A FIELDBOOK
GREAT MOUNTAIN FOREST

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DEVELOPMENT OF THE EASTERN DECIDUOUS FOREST

A BRIEF HISTORY

The eastern deciduous forest of North America describes a complex of forest types that covers the eastern third of the United States, southeastern Canada, and northeastern Mexico. It stretches north to south along the Atlantic coast from Maine to Florida, and extends in the west all the way from Minnesota down to central Texas. Ample precipitation throughout this region, combined with high variability in topography, soil type, and climate, make it one of the most diverse assemblages of temperate forests found anywhere in the world. Classifying distinct forest types within this region is difficult, as the ranges of individual species often overlap and grade into one another, and communities can exist in patchy formations according to landscape level shifts in slope, aspect, and microclimate. In general, moving northward along the Atlantic coast, forest assemblages shift from the fire-prone pine forests of the southeast up into oak-pine and oak-hickory communities. From there the forest changes to the northern hardwood communities which encompass most of New England, and finally the boreal coniferous forest which covers the bulk of Canada.

Great Mountain Forest sits at the nexus of several of these forest communities. Many areas are dominated by species of oak and hickory, particularly at high elevations and on dry, southern-facing aspects. The bulk of the forest, however, is composed primarily of eastern hemlock (*Tsuga canadensis*), American beech (*Fagus grandifolia*), sugar maple (*Acer saccharum*), and birches (*Betula* spp.), which are the typical species of the northern hardwood forest that extends from Massachusetts up through southern Quebec. There are also a few notable species outliers. In the area of the Forest with the lowest elevation—a small pocket in the southeast corner

View over the GMF canopy. Since it sits at the nexus of several distinct forest types, GMF is host to a wide diversity of plant species.

along Under Mountain road—there are tulip trees (*Liriodendron tulipifera*) and sassafras (*Sassafras albidum*), species common in the mixed mesophytic (moist) Central Appalachia and southern hardwood forests, but which are rare as far north as Litchfield county. Similarly, but oppositely, certain bogs and swamps in the Forest contain healthy communities of black and red spruce (*Picea mariana, Picea rubens*), which are closely associated with boreal habitats, and are certainly towards the southernmost extent of their range here in Connecticut. The convergence and intermixing of these forest types across one intact land unit makes Great Mountain Forest a fascinating place to study plant community dynamics.

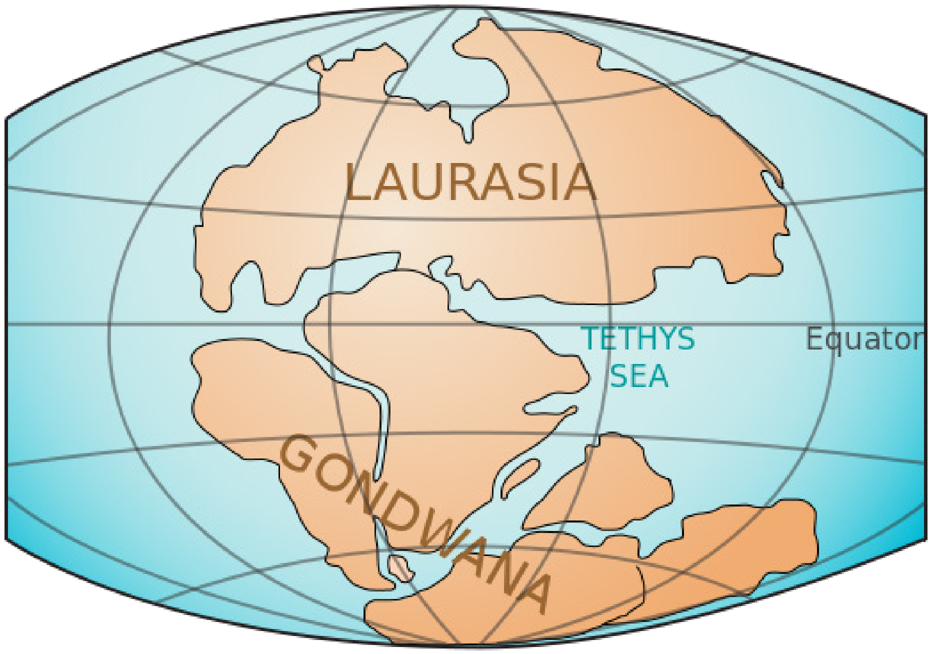
The current character of the eastern forests has been shaped by a number of powerful forces across different timescales. The activity of plate tectonics and dramatic fluctuations in climate across millions of years brought about the shape of the North American continent, and strongly influenced the evolutionary lineage that produced the tree species it contains. The freeze-thaw cycles of our current ice age have jumbled and mixed these species around the landscape for over two million years, appropriating them to their modern day ranges and combinations. The forests our generation knows are further fashioned by thousands of years of human management, which continues to transform the landscape in radical ways. To understand the context of this relationship between people and the forest, it is first necessary to outline the major geologic and evolutionary events which have molded our shared existence.

GEOLOGIC TIMESCALE (350-2.4 MYA)

In a sense, the origin of the eastern deciduous forest can be traced to the humble beginnings of the first forests of the world, which arose during the late Devonian around 350 million years ago (mya). These ancient woodlands looked very different from those we see today, composed mostly of giant lycopsids (clubmosses) and tree ferns that were well adapted to the increasingly hot and humid climate of the late Paleozoic. These plant groups would continue to dominate for several hundred million years until the rise of coniferous trees (gymnosperms) during the Triassic period. The woodland ferns, horsetails, and clubmosses that creep along the understory of modern temperate forests are miniature memories of their tree sized ancestors. Fossilized trunks of Stigmaria and Lepidodendron, (ancient clubmoss species) have been found that average 7 to 10 feet in diameter—far wider than any tree growing in eastern North America today.

By the beginning of the Permian period, all the major landmasses of the planet were fast converging towards one another. The Alleghenian orogeny was completed around 280 mya, when the ancient supercontinents Gondwana and Laurussia fused together to form the bulk of Pangea (literally, "all land" in ancient Greek). Pangea was so massive that the moist winds from the ocean could not reach its center. Heat given off from the interior helped raise global temperatures, melting glaciers around the South Pole. Forests, along with most land dwelling life forms in general, were confined to the relatively hospitable coastal regions. Conifers had been around since the late carboniferous (300 mya), but gained prominence in this harsher environment, possibly owing in part to their greater ability to cope with droughty conditions. By the first part of the Jurassic, some 190 mya, the forests of the world were dominated by gingkos, giant cycads, and ancient needle leaved trees, radiating all along the coastal plains of the unified continent.

Flowering plants (angiosperms) first appeared around 125 mya, during the beginning of the Cretaceous. By this point, Pangea had broken into smaller continents again. Laurasia separated from Gondwanaland, and itself split into more or less familiar forms of the northernmost



Map showing the relative positions of Laurasia and Gondwana during the breakup of Pangea, around 200 mya. Source: User:LennyWikidata [CC BY 3.0 (http://creativecommons.org/licenses/by/3.0)], via Wikimedia Commons

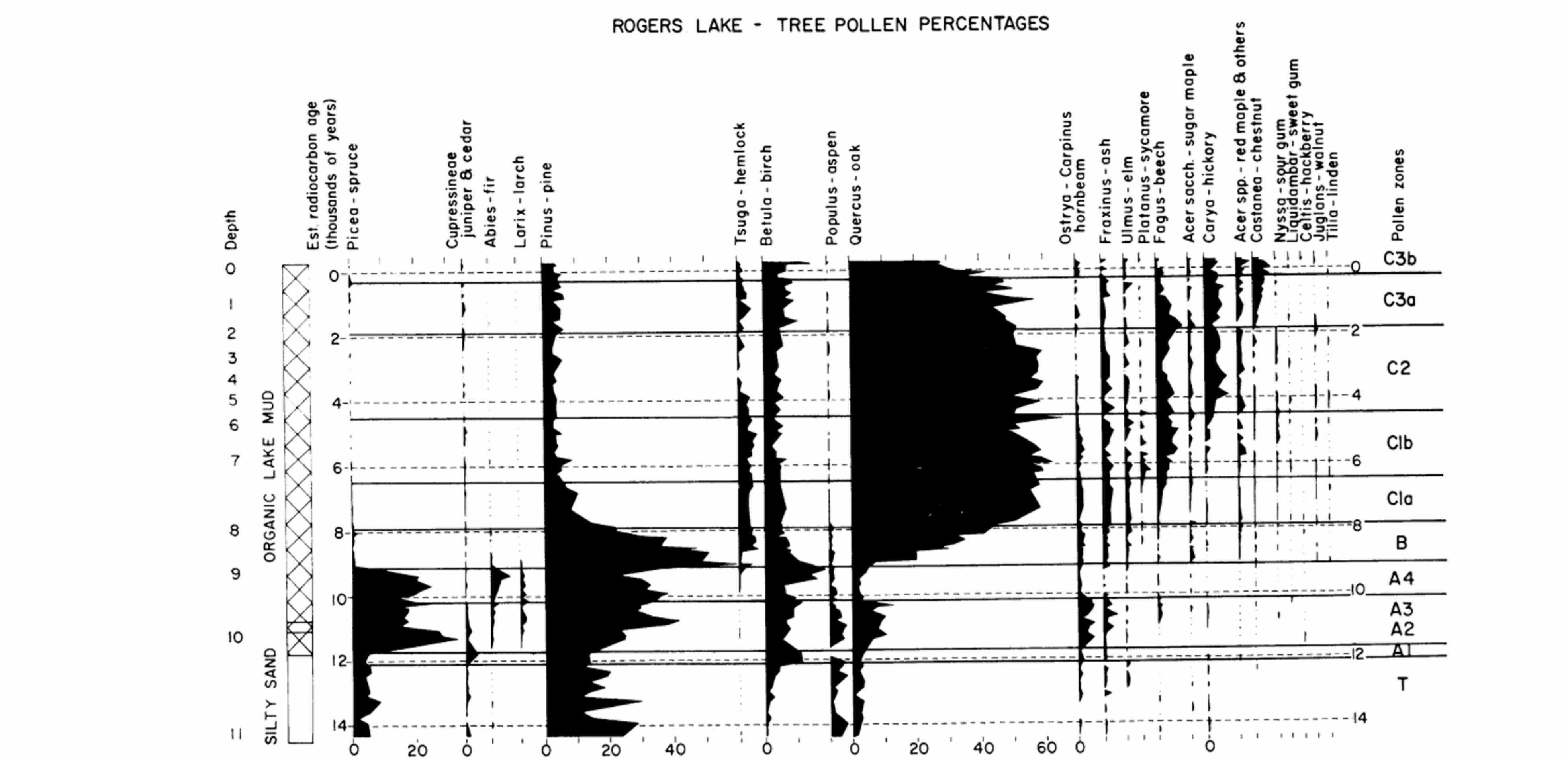
continents: North America, Europe, and Central Asia. Together these regions constitute the Holarctic (or Boreal) floristic kingdom, which is further broken into the Palaearctic (Old World) and the Nearctic (New World). Because they were united for a longer period before drifting apart and had episodic instances of contact thereafter, the forest flora of these regions are markedly similar. Whether in New England, Central Europe, or the plains of China, todays northern latitude temperate forests all contain related species of trees, shrubs, and herbs from the same families, such as the birches (*Betulaceae*), oaks, beeches, and chestnuts (*Fagaceae*), cherries and roses (*Rosaceae*), buttercups (*Ranunculaceae*), mustards (*Brassicaceae*), saxifrages (*Saxifragaceae*), and pines, firs, spruces, and larches (*Pinaceae*) extending into the circumboreal regions farther north.

Throughout most of the Cretaceous until about 75 mya, eastern North America was an island, still separated from the modern day Pacific coast region by the broad and shallow Bearpaw sea. An evergreen tropical forest of early flowering trees, including the magnolias, had gained prominence, growing larger and moving northward to form mixtures with early progenitors of ancient coniferous species such as the monkey puzzle tree (*Araucaria araucana*) and the dawn redwood (*Metasequoia glyptostroboides*) that were then dominant canopy trees. Early relatives of the pines (*Pinus* spp.) were present at this time, but existed mostly as small understory shrubs. The tropical climate of this period persisted well into the Paleogene, when a major cooling trend began around 33 mya. The forests shifted to a more temperate type, dominated by groups of deciduous broadleaved tree species that would look fairly similar to what we have today, with tulip-trees (*Liriodendron tulipifera*), various legume (*Fabaceae*) species, and oaks (*Quercus* spp.) becoming prominent in forest assemblages.

ENTERING AN ICE AGE (2.4 MYA - PRESENT)

Around 2.4 mya, the world entered a new ice age: an ongoing series of freeze-thaw cycles with corresponding periods of glaciation and inter-glaciation. As the Earth orbits the sun, slight shifts in the eccentricity, angle of tilt, and axis of rotation —known as Milankovitch Cycles— set long alternating phases of global heating and cooling into motion. Available geologic evidence collected from deep ocean sediments suggests that Earth has gone through at least 17 of these cooling/heating cycles (so far). In the eastern United States and Canada, tree species respond to these climatic fluctuations by shifting their range north or south in step with the movement of glaciers extending from the far north.

The last such cooling event began 35,000 years ago, and reached its peak about 18,000 years ago. At its glacial maximum, the Laurentide ice sheet covered 13.4 million square kilometers of land, and in the eastern United States, extended far enough south to cover almost all of Connecticut (including Great Mountain Forest). Forest distributions changed accordingly. Directly to the south of the glacier was a band of tundra that stretched across Long Island (itself a terminal moraine created by the ice) westward past the Appalachians. Below that was a large swath of spruce forest (*Picea*), which mixed with a collection of cold-hardy pines in today's Georgia and the Carolinas. Virtually all the temperate hardwood species so dominant in today's eastern forest were relegated to a tiny refuge in the southern half of the Florida peninsula. It is interesting to note that the north-south orientation of the Appalachian mountain chain permits the passage of tree species to and from glacial refugia. In Europe, temperate tree species migrating south from the expanding glacier ran up against the Alps, which run east-west, and many were trapped and extirpated. For this reason, and to this day, the forests of the eastern United States have a much



Graph showing relative abundances of tree species pollen collected from cores of increasing depth, and hence earlier deposition. Taken together, the data demonstrate a transition from spruce to oak forest over the past 12,000 years (from Davis 1969).

higher diversity of tree species than the forests of Western Europe.

By about 15,000 years ago, the climate warmed again, and the Laurentide ice sheet melted northwards. In its wake the glacier created "kettlepot" lakes—areas where meltwater accumulated in depressions formed by buried ice melting under sediment. By extracting sediment cores from the bottoms of these lakes and aging them using radiocarbon dating methods, paleoecologists can identify the species of pollen that accumulated from ancient trees. This information is used to reconstruct the historic forest compositions through time since the retreat of the glacier.

In a study from southern Connecticut, Davis (1969) analyzed pollen deposition in lake sediments, spanning a 14,000- year period up to the present day. The fossilized grains tell the story of tree species migration northward over time as the climate warmed and stabilized. From 14,000 to 12,000 years ago, Connecticut and much of southern New England was a tundra landscape. The pollen grains from this period are mostly herbaceous species that we currently associate with an Arctic flora. By 10,000 years ago, spruce and fir had moved in to become the prominent vegetation assemblage, with small populations of oak, white pine, hornbeam, alder, and ash. The less cold-hardy white pine was the dominant species by around 8,000 years ago, accounting for 50% of the total pollen accumulation. The boreal spruce, fir, and larch species decreased rapidly during this period, being outcompeted by the more temperate adapted tree species. They continued migrating north, closer to their modern day distribution. Following a heating and drying trend that lasted until about 6,000 years ago, oak species moved in to become more dominant across much of the Connecticut canopy, which is still the case today.

Forests and glaciers have been dancing north and south across the whole of eastern North America in this fashion for millennia. Tree species respond individualistically to shifts in climate as opposed to rigidly defined obligate communities, each according to its own growth rate, seed dispersal mechanism, and amplitude for tolerating ecological stressors. Each cooling and thawing sequence results in novel forest assemblages for which there are no equivalent modern counterparts—a phenomenon known as the "no-analog problem" (Brubaker 1988). For example, although the immediate post-glacial environment of Connecticut did resemble today's arctic tundra with its herbaceous plant distribution, pollen studies show evidence of some scattered oak individuals, which are unknown in today's arctic communities. Oaks as a general group took much longer to move northward because of their seed dispersal strategy. As a masting species, oaks drop large quantities of nutrient-rich nuts to satiate their dispersal agents (mostly squirrels, today) and have enough left over to germinate. The wind dispersed pines, however, are able to send their seeds much greater distances and in higher quantities to colonize newly habitable landscapes, which helps explain their dominance in the region several thousand years before oaks. In short, though paleobotanical data can provide useful insight when trying to determine how forest species and communities will respond to future shifts in climate, ultimately the novel conditions and non-predictable responses of species to changes in temperature and precipitation make it impossible to determine for certain.

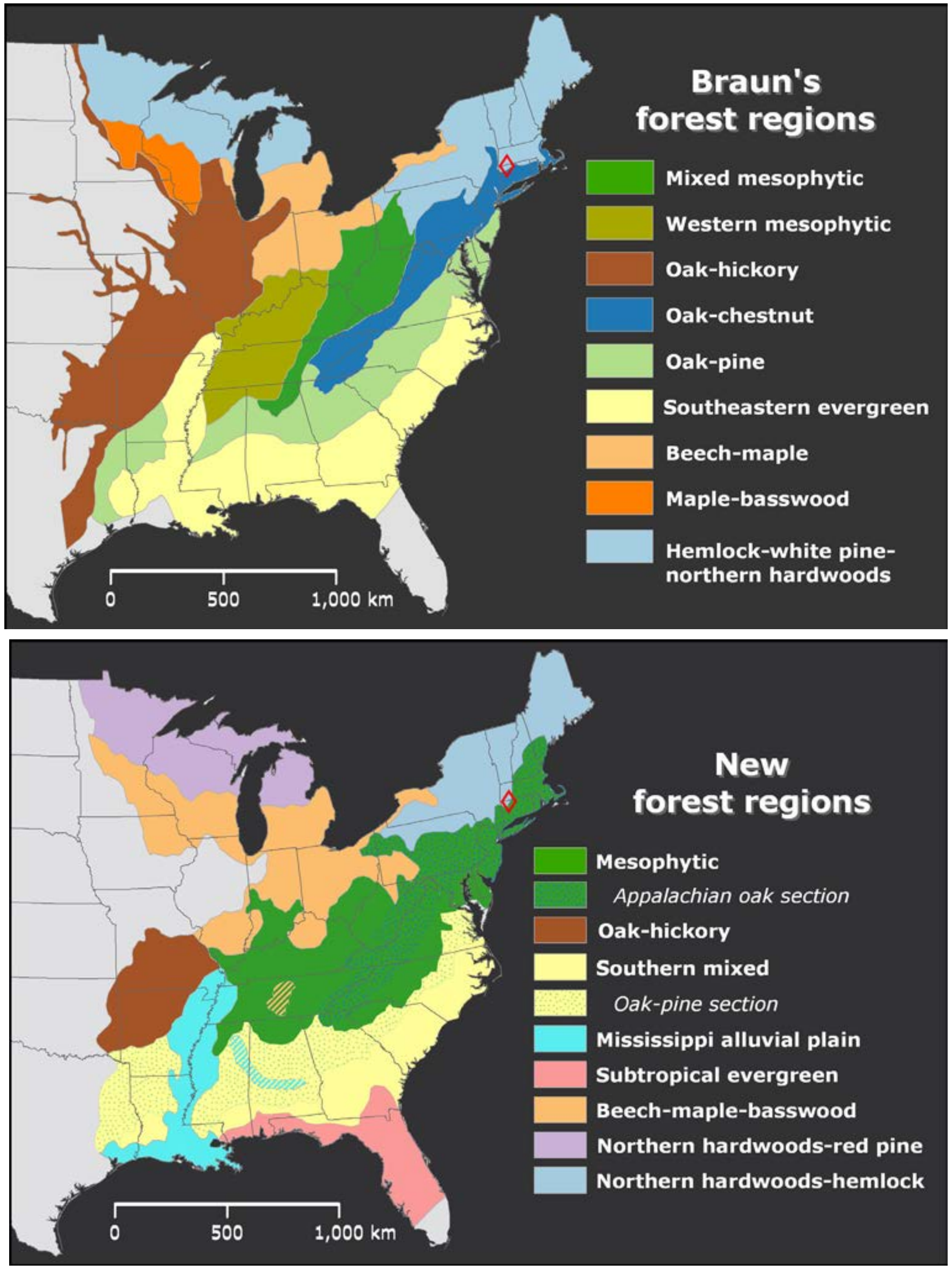
HUMAN RELATIONSHIPS (13,500 YA - PRESENT & FUTURE)

In addition to shifts in forest composition caused by geologic, evolutionary, and climatic agents, further changes wrought by anthropogenic means have interacted with these forces to shape the eastern deciduous forest as it exists today. For as long as the most recent glaciation has receded, there have been people here, manipulating the environment. American Indians have for thousands of years set fires in the forests, primarily in floodplain areas or along streams where conditions were most suitable for habitation. In some cases, entire tracts of the forest would be burned away completely, to create open grounds for agriculture or new settlements. When they moved on from these areas to find new sites, forests returned to the abandoned land, creating a patchwork of stand compositions and age classes. More often however, people would set lower intensity ground fires, which consumed all ground level fuel and vegetation but left the canopy trees mostly intact. This created more open, park-like forests, and promoted the growth of medicinal herbs and fire resistant, nut producing trees. It also created better habitat for wildlife, and made hunting these animals easier. It is thought that entire unique ecosystems, such as the grassy oak savannahs of the Midwest, were completely engineered and maintained by Native American fire usage.

The arrival of Europeans brought another dramatic restructuring of forests. The original colonies were founded, in part, to satisfy England's demand for high quality timber, particularly large old growth eastern white pine (*Pinus strobus*) that could be fashioned into ship masts for use in its long-running naval wars. Forests were decimated in a more or less systematic fashion heading westward, to feed the hungry needs of the new nation. Logging accelerated in pace over time to keep up with new demands for construction timber, and fuel for forges and early wood-powered trains. Within a few hundred years, virtually all the old growth trees in the east had been felled. Besides being much younger and denser, the regenerating forests tended to have vastly different species compositions, favoring early pioneer species like birches and pin cherries over shade tolerant, later successional species like sugar maple, American beech, and hemlock.

European settlers also existed under a land tenure system that promoted permanent clearing and "development" of private and publically owned property. Forested land became more and more fragmented as agriculture and new settlements proliferated across the landscape. Remaining forest stands had smaller cores and a greater proportion of edge habitat, which again promoted different guilds of plant and animal species. In New England, large portions of the landscape have filled back in with forest as agriculture moved westward and fields were systematically abandoned. These have been chipped away at since the 1970s with the sprawl of suburbia and other development projects. History seems to repeat itself, yet it seems unlikely that these high value properties with extensive rolling lawns will ever be abandoned the same way that the poor quality farmland was.

Under an increasingly globalized economy where goods are



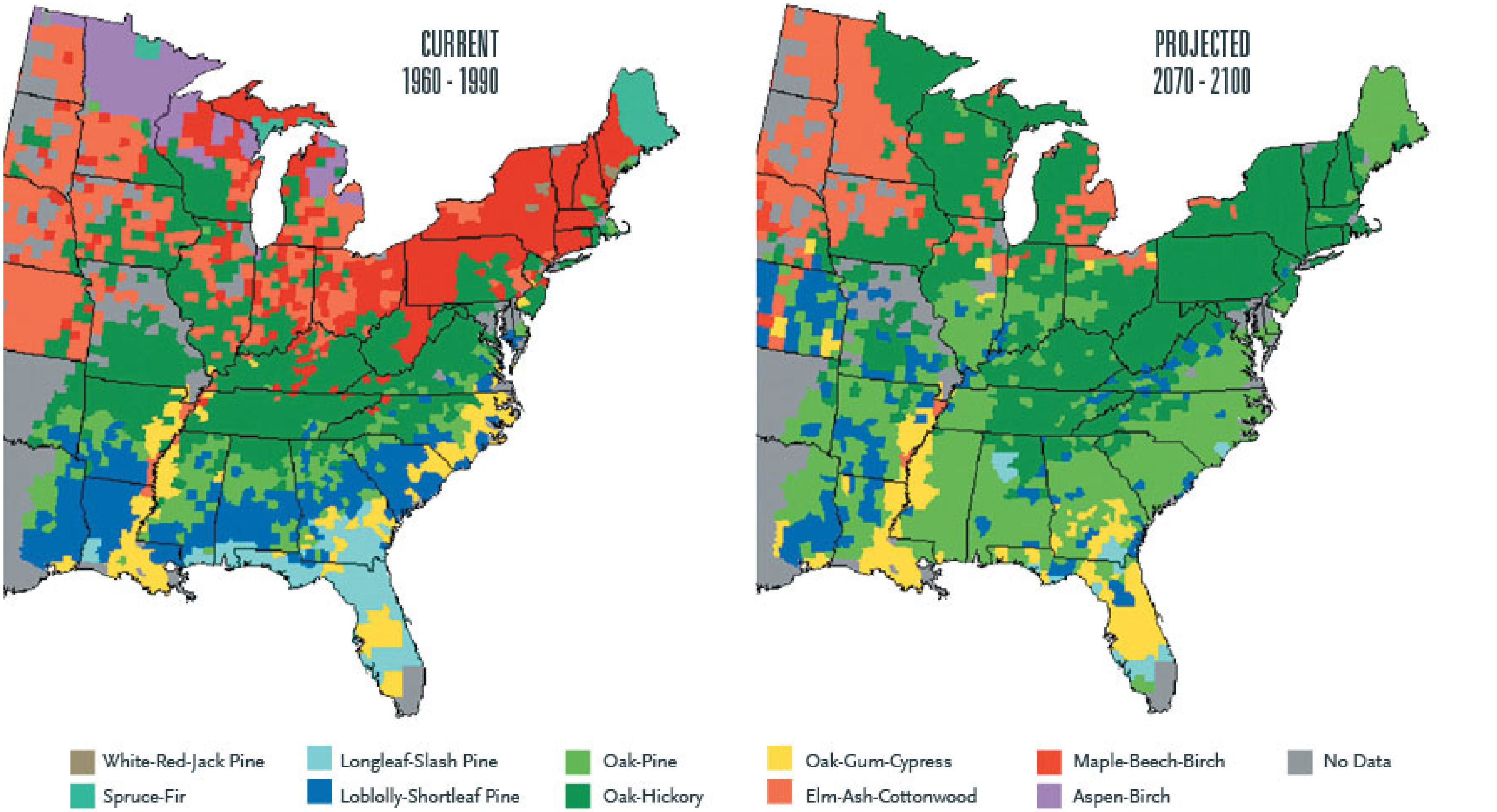
Maps of eastern US forest regions, by Lucy Braun in 1950 (top) and 2006 revision by James Dyer (bottom). The absence of American chestnut as a dominant community type has largely taken over by oaks and hickories. Great Mountain Forest (red diamond) sits at a critical transition zone between the Appalachian forest and northern hardwoods. Hardwoods (indicated by the red stars).

being shipped around the country in greater quantities and faster speeds than the world has ever seen, a whole suite of invasive plant and animal species have been introduced to the North American continent, sometimes with important consequences for the structure and health of eastern forests. Some of these are airborne fungal pathogens or insects that have the capacity to parasitize and make entire tree species functionally extinct. When the chestnut blight (*Cryphonectria parasitica*) was accidentally introduced to New York in 1904, it quickly spread throughout Appalachia and within decades exterminated virtually all American chestnut (*Castanea dentada*) within its natural range, destroying an estimated 4 billion trees. This in turn led to a restructuring of forest communities where the species was prevalent, as species with similar ecologies, such as the oaks and hickories, moved in to fill the void that the dead trees had left behind. In other instances, the invasive species are plants themselves that compete vigorously for growing space with the native vegetation. Species such as Japanese barberry (*Berberis thunbergii*), Tartarican honeysuckle (*Lonicera tartarica*), and Asiatic bittersweet (*Symphoriocarpus orbiculatus*) can quickly cover large swaths of land, inhibiting the natural regeneration of native tree seedlings. These species are of special concern to foresters who rely on natural seed sources to regenerate forestland following a harvest.

In addition to the preceding categories of anthropogenic landscape transformation, the future of the eastern deciduous forest is further complicated by the acceleration of human induced climate change. The rapid rise in temperature is expected to result in a dramatic shift in species composition and distribution as trees respond to new, possibly novel, site conditions. Knowing exactly what will happen is impossible, given the no-analog problem of forest assemblages through time, but it is possible to make predictions based on the observed physiological characteristics of individual species. Pioneering research at GMF led by Charles Canham and Stephen Pacala (Pacala et al. 1993, Pacala et al. 1996) led to the creation of a model to explain the process of forest growth. They collected the necessary data by performing rigorous measurements of all aspects of tree growth, down to minute details such as light dependent mortality and seed dispersal distances. Their SORTIE model is now the standard used around the world to predict shifts in the progression of forest development.

A 2003 report by the Pew Center on Global Climate Change (now Center for Climate and Energy Solutions) compiles the available information on the response of forests to climate change, based on different models of tree species migration patterns and atmospheric increase of

CURRENT-PROJECTED FOREST TYPES



Maps showing projected future shifts in the range and distribution of different forest types in the eastern United States, based on climate change predictions and the known ecological amplitudes of tree species (Iverson et al. 1999). Note the predicted north-westerly migration of loblolly-shortleaf pine communities, and the near complete extirpation of northern hardwoods from New England and the Midwest (Shugert et al. 2003).

CO_2. All, like the previous map based on the work of Iverson et al. (1999), suggest a general northward migration of forest communities. Most striking are the projected shift of southern loblolly/shortleaf pine ecosystems into the Central region, and the near complete replacement of Northern hardwoods by oak dominated systems in New England and the Midwest. In a sense, this community transition is a natural step in the ongoing freeze-thaw cycles of the current ice age. However, the heretofore unprecedented rapid pace of climate change wrought by human industrial practice may overwhelm certain tree species. Potentially vulnerable forest types, such as aging northern hardwoods and high elevation spruce-fir, may not be able to migrate quickly enough to respond to shifts in climate zones. The indefinite response of forests to climate change, compounded with the direct and indirect effects of other human enterprises, make the future character of the eastern deciduous forest hard to predict.

RESOURCES

Brubaker, Linda B. (1988) Vegetation History and Anticipating Future Vegetation Change. Pages 41-61 in J.K. Agee and D.R. Johnson, ed. Ecosystem Management for Parks and Wilderness. University of Washington Press, Seattle.

Davis, Margaret B. (1969) Climatic changes in southern Connecticut recorded by pollen deposition at Rogers Lake. Ecology 50: 409-422

Dixson, D., I. Jenkins, R. T. J. Moody, and A. Y. Zhuravlev. (2001) Atlas of Life on Earth. Barnes and Noble Books, New York.

Dyer, J.M. (2006) Revisiting the deciduous forests of eastern North America. Bioscience 56: 341-352

Iverson, Louis R., Anantha M. Prasad, Betsy J. Hale, and Elaine Kennedy Sutherland (1999) Atlas of Current and Future Distribution of Common Trees of the Eastern United States. United States Forest Service Northeastern Research Station, General Technical Report NE-265

Flannery, Tim (2001) The Eternal Frontier: An Ecological History of North America and its Peoples. Grove Press, New York.

Pacala, S.W., C.D. Canham, and J.A. Silander, Jr. (1993) Forest models defined by field measurements: I. The design of a northeastern forest simulator. Canadian Journal of Forest Research 23: 1980-1988

Pacala, S.W., C.D. Canham, J.A, Silander, Jr., and R.K. Kobe. (1996) Forest models defined by field measurements: II. Estimation, error, analysis, and dynamics. Ecological Monographs 66: 1-43.

Shugart, Herman, Roger Sedjo, and Brent Sohngen (2003) Forests & Global Climate Change: Potential Impacts on U.S. Forest Resources. Prepared for the Pew Center on Global Climate Change.