Ecosystem Response to an Imported Pathogen: The Hemlock Woolly Adelgid

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One of the provocative issues that have emerged in the field of ecology over the past few decades has concerned the question of whether individual plant or animal species may play a critical role in controlling ecosystem processes and determining major community characteristics—that is, are there really "keystone" species? In an era when species are being driven either locally or globally extinct, the possibility that individual taxa may be crucial for maintaining the integrity of ecosystems has become a major impetus for the study of biodiversity.

This issue has been the focus of considerable research in the northeastern United States in particular, in large part because the region has experienced a series of species eliminations or reductions in numbers primarily as a consequence of human activities. The decline of hemlock across its range 4,800 years ago due to an insect pathogen, followed by a very gradual recovery; the elimination of chestnut in this century by a fungal blight introduced from eastern Asia; the outbreak of gypsy moth on oak, aspen, and birch forests; and the purposeful elimination or drastic reduction of animal populations—wolves, passenger pigeons, deer, beavers, to name only a few—all have undoubtedly had major consequences for forest, aquatic, and wetland ecosystems across the Northeast, although they remain largely unquantified.

Widespread, abundant, long-lived, and extraordinarily shade-tolerant, eastern hemlock *(Tsuga canadensis)* has always been classified as a preeminent part of the "climax" forest that existed before European settlement. Thanks to the extremely dense shade and deep, acidic litter it produces, hemlock is able to determine forest composition and create distinctive wildlife habitats. Although it is currently found in greatest abundance on rocky ridges or talus slopes and in moist, cool ravines, hemlock grows on a broad range of sites, and, in fact, hemlock plays an important role in controlling ecosystems all across New England, from the rocky highlands through the mesic woodlands and riparian areas, and into the wetlands.

Now, nearly 5,000 years after a pathogen decimated hemlock populations across its entire range, an introduced insect, hemlock woolly adelgid, or HWA *(Adelges tsugae)*, threatens another catastrophe for hemlock, and at the same time offers an opportunity to examine the consequences for the ecosystems it occupies. In contrast to the case of the chestnut blight, whose effects we understand only partially, we hope to learn from the case of HWA what happens to a forest when its dominant species is lost.

It is important to point out that the HWA-hemlock system behaves very differently from other pathogen and pest systems. The damage caused by HWA is unlike that of chestnut blight, gypsy moth, dutch elm disease, or the related balsam woolly adelgid *(Adelges piceae)* in that HWA attacks overstory trees, saplings, and seedlings alike, and therefore has the potential to eliminate hemlock from a site within a few years. Moreover, hemlock trees lack the ability to sprout or refoliate after defoliation; consequently reestablishment can only occur from the seedbank or from seed transported from surviving trees. Hemlock seed typically remains viable only one growing season, although a few researchers have reported seed viability for up to four years. It is believed that on most sites, episodic establishment of hemlock occurs only infrequently, under unusual conditions related to the nature of the seedbed, moisture, and seed availability.

White-tailed deer often represent another obstacle to regeneration: many studies have shown that deer browse can severely reduce hemlock seedling densities. Deer herd density in Connecticut has more than doubled since 1980, resulting in high local population densities that change understory composition and structure. All these problems raise concerns about the long-term viability, stability, and composition of hemlock ecosystems. Many hemlock stands are scattered across the landscape on sites that have been protected from intensive human and natural disturbance. If hemlock is eliminated from even a portion of these sites, seed production will be eliminated or drastically reduced across broad geographic areas. It should be noted that it took eastern hemlock one to two thousand years to recover following the mid-Holocene decline 4,800 years ago.

In 1995 the Harvard Forest initiated a major research effort consisting of stand, landscape, and ecosystem components in central Connecticut along a 370-mile transect that extends from Long Island Sound to the Massachusetts border. To document the damage already caused by HWA since it arrived in 1985, we used aerial photographs to map each hemlock stand greater than three hectares (seven and a half acres). We have compiled extensive data on forest composition from 115 stands, which we have overlain on a GIS (Geographic Information Systems) map that shows other biological features as well as soil types and topographic characteristics. This map will facilitate our analysis of the way HWA spreads and help us determine whether the damage patterns observed in the present study are consistent across various types of landscape.

We also began to examine in detail the response of eight hemlock stands with differing levels of HWA infestation; the range of damage found in this sample was in general representative of conditions observed in dozens of stands throughout south-central Connecticut. Results after the second year of analysis of the eight sample stands showed continued deterioration of hemlock, with annual mortality levels ranging from 5 to 15 percent in stands that had already lost 20 to 95 percent of all overstory hemlock. All surviving hemlocks except those in one isolated stand are infested with HWA and have suffered moderate to severe canopy damage. Consequently, many of our study sites currently have a high proportion of standing dead snags or trees whose only remaining foliage is in the outer ends of upper branches.

In severely damaged stands, many dead treetops and boles have snapped off during recent windstorms, and deterioration in the surviving trees has continued due to

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This Tsuga canadensis *branch is infested with HWA ovisacs, located along the twigs at the base of the needles* the presence of secondary organisms such as hemlock borer, shoestring fungi, and conk fungi. The consequences of this continued mortality will be substantial pulses of woody debris, dramatic changes in the age, structure, and composition of forests, and altered wildlife habitat. Light availability as well as above- and below-ground space should increase as HWA spreads across the landscape. We have recently begun to study how these substantial changes in forest structure will affect the timing, magnitude, and duration of nitrogen cycling.

Our analysis of the effects of HWA damage shows dramatic changes in the understory microenvironment and in the response of vegetation to these changes. Particularly in stands that previously had a high percentage of hemlock in the overstory, black birch *(Betula lenta)* seedlings have established themselves prolifically, encouraged by the increased amount of light reaching the previously shaded forest floor. The organic layer in the soil under hemlock canopies appears to be an ideal substrate for germination of this wind-dispersed species. Several researchers have reported similar increases following partial cutting or tree mortality due to chestnut blight or windthrow. An increased abundance of black birch is also expected in less severely damaged stands in the future, since it is already present in the overstory and produces copious numbers of seeds.

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Severe HWA damage on the Guilford, Connecticut, study site. Note the dead hemlocks in the foreground and background, adjacent to trees that retain sparse canopies. Hemlocks typically die with their branch structures intact and gradually fall apart over three to ten years.

Seedlings of red maple and of several oak species were also present in low densities in most of our study sites; they may become more numerous in the future. The overall scarcity of hemlock seedlings in these forests suggests that neither they nor seedbanks will be of much help in hemlock reestablishment. Very few shrub species have colonized these stands; exceptions are bird-dispersed grape species *(Vitus)* and Virginia creeper *(Parthenocissus quinquefolia)*. Several opportunistic herbaceous species have also become established in low abundance throughout the study area, and invasion has already begun of several exotic tree, shrub, and herbaceous species that may increase and further affect revegetation processes in the future. Many factors, including pre-HWA site and soil characteristics, hemlock mortality rates, herbivore pressure, and the percentage of overstory space occupied by hardwood species, will also

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Black birch seedlings have established themselves prolifically under HWA-damaged hemlocks, encouraged by the increased amount of light reaching the previously shaded forest floor

play a role in determining the eventual composition of vegetation.

By documenting damage patterns and changes in forest structure and composition resulting from an introduced forest pest as they develop, we have gained valuable insight into the initial recovery processes of forests when a dominant species is removed. The results of this study and direct observations in dozen of stands throughout the state indicate that Connecticut forests are being severely impacted by HWA. To date, the rate and intensity of infestation is not attributable to any site factor or stand characteristic, and there is no apparent impediment to the widespread expansion of HWA and devastation of eastern hemlock across its range.

Varying degrees of HWA infestation at the stand level resulted in high hemlock mortality rates, pulses of downed woody debris, and dramatic changes in microenvironment characteristics due to overstory canopy gaps. These structural changes have initiated rapid vegetation responses in understories typically devoid of vegetation. In addition, our results suggest that some sites may experience a complete change in cover type from hemlock to forests dominated by birch, oak, and maple species. Under this scenario, forest composition and structure at the landscape level would become increasingly more homogenous. The outlook for hemlock persistence in southern New England forests is bleak. If HWA dispersal continues unimpeded, dramatic reductions of hemlock across broad geographical areas appear imminent unless natural or introduced predators of HWA are found.

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