discussions.

I shall try to address all of these considerations at least to some degree. Effective interdisciplinary cooperation will require that each gets our collective attention. My thoughts on this subject arise from the perspective of evolutionary ecology more than from population, community, or ecosystem ecology. I conduct most of my research in terms of the behavior of individuals in populations. My theoretical commitments are neo-Darwinian and my methodology primarily is that of microeconomics. Most of my empirical studies are in the form of ethnographic and simulation analyses. I work broadly within the tradition of ecological anthropology, studying both hunter-gatherers (Cree speakers, in northern Ontario) and peasant agriculturalists (Quechua speakers, in the Peruvian Andes). This orientation itself has a history (Winterhalder and Smith 1992), which assures it biases and limitations plus a few merits that I hope will be apparent.

HISTORICAL ECOLOGY

Historical ecology might mean several things: a commitment to certain theoretical principles, a methodology or form of investigation, a predilection to certain topics, or investigation within a framework provided by a certain set of concepts. At this early stage, probably any definition will be provisional. Nonetheless, the cross-disciplinary ambiguity, breadth, and nuance associated with the terms "history" and "ecology" beg explicit attention.

Ecology is the easier term. I take it to refer to the holistic study of relationships among living organisms or between them and the physical environment. The relationships may be dyadic (a predator and prey) or more complex (a community food web); explicit (parasite and host) or implicit (community stability); biophysical (ecotypic variation along a climatic gradient) or purely biological (competition). This definition encompasses a variety of more specific types of ecology—autecology, synecology, chemical ecology, population ecology, community ecology, ecosystems ecology, human ecology and so forth—most of which refer to self-evident topical specialities.

History is the more difficult term. History itself is the descriptive, chronological account of selected events given coherence and boundedness by reference to some theoretical proposition, analytical problem, or limitation of space or time. Adjectival uses of the word—as in our subject, "historical ecology"—are problematic and for our purposes perhaps meaningless. Strictly speaking, historical factors, causes, processes and the like do not exist. We can isolate such things as sociocultural or environmental causal factors or processes. Important properties of these may depend on their location in time, that is, they may have a *temporal dimension*. But we cannot define or isolate time itself as a causal variable or process. The same is true of (so-called) spatial variables or processes.

This fine distinction matters in at least two senses, one weak and one strong. In the weak sense it is slipshod usage, because it hides the fact that we are actually referring to the historical dimension of some unidentified type of variable or process. And in the strong sense, the adjectival form necessarily draws attention to a possibility that we wish to deny: that there is an ahistorical ecology.

What then are we to make of historical ecology, which for reasons just stated is a suspect combination of adjective and noun? I think we should mean the historical dimension in ecology and should use the reference not to distinguish a subset of ecological subject matter but rather to draw attention to a strong epistemological assertion: *a complete explanation of ecological structure and function must involve reference to the actual sequence and the timing of the causal events that produced them*. This assertion is a claim about the nature of ecological investigation, equivalent to the belief that it cannot be reduced to statements that might qualify as "laws" (Hull 1974:45–50). It is a claim with implications for theory and methodology, and for the kind of knowledge that we seek. It is a claim that is controversial in the philosophy of science (Hull 1974). Any explanation that cites only the type, number, and cumulative value of the independent variables is incomplete. It also must acknowledge their possible novelty and give attention to the actual order and timing of their impacts.

This raises the question, are all complex assemblages of linked and interacting parts historical? What properties make a system historical for purposes of analysis and management?

I will try to develop an answer from a simple beginning. Most everything has a narrative past, even a cobble. Obviously the same can be said for physical systems (a lightning storm) and mechanical systems, and for natural and anthropogenic ecosystems. Further, most things bear traces of this history. The cobble has a composition identifying certain parent materials, a structure that indicates its conditions of formation, and surface features that indicate its erosional exposure. This record may be highly imperfect, but it is directly observable, and the evidence, to the extent it is preserved, is usually interpreted by an expert with few uncertainties. On this much, historians and scientists might agree. Each also might find that past intrinsically worthy of study. A more difficult question follows: Does that history matter to our ability to explain the present or predict the future? What kinds of knowledge about an entity are dependent on the specifics of that narrative history? Are there important properties not discernible from present observation and analysis?

For the cobble we might do well without the narrative. We could reconstruct something of its origins, explain much about its present state, and in principle could predict its response to future conditions using data only from contemporary observation and experiment. The geologist who undertook this task might seek evidence of the cobble's history and might include it in his or her description, but strictly speaking the key scientific objective of explanation and prediction can be met without it. The cobble has a history and bears traces of it, but its narrative past is largely inconsequential to what we can learn and might want to predict about it. The cobble bares its soul; its extant "phenotype" is the full and direct expression of its essential properties. Without elaboration, I will claim that in principle the same is true of any physical system.[1]

This is not the case for living systems—for simplicity, exemplified here by an individual organism. The phenotype of an organism is a partial and indirect manifestation of a special kind of history, a functional history recorded by natural selection in its underlying genotype. The genotype thus is both a record of a species' past and a program for its current adaptive interactions with the environment. It is especially important that this historical record cannot be determined directly from the genotype, nor can it be fully discerned from the organism's present phenotype, which is observable only after the transformations occurring during a particular ontogeny.

For this reason, the full set of functional relationships that would enable us to predict the phenotype for each genotype in all possible environments (technically, the norm of reaction) is effectively "hidden" to analytical view (Lewontin 1974). The history that matters to living organisms, the one they carry into their future interactions with their environment, is a single, somewhat *opaque* layer beneath the entity we observe. Unless we recover it as history, through knowing the temporal past of the organism, this information is not directly accessible. Evolved beings do not bare their souls; their phenotypes only partially and indirectly reveal their essential properties.

Using an analogy, this is much like the "hiddenness" of the dynamic properties of ecosystems (technically, the phase or domain of attraction map; see below).[2] Functional ecosystem properties that we need to understand (e.g., resilience) reflect an equally deep and obscured history. As in the case of genotype-environment interactions, these properties remain potent but are incompletely and only indirectly revealed in the manifest form and behavior (phenotype) of the extant system. As with phenotypes, feasible manipulation of extant ecosystem processes provides only a limited ability to explain and predict. An ecosystem is an indirect manifestation of its own special kind of history, a functional history arising from the partial coevolution and adjustments of the species composing it. Without knowledge about the system's actual history, our understanding is quite limited.

The inability of biologists to decipher the properties of evolved creatures fully, or those of the ecological systems composed of their interactions, by studying their extant form gives substance to the claim that their full understanding requires historical analysis.

ENVIRONMENTAL HISTORY

Historical ecologists and environmental historians ought to be natural allies. For this reason, it may be instructive to compare the evolutionary view of history developed above with that of the latter group, especially the essays of Bailes (1985), White (1985), and Worster (1984, 1988a). This group has its intellectual origins in the work of Walter Prescott Webb and James Malin, but it has flourished recently with studies of the relationships among the natural (physical) environment and American society and social institutions. Environmental historians initially focused on leaders of the conservationist and preservationist movements, and on the relationship of the frontier and wilderness to American culture and politics. Specific topics include the history of the dust bowl, the development and impact of western lands irrigation, the creation of national parks, the relationship between environmentalism and scientific ecology, and the emergence of governmental regulation of environmentally sensitive activities.

Although environmental history began as a form of intellectual or institutional history, it more recently has turned to examinations of the political and economic implications of the topic. The reciprocal relationship between culture and nature has been revealed in several dominant themes: the European expansion and colonization of the New World (by people, weeds and animal pests, domesticates, and diseases), the expansion of market capitalism as the dominant global mode of economic action, and the expansion of science as a disciplined basis for pursuing mastery over nature. Worster (1988a:289) describes this self-consciously "revisionist effort" as one dedicated to writing historical narratives that recognize and document the role of the "earth as agent and presence in history," as a source of "fundamental forces." He adds, environmental "damage had itself become an historical force, threatening to bring down political regimes, disrupt social patterns, and force fundamental economic and technological change." (Worster 1988b:17).

Worster recognizes three levels for the analysis of human ecology: the organization and functioning of nature (which he allocates to the discipline of biological ecology and paleoecology); the realm of material culture, that "age-old dialogue between ecology and economy" (1988a:301) (where ecological anthropology holds sway); and the realm of mental culture, of perception, meanings, and values (where environmental historians and anthropologists divide duties along the axes of Western and non-Western peoples, history, and archaeology). Worster especially looks to ecological anthropologists for guidance and inspiration, because they "are among the most wide-ranging and theory-conscious observers of human behavior" (1988a:299). The contrast between his evaluation of anthropology, and geography and history, is instructive:

> Geographers, like historians, have tended to be more descriptive than analytical. Taking place rather than time as their focus, they have mapped the distribution of things, just as historians have narrated the sequence of events. Geographers have liked a good landscape just as historians have liked a good story. Both have shown a love of the particular and a reluctance to easy generalizing. (Worster 1988a:306)

Worster (1984) identifies ecological anthropology with the work of Julian Steward and his students, noting the influence on Steward of Karl Wittfogel and their joint commitment, historian and ecological anthropologist alike, to historical, comparative environmental studies. "So far has this study [of ecological anthropology] progressed that now it is the historian's turn to become learner and follower, seeking to apply the anthropologist's approach to the investigation of past societies" (1984:6).

When Worster comes to examine the "specific ways in which an ecological approach to history can be pursued, to ask what it can seek to do, what its limits are, and why its time at last has come" (1984:16), however, the results are disappointing. There is the admonishment that history itself has no theory to contribute to this task, being instead more a "clustering of interests." There is advice that "all generalizations must be rooted in specific times and places." There is acknowledgment of differences of subject matter (historians deal with written records of the modern era, etc.), and a short list of potential topics for interdisciplinary study.[3] But there is little about theory or methods, or even a clearly enunciated sense of the potential interdisciplinary meaning(s) of history in analyses that would combine natural science, social science, and humanism. Whatever its potential, the possible alliance of human ecologists and environmental historians is not yet set within an analytical framework that can encompass them both.

Because they are evolved creatures or aggregates of evolved creatures, biological entities—from individuals to systems—have properties that make them historical in ways that are central to their *scientific* analysis. Ecologists thus have special reasons to pay attention to history. Historians have recently discovered the importance of ecological variables to their (more humanistic and socially oriented) analyses of American landscape, culture, and institutions. It is encouraging and a little daunting that historical ecology, as pursued by anthropologists, might provide a meeting ground for these endeavors.

It may be useful to recall that ecology began in the nineteenth century, fresh on the vivid discovery that the geological and biological realms imperfectly preserved, and were the product of, an actual (evolutionary) record of past events. The earth and natural worlds had history; the scholars who studied these realms thought of themselves as "natural historians." It is an important endeavor of this volume that we produce a concept of history that is congenial to scientific endeavor and a concept of ecology that is congenial to the historian. Nothing less will sustain our sense (based in experience and practical concern) that an undertaking called "historical ecology" is essential; nothing less will inspire the interdisciplinary collaboration it requires.

A beginning definition that is rooted in the natural science component of our subject would include the following: historical ecology undertakes the temporal (diachronic) analysis of living ecological systems that in principle is necessary to analyze their structural and functional properties fully.

CONCEPTS

Some of the most powerful contributions of the natural historians were temporal concepts (e.g., descent with modification, gradualism). This volume is about concepts, of which ecosystem is an example. We might ask then, what is a concept? What kind of scientific work do we mean it to do? A cursory sampling of philosophy of science books indicates that three (Hull 1974; Thomas 1979; Toulmin 1953) have no explicit reference in the index or table of contents to the idea of a concept. Two (Hempel 1966; Schleffer 1967) contain index entries for the term but no explicit definition.

Neglect of the scientific status of concepts is widespread even in biology, which thrives on them. The evolutionist Ernst Mayr notes that important changes in concepts are seldom recorded or explicitly discussed in publications (1982:18) and have received little attention from the philosophy of science (1982:43). Mayr has repeatedly emphasized the "overwhelming importance" (1982:43) of concepts in the history of biology, arguing that the greater part of progress in the discipline and the reputation of leading figures has turned on the development and refinement of concepts:

> One can take almost any advance, either in evolutionary biology or in systematics, and show that it did not depend as much on discoveries as on the introduction of improved concepts. . . . Those are not far wrong who insist that the progress of science consists principally in the progress of scientific concepts. (Mayr 1982:24)

He argues that concepts have a place and significance in biology comparable to that of laws in physics. Among his list of eight propositions forming the basis of a philosophy of biology are "that the historical nature of organisms must be fully considered . . . [and] that the history of biology has been dominated by the establishment of concepts and by their maturation, modification, and—occasionally—their rejection" (1982:76).

Despite his attention to concepts, I have not found an explicit definition of concept in Mayr's (1982, 1988) writing. He does provide examples (population thinking, meiosis, natural selection, phenotype). He mentions that concepts are refined and articulated primarily by definition, and he refers to their flexibility and heuristic usefulness. He observes that they constitute a framework for organizing generalizations.

I propose this definition: *A concept is a statement that isolates and systematically defines relationships or processes thought to be especially worthy of analytic attention* (see Winterhalder 1984:303). A concept provides a framework for viewing facts selectively, with heed to certain of their attributes or relationships. Niche, surplus, and ecosystem are examples. Concepts are most useful when joined to appropriate theory, hypotheses, and methods. The ecosystem concept, for instance, "cannot substitute for theory that is coherent and that can yield testable hypotheses" (Gross 1984:254).

Concepts are not facts or theories (Rigler 1975) as they are commonly understood. Neither are they principles, which are statements of "a general or fundamental truth: a comprehensive and fundamental law, doctrine, or assumption on which others are based or from which others are derived" (*Webster's Third New International Dictionary* 1971). For instance, foremost among the principles of the natural historians is that of uniformitarianism (Simpson 1970); central to this volume is the claim that history is in principle important to ecological study. In one of the earliest attempts to list the generalizations of ecology systematically, in 1939 Allee and Park set out a list of nine "principles" (law of the minimum, adaptation, community, succession, etc.; see McIntosh 1976:358–59). All of them would be termed *concepts* according to the present definition.

If we can take the history and philosophy of evolutionary biology as a reliable guide, concepts are likely to be important components in the science of historical ecology. They fully merit the explicit attention assigned them in the organization of this volume; they provide a meeting ground for the interaction of environmental historians and human- and bioecologists.

The Ecosystem Concept

Ecology as a professionally organized and self-conscious discipline postdates the beginning of the twentieth century.[4] The explicit formulation and expansion of what we know as ecosystem ecology occurred only after World War II (McIntosh 1976, 1985). It was propelled by scientific advances in nonbiological fields during the war, although it had antecedents much earlier. It rested especially in the holistic practices of the natural historians and their vision of an integrated and "balanced" nature. Reference to three "milestone" studies will provide a highly schematic sense of this complex history.

The entomologist-limnologist Stephen A. Forbes, chief of the Illinois Natural History Survey, provides an early and influential example of an ecosystem view. His 1887 study, "The Lake as a Microcosm" (Forbes 1925), articulated a holistic vision of a lake as a complex of interacting physical and biotic processes. Forbes (1925:537) wrote:

> [A lake] forms a little world within itself. . . . Nowhere can one see more clearly illustrated what may be called the sensibility of such an organic complex, expressed by the fact that whatever affects any species belonging to it, must have its influence of some sort upon the whole assemblage. . . . a comprehensive survey of the whole [is] . . . a condition to a satisfactory understanding of any part.

Forbes detailed the life forms found in the lakes of Illinois, gave examples of their manifold interconnections through predation and competition (what he called "remote and unsuspected rivalries" [Forbes 1925:548]), and went on to describe the remarkable "steady balance of organic nature, which holds each species within the limits of a uniform average number, year after year . . . the little community secluded here is as prosperous as if its state were one of profound and perpetual peace" (1925:549). To explain this stability, Forbes argued:

> Two ideas are thus seen to be sufficient to explain the order evolved from this seeming chaos; the first that of a general community of interests among all the classes of organic beings here assembled, and the second that of the beneficent power of natural selection which compels such adjustments of the rates of destruction and of multiplication of the various species as shall best promote this common interest . . . even here, out of these hard conditions, an order has been evolved which is the best conceivable. (Forbes 1925:550)

According to Forbes, this "beneficent order" is maintained by natural selection, competition, and predation, all "laws of life" that determine an equilibrium, a state that is "steadily maintained and that actually accomplished for all the parties involved the greatest good which the circumstances will at all permit" (quoted in McIntosh 1985:59). Forbes's vision of the balance of nature sounds as if it were inspired as much by Adam Smith as by Linneaus.[5] Developed by pioneering limnologists such as E. A. Birge and C. Juday, this approach became influential in the community ecology studies that occupied the early days of the discipline (1920s to 1950s). It focused on photosynthesis, respiration, decay, and processes controlling lake productivity.

A second important event in the development of ecosystem ecology was Lindeman's 1942 paper, "The Trophic-Dynamic Aspect of Ecology." Also a limnologist, Lindeman added a theoretical emphasis to the holistic, biophysical view by emphasizing quantitative study of trophic function, energy and materials flows and transfers, and the relation of these processes to seasonal and longer-term changes in the community of organisms. The period immediately following World War II saw a great expansion of funding for ecosystem studies based on Lindeman's work, from the National Science Foundation (founded in 1950) and the Atomic Energy Commission. The field developed around a trophic-functional orientation, through studies of productivity and nutrient cycling. The emphasis was often on the abiotic components and processes of ecosystems, on large-scale computer models, and on application of ideas from cybernetics, general systems theory, and operational research. By 1964 Eugene Odum could state:

> *The new ecology is thus a systems ecology*—or, to put it in other words, the new ecology deals with the structure and function of levels of organization beyond that of the individual and species. (Odum 1964:15; emphasis original)

In fact, the third highlight may well be the epitome of this approach: Odum's (1969) *Science* article, "The Strategy of Ecosystem Development." In this influential article, Odum presented a successional model of the components and stages of ecosystem development. The process was presented as one of orderly, directional, and predictable development, culminating in the maximization (or minimization) of various structural and functional properties of the community. Among the twenty-four different attributes listed in the model were such things as biomass, productivity, diversity, and homeostasis. According to Odum, these trends were based on fundamental evolutionary principles related to energy dynamics, which have "parallels in the developmental biology of organisms, and also in the development of human society" (Odum 1969:262). The paper was rich in generalizations that proved attractive to natural and social scientists (Winterhalder 1984): as an example, "quantity production characterizes the young ecosystem while quality production and feedback control are the trademarks of the mature system" (Odum 1969:266). Citing these and other generalizations, Odum argued that "the framework of successional theory needs to be examined as a basis for resolving man's present environmental crisis" (1969:262).

Although not all ecosystem studies are systems ecology (see discussion in McIntosh 1985:202–7), a systems approach drawing theoretical inspiration from engineering and the physical sciences has been dominant (Golley 1984). Proponents of an ecosystem approach emphasize its holistic orientation to a degree that recalls the organismic analogy of Clements (see below). Odum described the ecosystem as "the *basic unit* of structure and function" for ecological analysis (1964:15; emphasis added). Woodwell and Botkin (1970:73) note that "There is something rejuvenating in the tacit but progressive acceptance of Clements's classical assertion that the community is an organism." In debates provoked by the creation and evaluation of the International Biological Program (IBP 1964–74), proponents made an impassioned defense of the holistic, systems approach: "Although systems analysis is most commonly encountered in ecology as a method, principally the mathematics model, it has overtones of a philosophy . . . or even . . . an ideology" (McIntosh 1985:232).

The influence of the ecosystem concept is pervasive in human as well as biological ecology (Moran 1984).

Community and Succession

The other guiding concepts of ecology prior to World War II were those of succession and community, developed primarily in the work of F. E. Clements (McIntosh 1985). Clements made his first systematic statements on the concept of succession as early as 1905; the classic description is his 1916 book, *Plant Succession,* and the 1936 paper, "Nature and Structure of the Climax." In Clements's view, succession is the regular process of development of a plant community after a disturbance. The species composition and physiognomy (three-dimensional form) of the community pass through a regular sequence of changes until they reach a stable, self-replicating climax determined by external climatic factors (typically temperature and moisture). These climatic factors are themselves stable, so the climax persists unchanging for a long period over large regions. Disturbance is external and rare. Whatever the character and impact of a perturbation, hence whatever the state from which succession is initiated, it will converge to a pathway of development that leads again to the climax.

Clements was the "premier American plant ecologist" (McIntosh 1985:354), and his ideas dominated the subject during the decades of the twenties, thirties, and forties. They exerted considerable influence even after the focus had shifted to ecosystem questions (see citation of Woodwell and Botkin, above). The climax community was a stable equilibrium, its structural and functional integrity like that of an organism. Systems ecologists adopted large parts of this conception, merely shifting its application from the biotic components of the community to more inclusive energy and geochemical relationships, and from analysis of structure to that of function.

The past two decades have seen strong critiques of both systems ecology and the concept of succession developed and promoted by Clements. Before summarizing them, I want to note an influence common to both approaches: Herbert Spencer. McIntosh (1985:43) observes that Clements's ideas had their origins in German idealism and in "Herbert Spencer, a source he shared with the premier American animal ecologist S. A. Forbes." McIntosh (1985:254, citing Tobey 1981) notes that "Clements's holistic organismic views were influenced by reading Herbert Spencer and his association with social scientists of similar persuasion":

> Clements's theories were extremely controversial, and the persistence, intensity, and inconclusiveness of much of the controversy suggest a philosophical as well as an empirical problem. . . . Clements . . . formalized ideas about the holistic nature of communities as organisms which were widespread, if not universal, among other progenitors of animal ecology, oceanography, and limnology. (McIntosh 1985:43)

Forbes himself attributed certain of his ideas to Spencer (McIntosh 1985:65). Spencer's influence is evident in the emphasis on organismic analogy, ontogeny (succession), equilibrium, and system determination of directional change.

Spencer of course had a direct but much more apparent impact on anthropology. As a consequence there is a long and incomplete but very public struggle to escape from his legacy of determinism, evolutionism, and ontogenetic and organismic analogies. Spencer's similar influence on ecological concepts in the biological sciences is less well appreciated, and it would be an especially ironic twist to intellectual history if human ecologists inadvertently gave Spencer new influence by adopting a bioecology influenced by his ideas.

I want to focus on one particular problem with the ecosystem concept produced within the Spencerian legacy: the claim that ecosystems function as organisms. It is an important claim because if ecosystems are cybernetic in this manner then a sufficient explanation can end when the equilibrium has been characterized. Deviations are due to incidental, exogenous factors, typically of limited duration and impact. System history is of little or no consequence. But the cybernetic characterization is not uniformly accepted (cf. Engelberg and Boyarsky 1979; Patten and Odum 1981) and not that clearly manifested in empirical studies. The information circuits that could provide negative feedback are not evident. Most important, the only theory that we have to account for design in nature, neo-Darwinism, does not give us reason to expect homeostatic design of functional relationships *at the level of ecosystems* (see below).

The description of ecosystems as balanced, cybernetic entities has also suffered from revised views of succession and community (Drury and Nisbet 1973; Horn 1974). There are multiple inconsistencies between Clements' view and empirical studies. The sequence of changes during succession is not so regular as once was thought, nor is sequential replacement of species always the case. Disturbance is more pervasive in its effects and more common than was originally realized; it is often endogenous in origin and character, resulting from properties of the community itself (recurrent disease or parasitic outbreaks, cycles of senescence, predator-prey cycles, etc.). Rather than one climatically determined climax, alternative stable-state communities may be possible in a given locale, also determined in part by endogenous factors (Holling 1986:298–300). Many of the generalized structural-functional patterns thought to be associated with succession (Odum 1969) are riddled with exceptions.

In an alternative view, succession can be explained in terms of statistical patterns of replacement rather than the organismal development (ontogeny) of a cybernetic community (Horn 1974). Ecologists now speak of "blurred successional patchworks," "gap phases," and "moving mosaics" as ways of characterizing the highly localized dynamics of ecological disturbance and succession (Picket and White 1985). If they speak of an equilibrium, it is a statistical statement referring to a stabilized distribution of vegetational patches taken over a region large enough to even out the local dynamics and irregularities. Even the descriptive sense of a community as a distinctive, bounded, and nonarbitrary assemblage of biota has been replaced to some extent by a more individualistic view. Species respond somewhat independently to environmental gradients and in their collective distribution meld together and replace one another in a more continuous fashion than the community concept implies.[6]

The ecosystem and community concepts with their embedded organismic analogy have had a tremendous influence on social scientists pursuing interdisciplinary analyses of human ecology (Winterhalder 1984:302). But we ought to be wary of these ideas. They yet are imbued with Spencerian ideas based in organismic analogy and equilibrium, and their most potent contemporary theoretical expression is a form of systems theory that likewise places its emphasis on cybernetics and homeostasis. In either case, they grant little or no analytical room to history. Furthermore, the ecosystem concept offered us by the biologists is a curiously *social* construct: its origins were strongly influenced by the social evolutionary theories of Spencer, and its current theoretical interpretation is fixed to cybernetic devices engineered by human beings. We should worry (and I take this to be the substance of much recent critique), however, about whether or not it is also an appropriate *natural* construct. Without being aware of it, human ecologists may be borrowing back from the biologists disguised versions of some of our own outdated and less salutary ideas.

EVOLUTION, ECOLOGY, AND HISTORY

Throughout the development of ecology there has been a tension over the appropriate level of analysis: individual, population, community, or ecosystem. While system ecologists have sometimes insisted that the ecosystem itself has functional integrity as an evolutionary unit (for example, "the ecosystem can be taken to consist of biotic and abiotic components that change and evolve together, and the term ecosystem implies a unit of coevolution" [Patten 1975; quoted in McIntosh 1985:239]), others disagree ("There is in the community no center of control and organization . . . and no evolution toward a central control system. . . . Community organization is a result of species evolution and species behavior" [Whittaker and Woodwell 1972:150; also quoted in McIntosh 1985:239]).

Advances in evolutionary theory in the past twenty years support Whittaker and Woodwell. Neo-Darwinian mechanisms of evolution lead us to expect that adaptive design is a routine property of individuals, a less common property of kin or unrelated intraspecies groups, and occasionally a property of very limited sets of coevolved organisms (as in cases of interspecific mutualism). Beyond these levels, unless we can interpret the properties of more complex aggregates as emergent and thus incidental results of adaptive design at lower levels, we ought to be skeptical. Further, if there are emergent properties, we are obliged to be quite cautious in appraising them using cybernetic, homeostatic, organismic models. Forbes's appeal to Darwinism as the source of harmony and balance in natural systems (cited above) and all of the like appeals subsequent to him must grapple with the trenchant hostility of neo-Darwinian theory to such interpretations.

Evolutionary theory adds to the doubts expressed about the concepts of community and ecosystem ecology. It is more supportive of the historical endeavor proposed in this volume. For instance, Lewontin (1966) has identified two properties which generate what he calls the "historicity" of evolution. First, the extent to which organisms incorporate and retain experience with past environments in their adaptive repertoire influences whether they will experience recurring environmental challenges as predictable or capricious. Most genetic systems have a limited memory, and the organism will experience even recurring events as capricious if they occur at intervals longer than the retention of the relevant adaptive information. Second, adaptations are a response to an exact historical sequence of environmental conditions. It is relatively easy to show through computer simulation that selective regimes with like normative qualities but differing in their exact sequences of environmental perturbations will produce different evolutionary pathways and outcomes. This occurs because a gene system with allele frequencies approaching fixation (i.e., approaching 0.00 or 1.00) is less responsive to selection of a certain intensity than is one with more equal allelic distributions (say, 0.45 and 0.55 for a two-allele locus).[7] If subjected to the same selection pressures, they will behave differently. The "historical accident of the order in which the environments occur necessarily changes the long-time life history of a population" (Lewontin 1967:86). The key to this result is a nonlinear relationship between perturbation and response—one in which the magnitude of the response is sensitive to the preexisting state of the organism. It is likely to be a widespread feature of natural and sociocultural systems.

Building on these evolutionary ideas, Lewontin (1969) analyzes the claim that the history of an ecosystem is unimportant to its present state. At least three assumptions are implicit in this view—the system has one stable configuration, it is in that state, and how it got there is dispensable to analysis. Each assumption can be questioned. Multiple stable states are empirically known; the claim that a system is at a stable state already presumes we know something about its history; and finally, analysis at a stable state cannot provide information about how the system will evolve or respond to stress or perturbation. Lewontin's observations are among the reasons that extant phenotypes of evolved beings cannot fully reveal their origins or future behavior (see above).

Advances in evolutionary ecology have also drawn attention to the importance for adaptation of spatial heterogeneity and temporal dynamics in natural environments. Unfortunately, normative description and averaging statistics (e.g., mean temperature, average biomass of resource species) characterize most studies of environment found in the human ecology literature. Ecological factors typically enter the analyses as static and predictable variables, shorn of their dynamic, discontinuous, unpredictable, and especially their historical qualities. This has been the case even though virtually all of the various analytical approaches guiding ecological anthropology studies suggest that temporal variance and spatial heterogeneity drive ecological adaptation (Winterhalder 1980:136).

The adaptive content of human-ecological systems is a response to the extremes of environmental variability they have experienced; virtually all of their adaptive crises occur at these extremes. Thus, it is important to come to an understanding of what constitutes an analytically sufficient environmental description, one more cognizant of history, and to find the concepts that will produce it. Here we must delve into what Worster

(1988a:290) calls, one hopes with some bemused respect, the "outlandish language" of the natural scientist.

Patchiness

The distribution in space of ecological communities is locally heterogeneous and quite labile. In the place of succession and climax, ecologists are developing a more differentiated and dynamic vision of the spatial qualities of communities. Disturbance is seen as a regular element of the system itself, and although there are patterned responses to perturbations, it is the processes of adjustment that are taken to be fundamental.

The set of ideas mobilized around the concepts of *patch* and *patchiness* (Pickett and White 1985; Wiens 1976) is an important component of this shift. A patch is an ecologically distinct locality in the landscape; it is problem- and organism-defined, relative to the behavior, size, mobility, habits, and perceptive capabilities of the population being studied. For an herbivorous insect, individual leaves may operate as patches; for an ungulate, isolated mountain meadows or localized areas of fire-regenerating brush might represent patches. In general, patches are localized discontinuities in the landscape which affect behavior; they are assessed in terms of properties like the number of patch types and their size, quality, turnover and developmental dynamics (e.g., succession), and distribution.

A related concept is *grain*. Grain is established by the mobility of the organism relative to the scale of patchiness and by the ways in which the organism responds to environmental heterogeneity. A coarse-grained environment is one in which patches either are much larger than the typical range of the organism or are utilized very selectively. In either case, the organism uses selected portions of the landscape disproportionately. A fine-grained environment has a small scale relative to the organism's mobility, or patches are utilized generally. In this case, the organism encounters and uses patches more or less in proportion to their representation in the habitat. Patchiness has become a basic feature of analyses of such evolutionary ecology topics as habitat selection, foraging behavior, life-history strategies, and population dynamics (see Southwood 1977; Wiens 1976, 1985); it also has become a basic feature of ecological management practices (Pickett and White 1985).

The boreal forest of northern Canada is a particularly good example of a patchy environment (see Winterhalder 1983a). Edaphic differences associated with low-relief landforms (uplands of kames and eskers; basement shield; rivers and kettle-lake depressions) coupled with recurrent disturbances (fires; animal activities, such as flooding from beaver dams; and toppling of trees by wind and snow) create a dynamic and highly heterogeneous landscape. Each patch type has a set of associated resource species and dynamics; each presents unique subsistence opportunities and impediments. Knowledge of this spatial variation is essential to studies of the productivity and dynamics of boreal forest resources and to analysis of the tactics of the Cree foragers who harvest and live from them (Winterhalder 1983b).

Persistence and Predictability

Patterns of temporal variation and long-term change are also important. If patchiness summarizes the state of environmental heterogeneity in space, the concepts of persistence (Botkin and Sobel 1975) and predictability (Colwell 1974) help to characterize the range and regularity of variation in environmental states in time. An organism's experience mingles the space and time dimensions, but it is analytically difficult to treat them simultaneously and their effects are often different.

Persistence (Botkin and Sobel 1975) is a term meant to characterize the natural dynamics of time-varying ecosystems without assuming that they have a static equilibrium (a condition to which they will always return following a disturbance, the classical definition of succession to a climax being an example). Persistence implies that the system characteristics of central interest fluctuate within defined boundaries, which may be more or less "stringent" (i.e., encompass fluctuations of lesser or greater magnitudes). Within a certain time interval, the fluctuations may be either "recurrent" (a repetition of a particular state of the system) or "transient" (the state does not repeat). In this view, a perturbation alters the future states that otherwise would have occurred by changing boundaries of persistence or the likelihood and frequency of recurrent or transient states of a particular type. Persistence and the related terms have the important advantage that they can characterize regular or irregular fluctuations without implying that the system possesses qualities of homeostasis or static equilibrium.

Persistence describes the expected magnitude of fluctuations, but it says nothing about the regularity or patterning of recurrent states. Colwell's (1974) concept of predictability fills this gap by providing a quantitative characterization of periodic phenomena with a simple measure based on information theory. Seasonal amounts of rainfall over a period of years will serve as an example. To simplify we consider four seasons (spring, summer, fall, and winter) and rainfall in three categories (low, medium, and high). If knowledge of the season (time) is enough to determine with complete confidence the quantity of precipitation (state), then rainfall is maximally "predictable." Conversely, if any category of precipitation amount is equally likely in each season, predictability is at a minimum. Predictability can arise from "constancy" (the same state category obtains for all time seasons for all years), from "contingency" (a different state category pertains for each season, but in exactly the same pattern for all years), or some combination of the two. In practice, Colwell's measure is easily calculated, with predictability being the simple sum of constancy and contingency, measured on a scale of 0 to 1 (i.e., $[0 \leq P \leq 1]$; $P = C + M$).

An example of an analysis that uses the concept of predictability can be drawn from human ecology studies in southern Peru (see Winterhalder in press). The data are monthly precipitation records from weather stations located on the eastern escarpment of the Andes, an area of intensive, dry-farming peasant agriculture. In this case the study objective is an analysis of the roles and relative importance of production, storage, and exchange decisions in mitigating subsistence risk arising from drought and frost. Both for the local analysis and for regional comparisons, it is important to know the degree and regularity of fluctuations in seasonal precipitation. In this case the relationship between altitude and the predictability, constancy, and contingency of monthly precipitation is quite regular. Although predictability owing to contingency (seasonality) increases with elevation, the increase is not sufficient to offset the large drop in predictability owing to constancy. Overall the predictability of the monthly distribution of rainfall declines at the higher altitudes, indicating that subsistence risk increases with elevation.

Ecological studies have demonstrated regularities of ecosystem structure and function, but most of these regularities are empirical generalizations that have not been set within a solidly established theoretical framework. Commitment to "benign" system-level functionalism (homeostasis, balance, harmony, etc.) is a matter of much faith and very limited experience. Emergent properties like stability and resilience may characterize an ecosystem, even though they are not an (organismic) adaptation of an assemblage of species (in the sense of a quality designed by natural selection). Evolutionary theory suggests that we should be skeptical of attributing cybernetic properties to high-level entities like ecosystems, and it gives us additional reason to believe that history itself is important in the scientific analysis of ecological questions. Here is a natural collaboration, in which the natural and social scientist can profit from the methods and attentions of environmental historians.

In pursuit of historical ecology, we might be tempted to produce chronologies of highly detailed environmental information. But narrative ecohistory is not the entire answer. For some scientific goals, we also need theoretically sensitive means of summarizing the descriptive detail of environmental variability without succumbing to it. This is precisely the kind of scientific work for which concepts like patch, persistence, and predictability are suited. Although none of these concepts fully captures history in its narrative sense of sequence, timing, and uniqueness, they do generalize some of the key effects of this history on properties of ecological systems.

ADAPTIVE MANAGEMENT

By claiming that our subject is historical in principle, we place certain limits on our confidence in prediction, whether it is based on theory, empirical generalization, simulation, or analogy. Quite beyond our considerable present-day ignorance about the structure and function of complex human-ecological systems—ignorance that we can hope to diminish—these systems will always contain the possibility of novelty and capriciousness. Their specific histories, which may be only partially known to us, contain implications for their future development. All of this reduces our certainty about how these natural and anthropogenic ecosystems will function, especially when exposed to stress. History compels us to allow for the unexpected.

Adaptive management is Holling's term for the research and policy consequences that follow from acknowledging these sources of uncertainty (Holling and Goldberg 1981; Holling ed. 1978; Holling 1986). Holling begins by stating four basic properties of ecological systems (Holling and Goldberg 1981:83): (1) they have systemic qualities (there are complex interactions or connections among parts); (2) they are historical (current behavior is shaped by past events); (3) they are spatial (local behavior is shaped by surrounding events); and (4) they are nonlinear (key interactions may be characterized by lags and thresholds). These qualities are important, but they also are sometimes exaggerated or misunderstood (Holling ed. 1978). For instance, only certain of the connections within an ecosystem matter (we need not study everything to understand the behavior of the system); the effects of events are localized and heterogeneous across space (we cannot assume that the impact of an event gradually diminishes with distance); abrupt shifts in system behavior are always possible and are difficult to anticipate; and variability, not constancy, is fundamental.

Linked to these properties is a distinction between two ways of conceptualizing the structural properties of ecosystems: *stability* and *resilience.*

> Stability . . . is the propensity of a system to attain or retain an equilibrium condition of steady state or stable oscillation . . . resist any departure from that condition and, if perturbed, return rapidly to it . . . a classic equilibrium-centered definition. . . . Resilience . . . is the ability of a system to maintain its structure and patterns of behavior in the face of disturbance. (Holling 1986:296)

The difference between these terms can be visualized in terms of a simple diagram (technically, a "phase portrait") representing the behavior of two ecosystem variables (fig. 2.1). In a simple system the axes might be the population sizes of two interacting species. So long as the two variables remain in central portions of the *domain of attraction,* small disturbances are absorbed with modest and perhaps temporary quantitative changes in the system. However, if the variables move across the boundary or the boundary shifts so that it passes over their position, unstable, qualitative changes can result.

Stability focuses on maintenance of an equilibrium and ecosystem conditions near it. It might refer to a stable equilibrium point, cycle, or trajectory. As an analytical or policy concept it emphasizes low variability and resistance to change. It contains the presumption that incremental change will have a predictable, incremental effect, and that the relationship between the variables will reliably signal this effect. In contrast, resilience focuses on the size and form of the domain of attraction, on the behavior of the variables near its boundary, and on the susceptibility of the domain to contract under differing ecological or management conditions. It emphasizes nonequilibrium events and processes, variability, and adaptive flexibility. From a resilience perspective, incremental change may not reliably signal its effect. If a boundary is reached, the effect will be abrupt, unpredicted, and disproportionate to the cause—a surprise.

System resilience is determined by history and is linked to properties like diversity and complexity, although these relationships are only partially understood and they provide generalizations of limited reliability. For

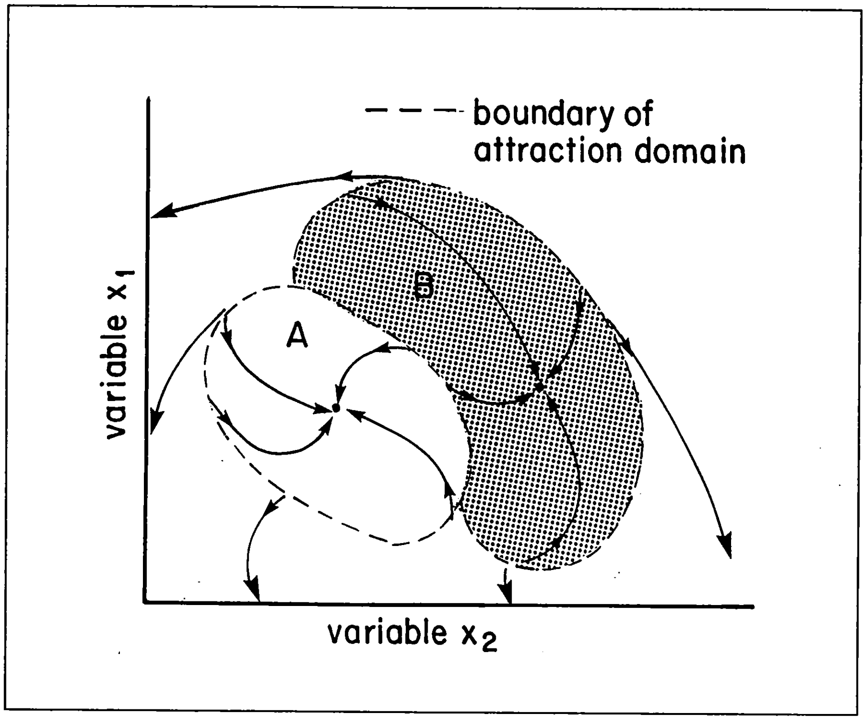

Figure 2.1. Domains of attraction for a system of two variables and two alternate stable states (A and B). A perturbation that displaces the variables to a point within their present domain of attraction will be followed by a regular return to the equilibrium. However, if the position of the variables crosses a boundary, either because they are perturbed or because the boundaries of the domain shift or contract, then the system will abruptly make a qualitative shift from one to the other domain of attraction or from an attraction domain to extinction. (After Holling 1973)

instance, complexity, measured as connectedness, seems to reduce system resilience; homogenization of systems spatially increases their connectedness, etc. The descriptive properties of ecosystems may not provide reliable or highly generalized clues about their functional responses to change.

A resilience-oriented view draws attention to important properties of ecosystems. Multiple domains of attraction can characterize a set of interacting elements; system behavior becomes discontinuous at the boundaries of these domains; the boundaries themselves can shift. The combination of complex interactions, hidden functions and the limited reliability of extrapolation from the effects of observed changes make prediction difficult. Experimentally we might be able to make localized measurements of the effect on x_2 of varying x_1 (see fig. 2.1), but except in a few exceptionally well documented cases, we cannot "see" the underlying phase map. Like the norm of reaction (see above), it is effectively hidden to us in the cases that matter, those that are complex and not amenable to laboratory or experimental manipulation. The effect of a disturbance can be measured only by observing its actual impact, a prohibitive and in some circumstances risky experimental procedure, or by attempts to simulate the response. Thus it is especially important that we examine the consequences of past impacts to try to assess system resilience. And that returns us to history: "All the facets of the problem of stability of ecosystems are pervaded by history" (Margalef 1969:29).[8]

Holling's approach relies on a generally accepted principle of ecosystem studies: systems that have experienced variation, that are spatially heterogeneous, and that are more complex (but lack high degrees of connectedness) are likely to be more resilient. Nonetheless, as Holling puts it, we should expect surprises from ecosystems-qualitative departures from our expectations about causes, system behavior, and the consequences of intervention. We should analyze and plan based on a "presumption of ignorance" (Holling and Goldberg 1981:79) and the "inevitability of uncertainties" (Holling 1978:5). We should minimize risk by focusing on boundaries rather than equilibria. These actions would acknowledge that "what a complex system *is doing* seldom gives any indication of what it *would do* under changed conditions" (Holling 1978:4; emphasis in original). Management objectives consistent with this view would include recommendations such as the following:

> Actions [should be] limited in scope and diverse in nature . . . [C]omplexity is a worthwhile goal in its own right . . . [We should] adopt a more boundary oriented view of the world. (Holling and Goldberg 1981:91)

In the terminology of Botkin and Sobel (1975), it would be better to manage for the recurrence of desirable states than constantly try to force an ecosystem to maintain a particular state.

The methodological specifics of Holling's ecosystem models are beyond the scope of this paper, as are the details of his policy recommendations, especially those related to institutions and development. It is enough to note here that current approaches to policy almost universally adopt an equilibrium view; thus much environmental and developmental policy attempts to suppress temporal variation (e.g., fire control), homogenize spatial heterogeneity (monocrop tree planting), and introduce connectedness (industrial-scale timber harvesting), all of which promote constancy and stability at the expense of variability and resilience. As a consequence, environmental systems become ever more liable to surprise us, unpleasantly.

The concept of adaptive management captures some of the policy implications of a scientific commitment to historical ecology. It is an attempt to formulate development and policy tactics that recognize (1) the importance of ecosystem history, (2) uncertainties in our ability to predict ecosystem behavior, and (3) the desirability of focusing on change and resilience rather than attempting to guarantee stability.

CONCLUSIONS

Historical ecology (historical factor, historical process) is a misnomer, unless we take it to represent an epistemological commitment to the temporal dimension in ecological analysis. This commitment rests in part on the claim that knowledge of the history of natural systems is an indispensable part of their *scientific* analysis. The structural and functional properties of organisms, communities, and ecosystems must be sought in their history because they are only partly revealed in their extant form. It is evident from the history of biology that concepts are an appropriate focus of our endeavor, so long as we are sensitive to the theory and methods that accompany them. It will be a prime challenge of historical ecology to find or to generate concepts that will promote collaborative work among social and natural scientists, especially environmental historians, anthropologists, and geographers.

To succeed in being historical, however, practitioners of ecological analyses must be wary of concepts like succession or ecosystem, which derive from or continue to rely heavily on organismic analogies or cybernetic theory. They trace a record of deep ambivalence about the place of history in ecological analysis. More promising are concepts like patch, persistence, predictability, stability, and resilience, which direct attention to the spatial and temporal dynamics of ecosystems and to the effects of history on their current and future functioning. From a policy and planning perspective, the uncertainties inherent in predicting ecosystem behavior argue for an approach like that of adaptive management.

Notes

1. In practice, however, the scientist may find it expedient to look to the past for information in order to replace current knowledge that is incomplete or not easily supplied by experimentation.

2. The analogy is useful, but it should not be pushed too far. Ecosystems are not individuals (superorganisms), and they do not have adaptive, information-preserving capacity comparable to the genotypes produced by natural selection.

3. These are "the rise and evolution of industrialism and . . . capitalism" (Worster 1984:17), "the frontier" (p. 18), and the "regulation of exploitative behavior" (p. 18).

4. In 1902, a letter published in the journal *Science* complained about an article that had used the word "ecology" without explanation, noting that it was not an entry in the standard dictionaries of the era (McIntosh 1985:354).

5. Humans were seen as elements with qualities foreign to this formulation, as intruders and a source of disturbance: "There is a general consent that primeval nature, as in the uninhabited forest or the untilled plain, presents a settled harmony of interaction among organic groups which is in strong contrast with the many serious maladjustments of plants and animals found in countries occupied by man" (cited in McIntosh 1985:74).

6. Anthropologists will be familiar with an instructive parallel: the breakdown of the typological description of human races with empirical evidence that the different measures of human variation were clinal and to a large degree expressed independently of one another.

7. This has the curious consequence that the highly imbalanced allelic systems contain more information about selection pressures in their remote than their immediate past (because they are relatively insensitive to recent selection pressures), whereas the reverse is true of gene systems with more equal allelic frequencies (they are very sensitive to selection, hence contain information mainly about the immediate past; Lewontin 1967:87). The same cannot be said of the cobble mentioned earlier. This capability for historical acquisition or loss of buffering is a key difference between living and nonliving entities.

8. A particularly interesting example of such an analysis, combining information from the disciplines of marine population biology and archaeology, is Simenstad, Estes, and Kenyon's (1978) demonstration of alternate stable states in the prehistoric Aleut subsistence system.

Bailes, K. 1985. Critical issues in environmental history. In *Environmental History: Critical Issues in Comparative Perspective*. K.E. Bailes. ed. Pp. 1-21. Lanham, MD: University Press of America.

Botkin, D.B., and M.J. Sobel. 1975. Stability in time-varying ecosystems. *American Naturalist* 109: 625-646.

Clements, F.E. 1936. Nature and structure of the climax. Journal of Animal Ecology XXIV: 252-284.

Colwell, R.K. 1974. Predictability, constancy and contingency of periodic phenomena. *Ecology* 55: 1148-1153.

Drury, W.H., and Nisbet, I.C.T. 1973. Succession. *J. Arnold Arboretum Harvard University* 54: 331-368.

Engelberg, J., and L.L. Boyarsky. 1979. The noncybernetic nature of ecosystems. *The American Naturalist* 114: 317-324.

Forbes, S.A. 1925 [1887]. The lake as a microcosm. *Illinois Natural History Survey Bulletin* 15: 537-550.

Golley, F.B. 1984. Historical origins of the ecosystem concept in biology. In *The Ecosystem Concept in Anthropology*. E.F. Moran, ed. Pp. 33-49. Boulder, CO: Westview Press.

Gross, D.R. 1984. Ecosystems and methodological problems in ecological anthropology. In *The Ecosystem Concept in Anthropology*. E.F. Moran, ed. Pp. 253-263. Boulder, CO: Westview Press.

Holling, C.S. 1973. Resilience and stability of ecological Systems. *Annual Review of Ecology and Systematics* 4: 1-23.

Holling, C.S., ed. 1978. *Adaptive Environmental Assessment and Management*. Chichester: John Wiley & Sons.

Holling, C.S. 1986. The resilience of terrestrial ecosystems: local surprise and global change. In *Sustainable development of the Biosphere*. W.C. Clark and R.E. Munn, eds. Pp. 292-317. New Rochelle, NY: Cambridge University Press.

Holling, C.S., and M.A. Goldberg. 1981. Ecology and Planning. In *Contemporary Anthropology: An Anthology*. D.G. Bates and S.H. Lees, eds. Pp. 78-93. New York: Alfred A. Knopf.

Horn, H. 1974. The ecology of secondary succession. *Annual Review of Ecology and Systematics* 5: 25-37.

Hull, David L. 1974. *Philosophy of Biological Science*. Englewood Cliffs, NJ: Prentice-Hall.

Lewontin, R.C. 1966. Is nature probable or capricious. *BioScience* 16: 25-27.

Lewontin, R.C. 1967. The principle of historicity in evolution. In *Mathematical Challenges to the Neo-Darwinian Interpretation of Evolution*. P.S. Moorhead and M.M. Kaplan, eds. Pp. 81-88. Philadelphia: Wistar Institute Press.

Lewontin, R.C. 1969. The meaning of stability. *Brookhaven Symposia in Biology* 22: 13-24.

Lewontin, R.C. 1974. The analysis of variance and the analysis of causes. *American Journal of Human Genetics* 26: 400-411.

Lindeman, R.L. 1942. The trophic-dynamic aspect of ecology. Ecology 23: 399-418.

Margalef, R. 1969. Diversity and stability: A practical proposal and a model of interdependence. *Brookhaven Symposia in Biology* 22: 25-37.

Mayr, E. 1982. *The Growth of Biological Thought: Diversity, Evolution, and Inheritance*. Cambridge, MA: Harvard University Press.

Mayr, E. 1988. Is biology an autonomous science? In *Toward a New Philosophy of Biology: Observations* of an Evolutionist. Cambridge, MA: Harvard University Press.

McIntosh, R P. 1976. Ecology since 1900. In *Issues and Ideas in America*. B.J. Taylor and T.J. White, eds. Pp. 353-372. Norman, OK: University of Oklahoma Press.

McIntosh, R.P. 1985. *The Background of Ecology: Concept and Theory*. Cambridge: Cambridge University Press.

Moran, E.F. 1984. *The Ecosystem Concept in Anthropology*. Boulder, CO: Westview Press.

Odum, E.P. 1964. The New Ecology. *BioScience* 14: 14-16.

Odum, E.P. 1969. The strategy of ecosystem development. *Science* 164: 262-270.

Patten, B.C., and E.P. Odum. 1981. The cybernetic nature of ecosystems. *The American Naturalist* 118: 886-895.

Picket, S.T.A., and P.S. White, eds. 1985. *The Ecology of Natural Disturbance and Patch Dynamics*. Orlando, FL: Academic Press.

Rigler, F.H. 1975. The concept of energy flow and nutrient flow between trophic levels. In *Unifying Concepts in Ecology*. W.H. van Dobben and R.H. Lowe-McConnell, eds. Pp. 15-26. The Hague: Dr. W. Junk B.V., Publ.

Simenstad, C.A., J.A. Estes and K.W. Kenyon. 1978. Aleuts, sea otters, and alternate stable-state communities. *Science* 200: 403-411.

Simpson, G.G. 1970. Uniformitarianism. An inquiry into principle, theory, and method in geohistory and biohistory. In *Essays in Evolution and Genetics in Honor of Theodosius Dobzhansky*. M.K. Hecht and W.C. Steere, eds. Pp. 43-96. New York: Appleton-Century-Crofts.

Southwood, T.R.E. 1977. Habitat, the templet for ecological strategies? *J. Animal Ecology* 46: 337-365.

White, R. 1985. American Environmental History: The Development of a New Historical Field. *Pacific Historical Review* LIV: 297-335.

Wiens, J.A. 1976. Population responses to patchy environments. *Annual Review of Ecology and Systematics* 7: 81-120.

Wiens, J.A. 1985. Vertebrate responses to environmental patchiness in arid and semiarid ecosystems. In *The Ecology of Natural Disturbance and Patch Dynamics*. S.T.A. Picket and P.S. White, eds. Pp. 169-193. Orlando, FL: Academic Press.

Winterhalder, B. 1980. Environmental analysis in human evolution and adaptation research. *Human Ecology* 8: 135-170.

Winterhalder, B. 1983a. History and ecology of the boreal zone in Ontario. In *Boreal Forest Adaptations: The Northern Algonkians*. A. T. Steegmann, Jr., ed. Pp. 9-54. New York: Plenum Press.

Winterhalder, B. 1983b. Boreal foraging strategies. In *Boreal Forest Adaptations: The Northern Algonkians*. A. T. Steegmann, Jr., ed. Pp. 201-241. New York: Plenum Press.

Winterhalder, B. 1984. Reconsidering the ecosystem concept. *Reviews in Anthropology* 12: 301-313.

Winterhalder, B. 1991. Rainfall and temperature patterning and predictability with respect to water management in the central Andes of southern Peru. In *Irrigation at High Altitudes: The Social Organization of Water Control Systems in the Andes*. W. Mitchell and D. Guillet, eds. Society for Latin American Anthropology (in press).

Winterhalder, B., and E.A. Smith. 1991. Evolutionary ecology and the social sciences: An introduction. In *Ecology, Evolution and Human behavior*. E.A. Smith and B. Winterhalder, eds. (ms., 42pp.; volume under contract to Aldine de Gruyter).

Woodwell, G.M., and D.B. Botkin. Metabolism of terrestrial ecosystems by gas exchange techniques: The Brookhaven approach. In *Analysis of Temperate Forest Ecosystems*. D.E. Reichle, ed. Pp. 73-85. New York: Springer-Verlag.

Worster, D. 1984. History as natural history: An essay on theory and method. Pacific Historical Review LIII: 1-19.

Worster, D. 1988a. Appendix: Doing Environmental History. In *The Ends of the Earth: Perspectives on Modern Environmental History*. D. Worster, ed. Pp. 289-307. Cambridge: Cambridge University Press.

Worster, D. 1988b. The vulnerable earth: Toward a planetary history. In *The Ends of the Earth: Perspectives on Modern Environmental History*. D. Worster, ed. Pp. 3-20. Cambridge: Cambridge University Press.

HISTORICAL ECOLOGY

CULTURAL KNOWLEDGE AND CHANGING LANDSCAPES

Edited by

CAROLE L. CRUMLEY

SCHOOL OF AMERICAN RESEARCH PRESS
SANTA FE, NEW MEXICO

1994