Reading the Landscape: Primary vs. Secondary Forests

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In much of the eastern United States, the forests within a region vary enormously. Some forests are young thickets while others consist of old, majestic trees. There are oak forests and there are maple forests; some are wet, others dry. Distinguishing between primary and secondary forests can help to explain some of the variation.

"Secondary forests" are those growing on land that was once cleared for farming, and "primary forests" are on land that has never been cleared for agriculture. Both primary and secondary forests are common in the eastern United States, and their distribution is largely a function of land history. How land has been used, in turn, has been strongly influenced by intrinsic features such as soils and topography. In prime agricultural regions secondary forest is generally uncommon because little farmland has been abandoned. In mountainous regions secondary forest is also uncommon, in this case because very little land is suitable for farming. In other areas where agriculture was widely practiced and then substantially abandoned, secondary forests are common today. This essay focuses on why and how these two kinds of forest differ and, using the example of beech trees, discusses the process of succession that occurs when land is reverting from agricultural use to forest.

The term "primary" forest should not be confused with "old-growth" forest—forest free from significant human disturbance or influence. The few old-growth stands that exist today in the eastern United States are all primary forests, but the reverse is not true. The vast majority of primary forests are not old growth because they have been substantially disturbed by the activities of people, most commonly by logging and grazing. Despite having been disturbed in various ways, often repeatedly, primary forests have had continuity of forest habitat for thousands of years.

Looking for Clues

Trying to decipher the history of forests when walking in the woods is fun and informative. Sometimes it is easy. Younger secondary forests (say twenty to forty years since farming) are readily recognizable from their scrubby or thicket-like structure, the absence of large trees or stumps, and the presence of some trees with open, spreading growth forms resembling specimen trees in lawns. As secondary forests age, however, they gradually take on some of the appearance of primary forests. After sixty or ninety years or more, they can be more difficult to distinguish and closer scrutiny is required.

One useful clue is the degree of undulation in the ground surface. Conspicuous irregularities are normally present in the ground surface of primary forests, the result of centuries of tree-uprooting by wind. The mounds and pits, as these small-scale topographical features are called, tend to be on the order of one to two yards across. In contrast, the ground under secondary forests is relatively level because over the years agricultural plowing smoothed the surface of the ground.

Other features useful in distinguishing primary from secondary forests can be seen at the

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The initial stage of pit-and-mound formation. In this photo of red pine trees (Pinus resinosa) *uprooted by wind, the mounds are the root balls and the pits are the original locations of the root balls*

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When soil is displaced by an uprooted tree, a mound and a closely associated pit are formed The pits and mounds in this photo, of Hemlock Hill in the Arnold Arboretum, were created nearly sixty years ago, in the hurricane of 1938

A well-defined edge (above the arrow) between an older primary forest to the right and a younger secondary forest to the left. Note the profusion of spreading branches on the left side of the edge.

Secondary forest grows on both sides of this older hedgerow of trees, which runs from the left foreground of the picture to the center rear. Note the spreading branches growing out on both sides of the hedgerow.

edges of stands. One hundred (or more) years ago, when the sites that today support older secondary forests were still being farmed, the edges of farm fields were commonly either hedgerows or primary forest. Many of the trees that once grew on the edge of these fields retain evidence of their former edge environment. Specifically, trees on the edge of a primary forest adjacent to secondary forest will show a pronounced asymmetry in their branching, with more large, nearly horizontal, low-to-the-ground branches on the formerly sunny side. Older hedgerows with older secondary forest on both sides will likewise show evidence of a remnant branching pattern, but in this case large, spreading branches grow out on both sides of the trees. Sometimes, the large, spreading branches have died but their former existence can be deciphered from the large, bulging branch bases along the trunk.

Rocks can also tell a story. Rock piles or walls are common occurrences along the edges of secondary forest, generally indicating that the rocks were moved to the edge of the field to facilitate plowing. Sometimes it is unclear at first from which side of an edge the rocks came, but a bit of sleuthing usually reveals the answer. For example, two common situations are (1) an edge between primary and older secondary forest and (2) two older secondary forests separated by a hedgerow that was present when the forests were fields. Suppose that the edges in both situations contain rock piles. Which site did the rocks come from, and how can you be sure?

In the first situation, the secondary forest would have relatively smooth ground, the result of previous plowing, and thus the rocks must have been removed from that site; the adjacent primary site, in contrast, would show mounds and pits. Confirmation should come from the branching pattern of the edge trees: many more large, spreading branches should be growing out into what is now the secondary forest. In the second situation, mounds and pits would most likely be absent from both sites, suggesting that the rocks came from fields that were on both sides of the hedgerow. If the branches of the larger hedgerow trees are growing outward on both sides, this would confirm secondary forest on both sides of the hedgerow.

How Do They Differ In Species?

Secondary forests contain more sun-loving, open habitat plants than do primary forests. Examples are *Cornus racemosa* (gray dogwood), *Lonicera* spp. (honeysuckle), *Rhamnus cathartica* (buckthorn), and *Solidago rugosa* (goldenrod). These open habitat species typically invade early in old field succession; they are present in secondary forests because they can persist, at least for a while, in a shady forest understory. A number of the open habitat shrub and herbaceous plants are exotic species, and thus another difference between primary and secondary forests is that the latter have more exotic (nonnative) plant species.

There are other noteworthy differences in species, if we consider just the common plants of primary forests. Secondary forests contain a subset of the forest plants and animals found in primary forests; a few examples of plants that are common in each kind of forest in the northeastern United States are listed in Table 1. Even within a group of closely related species, we sometimes find that one species is common only in primary forests, while another is common in both secondary and primary forests, as shown in Table 2. For example, in central New York (and elsewhere) *Acer rubrum* (red maple) is common both in primary and secondary forests whereas *A. saccharum* (sugar maple) is abundant in primary forests but is seldom abundant in secondary forests. Where forest plants are present in secondary as well as primary forests, we can assume that they colonized the secondary forest sites from the primary forests and hedgerows that surround most fields. Why have some forest plants been so successful in colonizing secondary forests from source populations in primary forests and hedgerows?

To answer this question, consider the different land-use histories of primary and secondary forests. Clearing of the original forests, combined with the sustained use of a site for agriculture for the better part of a century, would eliminate the forest plants and animals present at the time of clearing. Thus, when a farm field is abandoned, primary forest plants and animals can colonize it only if they can get there from nearby forests and hedgerows. The distances over which forest species must travel in order to

Table 1. A list of selected plants that are characteristic of primary or secondary forests in the northeastern United States

Primary	Secondary
Fagus grandifolia (American beech)	*Acer rubrum* (red maple)
Acer saccharum (sugar maple)	*Fraxinus americana* (white ash)
Tilia americana (basswood)	*Pinus strobus* (white pine)
Tsuga canadensis (hemlock)	*Cornus racemosa* (gray dogwood)
Polystichum acrostichoides (Christmas fern)	*Viburnum dentatum* (arrowwood viburnum)
Trillium grandiflorum	*Botrychium virginianum* (grape fern)
Dentaria diphyllum (toothwort)	*Lycopodium flabelliforme* (ground pine)
Caulophyllum thalictroides (blue cohosh)	

Table 2. Examples of plant differences between primary and secondary forests in the northeastern United States

	Primary	Secondary
Trees	*Acer rubrum* (red maple) *Acer saccharum* (sugar maple)	*Acer rubrum*
Shrubs	*Viburnum dentatum* (arrowwood viburnum) *Viburnum acerifolium* (mapleleaf viburnum)	*Viburnum dentatum*
Herbs	*Dryopteris austriaca* var. *spinulosa* (spinulose wood fern) *Polystichum acrostichoides* (Christmas fern)	*Dryopteris austriaca* var. *spinulosa*

colonize abandoned farmlands are often not great—perhaps fifty to several hundred yards—but they are nonetheless significant because plant species differ so much in seed dispersal ability. Some forest species are much better than others at dispersing seeds to abandoned fields. Thus one reason secondary forests differ in species from primary forests is that they contain species with better dispersal capabilities. I suspect this explains why secondary forests contain herbaceous plants with tiny spores that drift long distances on the wind, such as spinulose wood fern.

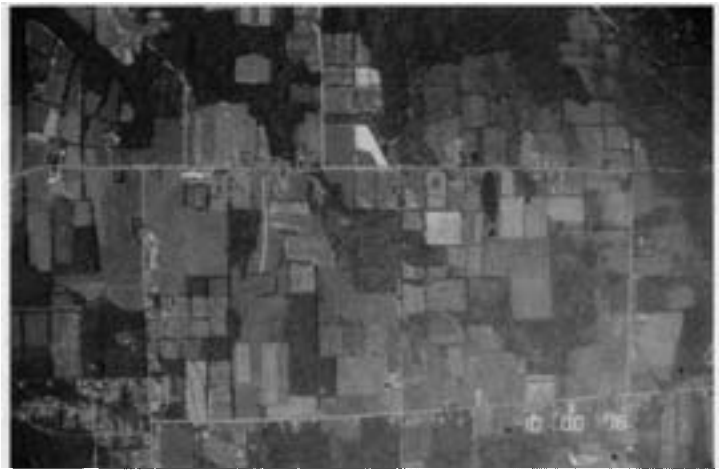
But not all forest species capable of dispersing to abandoned farmlands are well represented in secondary forests. Some shade-tolerant forest species are uncommon in secondary forests, perhaps because they cannot tolerate the sunny, open conditions of rundown, abandoned fields. And finally, plants may be uncommon in secondary forests because of seed size. Small seeds give rise to small seedlings, which compete poorly with the dense meadow vegetation of abandoned farm fields. The scarcity in secondary forests of the primary forest species listed in Table 1 can presumably be explained by one or more of the three factors just described.

The Case of Beech Tree Colonization

Beech *(Fagus grandifolia)* behaves quite differently in secondary forests than it does in primary forests, and the pattern of its invasion

Investigating Two Centuries of Change

In the eastern United States, the mixture of forest and open nonforest land has changed dramatically over the last two hundred to three hundred years. A recent study estimated how much forest was present in rural Tompkins County, central New York, in 1790, 1900, 1938, and 1980. Our estimates were drawn from a variety of sources. We used contemporary information for 1790, 1938, and 1980. Records from the original land surveyors indicated that in 1790, 99.7% of the county was covered in forest. By carefully examining aerial photographs taken in 1938 and 1980 we determined the amount of forest present at those times: 28.5% in 1938; 50.7% in 1980. Old agricultural census records revealed that the maximum acreage in farmlands occurred between 1890 and 1900. This was a key date because the amount of forest in Tompkins County would have been at its lowest when the amount of agricultural land was at its maximum. Before 1890, forest was still being converted to agricultural land; after 1900, agricultural lands were being abandoned. Fortunately, the short time interval between 1900 and 1938, when the earliest aerial photographs were taken, meant that we could distinguish on the 1938 photos young forest growing on abandoned agricultural fields from older forest that had been present in 1900. By this means we estimated that only 19.4% of the county was forested in 1900. Thus, in only two hundred years, the landscape of Tompkins County changed from being all forested, to mostly agricultural, to an equal mixture of agricultural and forest lands today.



In studying how much of Tompkins County's forest was once cleared for agriculture, we made extensive use of aerial photographs. This one shows primary forest as well as abandoned agricultural fields in the process of becoming secondary forest.

The major kinds of vegetation present in 1790 are here today: oak forests, swamp forests, and various forests with sugar maple, basswood, beech, hemlock, and other trees. Cattail marshes, other marshes, beaver meadows, and alder thickets are some other landscape components present today and in 1790. There are also present today landscape components that were rare or absent in 1790. Examples are active and abandoned cow pastures and abandoned crop fields (old field succession). Thus, we see that landscape components have changed both quantitatively and qualitatively over the last two hundred years. Many of the original components are still with us, but we have less of each one. At the same time we have some distinctly new components.

How general are the results from Tompkins County? The results probably apply to many parts of the eastern United States, provided that allowance is made for differences in both the dates and the amount of forest cleared. For example, the chronology would be shifted earlier in southern New England.

This information is based on two collaborative studies, which are cited at the end of the article B E Smith, P L Marks, and S. Gardescu, 1993, and P L Marks and S Gardescu, 1992

illustrates one of the general principles underlying plant succession. I first noticed that beech was showing an interesting pattern about ten years ago when I was studying forests around Ithaca, New York, to determine whether each stand was primary or secondary. After a while I realized that if I saw a stand with large beech trees—trunks greater than about fifteen inches in diameter—invariably the forest had not been cleared for agriculture. (Incidentally, the reverse was not true. Not all forests that lacked large beech trees had been farmed. Some were primary forests, but the soil was too wet or too dry for beech.)

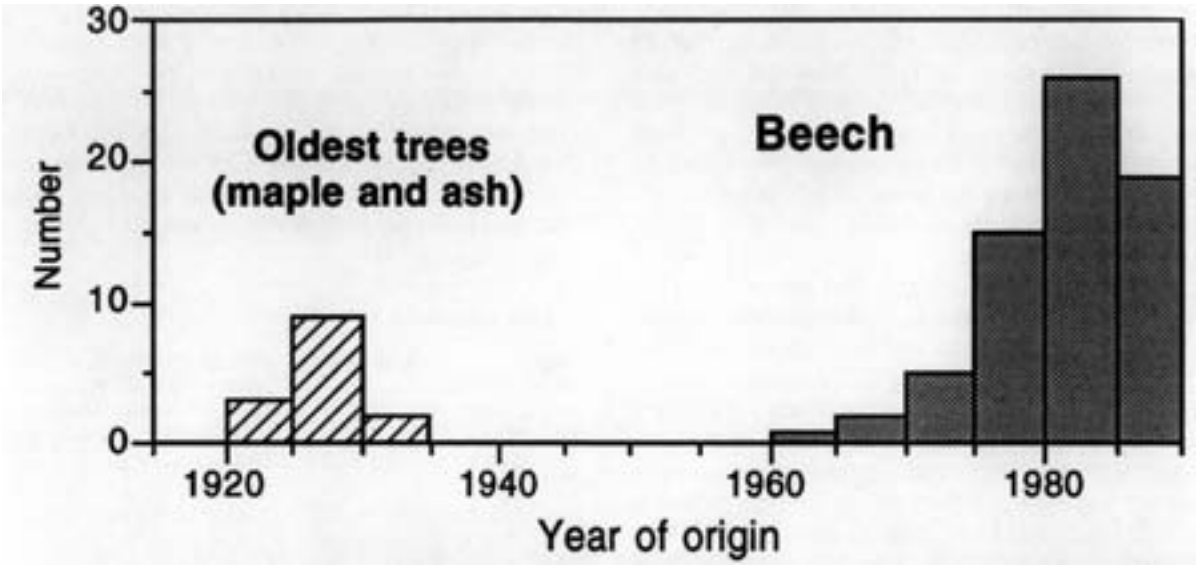
Subsequently I began to notice the widespread occurrence of beech seedlings and saplings in secondary forests, the same forests that lacked large beech trees. Apparently, secondary forests were being invaded by beech, since there were small, vigorously growing beech in the understory but no large beech trees in the overstory. On my own land, there is a well-defined edge between secondary and primary forest. The primary forest contains lots of beech, ranging from large trees to small stems. The adjacent secondary forest grew up in a field where agriculture had been abandoned around 1920, an estimate derived from examining old aerial photographs and deed records. Maples, pines, and ashes, but not beech, are among the dominant, tall tree species in the secondary forest today. These trees are sixty or seventy years old, having invaded the field within a decade or two after the last time crops were grown. In the understory, seedlings and saplings of beech are common. Many of the large beech in the adjacent primary forest are close to the edge of the secondary stand, and there is every reason to think that these trees have produced large numbers of beech seeds for a hundred years or more. Nevertheless, beech has been able to invade the former agricultural site only in the last couple of decades. Why? Why has it apparently taken so long for beech seedlings to get started after the field was abandoned?

Students in the plant ecology course at Cornell University have studied beech invasion in secondary forests, and it is instructive to examine some of their results. In several older secondary forests—on land that was last farmed

Beech leaves remain on saplings and lower tree branches throughout winter, making it easy to spot beech in a forest when other deciduous trees are leafless.

about seventy years ago—the density of beech seedlings and saplings is about one stem per hundred square feet, dense enough to produce a beech forest in the future if most of these stems survive. The ages of the beech invaders are revealing, as can be seen in the graph on the next page. In the secondary stand on my own land, beech began to invade about forty years after abandonment—thirty to forty years after the other tree species got started. The beech invasion continues, and most of the beech seedlings and saplings became established in the last twenty years. However, we can't tell whether the low density of beech dating from the 1960s and early 1970s is due to mortality or to a gradual beginning of the invasion.

More specifically, how might we explain the failure of beech seedling establishment in the first forty years following agricultural abandonment and the clearly successful establishment over the ensuing twenty-five years? As with vir-



Abundances of different ages of beech seedlings and saplings (in gray), and of the oldest trees of other species (diagonal lines), showing the years in which they originated, in a secondary forest that developed on farmland abandoned about 1920. (Younger maple and ash are not shown.)

tually all such questions in the science of ecology, there is more than one plausible answer. First, although as I have suggested above beech seeds have no doubt been available throughout the past seventy-five years, perhaps seeds began dispersing into the site only after it had become a forest, rather than in its earlier stages of meadow or thicket. In this part of the world, around forty years are necessary for an abandoned agricultural field to develop into young forest through natural succession. A second possible answer is that beech seeds have been dispersing into the site for the entire seventy-five years but were unable to become established as seedlings until something changed about thirty years ago.

How do beech seeds disperse from one place to another? What sorts of changes might have occurred thirty years ago that could have favored the establishment of beech seedlings? The answer to the first question hinges on the behavior of the animals that disperse beech seeds. Beechnuts are contained in prickly burs, which hold two shiny brown triangular nuts, each the size of a small acorn or a large lima bean. The burs open in early fall, at which time the seeds are eaten by birds such as blue jays, grouse, and turkeys, and by mammals ranging from chipmunks and squirrels to fox and deer. Of these animals, blue jays, squirrels, and chipmunks do carry beechnuts away from the trees, burying them to eat later. Blue jays, for example, can carry up to fourteen nuts at a time and may fly several miles from the beech trees back to their feeding territories, where they bury the nuts individually beneath the leaf litter covering the soil. When food is abundant in the fall of the year, these animals store beechnuts, acorns, and other tree seeds in their feeding territories, returning over the winter to eat the nuts. Even though the number of nuts left behind may be a small fraction of the number stored in the feeding territory, these seeds have been "planted" by the animal and thus stand a good chance of germinating and becoming established as seedlings.

The explanation for the delay in beech invasion could involve the behavior of the dispersal agent. It may be that blue jays, squirrels, and chipmunks bury beechnuts mainly in forests. In other words, forty years or so are required to produce the kind of habitat where these animals bury nuts. There is an alternative explanation, however. Blue jays, and for shorter distances, chipmunks and squirrels, could be burying beechnuts during most or all of the forty years

from farm abandonment to young forest, but the uneaten nuts may seldom become vigorous seedlings during this early period because beech seedlings require shade to keep their roots from drying out. Several decades would therefore be needed to produce the forest conditions that permit beech seedlings to thrive.

Whatever the reasons for the delay in beech invasion into post agricultural forest, the phenomenon illustrates one of the earliest theories about how succession works—namely, that the first invading plants alter the characteristics of a site in ways that favor invasion by other plants. These first invaders might cast shade that favors plants that do better away from direct sunlight. Or they might be legumes that fix nitrogen and thus favor plants that do better in richer soil.

But this process of "facilitation"—of early invaders facilitating later invaders—is not the only determinant of succession. When—or even whether—a species invades involves an element of chance. For example, a tree species might invade an abandoned field if it happens to be common around the edges of the field, or if it has a good seed year during a critical decade of succession, or if the weather is favorable during a critical stage in the life cycle (for example, during seed germination). In the case of delayed invasion of beech in secondary forests, both of the likely explanations appear to involve facilitation: Before beech trees can become established, an abandoned farm field apparently must become young forest either to encourage burial of beechnuts by animals, or to provide the environmental conditions that allow beech seedling establishment, or both.

The history of the landscape cannot be read with certainty, but that hasn't stopped historically minded ecologists from thinking about it. There is much to learn about today's landscapes by developing a picture of how they were in the past. Because landscapes are constantly changing, especially under the influence of humans, there are striking contrasts between contemporary and historical landscapes. Such contrasts help our present understanding by revealing how recently certain kinds of habitats, which we may take for granted, have become part of the landscape. At the same time, other elements of the landscape are relatively old; they are present today and were also present hundreds of years ago. Deciphering the landscape's history enriches our understanding by allowing us to see it as dynamic, as something that has changed from an earlier condition, and that is still changing today.

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