In the eastern half of North America, the eastern and Carolina hemlocks are under attack from the hemlock woolly adelgid, which is transforming their forest ecosystems. These species may yet survive, in part because of special ecological conditions and also multi-agency cooperation.

# THE PLIGHT OF THE HEMLOCK

IN EASTERN FORESTS

he forests on North America's East Coast from Canada to Alabama are threatened by an exotic and invasive forest pest that is both tiny and formidable the hemlock woolly adelgid (HWA). As a foundation species, hemlocks fundamentally shape the ecosystems and ecosystem processes in the areas

where they occur. Their loss would have major ramifications for the structure and composition of eastern forests. Nevertheless, the history of hemlocks in eastern North America is a story of decline and resilience, and unique opportunities for conservation lie before us, now and in the future.

# A MINIATURE BUG WITH OUTSIZED EFFECTS

At just 0.8mm in length and often nearly invisible to the naked eye, the hemlock woolly adelgid is primarily to blame for the severe decline of eastern North America's two native species of hemlock: the eastern hemlock, *Tsuga canadensis* (L.) Carr., and the Carolina hemlock, *Tsuga caroliniana* Engelm. Two other factors further stress trees already weakened by HWA: other pests and pathogens, and a changing climate with increased incidences of drought and rising temperatures.<sup>1</sup>

The tiny, aphid-related HWA (Adelges tsugae Annand [Hempitera:

Adelgidae]) is a sucking insect native to Japan and was first identified in eastern North America near Richmond, Virginia, on nurserygrown southern Japanese hemlock (*Tsuga sieboldii*) in 1951.<sup>2</sup> The adelgid is also found in the western United States and, although all hemlock woolly adelgid in the United States is the same species, the western adelgid is considered to be a different lineage, possibly originating in China. In Asia, HWA depends on Tigertail spruce (*Picea torano*) to complete its lifecycle and reproduce sexually.

The lack of Tigertail spruce in North America also helps explain why in the eastern U.S., HWA reproduces asexually.<sup>3</sup> Every individual is essentially genetically identical, female, and capable of reproducing twice each year, and with abundant hemlock hosts in eastern forests, HWA has reproduced rapidly.<sup>4</sup> Incapable of moving on their own (in North America, HWA is sessile for most of its life), these insects disperse via wind, birds, mammals (including people), and vehicles. HWA was first detected in Shenandoah

BY SARA DEFOSSET



White woolly egg sacks at the base of each hemlock needle are classic signs of hemlock woolly adelgid infestation. While these egg sacks are the most visible part of the insect's life cycle, they are not present year round. At times, the adelgid is nearly invisible to the naked eye. The eggs (pictured on the right with an adult) are 0.25mm long by 0.15mm wide; adults are just 0.8mm long.

National Park in Virginia in the 1980s; by the early 2000s, its reach was significant and devastation was widespread.

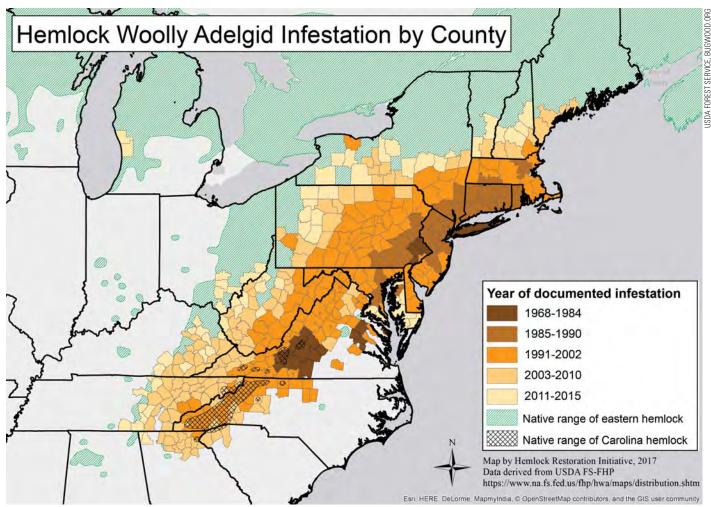
In 2002, the pest was discovered in the Great Smoky Mountains National Park in the southern Appalachians, home to 200,000 acres of old-growth forest, *35*,000 of which have a significant hemlock component. By 2006 hemlock mortality was evident in the park, especially where there were dense populations of large, old growth trees. Drought arrived in 2007–2008, accelerating hemlock decline. The world's largest known eastern hemlock, the "Caldwell Giant," was dead from HWA before the tree was even discovered.<sup>5</sup> HWA has progressed more rapidly and been more destructive in the southern Appalachians than originally expected, likely because of a combination of factors—drought, hemlock abundance, exceptionally large trees, and mild temperatures. In other parts of the eastern hemlock range, cold winters and hot summers have slowed its advancement.<sup>6</sup>

The hemlock woolly adelgid kills trees slowly, affixing itself to the base of a hemlock needle and feeding on the tree's starch reserves. HWA feeding interferes with the tree's ability to take up water and nutrients, producing a drought-like response that some researchers have likened to an allergic reaction. As a result, the hemlock's needles take on a gray and dusty appearance and begin to drop. Increasingly unable to photosynthesize as it loses its needles, the tree slowly dies from the bottom up. Trees can succumb to the pest in as little as four years, but in some cases this takes much longer.<sup>7</sup> Large trees, which require the movement of more water and nutrients to their crowns, appear to be the most vulnerable.

Adelgid populations native to Asia and the Pacific Northwest do not have the same devastating effects. Even eastern hemlocks relocated to these areas do not succumb to adelgid pressure as they do on the East Coast, perhaps because western and Asian hemlocks coevolved with HWA and native predator insects. Western trees may remain healthy even when infested with HWA because a delicate predator-prey relationship between HWA and other native insects has been established over thousands of years of evolutionary history. It is also possible that western and Asian hemlock species have some form of innate resistance that allows them to tolerate the pest and remain healthy even when infested.8 On the East Coast, however, HWA has no specialized, native predators, and neither eastern nor Carolina hemlock has any natural resistance to HWA. Specialized HWA predators and possible genetic resistance-present in the native range of other hemlock species-are hopeful signs for researchers and natural resource managers working to slow and stop HWA in the East.

### **HEMLOCKS IN THE ECOSYSTEM**

At least ten distinct species of hemlock exist in the world today. A new species, *Tsuga ullengensis*, which occurs on Ulleungdo Island in Korea, was delineated in 2017 by Holman et al.<sup>9</sup> All occur at roughly the same latitude.<sup>10</sup> Most are found in Asia; North America is home to four species and the southern Appalachians are home



HWA first arrived in the eastern United States sometime before 1951. It has since spread throughout nearly the entire range of eastern hemlock.

to two, the eastern (Canadian) hemlock and the Carolina hemlock. The latter has an extremely limited range: endemic to the southern Appalachians, it occurs primarily in western North Carolina, with a few small pockets in neighboring states. The eastern hemlock, on the other hand, dominates the eastern forest landscape, occurring up and down the East Coast from Canada to Alabama, and spreading as far west as Minnesota.

In southern Appalachian forests, Carolina and eastern hemlock occupy distinct ecological niches. The Carolina hemlock is a relatively small tree reaching heights of 40 to 60 feet.<sup>11</sup> It is found on drier ridge tops, bluffs, and rocky outcroppings. Its primary importance lies not in its dominance but in the contribution it makes, as a rare species, to global biodiversity. It appears to be more closely genetically related to its Asian cousins than to its eastern North American counterpart.<sup>12</sup>

The eastern hemlock is a forest giant. Called the "redwood of the East," it can live for more than 500 years and reach heights of more than 170 feet.<sup>13</sup> It is typically found in riparian areas growing along headwater streams, in moist, shady groves, and on northfacing slopes.<sup>14</sup> Many of the special services it delivers follow from its "shady" character. Eastern hemlock possesses the ability to persist for decades and even centuries in the near complete shade of the forest understory (where other trees would languish) in anticipation of a disturbance that will provide light and space for it to shoot up and join the forest canopy.<sup>15</sup> Like the redwood, it remakes the forest in its own image, creating around itself a particular ecosystem that

differs significantly from hardwood forests and in which it and many other plant and animal species thrive. It is also among the most genetically distinct of all the hemlock species; perhaps that contributes to its pronounced vulnerability to HWA pressure.<sup>16</sup>

The foliage of the eastern hemlock is dense, dark green, nitrogen rich, and-by benefit of being evergreen-available yearround. It reaches from the forest floor to the canopy, creating a ladder used by wildlife for habitat and mobility. Hemlock foliage is an important source of food and shelter in eastern forests, particularly in winter, when hardwood trees are dormant. The forest floor in hemlock groves tends to be more open than in other parts of the forest, and the temperature difference that hemlocks create is apparent. One need only step into a grove in summer to notice its distinctive coolness. The shady, cove-like environment created by hemlock stands is important for forest diversity in a general sense and specifically, in terms of plant and animal biodiversity in both aquatic and terrestrial environments. Hemlock groves break up the otherwise homogeneous character of hardwood forests, offering a microclimate and providing a moist, green island favored by many species.<sup>17</sup>

Shady hemlock groves provide ideal habitat for delicate native plant communities. Some species are found almost nowhere else. Pirate bush (*Buckleya distichophylla*), for example, is endemic to a small region of the southern Appalachians; it is a federal species of concern and appears on North Carolina's threatened species list. Hemlocks are considered a primary host for this hemiparasitic species. Also strongly associated with hemlock forests are numerous bird and animal species, including white-tailed deer, for which young hemlock foliage is a preferred browse, and as many as 90 bird species. Some warblers nest exclusively in hemlocks.<sup>18</sup>

The same shading, sheltering, and temperature-regulating services that the hemlocks deliver on land, they also deliver to the aquatic environments of headwater streams and waterways. In southern Appalachian watersheds, eastern hemlocks make up about 10 percent of total basal area but tend to be concentrated along riparian corridors. At one study site researchers found that hemlock occupied only 6 percent of basal area overall but 26 percent of basal area in the riparian corridor.<sup>19</sup> Hemlock roots hold stream banks in place, and their branches shade the water, keeping water temperatures stable, cooler, and more oxygenated-a necessary condition for cold-water species like brook trout. Their dense foliage intercepts precipitation, preventing nutrient runoff and sedimentation. Researchers have found that streams in watersheds affected by HWA show higher concentrations of micronutrients like chlorine and copper that can harm aquatic life.<sup>20</sup> Indeed, hemlock-dominated watersheds contain more aquatic biodiversity than streams that drain hardwood forests. In a 2003 study, brook trout and brown trout were nearly three times more likely to occur in streams draining hemlock forests than hardwood forests.<sup>21</sup>

Because their needles transpire more slowly and at a more constant rate than the leaves of their hardwood neighbors, hemlocks make more water available to watersheds during the growing season. If hemlocks are replaced by thirstier hardwoods, less water will be available during the warm months, when it is needed most. During winter, when hardwood trees are dormant, hemlocks along waterways are still taking up excess water during peak flow events, making flooding less severe. Thus, hemlocks both provide water to watersheds and, conversely, remove excess water, and their decline compromises the provisioning and regulating ecosystem services they deliver.<sup>22</sup>

The loss of hemlocks also takes a toll on less tangible ecosystem services like aesthetic beauty, cultural value, and outdoor recreation. Standing dead trees in forests can pose hazards to visitors, and their fuel dramatically increases wildfire danger. Trees that die along streams end up in the water, where the large woody debris makes waterways less navigable; with the decay of their root systems, erosion and sedimentation follow. And, of course, standing in a grove of dead trees does not have the same emotional and spiritual resonance that a thriving, healthy forest provides. Like the redwood, the eastern hemlock holds a special place in the public imagination. Its rare ability to instill in its beholders a feeling of wilderness and sense of place has not been lost on generations of poets, artists, scientists, and naturalists who have often expressed their affection for this tree.<sup>23</sup> When taken as a whole, no other forest tree in eastern North America is equipped to deliver the diversity of services provided by the eastern hemlock.

## **HEMLOCKS IN HISTORY**

Many of us see the decline of eastern hemlock in Appalachian forests as a devastating phenomenon; however, if we examine the ecological history, we find a precedent for the loss of foundation species—and the loss of hemlock from eastern North American forests in particular.<sup>24</sup> After all, humans and forests live at very different time scales. What we experience in our human



Carolina hemlocks, endemic to the southern Appalachians, are typically found high up on ridge tops and rocky outcroppings. As a rare species, they are important contributors to global biodiversity.

lifetimes as profound change may be only a fleeting moment in the life of a forest that has evolved over thousands of years.<sup>25</sup> Although large-scale disturbances to eastern hemlock populations have occurred at least twice before in prehistory, and again in relatively modern history, we nonetheless feel the current loss of eastern hemlock deeply.

One such decline of eastern hemlock in Appalachian forests began during the mid-Holocene epoch, around 6,000 years ago. A more than tenfold decrease in eastern hemlock populations lasted approximately 1,000 years. Researchers believe it was likely the result of pathogens, insects, a changing climate, or some combination of these factors, much as we are experiencing today.26 The arrival of European colonists in North America marked the beginning of another decline for the still rebounding, slow-growing eastern hemlock, as land was cleared for agriculture and hemlocks were harvested for the tannins in their bark and for timber. With the exception of a few old-growth pockets, today's eastern North American and Appalachian forests are second-growth, still actively recovering from having been clearcut in or before the late 1800s.<sup>27</sup> David R. Foster, director of the Harvard Forest, has remarked that eastern forests are "old by our standards but they have only been growing a couple of centuries. It takes 500 years to come back from a hit to anything like a steady state. We're less than midway towards that point and the hemlock woolly adelgid is going to stop that. It's going to divert the forest into another transition."28

The history of the eastern hemlock illustrates that forests, as constant as they may seem to us, are defined by change. Eastern hemlocks today face pressures that are at once different and the same as those they have overcome in the past. Although hemlock is no longer sought after for its tannin-rich bark and its stands are typically safe from logging by benefit of their inaccessibility and the timber's limited commercial value, the combination of the exotic hemlock woolly adelgid and the changing climate recalls the ancient problems that brought down the hemlock in the past. These pressures are exacerbated by human activity: as our human realm becomes ever busier and more interconnected, we can expect to see more species decline in the years to come, particularly in sensitive areas like the southern Appalachians.

Is there a role for human intervention in preventing this decline, and how prominently will the eastern hemlock figure in our future forests and landscapes? This current period of hemlock decline is clearly the result of human activity. With the movement of goods and services around the globe expected to increase in the coming decades, perhaps eastern hemlock is now poised to take on a new role in human consciousness, one that is less material and more instructive. For Foster, "hemlock provides a compelling record of change" that will undoubtedly inform forest management and conservation efforts as we confront intensifying ecological change and learn to navigate in a world where "species collapse is less and less a surprise."29 Our practical resources, our physical health, and our emotional well-being are so bound up with our forests that managing the hemlock woolly adelgid is as important for conservation of our way of life as it is for the trees themselves. The conspicuous loss of a foundation species presents an opportunity to reimagine conservation planning and develop an effective intervention that will halt its decline, eventually restore hemlocks to long-term health in our forests, and inform responses to the next invasive pest or pathogen that is surely coming.

Unlike the American chestnut, which disappeared from eastern

forests a century ago because of an exotic fungal pathogen, hemlock populations have not been subject to heavy timber harvesting and so retain a genetic diversity that will allow for potential adaptation and healthy population growth in the future. Moreover, whereas chestnut blight can live indefinitely in the forest, biding its time on other hosts,<sup>30</sup> HWA is extremely host specific, and therefore more straightforward to manage. And unlike the invasive emerald ash borer, which, by the time it is detected in a tree, the opportunity for action has passed. HWA can take four to ten years— and in many cases, much longer—to kill a hemlock.<sup>31</sup> These differences create a window of opportunity.

### **RESPONSES AND SOLUTIONS**

For many managers working on issues of forest health, the decline of the hemlock is only one among many pressing forest health concerns that compete for funding, personnel, and research. In one southern Appalachian state, however, a state where few trees not chemically protected remain healthy, a program is now addressing hemlock specifically, synthesizing information, and coordinating efforts for combating HWA. With funds awarded from a settlement with the Tennessee Valley Authority, Steve Troxler, North Carolina's Commissioner of Agriculture, began the Hemlock Restoration Initiative (HRI) in 2014. The U.S. Forest Service's Forest Health Protection program began providing matching funds the following year. WNC Communities, a 501(c)(3) nonprofit organization based in Asheville, North Carolina, with a 70-year history of successful rural development and forestry projects in the region, was chosen to administer the program, giving HRI greater flexibility than is enjoyed by similar programs administered through government agencies.



Technicians from HRI perform systemic treatments using a low-volume soil drench method to protect hemlocks from hemlock woolly adelgid.



The Hemlock Restoration Initiative works with the Landcare Committee for the town of Montreat, North Carolina, to release HWA predator beetles. Insects that are especially adapted to feed on hemlock woolly adelgid are considered a critical aspect of long-term hemlock conservation.

HRI works with partners and other restoration initiatives at all levels—from private citizens and homeowners to scientists, researchers, natural resource managers, and conservation-based nonprofits, in addition to local, state, and federal governments. Its mission is to restore eastern and Carolina hemlocks to their native habitats throughout North Carolina, mitigate damage to hemlocks and their associated ecosystems caused by HWA infestation, and ensure that hemlocks survive to maturity on North Carolina's public and private lands. The plan for hemlock restoration in North Carolina comprises short-, middle-, and long-term methods for combating HWA and ensuring hemlock survival.

In the short term, the only way to protect an individual tree from HWA is to treat it with a systemic, neo-nicatinoid insecticide, most commonly imidacloprid, and for heavily-infested, stressed trees, dinotefuran (name brand "Safari"). In most cases a simple, inexpensive soil drench application is effective, making at-home treatment possible for most homeowners. However, for very large forested properties on North Carolina's nonfederal public lands, HRI works with land management professionals, volunteers, and hired crews to chemically treat hemlocks. In 2017, HRI and its partners treated nearly 12,000 trees.

To treat ecologically significant trees on private lands, HRI is working with county governments, local land conservancies, and North Carolina cooperative extension services in a pilot cost-share program which offers financial assistance for private homeowners whose properties meet certain criteria. With some initial successes, this program may be replicated in counties throughout the state and beyond. If a tree is relatively healthy, an initial chemical treatment can ensure its survival for five to seven years, effectively buying time while longer-term strategies come to fruition.

The use of biological controls constitutes the middle-term approach to HWA management. Most of the insects used for biological control are predator beetles collected from the wild in the Pacific Northwest and Japan or reared in labs. Before release on the East Coast, each goes through a six- to ten- year vetting process by the federal Animal and Plant Health Inspection Service. Each species has advantages and disadvantages, and none are likely to be silver bullets, but, together, they are considered essential components of long-term HWA control.

HRI has established local insectaries where predator beetles can breed and become established and later be collected and distributed. These insectaries will increase the number of HWA predators present in southern Appalachian forests and reduce dependence on resource-intensive procurement methods, like wild collection or lab production. Many thousands of predator beetles have been released in North Carolina and elsewhere, and additional predator species are under evaluation. More research is needed to determine their long-term effectiveness for combating HWA, but the predator insects are reproducing and spreading to new areas. These predators will never exterminate HWA; instead, the intention is to establish predator populations of sufficient size to keep pest populations at a level that trees can tolerate. Because of the length of time required to vet, raise or collect, and establish new predator populations, biological controls are not well suited for immediate intervention to stop hemlock decline. They are a landscape-level approach intended to reduce ongoing dependence on chemicals and keep adelgids in check in eastern forests.

For the long term, HRI's partner scientists, some of whom are based in the southern Appalachians, are working to conserve the diverse genetic lineage of the eastern and Carolina hemlocks, identify the mechanisms for resistance in Asian and western hemlock species, define the growing conditions that hemlocks like best, and refine the silvicultural techniques that will inform forest restoration in the aftermath of HWA.

A group called Camcore, at North Carolina State University, is establishing seed banks and ex situ conservation plantings and

populations of hemlocks in South America and other places where HWA is not present, so that hemlock genetic diversity can be preserved and available for future restoration efforts. The Forest Restoration Alliance, also with ties to the university, conducts a selection and breeding program for pest resistance in hemlocks, using the model outlined by the American Chestnut Foundation, aimed at one day creating an eastern hemlock that is able to resist or tolerate the adelgid. Camcore has teamed up with U.S. Forest Service researchers, based at the Southern Research Station in Asheville, to study the effects of light exposure and competition release on HWA populations and hemlock health to inform future management approaches and restoration techniques. Numerous other researchers and managers are working similar projects in the Appalachian region and beyond.

The integrated approach being taken by various organizations and individuals is defining how we cope with future ecological changes and how we conceive of forest management and forest health in the years to come. The long-term effects of eastern hemlock decline remain to be seen, but changes are already apparent as dying hemlocks are being replaced by early successional species like red maple, tulip poplar, and rhododendron. If hemlock loss accelerates, these processes will dramatically alter the structure and composition of our forests.

The history of the hemlock is a reminder that this type of change is inevitable, but inevitability does not mean that conservation efforts are a lost cause. On the contrary, the history of the hemlock is one of persistence and resilience. Now human intervention is helping to conserve both the tangible and the intangible services provided by hemlock that have so shaped our landscapes and our lives, spare this majestic species from relegation to arboreta and special collections, and restore it to its place of prominence as the "long-lived champion of the untamed woods."<sup>32</sup>

Sara deFosset is the Outreach Associate with the Hemlock Restoration Initiative in Asheville, North Carolina. For more information about the organization's work, contact HRI at www.savehemlocksnc.org.

### NOTES

- Aaron M. Ellison, Michael S. Bank, Barton D. Clinton, Elizabeth A. Colburn, Katherine Elliott, Chelcy R. Ford, David R. Foster, et al., "Loss of Foundation Species: Consequences for the Structure and Dynamics of Forested Ecosystems," *Frontiers in Ecology* 3(9) 2005: 485.
- 2. Nathan P. Havill and Michael E. Montgomery, "The Role of Arboreta in Studying the Evolution of Host Resistance to the Hemlock Woolly Adelgid," *Arnoldia* 65(3) 2008: 4.
- 3. In Japan and the western United States, "the typical adelgid life-cycle involves alternation between spruce (Picea) primary hosts where they form galls and where there is a sexual generation, and other conifer secondary hosts where reproduction is strictly asexual." Nathan Havill, Michael Montgomery, and Melody Keena, "Chapter 1: Hemlock Woolly Adelgid and Its Hemlock Hosts: A Global Perspective," in *Implementation and Status of Biological Control of the Hemlock Woolly Adelgid*, U.S. Forest Service Publication FHTET-2011-04 (2011), 7.
- 4. Havill et al., "Hemlock Woolly Adelgid and Its Hemlock Hosts," 7-8.
- Will Blozan, "The Last of the Giants: Documenting and Saving the Largest Eastern Hemlocks," *American Forests* (Spring 2011), http://www.americanforests.org/magazine/article/the-last-of-the-giants/.
- 6. Havill et al., "Hemlock Woolly Adelgid and Its Hemlock Hosts," 8.
- Evan L. Preisser, Kelly L. F. Oten, and Fred P. Hain, "Hemlock Woolly Adelgid in the Eastern United States: What Have We Learned?" *Southeastern Naturalist* 13, Special Issue 6 (2014): 4.

- Kelly L. F. Oten, Scott A. Merkle, Robert M. Jetton, Ben C. Smith, Mary E. Talley, and Fred P. Hain, "Understanding and Developing Resistance in Hemlocks to the Hemlock Woolly Adelgid," *Southeastern Naturalist* 13, Special Issue 6 (2014): 148.
- Garth Holman, Peter Del Tredici, Nathan Havill, Nam Sook Lee, Richard Cronn, Kevin Cushman, Sarah Mathews, Linda Raubeson, and Christopher S. Campbell, "A New Species and Introgression in Eastern Asian Hemlocks (Pinaceae: Tsuga)" Systematic Botany, 42(4):1–15, http://www.bioone.org/ doi/full/10.1600/036364417X696474.
- 10. Havill and Montgomery, "The Role of Arboreta," 5.
- 11. Virginia Tech, Department of Forest Resources and Environmental Conservation, "Carolina hemlock Pinaceae, *Tsuga caroliniana*," http://dendro.cnre.vt.edu/dendrology/syllabus/factsheet.cfm?ID=143.
- 12. Havill and Montgomery, "The Role of Arboreta," 8.
- 13. Blozan, "The Last of the Giants."
- U.S. Department of Agriculture, Natural Resource Conservation Service, "Plant Guide: Eastern Hemlock, *Tsuga canadensis* (L.) Carr.," https://plants. usda.gov/core/profile?symbol=TSCA.
- H. A. Fowells, "Silvics of Forest Trees of the United States," Agriculture Handbook 271 (Washington, DC: U.S. Department of Agriculture, Forest Service, 1965), 608–09.
- 16. Havill and Montgomery, "The Role of Arboreta," 8.
- David R. Foster, Hemlock: A Forest Giant on the Edge (New Haven: Yale University Press, 2014), 6.
- 18. Mariko Yamasaki, Richard M. DeGraaf, and John W. Lanier, "Wildlife Habitat Associations in Eastern Hemlock—Birds, Smaller Mammals, and Forest Carnivores," in *Proceedings: Symposium on Sustainable Management of Hemlock Ecosystems in Eastern North America* GTR-NE-26 (Newtown Square, PA: U.S. Forest Service, Northeastern Research Station, 2000), 135–36.
- Steven T. Brantley, Chelcy Ford Miniat, Katherine J. Elliott, Stephanie H. Laseter, and James M. Vose, "Changes to Southern Appalachian Water Yield and Stormflow after Loss of a Foundation Species," *Ecohydrology* 1521 (2014): 3.
- 20. Misty Dawn Huddleston, "Riparian Ecosystem Response to Hemlock Woolly Adelgid (*Adelges tsugae*) Induced Eastern Hemlock (*Tsuga canadensis*) Mortality in the Great Smoky Mountains National Park, USA," (PhD diss., University of Tennessee, 2011), iv, http://trace.tennessee.edu/utk\_graddiss/1194.
- 21. Robert Ross, Randy Bennett, Craig Snyder, John Young, and David Lemarie, "Influence of Eastern Hemlock (*Tsuga canadensis L.*) on Fish Community Structure and Function in Headwater Streams of the Delaware River Basin," *Ecology of Fresh Water Fish* 1 (2003): 60–65.
- 22. Brantley et al., "Changes to Southern Appalachian Water Yield," 1.
- 23. Some examples: Henry Wadsworth Longfellow, *Evangeline, A Tale of Acadie* (1847); Robert Frost, "Dust of Snow" (1920); Joan Mitchell's painting *Hemlock* (1965); and John Grade's sculpture *Middle Fork* (2015).
- 24. Yan Zaho, Zicheng Yu, and Cheng Zhao, "Hemlock (*Tsuga canadensis*) Declines at 9800 and 5300 cal. yr BP Caused by Holocene Climatic Shifts in Northeastern North America," *Holocene* 20(6): 877–86.
- 25. Paul A. Delcourt, *Introduction to Quaternary Ecology: A Paleoecological Perspective* (London: Chapman and Hall, 1991), 1.
- 26. W. Wyatt Oswald and David Foster, "Middle-Holocene Dynamics of *Tsuga canadensis* (eastern hemlock) in Northern New England, USA," *Holocene* 22(1): 71–78; and Zaho et al., "Hemlock (*Tsuga canadensis*) Declines," 1.
- Anthony W. D'Amato, David A. Orwig, and David R. Foster, "Understory Vegetation in Old-growth and Second-growth Tsuga canadensis Forests," *Forest Ecology and Management* 257(2009): 1043–52.
- 28. Foster, Hemlock, xvii.
- 29. Foster, Hemlock, 10, xv.
- 30. D. Rigling and S. Prospero, "Cryphonectria parasitica, The Causal Agent of Chestnut Blight: Invasion History, Population Biology and Disease Control," *Molecular Plant Pathology* (January 31, 2017), https://www.ncbi. nlm.nih.gov/pubmed/28142223.
- 31. Karen Chavez, "Emerald Ash Borer Decimating Trees in WNC," *Asheville Citizen Times*, September 8, 2016, http://www.citizen-times.com/story/news/local/2016/09/08/emerald-ash-borer-decimating-trees-wnc/89557230/; and Jordan D. Marché II, "Fool Me Twice, Shame on Me: The Emerald Ash Borer in Southeastern Michigan," *Forest History Today* (Fall 2012): 5–15.
- 32. Foster, Hemlock, 2.