

Hemlock's Future in the Context of its History: An Ecological Perspective

David R. Foster¹

In October of 1852, Henry David Thoreau went for a stroll through a chestnut forest in Concord, Massachusetts and recorded the following impressions of a vibrant ecosystem:

"The chestnut leaves already rustle with a great noise as you walk through the woods, as they lie light, firm, and crisp. Now the chestnuts are rattling out. The burs are gaping and showing the plump nuts. They fill the ruts in the road, and are abundant amid the fallen leaves in the midst of the wood. The jays scream, and the red squirrels scold, while you are clubbing and shaking the trees. Now it is true autumn; all things are crisp and ripe".

Thoreau's many writings on chestnut (*Castanea dentata* (Marshall) Borkh.) are diverse and remarkably insightful for modern ecologists who seek to understand the former role of this species in New England forests. For example, his journal observations range from nut dispersal by squirrels and passenger pigeons, to the sprout behavior and growth rate of the trees, to forest structure and dynamics, and on to the many land-use practices associated with the human use of chestnut for wood, fuel, and food (Foster 1999). Thoreau's observations are revealing precisely because they pre-date the arrival of the chestnut blight to eastern North America and, unlike any historical reconstruction that we might attempt today, they are unbiased by the slightest inkling of the fate of the species.

In like fashion, most of the contributors to the symposium *Sustainable Management of Hemlock Ecosystems in Eastern North America* began their research on hemlock (*Tsuga canadensis* (L.) Carriere) forests before the hemlock woolly adelgid (*Adelges tsugae* Annand) became such a clear threat to the forests of eastern North America. Today, however, all hemlock researchers must undertake their studies with the knowledge that the adelgid, which arrived in Virginia in the early 1950s, spread into New England in 1985, and is now widely established across 11 eastern states, is spreading at a rate of 20-30 km per year and is leaving devastated hemlock stands in its wake (Orwig and Foster 1998). As hemlock, one of the most shade-tolerant and long-lived tree species in the Eastern U.S., is succumbing to an introduced pathogen, we find ourselves in the position of chestnut researchers in the early 1900s, questioning the future and fate of a dominant and very important tree species. The adelgid also raises the immediate question as to whether sustainable management of hemlock forests is, itself, a viable concept.

In areas of heavy adelgid infestation hemlock ecosystems are undergoing major changes in structure, composition, and ecosystem function (Orwig and Foster 1998). Interpretation of the long-term consequences of this disturbance and approaches to the management of

hemlock forests within and outside the current range of the adelgid, can gain insights from studies of the past dynamics of hemlock. Below, I review these dynamics with the broad objective of highlighting many of hemlock's characteristics and its long-term history in New England. In particular, I focus on the major ecological lessons that emerge from this 10,000 year legacy (Foster and Motzkin 1998).

Post-glacial Migration of Hemlock

Using an array of paleoecological sites across eastern North America it has been possible to determine the history of post-glacial movement of the major tree species upon deglaciation and climate warming (Davis 1981b). By comparing the dynamics of hemlock and other species from northeastern forests, the following observations and important ecological insights emerge: (1) taxa like hemlock, beech (*Fagus grandifolia* Ehrh.), maple (*Acer*), and chestnut, which co-occur in our forests and have strongly overlapping range distributions today, have strikingly different, individualistic histories. These histories include different glacial refugia, contrasting migration rates and pathways, and subtly different modern distributions; (2) co-occurring species also have very different New England histories. For example, whereas chestnut arrived and expanded broadly across the region only within the past 2000 years, hemlock has been present and abundant for more than 8000 years; (3) these differences in species history appear to be driven by ongoing and essentially continuous change in climate and differences in species physiology, population biology, and growth characteristics. Particularly important is the complex nature of climate change, which involves variation in quantity and seasonal distribution of temperature, precipitation, and growing season length, as well as ongoing changes in the earth's atmosphere.

Long-term Dynamics of Hemlock Forests

As background for ecology, conservation, and management, long-term records of local stand dynamics provide essential information (Foster et al. 1996). Unfortunately, such data are impossible to retrieve from standard sampling methods or even long-term records and permanent plots. However, an unusual application of paleoecology, which involves the stratigraphic analysis of sediments in very small basins like vernal pools, small hollows, and confined wetlands, enables us to develop lengthy chronologies at a stand scale. The pollen deposited in these basins, and therefore the vegetation record, derive primarily from within 50-m distance.

In one study using this approach a 9500-yr record was obtained from a mature hemlock forest in the Harvard Forest in Petersham, Massachusetts (Foster and Zebryk 1994). Major results and insights include: (1) hemlock was locally abundant for 8000 years, having invaded sites

¹Harvard Forest, Harvard University, Petersham, MA 01366

previously dominated by spruce (*Picea*) and then pine (*Pinus*) and oak (*Quercus*); (2) through time, the relative abundance of hemlock and of associated species have changed as the climate changed and as new tree species migrated into the region; (3) major disturbances occurred approximately every 1000 years and included: fire, marked by discrete layers of charcoal, at 7650, 6650, 6150, and 1900 years BP (before present); the hemlock decline at 4700 years BP; and European settlement at 250 years BP; (4) following each disturbance the abundance of hemlock declined abruptly and gradually recovered over a 500+ year period; and (5) the species that replaced hemlock following each disturbance varied through time as a consequence of changes in the species pool: from 8000-2100 BP birch, oak and pine increased as hemlock declined, but since chestnut arrived in the region 2000 years ago it has been the major species increasing after disturbance.

Ecological Consequences of the Mid-Holocene Hemlock Decline

Approximately 5000 years BP hemlock suffered a major decline in abundance across its entire range. Due to the synchronous, widespread, and single-species nature of the decline it has been interpreted as a consequence of outbreak of a pathogen like the eastern hemlock looper (*Lambdina fiscellaria* Gven.), as opposed to climate change (as previously believed) or aboriginal impact (Davis 1981a). Support for this interpretation has been provided by subsequent studies, particularly the identification of large numbers of looper fossils in sediments contemporaneous with, and containing pollen and macrofossil evidence for, the hemlock decline (Bhury and Fillion 1996). Interestingly, the hemlock decline represents the only documented outbreak of a natural pathogen in the paleoecological record.

Detailed paleoecological studies provide interesting insights concerning the nature of the hemlock decline and subsequent ecosystem dynamics (Fuller 1998, Hall and Smol 1993, Foster and Zebryk 1993), including: (1) the decline appears to be a two-stage process in which an initial decrease and temporary recovery was followed by a major, enduring decline; (2) the intensity of the decline and residual abundance of hemlock varied geographically and perhaps on a landscape scale, however, across the range of hemlock the species appears to have survived in small, but widespread, populations; (3) the species replacing hemlock varied geographically and also through time as succession occurred; (4) hemlock abundance after the recovery was oftentimes quite different than before the decline; and (5) the forest disturbance exerted a marked impact on adjoining aquatic ecosystems. In summary, although hemlock showed the potential to recover from, or perhaps evolve resistance to, a major pathogen, the recovery process required 1000 years or more.

Regional Forest Response to Land Use: Interaction of Disturbance and Climate Change

The most rapid change in forest composition in New England during the post-glacial period was initiated by European settlement and land-use activity (Jacobson et al. 1987). Importantly, although this human disturbance initially involved rapid deforestation and increased agricultural activity, over the past 150 years this process has largely been reversed by agricultural decline and natural reforestation (O'Keefe and Foster 1998). Today in New England a largely forested condition prevails in which forest height and tree size are increasing. Among the most important and relevant questions for ecological studies and forest conservation and management in this region are: What are the consequences of this land-use history on forest ecosystems? And, To what extent does modern forest composition parallel pre-European forest composition? To address these questions on a broad scale we examined paleoecological records (<2000 years), historical data, and modern stand characteristics in a region of north-central Massachusetts, extending from the Connecticut Valley Lowland (30-50 m a.s.l.) through the Central Upland (300-400 m a.s.l.) to the Eastern Lowland (< 100 m). Sampling sites are distributed throughout this region, which encompasses a subtle climate gradient.

Findings include: (1) the major compositional dynamic across the region (and much of the northeast) involves a decline in hemlock and beech and increase in birch, oak and red maple since settlement; (2) at the time of European settlement the major forest types and tree species varied geographically: Oak-Hickory forests were abundant in the warmer, lower, southern areas and Northern Hardwoods (maple, beech, birch (*Betula*), maple)-Hemlock forest increased in the cooler, higher and northern areas. However, through time, the history of land use apparently caused a homogenization of the regional vegetation. Today, there is no geographic pattern or statistical relationship between species abundance or forest type and climate (Foster et al. 1998); (3) paleoecological data corroborate these findings but indicate that part of this dynamic, specifically the decline in hemlock and beech, was actually initiated approximately 500 years before present (Fuller et al. 1998). This early forest change was apparently linked to climate change, notably the Little Ice Age, a cooler, drier and more variable period; and (4) consequently, it is potentially misleading to interpret post-settlement forest change in the absence of a thorough understanding of pre-settlement dynamics and environmental change.

Post-settlement Dynamics and the Development of Old-growth Characteristics in Hemlock Forests

Hemlock forests dominated by large trees on sheltered sites represent some of the oldest and most mature stands across southern New England (Foster and O'Keefe 2000). Due to their many old-growth characteristics, lack of recent disturbance, and apparent stability, these forests have been interpreted by many researchers as natural and as possible examples of the pre-settlement vegetation (Nichols 1913, Spurr 1956). Most of these forests occur on sites that were never cleared historically but it is very likely that most were

cut once to several times early in the region's history (O'Keefe and Foster 1998). Recently, a number of studies have sought to investigate the history of these stands over the past few hundred years using pollen analysis of the stratigraphic record contained in small hollow or vernal pools (see Long-term Stand Dynamics, above) and organic humus layers in conifer forests.

In studies in north central Massachusetts, Foster *et al.* (1992) and McLachlan *et al.* (1999) analyzed deep (15-25 cm) humus layers in such hemlock forests and revealed a very consistent record of their developmental history: (1) although appearing natural, mature and relatively stable, each of these stands underwent major changes over the last 400 years, generally involving conversion of a pre-settlement forest of mixed hardwoods (beech, birch, oak) and conifer (white pine and hardwood) to a sprout hardwood forest of chestnut or birch upon heavy cutting in the 18th or 19th C. The subsequent development of a hemlock-pine-hardwood forest has occurred through time, low human impact, and the advent of the chestnut blight; (2) these dynamics have resulted in two or three forest types on these sites over time, each with little similarity to each other; and (3) the development of mature forest with many old-growth characteristics has resulted in spite of (and perhaps partly due to) a history of human activity.

Hemlock's Latest Dynamic: Response to the Hemlock Woolly Adelgid

In 1985, the hemlock woolly adelgid crossed Long Island Sound into Connecticut and began to advance northward through New England. Considerable effort and money have been expended in attempts to control the adelgid through chemical and biological means, but surprisingly little work has focussed on the adelgid's ecological impact (however, see articles by York *et al.* and Orwig and Foster, this volume). In 1994, the Harvard Forest launched a broad program led by Dr. David Orwig to study the progression and ecological consequences of the adelgid in New England. Across a study region extending from Long Island Sound to northern Massachusetts and encompassing the Connecticut River Valley (100 x 250 km), this project seeks to: (1) map all hemlock forests using pre-adelgid air photos; (2) determine the regional pattern of adelgid infestation, assess its impact on the vigor and mortality of hemlock, and interpret these patterns in terms of environmental factors, distance from the Connecticut coast, and time; (3) assess forest ecosystem changes in terms of structure, composition and function (particularly nitrogen dynamics) and interpret these in relationship to changes in the forest environment; and (4) quantify the extent of increased logging of hemlock prompted by adelgid damage and contrast the ecological effects of logging with the "natural" process of mortality generated by adelgid.

Results to-date provide a very sobering view of the state of hemlock in southern New England and an equally pessimistic prognosis for the species throughout its range: (1) the hemlock woolly adelgid is widespread in

Connecticut and southern Massachusetts and is continuing to spread at a rate of 20-30 km per year; (2) along the latitudinal and temporal gradients of infestation there is a gradient in mortality and tree vigor, with extensive mortality occurring throughout southern and central Connecticut; (3) no infested hemlock tree or hemlock forest exhibits any sign of recovery, there is no evidence for any site or environmental factors that mitigate mortality, and trees of all size are affected; (4) as hemlock declines in vigor and as understory light levels increase, hardwood species, especially black birch (*Betula lenta* L., establish and grow rapidly; and (5) the major landscape-level consequence of the adelgid is to greatly reduce the complexity and diversity of forest and habitat structure and composition.

Conclusion

Eastern hemlock is very much a species in transition. Whether one's perspective is that of a landowner, forest manager, or conservationist seeking to manage landscapes for multiple sustained purposes, or that of an ecologist interested in interpreting the modern characteristics of ecosystems, it is impossible to consider hemlock forests without some doubt about its long-term viability. Ironically, in an era of extensive concern for global environmental change it is another manifestation of globalization – the movement of exotic organisms – that is changing the southern New England landscape most rapidly. Hemlock mortality and widespread logging of hemlock (more than 4 million board feet of hemlock were cut in Connecticut and Massachusetts in 1998 by Re-Gen, Inc. alone; D. Whitney pers. comm.) are transforming large areas from old, conifer-dominated forest to stands of young, rapidly growing hardwoods. The potential for the adelgid to spread is great and this, in itself, is becoming a strong force encouraging land-use and land-cover changes through "pre-emptive logging" well outside the insect's current range.

The long-term history of hemlock illuminates the discussion of the future of our forests in an adelgid world. Forests are remarkably resilient and the declining and dying hemlock forests will be rapidly replaced by hardwood species such as black birch. The decline will be associated with nutrient pulses to the groundwater and aquatic ecosystems as well as local changes in microenvironment that will have additional repercussions for terrestrial and aquatic ecosystems. For most people, outside those who discover new views or dead landscaping in their backyards or devastated hiking trails and shady ravines, the changes may be largely overlooked. However, the dynamics initiated by the adelgid will be permanent, in human terms. Even if the adelgid could be controlled completely, even if a full restocking of hemlock seedlings could be established, in those stands where the decline is well advanced and mortality is widespread the recovery of hemlock forests will be hundreds of years in the making.

Thus, we should cherish our opportunity to view hemlock in the manner that Henry Thoreau viewed the chestnut, as a vibrant and ecologically unique part of our landscape.

Meanwhile, there will be a nagging reminder of hemlock's past and future in the back of our minds.

Acknowledgements

Most of the research described in this review was conducted by researchers at the Harvard Forest, which provided support along with the A.W. Mellon Foundation, the National Science Foundation (through the Long Term Ecological Research program and Division of Environmental Biology), and the Competitive Grants program of the U.S. Department of Agriculture. Discussions with S. Clayden, J. Fuller, J. Hadley, J. McLachlan, G. Motzkin, J. O'Keefe, D. Orwig, P. Schoonmaker, and T. Parshall have broadened my understanding of hemlock ecosystems. I greatly appreciate the invitation of the symposium organizers, Paul Sendak and Ken Demaris, for inviting this keynote address.

Literature Cited

- Bhury, N.; L. Filion. 1996. **Mid-Holocene hemlock decline in eastern North America linked with phytophagous insect activity.** *Quaternary Research*. 45: 312-320.
- Davis, M. B. 1981a. **Outbreaks of forest pathogens in Quaternary history.** In: Proceedings of the IV International Palynological Conference, Lucknow (1976-77). 3: 216-227.
- Davis, M. B. 1981b. **Quaternary history and the stability of forest communities.** In: West, D. C.; Shugart, H. H.; Botkin, D. B., eds. *Forest Succession, Concepts and Application*. Springer-Verlag, NY: 132-153.
- Foster, C. H. W.; Foster, D. R. 1999. **Thinking in forest time. A strategy for the Massachusetts forest.** Harvard Forest Paper 24.
- Foster, D. R. 1999. **Thoreau's Country. Journey Through a Transformed Landscape.** Harvard University Press, Cambridge.
- Foster, D. R.; Aber, J.; Bowden, R.; Melillo, J.; Bazzaz, F. 1997. **Forest response to disturbance and anthropogenic stress.** *BioScience*. 47: 437-445.
- Foster, D. R.; Motzkin, G. 1998. **Ecology and conservation in the cultural landscape of New England: lessons from nature's history.** *Northeastern Naturalist*. 5: 111-126.
- Foster, D. R.; Motzkin, G.; Slater, B. 1998. **Land-use history as long-term broad-scale disturbance: regional forest dynamics in central New England.** *Ecosystems*. 1: 96-119.
- Foster, D.; O'Keefe, J. 2000. **New England forests through time. Insights from the Harvard Forest Dioramas.** Harvard Forest and Harvard University Press.
- Foster, D. R., Orwig, D. A.; McLachlan, J. 1996. **Ecological and conservation insights from retrospective studies of old-growth forests.** *Trends in Ecology and Evolution*. 11: 419-424.
- Foster, D. R.; Zebryk, T. M. 1993. **Long-term vegetation dynamics and disturbance history of a Tsuga-dominated forest in New England.** *Ecology*. 74: 982-998.
- Foster, D. R.; Zebryk, T.; Schoonmaker, P. K.; Lezberg, A. 1992. **Post-settlement history of human land-use and vegetation dynamics of a Tsuga canadensis (hemlock) woodlot in central New England.** *Journal of Ecology*. 80: 773-786.
- Fuller, J. L. 1998. **Ecological impact of the mid-Holocene hemlock decline in southern Ontario, Canada.** *Ecology*. 79: 2357-2351.
- Fuller, J. L.; Foster, D. R.; McLachlan, J. S.; Drake, N. 1998. **Impact of human activity on regional forest composition and dynamics in central New England.** *Ecosystems*. 1: 76-95.
- Hall, R. I.; Smol, J. P. 1993. **The influence of catchment size on lake trophic status during the hemlock decline and recovery (4800 to 3500 BP) in southern Ontario Lakes.** *Hydrobiologia*. 269/270: 371-390.
- Jacobson, G. L.; Webb, T.; Grimm, E. 1987. **Patterns and rates of vegetation change during the deglaciation of eastern North America.** In: Ruddiman, W. F.; Wright, H. E., eds. *North America and adjacent oceans during the last deglaciation*. Vol. K-3 of the *Geology of North America*. Geological Society of America, Boulder, CO.: 277-288.
- McClure, M. S. 1991. **Nitrogen fertilization of hemlock increases susceptibility to hemlock woolly adelgid.** *Journal of Arboriculture*. 17: 227-230.
- McLachlan, J.; Foster, D. R.; Menalled, F. 1999. **Anthropogenic origins of late-successional structure and composition in four New England hemlock stands.** *Ecology*. In press.
- Nichols, G. E. 1913. **The vegetation of Connecticut II. Virgin forest.** *Torreyia*. 13: 199-215.
- O'Keefe, J. F.; Foster, D. R. 1998. **An ecological history of Massachusetts.** In: Foster, C. H. W., ed. *Stepping back to look forward: A history of the Massachusetts forest*. Harvard Forest and Harvard University Press, Petersham and Cambridge: 19-66
- Orwig, D. A.; Foster, D. R. 1998. **Forest response to introduced hemlock woolly adelgid in southern New England.** *USA. Bulletin of the Torrey Botanical Club*. 125: 60-73.
- Spurr, S. H. 1956. **Forest associations in the Harvard Forest.** *Ecological Monographs*. 26: 245-262.