CHAPTER 8

Forest Landscape Patterns, Structure, and Composition

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The forests of New England are incredibly varied, from 400-year-old hemlock stands in dark ravines to young hardwood forests that stretch across the rolling uplands, and from spruce swamps overlying deep peats to stunted pitch pines on dry ridge tops. Earlier we related much of this regional variation in forest composition to broad gradients in environment and disturbance history and illustrated that vegetation composition has been highly dynamic over time in response to changing climate and a wide range of natural and anthropogenic disturbances. However, as we shift our attention from this regional and long-term perspective to the variation in vegetation that we observe across the modern landscape, we need to consider the factors that control local differences in forest composition and structure. Why is it that we find mature hemlock stands immediately adjacent to younger hardwoods or gradual transitions between forests in one locality and very sharp breaks separating stands in other areas? Do the factors that control the distribution of tree species in a particular forest or landscape also control understory plants, or are different life-forms of plants sensitive to different environmental and historical factors? How does a region's disturbance history play out locally, and does it exert a persistent influence on vegetation patterns, even long after the disturbances have ended?

To answer these questions, we have investigated modern forest patterns on a range of sites and have studied the mechanisms that control these patterns. A major goal has been to test the commonly held notion that variation in vegetation primarily responds to differences in current site conditions as opposed to historical factors. In particular, we wished to determine the extent to which modern vegetation patterns reflect wind, fire, and especially land-use disturbances over past centuries, rather than current environmental conditions. Given the tendency for scientific research to become increasingly reductionist, understanding the relative importance of historical legacies versus current conditions provides important insights to our science.

Background

Studies in North America and Europe have found that modern vegetation composition and species diversity are strongly influenced by historical factors as well as modern site conditions. In particular, several investigations, including many originating from the Harvard Forest, have suggested that land-use activities may alter species composition or richness for many centuries, long after the disturbances have ended. Disturbance history may influence subsequent species composition in several ways as disturbance may

- alter physical site conditions directly and thereby influence subsequent plant performance and competitive interactions, or change the suite of species that can potentially occupy a site;
- allow for the establishment of species that are then able to persist for long periods of time, even on sites where they would, in the absence of disturbance, be unable to establish or compete effectively; or
- remove species that are extremely slow to recolonize, even in the absence of altered resource conditions.

For instance, plants with slow rates of dispersal or establishment may be absent from a site for decades or centuries, not because the site is unsuitable, but simply because the species was removed by a prior disturbance and has not had sufficient time or opportunity to recolonize. Because species' distribution patterns may be controlled by current environmental conditions and/or historical factors, a major challenge for ecological study is to evaluate the relative influence of these factors on modern vegetation, and to determine how the relative importance of contemporary conditions versus history changes with time since disturbance.

The possibility that legacies of past disturbance may endure to control forest structure and composition long after the direct evidence of the disturbance has disappeared has important ramifications for our understanding of forest ecosystems and for our attempts to manage them for resources and conservation values. However, evaluating the influence of historical disturbances is difficult because specific land-use activities and other disturbances are typically restricted to particular types of sites. For instance, even if we are able to determine that certain species occur primarily in areas that were used historically for crop cultivation, it is often difficult to know whether these species occur on these sites because they were formerly cultivated or because the species prefer the types of soils and locations that farmers selected historically for intensive agriculture.

We adopted a number of approaches to address this problem of confounding factors. On sites where soils and other physical conditions are relatively homogeneous but where land-use history varies, we were able to test land-use effects that are independent of variation in environment.

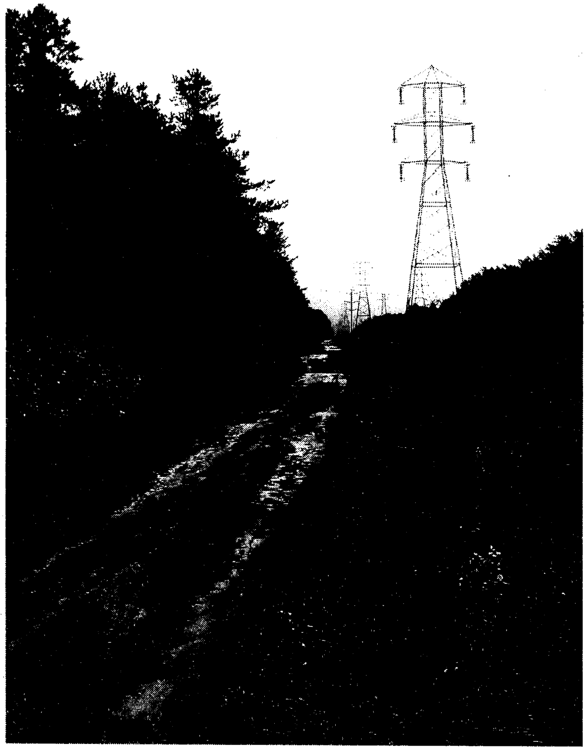

Figure 8.1. The Montague Plain is a flat and sandy outwash plain dominated by forests of pitch pine, oak, and scrub oak. The homogeneous soil conditions enable us to examine the effect of land use and other disturbances on vegetation patterns. Photograph by D. R. Foster.

Basically, this approach is akin to an experiment in which all factors but the one of interest (in this case, history) are controlled and held constant. On more complex sites, which is the typical situation in New England, we developed very detailed information about history and site conditions in order to help us interpret the relative contribution of each.

Our intensive study of the Montague Plain (Figure 8.1), a level outwash plain in the Connecticut River Valley that has limited environmental variability, allowed us to evaluate the effects of historical disturbances without the confounding effects of differing initial site conditions. Results from that investigation document the overwhelming influence of historical land-use activities on modern vegetation patterns. They also identify several species that have not recolonized former agricultural lands in 50 to more than 100 years since these farmlands were abandoned. Using these results, we initiated detailed studies of nutrient cycling and population demography at Montague to determine the mecha-

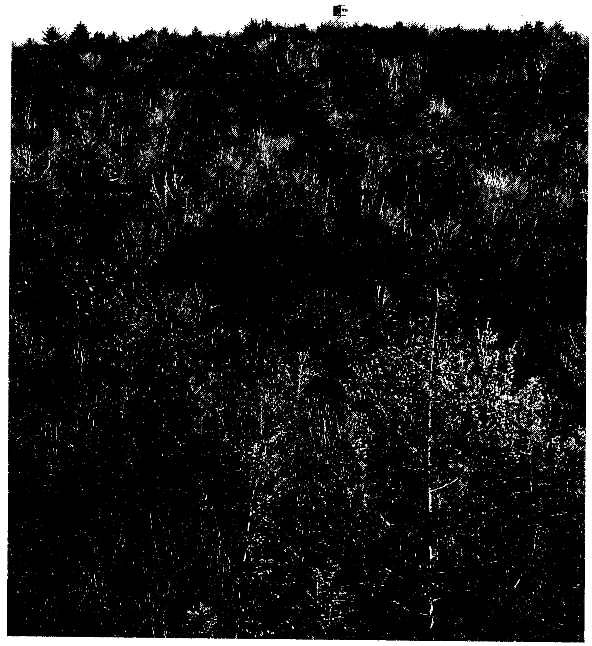

Figure 8.2. The locally varying environment on the rolling uplands including the Prospect Hill tract makes it more difficult to separate the influences of environmental factors and disturbance history on vegetation patterns. This northward view from the canopy tower near Hemlock Hollow toward the fire tower on Prospect Hill captures some of the topographic variation and the subtle changes from hardwood (lighter tones) to white pine and hemlock (darker). Photograph by D. R. Foster.

nisms by which historical factors may exert persistent influences on vegetation patterns and ecosystem properties.

We conducted similar investigations on the Prospect Hill tract of the Harvard Forest (Figure 8.2), a more complex upland site with highly variable physiography and a complicated history of both natural and human disturbances. This site is particularly appropriate for such research. It is representative of a much broader region in terms of vegetation, site conditions, and disturbance history, and ninety years of research enabled us to compile unusually detailed historical records. Thus, on Prospect Hill we can evaluate the influence of history and environment on modern vegetation in a way that is not possible for most sites.

Here we present some of the major findings of these community and population studies. We begin with an overview of disturbance history on Prospect Hill and present our understanding of the factors that control modern vegetation patterns on this site. We then present a similar analysis for the Montague Plain and compare disturbance histories and vegetation responses among these two sites. The results of population studies that seek to identify the mechanisms by which disturbance may exert persistent influence on vegetation is presented through a case study of wintergreen *(Gaultheria procumbens),* a species whose modern distribution is, on sites such as Montague Plain, strikingly controlled by historical land-use practices. Finally, we conclude with some thoughts on the implications of our findings for understanding modern community patterns in regions that have long and varied histories of natural and human disturbances.

Prospect Hill

Disturbance History

Before European settlement, the Prospect Hill tract was largely forested, and there is no evidence to suggest land clearing by native people (see Chapters 4 and 6). The wealth of historical records, including ownership and land-use maps, census data, and extensive stand records and forest inventories, enabled us to develop a detailed picture of the changing landscape (Figure 8.3). We sought to corroborate these historical sources in our extensive fieldwork by recording observations on land-use artifacts such as plow mounds, stone piles, dams, and cellar holes. In addition, we examined soils to determine the degree to which they had previously been disturbed by agricultural practices. On sites that were formerly cultivated, a distinct plowed surface soil horizon (Ap horizon) remains visible for many decades, enabling us to identify and map former cultivated fields. By combining field observations and historical sources, we determined that approximately 16 percent of the area remained wooded in the mid-nineteenth century. Approximately 7 percent has deep soil disturbance, indicating crop cultivation, and an additional approximately 15 percent has shallow soil disturbance, suggesting that it was lightly plowed or harrowed historically and most likely used as improved pasture. Fields (plowed areas and improved pastures) were established primarily on well-drained soils, whereas rough pastures, which lack any visual evidence of soil disturbance but were known from historical records to have been cleared, occurred on a wider range of soils, both drier and wetter. The permanent woodlands were largely restricted to swamps, poorly drained soils, or rocky sites. Beginning in the second half of the nineteenth century, widespread reforestation occurred, and by the early 1900s, most of the fields had been abandoned and allowed to revegetate naturally or had been planted to conifer plan-

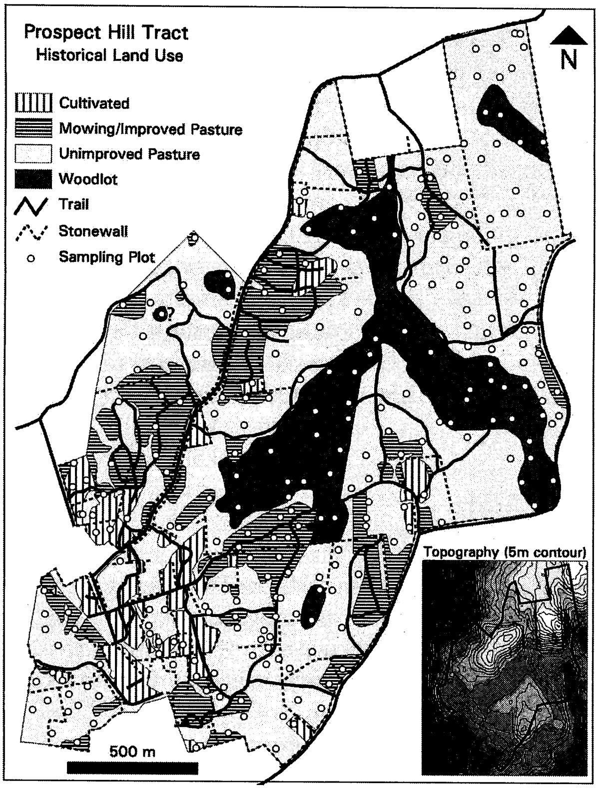

Figure 8.3. Map of historical land use on the Prospect Hill tract, indicating areas that remained wooded through the historical period (dark) and that account for only 16 percent of the 340-hectare tract. Former cultivated areas (vertical lines) and improved pastures/hay fields (horizontal lines) have soils that show evidence of past plowing, whereas in areas formerly in unimproved pasture (light shading) the forest vegetation was cleared but soils were not significantly altered. Dots indicate the location of vegetation sampling points. Modified from Motzkin, Wilson et al. 1999, with permission from Opulus Press.

tations. Continuously forested sites as well as secondary forests on old agricultural fields were cut frequently for a variety of forest products. Silvicultural activity since the establishment of the Harvard Forest included planting of conifers, harvesting of old-field white pine stands, and selective cutting of hardwoods and mixed stands.

Several additional disturbances also affected these forests during the twentieth century, including the chestnut blight beginning in 1913 and the 1938 hurricane. On the Prospect Hill tract, 21 percent of the forest sustained more than 50 percent damage to the overstory from the hurricane, and 10 percent sustained more than 75 percent damage (Figure 8.4). In addition, a few wildfires occurred during this century, the

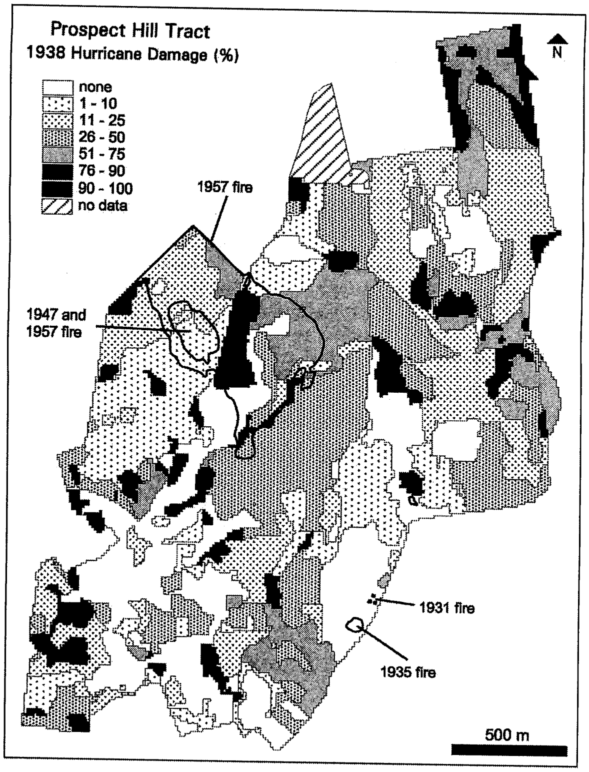

Figure 8.4. Damage to forest stands on the Prospect Hill tract of the Harvard Forest from the Great New England Hurricane of 1938. The areas affected by wildfires in 1931, 1935, 1947, and 1957 are also indicated. Modified from Motzkin, Wilson et al. 1999, with permission from Opulus Press.

largest in 1957, covering about 9 percent of the area. Ice, snow, and windstorms, as well as outbreaks of several forest pathogens, have also damaged the forest periodically.

Controls on Modern Vegetation Patterns

SPECIES COMPOSITION

On a complex landscape such as the Prospect Hill tract, many factors can influence vegetation patterns. In addition to determining the disturbance history, we therefore analyzed soil texture and chemistry (see Chapter 9) and related these to the variation in vegetation. Our results suggest that species respond individualistically to many environmental and historical factors, with each plant species exhibiting a unique pattern. However, three dominant factors are strongly correlated with the distributions of many species: historical land use, soil drainage, and the ratio of carbon to nitrogen (C:N ratio) in the soil. The current vegetation is strongly related to land-use history, with, for example, hemlock stands largely restricted to primary (never-cleared) sites, red maple stands mainly on old unimproved pastures or woodlots, oak-maple stands on former pastures and some tilled fields, and pine-oak stands and plantations on old pastures and plowed fields but generally not on continuously wooded sites. For some species, both spatial distribution and abundance are strongly influenced by nineteenth-century land use (Figure 8.5). For instance, white pine, staghorn clubmoss *(Lycopodium clavatum),* and Canada mayflower *(Maianthemum canadense)* occur more frequently or abundantly on former agricultural fields than in continuously forested areas. In contrast, several species are more frequent or abundant on continuously forested sites, including hemlock *(Tsuga canadensis),* witch hazel *(Hamamelis virginiana),* and several bryophytes (for instance, *Calypogeia fissa* and *Brotherella recurvans*).

These findings support studies from eastern North America and Europe that have identified species that are largely restricted to continuously forested sites and that are slow to recolonize areas once they have been removed. Several mechanisms may contribute to this pattern. For some species, dispersal, establishment, or other biological limitations may restrict colonization (see the case study of wintergreen below). In addition, the abundance of hemlock, which casts deep shade and forms deep, acidic litter, in continuously forested sites significantly influences the understory environment and composition. In some instances this relationship is quite strong, as in the case of the liverwort *Lepidozia reptans,* which is found on Prospect Hill almost exclusively in association with a hemlock overstory.

SPECIES RICHNESS

Studies that have evaluated the influence of historical land use on species richness (the number of species per unit area) have differed in their results. Whereas several studies, including those of George Peterken in Britain, have found that primary woodlands or old secondary woodlands adjacent to primary woodlands are species-rich relative to more recent and isolated secondary stands, others have found no difference across differing land-use histories, or that more recently or intensely disturbed sites may actually support a greater number of species. However, it should be noted that in some instances where total species richness does not vary by land use, the number of "true woodland species" (that is, species that are restricted to woodland habitats) may still differ. In our study, the number of bryophyte (moss and liverwort) species does not differ according to historical land use, whereas the number of trees, shrubs, and herbaceous species does differ, with the fewest species in continuously forested stands. Although some of this effect may result from the persistence of a few weedy species on former

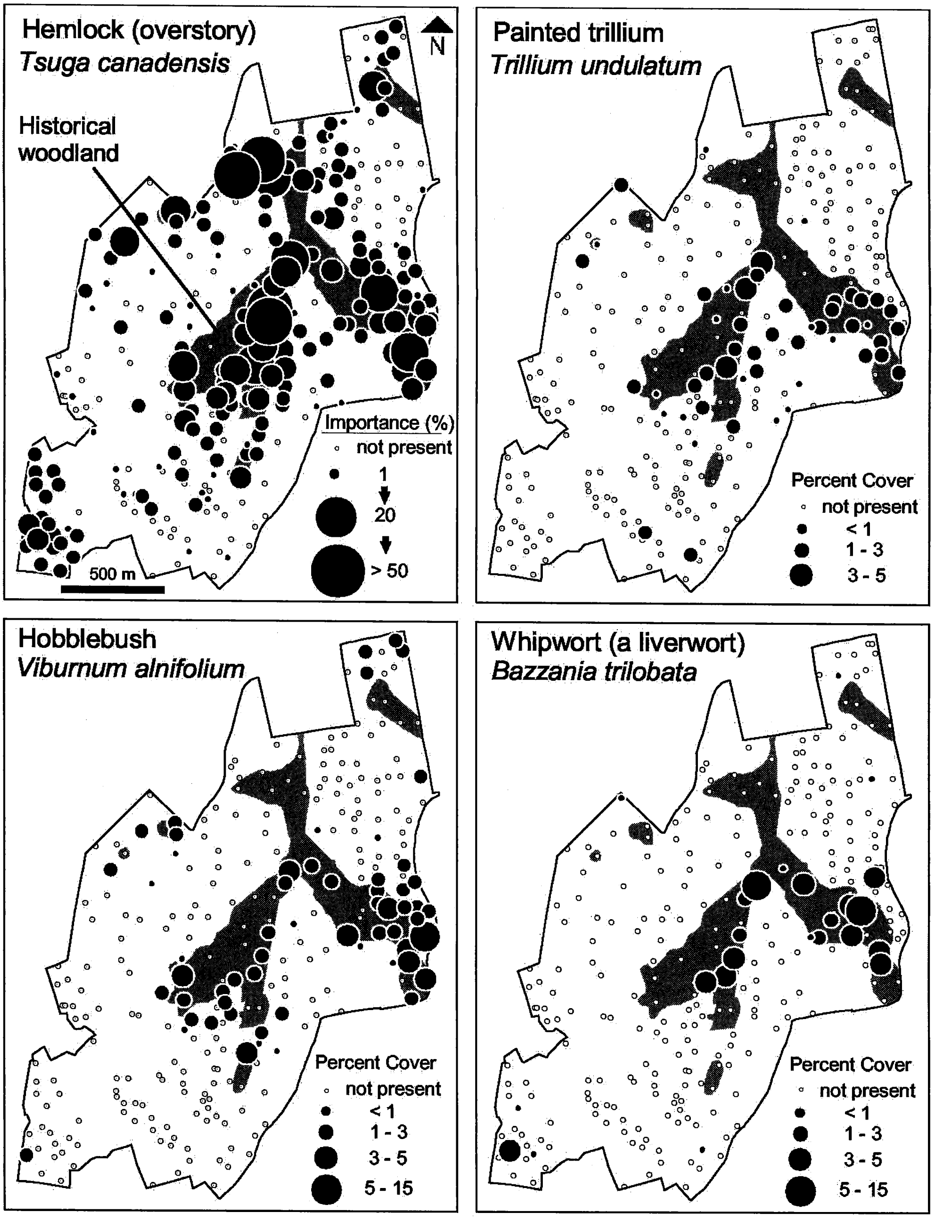

Figure 8.5. Distribution and abundance of plant species characteristic of continuously forested sites on the Prospect Hill tract of the Harvard Forest. These species are less abundant and less common today on sites that were cleared for eighteenth- and nineteenth-century agriculture. Based on Motzkin, Wilson et al. 1999.

agricultural sites, it is likely that the inability of many species to tolerate low light in dense hemlock stands is a major factor limiting richness in primary woodlands. Thus, historical land use can affect species richness and composition both directly and indirectly. Interestingly, continuously wooded sites with a history of least intensive land use have the smallest number of species.

Many species also vary in distribution according to differences in soil drainage and C:N ratios. Soil drainage strongly influences the mosses and liverworts, whereas many tree species tolerate a wide range of moisture conditions, from relatively dry to fairly wet. Some species vary according to C:N ratios, which are highest in hemlock stands on permanently wooded sites and lower in vegetation on former agricultural fields. In general, gradients in calcium and magnesium concentrations and pH do not strongly influence species distributions in this landscape, perhaps because soils are fairly uniform. These results differ somewhat from those of other studies (for example, the work by Peet and Christensen 1980, Balter and Loeb 1983, and Cowell 1993) that examined a broader range of site conditions than those that occur on Prospect Hill.

In addition to those factors that strongly influence modern vegetation, it is instructive to consider variables that, rather surprisingly, are not closely associated with forest patterns. For instance, the 1938 hurricane clearly had a major effect on forest structure and overstory composition, as it damaged most stands and generated dramatic structural effects, including downed trees, windthrow mounds, and damaged crowns that are apparent sixty years later. However, despite dramatic wind impacts on both overstory composition and structure, our study indicates that the degree of 1938 hurricane damage helps to predict the modern distributions of only a few species such as thread moss *(Atrichum angustatum),* which is frequently found on old tip-up mounds. What explains this seemingly contradictory result? Several factors offer partial explanations: (1) understory species may be relatively independent of overstory structure and composition, particularly as herbs, shrubs, and small trees may be undamaged by wind or capable of rapid resprouting; (2) sufficient time may have passed since the hurricane to obscure many of the initial and successional effects; (3) hurricane damage may have been sufficiently widespread and varied that our stand-level data are inadequate to detect effects on the understory flora; and (4) logging and related salvage activity, which was widespread after the hurricane, may have obscured wind effects.

In addition, we suspect that part of our inability to detect significant hurricane effects may be a common problem in ecological sampling: we are able to measure current environmental conditions and vegetation patterns, but we are unable to evaluate directly the difference between what the landscape is and what it would have been if the disturbance had not occurred. Thus, effects of widespread disturbances such as wind, logging, or pathogens, though important, may go undetected.

Land Use, Soils, and Vegetation on Montague Plain

The difficulty of separating historical and environmental effects on vegetation in the complex landscape of Prospect Hill prompted us to investigate more homogeneous sites. We hoped that by limiting variation in topography, soils, and drainage, we could study the mechanisms by which historical disturbances influence vegetation in the long term. Several of these studies were conducted on the Montague Plain, a large sandy plain in the Connecticut River Valley (Figure 8.1). This site is ideal for such studies because it is homogeneous with respect to soils and yet supports a range of vegetation and prior land use. Using a combination of historical sources and field studies similar to those on Prospect Hill, we pieced together the site history, which is somewhat different from that of most upland areas. Although the land on Montague Plain was first divided and assigned to owners in the mid-eighteenth century, historical records indicate that widespread forest clearing did not occur until after 1830. During the mid-nineteenth and early twentieth centuries, much of the plain was used for agriculture. In fact, because plow horizons are distinct in these soils, we were able to determine that approximately 80 percent of the site was plowed historically (Figure 8.6). By the late 1930s, most of the site had been agriculturally abandoned and was reforesting naturally. Because this is an extremely sandy site, pitch pine, which is tolerant of dry conditions, was the dominant overstory species to become established on these old fields.

Interestingly, even though the fields were generally abandoned 75 to more than 100 years ago, the modern forests on these sites still differ substantially from adjacent areas that were never plowed (Figure 8.7). Some weedy species are more common today in the forests that established on fields than in nearby unplowed sites, whereas some characteristic "pine barrens" species are abundant on historically unplowed sites but have not successfully recolonized areas that were cleared for agriculture (Figure 8.8). We suspect that pine barren species such as wintergreen and huckleberry were formerly widespread across the entire plain, that they were eradicated from most of the area by plowing, and that they are currently restricted because of severe limitations in their ability to recolonize. In fact, on this and similar sites in the Connecticut River Valley, the presence of wintergreen and huckleberry is a strong indication that the site was never cleared and plowed. Consequently, boundaries between unplowed and formerly plowed sites are often visible as distinct breaks in understory vegetation, with the restricted species having spread only a few meters onto former fields.

Among the species whose modern distributions are strongly deter-

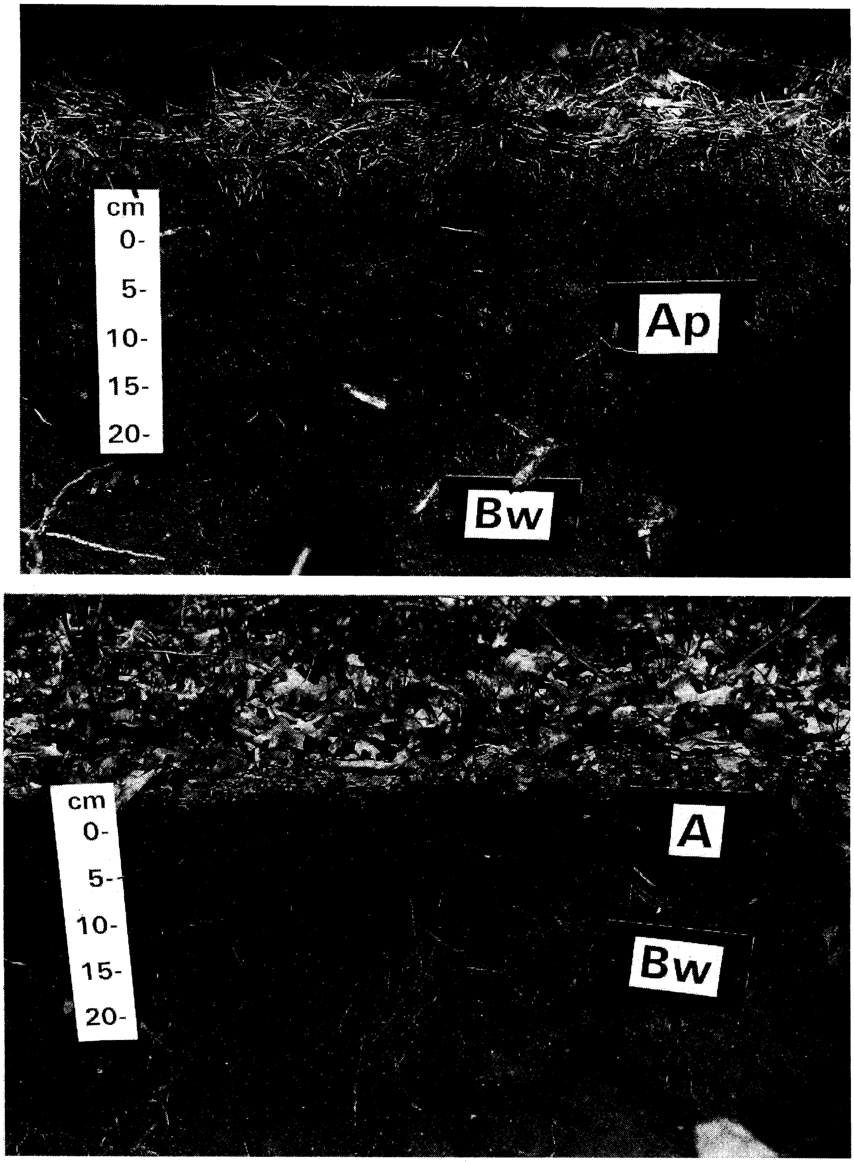

Figure 8.6. Soil profiles from two sites on the Montague Plain with contrasting land-use histories. Top: Pitch pine forest on a site that was cleared and plowed for agriculture during the nineteenth century. A deep, homogeneous Ap "plow horizon" extends to 20 centimeters and persists despite 100 years of forest growth. Bottom: Scrub oak stand on a continuously forested site. The undisturbed and shallow upper (A) soil horizon grades gradually downward in appearance and color. Photographs by A. Allen, from Motzkin et al. 1996, reprinted with permission from the Ecological Society of America.

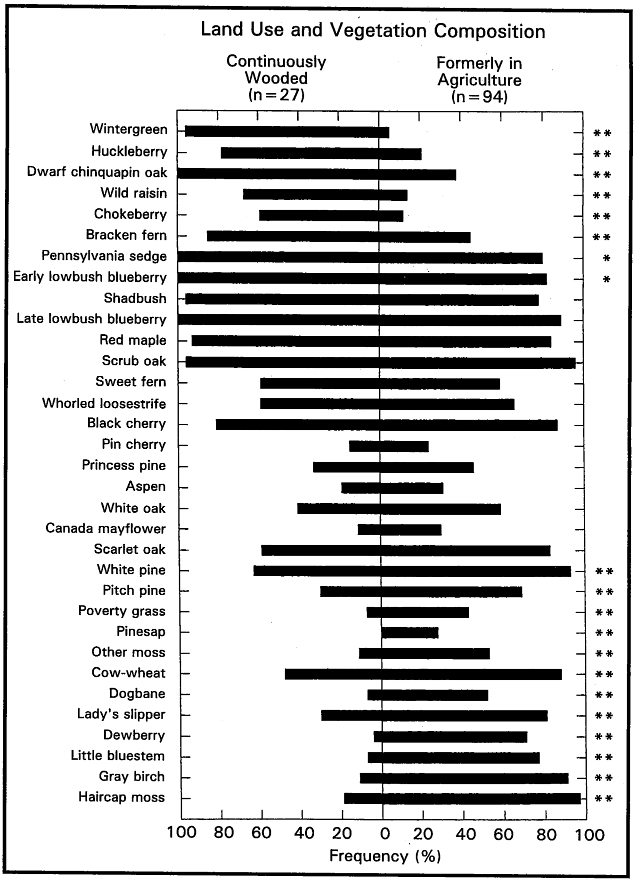

Figure 8.7. The influence of land-use history on current vegetation composition on the Montague Plain. The frequency of occurrence of common species (occurring in more than 20 percent of plots) illustrates that some species are highly restricted to areas continuously in woodland, others are preferentially found on sites previously in agriculture, and others are widespread and relatively indifferent to prior land use. Asterisks indicate significant differences; *$p < .05$, **$p < .01$. Modified from Motzkin et al. 1996, with permission from the Ecological Society of America.

mined by past land use, wintergreen *(Gaultheria procumbens)* is the most striking (Figure 8.9). We found this creeping species in 96 percent of plots that had never been plowed but in fewer than 5 percent of plots on former fields. Because our soil and environmental analyses indicated that most conditions were identical across these land-use boundaries, we looked in detail at the population demography of wintergreen to determine why it recolonizes these sandy old fields so slowly.

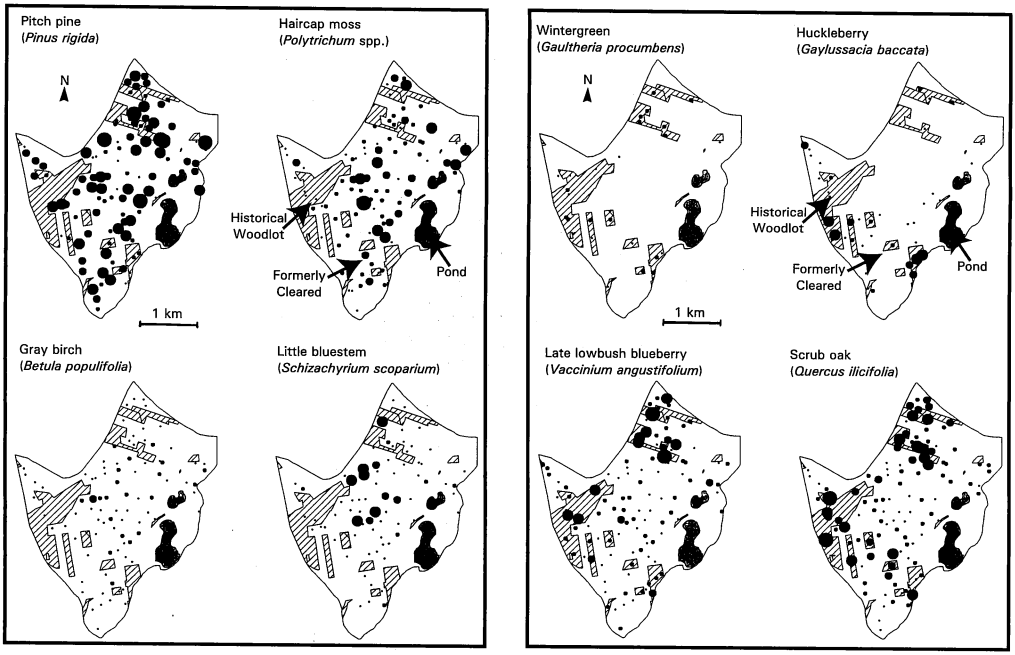

Figure 8.8. The influence of land-use history on patterns of species distributions on the Montague Plain. Distribution and abundance of species characteristic of formerly plowed areas (left) and sites that were never cleared for agriculture (right). White areas were cleared and plowed for agriculture but were abandoned and currently support forest that is 50 to more than 100 years old. Diagonal shading indicates continuously wooded areas. Modified from Motzkin et al. 1996, reprinted with permission from the Ecological Society of America.

We hypothesized that if plowing and agriculture had altered resources such that formerly plowed sites are now less suitable for wintergreen, then it should exhibit decreased size, vigor, or growth rates on these sites. In order to test this hypothesis, we compared plant characteristics that are associated with population establishment and growth (such as flower and fruit production, seed germination, growth, and survivorship) on wintergreen growing on plowed versus unplowed sites. We found no evidence of successful wintergreen colonization of former fields through sexual reproduction. In fact, we determined that on formerly plowed sites, wintergreen is restricted to areas adjacent to unplowed sites, from which it has spread vegetatively an average maximum distance of only 10 to 14 meters in the 50 to more than 100 years since these fields were abandoned. However, our findings do not support the notion that former plowed fields are unsuitable for wintergreen. In fact, contrary to this prediction, we found that for many demographic

Figure 8.9. Wintergreen *(Gaultheria procumbens),* an ericaceous herb that is slow to expand from primary forests into previously plowed areas in the sand plain environment (see Figures 8.7 and 8.8) but is quite widespread across forests of different land-use history on the mesic uplands like the Prospect Hill tract. Photograph by J. Gipe.

parameters, wintergreen performed as well on formerly plowed sites as on unplowed sites, or in some instances actually performed better on the old fields. For instance, germination, seedling longevity, and rhizome growth rate were greater on plowed versus unplowed sites.

Thus, it seems that on the sand plain, wintergreen's absence from many former fields is not a result of agricultural modification of environmental conditions, but rather comes from inherent biological limitations on the species' ability to colonize new sites. The current distribution of wintergreen on this and similar sites thus apparently results from historical factors rather than from current site conditions. Interestingly, wintergreen does not display the same degree of restriction to continuously wooded sites on the Prospect Hill tract or other moist upland areas. On these sites it more readily spreads from old woodlands onto recently abandoned land and is now widespread in forests across many former land uses. This indicates that even for individual species, responses to historical factors are complex and may vary according to local site conditions.

Comparing Prospect Hill with Montague Plain

Prospect Hill and Montague Plain may be thought of as representing points on the continuum of land-use impacts. Although approximately 80 percent of Montague Plain was plowed historically, our analyses suggest that this disturbance resulted in relatively minor long-term alteration of physical and chemical soil properties, presumably because of the short duration and low intensity of historical agricultural use of this marginal site. However, even without prolonged, intense disturbance, the long-term effects of land use on modern vegetation are striking as a result of species differences in colonization ability. It is reasonable to conclude that on sites where the duration or intensity of agricultural use was greater, resulting in altered site conditions, subsequent vegetation patterns would reflect the confounding effects of recolonization limitations and altered site conditions. Such an interaction is thought to be significant in many European ecosystems and undoubtedly applies to broad areas of North America that have a long history of intensive agriculture. Our results suggest that this may also be the case for much of Prospect Hill and the broad uplands of New England. Although the total percentage of land cleared is comparable on Prospect Hill and Montague Plain, crop cultivation on the former was less widespread but more intensive and of longer duration, resulting in more pronounced, long-term soil modification. This contributes to the persistent influence of historical land use on modern species distributions, despite the considerable length of time (75 to 160 years) that has passed since agricultural abandonment, a time during which species could have shifted their distributions in response to more recent disturbances or to more closely reflect variation in contemporary site conditions.

Conclusions

Why is it that on some sites the influence of history on modern vegetation is so striking, whereas on others it is more difficult to detect? Several factors are apparently important. The history of land use across the northeastern United States is varied and complex. Whereas some areas were cultivated intensively for many years, others were never entirely cleared for agriculture but were managed as woodlots and were cut repeatedly. Even on individual sites, the sequence of land uses is complex and is generally impossible to reconstruct fully. For instance, many sites that were cultivated for crop production were subsequently used as pastures and, after farm abandonment and succession to forest, were cut repeatedly or burned. Thus, despite our most rigorous efforts to determine historical land-use practices, our knowledge of the history of any particular site is always incomplete and, because of its complexity, is not easily quantified. In addition, environmental variability differs considerably among sites. Although sites like Montague Plain are extremely homogeneous, most of the northeastern landscape is much more like Prospect Hill, with its varied terrain, drainage patterns, and environmental conditions. The fact that land-use history is frequently correlated with environmental variability tends to restrict our ability to identify clear land-use impacts, even on sites where they occur. Finally, our flora are quite varied and each species responds to this complex history as well as to environmental gradients in different ways and at different rates, making it difficult to generalize to any great extent. Similar to wildlife assemblages, when we sample New England's vegetation at any point in time, we are observing species at different positions in their response to and recovery from historical disturbances. For instance, although some species may have largely recolonized sites that were occupied before the agricultural period, others have moved only a few meters onto old farmland. For species with severe limitations on dispersal or establishment, decades or centuries may be needed for them to spread onto old fields.

Thus, while there is no simple answer to the question of the relative importance of environment versus history in controlling modern vegetation patterns, we can clearly find evidence for the strong influence of both factors. When we look closely with a view that is strongly informed by historical information, we see that landscape patterns of species assemblages and individual species distributions in New England continue to be influenced by historical land-use activity. This is true despite the passing of a century or more since the abandonment of most former agricultural sites, and the occurrence of many more recent disturbances, such as the 1938 hurricane, fire, numerous pathogens, and twentieth-century logging, that could have obscured the effects of earlier land-use practices. We conclude that modern assemblages and species distribution patterns are only partly the result of contemporary environmental conditions and that for some species, modern distributions may be controlled more by historical factors than by variation in current resource conditions.

These results have important implications for the use of standard community ecological data and analyses to interpret community composition and dynamics. Studies at the Harvard Forest and throughout the northeastern United States have documented the dramatic landscape transformations that occurred during the historical period as a result of changing land-use practices and natural disturbances. In fact, it is likely that the distribution and abundance of every species on the modern landscape have been significantly altered by historical disturbances. Our limited ability in complex landscapes to identify such influences results in part from the factors described above, and also from the limitations of our approaches in quantitative community ecology that typically enable us to measure current environmental conditions and vegetation patterns well but do not allow us to adequately evaluate what the landscape would have been if historical disturbances had not occurred. Thus, the effects of widespread and complex disturbances such as historical land use, wind, or pathogens, though important, may go undetected. We do not suggest that these factors be ignored as untractable; on the contrary, they must be rigorously analyzed using as complete historical and environmental investigations as possible. However, we must also recognize the potential importance of factors that, though not easily quantified, may exert a strong and persistent influence on the landscape.