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REPORTS

EFFECTS OF ECOLOGICAL AND PALEOECOLOGICAL PATTERNS ON SUBSISTENCE AND PALEOENVIRONMENTAL RECONSTRUCTIONS

Frances B. King and Russell W. Graham

Spatial and temporal variations in human populations are, to a large extent, determined by the environmentally controlled distribution of biotic and abiotic resources. While archaeologists generally recognize this relationship, many fail to fully appreciate the complexity of either the changing environment, the ecological literature, or applications of ecological data to archaeological problems. It is important to apply modern ecological principles to archaeological problems, but the novelty of the principle should not preclude the nature of the problem to be solved. For example, the concepts of ecotone and edge effect are still applicable to archaeological problems concerning biotic boundaries such as those between forest and grassland even though it may be more appropriate to use an individualistic approach in research designs concerned with diffuse environmental and biotic gradients.

Archaeology is presently evolving to show a more interdisciplinary approach by its researchers, an attitude which is reflected in greater consideration of the physical environment and increasing interaction with the work of allied scientists such as geologists and paleoecologists. It is increasingly accepted that human populations form a living ecosystem, tied to their environment and responding to the same types of external regulatory mechanisms as other organisms, though in part adapting to environmental change by cultural evolution (Ford 1977). The problems inherent in successfully integrating and synthesizing multidisciplinary data into an interdisciplinary product have been discussed by Butzer (1975), while Rhoades (1978) issued a much needed warning about the dangers of oversimplifying ecological concepts when applying them to archaeological situations. In this paper we discuss the development of these concepts and attempt to clarify their present status and to evaluate their pertinence to archaeological problems. Our viewpoint is that of paleoecologists who frequently work with archaeologists on problems of mutual interest, and as such it may offer some new ideas to the archaeologist himself working with such data.

One of the goals of ecology is to ascertain the causes of distribution and abundance of organisms. This field concerns itself not only with single organisms, but with populations, with biotic communities of numerous species, and with ecosystems which include both the biotic community and its abiotic environment. If it is difficult to study an organism without taking into account its biotic and physical environment, it is nearly impossible to study a community without first knowing something about the organisms of which it is comprised. Archaeology is tied closely to the study of communities and ecosystems since it deals with sequences of social and cultural evolution under diverse environments.

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COMMUNITY

The term "community" is as fundamental to discussions of groups of closely interacting plants and animals as it is to discussions of groups of people living together in small social units within larger ones. The idea of the plant community as such a basic unit was recognized as early as the 1700s, although the concept of biotic (plants and animals) communities was not employed until the beginning of the twentieth century (Clements and Shelford 1939). By then, the significance of the biotic community had been fully recognized, more or less independently, by a number of researchers (Clements 1905, 1916; Shelford 1913; Vestal 1913, 1914). The term "biome," referring to a group of related biotic communities, was first introduced as the basic concept in climax and succession by Clements in 1916.

There are numerous working definitions for the biotic community in modern ecological literature (e.g., Curtis 1959; Krebs 1972; Odum 1959; Oosting 1956; Shelford 1963; Whittaker 1970), but they all can be categorized as being either an organismic (classification) or an individualistic (gradient analysis) definition. Both definitions have supporters, and it is critical for readers attempting to understand and apply the ecological literature of a region to realize the background and biases of the ecologists who have worked in that area.

The organismic school, which began with Clements (1905, 1916), contends that communities are like organisms, with both structure and function. In this sense, communities have discrete boundaries, and those with similar environments and histories will be composed of similar diagnostic species. In this scheme, the biome is the basic community unit, comprising discrete entities into which it can be subdivided.

The individualistic viewpoint emphasizes the species rather than the community and was advanced by Gleason (1926) as an alternative hypothesis to the biome. Study of the principle was subsequently expanded by such ecologists as Curtis (1955, 1959), McIntosh (1967), Terborgh (1971), Whittaker (1951, 1953, 1956, 1967, 1970), and Whittaker and Niering (1965). The basis of this principle is that communities are not integrated units with discrete boundaries but are collections of populations requiring similar environmental conditions. Because the ecological requirements of the individual species differ, sharp boundaries between "communities" do not exist.

Available data tends to support the individualistic concept of the community as more closely reflecting the actual situation. Communities are not discrete units but grade continuously in time and space. However, the concept of community can still be used within the context of the individualistic system. Just as the spectrum of colors can be discerned in the continuum of the wave length of light, so can communities be recognized in the environmental gradient continuum (Whittaker 1970). In both the neontological (Pielou 1969) and the paleontological record (Valentine 1966, 1973; Webb and Bryson 1972; Kay 1979), communities can be identified along an environmental gradient by statistical (e.g., factor analysis) segregation of dominant species. The plant and animal life of any large area is so complex that it must be separated into subdivisions if they are to be studied, described, or compared with similar stands in other habitats. Thus, the community remains an important tool for the study and comparison of segments of the gradient, as well as a useful concept for anyone attempting to map plant or animal distributions.

Even researchers who strongly support the continuum approach sometimes feel that it is advantageous to consider vegetation from the classification perspective when major communities are being discussed or compared (Whittaker 1970:51). Such major communities (i.e., biomes) are generally characterized not merely by dominant species but by distinct growth forms and other adaptations to diverse environments as well. While it may be impossible to point to a sharp transition between two adjacent types of deciduous forest for example, because trees are similar in size and growth form, the transition between vegetation types exhibiting two entirely different growth forms (e.g., deciduous forest and prairie) is often more readily apparent.

General appearance, or physiognomy, is a useful method of delineating communities (R. Smith 1966:22). Since animal distributions are often more closely related to the structure of vegetation than to species composition (e.g., MacArthur and MacArthur 1961), classification by physiognomy will also relate both the plants and animals of an area. In areas where habitats (backwater lakes, sand dunes, bluffs) are well defined, physiography can be used as well.

To subdivide a physiognomically similar area, finer subdivisions are frequently based on species composition, a system which works much better with plants alone than with animals or with both (R. Smith 1966:23) since communities defined on the basis of plant composition have little relationship to animal distributions. Therefore, the smaller the communities into which the vegetation of an area is divided, the more poorly the animals are represented.

If a community complex is being subdivided along a continuum, it is still divided into units on the basis of species composition. These units are then correlated with an arbitrarily divided environmental gradient, for example: wet, wet mesic, mesic, dry mesic, and dry. Frequently the ecologists who work in areas where there are sharp natural boundaries between vegetation types perceive vegetation from a classification viewpoint, while those who work with closely related communities see them oriented along a gradient.

ECOTONE

The concept and use of the term "ecotone" is more controversial than even that of the community. The term is primarily associated with the classification system. C. H. Merriam (1890) was one of the first to acknowledge the concept of ecotone by his use of "transition life zones" in his seminal study of the life zones of the San Francisco Mountains, Arizona. However, the term "ecotone" was first used by Clements (1904:153) when he defined it as a habitat stress line. Later, following the earlier work by Livingston (1903), Clements suggested that "the limiting line or ecotone of a . . . province is a composite obtained from the limits of principal species and checked by the limits of species typical of the contiguous vegetations" (Clements 1905:304; Curtis 1959:15).

Several important points made in the original definition must be emphasized. First, the original definition of ecotone was concerned strictly with plant communities and did not consider faunal distributions. This distinction was followed by most later workers. In Clement's original statements (1904, 1905), the ecotone was recognized as a boundary between two contiguous vegetational aggregations. The area of the ecotone was composed of a composite of species from the two aggregations and was defined by the distributional limits of the principal (dominant) species. Later, Clements (1916:139-140) expanded on his concept of the ecotone (or tension zone) and unfortunately applied the concept to all levels of floral organization. It is this broad application by Clements that has led to the confusion surrounding the term "ecotone" in later studies.

In addition, some more recent ecologists (Margalef 1968:40) have used ecotone as a boundary between ecosystems (an ecosystem includes both biotic and abiotic interactions, e.g., shore between marine and terrestrial ecosystems). In this sense, the concept of ecotone not only incorporates an organic component (flora and fauna), but it also includes all of the inorganic environmental parameters incorporated into the ecosystem as it was originally defined by Tansley (1935:299). Other ecologists (e.g., Shelford 1963:16) have employed "ecotone" as a boundary between even larger communities such as biomes. In this sense, the ecotone may cover a broad geographical area and constitute a transitional community within itself (e.g., subarctic forest).

Kendeigh (1961:30) carried the ecotone concept back to Clement's (1916) idea by defining it as a transition between any plant aggregations irrespective of their size or scale. Thus, Kendeigh recognized ecotones between biomes as well as between successional stages that occur as a result of environmental change or disturbance. In this sense, the ecotone is a temporal transition as well as a spatial one and is, therefore, of even more potential interest to the archaeologist.

It was stated above that in some situations there are relatively sharp boundaries between vegetation types while in others there are not and that the organismic and individualistic concepts of the community were developed by ecologists who were to some degree influenced by the communities with which they were working. The concept of ecotones developed out of the organismic school and, like the organismic concept of the community, it applies best to situations where there are sharply defined boundaries. In areas where there is a gradual transition between vegetation types, forming a gradient, the concept of the ecotone breaks down. In such situations, an ecotone

can not be easily delineated and neither can a point location (e.g., archaeological site) be readily described in reference to it, necessitating generalized statements of the type: "within the broad ecotone" rather than "15 km from the ecotone."

The most conspicuous and important ecotone in North America is probably that between the eastern deciduous forest and the prairie. The ecotone between these two adjacent communities stretches from Canada to Mexico and the relationship between them was well described by Curtis (1959:302) as follows:

Grass dominated plant communities can exist on a large scale only within a particular climatic regime, one that is characterized largely by an excess of evaporation over available rainfall. Within the area with this climate, soils and topography are of minor importance. Towards the humid border conditions tolerable to both grasslands and forests may exist. In this ecotonal region, certain soils and certain topography may favor one over the other. On the majority of sites, presence or absence of prairie was probably determined by fire. In still more humid regions to the east, grasslands can occur only on special topographically dry sites—regardless of fire.

It is such boundaries that are most sensitive to environmental change, not the interiors of the plant communities. With a little more moisture trees can become established in exposed situations where they did not previously grow; with a little less, the trees that are already there fail to reproduce and are replaced by prairie plants. Paleocologists seek out such boundaries, knowing that along them will be found the records of plant and animal migrations reflecting the varying climates of the past. A classic study of the history of the forest-prairie border is that of J. H. McAndrews (1966) who discusses the east-west movements of the border across a transect in north-central Minnesota over the last several thousand years based on pollen records. The same type of time transgressive phenomena is seen by J. King (1981) in the development of the prairie in Illinois and by Kay (1979) in the development of the forest-tundra transition zone of the Northwest Territories of Canada.

Indian settlement patterns sometimes also reflect the forest-prairie border. For example, Hickerson (1965) showed that the historic Chippewa in Minnesota and Wisconsin lived in the forest to the north of the boundary, while the Sioux lived in the prairies to the south and that a buffer zone existed between the two. Although this buffer zone existed for cultural reasons, it also corresponded to the forest-prairie ecotone, which was the zone of greatest plant diversity and, incidentally, the one which provided the best deer habitat as well. When tensions between the two tribes were high and the buffer zone was enforced, there were many deer available on the peripheries of the zone to individuals who would risk entering the proscribed area. When the tribes tolerated one another and both hunted within the zone, the deer herds would be depleted to the detriment of all.

The prairie-forest border does not always act as a cultural boundary between groups, however, and shifts in aboriginal subsistence activities in response to environmental changes are recorded in many archaeological sites situated in the transition zone. One example is that of Rodgers Shelter, a deeply stratified site on the western border of the Missouri Ozarks. At this site, the archaeological record indicates a shift in hunting emphasis from deer to small game and grassland species during the effectively drier mid-Holocene (Hypsithermal) when prairie species invaded the area (J. King and Allen 1977; Klippel et al. 1978; McMillan 1976:228).

While food resources may be most diverse along such an ecotone, there is at the same time less stability, since fruit and nut crops frequently fail because of drought or other stress. It is in some ways, therefore, more dangerous to live here than in the interior of the forest where resources are more dependable if somewhat less diverse. The Indians of such an ecotonal region would be expected to have been relatively more flexible in resources exploited, scheduling, and settlement patterns. If a group customarily gathered together in the fall to collect nuts and hunt deer from a large base camp, that might occasionally be out of the question if the nut crop was poor and the deer scanty.

EDGE EFFECT

The term "edge effect" is defined as the tendency for increased variety and density at community junctions (Odum 1959:278). It should be noted that this is merely a tendency, not a universal phenomenon. As communities become more distinct and the boundaries between them sharpen, the amount of environmental change that exists over a relatively short geographical distance increases as do potential diversity and density. The greatest increase in diversity and density probably occurs when one type of vegetation has a sharp contact with another as a result of disturbance (fire, logging, etc.). Along such a boundary, the environment has been made artificially suitable for the plants of the second community although basic physical factors, such as soil and gross climate, remain suitable for the first. One of the most important types of such an ecotone is the forest edge.

Ultimate growth of plants (including species density, size, absolute density) is always controlled by some limiting factor, e.g., soil nutrients, moisture, sunlight, heat, cold, etc. Frequently in a forest situation the limiting factor to understory growth and fruiting is available light. As Whitaker (1970:17) states in reference to a shrub population growing in the shade of a tree canopy, "It may be true both that the shrubs are physiologically adapted to grow and reproduce successfully at this light intensity and that the shrub population could be much denser in the absence of trees competing with the shrubs for light." At the forest "edge," light ceases to be limiting, and density and species diversity of forest understory plants increase proportionately, while light is sufficient to allow growth of grassland species as well. This is the so-called "edge effect." However, the edge is also drier than the forest interior because of increased light and air circulation, and not all plants are favored. For example, the density of trees is often less at the edge than in the forest interior.

A forest edge area generally contains more biomass in the form of understory shrubs and herbs than the interior of a mature forest where relatively more of the biomass is tied up in the form of wood in the tree canopy. For many species, low light intensity favors vegetative development at the expense of flowering and fruiting, and it has sometimes been suggested that an overstory be thinned to improve fruit production by certain species. The increase in usable food biomass at a forest edge (increasing the carrying capacity) and the increase in species diversity are naturally reflected in the increased abundance of animals linked to those plants. Many wildlife species value the edge and occupy it when fruits are ripe or the browse succulent. They will do so, however, whether the edge is natural or artificial. Long before man began to consciously create "edge," he was increasing it by burning to increase game and human plant resources (F. King 1978). Before that, it was created naturally by fire as well as by wind storms or individual dead trees falling and creating openings in the forest. These openings were then rapidly occupied by characteristic successional or edge plants. Every hunter knows that game will not be as abundant in a mature forest as in a brushy open woods, whether that brushy woods is oriented along an edge or not.

While an ecotone may be characterized by a greater species diversity, this diversity is not always reflected by a greater diversity of food resources. Fitting (1966) shows this to be the case along the border between the deciduous and coniferous forests in Michigan. Since there are almost no food resources in mature conifer forests, one goes from a relatively high diversity and density of food plants in the deciduous forest to a low diversity and density in the coniferous forest. The transition has an intermediate rather than the high diversity and density that one might expect. This possibility—that the ecotone is not always potentially more productive than the adjacent communities—is one that must always be considered in attempting to reconstruct the importance of vegetational boundaries to aboriginal settlement patterns.

ENVIRONMENTAL RECONSTRUCTIONS

It has been stated above that plants are spatially distributed in response to a series of environ-

mental variables, often arranged as gradients. These variables, whether they be temperature, precipitation or soils, have varying degrees of importance to any given species. Some plants are tightly controlled by one variable, others are tolerant of a wide range of environmental variables. Decreased available moisture might shrink the range of one species or limit its distribution within that range, while a temperature change might have little effect. At the same time, another species might be very sensitive to a few days shorter growing season. Unfortunately, limiting variables are usually not so simple as average annual precipitation or temperature. Extremes of heat and cold or of precipitation, the length of the growing season, seasonal distribution of moisture or a combination of such factors may influence various plants. High temperatures speed evaporation and so reduce the amount of available moisture, even though precipitation might remain the same. Therefore, just being able to reconstruct mean annual precipitation or temperature for the past does not automatically reconstruct the spatial or temporal differences that might have existed in the plant communities which emerged in response. In addition, there is also the problem of differential migrations of plant species into an area as a result of climatic change.

The distributions of animals are primarily determined by either the distribution of the plant foods on which they depend or on the distribution of prey species so controlled. Again, animals show varying tolerances by the range of habitats in which they can exist. While plant distributions can frequently be shown to correspond to basic environmental factors of climate or soils or topography, many animal distributions are more complex, since an animal species dependent on only one type of habitat or plant food is likely not to survive serious destruction of that habitat. A prime example is the Kirtland's Warbler (*Dendroica kirtlandii*). This bird nests in 8-10-foot tall jackpines with a certain density and little understory. While these birds may have been more common prior to settlement when uncontrolled fires swept periodically through the forest, maintaining it in a perpetual state of rejuvenation, they have become nearly extinct since man has been altering the age classes of their forest habitat. Figure 1 shows examples of a tolerant and widespread plant species (chokecherry, *Prunus virginiana*) and animal (white-tailed deer, *Odocoileus virginianus*) as well as that of paper birch (*Betula papyrifera*) whose southern limit of distribution coincides with a mean July temperature of 21 °C (70 °F) and that of moose (*Alces alces*) whose southern limit approximates that of the boreal forest.

If communities existed as discrete units, they might be expected to react as units to environmental change and paleoecological reconstructions could be directly based on modern analogs. However, if each species reacted individually in response to environmental change through time as they have been shown to do through space, then plant communities would be constantly changing and their species composition would not necessarily be the same as modern analogs (Graham 1976, 1979). Thus, it is not always appropriate to directly apply characteristics of modern communities when reconstructing the past environments. Pollen studies of vegetational history show that plant assemblages have continually changed through the prehistoric record, with each species generally responding individually to environmental change. There are modern pollen assemblages (reflecting plant communities) which have no analog in the past and others from the past which represent plant communities which do not exist today. J. King (1974), for example, reported as much as 92% spruce pollen in samples from a late Wisconsinan glacial record in the Missouri Ozarks, which apparently represented a spruce-dominated forest unlike any modern boreal forest. Such differences between the pollen records of late Wisconsinan boreal forests and modern forests have been explained by differential species migration rates and the existence of plant communities unlike those at present (Webb and Bryson 1972; Wright 1968a). A similar explanation has been applied to late Wisconsinan mammalian assemblages in the eastern United States (Graham 1976). For example, some northern boreal species that have similar distributions today had different southern limits in the late Pleistocene. The yellow-cheeked vole (*Microtus xanthognathus*), which today occurs in far northwestern North America, has only been found in late Pleistocene deposits in the Midwest and eastern United States (Figure 2A). On the other hand, caribou (*Rangifer tarandus*) has a more southerly distribution today than *M. xanthognathus*, but its late Pleistocene southern limit was further north in the Midwest though about the

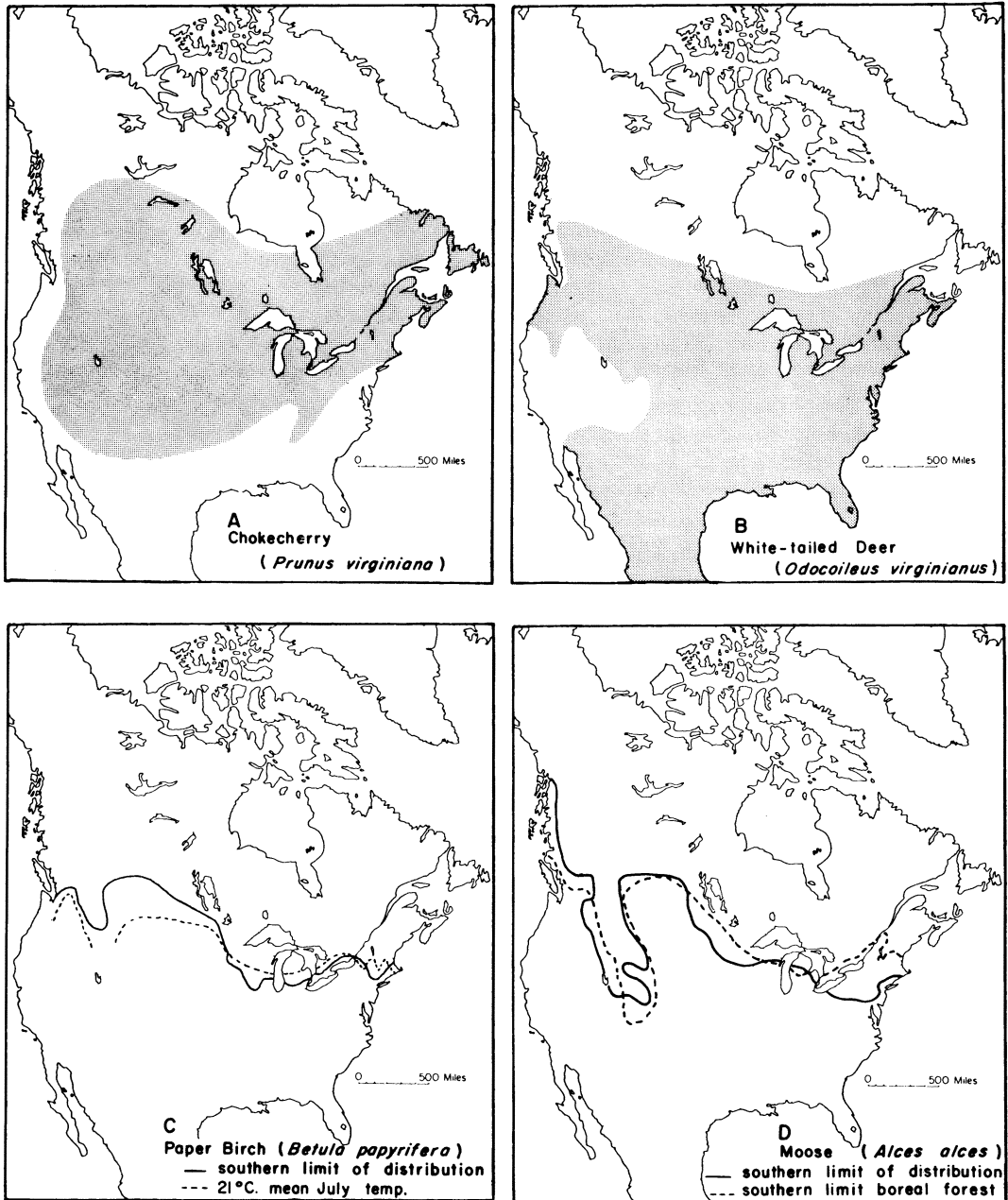


Figure 1. Examples of the distribution of tolerant, widely distributed plant and animal species (A and B) and intolerant species whose distribution is controlled by one primary variable (C and D).

same in the East (Figure 2B). At the same time, muskoxen (*Ovibos moschatus*) and collared lemmings (*Dicrostonyx* spp.), which are restricted to the arctic tundra today, ranged almost as far south as the yellow-cheeked vole and the caribou during the late Pleistocene (Figures 2C and 2D).

This does not mean that attempts cannot be made to reconstruct past communities. If there is a good record of past vegetation (such as pollen or plant macrofossils), it should be possible to deter-

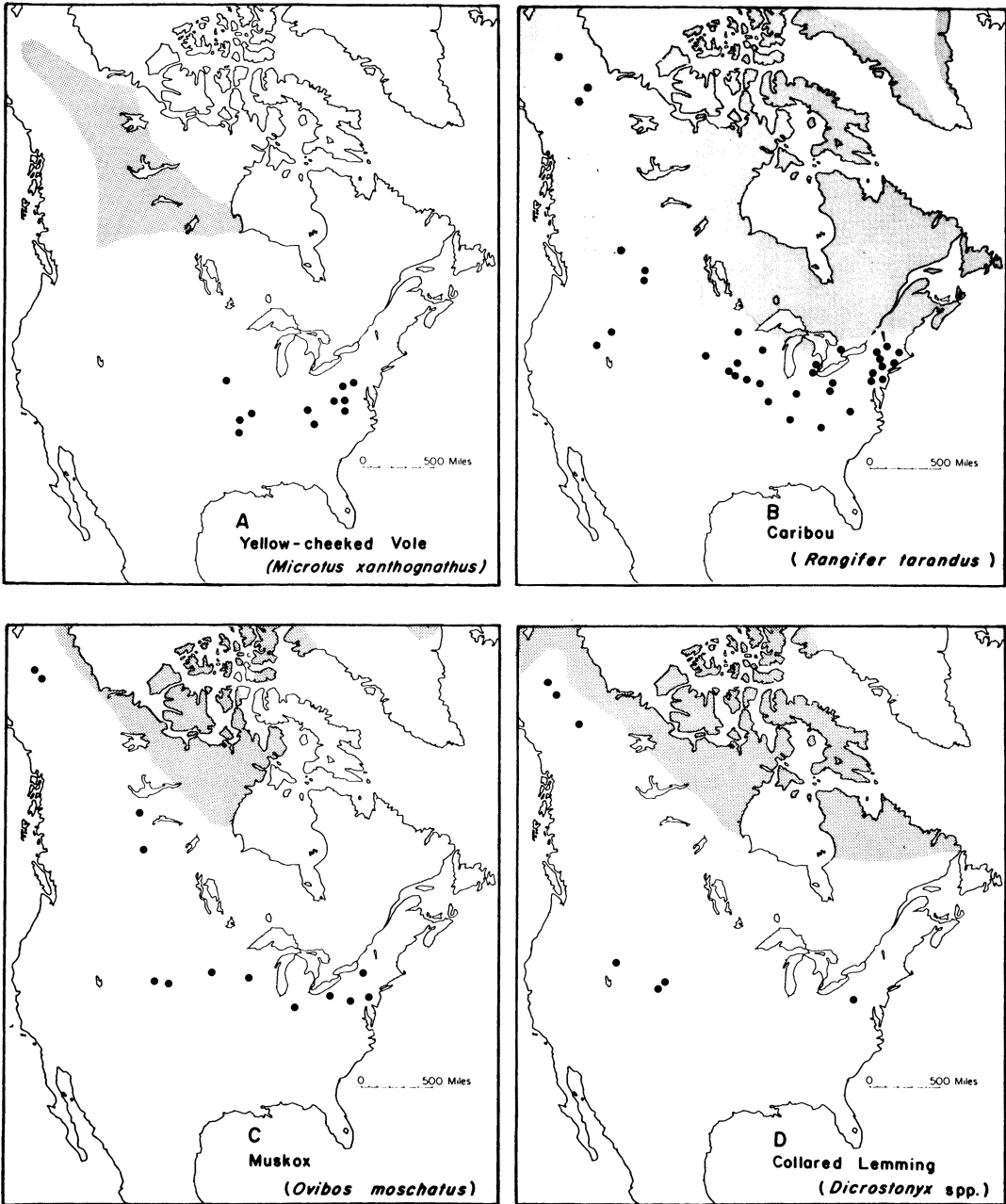


Figure 2. Comparison of the modern (shaded area) and late Wisconsinan (dots) distribution of some mammals in the eastern United States (from Graham 1979).

mine the dominant plants of the community, as well as many lesser species. It is impossible however, on the basis of such data, to project the point in time when rare species and those not represented in the fossil record entered the community. Likewise, it is impossible, on the basis of such data, to quantify past plant food resources or biomass, much less the animal communities living off those plants. It should also be pointed out that community reconstructions based on gra-

dient analyses are no more applicable in reconstructing the past than those based on modern analog communities, since the gradient itself has been altered, not just the position along the gradient.

In addition, this does not mean that qualitative differences cannot be shown, especially differences in the dominant plants and animals. For a plant or animal to have been an important human resource, it must have been common enough in the environment (i.e., dominant) to have warranted its exploitation. Therefore, we do not have to worry about the spatial or temporal distribution of minor species. By considering primarily dominants, which are also used to characterize communities, we avoid many of the problems inherent in attempting to reconstruct paleovegetational gradients.

APPLICATIONS TO ARCHAEOLOGY

One of the most important factors influencing aboriginal peoples is obviously the environment and its effect on the spatial and seasonal distribution of biotic resources. Since settlement, distribution was in great part determined by the location of specific resources, correlation between habitation sites and these resources should provide important clues for understanding subsistence and settlement systems. Reconstruction of the environment is therefore crucial to the increasingly more sophisticated models which archaeologists wish to develop. In addition, the more detailed environmental reconstructions can be made, the more useful they are in determining man-land relationships.

It would be futile to list all of the applications of ecological models to archaeological studies. Furthermore, the "correct" application of ecological models is not cut and dried but is dependent upon the nature of the biological record recovered and the specific questions the archaeologist wishes to answer. We believe it is more productive to categorize the major pitfalls environmental archaeologists might face and suggest ways of avoiding them.

There are two major types of errors with several corollaries, any combination of which might be incorporated into environmental models:

Error Type I - assuming stability or change in an environment where it does not exist

Corollary A - overestimating or underestimating effect of environmental change on human ecology

Corollary B - confusing culture system changes with environmental changes and vice versa

Error Type II - inappropriate application of an ecological/environmental analog

Corollary A - oversimplification of paleoenvironmental reconstruction

Corollary B - overextending paleoenvironmental reconstruction beyond limits of data base.

Type I errors can be avoided by having a good paleoenvironmental record with independent checks such as pollen, plant megafossils, vertebrates, invertebrates, geomorphology, etc. It is also important to check environmental data derived from the archaeological site against an independent record such as a paleontological record of the same temporal and spatial context whenever possible. Such an independent check will help eliminate errors falling under corollaries A and B. Thus, it is advantageous for an archaeologist to work in an area with a well-established paleo-

environmental record or to design research so it incorporates such studies. For example, well-integrated paleoenvironmental records (i.e., pollen, plant megafossils, vertebrates, invertebrates, geology, and soils) for the Missouri Ozarks (Wood and McMillan 1975) provide a good framework for paleoenvironmental archaeological studies. Similar interdisciplinary approaches with a regional framework have been applied at the Cherokee site, Iowa (Anderson and Semken, in press), and the Jones-Miller site, Colorado (Stanford 1974), just to mention two.

Because environmental and climatic change have been poorly known in the past, such changes have generally been ignored in producing human adaptation models. Thus, the assumption of stability has generally been more of a problem than overestimations of change. Workers in many regions are finding that climatic change has been important in the past. For example, Braun (1974:594) showed that postglacial climatic changes resulting in temperature drops and sea-level rises in eastern New England were responsible for changes in mollusk habitats and availability, which were in turn reflected in the archaeological record. The possibility remains for such internally initiated cultural changes as those to which changing adaptive strategies have previously been attributed; however, climatic change must now be recognized as a significant factor in the evolution of subsistence patterns in this area. It has been suggested (Griffin 1960; Vickery 1970) that climatic cooling, rather than cultural "climax," cultural "fatigue," or warfare, was a significant contributing factor in the decline from Hopewell to Late Woodland culture in the northern Mississippi Valley and Great Lake region, a suggestion that has been further substantiated by pollen studies in the area (Jones and Kapp 1972). The origins of agriculture in the Near East may reflect an important climatic shift at the end of the Pleistocene which resulted in the migration, about 11,000 years ago, of certain food plants into areas where concomitant cultural changes led to their domestication (Wright 1976).

Two competing views (Bettinger 1977) regarding the nature of human adaptation in the Great Basin are examples of corollary A. One hypothesis (Jennings 1957, 1964, 1968) contends that diffuse subsistence patterns as defined by Cleland (1966:44) remained broadly similar for more than 8,000 years despite long-term postglacial climatic and environmental fluctuations. If such a hypothesis is incorrect, then it would be an example of underestimating the effect of environmental change on human ecology. On the other hand, an alternative hypothesis (Baumhoff and Heizer 1965; Davis 1966; Heizer 1956; Napton 1969) contends that focal subsistence patterns (Cleland 1966:42) were dramatically affected by climatic changes. If such a position is incorrect, then it would be an example of overestimating the effect of environmental change on human ecology. Bettinger (1977, 1979) believes that available data tend to support the second hypothesis.

A confusion of cultural and environmental changes can best be avoided by comparing the environmental data from an archaeological site with the regional picture. For example, in an early study at the Koster site, botanical remains (particularly the abundance of hickory nuts) from the Middle Archaic occupation suggest that the forest environment of the Hypsithermal was relatively stable (Asch et al. 1972). In contrast, regional vegetational studies (J. King and Allen 1977; Wright 1968b) and geomorphological studies at Koster (Butzer 1978) indicate major environmental and vegetational changes during this period.

Hickory trees occur in a wide variety of habitats as far west as central Kansas, although to the West they become restricted to increasingly protected niches. An individualistic model would suggest that mid-Holocene environmental changes (Asch et al. 1972:22; Butzer 1978:412-413; J. King and Allen 1977:319) may have caused reduction or elimination of upland forests while the relatively mesic forests on the lower slopes adjacent to Koster may have retained many of their floristic constituents, although perhaps with a different composition (relative abundance of various species) and different structure (relative density of trees, shrubs, and herbs). Hickory nuts would continue to be available, although their abundance would be less and the ratio of various species might be altered. However, if hickory nuts remained a first-line resource despite decreased availability, selective utilization may have masked environmental change, and the two types of environmental data may not actually be inconsistent at all.

In other cases, changes from focal to diffuse subsistence might give the impression of climatic change (Asch et al. 1972; Styles 1978) because resource stress can be caused by either population

growth or environmental change with identical human reaction. For example, Styles (1978) suggests that Middle to Late Woodland subsistence changes in the Lower Illinois River Valley are the result of population growth rather than climatic change. While it is difficult to separate environmental and culture system changes, evidence such as greater site density and more localized exploitation of a more diverse resource base seems to indicate cultural rather than climatic change (Styles 1978).

Appropriate application of ecological/environmental analogs (avoidance of Error Type II) will depend upon the completeness of the environmental data base and the questions the archaeologist wishes to answer about man-environment relationships. Late Pleistocene environmental reconstructions that employ modern vegetational and faunal zones as direct analogs are an oversimplification of environmental reconstruction, because Late Pleistocene communities were different from modern ones (Graham 1976, 1979). The different environmental patterns of the Late Pleistocene may have far-reaching implications for human adaptive strategies (Brown and Cleland 1968; Graham 1979). It may also be an oversimplification to assume that Holocene communities have been the same throughout time, because vegetational studies (e.g., Davis et al. 1975) have illustrated some important changes in community structure, though Holocene communities may not have been as different from one another as from Pleistocene communities. Therefore, the accuracy of "ecosystem similarity" (B. Smith 1979) may decrease with increasing antiquity of the archaeological site.

The importance of adequate data on which to base interpretations and conclusions is exemplified by Adams (1979), who found that the average length of the growing season at the Hopi mesas in northeastern Arizona is much longer than had been previously reported and that the assumption that in farming the broad valleys the Hopi are growing maize in an area with a marginal growing season is erroneous. The use of incorrect data has, he feels, skewed the interpretation of the cultural ecology of horticultural groups in the Southwest (Adams 1979:292).

Applications of individualistic and zonal models may vary from site to site dependent upon the problems being studied and on the magnitude of, and sensitivity of biota to, environmental changes. If the important changes can be recognized, individualistic models may be of more value for the study of focal subsistence, low-magnitude environmental changes, or areas such as floodplains of large rivers or centers of major vegetational formations which may be buffered against large-scale changes. For example, shifts in individual species of mussels within the Pomme de Terre River may reflect increased moisture during the Late Archaic and Woodland times which would also have influenced subsistence patterns (Klippel et al. 1978). F. King and Roper (1976:147-148) suggested that differences in the plant remains recovered from two Middle Woodland to early Late Woodland sites in central Illinois may have been the result of the differing effects of "climatic amelioration" (i.e., warming and/or drying) in an already droughty ecotonal situation and on the adjacent bottomland.

Hunting and gathering subsistence strategies for the Bighorn Basin as reconstructed by Frison (1978:343-361) are best explained by individualistic models. For instance, grassland areas that were generally favorable for large herbivores were apparently not used extensively for communal bison kills because the species composition of grass communities would not support large bison herds. However, in the western areas of the basin grassland communities supported significant bison herds, and as a result communal kills are known (Frison 1978:347). Also, utilization of particular plant species along an altitudinal gradient (Frison 1978:351) is dependent upon the tolerance limits of individual species.

Zonal models may be more applicable to sites located at the edges of major vegetational zones or in cases where the magnitude of environmental change is high or where the biota is very sensitive to environmental change. Sørensen (in press) has successfully used zonal models to show shifts in bison subsistence in western Iowa in response to major shifts between grassland and forest. Likewise, McMillan (1976) has applied a similar model to subsistence patterns at Rodgers Shelter, and Klippel and Maddox (1977) have used zonal models to explain Archaic settlement patterns in the Sangamon River drainage of central Illinois.

As has been stated above, plant and animal assemblages cannot be precisely reconstructed and

projected into the past. It is, unfortunately, impossible to develop detailed distribution maps of important "microvegetation" zones or to quantify the resources of such zones in a meaningful manner. It is probably just as well therefore that as Flannery (1971) observed, primitive people rarely rely on "environmental zones" or even "microenvironments"; rather they rely on small series of individual plant and animal genera whose ranges may intersect several environments. For while it may be impossible to reconstruct total communities or environmental zones, it should be possible to develop the knowledge of a few key taxa necessary to fairly accurately quantify those resources and to project variations in their relative abundance and distributions back through time as they may have responded to environmental change. This will be most easily done for those species that have left good fossil and archaeological records. It is in this situation where the understanding of ecological concepts, such as the individualistic hypothesis, becomes most important, since these concepts are fundamental to the relationships of plants and animals, including man, to one another and to their environment.

The concepts of ecotone and edge are especially important to archaeology—not merely because of greater resource availability or diversity along ecotones, because this is not always the case, but because shifts in aboriginal subsistence activities in response to climatically induced environmental change occur first along the affected ecotones. These areas are of greatest potential value to archaeologists interested primarily in man's relationship to the environment rather than in social or cultural development which might best be studied away from the ecotone in areas that have been less affected by environmental change.

Before ecological models are employed to explain spatial or temporal settlement-subsistence changes, however, the environment must be thoroughly understood through the application of data from independent disciplines. The modern plant and animal assemblages must be recognized and tied to their limiting factors of pedology and climate. In addition, if an archaeological site lies near an ecotone, the importance of that ecotone must be determined. This applies whether it is a sharp boundary produced by geology or disturbance or the more diffuse product of climate. It probably matters little if a site lies on an ecotone if the two adjacent communities have comparable plant and animal resources in terms of ease of exploitation, food value, seasonal availability, and so forth. Only when there is a spatial and temporal difference in resources will scheduling and settlement patterns be affected and will there be adequate change so that the homeostatic mechanisms maintaining stable cultural relationships and subsistence activities may be altered. As with any paleoecological record, the more sensitive the region and the more change that has occurred there through time, the more information there will be available about the adaptations of communities to that change, be they human or otherwise.

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