Landscape History and Ecological Change

Norman L. Christensen

North American ecologists have a long tradition of studying "natural" or undisturbed ecosystems. In addition to the innate affection for wilderness that likely initially enticed most ecologists to their discipline, practical reasons have prompted this focus. Ecologists seek to identify and understand the factors regulating the distribution and abundance of organisms. Interpreting the complex relationships between organisms and their environments is complicated by the variation in ecological communities caused by disturbances and past human interventions. Ecologists can control the effects of these external variables on their research by studying undisturbed ecosystems.

Yet ecologists have for some time recognized that their concentration on natural ecosystems is, in many cases, rather naive or even misleading. During the past several years, the emphasis of their research has shifted to the consequences of past historical events for the current structure and function of ecosystems. Several factors account for this shift.

First, it has become obvious that the research emanating from the focus on natural ecosystems suffers from serious limitations. Although statistically significant relationships between the distribution of organisms and existing environmental conditions have allowed us to construct predictive models, such models often account for only a small part of the observed variation among ecosystems.[1] We are forced to conclude that the unexplained variation is due either to unmeasured variables or to past events.

Second, we are increasingly aware of the longevity of historical impacts. For many years, ecologists assumed that the importance of the historical impacts of human interventions would diminish to insignificance given sufficient time for succession to "heal the wounds." In recent years, however, this assumption has been seriously questioned. Many plants, especially forest trees, live a long time. Because of this longevity, past environmental conditions play a significant and continuing role in the structure of most forest ecosystems.

Third, we are beginning to understand that the processes regulating the structure and function of ecosystems function on a spatial scale much larger than the conventional ecological study unit—the population or stand. As ecologists turn their attention to landscape-scale patterns and processes, they cannot avoid accounting for influences stemming from human uses of the land. Even segments of a landscape that have not been directly disturbed are influenced by the human factors affecting surrounding areas. A small plot of undisturbed woods preserved in the midst of an otherwise urban landscape differs markedly

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[1] Norman L. Christensen and Robert K. Peet, "Convergence During Secondary Forest Succession," *Journal of Ecology* 72 (March 1984): 25–36.

from a similar plot surrounded by undeveloped forest. Thus past land use patterns may influence the structure of wilderness remnants that appear not to have been directly altered by human activities.

Finally, the influence of human interventions in the environment will continue to grow in the future. Thus the most compelling reason to study the effects of past history on the current structure of ecosystems is our desire to make informed predictions about future changes in the ecosystem.

This essay presents an overview of this new area of ecological research. I shall discuss the use of the term "history" among ecologists and assert that our views of the effects of historical events on ecosystems are colored by our understanding of the nature and mechanisms of ecosystem change. Having established that past history does affect current ecosystems, I shall discuss several approaches to deciphering the historical record from the structure of the ecosystem. In addition, I shall describe examples that demonstrate how purportedly simple historical effects are often brought about by complex influences. I shall also demonstrate the importance of historical studies to our understanding and management of current ecological problems. I shall argue, in conclusion, that the history of land use and the succession of ecosystems are directly linked: future land use depends in large part on the nature of ecosystem change, which, in turn, is often initiated and affected by patterns of land use.

The Ecologist's View of History

Ecologists often use the terms "history" and "historical effect" in their most generic senses. In the ecological literature, any property of an ecosystem that is a consequence of some past event, whether or not caused by humans, is often said to be "due to history."[2] Indeed, variations in ecosystem characteristics not attributable to current environmental conditions are often simply attributed to "historical effects." I do not wish to defend ecologists' lax use of these terms. Rather, I feel it illustrates a very basic philosophical difference between the central interests of the disciplines of history and ecology.

The historian most often focuses on humans and the human condition; the ecologist on the causes of ecological variation. This is not to say that ecologists are not interested in humans, but rather that ecologists view humans simply as one factor altering the environment. When, for example, an ecologist studies the effects of a forest fire on the forest ecosystems, the event has the same ecological consequences regardless of its origin. Whether the forest fire was started by a lightning strike or by human activity is thus of little consequence to the ecologist. Furthermore, the ecologist may not be equipped to answer the question of exact causes. Many "natural" and human-caused events have similar ecological consequences, so ecological data alone are often insufficient to identify the specific agents of past disturbance.

The Role of History in Changing Landscapes

Since Henry Chandler Cowles's description of the patterns of vegetation change on sand dunes surrounding Lake Michigan,[3] American plant ecologists have been preoccupied with studies of succession, or ecosystem change following disturbance. Frederick E. Clements, influenced by Cowles's work and his own observations of prairie ecosystems, developed a comprehensive theory describing the mechanisms and patterns of successional change that was the mainstay of plant community ecology for nearly half a century.[4] According to this theory, the primary forces driving successional change are biotic reaction and competition. Clements coined the phrase "biotic reaction" to describe the influence of organisms on their environment. An example of a biotic reaction is the mechanical and chemical weathering of soil caused by plant roots. "Competition" refers to the effects of one organism on another that uses a common shared resource in short supply.

Figure 1 is a diagram of the pattern of succession as described by Clements's theory. The process is initiated by a disturbance resulting in "nudation." Clements realized that the considerable variation among disturbances in postdisturbance environments would greatly affect the rate and trajectory of this process. Disturbances that leave habitats devoid of soil (e.g., volcanic eruptions, glaciation, etc.) initiate so-called primary succession and typically produce very slow rates of invasion and successional change. Successional change is much more rapid following disturbances such as fire and land clearing in which soil and even some surviving plants are left (secondary succession). Nevertheless, Clements thought that the general mechanisms of successional change were the same in both cases. Early invading organisms (pioneers) establish and alter the environment in such a way as to favor the establishment and growth of other potential migrants over themselves. In the same manner, these migrants change their environment so that they too eventually are replaced. This process of replacement continues until a community of plants (and animals) is established that alters the environment to one that favors their own reproduction. This is the climax.

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[2] See for example William H. Drury and Ian C. T. Nisbet, "Succession," *Journal of the Arnold Arboretum* 54 (July 1973): 331–68, or several of the papers in Darrel C. West, Herman H. Shugart, Jr., and Daniel B. Botkin, eds., *Forest Succession: Concepts and Application* (New York: Springer-Verlag, 1981).

[3] Henry C. Cowles, "The Ecological Relations of the Vegetation on the Sand Dunes of Lake Michigan," *Botanical Gazette* 27 (February 1899): 95–391.

[4] Frederick C. Clements, *Plant Succession: An Analysis of the Development of Vegetation*, Carnegie Institute of Washington Publication 242 (Washington, D.C.: Carnegie Institute of Washington, 1935). For a lucid history of the Clementsian school of ecology see Ronald C. Tobey, *Saving the Prairies: The Life Cycle of the Founding School of American Plant Ecology, 1895–1955* (Berkeley: University of California Press, 1981).

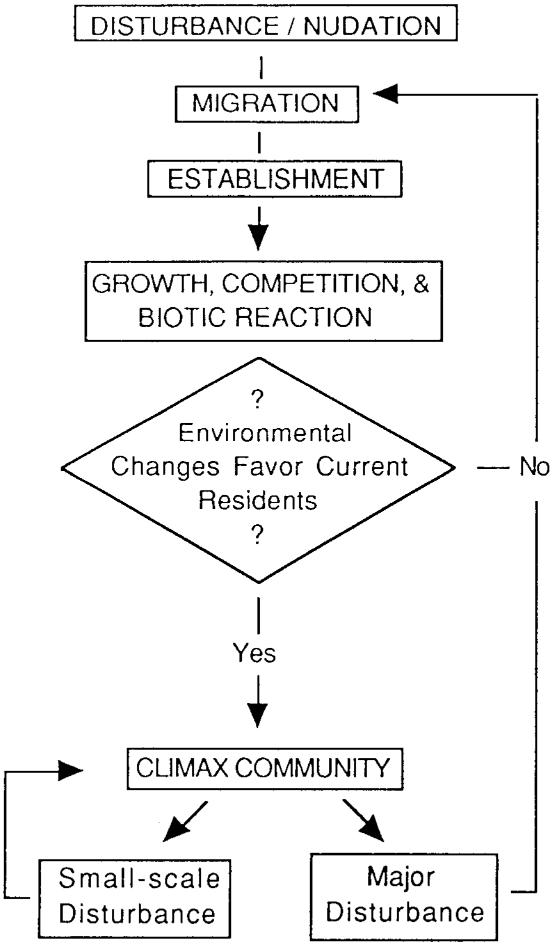

Figure 1. Diagram of processes in ecological succession as proposed by Frederick E. Clements.

One of Clements's central assertions was that regardless of the types or varieties of disturbances that initiated successional change on a landscape, succession inexorably leads to a single climax community whose composition is determined by the characteristics of the region's climate.[5] Although the pioneer vegetation surrounding a kettle lake and that growing on an outwash plain on a recently deglaciated landscape initially have little in common, biotic reactions result in increased environmental similarity, and this results in increasing similarity among later successional communities. Similarly, the vegetation of a field recently abandoned from row crops and another abandoned from pasture may be quite different, but successive communities in these two fields will become increasingly similar.

Clements's notion of ecological convergence has important consequences for both the historian and the ecologist. If true, it suggests that historical effects are eventually erased by succession and that the structure and composition of relatively late successional ecosystems may contain little information about their past history. To the ecologist, it also indicates that if one simply waits long enough, historical events and patterns of past disturbance will become relatively unimportant.

Certain of Clements's assertions, such as the notion of a single ultimate climax or "monoclimax," were questioned rather quickly.[6] Ecologists recognized that local soil and hydrological conditions greatly influenced the structure and function of ecosystems and that these conditions were not likely to be changed by biotic reaction, even over long time spans. Thus developed the theory of "polyclimax," an accommodation to explain why vegetation was not homogeneous over large regions, but rather varied continuously along environmental gradients.[7] Nevertheless, many of the central tenets of Clements's paradigm were widely accepted by ecologists until the 1960s.[8]

Nearly all successional studies up to the 1960s were based on comparing at a single point in time ecosystems of varying successional age. Such studies assumed that the younger samples would eventually look like the older samples and that the older samples once looked like the younger ones. The mechanisms that drive successional change were, for the most part, taken for granted: very few studies actually rigorously demonstrated the roles of biotic reaction or competition in driving successional change. Gradually, however, some ecologists came to realize that the available data were not sufficient to support the major assumptions of Clements's model.

Some of the critics began to argue that pioneer species usurped available resources and prevented subsequent invasion until they began to decline, instead of preparing the way for subsequent invaders. Thus they argued that succession was driven by dispersal and competitive exclusion; if later successional species had access to a site, they could invade recently disturbed habitats.[9] Other ecologists argued that many successional sequences were a simple consequence of differential longevity. Most species that eventually invaded a site arrived early, and those that lived longest (e.g., broad-leafed trees) formed the eventual climax community.[10]

Suffice it here to say that both of these patterns have been shown to be important in one or another ecosystem. The notion of convergence has not been entirely abandoned, but patterns of convergence, if and when they occur, have

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[5] Frederick E. Clements, "Nature and Structure of the Climax," *Journal of Ecology* 24 (February 1936): 252–84.

[6] Henry A. Gleason, "The Individualistic Concept of the Plant Association," *Bulletin of the Torrey Botanical Club* 53 (January 1926): 7–26.

[7] See Henry I. Oosting, *The Study of Plant Communities*, 2nd ed. (San Francisco, California: Freeman, 1956), pp. 252–64, and Rexford F. Danbenmire, *Plant Communities* (New York: Harper and Row, 1968), p. 240, for discussions of polyclimax.

[8] Eugene P. Odum, "The Strategy of Ecosystem Development," *Science* 164 (1969): 262–70.

[9] Joseph H. Connell and Ralph O. Slatyer, "Mechanisms of Succession in Natural Communities and Their Role in Stability and Organization," *American Naturalist* 111 (1977): 1119–44.

[10] Frank G. Egler, "Vegetation Science Concepts: 1. Initial Floristic Composition—A Factor in Old Field Vegetation Development," *Vegetatio* 4 (no. 4, 1954): 412–17; Frank G. Egler, *Nature of Vegetation: Its Management and Mismanagement* (Bridgewater: Connecticut Conservation Association, 1976), pp. 165–66.

been shown to be far more complex than originally envisioned by Clements. Consequently, the last twenty years have witnessed the nearly complete demise of Clements's theory of succession.[11]

The alternative successional models postulate an important difference in the role past history plays in ecosystem structure. For example, if most eventual climax species do indeed arrive early and simply live longer, disturbances may have long-range ecological consequences—lasting for centuries and longer.

One of the most significant changes to occur in ecologists' views of successional change is the realization that, even on the scale of decades and certainly on the scale of centuries, environments are not static. Palynologists have demonstrated that the vegetation of North America has been in a continuous state of flux for the past forty thousand years. Most ecologists agree that such variation has been the norm since the Pleistocene.[12] It is now generally recognized that natural disturbance cycles, involving such agents as fire, wind, or pathogens, are a normal part of most landscapes and that few ecosystems ever achieve a steady-state climax.[13] Furthermore, abundant data convince us that humankind has influenced the composition and structure of nearly all North American ecosystems for nearly ten thousand years. Because the properties of environment (i.e., the factors affecting the relative success and performance of organisms) are not static, ecologists have come to recognize that it is generally hopeless to try to understand environmental dynamics in the absence of human influences.

The Historical Record in the Ecosystem

Ecologists generally agree that past events influence the properties of current ecosystems. They vary, however, in deciding which features of ecosystems ought to be used to reconstruct past history. What follows is a brief review of ecological approaches to identifying the influences of past events. It is important to note that these approaches may tell us a good deal about *what* has happened in the past, but they only rarely tell us *why*. For example, forest data may identify a period of high tree mortality fifty years ago, but such data are unlikely to indicate the cause of tree death.

The architecture or physical structure of a forest stand or the individual trees within it may provide information about its past. In southeastern pine forests the diameter-to-height ratio of the dominant trees correlates highly with growth conditions (such as initial stand density) in the abandoned field in which they establish.[14]

Mark McDonnell and Edward Stiles show that variations in the physical structure of forest stands that regenerate from abandoned agricultural fields may determine the spatial patterns of different tree species within such stands.[15] Such significant historical variations include the size of the field and the presence or absence of agricultural debris, fence posts, and other structures affecting the behavior of animals that disperse tree seeds into such fields.

As forests develop and mature, a forest floor of litter and woody debris begins to accumulate. Fires add charcoal to the soil. Trees blown over by wind create tip-up mounds and pits, churning the soil and altering microtopography. In order to reconstruct the disturbance history of a forest stand in the Pisgah Forest of southwestern New Hampshire, J. D. Henry and J. M. A. Swan excavated a tenth-acre site using much the same techniques an archaeologist might use to excavate a site of suspected past human habitation. They took a census of the living vegetation, measured woody debris, and used various techniques to infer the year of death for downed and decayed logs. They excavated the soil to determine the location of long-decayed logs and deposits of charcoal. Then they analyzed their data to reconstruct the history of disturbance in this stand back to 1665.[16]

Carbon dating of charcoal from soils beneath forests in the Amazon Basin has been used to document patterns of human land use and burning over the past several centuries.[17] Thomas Bonnicksen and Edward Stone use a similar approach to reconstruct past stand structure and history in the giant sequoia forests of the central Sierra Nevada.[18] By linking their reconstructions to features of the forest that can be discerned from aerial photographs, they then extend their analysis to a landscape encompassing hundreds of square kilometers. These researchers suggest that this method might be used by agencies such as the National Park Service to determine the precolonial structure of ecosystems when designating wilderness in areas that have been altered by human activities.

Although such studies are of some use in documenting past episodes of disturbance, they suffer from several shortcomings. Of these, perhaps the most important is their limited scope. They typically focus on relatively small areas (usually

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[11] Unlike the scientific revolutions described by Thomas Kuhn in *The Structure of Scientific Revolutions* (Chicago, Illinois: University of Chicago Press, 1962).

[12] Paul A. Delcourt and Hazel R. Delcourt, *Long-Term Forest Dynamics of the Temperate Zone* (New York: Springer-Verlag, 1987), pp. 5–16.

[13] This recognition has led ecologists to view landscapes as mosaics of patches recovering from disturbance. See Peter S. White, "Pattern, Process, and Natural Disturbance in Vegetation," *Botanical Review* 45 (July–September 1979): 229–99; and several chapters in Steward T. A. Pickett and Peter S. White, eds., *The Ecology of Natural Disturbance and Patch Dynamics* (New York: Academic Press, 1985).

[14] Robert K. Peet and Norman L. Christensen, "Competition and Tree Death," *BioScience* 37 (September 1987): 586–95.

[15] Mark I. McDonnell and Edward J. Stiles, "The Structural Complexity of Old-Field Vegetation and the Recruitment of Bird-Dispersed Species," *Oecologia* 56 (January 1983): 109–16.

[16] J. D. Henry and J. M. A. Swan, "Reconstructing Forest History from Live and Dead Plant Material: An Approach to the Study of Forest Succession in Southwest New Hampshire," *Ecology* 55 (Summer 1974): 772–83.

[17] Robert L. Sanford, Juan Soldarriaga, Kathleen E. Clark, Christopher Uhl, and Raphael Herrera, "Amazon Rainforest Fires," *Science* 227 (January 1985): 53–55.

[18] Thomas M. Bonnicksen and Edward C. Stone, "Reconstruction of a Presettlement Giant Sequoia–Mixed Conifer Forest Community Using the Aggregation Approach," *Ecology* 63 (August 1982): 1134–48.

a few hundred square meters), and thus they seldom provide a statistically meaningful history of change for entire forest stands, much less landscapes or regions.

Another problem is the accuracy of the data collected. Several researchers have questioned the precision of dating disturbances on the basis of dead debris on and in forest soils.[19] Because disturbances are often spatially heterogeneous, they will not leave behind uniform accumulated debris or charcoal throughout a forest. Furthermore, the technical problems in making such estimates are numerous and are complicated by the varying rate of decay of such debris among locations and tree species. From a practical standpoint, the labor-intensive and destructive nature of such methods is another major drawback.

The species that compose a forest community can also provide information about its past. The presence of shade-intolerant trees in the forest canopy is usually a sign of past disturbance. This is true today in the southeastern United States, where shade-intolerant trees such as pine or tulip tree in the forest canopy provide a reliable measure of the nature and extent of past disturbance.[20] In the western United States, however, this generalization does not hold. Western land management policies that excluded natural wildfire eventually allowed shade-tolerant trees to invade the understory of relatively open mixed-conifer forests.[21]

In forest ecosystems in which species that dominate late in succession actually establish relatively early, the distribution of such species may provide evidence of the nature of disturbance or the immediate postdisturbance environment. In southern New England, for example, secondary forests dominated by birch likely became established in fields that had been row cropped before they were abandoned. On the other hand, redcedar predominates in forests established in old pastures.[22]

Even some herbaceous plants indicate past forest history. For example, in forests of the southeastern U.S. piedmont, the common garden periwinkle (*Vinca minor*) is a faithful indicator of the location of old homesites and graveyards. The distribution of specific herbs in the woods of Great Britain is an important tool used to recognize "ancient woods" (i.e., forest stands that have never been totally cleared and cultivated).[23]

Our primary source of information about changes in ecosystems over hundreds or thousands of years is fossil pollen. The often ornately sculpted walls of pollen grains are unique to specific plant taxa and are very resistant to decay. The often ornately sculpted walls of pollen grains are unique to specific plant taxa and are very resistant to decay in anaerobic sediments such as those found in bogs and lake bottoms. The pollen grains accumulating in the sediment of such sites record changes in the vegetation of such an environment through time. Scientists compare the patterns of such change among different sites to reconstruct vegetation change on whole continents and over very long time spans.[24] In some cases lake sediments are "varved" or deposited in such a way that scientists can differentiate individual years. Such records have been used to reconstruct the history of fires on boreal forest landscapes in Canada.[25]

During the past decade a number of researchers have used palynology to chronicle changes in forests and forested landscapes caused by human land use. For example, Emily Russell has coupled palynological and archival studies to reconstruct patterns of vegetation change in northern New Jersey from precolonial times to the present.[26] James Clark has recently published a similar study for New York.[27]

The studies by Grace Brush and Frank Davis of sediment cores taken from multiple locations in Chesapeake Bay provide an excellent example of the power of these techniques.[28] Brush and Davis discern changes in the extent of deforestation surrounding the bay by examining fossil pollens and comparing the relative amounts of oak and ragweed pollen. They also use the pollen record to trace major forest events such as the decline of the American chestnut. They analyze fossil-diatom populations to document variation in salinity and relate these to changes in rainwater runoff caused by changing land uses. They use the sediment record to trace changing agricultural practices as evidenced by widespread eutrophication and rapid siltation.

Several factors affect the value of palynological research. First, it may be limited by the availability of appropriate depositional environments. Second, it may fail to isolate short time spans adequately. Third, it may fail to isolate the

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[19] This approach is reviewed by Nathan R. Stephenson, "Use of Tree Aggregations in Forest Ecology and Management," *Environmental Management* 11 (January 1987): 1–5.

[20] Andrew M. Greller, "Deciduous Forest," in *North American Terrestrial Vegetation*, edited by Michael G. Barbour and William D. Billings (Cambridge, England: Cambridge University Press, 1988), pp. 288–316; James R. Runkle, "Disturbance Regimes in Temperate Forests," in *The Ecology of Natural Disturbance and Patch Dynamics*, ed. Pickett and White.

[21] A. Starker Leopold, Stanley A. Cain, C. M. Cottam, J. N. Gabrielson, and T. L. Kimball, "Wildlife Management in the National Parks," *American Forests* 69 (April 1963): 32–35 and 61–63.

[22] Emily W. B. Russell, "Vegetation Change in Northern New Jersey since 1500 A.D.: A Palynological, Vegetational, and Historical Synthesis" (Ph.D. thesis, Rutgers University, 1979).

[23] For examples see George F. Peterken, "Long-Term Changes in Woodlands of Rockingham Forest and Other Areas," *Journal of Ecology* 64 (March 1976): 123–46; Oliver Rackham, *Ancient Woodland: Its History, Vegetation and Uses in England* (London, England: E. Arnold, 1980).

[24] The use of these techniques for temperate forests of North America has been recently reviewed by Paul A. Delcourt and Hazel R. Delcourt, *Long-Term Forest Dynamics of the Temperate Zone.*

[25] Les C. Cwynar, "The Recent Fire History of Barron Township, Algonquin Park," *Canadian Journal of Botany* 55 (June 1977): 1524–38; Les C. Cwynar, "Recent History of Fire and Vegetation from Laminated Sediment of Greenleaf Lake, Algonquin Park, Ontario," *Canadian Journal of Botany* 56 (January 1978): 10–21.

[26] Emily W. B. Russell, "Vegetation Change from Precolonization to the Present: A Palynological Interpretation," *Bulletin of the Torrey Botanical Club* 107 (July 1980): 432–46.

[27] James S. Clark, "Coastal Forest Tree Populations in a Changing Environment, Southeastern Long Island, New York," *Ecological Monographs* 56 (September 1986): 259–77.

[28] Grace S. Brush and Frank W. Davis, "Stratigraphic Evidence of Human Disturbance in an Estuary," *Quaternary Research* 22 (1984): 91–108.

extent of the landscape contributing materials to the sediment core. For example, evidence of pollen of a certain species may sometimes reflect highly localized activities, and sometimes reflect landscape-scale patterns of land use. Despite the difficulties, however, this approach has proven to be very useful, especially when coupled with archival data documenting land use changes.

Dendrochronology, the study of annual growth rings in trees, is a very useful tool for studying forest history. Tree reproduction in many forest ecosystems occurs in episodes associated with major disturbances. Thus the distribution of ages in a population (trees of one species within a stand) is often a sensitive indicator of the history of disturbance in the stand.[29] In even-aged forests that regenerate following disturbance (fire, land clearance, windthrow), the pattern and distribution of stands of different ages reveal the history of disturbance.[30]

Properly calibrated, the relative width of tree rings provides a measure of changes in tree growth. In habitats where tree growth is tightly correlated with climatic variation (usually extreme environments), dendrochronology has been used to reconstruct patterns of climatic change over millennia.[31] In more hospitable habitats, tree growth is often regulated by competition from other trees. Thus the changing widths of tree rings in such forests may indicate an event such as cutting or disturbance that reduces competition among surviving trees.[32]

The history of fire on forested landscapes can often be discerned by studying fire scars. The date of a fire can be determined by the location in the tree-ring record of scars left by a fire-caused wound. Successive fires tend to rescar a tree in the same location, providing a continuous record of fire near that tree. Collected and mapped for many forest stands and large spatial scales, such data provide a history of fire frequency and behavior over entire landscapes.[33]

Problems in Reconstructing the Past from the Present

One of the most active areas of research on forest succession is the development of computer simulation to depict and predict patterns of forest change following disturbance.[34] Such models couple the physiological and life-history characteristics of forest species with data on climate, site environment, and disturbance to simulate change in forest structure. They allow us to predict with some degree of confidence the future status of a particular forest stand or forested landscape from appropriate data on the current status of that stand or landscape. It should be noted that our confidence in such models declines with the specificity of the prediction required and the length of time over which we try to predict.

Some researchers have suggested running the prediction models backward to reconstruct a description of a site at some past time.[35] Unfortunately, this technique is unlikely to be effective, primarily because successional change results in convergence of forest properties only in a manner far more complex than was envisioned by Frederick Clements.[36] Thus on most landscapes, the range of past situations that might have led to an existing forest structure is considerably greater than the range of possible future states. In predicting the future we assume the absence of historical "accidents" such as fires, wind storms, or human actions; we can make no such assumption for the past. Nevertheless, reconstructive computer simulation may be useful in defining the *range* of possible past forest states or disturbances or in exploring the possible consequences of past historical accidents.

Causation and Correlation

Although the current structure of a forest may allow us to infer specific properties of that forest at various times in the past, we can do little more than speculate about the specific *causes* of those properties. We may be able to attribute some characteristic of a forest or forest landscape to an event in its past history and yet be able to say little about that event. Thus we may infer from an even-aged population of shade-intolerant trees that a stand was initiated by a disturbance as old as the trees themselves. But lacking any additional information, we have no way of knowing the exact nature of this initial disturbance (e.g., "natural" or man-caused).

Variations in the relative abundance of shortleaf pine (*Pinus echinata*) and loblolly pine (*Pinus taeda*) in forest stands regenerating on abandoned agricultural land on the eastern piedmont of North Carolina illustrate the complexity of sorting out the causes behind even relatively simple observations. Both of these pines invade recently abandoned fields and eventually form even-aged stands. Because

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[29] Craig G. Lorimer, "Age Structure and Disturbance History of a Southern Appalachian Virgin Forest," *Ecology* 61 (October 1980): 1169–84. This paper is an excellent example of the use of these techniques to decipher the past history of a single forest.

[30] The application of such methods to reconstructing the fire history of a large portion of the Yellowstone National Park is described by William H. Romme, "Fire and Landscape Diversity in Subalpine Forests of Yellowstone National Park," *Ecological Monographs* 52 (June 1982): 199–221.

[31] Harold C. Fritts, *Tree Rings and Climate* (New York: Academic Press, 1976), 567 pp.

[32] See, for example, Stephen H. Spurr and Burton V. Barnes, *Forest Ecology*, 3d ed. (New York: John Wiley, 1980), p. 381.

[33] Romme, "Fire and Landscape Diversity in Subalpine Forests"; Myron L. Heinselman, "Fire in the Virgin Forests of the Boundary Waters Canoe Area, Minnesota," *Quaternary Research* 3 (1973): 329–82; Bruce M. Kilgore and Dean Taylor, "Fire History of a Sequoia–Mixed Conifer Forest," *Ecology* 60 (February 1979): 129–42.

[34] Herman H. Shugart, Jr., *A Theory of Forest Dynamics: The Ecological Implications of Forest Succession Models* (New York: Springer-Verlag, 1984).

[35] This approach has been suggested by Bonnicksen and Stone, "Reconstruction of a Presettlement Giant Sequoia–Mixed Conifer Forest Community," as a means of determining past forest structure. They propose that such a method would allow the National Park Service to know the presettlement forest structure of ecosystems that have been altered by humans.

[36] For example, see Norman L. Christensen and Robert K. Peet, "Convergence during Secondary Forest Succession."

they are unable to reproduce in their own shade, they are replaced in 75 to 150 years by broad-leafed deciduous hardwoods (figure 2).

A census of stands in the piedmont region reveals rather marked differences in the relative abundance of these two species during the last two centuries. These differences seem to depend on the age of the pine stand, i.e., the time when it was abandoned (see table). There is no doubt that shortleaf pine was a more successful invader in fields abandoned during the nineteenth century than in those abandoned after 1930. But at least five distinct types of historical change might account for this observation: in landscape pattern, in silviculture and forest demography, in site conditions, in patterns of land use and abandonment, and in the general environment.

Variations in the Distribution and Abundance of Loblolly and Shortleaf Pine

	Stands established before 1900		Stands established after 1930	
	Frequency (percent)	Biomass (percent)	Frequency (percent)	Biomass (percent)
Shortleaf (small seeds, uplands, adapted to "poor" sites)	92	45	37	10
Loblolly (larger seeds, bottomlands, grows best on fertile sites)	37	50	100	90

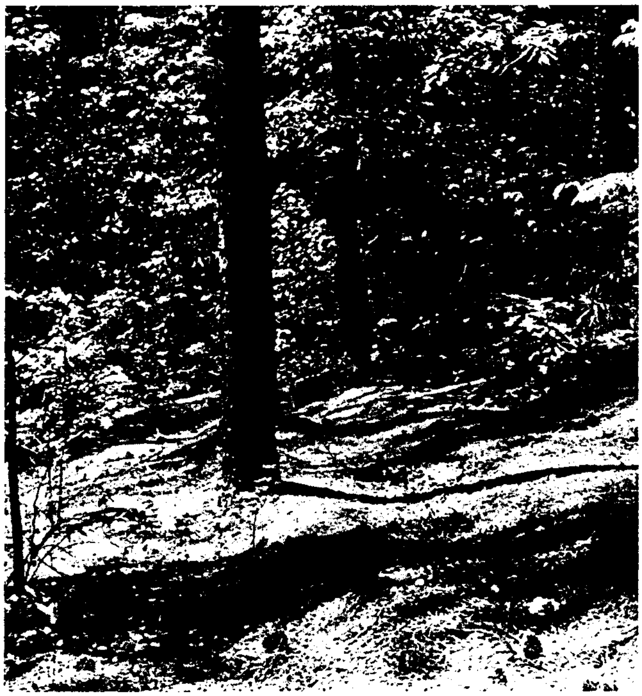
Source: Author's unpublished data from Duke Forest, Durham, North Carolina.

Fields abandoned during the nineteenth century stood in landscapes very different from the landscapes surrounding fields abandoned during the twentieth century. Prior to 1900 a newly abandoned field was something of an island in a "sea" of other fields (abandoned and cultivated), so there was unlikely to be a nearby seed source of forest trees. By this century, reforestation of the landscape was well underway, and newly abandoned fields were likely to be close to a source of tree seeds.[37]

The "natural" or precolonial habitats of the shortleaf and loblolly pines differ. Shortleaf pine occurs naturally on rocky, shallow upland soils; loblolly in bottomland areas. Seeds of shortleaf pine are considerably smaller and more widely dispersed than those of loblolly. The shortleaf's preferred upland location and wider dispersal range may have given it an advantage as an invader in the isolated fields of the nineteenth-century landscape. But after dispersal became less important (such as on the reforested landscape of the mid-twentieth century), loblolly pine may have been the better competitor.

Figure 2. Successional change following agricultural land abandonment in the North Carolina piedmont. All photographs provided by author.

2a. Immediate post-abandonment field; historical factors such as agricultural practices and season of abandonment significantly influence patterns of plant invasion.



2c. A forty-year-old pine stand in which agricultural furrows are still obvious.

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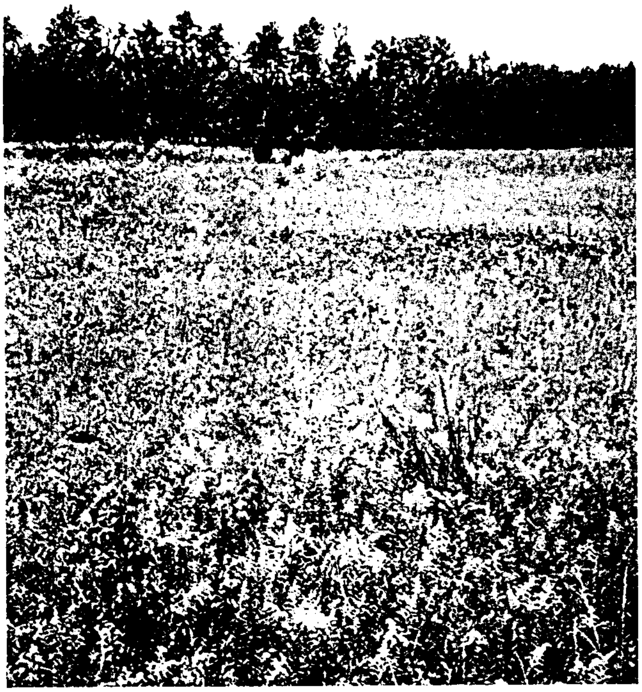
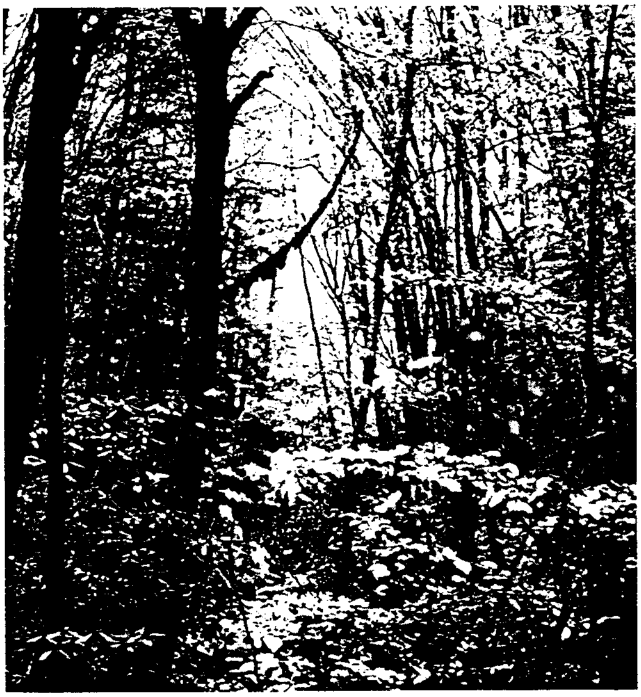
[37] Henry J. Oosting, "An Ecological Analysis of the Plant Communities of Piedmont, North Carolina," *The American Midland Naturalist* 28 (July 1942): 1–126.



2b. Five-year-old field; patterns of field disturbance, year-to-year variations in climate, and activities adjacent to the field influence establishment of tree species.



2d. A mature hardwood forest; species composition and population structure bear witness to past historical events.

On all but the poorest sites, loblolly pine grows more quickly than shortleaf pine. For this reason loblolly is generally favored for silvicultural plantations. Thus rapid growth plus silvicultural selection may have greatly increased the "seed rain" of loblolly pine compared to shortleaf pine.

The environmental characteristics of fields abandoned a century ago may have been quite different from those of fields abandoned more recently. For example, nitrogen and phosphate fertilizers and lime were rarely used on cropland prior to about 1920. Thus fields abandoned during the nineteenth century were probably considerably more sterile than their twentieth-century counterparts.[38] Shortleaf pine is known to compete more effectively with loblolly pine on sterile soils than on nutrient-rich soils.

As a consequence of variations in the chemical makeup of the parent rock underlying the eastern piedmont, soil conditions vary considerably over spatial scales of tens and hundreds of meters. The distribution of sites favoring one species over another was further complicated by economic and other factors, which produced regional patterns of land clearing and development that were sometimes very different from patterns of subsequent abandonment. The poorest sites (least fertile, driest, etc.) were most likely to be abandoned first; somewhat more fertile sites were probably not abandoned until later. Given shortleaf pine's increased competitive ability on poor sites, its abundance in old stands may simply reflect the bias in the pattern of abandonment.

Finally, we cannot rule out the possibility that general environmental conditions during the latter half of the nineteenth century might have favored shortleaf, whereas those of 1930–89 might have favored loblolly pine. There is, for example, ample indication that climatic conditions have changed between these two periods. Then too, the relative success of these two species over the past century might have been influenced by changes in competition from other tree species or changes in the importance of fungal or insect pathogens.

Forest Decline: An Example of the Importance of Understanding History

Forest decline (regionwide decreased production or increased mortality of trees) is one of the most daunting problems currently facing forest ecologists. Where pathological symptoms are clear and impacts obvious, forest ecologists are occasionally successful in identifying the specific causes of such decline—even if they cannot remedy the problem. Such is certainly the case with respect to the impact of atmospheric pollutants and acidic precipitation on forested areas near industrial centers in central Europe.

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[38] Stanley W. Trimble, "Man-Induced Soil Erosion on the Southern Piedmont 1700–1970" (Ph.D. thesis, University of Wisconsin, Milwaukee, 1973), 180 pp.

In other areas, evidence of decline is more subtle and potential causes more complex.[39] It is clear, however, that historical patterns of land use are often a significant factor explaining forest decline.

The alleged decline of successional pine forests on the piedmont of the southeastern United States illustrates the potential contribution of land use history to explaining forest declines. Analysis of regional forest census data (gathered over the past thirty years) in the piedmont region suggests that the growth increment of several important southern pines has declined by as much as 25 percent in some areas.[40] Recall that most of these forests have regenerated on land abandoned by humans from nonsilvicultural land uses. Given the current dependence of the southeastern timber industry on these species, the financial consequences of a decline of this magnitude are substantial.

When forests have declined on other landscapes, scientists have frequently been able to help diagnose the cause. This is not the case in the southeastern piedmont: the southern pines have displayed no cause-specific symptoms. But assuming that the data are reliable, there are several possible explanations for the decline: competition from invading broad-leafed hardwoods, pests, widespread drought, increased atmospheric deposition (acid rain and ozone), forest aging, and land use.[41] Although atmospheric deposition has received the most attention, historical explanations may be much more likely.

Change in the successional forests of the southeastern piedmont follows a very predictable pattern for secondary forests in general (figure 2). In this pattern, tree populations are initiated during an establishment phase (the old field). As trees grow and their canopies begin to intersect, competition begins to regulate growth and result in mortality of smaller, slower-growing individuals. This initiates a thinning phase during which overall stand growth is rapid, but mortality continues. Eventually such stands thin to the point where additional mortality begins to create openings in the forest canopy. Growth of the surviving trees is not sufficient to replace the biomass lost through mortality of large stems, and stand biomass begins to decline. Growth in height of surviving trees may also decline at this time. During this transition phase, if there is no intervention, deciduous hardwoods replace pines to form a mixed deciduous forest. In short, decline is a normal expectation in forest stands in which the successional process is not arrested by cutting.

Foresters are very familiar with the trajectory of change described above, and they ordinarily harvest a stand before it reaches the transition stage. However, most of the forested land in the Southeast is not being managed by foresters.

Furthermore, abandonment of land from agriculture or other nonforest uses has not been continuous during the past 150 years. Rather, reforestation has been initiated in pulses associated with historically important events such as Reconstruction and the Great Depression. Thus the various stages of succession represented in figure 2 are not distributed naturally over the landscape; rather, their abundance reflects the history of land use and abandonment. What appears to be widespread decline may simply reflect the synchronous onset of the transition stage of stand development in many forest stands affected by the same large-scale historical events.

Whether this is the correct explanation for the phenomenon has yet to be decided. Only a comprehensive study of the history of land use and abandonment in this region can resolve the issue. The example does, however, demonstrate the potential contribution of historical studies to our understanding of contemporary environmental problems.

Historical Ecology as a Predictive Endeavor

Much of our preoccupation with the past is related to our interest in predicting the future. By studying past ecosystem change, ecologists have developed elegant models that can, with reasonable accuracy, predict the properties of future forests. Similarly, studies of patterns of past human behavior on landscapes provide us with likely scenarios for patterns of future land use. The necessity of understanding the interrelationships between ecological and historical change in order to create realistic predictive models is becoming increasingly clear. Again, the example of the relationship between land use and old-field succession in the southeastern piedmont illustrates this point.

Old-field succession is a creation of human land use and agricultural development. Although old fields may in some ways mimic natural disturbances that might have occurred on this landscape prior to human intervention, ecosystems such as broom-sedge fields and even-aged pine forests are unique to abandoned agricultural fields and are a consequence of past human history. Reciprocally, successional processes have altered the course of human history on the landscape. Rapid invasion of herbs in abandoned fields provided the basis for the fallow-field system of crop rotation used in the early nineteenth century.[42] The permanent abandonment of land later in that century resulted in the establishment of the extensive pine stands that now sustain the modern timber industry in this region.

For the foreseeable future, extensive abandonment of agricultural land such as occurred during the first four decades of this century is unlikely. Furthermore, unless considerable postharvest site preparation is done, cut pine stands will be replaced with a mixture of hardwood species and some pines. In addition, forest stands are now developing in a matrix of increasing urban development. Just as surely as our use of the landscape will affect the course of ecosystem change, that change will alter the values of the landscape for future human use. Can there be any doubt of the value and need for the collaboration between historians and ecologists? ▲

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[39] Louis F. Pietelka and Dudley J. Raynal, "Forest Decline and Acidic Deposition," *Ecology* 70 (February 1989): pp. 2–10.

[40] R. M. Sheffield, Noel D. Cost, William A. Becktold, and Joseph P. McClure, "Pine Growth Reductions in the Southeast," *USDA Forest Service Resource Bulletin* SE-83 (1985), p. 90.

[41] Ibid.; Alan A. Lucier, "Summary and Interpretation of USDA Forest Service Report on 'Pine Growth Reductions in the Southeast,' " *Technical Bulletin of the National Council of the Paper Industry for Air and Stream Improvement* 508 (1986), p. 12.

[42] Albert Cowdrey, *This Land, This South: An Environmental History* (Lexington: University of Kentucky Press, 1983).