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Ecosystem to regional impacts of introduced pests and pathogens: historical context, questions and issues

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Infestation by exotic pathogens and pests, and the resulting decline in native species is an important ecological, economic and evolutionary process that may alter ecosystem structure and function, and exert devastating impacts on natural resources and aesthetic conditions (Castello *et al*., 1995; Enserink, 1999; Everett, 2000). Introduced pests may dramatically change forest composition, structure and microenvironment; alter critical ecosystem processes such as nutrient cycling and retention; and increase ecosystem susceptibility to further disturbances, including invasion by exotic plants and animals (Vitousek, 1986; Ramakrishnan & Vitousek, 1989; Mack & D'Antonio, 1998; Mack *et al*., 2000). In the north-eastern USA, pathogen outbreaks have occurred historically and increasingly in the last century (Table 1; Castello *et al*., 1995; Liebhold *et al*., 1995; O'Keefe & Foster, 1998; Hall *et al*., 2002), and have initiated precipitous declines in such dominant species as chestnut, elm and beech (Liebhold *et al*., 1995). Importantly, outbreaks often lead to shifts in harvesting strategies of host trees, including increases in both the amount and rate of pre-salvage and salvage logging (Frothingham, 1924; Irland *et al*., 1988; Radeloff *et al*., 2000), potentially generating more profound ecosystem disruption than the pest or pathogen itself.

Despite historical and ongoing introduction of pests and pathogens into forest ecosystems, there remains a critical lack of information regarding the factors controlling their impact across a range of spatial scales as well as the response of forest ecosystems and associated wildlife species to the selective mortality of dominant tree species. There has also been precious little attempt to place the understanding of these responses into a broad framework of ecosystem perturbation and recovery. Broad questions include: What regional, landscape, site and stand factors control the pattern of forest decline and mortality? What is the magnitude and trajectory of vegetation and microenvironment responses initiated by the selective removal of a dominant tree species and how do these affect ecosystem processes? How do pre-emptive logging and forest species decline because of the exotic pests differ in their impacts on forest structure, composition and ecosystem function? and finally, how do wildlife species respond to these species-selective processes? Because of the global movement of pests and pathogens, answers to these fundamental scientific questions are essential for understanding the function, dynamics and management of forests world-wide and for the development of appropriate management responses in forest ecosystems.

One of the best-known examples of overstory loss in North America occurred following the introduction and subsequent spread of chestnut blight (*Cryphonectria parasitica*). This fungal disease effectively eliminated overstory chestnut (*Castanea dentata*) from forests extending from Maine to Georgia in the early twentieth century and dramatically altered the structure and composition of eastern deciduous forests (Liebhold *et al*., 1995). Unfortunately, despite a good understanding of the compositional and structural changes generated by this blight, we know very little concerning ecosystem response to the loss of chestnut. Similarly, impacts of chestnut loss on wildlife species are also largely unknown, outside the anecdotal information that squirrel populations crashed with the loss of chestnut mast, woodpeckers apparently increased because of the food and habitat in dead trees (cf. Smith *et al*., 2000), and seven moth species that fed exclusively on chestnut are now extinct (Opler, 1978).

The recent unimpeded infestation of the hemlock woolly adelgid (*Adelges tsugae*; HWA) across the north-eastern USA provides an unusual opportunity and critical imperative to examine the ecological consequences of the removal of a core tree species, eastern hemlock, on forest composition, structure and function, as it occurs. The HWA, an introduced aphid-like insect from Japan that attacks and kills eastern hemlock, is generating widespread mortality and initiating intensive logging of hemlock from

Table 1 List of exotic pests and pathogens that have caused or threaten to cause dramatic tree declines in forests of the eastern USA

Pest/pathogen	Date introduced	Species affected
Gypsy moth (*Lymantria dispar*)	1869	*Quercus*; other hardwood species
Beech bark disease (*Nectria coccinea* var. *fraginata*)	1890	*Fagus grandifolia*
Balsam woolly adelgid (*Adelges piceae*)	1900	*Abies balsamea, A. fraseri*
Chestnut blight (*Cryphonectria parasitica*)	1904	*Castanea dentata*
White pine blister rust (*Cronartium ribicola*)	Early 1900s	*Pinus strobus*
Dutch elm disease (*Ophiostoma ulmi*)	1930	*Ulmus americana*
Hemlock woolly adelgid (*Adelges tsugae*)	1950s	*Tsuga canadensis, T. caroliniana*
Butternut canker (*Sirococcus clavigigenti-juglandacearum*)	1967	*Juglans cinerea*
Dogwood anthracnose (*Discula destructiva*)	1978	*Cornus florida*
Asian longhorn beetle (*Anoplophora glabripennis*)	1996	*Acer, Betula, Populus, Ulmus* spp.

North Carolina to New Hampshire and threatens to produce a range-wide decline or elimination of this ecologically, culturally and economically important species (Orwig & Foster, 1998, 2000).

The array of hemlock forests in different stages of infestation present a model system to investigate the ecological processes associated with selective species removal. Hemlock is one of the most abundant, long-lived and shade-tolerant trees in the northeast and plays a unique role in forest ecosystems (Rogers, 1978). This important conifer provides vital habitat to many birds, mammals and forest carnivores (Yamasaki *et al*., 2000). Because of the hemlock's role as a core species, controlling forest understory environments and composition, HWA infestation or logging may initiate ecosystem responses that exceed those resulting from previous forest pathogens (Foster, 2000). The deep shade and thick, acidic litter in stands result in cool, damp microclimates, low light availability, depauperate understories and slow rates of nitrogen cycling (Lutz, 1928; Rogers, 1978, 1980; Aber & Melillo, 1991). Consequently, progressive decline from HWA or abrupt overstory removal by logging could generate a lengthy and dramatic period of forest reorganization leading to completely new forest types, changes in wildlife assemblages (Benzinger, 1994), and profound ecosystem impacts, including accelerated decomposition, nutrient losses, nitrogen export to streams and erosion (Foster *et al*., 1997). In addition, hemlock's dominance in wetlands and riparian areas enhances the vulnerability of aquatic ecosystems to these changes (Snyder *et al*., 2002).

Several contributors to this section address the ecological importance of the selective removal of dominant tree species by exotic pests and pathogens across the landscape. Orwig *et al*. (2002) document the distribution of HWA, its rate of spread and its impact on tree vigour and mortality in southern New England. In addition, they discuss the important environmental, stand, and landscape factors controlling the spread and impact of HWA. The subsequent study by Kizlinski *et al*. (2002) contrasts the rate, magnitude and quality of vegetation and ecosystem responses to HWA vs. logging and relates these to differences in site conditions, microenvironmental change and disturbance intensity. To examine the effect of overstory species removal on wildlife, Tingley *et al*. (2002) document avian response to the HWA-induced decline of hemlock. This section concludes with Paillet's (2002) thorough review of the history, decline and the ongoing transformation of American chestnut in eastern USA forests. Collectively, these papers shed light on forest ecosystem response to the selective removal of a dominant species by introduced pests. In a modern global world in which organisms move freely to new environmental and ecological settings the introduction of pathogens, followed by major changes in natural ecosystems, will become an increasingly important ecological process with major economic, conservation and social implications.

DAVID A. ORWIG

Harvard University,
Harvard Forest,
Petersham,
MA, USA

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BIOSKETCH

David A. Orwig is a forest ecologist at Harvard Forest interested in dendroecology and the role of land-use history and disturbance on forest dynamics. His current research integrates community, landscape, and ecosystem approaches in examining the ecological consequences of an invasive insect pest in hemlock forests of New England.