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Quaternary landscape ecology: Relevant scales in space and time

Hazel R. Delcourt[1] and Paul A. Delcourt[2]
[1]Department of Botany, Graduate Program in Ecology and Center for Quaternary Studies of the Southeastern United States, University of Tennessee, Knoxville, TN 37996; [2]Department of Geological Sciences, Graduate Program in Ecology and Center for Quaternary Studies of the Southeastern United States, University of Tennessee, Knoxville, TN 37994

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Abstract

Two primary goals of landscape ecologists are to (1) evaluate changes in ecological pattern and process on natural landscapes through time and (2) determine the ecological consequences of transforming natural landscapes to cultural ones. Paleoecological techniques can be used to reconstruct past landscapes and their changes through time; use of paleoecological methods of investigation in combination with geomorphic and paleoethnobiological data, historical records, and shorter-term ecological data sets makes it possible to integrate long-term ecological pattern and process on a nested series of temporal and spatial scales. 'Natural experiments' of the past can be used to test alternative hypotheses about the relative influences of environmental change, biological interactions, and human activities in structuring biotic communities within landscape mosaics.

On the absolute time scale of the Quaternary Period, spanning the past 1.8 million years, current distributional ranges of the biota have taken shape and modern biotic communities have assembled. Quaternary environmental changes have influenced the development of natural landscapes over time scales of centuries to hundreds of thousands of years; human cultural evolution has resulted in the transformation of much of the biosphere from natural to cultural landscapes over the past 5,000 years. The Quaternary extends to and includes the present and the immediate future. Knowledge of landscape changes on a Quaternary time scale is essential to landscape ecologists who wish to have a context for predicting future trends on local, regional, and global scales.

Introduction

The Quaternary Period encompasses approximately the past 1.8 million years of geologic history (Bowen 1985). The Quaternary includes two subdivisions of time: (1) the Pleistocene Epoch, which lasted from about 1.8 million years ago until 10,000 years ago; and (2) the Holocene Epoch, from 10,000 years ago to the present (Fairbridge 1983). The Quaternary is characterized by alternating episodes of glacial and interglacial climates. Each glacial-interglacial cycle lasts about 100,000 years (CLIMAP 1976), of which 90,000 years are relatively cold, and during which continental glaciers develop and expand at middle and high latitudes. Approximately 10,000 years of each climatic cycle are characterized by warm climate, for example the current, or Holocene, interglacial interval. The Quaternary Period is also defined on the basis of minimal evolution or extinction of both terrestrial and marine flora and fauna (Lyell 1834; Kurtén and Anderson 1980). Two major exceptions to this are the evolution of *Homo sapiens* about 400,000 years ago (Bowen 1985) and the late-Quaternary extinctions of numerous species of megafauna, for example, occurring in North America at the end of the Pleistocene, 10,000 years ago (Martin and Klein 1984). For the late-Quaternary time interval, corresponding to the most recent glacial-interglacial cycle, an absolute chronology of events is available through radiocarbon dating, an isotopic-dating' technique useful to about 80,000 years Before Present (yr B.P.). The late Quaternary is characterized by major changes in species distributions and composition of biotic communities; only during the Holocene interval have modern distributional ranges of the biota taken shape and contemporary biotic communities assembled (Kurtén and Anderson 1980; Davis 1981, 1983; Huntley and Birks 1983; Nilsson 1983; Graham 1986; Graham *et al.* 1987; Delcourt and Delcourt 1987a; Ritchie 1987).

The Quaternary Period represents not only a portion of the history of life on earth, but it also includes the present day and will extend into both the immediate and the distant future. Paleoecological studies that reconstruct late-Quaternary landscape changes (Berglund 1986) thus can be designed to dovetail with other methods of 'investigation, including historical records and shorter-term data sets, to integrate landscape patterns and processes on a nested series of temporal and spatial scales in ecological time. An appreciation of past changes in both environment and biota is imperative for evaluating the current trajectory of change in landscapes (Delcourt *et al.* 1983a; Jacobson and Grimm 1986; Clark 1986). Histories of landscape development that can be reconstructed using paleoecological techniques provide long-term 'experiments of the past' ('natural experiments' *sensu* Diamond 1986) that give a basis for testing alternative hypotheses about the relative influences of environmental change, biological interactions, and human activities in structuring biotic communities within landscape mosaics (Delcourt and Delcourt 1987a, b).

Changes in landscapes on a Quaternary time scale have been two-fold: (1) changes in climate and in geomorphic processes have affected vegetational patterns and processes on natural landscapes on the scale of hundreds of years to hundreds of thousands of years (Wright 1984; Kutzbach and Wright 198.5); and (2) human activities have greatly modified the biosphere, particularly over the past 5,000 years, resulting in the widespread conversion of natural landscapes to cultural ones (Barker 1985; Behre 1986). Long-term changes in natural landscapes, which are defined here as those landscapes without substantial human intervention, include shifts in species ranges and ecotones between communities, changes in the mosaic of vegetation patches and community composition, and dynamic interactions of geomorphic processes with vegetational processes. Human modification of landscapes has involved changes in community composition, extensions or truncations in the ranges of plant and animal species, changes in the proportion of forest to nonforest land, and changes in disturbance regimes that have favored perpetuation of invasive, weedy (ruderal) species (Delcourt 1987).

In Europe, the ecological effects of prehistoric as well as historic human activities are widely appreciated by landscape ecologists (Naveh and Lieberman 1984). In North America, primary emphasis has been placed on understanding of energy transfer, nutrient flow, and changes in heterogeneity of natural landscapes on a short time frame of years to decades (Risser *et al.* 1984). Over a longer time scale of the past several hundred years, the effects of land conversion and forest fragmentation since Euro-American colonization also have been considered integral to developing concepts in North American landscape ecology (Burgess and Sharpe 1981; Turner 1987).

In this paper, we emphasize the potential for the Quaternary paleoecological record to contribute a wealth of information relevant to the developing subfield in Quaternary Landscape Ecology. First, we review the specific environmental forcing functions and biotic responses that result in landscape-scale ecological patterns and processes. Then we consider several aspects of development of an integrated, interdisciplinary research design that are necessary for successful integration of data within a nested hierarchy of space-time domains. We illustrate the relevance of this approach to understanding the dynamics of both natural and culturally influenced landscapes using examples from our

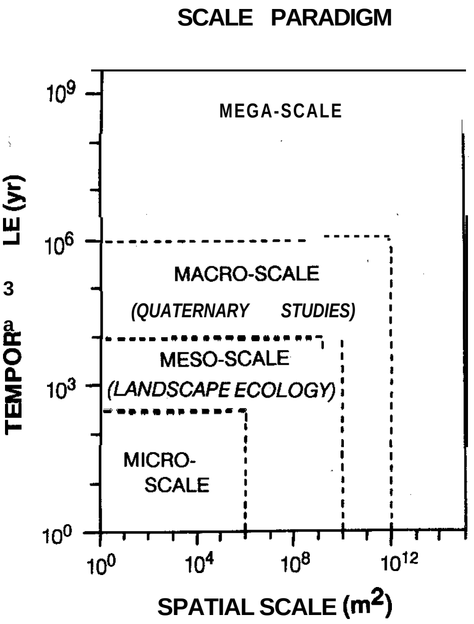

Fig. 1. Spatial-temporal domains for a hierarchical characterization of environmental forcing functions, biological responses, and vegetational patterns.

research in the southern Appalachian Mountains within the southeastern United States. Finally, we identify several fundamental issues in ecology that can be resolved by an integrated, interdisciplinary approach to Quaternary Landscape Ecology.

Spatial and temporal scale as an organizational paradigm in landscape ecology

Environmental forcing functions, biotic responses, and patterns of organization of communities on terrestrial landscapes vary on all scales in space and time (Delcourt *et al.* 1983a). A successful research design first defines the scale at which the phenomenon of interest can be observed, and then selects methods of analysis appropriate to resolving ecological pattern and process at that spatial-temporal scale. An operational scale paradigm into which landscape ecology can be incorporated includes micro-scale, meso-scale, macro-scale, and mega-scale spatial-temporal domains (Figs 1 and 2). These domains, as defined here, are modified from the hierarchical scheme first developed in Delcourt *et al.* (1983a). It should be noted that the bounds placed on the dimensions of these domains represent a generalized overview for the purpose of illustrating relationships. In any particular case study, the dimensions chosen for study may be within one of these arbitrary domains, or they may cross'the boundaries in order to arrive at an appropriate scaling relative to the generation times of the organisms studied or to the recurrence intervals for disturbances or of environmental changes relative to the ecosystems investigated.

Micro-scale domain

The micro-scale domain (Figs 1 and 2) has a duration of from 1 yr to 500 yr, and a spatial dimension of 1 m^2 to 10^6 m^2 (100 ha). The micro-scale is the domain of interest for the landscape manager, the process geomorphologist, and population and plant-succession ecologists. On this spatial-temporal scale; seasonal patterns of temperature and precipitation as well as longer-term weather trends and climatic fluctuations of decades to centuries are important stimuli to both plant and animal populations. Local to widespread disturbances of relatively short duration, such as wildfire, windthrow, and clearcutting have immediate effects on community composition (Pickett and White 1985). Geomorphic processes operative on this scale include soil creep, movement of sand dunes, debris avalanches, slumps, fluvial transport and deposition, and cryoturbation (Swanson *et al.* 1988). Biological responses to weather and climate changes, as well as to geomorphic and other kinds of disturbance events, include cyclic changes in animal populations, gap-phase replacement of forest trees, and plant succession on abandoned agricultural fields. These events thus affect vegetation at levels from individual plants to large forest stands, and occur on areas extending from the size of sample plots up to first-order stream watersheds, for example, the experimental watersheds within the Coweeta Basin (Fig. 3) in western North Carolina (Swank and Crossley 1988), or small second-order stream watersheds. Examples of changes in the landscape mosaic on this time scale include forest

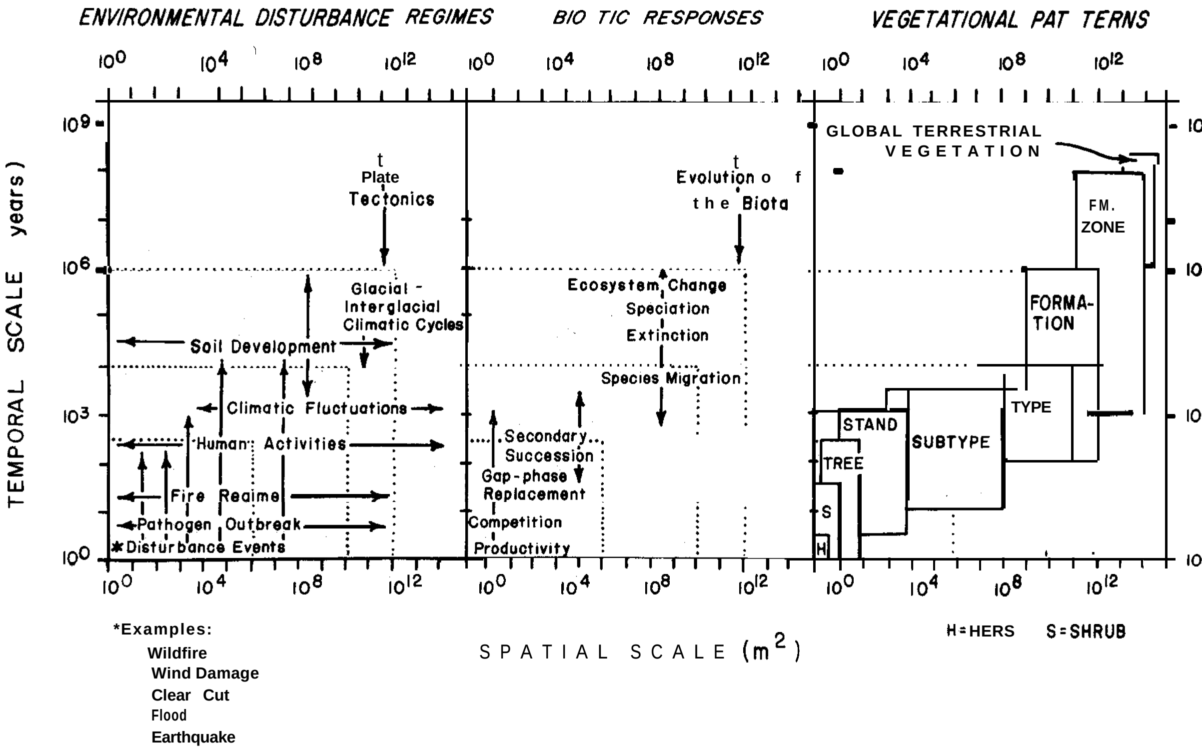

Fig. 2. Environmental disturbance regimes, biotic responses, and vegetational patterns viewed in the context of four space-time domains (modified from Delcourt *et al.* 1983a).

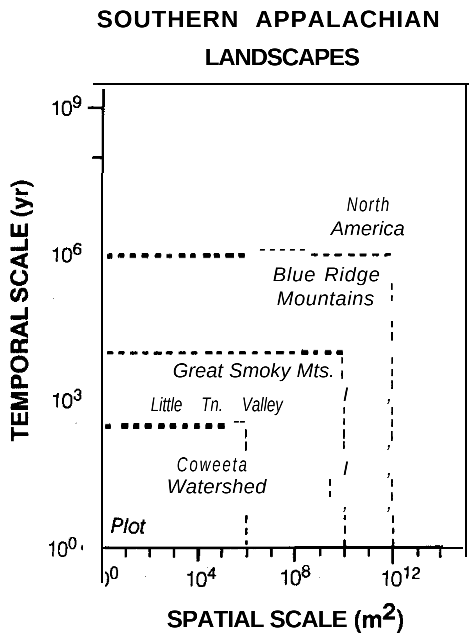

Fig. 3. Classification of study areas nested within the hierarchical framework of spatial-temporal domains.

fragmentation, with changes in relative size of forest and nonforest patches, increases in forest edge, and changes in available corridors due to land clearance (Forman and Godron 1981; Burgess and Sharpe 1981).

Meso-scale domain

The meso-scale domain (Figs 1 and 2) extends in time from 500 yr to 10,000 yr and in space from 10^6 m² (a physical feature averaging 1 km in width) to 10^{10} m² (100 km width). This domain encompasses events occurring over the last interglacial interval, the Holocene, and on watersheds of most second-order streams such as (Fig. 3) the Coweeta Basin (Swank and Crossley 1988), the Little Tennessee River of East Tennessee (Delcourt et *al.* 1986), mountain ranges such as within the Great Smoky Mountains National Park (White and Wofford 1984), and extending up to 1” latitude *x* 1” longitude (1/2 of a U.S.G.S. 1:250,000 topographic or geologic quadrangle; Olson **et al.** 1976). On the meso-scale, changes in geomorphic and climatic regimes effect changes in dynamics of patches in a landscape mosaic. Species migrations and ecotone displacements occur on this scale in response to changes in environmental gradients and predominant disturbance regimes. Long-term changes in the landscape mosaic occur on second-order and larger stream watersheds as well as on other large landforms. Within this domain, human cultural evolution has resulted in the transformation of natural landscapes to cultural ones.

Macro-scale domain

The macro-scale domain (Figs 1 and 2) lies largely within the research sphere of the Quaternary scientist. Within this domain, natural phenomena operate at temporal scales from 10,000 yr to 1,000,000 yr and at spatial scales ranging from 10^{10} m^2 (physical features averaging 100 km width) up to 10^{12} m^2 (1,000 km width). This domain spans in time from one to many glacial-interglacial cycles and in space an area of a physiographic province, such as the Blue Ridge Mountains of eastern North America (Fig. 3), to that of a subcontinent (Delcourt and Delcourt 1987a). On this scale, speciation and extinction become important biotic responses along with subcontinental-scale migrations and displacements of biomes. Changes in landscape heterogeneity occur on a macro-scale across entire physiographic regions, with consequent changes in the make-up of ecoregions *sensu* Bailey (1976).

Mega-scale domain

The mega-scale domain (Figs 1 and 2) encompasses 1 million yr to 4.6 billion yr (the age of the Earth) and includes areas > 10^{12} m^2 (land features > 1,000 km in average width). This scale ranges from continental, for example, North America (Fig. 3), to hemispheric and global and includes the majority of geologic time during which plate tectonics have changed the configurations of continents and ocean basins, the biota has undergone major episodes of evolution and extinction, and the linkages between the lithosphere, cryosphere, and biosphere have developed (Frakes 1979).

Hierarchical relationships

This scale paradigm inherently is built upon an implied set of hierarchical relationships (Allen and Starr 1982; Delcourt **et al.** 1983a; O'Neill **et al.** 1986; Urban **et al.** 1986; Delcourt and Delcourt 1987a). Micro-scale, meso-scale, macro-scale, and megascale domains, as we define them in this paper, are a nested series of spatial-temporal configurations, each bounded by the next larger scale and each integrating all the patterns and processes ongoing at lower levels within the hierarchy.

Many ecological patterns and processes of direct relevance to landscape ecologists are resolvable at the interface between the micro-scale and the meso-scale domains. Whereas it seems of less immediate interest for some landscape ecologists to understand the macro-scale biogeographic changes that occurred in the Pleistocene (Urban et **al.** 1986), meso-scale events occurring during the Holocene are clearly relevant to all landscape ecologists, as these events of the present interglacial period have shaped the landscapes that were observed at the time of Euro-American settlement of North America (Williams 1982; Clark 1986). Landscape ecologists include not only the subset of ecologists concerned with integration of short-term ecological patterns and processes over relatively broad areas (Turner 1987); landscape ecologists must also concern themselves with understanding the long-term changes in ecological patterns and processes on landscapes (Risser 1987).

Developing an integrated research design

If Quaternary Landscape Ecology is to become a productive interface between neo-ecology and Quaternary paleoecology, it will be important for landscape ecologists to be aware of and to use effectively the full spectrum of investigative tools available for evaluating landscape change.

The history of forest stands and disturbance regimes

A number of methods are in common use for determining the modern composition and history of individual forest stands and the disturbance regimes that have influenced their development (Mueller-Dombois and Ellenberg 1974; Pickett and White 1985). Inferences about stand history can be made from age-class data and present stand composition (Harcombe and Marks 1978; Peet and Christensen 1980). Systematic excavation of the forest floor reveals not only changes in stand composition but the history of windthrow disturbance (Henry and Swan 1974; Oliver and Stephens 1978). Historical documents give insights about the influences of human disturbance on stand composition (Pyle and Schafale 1988). Tree ring counts and fire scars are used to establish recurrence intervals of fire that affect forest stand composition (Heinselman 1973; Romme 1982; Romme and Knight 1982). Analysis of macroscopic and microscopic plant remains including pollen grains and charcoal particles preserved in woodland hollows' (Bradshaw 1981a, 1981b; Heide 1984) can extend the known history of individual forest stands over time intervals as long as nine thousand years. A series of individual site-intensive studies can be summarized to formulate patterns of forest history on a regional scale (Pyle and Schafale 1988).

The presettlement vegetation mosaic

Mapping landscape patterns on the meso-scale to interpret the presettlement vegetation mosaic as a point of departure for land-use history studies (Marschner 1959) can be accomplished with several complementary kinds of data sets. The most widely used are the records of the General Land Office Surveys (Bourdo 1956, 1983; Delcourt and Delcourt 1977; Grimm 1984). The GLOS records are limited in geographic coverage to the region west of the Appalachian Mountains and beyond the original 13 colonies (Pattison 1970). Other kinds of historical documents including ethnohistoric accounts and diaries can provide useful in reconstructing landscape changes since the time of Euro-American settlement (Cronon 1983). Pollen assemblages from presettlement horizons in lake sediments constitute another complementary form of information concerning the landscape mosaic (McAndrews 1966; Davis *et al.* 1986). All of these kinds of data require careful interpretation within the limitations of uncertainty inherent in the methods. Special training may be required in the correct use of historical documents (Cronon 1983) or in the proper interpretation of the fossil pollen record (Faegri and Iversen 1975; Birks and Gordon 1985; Berglund 1986) in order to avoid pitfalls.

Landscape changes prior to Euro-American colonization of North America

Geomorphic and other geologic evidence of change in configuration of hillslopes, stream courses, terraces, and in recurrence intervals of geomorphic disturbance events can be obtained through radiocarbon dating and stratigraphic interpretation of sedimentary deposits (Mills and Delcourt 1989). Changes in the vegetation mosaic through the Holocene interval are interpretable from pollen and plant-macrofossil evidence preserved in lake sediments (see Bryant and Holloway 1985 for complete bibliographies to all North American literature in Quaternary pollen analysis). Paleolimnologic evidence of changes in water quality and coupled watershed-lake ecosystems is available in the form of fossil diatoms, cladocera, biochemical pigments, and in stratigraphic profiles of elements such as nitrogen and phosphorus (Likens 1985; Binford *et al.* 1987; Davis 1987). Evidence of prehistoric land use can be gleaned from the archaeological and paleoethnobiological (both floral and faunal) record (Butzer 1982; Dincauze 1987; McAndrews 1988).

An interdisciplinary approach

Lists of the kinds of tools and observations that can be made, especially when explicitly tied to the appropriate scale of resolution, can serve as helpful guides to developing a comprehensive research design for gathering and tabulating data for inclusion in a time-series of Geographic Information System (GIS) data bases for subsequent mapping (Meentemeyer and Box 1987). Integration and understanding of Quaternary landscape history requires development of a well-designed research strategy, followed by synthesis and effective interpretation. Dincauze (1987) has emphasized the need for effective interdisciplinary research designs in environmental archaeology ('prehistoric human ecology' *sensu* Butzer 1982). The need for anthropologists to have a thorough understanding of the underlying assumptions in other paleoenvironmental disciplines and to be cautious about borrowing data sets from other fields (Dincauze 1987) is also applicable to the field of landscape ecology. Landscape ecologists must become broadly based if our field is to mature from a descriptive/correlative phase of scientific endeavor to an experimental/hypothesis-testing phase (Risser *et al.* 1984).

An integrated, interdisciplinary approach to Quaternary Landscape Ecology includes the following elements: (1) identification of the problem to be addressed (specific hypothesis to be tested); (2) bounding the problem in a spatial-temporal domain appropriate to its resolution; (3) selection of methods appropriate to investigation of the problem, employing specialists to develop data sets or provide advice when necessary (a comprehensive summary of paleoecologic techniques is found in Berglund 1986); (4) collection of data in a statistically valid way; (5) interpretation of results of each independent line of evidence within the limitations of the techniques available; (6) integration of the data from an ecological perspective in terms of inferred dynamics of landscape patterns and processes, using map series, descriptive or quantitative models, and scenarios; and (7) use of resulting scenarios as tests of hypotheses originally proposed.

The examples that follow are from our recent work in the central and southern Appalachian Mountain region. These case studies illustrate the potential of the interdisciplinary approach of the Quaternary scientist for reconstructing long-term changes in natural landscape mosaics, as well as for evaluating the ecological consequences of prehistoric human activities.

Late-Quaternary landscape history in the central and southern Appalachian Mountains

Methods of investigation and site selection

We have studied the late-Quaternary history of the central and southern Appalachian Mountains from a transect of sites distributed from 500 m to over 1,500 m elevation from eastern West Virginia south to western North Carolina. Methods of investigation included (1) field mapping of local and regional vegetation in each study area; (2) field mapping of geomorphic landform features and geologic deposits in each study area; (3) compilation of historic records of logging and other disturbances at each site; (4) paleoecological analyses of peat or lake sediment cores collected from bogs and fens in West Virginia and North Carolina, from the former lake at Saltville, Virginia, and from natural lakes in East Tennessee; (5) establishment of absolute chronologies for late-Quaternary vegetation and geomorphic events in each study area. These paleoecological records extend back in time from 1,500 yr B.P. to 17,000 yr B.P.

Our series of coordinated studies was designed to gather available evidence to test the long-held hypothesis that the modern species richness and composition of biotic communities in the southern Appalachians can be explained by the two major factors most frequently cited in scientific literature: (1) the great length of time (260 million yr) since the Appalachian Mountain chain was affected by significant tectonic uplift or by marine submergence (thereby providing habitat continuity for persistence of vegetation types of presumed great antiquity, such as the proposed Tertiary relict cove hardwoods forest of Cain [1943]); and (2) the present-day configuration of elevation and slope aspect of the landforms, the modern disturbance regime, and the resulting diversity of habitats distributed along an environmental gradient of more than 2,000 m elevational range (Whittaker 1956). Alternative hypotheses that we proposed included

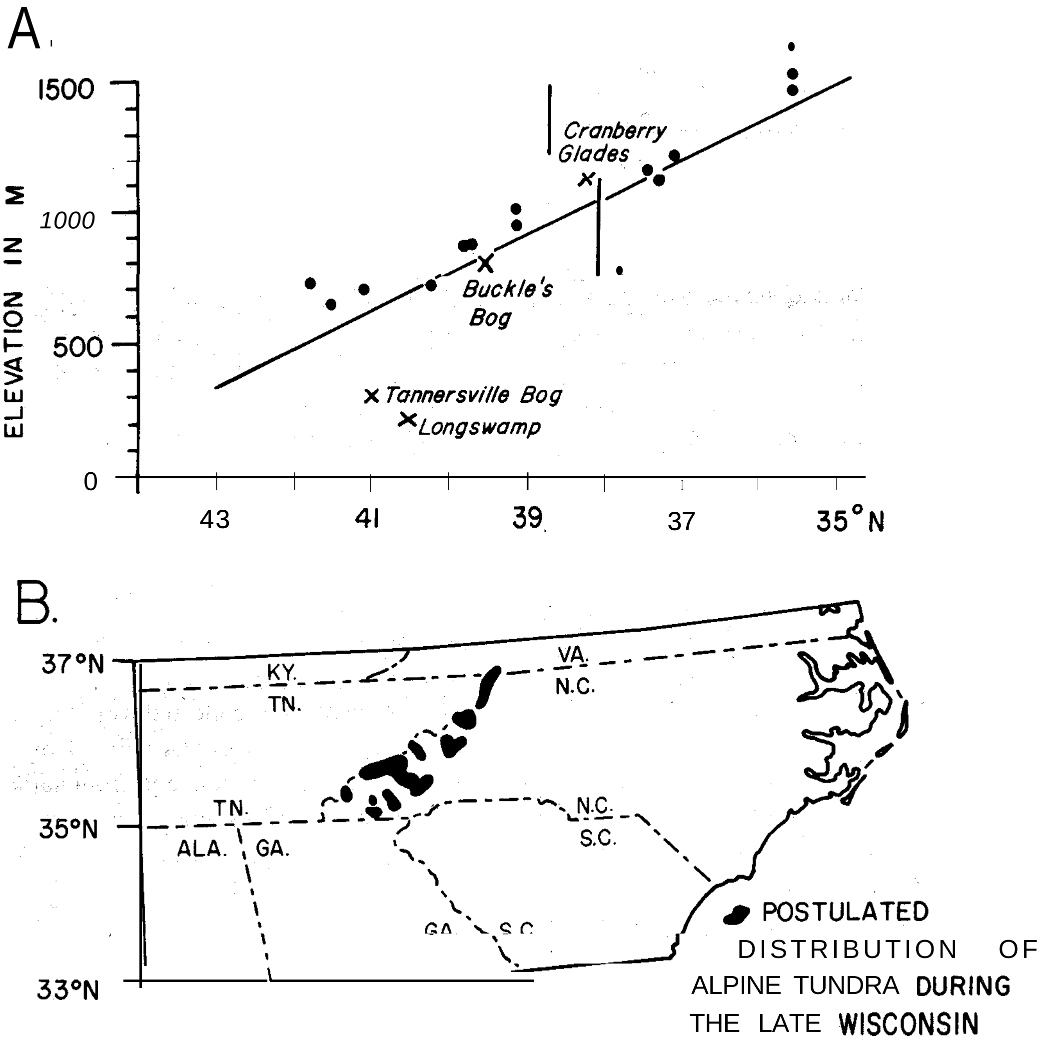

Fig. 4. Late-Quaternary periglacial environments of the central and southern Appalachian Mountains: (A) Distribution of relict, periglacial sorted, patterned-ground features (designated by solid dots) and selected montane bog sites (designated by X's), plotted along an elevational and latitudinal transect; (B) Postulated distribution of alpine tundra during the full-glacial interval (from Delcourt and Delcourt 4985).

(1) climatic changes during the past 10,000 to 100,000 years that would have induced both northward and southward migrations of plant and animal species as well as speciation events; and (2) changes in geomorphic disturbance regimes during the late-Quaternary interval (linked to changes in temperature and precipitation) that would have provided opportunities for rare species to persist within the prevailing vegetation mosaic.

In the course of this research project, we, our students, and other colleagues have documented the quantitative relationship of both the local and regional composition of modern forests to pollen rain (Delcourt et *al.* 1983b; Delcourt and Pittillo 1986), evaluated the geomorphic and vegetational history at individual sites (Delcourt and Delcourt 1986; Larabee 1986; Shafer 1984, 1985, 1988), and prepared summaries of the major biogeographic changes that have occurred during the late-Quaternary interval for the central and southern Appalachians (Delcourt 1985; Delcourt and Delcourt 1984, 1985, 1986, 1987a).

Relationship of geomorphic changes to landscape history

At mid- and high elevations in the central and southern Appalachian Mountains, conditions during the last glacial maximum of the Pleistocene (20,000 yr B.P. to 16,500 yr B.P.) were characterized by intense periglacial environments in which the ground was perennially frozen. Evidence for discontinuous permafrost during the Pleistocene is in the form of both paleovegetation localities for alpine tundra (Maxwell and Davis 1972; Watts 1979; Larabee 1986) and relict geomorphic features that were produced under a former climatic regime with mean annual temperatures as low as -8°C (Péwé 1985; Mills and Delcourt 1989). Periglacial geomorphic features including stone polygons, stone stripes, block fields, and boulder streams have been mapped throughout the Appalachian region (Michalek 1968; Clark 1968; Shafer 1984, 1988). The elevational and latitudinal distribution of these relict, periglacial features corresponds well with the distribution of paleoecological localities with plant-fossil assemblages representing tundra vegetation that are radiocarbon-dated from the last glacial maximum (Fig. 4a). By extrapolation of this elevation-latitude relationship for the upper tree-line limit during full-glacial time, we have inferred (Delcourt 1985; Delcourt and Delcourt 1985, 1987a) that the potential area of alpine tundra in the southern Appalachians extended to the summits of the highest mountain peaks above approximately 1,500 m elevation (Fig. 4b).

With climatic warming in the late-glacial interval, which began as early as 16,500 yr B.P. at 35°N latitude (Delcourt 1979), mean annual temperatures at high elevations increased from -8°C up to about 0°C (Shafer 1984, 1988; Delcourt and Delcourt 1985; Fig. 5), crossing-a climatic threshold governing geomorphic processes (Mills and Delcourt 1989). With an increase in mean annual temperature, both the frequency and intensity of freeze-thaw cycles would have been augmented during the late-glacial interval from 16,500 yr B.P. to about 10,000 yr B.P. (Péwé 1985). Sediment particles in all size ranges from boulders to silt and clay were produced during late-Pleistocene periglacial climates, with intense freeze-thaw cycles creating sorted patterned-ground features such as stone polygons and stone stripes (Clark 1968; Péwé 1985). Most of the periglacial sediments remained perennially frozen in place until the late-glacial climate warmed sufficiently for processes such as solifluction to move the materials downslope (Mills and Delcourt 1989).

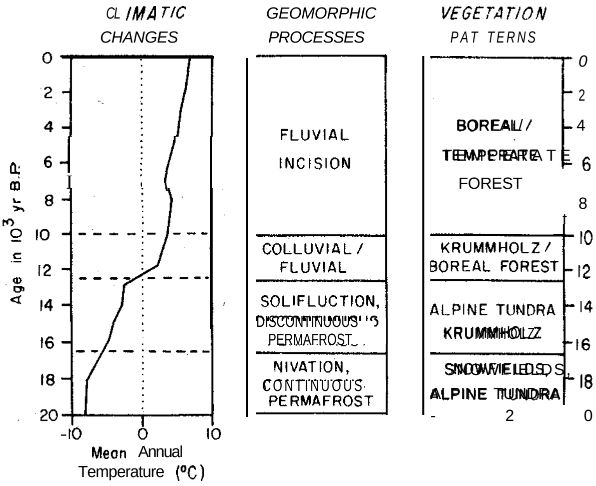

Fig. 5. Late-Quaternary landscape model for interactions of climate, geomorphology, and vegetation at elevations above 1,500 m in the southern Blue Ridge Physiographic Province (from Delcourt and Delcourt 1985).

Solifluction and active colluvial movement of boulder streams were the predominant geomorphic processes through the late-glacial interval (Fig. 5). At Flat Laurel Gap, in western North Carolina, reactivation of solifluction‘ lobes and boulder streams persisted into the early Holocene to as recently as 7,800 yr ‘B.P. (Shafer 1984, 1988; Mills and Delcourt 1989). This geomorphic activity would have been a major form of physical disturbance that may have affected the rate of reestablishment of both boreal and temperate trees on hillslopes throughout the region. Boulder streams have been mapped to as low an elevation as 600 m in the Great Smoky Mountains of East Tennessee and western North Carolina (Michalek 1968).

With the onset of Holocene interglacial climatic

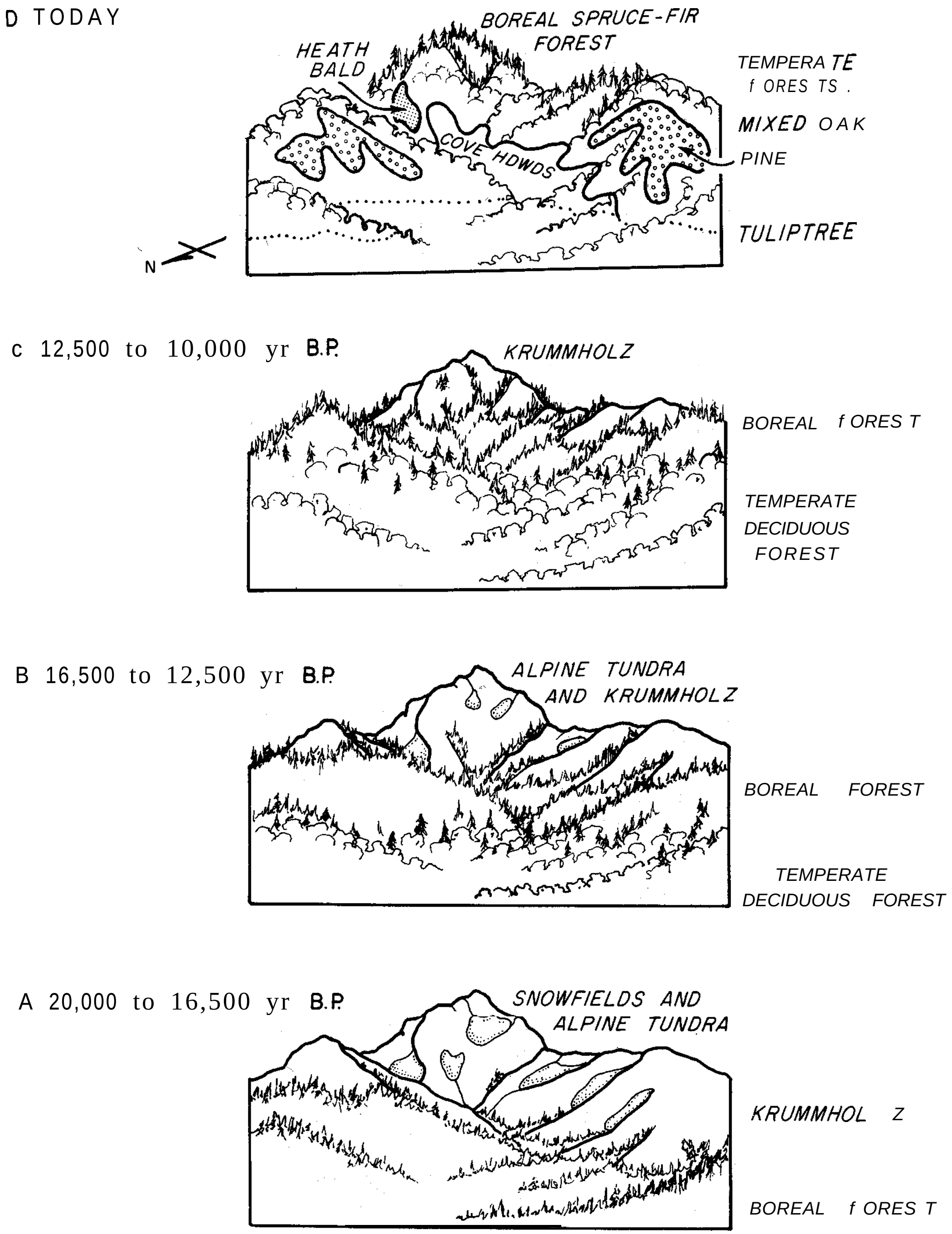

Fig. 6. Long-term landscape changes on Mt. LeConte, Great Smoky Mountains National Park (from Delcourt and Delcourt 1985).

conditions, a major geomorphic threshold was passed, resulting in the replacement of periglacial colluvial processes by temperate fluvial processes (Fig. 5). A decrease in the frequency and intensity of freeze-thaw cycles resulted in stabilization of slopes and inactivation of boulder streams. Fluvial processes became predominant, influencing the distributions of plants on the montane terrain (Hack and Goodlett 1960), but only limited stream incision has occurred during the Holocene (Mills and Delcourt 1989).

Consequences of late-Quaternary history for landscape ecology: tests of hypotheses

Through the late-Quaternary interval, climate change has been a major forcing function for landscape change in the southern Appalachian Mountains. During times of periglacial climate, cryoturbation was the primary geomorphic disturbance regime. The combination of cold temperatures and freeze-thaw churning of the soil resulted in a landscape mosaic that consisted of permanent snowfields and alpine tundra at mid- to high elevations in the central and southern Appalachian Mountains (Delcourt and Delcourt 1985; Figs 5 and 6). Paleoecological sites at relatively low elevations, such as Saltville, Virginia (Delcourt and Delcourt 1986), document species-rich boreal forest below 500 m elevation during full-glacial times.

With late-glacial climatic warming, thresholds were crossed for both fundamental geomorphic processes and cold-hardiness tolerances of plant species. Krummholz and boreal forest began to establish populations farther upslope, interfingering with alpine tundra (Delcourt and Delcourt 1985; Figs 5 and 6). Solifluction moved large quantities of sediment downslope, and active boulder streams funneled mineral debris through mountain ravines and coves. Both fauna1 and paleovegetational records indicate that the late-glacial transition was characterized by increased patchiness of the landscape mosaic, resulting in coexistence of species of small mammals no longer sympatric (Graham 1986) and intermingling of boreal and temperate trees in communities unlike those of today (Delcourt and Delcourt 1986).

With postglacial climatic warming, hillslopes stabilized and fluvial activity became predominant in the southern Appalachian Mountains. Herbaceous plant species formerly characteristic of alpine tundra communities either became locally extinct or else were restricted to high-elevation sites kept open because of disturbances (White 1984). In the Holocene, natural disturbances maintaining grassy balds and populations of relict tundra species included fire, rock fall, and debris avalanches (Grant 1988) that resulted from storms associated with passage of hurricanes emanating from the Gulf of Mexico. During the Holocene, boreal forest spread upslope to the summits of the highest mountain peaks, and deciduous forest replaced boreal forest at mid- and low elevations (Figs 5 and 6). Modern cove hardwoods communities (Cain 1943; mixed mesophytic forest *sensu* Braun 1950) assembled as recently as 10,000 yr B.P. to 8,000 yr B.P.

It is now clear that climatic changes of the Quaternary have had profound effects on the landscapes of the southern Appalachians, not only in redistributing species across landforms, but in changing the rates and kinds of surficial geomorphic processes. Glacial-interglacial climatic fluctuations have enhanced the species richness of the Great Smoky Mountains and other mountain ranges of the southern Blue Ridge Province. The ‘great length of time’ (260 million years) potentially available for gradual accumulation and evolution of species can no longer be used as the major explanation for biotic diversity in the southern Appalachians. Cove hardwoods communities can no longer be viewed as relicts of an Arcto-Tertiary Geoflora (as proposed by Cain (1943) and Braun (1950)). Many of the sites now occupied by cove hardwoods forest were locations continually disturbed by active boulder streams until 10,000 yr B.P. to 8,000 yr B.P. During the last glacial-interglacial cycle, severe geomorphic disturbance and cold periglacial climate would not have favored establishment of temperate trees on Appalachian Mountain slopes until the present Holocene interglacial. The forest communities as we know them have assembled only recently, even relative to the maximum lifetimes of individual trees. The variation in community composition from site to site described as characteristic of mixed mesophytic forest and cove hardwoods forest (Cain 1943; Braun 1950) is now better explained by chance dispersal as deciduous forest species spread northward from glacial refuges in the Gulf Coastal Plain and throughout the southern Appalachian region in postglacial times (Delcourt and Delcourt 1987a).

Natural and cultural landscapes in the Little Tennessee River Valley

Dynamic changes in environment in the southern Blue Ridge Mountains on a late-Quaternary time scale have had important consequences for changing landscapes in adjacent physiographic provinces such as the Ridge and Valley Province of East Tennessee. Rock debris produced at high elevations during full-glacial times was eroded from hillslopes and transported by streams to lower elevations during the late-glacial and Holocene (Delcourt 1980; Delcourt *et al.* 1986). Consequently, in the Valley and Ridge Province of East Tennessee, streams such as the Little Tennessee River aggraded their floodplains during this time interval from 15,000 yr B.P. to 4,000 yr B.P. (Delcourt *et al.* 1986). Changing fluvial geomorphology during the late-glacial transition and the Holocene not only changed the nature of vegetation patches and corridors for movement of animals, but was central to the developing cultures of prehistoric Native Americans. Paleo-Indians first immigrated to the southern Appalachian region 12,000 yr B.P.; Native Americans subsequently lived primarily on aggrading floodplains and on adjacent, topographically higher stream terraces (Chapman 1985). Our investigations of landscape history in the Little Tennessee River Valley have concentrated upon testing whether changes in climate and geomorphology have been the major agents of vegetational change, or, alternatively, whether human activities beginning in late Paleo-Indian and early Archaic times about 10,000 yr B.P. and continuing to the present have had a significant role in altering the landscape mosaic through the Holocene interval.

Interdisciplinary methods of investigation

Geologic framework

Reconstruction of dynamic lanscapes during the time of prehistoric human occupation of the Little Tennessee River Valley was accomplished through geomorphic mapping of stream terraces and radiocarbon dating of Quaternary alluvial deposits underlying the terrace surfaces (Delcourt 1980). Nine sets of alluvial terraces occur within the study area; highest, oldest terraces have undulating land surfaces modified topographically by karst solution and collapse in underlying carbonate bedrock. Fluvial sediments associated with each stream terrace are derived from local sedimentary rocks in the Valley and Ridge Province, as well as metasedimentary rocks transported from the Blue Ridge Province, located to the east. The two youngest stream terraces contained wood and wood charcoal datable within the limits of the radiocarbon method. Wood from Terrace 2 (T2) was dated between about 27,000 and 32,000 yr B.P., indicating that sediment deposition in the T2 floodplain occurred at the transition from a relatively cold (Altonian stadial) time to a relatively warm (Farmdalian interstadial) interval. Wood and wood charcoal contained in sediments underlying the land surface of the youngest terrace (T1) date from 15,000 yr B.P. to 4,000 yr B.P.; the modern floodplain was formed when the T1 was incised 4,000 yr B.P. The timing of deposition of the T1 corresponds with the transition from maximum cold (Late Wisconsin glacial) conditions to maximum warm (mid-Holocene interglacial) conditions (Delcourt 1980). The beginning of deposition of T1 sediments corresponds with the late-glacial pulse of downslope solifluction and the early-Holocene change to predominance of fluvial processes in the adjacent Blue Ridge Province (Shafer 1984, 1988).

Archaeological record

The late-Pleistocene and Holocene chronology of geomorphic events in the Little Tennessee River Valley provides an environmental context that is critical for interpreting the archaeological record. The deeply stratified alluvial deposits of Terrace 1 contain a continuous sequence of human occupation of the Valley that extends back 10,000 years (Chapman 1985 and references cited therein). Using early-historic maps showing the distribution of major Indian towns (Timberlake 1762, *in* Williams **1927),** systematic testing was conducted on over 60 archaeological sites, of which some 25 sites were completely excavated (extensive summary and bibliography of archaeological studies in Chapman 1985). Extensive use of radiocarbon dating of or-

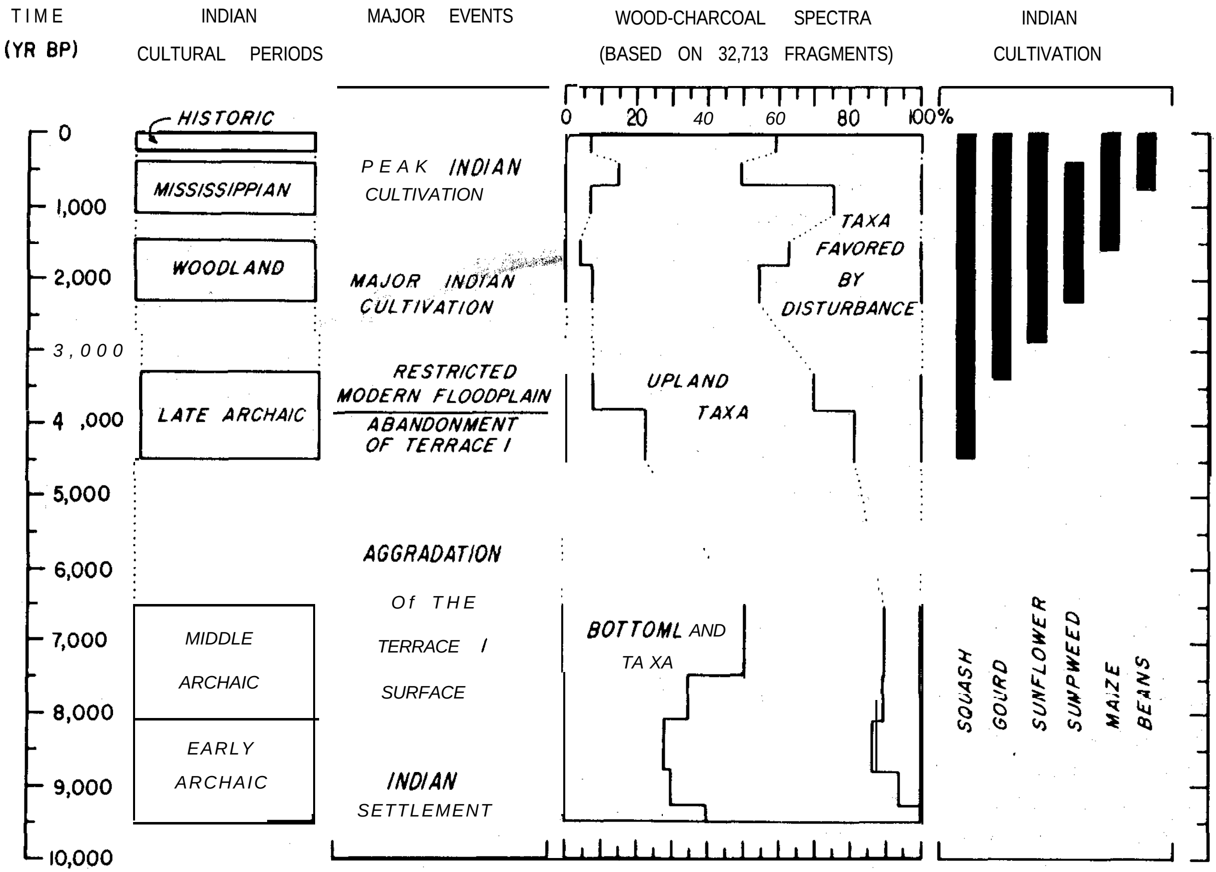

Fig. 7. Major Holocene cultural, environmental, and vegetational events within the Little Tennessee River Valley. The vertical bar for each cultigen corresponds to its temporal range, as preserved within stratified archaeological deposits (from Delcourt and Delcourt 1985).

ganic material (wood charcoal and carbonized fruits and seeds) from the stratigraphic horizons of human occupation provided an absolute chronology for the long-term cultural transformations reflected in changing types of projectile points and ceramic pottery (Chapman 1985).

Locations of hearths, post-holes representing habitation structures, and other archaeological features were systematically mapped at each buried, stratigraphic level (each representing a temporal horizon for a different culture) for subsequent spatial analysis. Ethnobotanical remains (13.7 kg of macroscopic wood charcoal and 7.7 kg of charred fruits and seeds from 956 excavated features) and zooarchaeological remains (animal bones and teeth) recovered from hearths and other archaeological contexts were identified, quantified, and interpreted in the context of Native American utilization of natural resources gleaned from the nearby landscape (Chapman and Shea 1981; Bogan 1982).

The ethnobotanical remains represent plant materials gathered for use as food, fuel, or for construction. Therefore, these plant remains represent a culturally biased record of vegetation composition. However, if it is assumed that people were gathering firewood from an area as close to the hearth site as possible, then the changes in relative representation of woody species in major ecological groupings can be used as a general indicator of changing landscape conditions in the vicinity of human habitations (Chapman *et al.* 1982). We used 32,713 fragments of wood charcoal that were identified to species to summarize the 10,000-year record of changing dominance of local bottomland (riparian) forest, upland forest, and early-successional (disturbed) forest within the valley (Fig. 7; Chapman et *al.* 1982).

Paleoecological record

As an independent record of changes in the vegetation mosaic through time, the fossil-pollen, plant-macrofossil, and charcoal-particle records from sediments of two ponds weredocumented for comparison with the archaeological record (Cridlebaugh 1984). The two sites chosen for paleoecological analysis (Figs 8 and 9) were (1) Tuskegee Pond, located near the Historic Cherokee town of Tuskegee on a mid-level Quaternary stream terrace 1.5 km from a major archaeological excavation of the T1 (Icehouse Bottom); and (2) Black Pond, located in the karst uplands about 4 km northeast of Tuskegee Pond. Small pond sites were chosen to reflect primarily the local (within 20 m radius of the site) and extralocal (20 m to 2 km radius of the site; Prentice 1985; Jackson 1988) contribution of fossil plant remains, with only a minor regional component to the pollen assemblages (Jacobson and Bradshaw 1981). Cross-comparison of the paleoecological records from the two sites, along with comparison of corresponding prehistoric changes in the ethnobotanical record, allows estimates of the area1 extent of land clearance and vegetational change during the Holocene along a gradient of human modification of the landscape, extending from the floodplain sites of continuous human settlement across higher alluvial terraces and into the uplands. The charcoal-particle record in the pond sediments provides an indication of changes in fire frequency through time, and changes in sedimentation rate indicate changes in erosion of hillslopes surrounding the ponds (Delcourt et *al.* 1986).

Synthesis of Holocene landscape history

More than 50 scientific publications, theses, and dissertations provide the evidence for particular aspects of the Holocene environmental, biotic, and prehistoric cultural data from the Little Tennessee River Valley (see references in Chapman 1985 and Delcourt *et al.* 1986). Here we characterize the major environmental and human forcing functions, landscape responses, and resulting changes in landscape patterns through time (Fig. 8) that can be inferred from both published and unpublished summaries of the geomorphic, archaeological, and paleoecological data.

In the early Holocene, in adjustment to the influx of sediment, the floodplain of the Little Tennessee River was aggrading in response to climatic warming that triggered erosion of sediments from nearby hillslopes in the Blue Ridge Province. Where the Little Tennessee River emerged from its relatively restricted, meandering channel carved through the Blue Ridge Province and flowed westward into the Ridge and Valley Province, its floodplain broadened and it became a braided stream, creating an anastomosing series of wide, riparian corridors (Fig. 8a). At the Icehouse Bottom archaeological site, pollen evidence from gley soils buried beneath alluvium indicates that by 9,500 yr B.P., the landscape was predominantly forested, with deciduous forest of oak (*Quercus*), chestnut ***(Castanea dentata),*** and hickory ***(Carya)*** probably widespread across the uplands of the Ridge and Valley Province. Species of ash ***(Fraxinus),*** elm (*Ulmus*), and willow ***(Salix)*** occupied bottomlands along stream courses and point bars of the aggrading floodplain. The pollen record from the early Holocene contains very little evidence of herbs such as grasses, sedges, and composites, indicating that openings in the forest were infrequent and probably confined to small, frequently disturbed areas along point bars, river-eroded outcrops of steep bluffs, and temporary hunting camps of PaleoIndian and early Archaic people. The incidence of wildfire was probably low in the mesic forested environment of the

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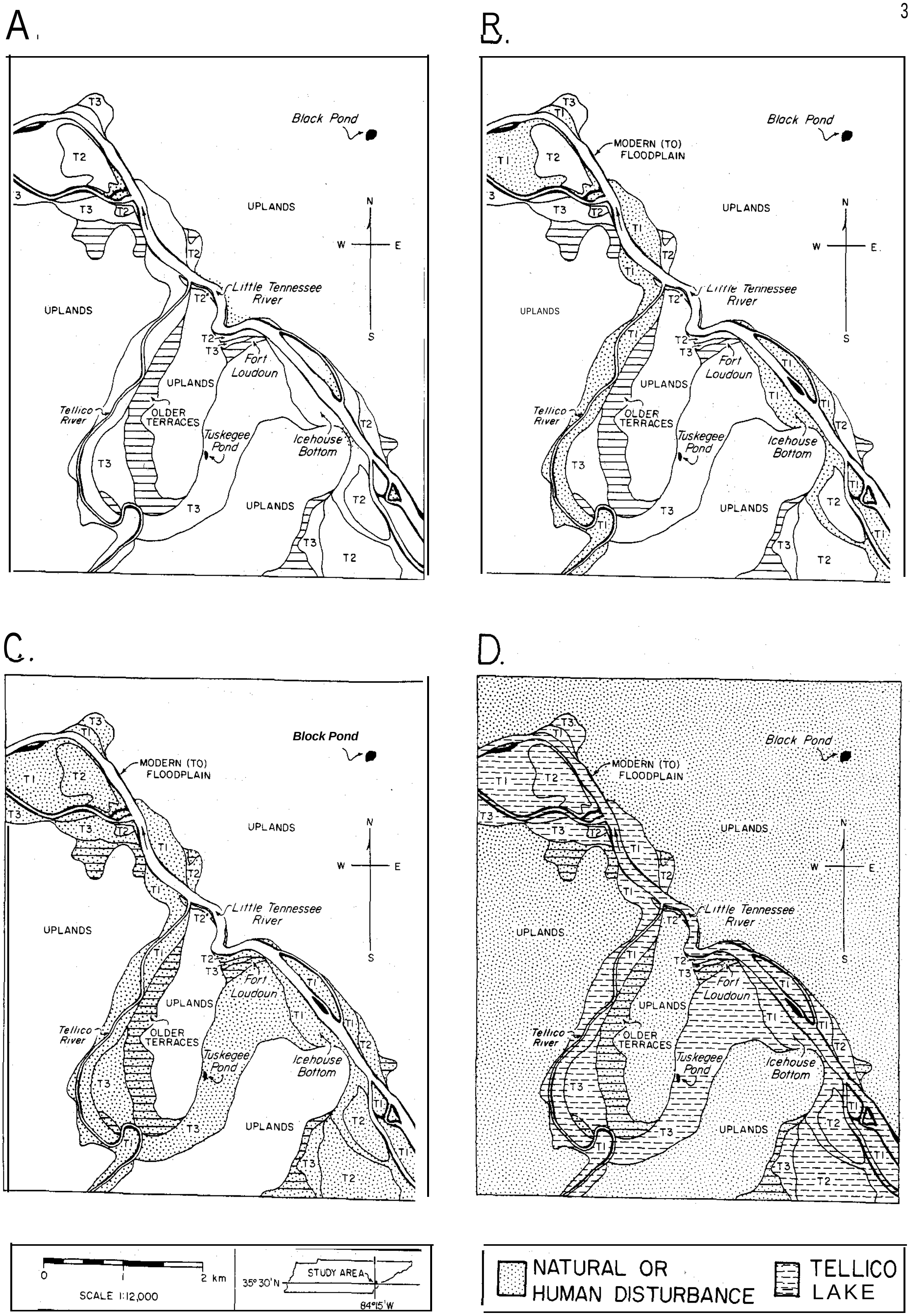
Fig. 8. Landscape reconstructions for the Little Tennessee River Valley, East Tennessee, showing the distribution of stream corridors and the mosaic of forest and nonforest vegetation. (A.) PaleoIndian cultural period, 12,000 yr B.P. to 10,000 yr B.P. (B.) Archaic cultural period, 10,000 yr B.P. to 2,800 yr B.P. (C.) Woodland and Mississippian cultural periods, 2,800 yr B.P. to 500 yr B.P. (A.D. 1,500). (D.) Historic cultural period, 500 yr B.P. (A.D. 1,500) to present.


A.
B.
C.
D.
Black Pond
MODERN (TO) FLOODPLAIN
UPLANDS
Little Tennessee River
Fort Loudoun
Tellico River
OLDER TERRACES
Tuskegee Pond
Icehouse Bottom
T1
T2
T3
N
S
W
E
0
1
2 km
SCALE 1:12,000
35°30'N
STUDY AREA
84°15'W
NATURAL OR HUMAN DISTURBANCE
TELLICO LAKE

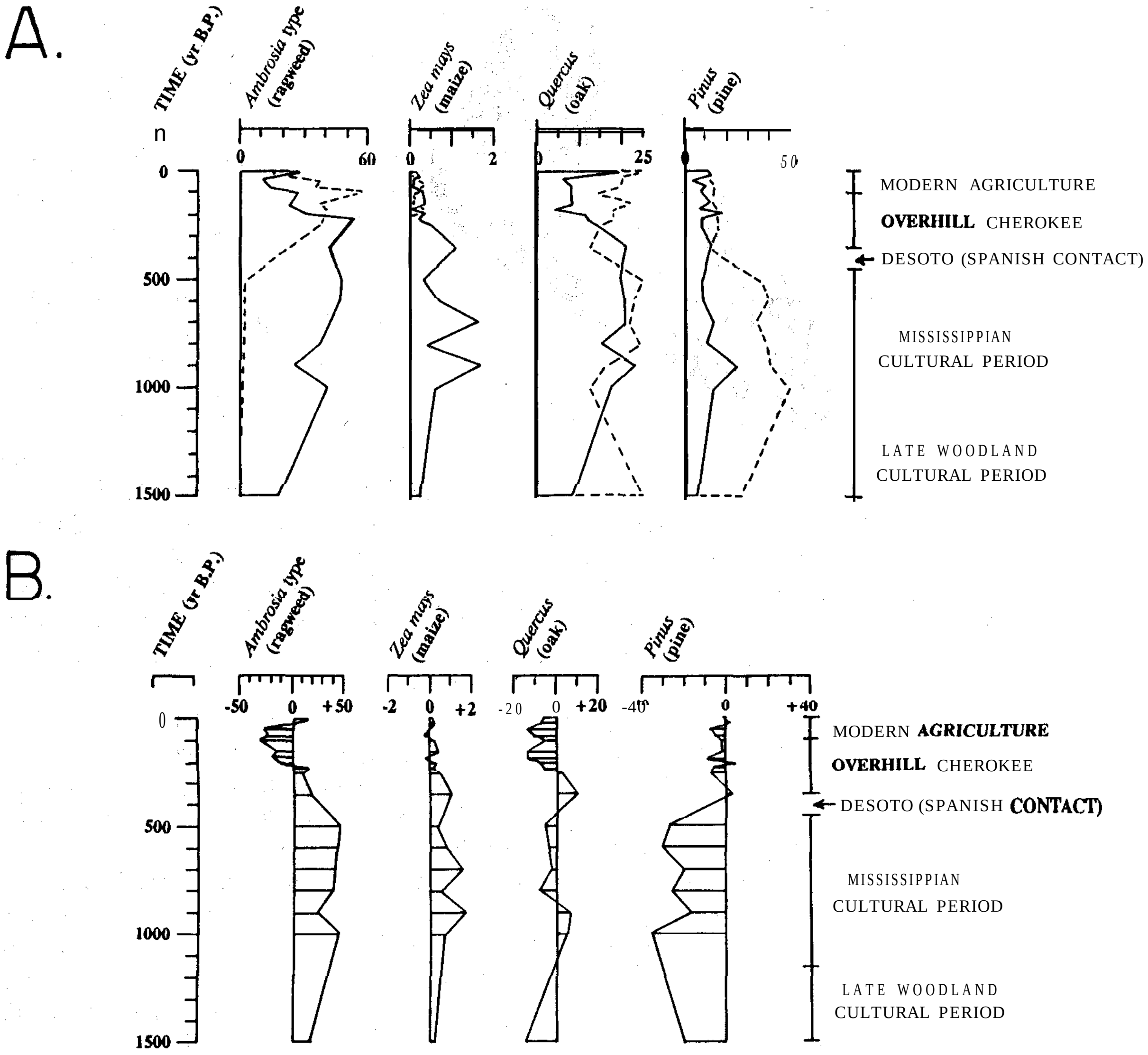


Fig. 9. (A.) Contrast diagram of Tuskegee Pond (solid curve) and Black Pond (dashed curve), Little Tennessee River Valley, for 1,500 yr B.P. to the present. Percentages are expressed as percent of arboreal pollen grains plus nonarboreal pollen grains and spores, excluding grains of obligate aquatic plants. (B.) Difference diagram of Tuskegee Pond minus Black Pond, Little Tennessee River Valley, for 1,500 yr B.P. to the present. Percentages are expressed as percent of arboreal pollen grains plus nonarboreal pollen grains and spores, excluding grains of obligate aquatic plants.

aggrading floodplain, although fire may have been used deliberately by Native Americans for hunting in game drives or to open the understory of upland oak-chestnut-history forests.

Through the Archaic cultural period (10,000 yr B.P. to 2,800 yr B.P.; Fig. 8b), the wood-charcoal record reflects primarily the utilization of bottomland trees that would have been readily available in the local environment of the aggrading floodplain (T1) surface. The ethnobotanical record of charred fruits and seeds was comprised mainly of mast trees, including husks of hickory nuts (*Carya*) and walnuts (*Juglans nigra*) as well as acorns of oak (*Quercus*). Hazelnuts (*Corylus*) and chestnuts were used to a lesser degree as plant foods by the aboriginal populations of Native Americans. After 4,500 yr B.P., the first cultigens were introduced, including squash *(Cucurbita pepo)* and gourd *(Lagenaria siceraria).* After 4,000 yr B.P., the T1 alluvial surface was incised and abandoned, forming the restricted modern floodplain; representatives of bottomland forest taxa diminished in the wood-charcoal record at that time, corresponding with the reduction in area of the bottomland habitat. However, as the Tl terrace became more well-drained, populations of early-successional plant taxa increased, including red cedar *(Juniperus virginiana),* pine *(Pinus virginiana),* cane *(Arundinaria gigantea),* and tuliptree *(Liriodendron tulipifera)* .

The incision and abandonment of Terrace 1 by the Little Tennessee River may have been a hydrologic response to climatic change at the transition from middle to late-Holocene times. Alternatively, it may have resulted from human modification of the landscape, including both deforestation and cultivation of garden plots. Based on the spatial distribution of habitations and other archaeological features, by 2,800 yr B.P., the end of the Archaic cultural period, we infer that all of the T1 surface was disturbed by the activities of Native Americans, no longer in original forest, but converted to clearings and in early stages of secondary succession (Fig. 8b). The landscape may have been kept open through the deliberate use of fire, and hearth fires may have escaped accidentally from control as well.

During the Woodland cultural period (2,800 yr B.P. to about A.D. 900; Fig. 8c), lifeways became more sedentary. Pottery was developed, and garden plots were cultivated. Crops included a diverse group of species often referred to as the 'eastern agricultural complex' (Ford 1985), such as sunflower *(Helianthus annuus)*, marsh elder *(Iva annua),* goosefoot *(Chenopodium),* and canary grass *(Phalaris caroliniana).* Fire would have been used by Woodland people to clear garden plots, fire pottery, and to cook food. Maize *(Zea mays)* was introduced by 1,775 yr B.P., and in the Mississippian cultural period, after A.D. 900, maize became the primary plant food in the diet. Increasing dependence on maize-required more intensive cultivation of the land in order to sustain increasing human populations. By A.D. 1,500, the proportion of early-successional plant species recorded in the wood-charcoal record increased to as much as 50% of all wood utilized by Mississippian people.

The pollen record from Tuskegee Pond (Delcourt *et al.* 1986) shows that by 1,500 yr B.P. maize cultivation extended to mid-level terraces at distances up to at least 1.5 km from the modern floodplain. Pollen of herbs today associated with agricultural fields *(i.e.,* ragweed *(Ambrosia* type)) was as much as 30% of the upland pollen assemblage from Tuskegee Pond as early as 1,500 yr B.P., indicating a very open landscape by late Woodland times. The record of charcoal particles from Tuskegee Pond sediments shows order-of-magnitude increases in the use of fire corresponding with the changes in major cultural periods of prehistoric and historic Native Americans. The paleoecological record from Black Pond, located in the uplands about 4 km away from the river, contained less than 5% ragweed pollen until about 400 years ago, after which ragweed percentages increased dramatically. With the records from the two paleoecological sites, it is possible to realistically constrain the area of human impact on the forest/nonforest mosaic through time (Figs 8c and 9a, b).

The paleoecological records from Black and Tuskegee ponds can be compared directly by means of a 'contrast diagram' (Janssen *et al.* 1985; Fig. 9a) and a 'difference diagram' (Jacobson 1979; Fig. 9b). These diagrams illustrate graphically that the two paleoecological sites have recorded distinctively different histories of vegetational change through the past 1,500 years that can be attributed to differences in land use by prehistoric Native Americans. Prior to Spanish contact in A.D. 1,540, deforestation and agriculture was restricted to lowlands along the Little Tennessee River, whereas after Euro-American settlement, the uplands were deforested of pine and converted to agricultural fields. Pollen percentages of ragweed *(Ambrosia* type) subsequently diminished in the lowlands, tracking the historic decline of Overhill Cherokee populations that formerly occupied valley bottoms and river terraces (Chapman, 1985). The dramatic differences in the pollen records from these two small pond sites indicates that their pollen source areas do not overlap to a substantial extent. Thus, small sites such as Black Pond and Tuskegee Pond, situated along an elevational transect and spaced 4.5 km apart in settings with different land use histories, can be used in combination to place spatial constraints on the area impacted by long-term human activities on a watershed of the scale of the Little Tennessee River (Figs 3 and 8).

Both archaeological and paleoecological evidence indicates intensified land use along the riparian corridor and on the lower and mid-level stream terraces of the Little Tennessee through the Woodland and Mississippian cultural periods. With progressive Indian clearance of forests on the floodplain and lower terraces, and with intensification of crop cultivation, the late-Holocene landscape was gradually converted into a mosaic consisting of permanent Indian settlements and cultivated fields, early-successional forests invading abandoned Indian old-fields, and remnants of original deciduous forest in the uplands. As the forests continued to be fragmented by the ever-enlarging agricultural fields, forest-edge habitat would have increased. This in turn would have provided additional browse that together with the greater extent of forest edge would have led to increases in the populations of deer and wild turkey, both abundantly represented in the zooarchaeological record (Bogan 1982).

In Historic times, with introduction of new technology such as the iron hoe, cultivation of the land became more efficient. This is reflected in the sediment record of Tuskegee Pond by an order-of-magnitude increase in sedimentation rate. Beginning with the Spanish, Euro-Americans introduced a series of domesticated plants, animals, and weeds, once again transforming the lifeways of the Historic Cherokee. Today's agricultural landscape (Fig. 8d) includes old-fields that are invaded by a mixture of native and introduced species. All of the landscape within the study area mapped in Fig. 8d is either in secondary succession or flooded beneath the Tellico lake impoundment.

Over the past 10,000 years of the late-Quaternary interval, the vegetation mosaic of the Little Tennessee watershed has undergone long-term and progressive modification, gradually being transformed from a natural landscape to a culturally maintained one. We conclude that, in the Little Tennessee River Valley, Native Americans were not living in balance with their environment, although at any given moment they may have perceived it as such, but rather they were part of and active agents within a dynamically changing landscape.

Priorities for future research

The case studies reviewed in this paper illustrate the potential for collaborative research among Quaternary paleoecologists, geomorphologists, archaeologists, and landscape ecologists to provide a productive approach to examining the long-term changes in both natural and cultural landscapes. Priorities for future research in Quaternary Landscape Ecology include:

1. Additional refinements in research design to make it possible to develop more quantitative reconstructions of the changes in area, shape, configuration, heterogeneity, and connectivity of landscape patches and corridors on a Quaternary time scale. This basic documentation will be useful as boundary conditions for studies of more recent landscape changes at, for example, Long-Term Ecological Research sites such as Coweeta in western North Carolina (Swank and Crossley 1988).

2. Development of definitive tests of landscape hypotheses such as Godron and Forman's (1983) predictions of changes in patch characteristics, corridors, and other landscape features along a gradient of human modification. Temporal tests of this landscape hypothesis would not only complement the spatial tests that can be accomplished by comparing the patterning of modern natural, managed, agricultural, suburban, and urban landscapes, but would also yield new insights such as timing of introduction of invasive weedy plant species. Such events of biological invasion may have major ramifications for subsequent changes in ecological relationships within communities (Mooney and Drake 1986; Crosby 1986), but the process by which these changes have occurred in prehistoric times may be knowable only by using paleoecological or archaeological methods of investigation.

3. Using available tools to help solve fundamental ecological problems at the interface between meso-scale and micro-scale domains. One example is investigating the nature of presettlement vegetation and its prior development. The notion of a 'virgin' and 'stable' presettlement vegetation *(circa* A.D. 1,500 to A.D. 1,800) is a baseline assumption for most contemporary research in North American plant ecology and for management of natural resources. Was the presettlement vegetation mosaic changing at the time of Euro-American settlement? If so, was it responding to climatic change, prehistoric human impacts, or some combination of forcing functions? What were the spatial and temporal patterns of these landscape dynamics on a meso-scale, and what were their relationships to sensitive ecotones such as the prairie-forest border?

4. Challenge to develop new testable hypotheses in landscape ecology that have central significance to all of ecology. These might center around scale-dependent interactions of perturbations, processes, and patterns such as: (a) the effects of changes in landscape heterogeneity on community assembly and population dynamics; (b) the relative influence of environmental change, biological interactions, and human activities in structuring communities; and (c) the effects of changes in the patchwork of the landscape mosaic for microevolutionary processes including selection for demographic characteristics in plant populations (investment in seed production and mechanisms for seed dispersal), the importance of changes in connectivity of corridors for animal migrations and/or extinctions, or the effects of changing size, shape, and configuration of vegetation patches for long-term sympatry of small mammals within a region.

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