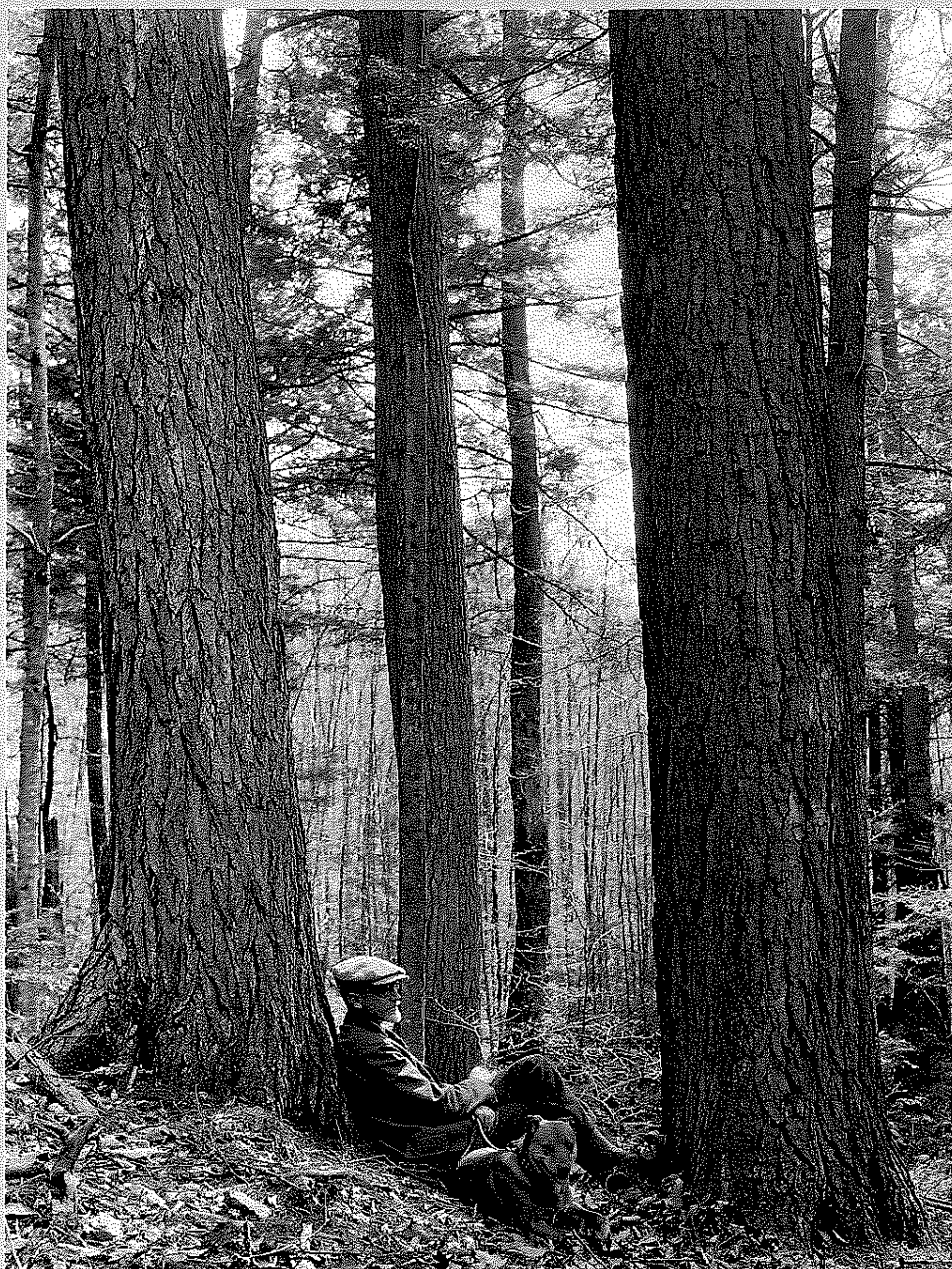

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Front cover: Glory-of-the-snow (*Chionodoxa* sp.) was in bloom at the foot of an Oriental beech (*Fagus orientalis*, accession 14586-A) on April 9, 2013. Photo by Kyle Port.

Inside front cover: R.T. Fisher, first director of Harvard Forest, and his dog Johnny amid old-growth eastern hemlock and eastern white pine on Harvard Forest's Slab City tract in 1925. Photo courtesy of Harvard Forest Archives.

Inside back cover: Spiraea prunifolia var. *simpliciflora* in bloom. Photo by Nancy Rose.

Back cover: A lone specimen of Siberian elm (*Ulmus pumila*) growing by a cultivated field in Hebei, China, photographed by John George Jack on October 4, 1905. Archives of the Arnold Arboretum.

BOOK EXCERPT

Hemlock: A Forest Giant on the Edge

David R. Foster, Editor

Editor's Note: Eastern hemlock (*Tsuga canadensis*) is an iconic tree species in northeastern forests and the Appalachian Mountains. It has faced peril in the past but is now faced with perhaps its most deadly threat—the invasive and devastating insect pest, hemlock woolly adelgid. In this new book, Harvard Forest director David Foster and several colleagues and scientific collaborators explore the history and ecology of and challenges to the majestic eastern hemlock.

Presented here by permission of the publisher is an excerpt from Chapter Three: *Prehistory to Present,* written by Wyatt Oswald, David Foster, and Jonathan Thompson. In the previous part of the chapter the authors describe the process of extracting 3-inch-wide, 3-foot-long sediment cores from a pond for later paleoecological analyses of the material.

Hemlock: A Forest Giant on the Edge
David R. Foster, Editor.
Written by Anthony D'Amato, Benjamin Baiser, Aaron M. Ellison, David Foster, David Orwig, Wyatt Oswald, Audrey Barker Plotkin, and Jonathan Thompson; Stephen Long, Consulting Editor.
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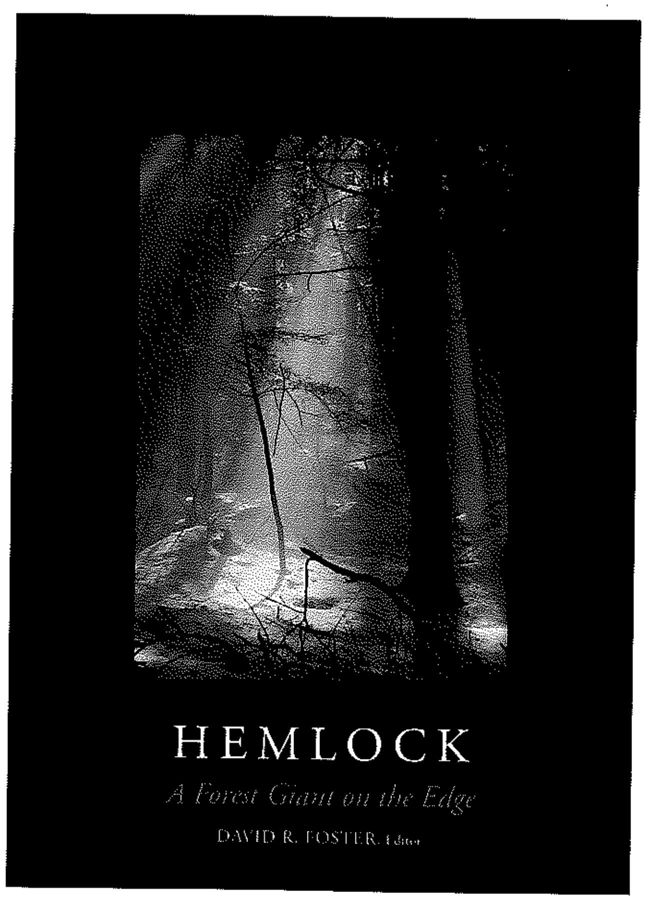


HEMLOCK has changed in abundance numerous times in the past, and it now faces an extreme threat from the hemlock woolly adelgid. As we seek to consider this new dynamic in perspective, we are fortunate that hemlock has left a remarkable array of records that shed light on its ecology under a wide range of conditions. These historical and paleoecological archives inform the field studies, experiments, and modeling activity that we undertake in the woods and back in the laboratory. A look at hemlock's fossil record helps us examine how hemlock has changed with the intense human activity in the past few centuries and allows us to assess how it might cope with the combination of insect onslaught, climate change, and ongoing human activity today and in the future. It also enables us to evaluate whether there is any hope that hemlock may stave off or recover from the population collapse associated with a new invasive organism.

We use a variety of tools and techniques to reconstruct the historical dynamics of the forest environment and vegetation, as well as individual tree species. To reach back furthest, we study pollen, other microscopic fossils, and diverse signatures of past environments that are preserved for millennia in the sediments of lakes, bogs, swamps, and other wetlands. More recent centuries and decades come alive in historical land-survey documents, field studies of old-growth forests, and tree rings that yield insights into the composition and structure of forest vegetation from the time of European arrival forward. In some cases, the particular qualities of hemlock provide a record that bridges prehistory and history. For example, by carefully dissecting the deep beds of needles that accumulate on the cool, moist ground beneath hemlock, we find pollen and other plant parts that yield a chronological record connecting the postglacial period with the time since European settlement. From these distinctive soil layers comes a record of changes in the composition of individual forest stands that can be linked to the evidence from tree rings, uprooted trees, and the many other clues that are present in the hemlock forest itself. Those of us conducting retrospective studies at the Harvard Forest have employed this full array of approaches, exploiting every opportunity to reconstruct the distribution, abundance, and dynamics of hemlock across New England and going back thousands of years into the past.

ONE HUNDRED and fifty years ago, Henry Thoreau mused in his journal on what stories might be gleaned from the pollen grains accumulating in small pools and ponds, but it took nearly a half century more for the Swedish naturalist and geologist Lennart von Post to first take advantage of this phenomenon in studying the history of plants over long periods. He published a report in 1917 showing that the grains of pollen identified in Scandinavian peats told an astonishing story of dynamic changes in vegetation composition.

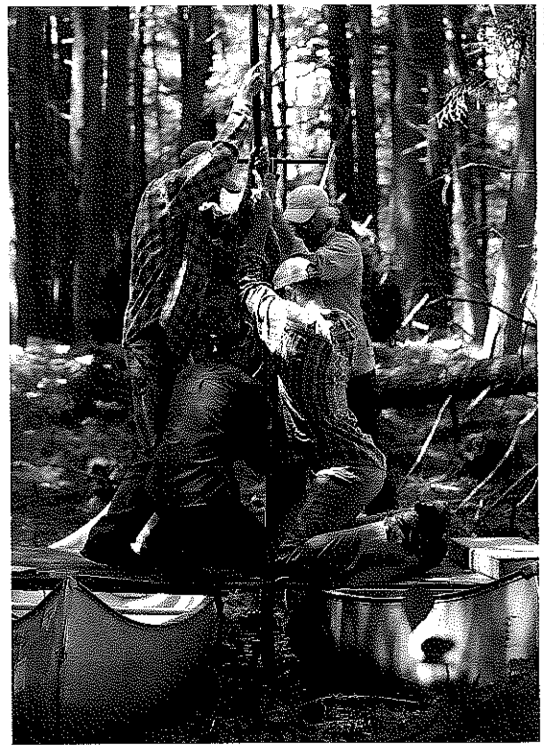
Two characteristics of pollen make it a particularly useful tool for interpreting the past. First, pollen grains are remarkably durable because they are shielded by an outer layer of complex chemical compounds that protect the sperms cells as they get transferred from the stamens to the pistils of flowering plants, or from male to female cones in conifers like pine or hemlock. Second, the pollen of different species and genera of plants is different enough to allow us to identify them. It comes in a wide range of shapes, sizes, and surface markings, all of which allow palynologists—the meticulous and patient scientists who toil over microscopes, examining these minute fossils—to separate and identify the pollen or spores of particular plants. Some pollen can only be distinguished at the level of the plant family (such as roses, buttercups, or peas) or at the genus level (as is the case for oak, which has many different species but unfortunately only a single type of pollen). In other cases, finer distinctions can be made, such as with the pines, the maples, the hickories, and the spruces, where many but not all of the species can be separated. But in the case of two of our most important species—hemlock and beech—we are fortunate that they can be identified individually. Indeed, the pollen of each of these species is rather distinctive. Hemlock pollen grains look like rough spheres with a fringe along their equators. By contrast, each beech grain has three deep furrows with circular pores in the middle. Palynologists puzzle over these and many other distinctions through their microscopes, with the assistance of reference materials, photographic keys, and colleagues. Over time—many years to a lifetime—the many different types of pollen have become readily distinguishable.

The different pollination strategies of individual species influence how reliably we'll find a particular tree's pollen in the cores we extract. Some species produce small amounts of pollen in an attractive flower to enlist the assistance of insects, birds, and even small mammals to transfer the tiny grains from the flower of one plant to that of another of the same species. The efficiency of this process and the characteristics of these pollen grains, which are often comparatively large, heavy, and sticky, ensure that very few errant grains end up in some sediment. That means that for many plants that use bright and showy flowers to attract the attention of pollinators, there is but a scant record in the mud. Among New England trees, the pollen of chestnut and maple, for example, is largely distributed by insects, so even though these species were or are often abundant, they are underrepresented in the pollen record. If, however, a plant relies on the wind to distribute its pollen grains— and most of our abundant trees such as oaks, birches, beech, and all of our evergreen species use this strategy—it's a different story. These species produce prolific amounts of pollen, each year sending clouds of pollen aloft so that some lucky few might happen upon a female flower.

The vast majority of these pollen grains miss their mark and end up in the sediments of lakes, wetlands, and forest soils. A large lake collects pollen not only from the adjacent vegetation, but also from plants in the landscape as far as ten to a hundred miles away. In contrast, pollen accumulating in vernal pools, small ponds, bogs, or soils is much more likely to be derived from nearby plants, including those hanging immediately above it. This means that records from those types of small basins reflect the local vegetation. Paleoecologists need to take these factors into account in their interpretation of records. They can also apply this knowledge to choose sites that sample the vegetation at either local or regional scales.

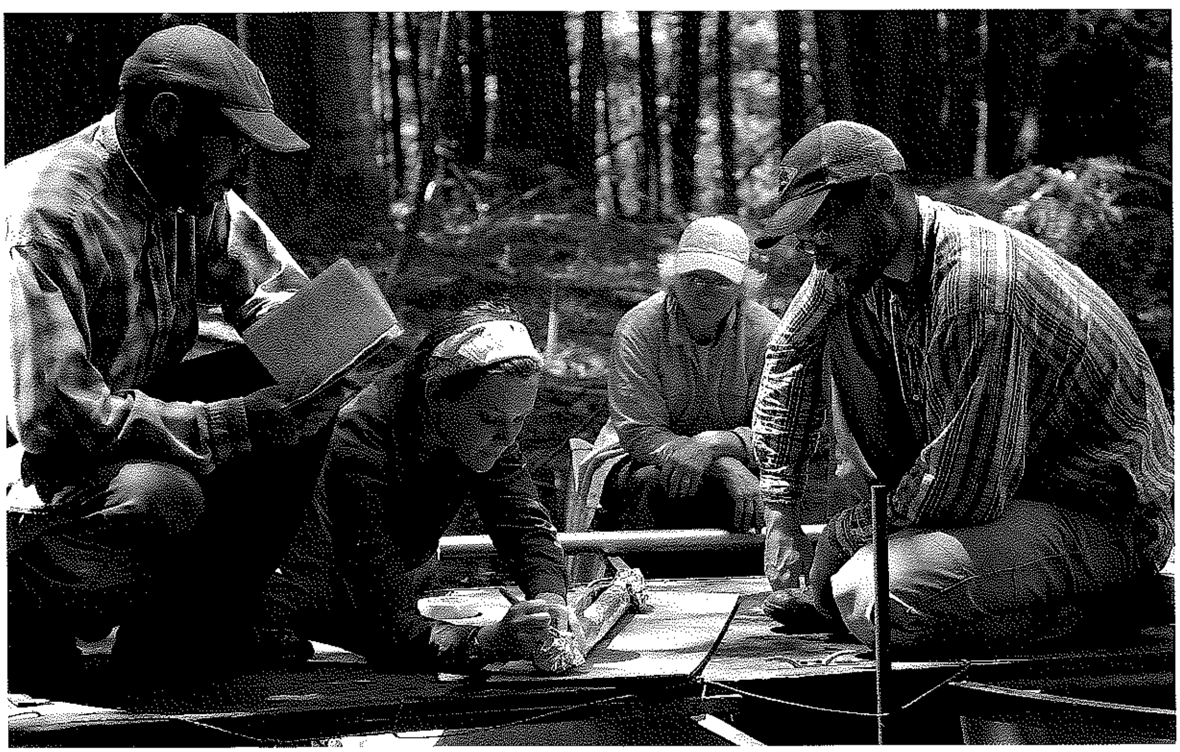
Regardless of the site, changes in the pollen grains found in successive layers of sediment indicate whether the composition of the vegetation has changed through time. The key to obtaining a good and continuous record is locating an environment with slow decomposition, in which such layers can accumulate gradually and remain undisturbed. We find such conditions in lakes, where fine-grained mineral and organic matter settle out as mud in the deepest areas and then are preserved in the cold and oxygen-poor environment. An alternative environment is wetlands, where waterlogged conditions inhibit decomposition, and the vegetation grows on a surface composed of the remains of

The top of an eastern hemlock (*Tsuga canadensis*) pokes above the canopy on the Prospect Hill tract of Harvard Forest.



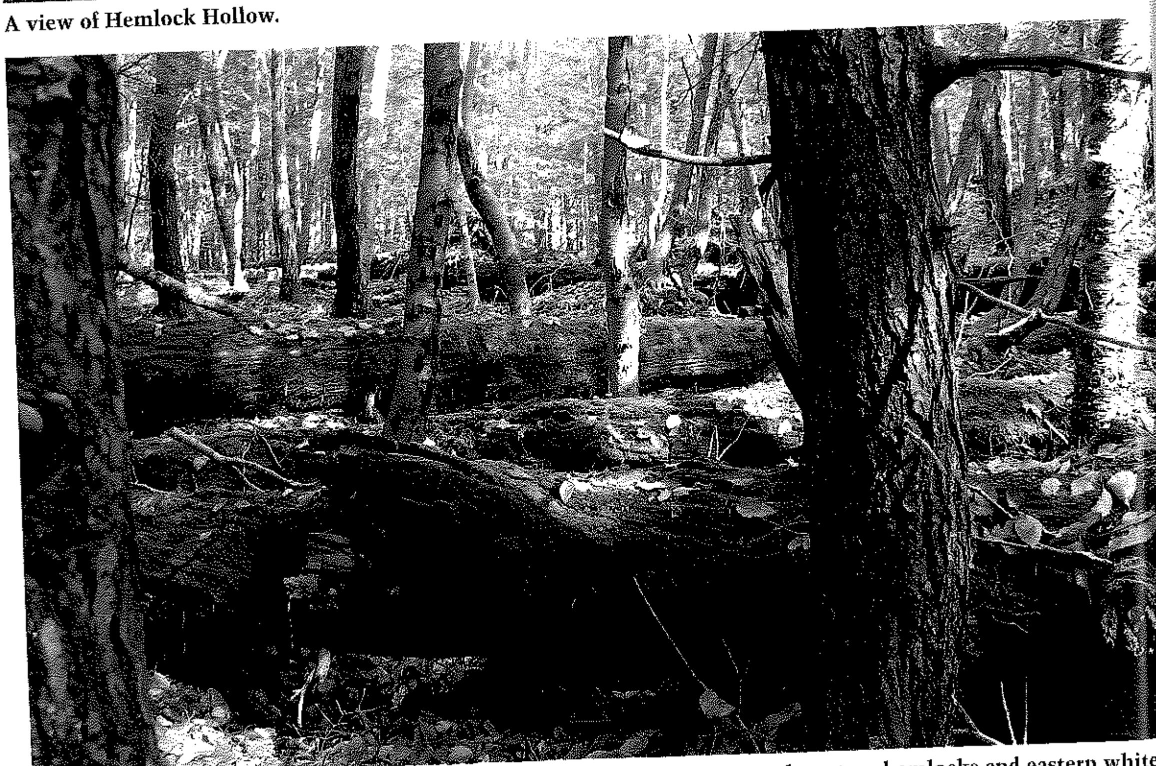
ALL IMAGES BY DAVID FOSTER

Researchers extract sediment cores from Harvard Forest's Hemlock Hollow.



An extracted sediment core is finished and labeled by researchers.

A view of Hemlock Hollow.



In Harvard Forest's Pisgah Tract in southwestern New Hampshire, old-growth eastern hemlocks and eastern white pines (*Pinus strobus*) that were blown down by the 1938 hurricane provide structure to the modern forest.

previous generations of plants. In New England, where glaciers scoured the earth surface during the last ice age, the duration of both of these sedimentary archives is limited to the period since the ice melted, the land surface stabilized, and the climate allowed the growth of plants. Thus, the oldest lake records span about twelve to fifteen thousand years, and many wetlands only extend back five or six thousand years.

MEANWHILE, back in the lab, we slice the cores into thin sections, half an inch or less in length, and carry out a series of treatments and analyses of the material. It's not just pollen grains that we seek. For instance, we want to know the age of the mud at different depths in the core, so we extract small samples of sediment or plant material and send them to a specialized (and expensive) laboratory that assesses the radiocarbon content of the material. We also measure the sediment's organic and mineral content or particle sizes to determine changes in the lake environment, including past droughts, which are often registered as layers of sandy, inorganic material. In combination with other chemical analyses, these sedimentary characteristics provide a detailed record of past variations in climate.

We isolate pollen grains as well as the spores from ferns and other early plants by subjecting mud samples to intense acid baths, washings, centrifuge spins, and sieving steps. It's remarkable that these intense treatments remove most of the organic and mineral material but leave a tiny residual fraction that contains the concentrated and quite intact pollen, along with bits of insects, charcoal, and other miscellaneous detritus. The tiny pieces of charcoal and insect remains, both of which are as highly resistant to decay as pollen, are sieved, identified, and counted under a microscope to provide information about past wildfire activity and insect outbreaks.

We mount the residue on microscope slides and examine them with high-powered magnification, carefully scrutinizing and identifying every pollen grain that is encountered. At any given level, a palynologist might identify 300 to 500 pollen grains through a painstaking process that can take anywhere from two to eight hours or more.

Pollen data tell us the relative abundance of different species. If 50 out of 500 pollen grains at a given level are identified as hemlock, this would yield a value of 10 percent. Knowing whether or not a species is a prolific pollen producer helps us to assess how well the relative abundance of its pollen corresponds to its actual abundance on the landscape. The pollen of insect-pollinated trees such as maple and chestnut rarely exceeds 5 percent of the total, whereas pine, birch, and oak can easily reach 10 to 20 percent or more. Considering these factors, we would assume that 5 percent chestnut means a significant presence. At its very crudest, a pollen diagram will show at what point in the past hemlock or any other plant was absent, rare, or abundant. In most cases, it will also reveal fascinating curves depicting the long-term variation in these species in relationship to other species and many environmental factors.

In well-studied regions such as eastern North America, many dozens of pollen records have been analyzed over the last few decades. In southern and central New England, the Harvard Forest group has analyzed cores from more than three dozen sites. We make the data available to everyone electronically on our website and collaborate with many people who use them. We also keep the cores from which samples have been taken in cold storage for our future needs and those of other scientists who may be interested in examining our records in more detail or for searching for other materials and clues in the mud. Our network of study sites enables us to understand how the environment and ecosystems have changed in certain places, and how geographic patterns of climate and vegetation have shifted through time. They also help us reconstruct the migration history of various trees, including hemlock, as they returned following the last glacier.

AT THE HEIGHT of the last glacial period, approximately 20,000 years ago, a mile-thick ice sheet covered the New England landscape, with its southern limit extending just to or slightly beyond the modern-day coastline. Pushing and carrying material southward like a combination of a bulldozer and conveyor belt, the immense glacier piled up linear landforms called moraines that today form the higher parts of Cape Cod, Martha's Vineyard, Nantucket, other coastal islands, and Long Island. We use the term "sea level" as if it were a constant, but with vast quantities of water stored on land in these continental ice sheets, the sea level then had dropped more than 300 feet. New England and other coastal regions extended thirty-five miles or more outward on the exposed continental shelf. Pollen records show that, during this peak of ice and cold global temperatures, hemlock thrived far south—in the valleys and hilly landscapes in the Southern Appalachians, where oaks, hickories, and tulip poplars thrive today. As the climate warmed and the ice melted back to the north, hemlock migrated northward, arriving in New England around 10,000 years ago. To get to the Northeast from the Southeast, populations of hemlock had to travel nearly 900 miles in approximately 5,000 years, a migration rate more rapid than we might expect based on our modern studies of the dispersal distances of the species in our forests today.

Most estimates of migration are based on standard observations of the dispersal of a parent tree's seeds and the establishment of new seedlings, which are then extrapolated over time. The small, winged seeds that drop from hemlock cones generally fall within 100 feet of the parent tree, and as a result hemlock moves more slowly across the landscape than most species. For example, in many New England forests today, hemlock has yet to travel the short distances required to return to stands from which it was extirpated two or three centuries ago. In contrast, the seeds of birches and pines may be dispersed 200 feet within a stand and more than 700 feet across an open landscape, enabling them to be highly successful at colonizing abandoned agricultural fields.

Given these factors, we would expect hemlock to be among the slowest of species to have migrated north after the ice age. Indeed, the characteristic slow movement of hemlock initially led to predictions that, during its northward march, it would have lagged well behind the availability of suitable environmental conditions that developed as the climate warmed. Rather surprisingly, however, all current evidence suggests that hemlock and the other major tree species migrated fairly rapidly, effectively keeping up with the climatic conditions that were able to support them. Consequently, the order in which the species arrived in New England fits nicely with our general understanding of their individual environmental requirements, as well as their modern distribution. Open, treeless tundra occupied the harshest climates in the early postglacial landscape. As the climate became more hospitable, the tundra was invaded by northern boreal species—spruce, larch, and birches. With further warming, white pine followed, and then came the truly temperate tree species, including hemlock. Far to the north, the tundra continued to follow the receding glacier toward the pole, and, where they could, boreal forest trees then seeded into the tundra.

Paleoecologists have struggled to reconcile the observed and expected rates of migration and have even given a name to this incongruity: Reid's paradox. The issue has emerged as one of great importance today because of the looming likelihood of rapid climate change and the question of how plants will respond and cope with new conditions. We are employing all sorts of approaches—genetics, simulation modeling, field and laboratory studies of dispersal, and pollen analysis—as we continue to grapple with the question. Have we overestimated the rates at which trees moved in the past, or are we underestimating their anticipated and potential future dispersal rates? One possible way to account for a more rapid past dispersal is to invoke a history of rare long-distance dispersal events, such as abrupt gusts and updrafts in wind that may loft a seed into the jet stream, or the rare flight of a bird in which it carries a seed for dozens of miles. In this way, a chance event can disperse seeds great distances. If such an event happened even once a decade, it may have been extremely important in shaping patterns of movement over centuries. We cite uncommon processes such as these in our modeling discussions when talking about the dispersal of insects like the hemlock woolly adelgid or the adaptations of plant species under future climates. As research on this dilemma progresses, the answers to these questions will have important implications for predicting the future shape of our forest ecosystems and for gauging the ability of many species to survive the expected changes in climate in coming decades.

The long-term history of hemlock also reveals the extreme malleability of forest types and assemblages, including those that are familiar to us today. Hemlock arrived in the northeastern United States about 2,000 years after white pine and 2,000 years before American beech, even though today it frequently grows alongside both these species, and we often think of them as members of the same plant communities. Given beech's similarity to hemlock in shade tolerance and suitability for forest canopies, and the manner with which they coexist in many places today, it is hard to imagine that hemlock grew in New England for 2,000 years without beech. Similarly, it was only with the arrival of hemlock that the New England landscape developed forests akin to the old-growth stands of white pine and hemlock studied by early ecologists and described in many Harvard Forest studies, including those by Richard Fisher, Bob Marshall, Tony D'Amato, and Dave Orwig. The contrasting histories of these various trees illustrate that species respond in highly individualistic ways to environmental change. Because conditions in the past were distinctly different from the present, we witness the species behaving in significantly different ways over time. The assemblages of plants and animals that are familiar to us today are actually quite ephemeral in deep time and space.

It is through such understandings that we've developed an ecological theory that accepts and explains the separate though interactive behavior of species. One of the earliest and best articulations of this theory came from a noted northeastern botanist—Henry Gleason of the New York Botanical Garden—who developed the "individualistic concept of ecology" in the early 1900s. This simple but revolutionary theory posited that the makeup of vegetation on a site was determined by the actions of the many individual species, each of which operated quite separately from others and according to its unique ecological qualities. Although this concept was debated for decades, some of the strongest evidence that led to its conclusive support came from paleoecological studies that showed the highly disparate behaviors of different tree species in migration and in response to climate change and to natural and human disturbances. While this understanding of plant behavior and ecology emerged from the past and helps us explain our current landscapes, it should also prepare us for unanticipated combinations of species to appear under the anomalous conditions expected for the future.

Dead trunks of American chestnut (*Castanea dentata*) intertwined with dying eastern hemlocks.

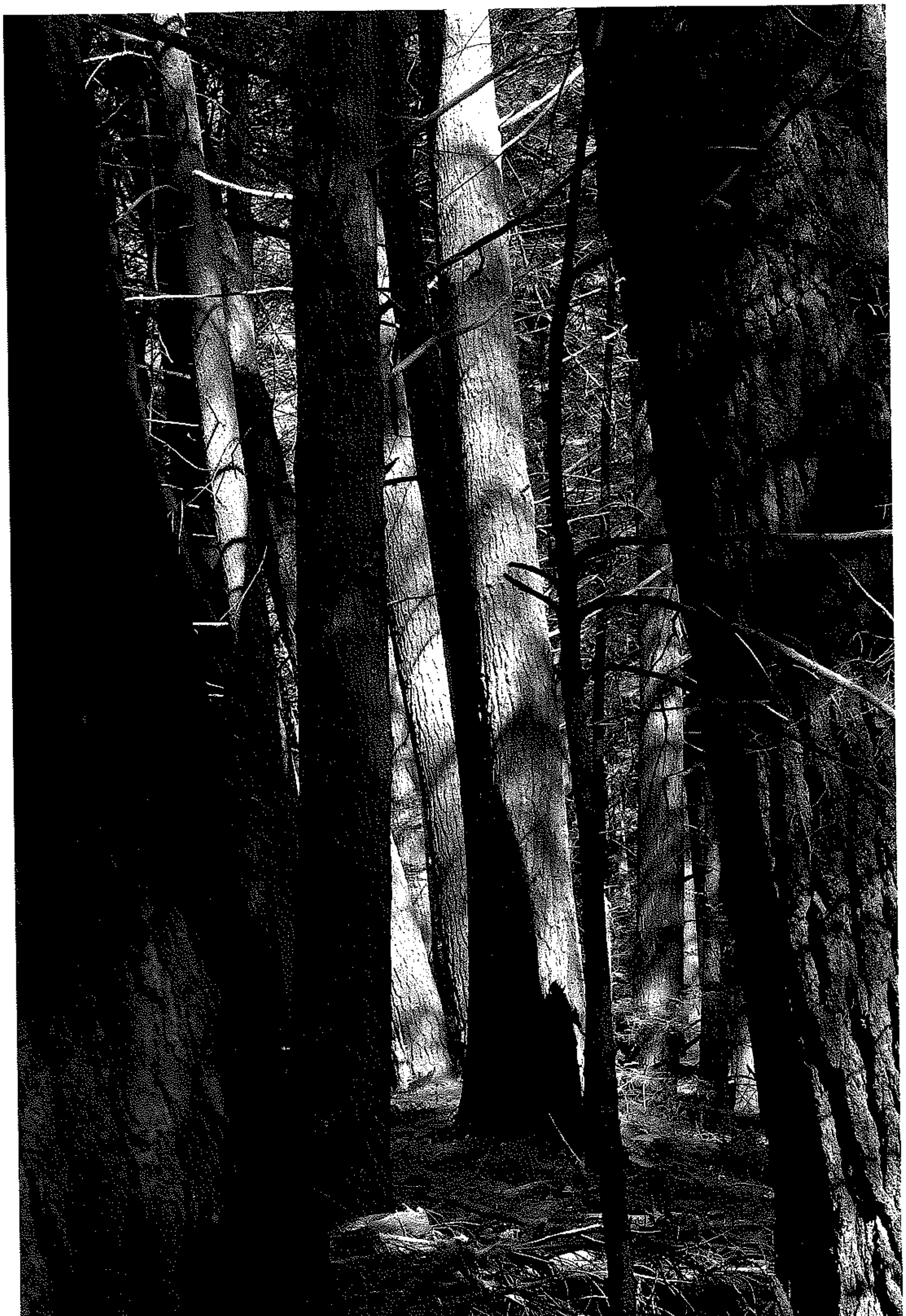
Coring dozens of ponds and bogs and examining tens of thousands of pollen grains preserved in their sediments has helped us outline the following picture of New England's prehistory. After a lengthy dry period, from around 11,500 to 10,000 years ago, during which white pine dominated the landscapes of the northeastern United States, hemlock increased in abundance across much of New England, then reached its peak population levels during a relatively warm and moist interval from 8,000 to 5,500 years ago. Beech had arrived to join hemlock in the region at that point, and with oaks, birches, and maples also present, and white pine and pitch pine already well established, the overall composition of New England forests was quite similar to what we find in our landscape today. Although the environmental conditions of that earlier time appear to have been well suited for hemlock, some of our recent research suggests that brief periods of cold climate occurred every few centuries, with deleterious impacts on hemlock in some parts of New England. Various lines of evidence, including chemical analyses of lake sediment records, show that the generally warm, moist conditions were interrupted occasionally by a century or so of cold, dry climate. And while hemlock and other species did not always respond uniformly to these events across the region, some of our relatively detailed pollen records feature abrupt, short-lived declines of hemlock, including significant population reductions at around 8,000 and 6,000 years ago. Hemlock certainly didn't disappear from the landscape during these events, but the pollen data do suggest that it became much less abundant during times of cold, dry conditions.

Then, around 5,500 years ago, hemlock experienced an abrupt, range-wide collapse. For about two millennia it nearly disappeared throughout its entire range in the Northeast before it rebounded about 3,500 years ago. Although it recovered greatly across the region, at most sites hemlock never returned to its predecline levels. This hemlock decline is one of the most thoroughly studied aspects of the postglacial vegetation history of North America, yet we still don't completely understand what caused it or sustained it. Conclusions drawn over the past three decades variously attribute hemlock's decline to a species-specific disease, a massive insect outbreak, a sustained shift to drier climate, a series of drought events, and a combination of these factors. It is now quite clear that climate was strongly involved and that in some ways the big decline was a larger version of the earlier declines witnessed during cold spells. If the trees weren't killed directly by drought, then the associated environmental conditions either stressed hemlock in ways that made it more susceptible to insects or disease or facilitated an unusual outbreak of a pest or pathogen. (It was this record of minor events leading to the major drought and decline in hemlock that our colleague correctly surmised he was seeing in the various layers of sand we observed that day on the raft in the middle of the lake.)

Hemlock eventually recovered, and pollen records reveal that it was again abundant in New England forests from around 3,500 years ago to the time of European settlement. Our studies of the sediments of Hemlock Hollow, a vernal pool hidden in the large hemlock forest on the Prospect Hill tract of the Harvard Forest, have yielded a detailed stand-scale record of forest changes over the last 10,000 years. The local nature of this record enables us to examine the fine-scaled ecological response of an individual forest to various changes in its environment. Here we can see that when disturbances occurred, including fires every 1,000 to 3,000 years, hemlock abundance dropped abruptly and then rebounded slowly, taking 500 years or more to recover to original levels. In the recovery from these major disturbances—intense events that we interpret to have killed most of the larger trees—the successional sequences brought back the species that we know so well and comply exactly with our understanding of the modern ecology of New England forests. For much of the pre-European period when hemlock declined, it was replaced around Hemlock Hollow by some combination of early successional and rapidly reproducing and growing species—white pine, birches, and other hardwoods—as well as more mid-successional, long-lived species such as oaks.

Everything changed when chestnut arrived. After spending the ice age in the southeastern United States, chestnut slowly migrated north and finally arrived in New England 2,000 years ago. At Hemlock Hollow we see chestnut employing its phenomenal ability to sprout and its rapid growth rate to become the dominant species when the populations of hemlock and other species were reduced by disturbance. This pattern occurred following fire and also after European settlement and the first episodes of logging in these forests. These disturbances affected both species, but chestnut bounced back quickly. Dead chestnut boles are a common sight in many hemlock forests today; it is clear from the fossil record at places such as Hemlock Hollow that the two species had a close and often reciprocal relationship in the more distant past. One other notable observation emerges from the long-term record at Hemlock Hollow: regardless of the nature of the disturbance or the successional species that followed it, in each case, hemlock recovered from the disturbance and eventually returned to dominance. These records offer other instructive insights into the broader nature of the New England landscape and its forests. The low abundance of charcoal in lake sediments confirms that there was little fire. Meanwhile, the long duration of hemlock dominance confirms that the region was only infrequently affected by fire or any other major disturbances: drought, wind, and ice. Similarly, there is no direct evidence of disturbance to or use of these forests by the dispersed populations of largely hunting and gathering American Indians who inhabited central New England. Thus, while we may assume quite correctly that change is a prominent factor in forest ecosystems, the paleoecological perspective demonstrates that New England hemlock forests experienced lengthy periods of relative stability.

We also have a detailed map of North American forests just before they were first cut and then cleared. For this we can thank a largely anonymous group of seventeenth- and eighteenth-century land surveyors. While walking the landscape and demarcating it into towns, sections, and ownerships, colonial surveyors recorded the presence of individual trees by their species and sometimes by their size. Ecologists have been using these accidental forest inventories to reconstruct presettlement forest composition for almost a century. By far the most common source for survey records has been the Public Lands Survey of the General Land Office, which was established by Thomas Jefferson and covered much of the midwestern and western states. But because southern New England was largely settled prior to the establishment of the General Land Office in 1785, its survey records are much less standardized. Survey-based reconstructions of New England forests typically rely on some type of town proprietor records. The English colonies deeded unsettled land in the form of regularly shaped towns, often about six miles square. In laying out the boundaries in these towns, surveyors identified and blazed "witness trees" as permanent markers at the corners of individual lots ranging in size from 1 to 160 acres. Longtime Harvard Forest collaborator Charlie Cogbill has spent decades amassing a comprehensive spatial database of these tree records from across the Northeast. The maps derived from his witness-tree data set have been analyzed by Jonathan Thompson to show how forest composition varied across the region.



Eastern hemlocks and eastern white pines along the Swift River in Petersham, Massachusetts.

Old eastern hemlocks and eastern white pines in Harvard Forest's Prospect Hill Tract.

In northern Maine, spruce, balsam fir, and white cedar dominated the landscape. Moving slightly southward into the rest of Maine, New Hampshire, and Vermont, hemlock, beech, maples, and red spruce were common, even reaching down along the broad uplands of the Berkshires in western Massachusetts and Connecticut. Oaks, pines, hickories, and American chestnut picked up from there and were prevalent in the south and along the coast. In broad detail, this pattern closely parallels the regional environmental gradient, with cooler and moister conditions to the north and warmer and drier conditions to the south. Hemlock became less common farther south and was found in increasingly smaller concentrations. Near the coast it would only have occurred in isolated stands in protected moist areas.

Pollen records provide context for the witness-tree snapshot of New England vegetation patterns, including some perspective on the dynamics that were under way when the European settlers arrived. For example, we can see that American chestnut was the last tree species to reach New England from its glacial refuge in the Southeast, arriving here only in the last 1,000 to 2,000 years. Meanwhile, hemlock and beech appear to have already begun a slow decline a couple of centuries before colonial deforestation commenced. The timing of these declines seems to coincide with the Little Ice Age, a relatively recent climatic interval (A.D. 1550–1850) that triggered physical and ecological changes in many regions of the world, including glacial advances farther north. It may seem counterintuitive that two species common in northern New England would be bothered by a shift to colder climate. It is quite possible, however, that conditions became both colder and drier, with both hemlock and beech suffering due to their relatively high moisture requirements.

The latter part of the Little Ice Age coincided with the expansion of European colonists across New England, transforming the land. Region-wide, up to 60 percent of the land was cleared for agriculture and the rest was cut—repeatedly in some places—with a peak in harvesting occurring in the late nineteenth and early twentieth century. Although forest once again covers more than 80 percent of New England, these second-growth stands are not the same as those of presettlement times. When we compare the witness-tree data with present-day forest composition, we find that some species are more common than they were centuries ago, such as early successional birches, red maple, and pines, including the old-field white pines that invaded abandoned agricultural lands. These light-seeded, fast-growing, and light-requiring species spread and grew rapidly across heavily disturbed areas, thriving after the intense farming and logging subsided. On the other hand, some species are less abundant than they were before European settlement. Species of mature forests, including hemlock and beech, are much less common than they were in the witness-tree surveys. Throughout the Northeast, hemlock declined as much as 10 percent over the last 400 years.

When we zoom back in from the region-wide scale to that of the individual landscape, we often see considerable evidence of land use in the characteristics of hemlock forests. In some cases, seemingly ancient hemlock stands have undergone much greater changes in their recent past than we might at first assume. These are the unexpected findings of a study led by Harvard Forest researchers Jason McLachlan and David Foster. They set out to reconstruct the histories of four old hemlock forests in central Massachusetts, using both tree-ring analysis of the largest trees and centimeter-by-centimeter analyses of pollen grains preserved in the approximately six-inch-thick layer of organic matter forming the top layer of the soil. They found that the stands, dominated today by hemlocks 100 to 200 years old, had experienced a series of disturbances over the last few centuries, including logging, windstorms, fires, and pathogen outbreaks. Indeed, early and mid-successional trees such as oaks, pines, and American chestnut had occupied those same stands at different times in the past. In many of the forests, it appeared as though today's dominant hemlocks may in fact owe their current good fortune to the removal of competing species by selective logging and the chestnut blight.

Like many of our other retrospective investigations of hemlock, this study of second-growth stands obliges us to change the way we think about the species, the forests it forms, and the way that nature operates. On one hand, forests that appear to be unchanging may be relatively recent in origin and shaped by processes that the species has never experienced before. On the other, although hemlock forests have been dynamic at times, the history of the species in New England has always been one of long-term dominance interrupted by infrequent abrupt declines. With such a decline spreading across the landscape today, we can expect another lengthy period with little hemlock followed by—we can only hope—its gradual return.

Wyatt Oswald is Associate Professor at Emerson College, David Foster is Director of Harvard Forest, and Jonathan Thompson is Senior Ecologist at Harvard Forest.