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Environmental Analysis in Human Evolution and Adaptation Research

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Human evolution and ecology analyses argue that environment is a major factor influencing biological and sociocultural adaptation, but they rarely analyze environmental properties. Multiple problems of perspective and method can arise from the normative and nondynamic environmental descriptions which pervade these analyses. This paper examines human adaptation frameworks to identify theoretical guidelines for environmental description in ways appropriate to available theories of biocultural evolution or congruent with known ecosystem qualities. Concepts and terminology are given for describing the spatial and temporal properties characteristic of ecosystems and central to hypotheses about ecological adaptation. These include: patchiness and grain; stability and resilience; persistence and recurrence; and predictability, constancy, and contingency. Field experience, theory, and the qualities of ecosystems themselves suggest that detailed, historical (long-term) environmental analysis is necessary to determine the role of ecological factors in human evolution and adaptation.

KEY WORDS: cultural ecology; adaptation; environmental analysis; human evolution; evolutionary ecology.

INTRODUCTION

A search for independent factors which can be incorporated into explanations of the origin, spread, and maintenance of biological, economic, and social adaptations has led a number of anthropologists to the physical and biotic environment of human populations (Anderson, 1973; Baker, 1962; Damas, 1969a; Harris, 1968; Hatch, 1973; Helm, 1962; Netting, 1971; Rappaport, 1971). Cultural ecology (Steward, 1955, 1977; Netting, 1971), cultural materialism

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(Harris, 1968), ecological anthropology (Anderson, 1973; Rappaport, 1971), human ecology, or some other variant (Vayda and McCay, 1975: 294) combine to provide a distinct field in contemporary anthropology. The pluralism of the schools is matched by the vigor of the endeavor, which has engendered extensive fieldwork. The most trenchant criticism of this work is that the ecological approach is merely functionalism recast in an idiom borrowed from biology (Hallpike, 1973; Orans, 1975; Salisbury, 1975; cf. Rappaport, 1977).

This paper considers problems related to the fundamental premise of the ecological approach, namely, that environmental factors provide significant, causative agents affecting human evolution and adaptation that are particularly susceptible to scientific investigation. The influence of such factors is indisputable, though the magnitude of their contribution to the variance observed in certain classes of human behavior is open to question. The problem is that the descriptions which accompany most ecological anthropology analyses are normative descriptions of common sense ecological features; the environment is presented as a static background characterized by averaging statistics. This normative approach conditions views of human adaptation in general and on specific issues in this area of research. More importantly, the way that environments are described in much anthropological writing provides information incompatible with the major theories available for analyzing human evolution and ecological adaptation.

The approach adopted here stems in part from questions posed a number of years ago by Mayr (1976a: 103): i.e., which qualities of environments give rise to certain classes of adaptations – genetic, developmental, demographic, and behavioral – and how can these environmental qualities be described so that they articulate with the theory necessary to account for specific adaptive forms within these classes. A premise of this work is that human evolution and adaptation analysis must be, at a minimum, consonant with the findings of evolutionary biology. Most important is the observation that ecological adaptations result from historical processes in natural ecosystems which have as their most important characteristics temporal variance and spatial heterogeneity. Anthropological studies, with some exceptions (e.g., Burch, 1972; Coe and Flannery, 1964; Schalk, 1977), give little attention to either, or to the historical qualities of natural environments. The present paper argues that it is deviations from static, normative patterns that engender evolutionarily significant events. Adaptations are often fitted to extreme rather than common conditions (Simpson, 1953). This paper argues for the importance of variability and range, as opposed to means, in the analysis of human ecological adaptation and evolution.

Following an historical note on the neglect of environmental description in ecological anthropology, I will outline the kinds of analytic problems that can occur because of the normative viewpoint adopted by anthropologists. I will review biological and anthropological approaches to human ecology analysis. Each is partial, but they overlap and provide an explicit agenda for appropriate environmental information and suggest qualities of its description. I then in-

roduce terminology and concepts for describing spatial heterogeneity and temporal fluctuations. I conclude that ecological analysis will have to become more conceptually and quantitatively rigorous before its analytic limits with respect to anthropological subjects can be determined. Careful environmental analysis is a necessary part of this.

ENVIRONMENTAL ANALYSIS IN ANTHROPOLOGY

Environmental analysis has received little attention in human ecology research. Despite increasing use of biological terminology and concepts (e.g., Rappaport, 1969a) the Stewardian emphasis on culture (1955, 1977) has persisted: "The theory of cultural ecology has less to say about the environment than about culture, and this is its strength" (Murphy, 1977: 22). Even in diachronic analysis "the environment is seen for the most part as stable," or as a "limiting and generally nondynamic factor" (Anderson, 1973: 187, 204). Anderson (1973: 203-207) traces this to several causes, including the functionalist approach which dominates human ecology:

The structural-functionalist approach and its dominant strategy of analysis encourage the treatment of ecology (generally meaning "environment") as a discrete component among other institutional components. Thus most ethnographies or problem-oriented studies begin with a chapter on the physical environment — the gross natural setting of the sociocultural investigation. Since the contents of the chapter are seldom referred to subsequently, we infer that such information is viewed as a backdrop, discretely separated from the primary components of the study.

Similarly, Lee (1976: 95) cites examples of ecological studies of hunter-gatherers which "suffer" from a "short time perspective" with respect to environmental factors. He argues that the hunter-gatherer adaptation is a "long-term one, and the observer can catch only a very short segment of the whole in a year." Citing experience with precipitation variability on the Kalahari desert, Lee states, "When an investigator reports an environment which is without significant regional or temporal variation . . . we may suspect that he has not looked into the matter carefully enough or long enough" (1976: 96; see also Yellen, 1976: 30-33). Yet the human ecology literature contains many reports of just this type.

Statements about the importance of detailed analysis, including attention to such periodic phenomena as droughts, do exist (Netting, 1971: 24).² But

² Nesbitt (1969: 181) draws attention to such environmental factors, but argues that information is often not available to anthropologists because of the locations in which they work. This is valid in some cases, but it is compromised by the observations that (1) pertinent information is sometimes available though difficult to find, and (2) lack of such information has rarely constrained ecological "explanation." Rather, anthropologists have often been content to assume that the "environment" is essentially what they experienced or monitored during fieldwork.

when one looks for quantitative information on spatial heterogeneity, on the range or variance of climatic factors, the densities or biomasses of flora or fauna or fluctuations in these variables, or similar information, the result is meager (Knight, 1974: 352).

PROBLEMS WITH NORMATIVE DESCRIPTIONS

Six kinds of problems can be anticipated in nondynamic evolutionary or adaptation analysis.

1. Normative environmental analysis risks matching observed behaviors (adaptations) to the wrong causes. Adaptations reflect the action of past environments on the genetic and sociocultural information that gives rise to human behavior; extant behavior only partially reflects or is fitted to present circumstances. Not only are environments historical entities with elements or combinations of elements that may always be more or less novel, but adaptation is not a frictionless process. It cannot perfectly match rates of response and qualities of adaptive traits to the rates, combinations, and qualities of events in the environment. It is always more or less behind present circumstances and compromised among competing goals and opportunities. If these constraints or historical ones (Cody, 1974) are great, or environmental change rapid or unpredictable, then adaptations can permanently fail to optimally match prevailing circumstances.

In population genetics it is observed that genotypic change "tracks" the optimum types defined by selective processes at any given point but usually fails to catch or match them (Diamond, 1977: 258-259; Lewontin, 1978: 216). Tracking is explained on the basis of constraints on the rate of potential genetic change directed to particular adaptive goals. These arise from the fact that mutation is independent of adaptive requirements, structural or behavioral preadaptations may not be available, linkage can slow the segregation and spread of loci, selection for rare alleles is very slow, and drift, genome integration, and other factors can operate in opposition to selection. Genotypes and gene frequencies are products of an historical sequence of past events, and only sometimes will they be consistent with present selective influences (Lewontin, 1966, 1967).

Different constraints operate on adaptive processes with respect to culturally informed aspects of behavior. Cultural evolution is sometimes treated as being highly flexible, in contrast to genetic evolution. But the contrast can be overdrawn. Culture, including the parts of cultural behavior that can be termed adaptations, rests on highly integrated and cohesive systems of belief (Geertz, 1973), which can resist rapid alteration of isolated elements or groups of elements. Change requires systematic adjustments of multiple interrelationships of belief, behavior, and goals, all of which require time (Salisbury, 1975: 140, 145).

Historical qualities of environments and genetic and cultural adaptive lag create the problem of mismatching between behavioral observations of an

ethnographic year and the environmental events of that year. Observed behaviors may not be adjustments to the present because contemporary circumstances are to some extent novel, or they may be results of events which occur only periodically and not during fieldwork. Neither possibility can be identified without historical treatment of environmental variance. This matching problem is significant because the qualitative nature of much cultural ecology, and its dependence on functional explanation, greatly reduce the possibility of identifying adaptive behaviors incorrectly associated with ecological causes.

2. It is also probable that part of the dynamism of human adaptive processes will be missed with a normative approach. In one respect this is a sample problem (Colson, 1976: 269): the ethnographic sample of environment-adaptation relationships is projected onto an indefinite past by way of an environmental constancy assumption. If an environment is dynamic in ways not perceived by the anthropologist, such a procedure will always underestimate the population's adaptive flexibility and repertory (Salisbury, 1975: 139-141).

Historical and archaeological work can also be prone to this difficulty. If some recoverable element of social life or technology does not change, it is sometimes assumed that adaptations were static. But the reliable information in this formula is the stability of the observed artifact. If it is related to ecological processes, e.g., a hunting tool, considerable adaptation may occur to preserve its constancy in the face of environmental perturbations. Since many adaptations are behavioral, and leave little direct evidence in historical or archaeological records, such dynamism is not easily assayed.

3. The assumption that environments are stable, or that change is either very gradual or abruptly cataclysmic, leads to the converse of problem 2: the failure to examine environmental sources of causation when rapid changes are recorded in historical or archaeological records. For instance, if an artifact assemblage changes rapidly it is often taken as a self-evident argument for migration, diffusion, or some other displacement of local cultural processes by cultural means. This need not be the case. Rapid and noncatastrophic changes are possible and perhaps not rare in ecosystems, and the recorded artifact change may represent a rapid adaptation of the indigenous population.

An excellent example is provided by Simenstad *et al.* (1978) in an analysis of the relationship between faunal components in a prehistoric Aleut midden and differing ecological communities in the same locale. Simenstad *et al.* (1978: 403) note that past interpretations of Aleut paleoecological evidence were based on an assumption that the resource base was stable and uniform. These studies invoked cultural explanations for changes in prey harvested over the 2500-year occupation. In contrast, Simenstad *et al.* provide extensive ecological and archaeological information which indicates that changes in harvests were caused by ecological transitions between local, alternative stable-state faunal communities. These transitions altered the assemblage of prey species available to the Aleut; they were probably initiated by over-harvest of a key component in the ecological community, the sea otter. These authors follow Sutherland (1974)

in arguing that explanation of this kind of environmental process often is found through examination of specific historical events. Environments are variable on multiple time scales. This, and the possibility of alternative stable states, makes it risky to eliminate *a priori* ecological explanations for certain types or rates of change in human communities.

4. Analysis based on the view that environments can be characterized typologically tends to match abstract environmental features with generalized features of the human sociocultural system. It proceeds by classification rather than by the study of process, and predominantly by qualitative rather than quantitative evidence. In this descriptive approach correlations produce the explanations for certain kinds of behavior. Although useful for initial study and organization, this procedure reveals little about the basic processes that link environment and human populations, and which produce adaptive change. It provides little guidance on what properties or features of environment the anthropologist should expect to find correlated with human sociocultural behavior.

5. A major impetus behind the formulation and expansion of cultural ecology has been the desire to free anthropology of the historical relativism of the early part of this century (Harris, 1968). This has left a continuing ambiguity about the relationship between history and the analysis of ecological adaptation and evolutionary change. The ambiguity runs through human ecology as a repeated tendency to view ecological adaptation as an ahistorical process (in non-Western societies) and its analysis as a nonhistorical science. Although it varies by author, cultural ecology is conceived as scientific study illuminating the regularities which articulate an adapted population with a stable environmental background, whereas historical analysis concerns itself with the less lawful and predictable residue of factors and events influencing (perhaps "disturbing") the adaptations of a particular group.³

The separation of history from ecology is often taken to be a legitimate distinction which characterizes the success of human ecology analysis. This is evident in the statement of Hatch (1973: 223-224) that cultural ecology arose from "the desire to root institutions in a substratum of forces or processes that are immune to the vicissitudes of history." Referring to Steward's concept of "historical reconstruction," Helms (1978: 180) states: "This perspective, though essential to concern with process and change, is neglected by many contemporary ethnologists who persist in subscribing at least in practice to the misguided contrast of science versus history."

Evolutionary and ecological studies belie this dichotomy (Sauer, 1977: 324-335). The science of evolutionary ecology is historical analysis with special features (Jacob, 1977: 1161). The presence of predetermined mechanisms (e.g.,

³Temporal aspects of the achievement of this stable adaptation are referred to a brief period in the indefinite past, prior to analysis. If historical factors are included as more recent causes of change they are usually those stemming directly or indirectly from colonial activities. Thus the ecology-history dichotomy is also expressed on the dimension of traditional-nontraditional (Western or Western-influenced) societies.

principles of Mendelian genetics for diploid organisms) does not obviate the historical nature of the context and parameters (e.g., population size and fluctuations, intensity and duration of selective influences, and so forth) necessary to complete an evolutionary explanation of adaptation (Lewontin, 1978: 218). To the extent that these and other necessary components are assembled to provide the temporal dimensions of evolutionary change, its analysis is a partially historical subject. Similarly, recent ecological analysis of species, communities, and ecosystems directs attention to the importance of temporal and spatial variability, and to the actual sequences of partially unpredictable or unique events, internal or external, in producing the structure and dynamics of these entities.

The history-ecology dichotomy is tenable only if environment is seen as static. In contrast, a more appropriate analysis enjoins cultural ecology and the vicissitudes of history through recognition that (1) environmental factors are partly historical, and (2) the ecologically and evolutionarily significant properties of those factors are also partly historical.

6. Adaptation, as Williams (1966) and Lewontin (1979) have pointed out, is an easily misused concept, particularly if applied in qualitative analysis of normatively idealized systems. Like functionalism, it can be invoked to explain almost any observation or set of alternative observations (cf. Mazess, 1975: 9), creating the impression that every social group is a "success story" (Colson, 1976: 264). Yet such critiques present anthropology with an uneasy situation. Adaptation presumably is the process creating much of what we would like to explain. But handling the concept operationally, using it to create reliable and logically satisfying analyses of the action it portrays, is difficult. The biologist has the full advantage of neo-Darwinism, which provides a specific framework and determines the parameters within which adaptation arguments are to be constructed. The parameters (e.g., mutation rates, variance available for selection) are important because they constrain certain hypothetical possibilities.

While the mechanisms and parameters of biocultural evolution are not well understood (cf. Durham, 1976; Thomas *et al.*, 1979) and hence offer less guidance, many of anthropology's difficulties in this respect are evident and avoidable. They arise because little attention is given to quantification of spatial diversity and temporal variance. The overly facile use of adaptation stems from treating evolution as a product of frictionless interactions, deterministic causes, and well behaved variables set against a static environmental background. In contrast, a first-order constraint on adaptation arguments lies in the recognition that evolutionary interactions contain thresholds and structural impediments, that causes are stochastic and unpredictable to some degree, and that variables need not be well behaved. With recognition of temporal variance and spatial heterogeneity adaptation becomes a much more contingent and constrained phenomenon. Adaptive analyses should be tied down to the physical limitations of events, rates, magnitudes, and distances of real environments. Hutchinson (1975: 511) identifies the importance of this type of question to evolutionary ecology with admirable brevity: "How big is it and how fast does it happen?"

Although they have other causes as well, each of these six kinds of problems rests on a view which assumes environmental stasis. This view conditions attitudes toward analysis and toward the origins and nature of adaptive behaviors in anthropologically studied peoples. It reinforces the notion that non-Western cultures are unchanging, and also produces analysis which by methodology alone is guaranteed to support the original assumption (Anderson, 1973: 203-207). That assumption is incorrect and both attitudes and methods must be reexamined. In Lewontin's words: "We cannot go out and describe the world in any old way we please and then sit back and demand that an explanatory and predictive theory be built on that description" (1974: 8).

THEORETICAL GUIDELINES FOR ENVIRONMENTAL ANALYSIS

Identifying the properties and features of environments most important in analysis requires three kinds of information: (1) biological qualities of the ecosystems taken to be the ecological environment of human populations; (2) the ecological requirements of prominent theoretical approaches to adaptation; and (3) analytic experience using certain approaches in conjunction with particular ways of handling environmental variability and heterogeneity. Of these (2) is discussed immediately below, and (1) throughout the remainder of the paper; (3) of course is contingent on future research.

The approaches considered here are: (1) the Slobodkin and Rapoport model of interactive adaptive responses, (2) social ethology, (3) hazards research, (4) evolutionary ecology, and (5) general evolutionary (population) biology. With the exception of the last mentioned – which illuminates several formal points about the responses of adaptive systems to environmental fluctuations – these are major methods used in adaptation studies, human and nonhuman. They are diverse, and for biocultural analysis each is incomplete. However, among them there is much overlap and agreement on what constitutes an analytically sufficient environmental description.

The Slobodkin and Rapoport Model of Interactive Adaptive Responses

Slobodkin and Rapoport (1974) analyze the process of adaptive responses to environmental events using game theory, with the special condition that persistence is the only appropriate evolutionary goal. Good adaptations in this view are those that allow the organism to minimize its chance of extinction when responding appropriately to an environmental perturbation (stress). The authors postulate a set of response mechanisms – behavioral, physiological, physiological acclimatization, demographic, and differential reproduction or survival affecting the population gene pool (see also Bateson, 1963; Slobodkin,

1968) – and outline hypothesized relationships among these and qualities of the eliciting environment. They argue that evolution should produce a matching of the time constants (rates) of the different response mechanisms to the frequency and duration of the stress, and an appropriate match of the resource commitments entailed in the response to the magnitude (or strain) of the perturbation. Such matching diminishes the organism's stakes in an environmental perturbation by amelioration of the stress and by reducing the investment of time, energy, structure, or other components of fitness necessary to do so. Resources, or adaptive capabilities, are thus preserved for future needs.

While the general scheme is biologically reasonable, its "precise operational implication . . . is not as simple or as obvious" (Slobodkin and Rapoport, 1974: 196). Particularly, it is unclear how different responses interact with respect to function, cost, effectiveness, initiability, and other, presumably linked, qualities. Slobodkin and Rapoport (1974: 196-199) hypothesize that the responses are variously and flexibly linked, with interactions structured by a principle of parsimony imposed by requirements of evolutionary effectiveness and efficiency. Deciding among these possibilities, and application of the model itself, however, requires careful and quantified measurement of the relevant parameters and variables.

The evolution and operation of this set of adaptive responses is contingent on the properties of eliciting environmental features: initiation rate, magnitude, duration, frequency, regularity, and others. Since response to one kind of event likely affects susceptibility, or the ability to respond, to other kinds, such information is necessary with respect to diverse features of the significant environment (Slobodkin and Rapoport, 1974: 193). The parameters mentioned all involved the study of variable historical aspects of ecosystems. A sufficient description contains information on periodicity, since "if each of two identical populations is confronted with environments which are identical in average properties but different in periodicity of fluctuations, they should develop different adaptations" (Slobodkin and Rapoport, 1974: 198). The frequency and regularity of recurring environmental perturbations are significant as well, especially for determining what kinds of environmental events select for learning abilities as an adaptive response. According to Slobodkin and Rapoport:

Learning is meaningful and valuable in responding to events which are reasonably irregular in their occurrence, so that strict genetic programming is impossible, but which recur with sufficient frequency that a lesson learned in early life can be put to use in later life. (1974: 192)

Novel events, those for which behavioral, physiological, or acclimatic responses are insufficient, perhaps because of magnitude, or those with very long durations or periodicities, should extend their effects to the other levels of response, eventually producing genetic change.

This model has the advantage of grounding the study of adaptation in a systematic, predictive theory. It structures hypotheses about the adaptive

responses expected in different environmental circumstances, and demands the use of quantitative data. These and other features make this model attractive to anthropologists (Vayda and McCay, 1975). Greenwood (1974) has suggested that it can assist understanding of peasant responses to their ecological and political-institutional environment, while Thomas (1973; see also Winterhalder and Thomas, 1978) applied it to analysis of human adaptation to chronic energy shortages in the high Andes.

Social Ethology

Social ethology, as defined by Crook (1970a, 1970b; Crook *et al.*, 1976), is distinguished by four characteristics: (1) social structure is viewed as a dynamic expression of interacting social and ecological factors with broad and flexible expression; (2) adaptation is seen as a complex product of immediate behavioral flexibility, changing social traditions, and genetic change; (3) individual adjustment to social environment is taken to be as important as that to external ecological factors; and (4) the source of behaviors (e.g., genetic, learned, etc.) is deemphasized in favor of analysis of the processes of social organization themselves. Social ethology is thus distinct from classical ethology with its focus on dyadic relationships expressed as species-specific behaviors, motivational analysis, and developmental studies of restricted behaviors.

The framework and methods of social ethology have been considerably developed, based on a rich accumulation of hypotheses and field observations. Primates, social carnivores, and cursorial ungulates have received special attention. Successive reviews by Crook and Gartlan (1966), Crook (1970a, 1970b), Denham (1971), Eisenberg *et al.* (1972), Kleiman and Eisenberg (1973), Clutton-Brock (1974), Crook *et al.* (1976), and Clutton-Brock and Harvey (1977) have traced this development.

The progress of social ethology studies has shown that a correlative approach using generalized features of habitat and social structure is inadequate:

Recent studies illustrate (i) the number and subtlety of the factors which need to be considered in fieldwork if advances in theory are to be made, (ii) the complex nature of the interaction between such factors and their variability between species and populations of the same species, (iii) the refined nature of the effects of ecological contrasts on social behaviour and (iv) the fact that, rather than simple correlations of traits, we are now comparing systems. (Crook *et al.*, 1976: 271-272)

Socioecological hypotheses have matched increasingly sophisticated information on social behavior on nonhuman animals only when detailed data on the microhabitat accompany analysis (Clutton-Brock, 1974; Clutton-Brock and Harvey, 1977: 4; Eisenberg *et al.*, 1972: 873). The kind of analysis performed has proven as important as its detail. Variables representing resource density

and distribution, fluctuations and predictability, regularity, and other properties have supplanted simpler habitat categories such as “savanna” or “woodland” (Clutton-Brock, 1974: 539-540; Crook *et al.*, 1976: 266).

Similarly, long-term study has proved important in isolating ecological sources of causation. The great variability of social structure within a species has focused attention on the history of local populations and their particular adjustments to microhabitat conditions, along with idiosyncratic aspects of their social traditions (Eisenberg *et al.*, 1972: 873). The attention given to rates of social change links social ethology to the temporal focus of the Slobodkin and Rapoport model: “Historical change in a social structure consists of several laminated and interacting processes with different rates of operation” (Crook, 1970b: 198).

Hazards Research

Vayda and McCay (1975) advocate a hazards research approach to the study of human ecology, emphasizing its similarity to Darwinian selection theory and its attention to the effectiveness of adjustments (which they feel necessary to offset misplaced attention to energy-flow and energy-efficiency adaptive criteria; cf. Smith, 1979). The authors include in their definition of hazards events with diverse sources (e.g., geology and religion), and they follow Burton and Hewitt (1974: 254) in suggesting that it is the properties of hazards, their “magnitude, extent, frequency, and other ‘hazard characteristics,’” that must be analyzed in the study of human adaptation. Barton (1969: 47), who is also cited by Vayda and McCay, bases a somewhat different typology of stress characteristics “on factors important to the response of the system to stress, rather than on those relating to its cause.” In its attention to environmental properties relative to adaptive responses the hazards research approach parallels that adopted by Slobodkin and Rapoport (1974).

Hazards research generally focuses on fairly rare or extreme events, which produces some drawbacks. Rarity means that fieldworkers are unlikely to encounter hazard events directly. High visibility can lead researchers to overlook low-level but frequent environmental stresses (Merton, 1969: xxv), which can be more important in shaping adaptive responses (Fig. 1C). Focus on extreme geophysical or biotic events may result in the exclusion of chronic hazards (Burton and Hewitt, 1974: 260; Barton, 1969: 53), and while a great deal can be learned about human reactions to such events, the contribution of catastrophic occurrences to evolution or adaptation may be quite small (Burton and Hewitt, 1974: 259, 266; Slobodkin, 1968: 200). There is an important distinction between disasters, which may have a relatively nonspecific (and hence nonselective) effect on the range of phenotypes, and extreme events, which affect or select

against specific phenotypes. Only the latter generate directional selection.⁴ Disaster events or extreme stress situations cannot be taken as simple magnifications (“natural experiments”) for analyzing the effects of selection less easily observable at lower intensities (cf. Brady and Laughlin, 1978: 289). Adaptive processes, including the biocultural, contain their own limitations; they are not sensitive to all degrees of perturbation in a linear fashion, nor to all kinds of perturbations. More precise statements will require experience with the kind of historical and dynamic analysis suggested here.

Evolutionary Ecology

Evolutionary ecology is based on the assumption that natural selection produces structures and behaviors which optimize components of an organism's fitness (Cody, 1974). Operationally it relies on the observation that simple graphic and mathematical models are often appropriate for generating hypotheses about expected adaptive results (Levins, 1966). Predator avoidance, reproductive behavior, and foraging are the components of fitness usually considered. In optimal foraging theory, for instance, spatial and temporal distributions of potential resources are taken to be independent variables in models that attempt to predict diet breadth, use of patchy habitats, foraging pathways, individual or group foraging, or exclusive use of foraging space (Krebs and Cowie, 1976; Pyke *et al.*, 1977; Schoener, 1971). Predictions rely on the assumption that organisms have evolved behaviors that maximize the net rate of energy intake while foraging (Smith, 1979).

Evolutionary ecology, and in particular optimal foraging theory, produces heuristic models incorporating environmental variables couched in terms of spatial pattern, temporal fluctuation, and quantity. Demonstration of some degree of environmental repeatability is basic (MacArthur, 1972: 59), while more specific data on such factors as density, dispersion or aggregation of prey types, movement of prey, the size and number of habitat patches, and the energetic values of different resources, is necessary to set the parameters and establish the variables of particular models. Moreover, the “types of environmental characteristics” to be examined and quantified must be reduced to analytically appropriate and operational expressions of the basic time and space dimensions (Southwood, 1977: 337, *passim*).

The degree to which environmental features depart from regular patterning over longer time periods is significant for the analysis of adaptive optimization.

⁴In a formal genetic analysis Haldane (1966: 174-179) has demonstrated that intense selection may inhibit the evolution of adaptive traits that would evolve with similar but more moderate selection pressures: “a change in the intensity of selection may reverse the relative fitness of two types” (1966: 179). Under certain conditions “*intense competition favours variable response to the environment rather than high average response*” (pp. 177-178, *Italics in original*), thwarting or reversing directional selection for an adaptive adjustment. Haldane (1966: 117-118) specifically relates his mathematical analysis to the effects that disasters would have on the evolution of natural populations.

Long-term observations are necessary to test predictions of the models (by observing adaptation alterations as independent variables change), and also to evaluate expectations that optimal or ideal behaviors are evolutionarily feasible. That short-term evaluation of ecological hypotheses can be unreliable has been established by Wiens (1977) in a summary of 10 years of evolutionary ecology study of resource use and competition in temperate grassland bird communities. Wiens' work shows that short-term adaptation studies predicated on assumptions of equilibrium, optimization, and homeostasis may confirm hypotheses that would be modified or even invalidated with longer term study and attention to environmental variability.

This approach has the advantage of producing specific, alternative hypotheses in such a way that both environmental properties and predicted behaviors can be operationally defined. Although developed in the idiom of Neo-Darwinism and genetic adaptation, many of the models can be applied to adaptive behavior in a broader, sociocultural sense (Pyke *et al.*, 1977: 138; Winterhalder, 1979b). Few anthropological applications are yet available, although Dyson-Hudson and Smith (1978) have adopted this perspective in an analysis of ethnographic evidence on territoriality, and a series of foraging studies using and evaluating the approach has been completed (Winterhalder, 1977; Winterhalder and Smith, in preparation).

Evolutionary (Population) Biology

The theory of population genetics (Cavalli-Sforza and Bodmer, 1971; Johnson, 1976; Lewontin, 1974; Wallace, 1968) relates to the present argument by way of a phenomenon Lewontin (1966) calls the "historicity" of adaptive responses to fluctuating environments.

Most long-term evolutionary change is thought to result from directional selection, that is, selection against one end of the distribution of a genetically conditioned phenotype influencing relative fitness. Figure 1 illustrates how the frequency distribution of environmental states interacts with the selective effects of those states to produce different distributions and intensities of selective action, and different effects on a population. Comparison of the four examples demonstrates that average environmental properties provide little (or misleading) information about selective processes. In these circumstances it is essential to focus environmental description on variability and the events which occur toward the end of the distribution of environmental states. If selection occurs at the limits of a distribution, then mean environmental variables will be insensitive measures of evolutionarily significant events. Additionally, observation of mean phenotypic changes over time provides only limited information about the causes of change, which operate elsewhere.

Historicity of adaptive response is expressed in two ways. First, the extent to which organisms incorporate a memory of past environments into their adaptive capabilities influences the degree to which they will experience recurring environmental factors as either probable or capricious (Lewontin, 1966, 1967).

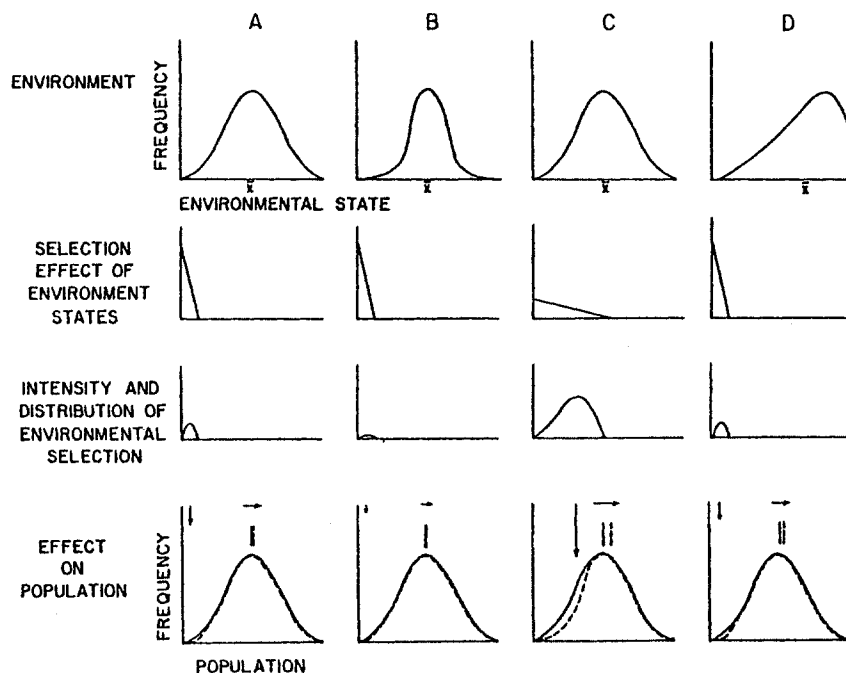


Fig. 1. Selection intensity and distribution as a product of the frequency of environmental states and their effects. A comparison of A with D shows that the relative intensity and distribution of environmental selection, and its effects on a population, depend on the frequency distribution of environmental states with different selective effects. Comparison of A with B demonstrates different selection outcomes for environments with the same average characteristics. Comparison of A and B with C shows that environmental states with low selection effects can produce significant selection intensities and population effects if they are sufficiently frequent. Comparison of A with D makes it apparent that mean environment can change with little or no effect on the magnitude and distribution of selection effects. Correct interpretation of the figure requires awareness that selection is probabilistic (see Mayr, 1976b: 36-37).

Because all organisms are limited in their ability to sample, integrate, and store such information, they will experience fluctuations with periods beyond their memory as novel. Adaptive capabilities will be constrained by the repeated novelty of the environmental factor. The adaptability of an organism is thus contingent on rates of its alternative adaptive responses and the extent and duration of the environmental memory contained in those responses, relative to rates and other properties of environmental fluctuations.

Second, the concept of historicity emphasizes that adaptations represent a response to an exact sequence of environments, and that a pathway of adaptive change need not bear any straightforward relationship to normative qualities (mean or variance) of the relevant habitat (Lewontin, 1966: 26-27, 1967, 1974:

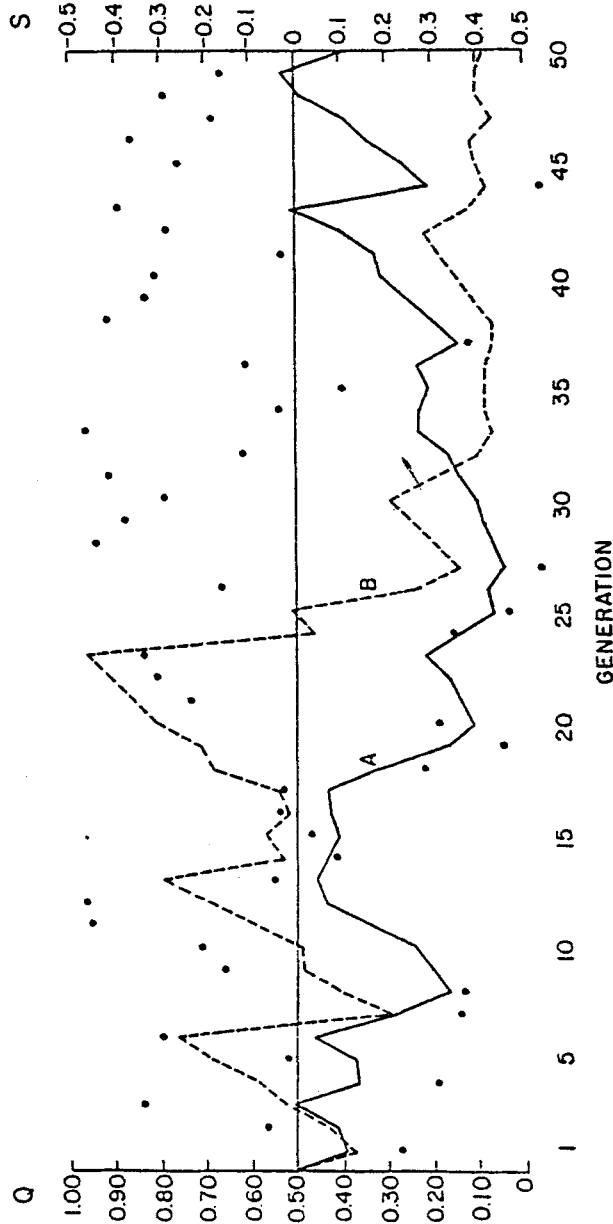


Fig. 2. Cross-generational history of gene frequencies (Q) in a randomly fluctuating environment (S). Dots give the environmental value (S), which varies randomly between -0.5 and $+0.5$. Positive environmental states select against one homozygote; negative states against the other; additivity is assumed. The solid line (A) shows the gene frequency changes caused by the sequence of environments shown. The dashed line (B) shows the gene frequencies which result from the same set of environments taken in reverse order. The average environmental state ($S = -0.07$) is the same for both curves; the average gene frequency represented by the solid line is 0.29 ; for the dashed line the average gene frequency is 0.37 . The graphs were obtained from a programmable calculator (Hewlett-Packard 25) using a pseudorandom number generator and the formula given in Lewontin (1967: 84). Based on Lewontin (1966, 1967).

270-271). This is illustrated for a simple genetic system in Fig. 2. Two points deserve emphasis: (1) the sensitivity of adaptive responses to particular environmental events depends on preexisting adaptations, in this case allele frequencies. Thus for population A, positive selective events in generations 18-20 and 24-27 produce a low allele frequency by generation 27. Even though selection values are predominantly in the other direction (negative) for the last 23 generations, this gene frequency recovers very slowly because rare alleles have a low sensitivity to selection. Thus gene frequencies can represent a set of environmental events in the distant past more than they do those of the more recent past. In contrast, an allele intermediate in frequency will reflect recent but not more distant past environmental selection. (2) Comparison of population A with population B (subjected to the same environments in reverse order) shows that the actual pathway of a population's adaptive history, as well as its mean response to a fluctuating environment, is dependent on the actual order of environmental events. Thus, "the historical accident of the order in which the environments occur necessarily changes the long-time life history of a population" (Lewontin, 1967: 86; see also Johnson, 1976: 134-135).

Despite the limitations of reliability, scope, or operational effectiveness, these adaptive approaches are in some respects systematically related. A significant example of interdependence concerns identification of constraints.

In the choice and application of evolutionary ecology models these are the factors assumed to be constant and which therefore can be ignored, or "written out" in the model's structure. In optimal foraging, for example, the models often assume a constant predator morphology, constant energy requirements, and so forth, in order to investigate a behavioral response – changing diet breadth – to changing prey abundances. However, every feature of an organism may be a product of and be affected by selection, and rarely has the historical precedence or structural or functional priority of adaptive features been established. This makes the decision to treat some features as constraints (constants) and others as variables by no means straightforward (Crook *et al.*, 1976: 265-266; Krebs and Cowie, 1976: 98; Lewontin, 1976; Pyke *et al.*, 1977: 138; Sahlins, 1976: 82-83). Crook *et al.* (1976) adopt an intuitive procedure based on their assessment of resistance to change: more resistant features become the constraints for more flexible ones. Morphology and neural features are cited, and a prominent place is given to constraints imposed by infant maturation rates (p. 267). Crook *et al.* point out, however, that "the causal relation between such traits (as to which may necessitate or facilitate the other) has rarely been resolved in thorough investigations" (1976: 266).

This question – which traits are labile and which conservative over the time span of the investigation? (and the related question: what is an appropriate time span?) – is fundamental to all five frameworks mentioned. Adaptation is a compromise among interrelated sets of behavioral and physiological functions, and study of a part of the system must assume fixity in the remainder. In social

ethology this is the question of which variables are dependent and which independent (Crook *et al.*, 1976: 266); in Slobodkin and Rapoport (1974: 197) it has to do with hierarchies; in evolutionary ecology it has to do with the choice of constraints built into models (Pyke *et al.*, 1977: 138). In addition to being fundamental, investigation of this question requires historical study of the lability and effectiveness of different types of adaptive adjustments relative to measured properties of dynamic environmental factors.

Although each of these frameworks has been presented as a distinct methodology, in practice they overlap and two or more are often used together by human ecologists. What emerges from them is a common theoretical attention to the dynamic, historical properties of adapting systems, and the corollary necessity of measuring and including in analysis environmental properties such as ranges, magnitudes, distributions, rates, and duration. The remainder of this paper provides some concepts and terminology for this kind of description.

SPATIAL HETEROGENEITY

All environments are characterized by an uneven distribution of the factors and processes that affect the adaptive success of organisms. Since complete and detailed data on such features are unwieldy and rarely provide theoretically useful information, parameters (variables or concepts) are required which summarize and reduce large amounts of data in ways that (a) preserve properties of the information relevant to the theory being used and (b) retain as much relevant information in the summary as possible. Analysis requires descriptions that recognize uniqueness while remaining sufficiently general that they can be used comparatively in different habitats.

Patchiness

Cox *et al.* (1973) discuss terminologies for large spatial scale (region, biome, habitat, etc.); the present material will focus on smaller scale "patches." The concept of patchiness derives from the observation that the environmental factors affecting the immediate behaviors and long-term evolutionary fitness of organisms are distributed discontinuously in space and time (Wiens, 1976). Multiple, overlapping scales of spatial heterogeneity are possible (Smith, 1972: 323). Consequently, Wiens defines a patch as an area "distinguished by discontinuities in environmental character states from [its] surroundings" (1976: 83); Levin and Paine (1974: 2744) as "a 'hole,' a bounded connected discontinuity in an homogeneous reference background." The flexibility of these definitions is intentional. Relevant boundary conditions are those with adaptive significance to the organism considered, or those which for some other reason are appropriate

for a particular analysis. Patchiness is "*organism defined*" (Wiens, 1976: 83, italics in original) and must be determined relative to the size, mobility, habits, and perceptive capabilities of the population studied. For most species two scales are primary: foraging range and migratory range (Southwood, 1977: 343). For humans, exchange can introduce a third scale determined by the extended interactions of trade (Wobst, 1978).⁵ Further, patchiness significant for one functional aspect of an organism's behavior or physiology may be different from that for another: that relevant to foraging may be of a quite different quality and scale than that relevant to microclimatic adaptation.

A related concept is grain, or the "grain response" (Wiens, 1976: 84). Grain can be "coarse," "fine," or some intermediate designation, where these terms are defined relative to (a) the relationship between the mobility of an organism and the scale of its significant habitat, or (b) the different ways that organisms utilize the spatial heterogeneity of their environment. The first of these assess grain relative to a fairly constant quality of the organism – its locomotor capacities – the second by patterns of the organism's movement relative to the environmental mosaic. In either case, a coarse-grained environment is one in which the organism uses portions of the habitat mosaic disproportionately (it specializes on certain patch-types), while a fine-grained response means that the organism encounters and uses patches in the actual proportion in which they occur. As with patchiness, grain is function-specific.

Wiens (1976: 85) has stated the relationship between patchiness and grain:

The concept of grain is best interpreted as a behavioral response to an environmental mosaic. Organisms may thus be characterized as coarse- or fine-grained only in reference to utilization of the resources associated with a particular life-history function, and categorization of species as fine-grained or coarse-grained without specifying the context is inappropriate. If "grain" refers to the nature of a behavioral response or utilization pattern, "patch" applies to the physical environments or resource units upon which the grain response is expressed.

Patchiness as such has not been quantified, though it is possible to identify its components. Overall patchiness is a function of the number of patches (or if classification is appropriate, the number of patch types) and the magnitude of the relative distinctions among them. It is also important to include a factor representing evenness of size and quality differences. Thus, "environments with

⁵Relevant scale for both time and space is important. Organisms are evolutionarily sensitive to and affected by factors expressed within limited ranges of possible time and space scales. The temporal range is determined by generation-span and adaptive memory; the spatial range by mobility and by distances associated with foraging, migration, and, in the case of humans, trade. The sensitive ranges are thus determined by the existing adaptations of the organism, but that does not mean that it is at some optimum defined by scaled features influencing fitness. Environmental fluctuations, adaptive lag, and the opportunism of evolution (Mayr, 1976b: 40) make such congruence unlikely. As the organism adapts to scaled features within the sensitive range, it shifts the margins of the range, creating new selective pressures and adaptive opportunities.

patches of grossly differing sizes . . . have a small 'effective number' of patches relative to an environment with patches of equal size" (Wiens, 1976: 85). Although patchiness is not in itself a parameter subject to quantified measurement, the environmental factors characterizing patches can and should be evaluated. These include the size and size distribution of each patch type, the relative differences in patch types with respect to the adaptive function studied, distances between patches, the distribution of patches, patch-type dynamics (e.g., succession), and so forth.

Harpending and Davis (1977) have developed a second way of characterizing heterogeneity, and a model relating their description to a series of predictions about hunter-gatherer subsistence behavior. The specific hypotheses concern group size, location, range and territoriality, and mobility. These are related to resource distributions (scatter and abundance) along linear transects by a procedure which uses combinations of sine waves to approximate a function representing the density (caloric value) of the resource (Harpending and Davis, 1977: 276-278). The predictions of this model are sensitive to variance in resource distributions, and to the phase relationships in the density of different resources, along with mean densities. It thus relates adaptive features of interest to operational and measurable variables describing environmental heterogeneity.

Landscape

Environmental qualities which define patchiness for terrestrial organisms can be termed landscape (Rowe, 1969), and include landform (geomorphology and geological parent materials), soils, vegetation and vegetation physiognomy, and micro- or local climate (animals are treated separately because of their mobility). Features of landscape combine with animal distributions to give a locality a particular adaptive quality related both to the resources and hazards found there, and to the impediments that landscape structure places between the organism, its resources, and its predators and conspecifics.

Geomorphology and soils represent stable elements of landscape, with obvious exceptions for floodplains and areas subject to volcanic disturbance, which may be highly differentiated.

Plants are the primary producers in ecosystems, fixed in location for most of their life-cycle, and are thus a relatively stable environmental factor influencing the dispersion and behavior of herbivores directly and that of carnivores indirectly. Vegetation provides an obvious landscape element for establishing patchiness.

For much of this century ecology followed the plant ecologist W. F. Clements, who suggested that vegetation communities progress through stages (succession) to a stable, geographically extensive climax determined by very slowly changing soils, geomorphology, and climate. Succession was seen as an "embryonic" development of a persistent "superorganism" – the climax – in

a model with a closed and deterministic character (Drury and Nisbet, 1973: 333). In recent years concepts of succession and climax have changed greatly (Wright and Heinselman, 1973). Ecosystems are now known to be mosaics of successional stages, a "blurred successional patchwork" (Horn, 1974: 30), with localized successional sequences initiated repeatedly by disturbances that are more or less unpredictable, frequent, and often endemic. A climax community is reached for local areas, but rarely over extensive geographic regions and rarely for long. Equilibrium is still an important concept, but the moving mosaic, or "gap phase" (see Wiens, 1976: 82), is now the focus of equilibrium studies. A balance between extinctions, recolonization, and succession may preserve a dynamic equilibrium of vegetational heterogeneity (Wright and Heinselman, 1973: 322), but the random qualities of these processes can also mean that "short circuits may prevent local patches from ever achieving equilibrium" (Levin and Paine, 1974: 2744). Wiens (1976: 85-90) has reviewed causes of spatial heterogeneity of vegetation.

The recognition that spatial heterogeneity of vegetation, aside from that resulting from geomorphology, soils, drainage, climate, or other physical factors, is the "natural" state of ecosystems again raises the importance of relative scale and its measurement. From a localized viewpoint the disturbance-succession cycle is one of abrupt followed by slower change in multiple elements of habitat, including productivity and species composition, but larger geographic regions may approach a dynamic equilibrium. Indeed, larger-scale (geographic) disturbances may be prevented by local instability (Wright and Heinselman, 1973). Whether it is localized instability or a geographic balance among the patches of a "moving mosaic" that affects human adaptation will depend on the exact scale of environmental events relative to human activities. The fact that ecosystem studies are now recognized as having an historical element (Wright and Heinselman, 1973: 320) has similar implications for the study of organisms adapting to them.

Mobile organisms may be spaced in three ways: randomly dispersed, clumped or aggregated, or regularly or uniformly spaced (see Brown and Orians, 1970: 239). All of these spacing patterns can be determined and expressed on a cardinal scale (Wiens, 1976: 83). Any of the three patterns can result from social factors, from the organisms' response to habitat patterns (including resources, predators, shelter, or physical hazards), or from both. Dispersion is described with respect to specified units (e.g., individuals may aggregate into family units, families themselves may be regularly spaced).

Dispersion refers to location at a particular point in time. Dispersal, which refers to movement patterns, requires separate terminology. Home range ("the area in which an animal normally lives, exclusive of migrations, emigrations or unusual erratic wanderings") and territory (an exclusive range roughly fixed over time, and defended by behaviors which successfully deter conspecifics from use),

Table I. Classification of Climatic Phenomena by Spatial Scale^a

Designation	Horizontal distribution	Vertical distribution	Example	Lifetime of corresponding meteorological phenomena
Microclimate	10^2 - 10^3 m	10^2 - 10^1 m	Greenhouse climate	10^1 - 10^1 sec
Local climate	10^2 - 10^4 m	10^1 - 10^3 m	Thermal belt on slope	10^1 - 10^4 sec
Mesoclimate	10^3 - 2×10^5 m	10^0 - 6×10^3 m	Basin climate	10^4 - 10^5 sec
Macroclimate	2×10^5 - 5×10^7 m	10^0 - 10^5 m	Climate zone Monsoon region	10^5 - 10^6 sec

^aAfter Yoshino (1975: 3, Table 1.1).

are the two dispersal terms most commonly in use (Brown and Orians, 1970: 240-242). Again these patterns can pertain to different social units.

The mobility and transient distribution pattern of many animal species make their dispersion a poor basis for patchiness descriptions. Dispersion may be strongly affected by landscape patchiness, however, so that various species are probabilistically associated with, for instance, the vegetation mosaic. Along with environmental factors, it is important to know how the study population is dispersed, since the distribution of an organism can itself create certain dispersion patterns in the habitat it experiences.

The climatic features relevant to human evolution and ecological adaptation are also expressed on multiple spatial scales, some of which are quite small (Table I). Yoshino (1975) has provided an extensive and detailed discussion of micro- and local climatology, emphasizing differentiation on these scales; Landsberg (1969) can be consulted for a set of worldwide climatic descriptions on meso- and macroscales.

The influence of spatial heterogeneity on evolutionary ecology processes has not received a great deal of attention (Levin and Paine, 1974: 2744). Many ecological models of interacting populations are "point models" with either no spatial dimensions or the assumption that space is homogeneous or else fully characterized by average qualities (Smith, 1972: 311). The competitive exclusion principle is an example (Winterhalder, 1979a). Yet studies of model ecosystems have shown that spatial heterogeneity is instrumental in producing stability and diversity in interacting populations which are normally destabilized by the temporal variability they experience (May, 1974; Smith, 1972). Further, a variety of subtle spatial conditions have a graded effectiveness in this respect (May, 1974: 34-44), suggesting that the phenomenon is pervasive. The kinds of

spatial heterogeneity which create diversity and stability in population interactions are expressed in the relationship of an organism to environment, and can be formed by the organism itself, by the environment, or by both (Roff, 1974a, 1974b).⁶

TEMPORAL VARIABILITY

Although I have separated description of spatial from temporal environmental properties, the distinction is less apparent to an organism. Spatial and temporal changes commingle, although this does not make them interchangeable with respect to their evolutionary results or analytic conceptualization. Moving from one habitat to another of a later successional stage has the same functional result as remaining in the first location while succession creates the change, but the alternatives have very different qualities with respect to locomotion costs, rate at which the change is effected, and other factors. And they require different kinds of description and analysis. There are general obstacles to treating space and time dimensions simultaneously (Orians, 1975: 140).

History in Natural Ecosystems

Natural ecosystems should be approached as historical entities. This is demonstrated by long-term studies which indicate nonrecurrent temporal changes, as well as by theoretical aspects of ecosystems which highlight the importance of historical analysis. With the development of reliable stratigraphic techniques using pollen (palynology) and macrofossils from vegetation, in addition to a variety of techniques for analyzing climate change, the extent and importance of temporal variability in climate and vegetation has become apparent. The boreal forest of Canada and the Great Lakes region, for instance, is characterized by unabated change in composition and structure since deglaciation approximately 11,000 years ago, due to interacting and partially random processes with differing time scales – the development of raw soils, changes in drainage due to geological and biotic causes, the differing lifespans and abilities of plants to migrate, colonize, and compete, climatic changes, and changes in the frequency

⁶More specifically, spatial heterogeneity has been shown to affect predator-prey relationships (Orians, 1975: 144-145); interspecific competition and the stability of competitive relationships (Smith, 1972); the genetic heterozygosity of a population (Levins, 1968); ecosystem stability and diversity (Smith, 1972: 324-327); population persistence and size (Roff, 1974a, 1974b); and foraging strategies (Charnov, 1976; Charnov *et al.*, 1976; Krebs and Cowie, 1976; MacArthur and Pianka, 1966; Pyke *et al.*, 1977; Schoener, 1971; Winterhalder, 1979b, 1979c). Orians (1971) and Southwood (1977) present a general discussion of these relationships; Wiens (1976) has provided an extensive review indicating the breadth of population and ecological processes influenced by spatial heterogeneity.

of disturbances such as fire (Davis, 1969; Heinselman, 1973; Rowe, 1966; Terasmae, 1973; Winterhalder, 1979d). Similar results can be demonstrated for a variety of terrestrial and aquatic ecosystems (e.g., Simenstad *et al.*, 1978; summaries in Botkin and Sobel, 1975; Holling, 1973).

Theory also points to the historical treatment of ecological processes. The supposition that the history of an ecological system is unimportant to its present configuration implicitly assumes (1) only one stable, i.e., a “globally stable” (Lewontin 1969: 16), configuration exists for the system; (2) the system is at that configuration; and (3) the route by which it got there is a dispensable portion of analysis. The first of these assumptions is questionable on ecological grounds – multiple stable points can characterize ecological systems (Holling, 1973; May, 1977; Sutherland, 1974). The second assumption has to be taken on faith, since historical analysis is necessary to demonstrate that the present relationships are globally stable, or indeed stable at all. Demonstration of local or short-term stability provides no information on global stability (Lewontin, 1969: 17). Finally, the analysis of ecological systems at globally or local stable points cannot provide information on how they undergo transformations (Lewontin, 1969: 23): it cannot tell how such systems evolve, or how they will respond to perturbations. Much of what ecological anthropologists would like to discover – how human ecological systems reach or depart from stable configurations, for instance – is lost or severely constrained if analysis dispenses with the study of historical routes of adjustment.

Temporal Scales

As indicated earlier, the investigator must identify scales of temporal variability appropriate for particular analyses. Biologists use generation time, a convenient and conceptually suitable measure of temporal events relative to the rates of genetic evolution (Slobodkin and Rapoport, 1974: 195; Southwood, 1977: 340). It is not clear if a corresponding unit exists for biocultural evolution, one with structural delimitations which can be integrated with generation time to produce an appropriate parameter. The choice of scale or scales then is dependent on the experience of the researcher with the behavior of the people studied.

Within the appropriate range particular scales can be identified by the temporal properties of relevant environmental features, using theoretical guidelines and conceptual recognition of environmental dynamics.⁷ In anthropological research attention has focused on seasonal variability, in part because it corresponds to the observation period of the “ethnographic year.” Less obvious

⁷Pyke *et al.* (1977) give examples for foraging behavior studies.

scales of temporal variation may, however, have an important and perhaps greater impact on certain adaptations:

Many environments, especially those in continental arid or semiarid regions or areas with high production concentrated into a short growing season (e.g. Arctic Tundra) are subject to both cyclic and erratic (unpredictable) climatic fluctuations that are large and occur over long time intervals. . . . These variations may be extreme and have major effects upon primary production and upon the resources available to consumers. The effects upon the evolution of and variation in resource-utilization traits may be profound (Wiens, 1977:592; see also Lee, 1976: 80-81).

A variety of terms and concepts has been suggested for summarizing temporal properties of varying environments, in response to the observations that significant ecosystem properties are historical.⁸

Stability and Resilience

Stability concepts in biology traditionally came from physics, and emphasize constancy and quantitative description of the frequency and amplitude of oscillations in some measure. Holling (1973) suggests that this equilibrium-centered view is unsuited to ecology, where qualitative results are important and equilibrium is of less concern than conditions for persistence:

An equilibrium centered view is essentially static and provides little insight into the transient behavior of systems that are not near the equilibrium. Natural, undisturbed systems are likely to be continually in a transient state; they will be equally so under the influence of man. (1973: 2)

Holling's reformulation begins with the "domain of attraction" (1973: 2-6), an idea based on the observation that state variables of a system can be perturbed and fluctuate within certain ranges, and yet may return by more or less regular oscillations to an equilibrium. If, however, the perturbation causes the variables to fluctuate beyond the domain of attraction the system shifts into another domain, or perhaps goes to extinction (Fig. 3). This kind of behavior can be predicted from stability theory, and it is evident in well documented field examples (Holling, 1973: 6-17). The observation that ecological systems have multiple stable states among their elements (Simenstad *et al.*, 1978; Sutherland, 1974) is equivalent to saying that they have more than one (local) domain of attraction for certain combinations of elements. In these cases, behavior of variables displaced from equilibrium, near the boundary, becomes difficult to predict and nonlinear with respect to disturbance magnitudes (May, 1977).

⁸ Climatologists have developed a terminology for describing temporal changes of climate on different scales (see World Meteorological Organization, Commission for Climatology, 1966). Terasmae (1975) gives a more accessible but less detailed description of these terms.

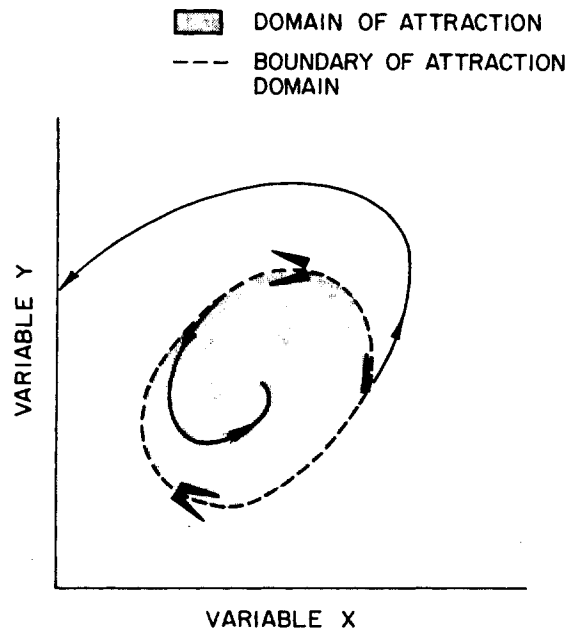


Fig. 3. Domain of attraction stability concept for a system of two variables. A perturbation shifting the variables to a point within the boundary of the attraction domain is followed by a cyclic return to equilibrium. However, a perturbation which moves the variables outside the domain of attraction results in unstable behavior and eventual "extinction" of one or the other variable. A system may have more than one domain of attraction. After Holling (1973: 4; see also Orians, 1975: 142).

Based on this model, Holling defines two properties to describe fluctuations in state variables (1973: 17). *Stability* refers to the "ability of a system to return to an equilibrium state after a temporary disturbance"; the less the fluctuation and the more rapid the return, the more stable the system. Stability assesses the degree of fluctuation about an equilibrium. *Resilience*, on the other hand "determines the persistence of relationships within a system"; it measures the ability of a system to absorb perturbations and yet maintain defined relationships among variables. A system that can absorb large disturbances and yet maintain these relationships, that is, not shift domains of attraction or go to extinction, is resilient. Stability refers to fluctuations from equilibrium; resilience to the size and form of the domain of attraction and the chance that disturbance will induce fluctuations that escape that domain.

Refinements or elaborations on stability and resilience are numerous. Loucks (1970: 19) has distinguished between short-term (e.g., successional) and

long-term (evolutionary) assessment periods for stability. Margalef (1969: 30) refers to two kinds of stability: persistence and adjustment stability, although he is pessimistic (pp. 25, 28) about the possibility of unambiguous definition or quantified measurement of these properties. Following Margalef's definitions, Sutherland (1974: 860) states that adjustment stability is the more general case, but that persistence is more commonly and easily measured. Stability is not equivalent to constancy; it is a dynamic concept. Perturbations and random factors can affect the system, imparting flux, yet if it remains close to some point and the flux has a statistical description related to the perturbations, it is properly termed stable (Lewontin, 1979: 21). Orians (1975: 141-143) identifies six meanings associated with stability (constancy, persistence, inertia, elasticity, amplitude, cyclic stability, and trajectory stability), but notes that these do not make up a unitary classification because they are neither independent nor fully comparable.⁹

Following Holling's (1973) terminology and ecological arguments, Vayda and McCay (1975: 298-299) have advocated replacing equilibrium-centered analyses in anthropology with studies focused on resilience. While the shift to a dynamic perspective is crucial, little will be gained if one vague concept (resilience) replaces another (stability). This concern arises because Vayda and McCay equate resilience with homeostasis, a term with a history of intuitive and indefinite uses in ecological anthropology.¹⁰ Precise use of these terms becomes manageable and they are more likely to articulate with theory when applied to specific properties or processes.

Generalities about the relationship between stability and other ecosystem properties are not yet reliable. Community studies indicate complex degrees and qualities of stability in ecosystems, and particularly that the much repeated and anthropologically popular notion that ecological complexity begets stability should be discarded or heavily qualified (Orians, 1975; Margalef, 1975; May,

⁹ Some order can be drawn through this information by noting that Holling's use of stability refers to short-term, adjustment stability, and in agreement with Lewontin (1969) he intends that the concept not imply constancy. Persistence stability (Margalef, 1969) is similar to resilience, as is Orians' "inertia" (Orians, 1975: 141) and May's (1975: 163) use of "dynamically robust" and "dynamically fragile" to characterize the extent to which model ecosystem parameters can fluctuate and the system remain viable in a certain configuration. However, as with stability, resilience is not a precise or easily measurable concept (May, 1975: 165).

¹⁰ There are reasons to keep these terms distinct. Homeostasis is an adaptive property of an organism; it can be analyzed as the product of natural selection acting on individuals. The temperature-regulating mechanism of mammals is an example. Resilience, however, is an emergent property of communities of co-adapting organisms and populations. It is not a product of natural selection at the level at which it is expressed, i.e., resilience is not an adaptation of communities of organisms, though it can be said to characterize them. Additionally, homeostasis connotes steady state, and negative feedback maintaining variables at a "set point." Resilience, in contrast, may, but need not, pertain to systems characterized by steady states in the absence of disturbance, or to systems having a "set point" for opposite variables. Cyclic stability (Orians, 1975: 143) systems can be resilient with no implication of an equilibrium set point. The lynx-hare cycle is an example (Holling, 1973).

1975). May (1975) postulates that communities in relatively constant physical environments will have populations co-evolved to a condition of dynamic fragility, whereas those in more rigorously fluctuating environments will co-evolve toward dynamic robustness. If true, this means that the ability of an ecosystem to absorb perturbations without change is directly related to the historical likelihood and degree of perturbation. This makes it difficult simply to observe ecosystems and tell which are the more robust or resilient, or more likely to persist (May, 1975: 164; Sutherland, 1974: 860).¹¹ In effect, “all the facets of the problem of stability of ecosystems are pervaded by history” (Margalef, 1969: 29).

Persistence and Recurrence

Botkin and Sobel (1975) have developed terms describing temporal variability which do not rely on an equilibrium assumption. They define equilibrium-centered stability as “static” stability, and provide evidence that long-term patterns of change in at least some ecosystems do not conform to the expectations of static stability. In particular, ecosystem histories do not always show recurrent convergence toward a particular state following disturbance.

Instead, these authors consider systems that are “‘naturally’ dynamic or time varying” (1975: 629). The function $x(t)$ describes some structural or functional ecosystem state of interest (e.g., species composition or productivity) at time t . All conceivable states of the system are denoted by S , which represents a set of real numbers; the initial state is denoted by $x_0 = x(0)$. States of the system for $t \geq 0$, $[x(t), t \geq 0]$, are termed its posterity. *Persistence* is characteristic of a posterity if its states remain within certain bounds about a specified value. Formally, “a posterity is θ -persistent about the point x' if $|x' - x(t)| \leq \theta$ for all $t \geq 0$ ” (Botkin and Sobel, 1975: 629; italics in orig.). The time interval is not necessarily infinite. Persistence depends both on the point about which the boundaries are constructed (x') and on their breadth θ . The breadth can be more or less *stringent*. Persistence characterizes magnitude of fluctuations without the assumption that an equilibrium state exists for the system.

Recurrence refers to repetition, and implies that some posterity comes arbitrarily close to a past state. Specifically, the “state x' is recurrent if for every $\delta > 0$ and $\tau > 0$ there is a $t \geq \tau$ such that $|x(t) - x'| \leq \delta$ ” (Botkin and Sobel, 1975: 631, italics in orig.). In this definition δ defines the arbitrary closeness that will be accepted as a repetition, and τ the minimum limit of the time period that will be considered. A state which does not recur is termed *transient*. The set of all states, the posterity, is made up either of recurrent or transient states; a

¹¹ Using similar reasoning, there is no direct basis for inferring, as do many anthropologists, that “complex, broad niches [or human adaptations] are intrinsically stable and more likely to prove successful than simple, specialized niches” (Hardesty, 1972: 465).

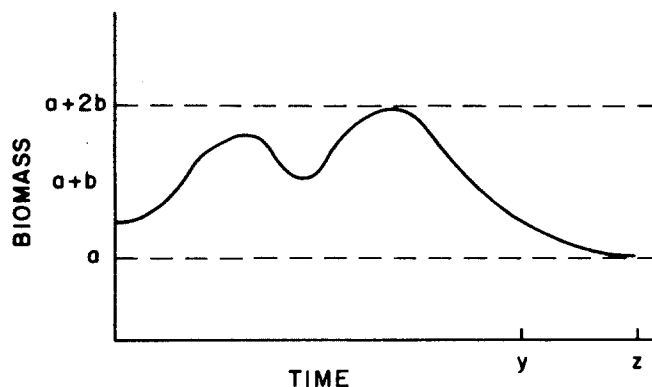


Fig. 4. θ persistence of a population represented by biomass. For this posterity (time interval 0 to z) the biomass is θ -persistent about x' if and only if $\theta \geq \max [x' - a, a + 2b - x']$. The value $2b$, or $2b$ relative to $(a + b)$, indicates the stringency of the neighborhood. For the posterity shown all states are recurrent up to time y , and transient for the interval y to z . After Botkin and Sobel (1975: 630).

posterity is defined as recurrent if all states are recurrent. These relationships are shown graphically in Fig. 4.

Predictability, Constancy, and Contingency

Colwell (1974) has defined three terms that summarize temporal fluctuations in periodic phenomena. His definitions are meant to clarify the often contradictory and vague use of words such as uniformity, regularity, and predictability. The major parameter is predictability, which is itself made up of two components, constancy and contingency. These terms have a critical advantage over others mentioned so far: they are amenable to precise and simple quantitative evaluation using information theory, and the properties they represent can be assessed statistically.

An environmental pattern is first characterized by time intervals of interest (e.g., seasons) within some longer period (e.g., a year), and second by two or more states (e.g., fruiting or nonfruiting of a tree). If the same seasonal pattern of the states is repeated for all periods considered, the phenomenon is maximally predictable. Knowledge of the season determines with complete confidence the state of the phenomenon (Colwell, 1974: 1148). Conversely, if any state is equally likely in any season, predictability is at a minimum.

Constancy is maximal if the state (e.g., fruiting) remains the same for all time intervals (seasons) in all periods observed (years); it is minimal when the state fluctuates within time intervals to the maximum extent possible. Thus, for

two seasons (A and B) and two states (fruiting and nonfruiting) constancy is maximal if the trees either fruit or do not fruit in both seasons for all periods observed. It would be minimal if the tree were always in fruit in one season and not in the other.

This latter case represents complete contingency: the state is different for each season but the pattern is the same for all periods. Conversely, if states are independent of seasons contingency is minimal. Constancy measures uniformity of states over time; contingency measures regularity of seasonally differentiated patterns over time (Colwell, 1974: 1152-1153).

While these terms provide explicit and quantitative evaluation of periodic environmental factors, in themselves they indicate nothing about the adaptive or evolutionary sensitivity of an organism to particular degrees of unpredictability; this must be established through knowledge of the organism. Additionally, similar degrees of predictability can have quite different evolutionary implications depending on whether they arise from constancy or contingency (Colwell, 1974: 1148).

This sequence of concepts – stability and resilience, persistence and recurrence, and predictability, constancy, and contingency – reflects a change from terms emphasizing constancy and equilibrium to those which depict and are able to describe ecosystems as temporally dynamic. They also reflect increasing attention to specificity and quantifiability. When applying these terms it is important to present overlapping characterizations of the factors that simultaneously affect an organism. In the case of a forager, for instance, regional synchrony of prey population fluctuations will affect the likelihood of adapting by migration; interspecific synchrony will affect the likelihood of adapting by shifting locally among alternative prey species. Further, even predictably fluctuating factors, if they have different periods or are out of phase, can give an environment an historical quality with respect to a population adapting to it.

CONCLUSIONS

Typological thinking remains commonplace in anthropology (Martin, 1974) and permeates descriptions of the environments to which humans adapt. This paper has argued that normative description using spatial and temporal averages of environmental factors destroys the information necessary to analyze human adaptations. I have presented terms and concepts for analyzing spatial heterogeneity and temporal variability in ways more appropriate to theory and more consistent with ecosystem qualities.

Environmental description must be suited to theory and adjusted to the spatial and temporal scales apposite to the organism (population) and function being studied. This aspect of “effective” environment (Netting, 1971: 9) generates special requirements for anthropological description. Human evolution is characterized by two factors which play only a limited role in nonhuman species

— exchange and cultural methods of storing and sharing information. These must be considered along with generation-time and foraging and migration ranges in setting spatial and temporal scales for biocultural investigation. How this is to be done has been addressed more by archaeologists than other anthropologists (cf. Wobst, 1978). It is a reasonable assumption that the seasonal cycle and the ethnographer's "home range" are on the lower ends, respectively, of the temporal and spatial scales which should be considered. The historical properties of ecological and evolutionary as well as human sociocultural processes (Colson, 1976: 269-270) are one reason that some of the most compelling analyses of human ecological adaptation come from ethnohistorians with ecological interests (e.g., Bishop, 1974; Ray, 1974; Rogers and Black, 1976; Salisbury, 1975).

The terms or concepts presented here become analytically meaningful when used as sufficient parameters in the context of theories and hypotheses, and when assessed by real situations. They should not be substituted for theory (Rigler, 1975: 15) or confused with established facts (Erich and Holm, 1962: 653). They are not, in some cases, mutually exclusive, nor do they provide a cohesive and complete description of environmental properties when taken together. Despite these drawbacks the terms underlie a perspective which is necessary to articulate human ecology analysis with its theoretical base, and with the qualities of actual environments. And, even with these restrictions, they generate an abundant set of relatively uninvestigated hypotheses about human evolution and ecological adaptation.

This paper has considered only a subset of possible influences on human behavior. It is not incongruous with the strict attention given here to ecological factors to suggest that the approach advocated would both improve the reliability of ecological explanation in anthropology *and* at the same time restrict its dominion. Ecological-functional arguments can be and are constructed with great facility; they prevail in much anthropological analysis. Detailed ecological writing bound to the dynamics and histories of real ecological systems, and constrained by the quantified parameters of evolutionary and adaptive processes, will probably limit some of the speculative hypotheses that have been advanced and accepted. In a critical review of ecological anthropology analysis, Salisbury (1975: 128, 144-145) argues that "a large number of cultural behaviours observed at any one time in a particular society are *not* aimed at adapting the population to the current physical environment."

Progress in human ecology research is more likely to come from intensive, ecologically sound analyses of the factors which can be shown to contribute to the variance observed in human adaptations than from the continued proliferation of cases which use functional arguments to claim that material, ecological factors provide preminent explanations of human behavior.

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