

# Loss of foundation species: consequences for the structure and dynamics of forested ecosystems

Aaron M Ellison<sup>1\*</sup>, Michael S Bank<sup>1</sup>, Barton D Clinton<sup>2</sup>, Elizabeth A Colburn<sup>1</sup>, Katherine Elliott<sup>2</sup>, Chelcy R Ford<sup>2</sup>, David R Foster<sup>1</sup>, Brian D Kloeppel<sup>3</sup>, Jennifer D Knoepp<sup>2</sup>, Gary M Lovett<sup>4</sup>, Jacqueline Mohan<sup>1</sup>, David A Orwig<sup>1</sup>, Nicholas L Rodenhouse<sup>5</sup>, William V Sobczak<sup>6</sup>, Kristina A Stinson<sup>1</sup>, Jeffrey K Stone<sup>7</sup>, Christopher M Swan<sup>8</sup>, Jill Thompson<sup>9</sup>, Betsy Von Holle<sup>1</sup>, and Jackson R Webster<sup>10</sup>

In many forested ecosystems, the architecture and functional ecology of certain tree species define forest structure and their species-specific traits control ecosystem dynamics. Such foundation tree species are declining throughout the world due to introductions and outbreaks of pests and pathogens, selective removal of individual taxa, and over-harvesting. Through a series of case studies, we show that the loss of foundation tree species changes the local environment on which a variety of other species depend; how this disrupts fundamental ecosystem processes, including rates of decomposition, nutrient fluxes, carbon sequestration, and energy flow; and dramatically alters the dynamics of associated aquatic ecosystems. Forests in which dynamics are controlled by one or a few foundation species appear to be dominated by a small number of strong interactions and may be highly susceptible to alternating between stable states following even small perturbations. The ongoing decline of many foundation species provides a set of important, albeit unfortunate, opportunities to develop the research tools, models, and metrics needed to identify foundation species, anticipate the cascade of immediate, short- and long-term changes in ecosystem structure and function that will follow from their loss, and provide options for remedial conservation and management.

*Front Ecol Environ* 2005; 3(9): 479–486

We are living in an era of unprecedented and rapid ecological change (Reid *et al.* 2005). Through habitat conversion, over-consumption of resources, and worldwide introductions of pests and pathogens, humans are causing species extinctions at a record rate: the sixth extinction crisis in the billion-year history of eukaryotic

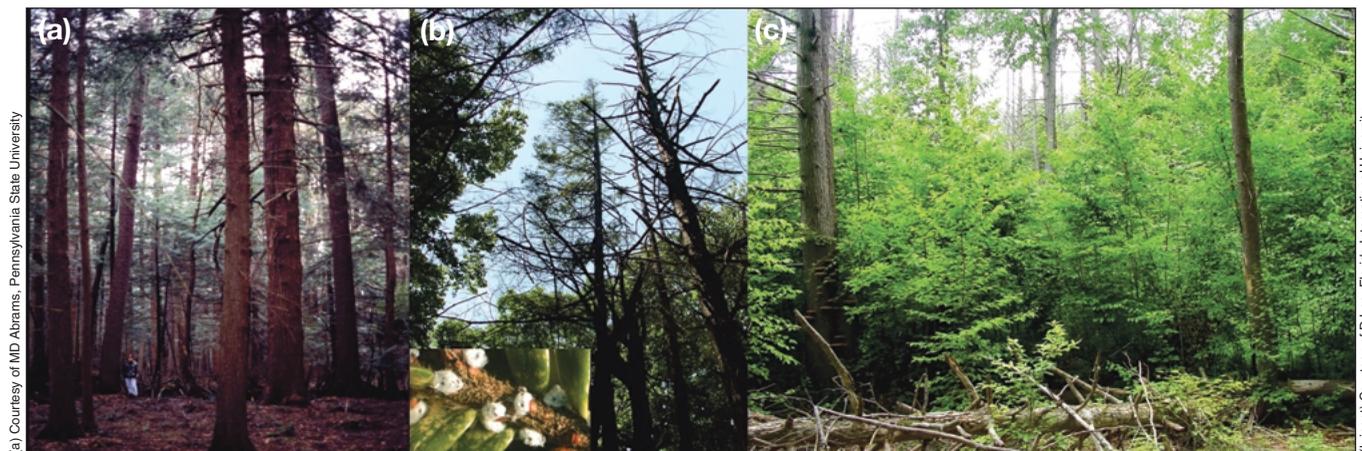
life on Earth (Eldridge 1998). The loss of a common or abundant foundation species (*sensu* Dayton 1972; see Panel 1), which by virtue of its structural or functional attributes creates and defines an entire ecological community or ecosystem, can have dramatic effects on our perception of the landscape and broad consequences for associated biota, ecosystem function, and stability. Foundation species differ from keystone predators (Paine 1966) in that the former usually occupy low trophic levels whereas the latter are usually top predators. They are also distinct from core species (Hanski 1982) in that foundation species are not only locally abundant and regionally common but also create locally stable conditions required by many other species. They also serve to stabilize fundamental ecosystem processes such as productivity and water balance.

Trees are most likely to be foundation species in forested ecosystems, as their architecture and functional and physiological characteristics define forest structure and alter microclimates, while their biomass and chemi-

## In a nutshell:

- In many ecosystems, a single foundation species controls population and community dynamics and modulates ecosystem processes
- The loss of foundation species acutely and chronically impacts fluxes of energy and nutrients, hydrology, food webs, and biodiversity
- Human activities, including logging and the introduction of exotic pests and pathogens, often functionally remove foundation tree species from forests
- Foundation species that are currently being lost from North American forests include eastern hemlock, Port-Orford cedar, and oaks

<sup>1</sup>Harvard University, Harvard Forest, 324 North Main Street, Petersham, MA 01366 \*(aellison@fas.harvard.edu); <sup>2</sup>USDA Forest Service Southern Research Station, Coweeta Hydrologic Lab, Otto, NC, 28763; <sup>3</sup>University of Georgia, Institute of Ecology, Athens, GA 30602; <sup>4</sup>Institute of Ecosystem Studies, Millbrook, NY 12545; <sup>5</sup>Wellesley College, Department of Biological Sciences, Wellesley, MA 02481; <sup>6</sup>College of the Holy Cross, Department of Biology, Worcester, MA 01610; <sup>7</sup>Oregon State University, Department of Botany and Plant Pathology, Corvallis, OR 97331; <sup>8</sup>University of Maryland, Baltimore County, Dept of Geography & Environmental Systems, Baltimore, MD 21250; <sup>9</sup>University of Puerto Rico, Institute for Tropical Ecosystem Studies, San Juan, PR 00931; <sup>10</sup>Virginia Polytechnic Institute and State University, Department of Biology, Blacksburg, VA 24061



**Figure 1.** (a) An old-growth eastern hemlock (*Tsuga canadensis*) stand, (b and inset) a stand declining following 10 years of infestation by the introduced hemlock woolly adelgid (*Adelges tsugae*), and (c) dense regeneration of black birch (*Betula lenta*) saplings on a site formerly dominated by eastern hemlock in southern Connecticut. Nearly all hemlock trees in this 150-hectare forest in southern Connecticut were killed in the mid-1990s by hemlock woolly adelgid.

cal makeup contribute substantially to ecosystem processes. Foundation tree species are declining throughout the world due to a number of factors, including introductions and outbreaks of nonindigenous pests and pathogens, irruptions of native pests, over-harvesting and high-intensity forestry, and deliberate removal of individual species from forests. We use three examples from North America to illustrate consequences for both terrestrial and aquatic habitats of the loss of foundation tree species: the ongoing decline of eastern hemlock (*Tsuga*

*canadensis*) resulting from an introduced insect and preemptive salvage logging; the local extirpation of white-bark pine (*Pinus albicaulis*) caused by interactions among a nonnative pathogen, a native insect, and human alteration of fire regimes; and the functional removal of American chestnut (*Castanea dentata*) by an introduced pathogen. Our examples focus on trees in systems we know best, but they are broadly representative of a wide range of foundation species and illustrative of their role in forests throughout the world (Panel 2).

#### Panel 1. The many definitions of foundation species

Following nomenclatural priority, we adopt Dayton's (1972) terminology and general definition of a foundation species: *a single species that defines much of the structure of a community by creating locally stable conditions for other species, and by modulating and stabilizing fundamental ecosystem processes.*

Subsequent authors, working in different habitats and apparently unaware of historical antecedents, have suggested terms with some or all of the attributes of foundation species, including:

**Core species** (Hanski 1982) are locally abundant and regionally common; associated **satellite species** are sparse and rare. An associated metapopulation model (the **core-satellite hypothesis**) explains relationships between a species' local abundance and its regional distribution.

**Dominant species** (Grime 1984) competitively exclude subordinate species by garnering a disproportionate share of resources and contributing most to productivity.

**Keystone predators** (Paine 1966) preferentially consume dominant competitors and enhance local biodiversity by preventing exclusion of weaker competitors. Holling's (1992) **extended keystone hypothesis** posits that all terrestrial ecosystems are controlled and organized by a small set of **keystone species**.

**Structural species** (Huston 1994) create physical structures of environments, produce variability in physical conditions, provide resources, and create habitat for **interstitial species**.

**Ecosystem engineers** (Jones *et al.* 1994) cause physical state changes in biotic or abiotic materials and modulate availability of resources to other species. Class 5 **autogenic ecosystem engineers** are directly analogous to Dayton's foundation species.

#### ■ The rise and fall of eastern hemlock

Majestic hemlock groves (Figure 1) evoke reverence, affection, and poetry (Frost 1923). Eastern hemlock (*Tsuga canadensis*), one of the most long-lived, shade-tolerant trees in North America, dominates about  $1 \times 10^6$  ha of forest from the southern Appalachians to southern Canada and west to the central Lake states (McWilliams and Schmidt 2000). In the north, hemlock typically occurs in nearly pure stands with species-poor understories. In the south, hemlock grows in mixed stands in narrow riparian strips and moist coves, often with dense understories of rhododendron (*Rhododendron maximum*). In hemlock-dominated stands, the combination of deep shade and acidic, slowly decomposing litter results in a cool, damp microclimate, slow rates of nitrogen cycling, and nutrient-poor soils (Jenkins *et al.* 1999). Canopies of evergreen hemlocks have a higher leaf area index and lower transpiration rates per unit leaf area than canopies of co-occurring deciduous trees (Catovsky *et al.* 2002). Although hemlocks have much greater whole-tree respiration rates in the spring and fall, when deciduous trees are leafless, during the summer hemlocks transpire about 50% of the total water released by deciduous trees (J Hadley unpublished). These characteristics of hemlock, along with its high snow-interception rates, mediate soil

moisture levels, stabilize stream base-flows, and decrease diel variation in stream temperatures. As a result, streams flowing through hemlock forests support unique assemblages of salamanders, fish, and freshwater invertebrates that are intolerant of seasonal drying (Snyder *et al.* 2002). Hemlock stands also shelter deer and other wildlife.

Populations of eastern hemlock have declined precipitously three times since the Pleistocene glaciation: approximately 5500 years ago, coincident with regional climate change and an outbreak of an insect similar to the extant eastern hemlock looper (*Lambdina fiscellaria*; Bhiry and Filion 1996); about 200 years ago, following forest conversion to agriculture, increases in fire, and extensive logging for timber and tannin (McMartin 1992); and from the mid-1980s to the present, due to an introduced insect, the hemlock woolly adelgid (*Adelges tsugae*; Figure 1). This rapidly spreading insect kills trees of all sizes and age-classes within 4–15 years of infestation (Orwig *et al.* 2002). Hemlock has no apparent resistance to the adelgid; it rarely recovers from attack (Orwig *et al.*

2002), and there are currently no effective biological or chemical controls of the adelgid in forested ecosystems. The insect's impact is further exacerbated by pre-emptive salvage logging, in which hemlock, which has modest economic value, is cut in anticipation of future infestation (Orwig *et al.* 2002).

Hemlock could functionally disappear from eastern forests in the next several decades. This species generally does not re-establish following adelgid-induced mortality (Figure 1), but is replaced throughout its range by hardwood species, including birch (*Betula* spp), oaks (*Quercus* spp) and maples (*Acer* spp) (Orwig *et al.* 2002). In the southeastern United States, hemlock is replaced by yellow poplar (*Liriodendron tulipifera*; J Vose *et al.* unpublished) when *Rhododendron* is absent. Decline of hemlock may lead to the local loss of its uniquely associated ants (Ellison *et al.* 2005) and birds (Tingley *et al.* 2002), cause regional homogenization of floral and faunal assemblages (Ellison *et al.* 2005), change soil ecosystem processes (Jenkins *et al.* 1999; Figure 2), and alter hydrological

## Panel 2. Additional examples of foundation species from forests around the world

**Bald cypress (*Taxodium distichum*)** dominates deepwater swamps of southeastern North America (Sharitz and Mitsch 1993). Its presence and density affect the water table and flow of sediment and nutrients, and control structure and composition of associated plant and animal communities (Sharitz and Mitsch 1993). Intensive logging and removal of bald cypress dramatically alter hydrology and nutrient cycling, reduce primary productivity, and increase sedimentation (Sun *et al.* 2001).

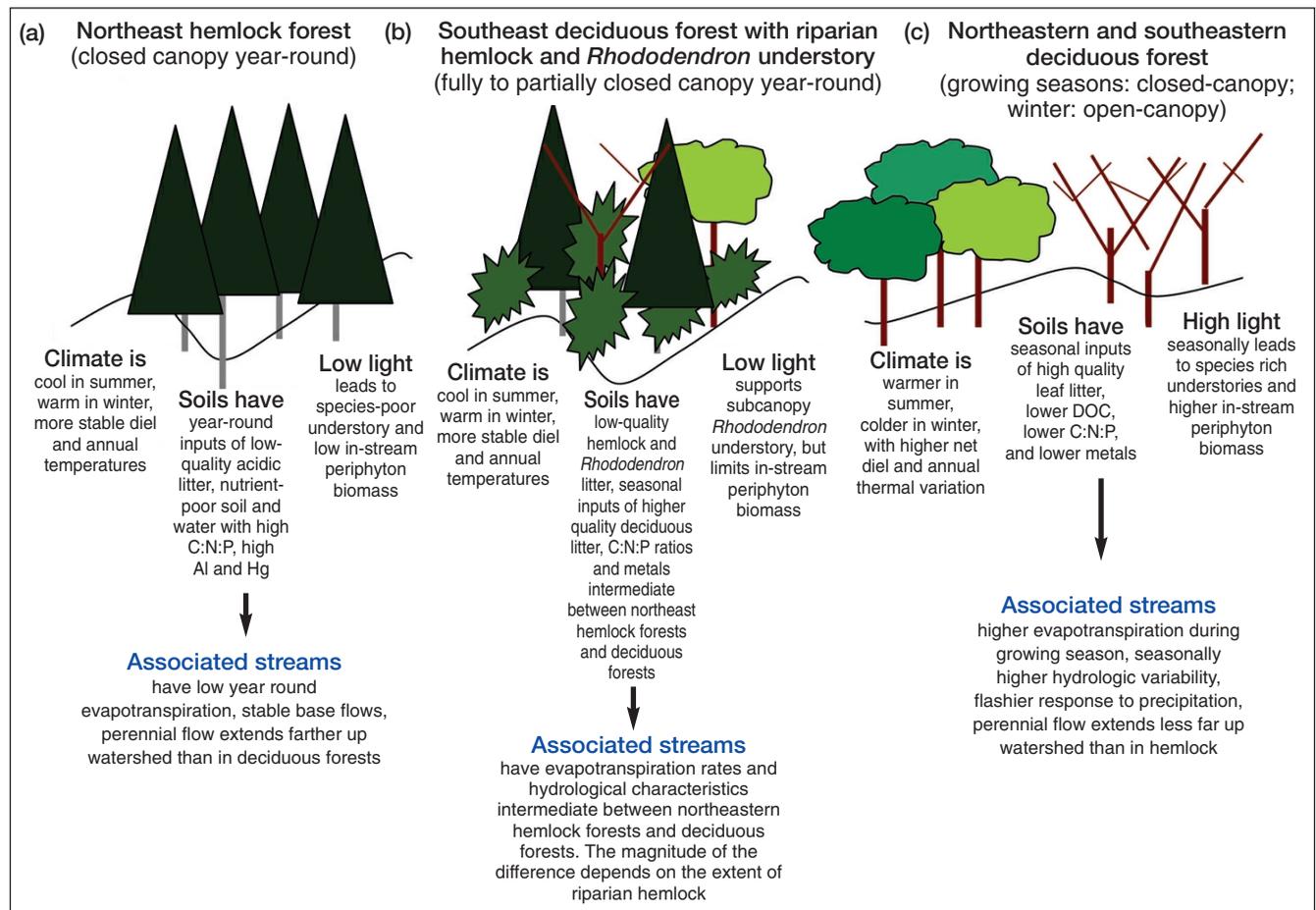
**Douglas fir (*Pseudotsuga menziesii*)** dominates young and old-growth forests at low and mid-elevations west of the Cascade Range and at higher elevations in the interior of the Pacific Northwest of North America. Live trees, snags, and fallen logs provide unique habitats for wildlife, including endangered and rare species such as the spotted owl (*Strix occidentalis*). The evergreen foliage controls light levels, microclimate, and gas exchange from the forest floor to the canopy (Parker *et al.* 2004). Logging alters C and N cycling, wildlife abundance, and plant successional dynamics (Halpern *et al.* 2005). Unlike the other foundation species discussed in this paper, Douglas fir is not currently threatened, as it is strongly favored by current forest management practices. However, many old-growth stands in the Pacific Northwest have been lost to logging over the past decades. High-intensity fires resulting from long-term fire suppression practices, introduced pests or changes in the ecological dynamics of native pests, or changes in forest management that pose mortality risks to old-growth Douglas fir stands could have important ecological impacts in the future.

**Fraser fir (*Abies fraseri*)** is a locally abundant endemic species that occurs in six discrete, high-altitude areas in the southern Appalachians (Hollingsworth and Hain 1991). There, Fraser fir defines high-elevation spruce-fir communities, with tightly associated animal and plant species. Fraser fir has been declining since the balsam woolly adelgid (*Adelges piceae*) was introduced in the 1930s (Hollingsworth and Hain 1991). Its loss increases the susceptibility of its co-dominant, red spruce (*Picea rubens*), to windthrow, and both species are suffering additional effects of climate warming and air pollution (Hamburg and Cogbill 1988).

**Jarrah** is a unique Australian forest type comprised mainly of *Eucalyptus marginata*. This species experiences mass collapse and sudden death following waterlogging, which increases infection of jarrah roots by zoospores of *Phytophthora cinnamomi* (Davison and Tay 1987), a soil-born pathogenic fungus introduced into Western Australia in 1921 that affects ~2000 of the 9000 extant plant species there (Wills 1992). Following invasion by *P. cinnamomi*, richness of woody perennial species in the jarrah understory declines significantly, whereas richness of monocots, herbaceous perennials, annuals, and geophytes are largely unaffected (Wills and Keighery 1994).

**Port-Orford cedar (*Chamaecyparis lawsoniana*)** is endemic to southwestern Oregon and northern California, grows on ultramafic and non-ultramafic soils, in riparian and upland sites, and occurs in the most diverse plant associations in the region. On ultramafic soils, Port-Orford cedar is often the only riparian tree species. It is a foundation species for both terrestrial and aquatic habitats: it recycles calcium to surface soils, provides shade, and stabilizes soil and stream banks (Hansen *et al.* 2000). Its highly rot-resistant wood provides habitat heterogeneity and alters hydrology. The non-native, water-dispersed, and generally lethal root pathogen *Phytophthora lateralis* has spread into virtually all natural forest stands from nursery plants infected in the early 1920s (Hansen *et al.* 2000).

**Mangroves (*Rhizophora* spp)** form dense, often monospecific stands in estuarine and coastal forests throughout the tropics; these forests have some of the highest reported net primary productivity of any ecosystem on the planet (Ellison and Farnsworth 2001). Removal of mangroves leads to rapid build-up of acid sulfides in the soil, increased shoreline erosion and sedimentation onto offshore coral reefs, and collapse of intertidal food webs and inshore fisheries (Ellison and Farnsworth 2001). More than 2% of mangrove forests are lost annually, as forests are cut for fuel, coastal development, and wood fiber used to produce rayon.



**Figure 2.** Conceptual model of shifts in terrestrial and aquatic ecosystem processes following loss of eastern hemlock from (a) northern and (b) southern forests, and (c) conversion to hardwood-dominated stands.

regimes (Figure 2).

The effects of adelgid-induced hemlock mortality on stream ecosystems will be extensive. For example, hemlock streams support significantly more taxa of aquatic invertebrates than paired mixed-hardwood stands, and nearly 10% of the taxa are strongly associated with the presence of hemlock (Snyder *et al.* 2002). Hemlock death may result in a rapid pulse of large amounts of wood that decays more slowly than coarse woody debris from hardwoods. Large hemlock logs in streams retain sediment and organic matter and create novel habitat types. In general, large hemlock logs are abundant in streams draining forests where hemlock is an important riparian species. Although logs from adelgid-killed hemlocks may persist in streams for decades to centuries, eventually the loss of hemlock will reduce in-stream wood, leading to a decline in sediment retention and productivity.

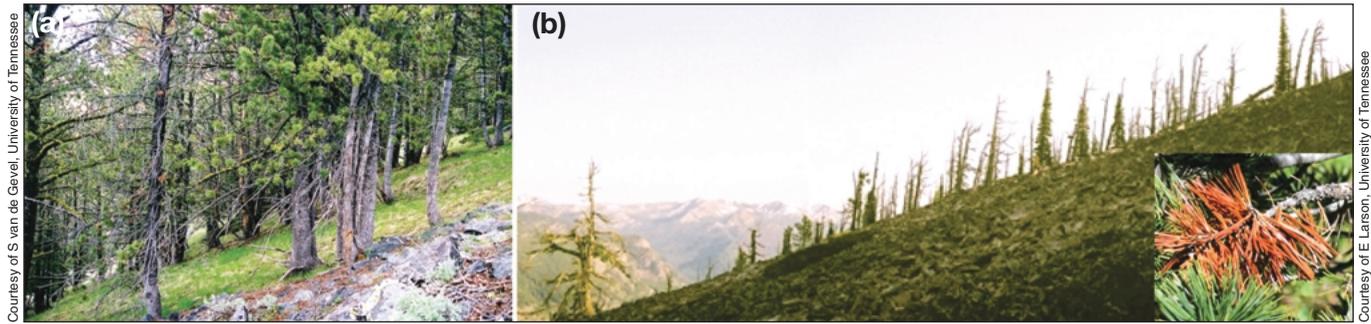
Logging of hemlock initiates more rapid and greater ecosystem changes than the adelgid because of the abrupt vegetation and environmental changes, removal of wood, soil scarification, and the presence of extensive slash left by logging operations (Kizlinski *et al.* 2002). Nitrogen availability and nitrification rates are significantly higher in cut forests than in adelgid-damaged ones, increasing the threat of nutrient losses and changing food availabil-

ity in nearby aquatic systems (Kizlinski *et al.* 2002; C Swan unpublished).

### ■ The shifting mosaic of whitebark pine

Whitebark pine forms extensive contiguous stands in high elevation forests of the Rocky Mountains of Wyoming, Montana, Idaho, and Alberta, and smaller disjunct populations in eastern and southwestern Oregon, California, and Nevada. This dominant late-successional species (Figure 3) grows as dense krummholz (stunted trees growing at or just below treeline at higher elevations forming a very low, cushiony mat) at its upper elevational limit, whereas at lower elevations and less extreme sites, it grows in association with other conifers and its dominance is maintained by periodic fire (Arno 2001). Whitebark pine has occupied its current range for approximately 8000 years. In western North America, extensive forests of whitebark pine, spruce (*Picea* spp) and poplar (*Populus* spp) developed after glacial retreat. As warming continued from 8000–4000 years ago, whitebark pine became restricted to high elevation sites (MacDonald *et al.* 1989).

Whitebark pine cover at upper elevations retards snowmelt and modulates runoff and stream flows (Farnes



**Figure 3.** High-elevation stands of whitebark pine (*Pinus albicaulis*). This species is transformed from (a) healthy stands to (b) dead stands through the interaction of fire suppression, the introduced pathogen *Cronartium ribicola* that causes white pine blister rust (inset), and the native bark beetle *Dendroctonus ponderosae*.

1990). At lower elevations, post-fire mid-successional whitebark pine stands provide shade and cool soil, facilitating establishment of diverse plant communities and associated cryptogams, invertebrates, and microbes, while its seeds serve as a major seasonal food source for many species of mammals and birds (Mattson *et al.* 2001).

Throughout its range, whitebark pine is declining due to the combined effects of an introduced pathogen, *Cronartium ribicola*, a native bark beetle, *Dendroctonus ponderosae*, and fire-suppression policies (Kendall and Keane 2001). The pathogen *C. ribicola*, which causes white pine blister rust, was introduced from Eurasia into western North America in 1910 on imported white pine (*Pinus strobus*) seedlings planted near Vancouver, British Columbia (MacDonald and Hoff 2001). After its introduction, *C. ribicola* spread in a series of episodic pulses throughout western North America and by the late 1930s was established throughout the west, where it devastated pine stands (MacDonald and Hoff 2001). Fire exclusion allowed further replacement of whitebark pine by more shade-tolerant species and at lower elevations promoted the growth of dense stands of lodgepole pine (*Pinus contorta*). In turn, lodgepole pine supports high populations of *D. ponderosae* beetles that disperse into adjacent whitebark pine stands when beetle populations irrupt. In a positive feedback loop, drought- and disease-stressed whitebark pines are further susceptible to beetle attack.

Loss of whitebark pine alters watershed hydrology immediately as flashiness of streams increases, and changes the dynamics of wildlife populations and succession over longer time scales. Cone crops of whitebark pine have declined due to interactions between white pine blister rust, fire exclusion, and bark beetles. Carrying capacities of species dependent on whitebark pine seeds have also declined with the cone supply of this irreplaceable species (Mattson *et al.* 2001).

### ■ The shrub that was a tree: American chestnut

American chestnut was once a foundation species in eastern North American forests (Figure 4). Chestnut and oak were co-dominants in the southern Appalachians for nearly 4000 years and reached the northeast from 2500–1500 years ago (Paillet 2002). Chestnut provided

important resources for wildlife and humans, and locally exerted a strong influence on ecosystem structure and function (Paillet 2002). Chestnut blight, caused by the canker pathogen *Cryphonectria parasitica*, was introduced from Asia in the late 19th century. The blight was first noted in New York in 1904, spread rapidly ( $\sim 37 \text{ km yr}^{-1}$ ) across the range of chestnut, and within 50 years had converted this stately tree to a rarely flowering understory shrub across approximately 3.6 million ha (Anagnostakis 1987).

Chestnut has a rapid growth rate and sprouting ability, wood with an extremely high tannin content, and leaves with a relatively low C:N ratio. Therefore, fundamental forest ecosystem processes, including decomposition, nutrient cycling, and productivity, probably changed substantially following chestnut's replacement by other species. Decomposition of chestnut wood is much slower than other co-occurring hardwoods and its high tannin concentrations could restrict the mobilization of nutrients in soils. Additionally, chestnut's fast growth rate (Jacobs and Severeid 2004) might have resulted in rapid sequestration of carbon and nutrients.

Chestnut dominated a wide range of environments and its decline is thought to have altered both terrestrial and aquatic processes. There is evidence to suggest that the abundance of chestnut along riparian corridors of the southern Appalachians was due to production of allelochemicals that prevented establishment of what we now consider "typical" riparian shrub and tree species, including eastern hemlock and rhododendron (Vandermaast *et al.* 2002). Ironically, therefore, the loss of one foundation species – American chestnut – may have facilitated the establishment of another – eastern hemlock – which in turn is now threatened.

In most forested headwater streams, autumn leaf inputs serve as the predominant energy base for aquatic ecosystems. Where chestnut was replaced by oak, relatively rapidly decaying chestnut leaves with high nutritional quality for aquatic macroinvertebrates were replaced by more slowly decaying oak leaves with lower nutritional quality (Smock and MacGregor 1988). As a consequence, leaf-processing and consumption rates would have declined, decreasing growth rates and adult body mass in macroinvertebrate shredder communities. Many



**Figure 4.** American chestnut. (a) Chestnut timber, Great Smoky Mountains of western North Carolina (circa 1910), a foundation species that was transformed in the mid-20th century to an understory shrub (b; small shrub in center) by the introduced pathogen *Cryphonectria parasitica*, which causes chestnut blight (c; chestnut in the Blue Ridge Plateau killed by the blight, circa 1946).

stream macroinvertebrates have life cycles closely synchronized to the dynamics of detrital decay, and this change in detrital quality undoubtedly affected the macroinvertebrate assemblage, although there are no data to support this supposition. Furthermore, slowly decomposing chestnut wood persists for decades in stream channels, altering channel structure and providing habitat for fish and invertebrates. For example, in an Appalachian headwater stream sampled in the late 1990s, Wallace *et al.* (2001) found that 24% of the large (> 10 cm diameter) woody debris still consisted of American chestnut that had died over 50 years earlier.

#### ■ Functional loss versus total loss

As foundation species decline, their control of ecosystem structure and processes may wane long before the species itself disappears completely. For example, as hemlock stands decline, tree death opens the canopy, drastically altering the understory microclimate and causing the loss of unique habitat. Similarly, shrubby chestnut contributes little to leaf area, wood production, or nuts, so that while it is still present in many forests, the American chestnut tree is functionally extinct.

The potential effects on ecosystem function and community composition caused by the loss of foundation species can be either exacerbated or ameliorated by patterns of decline in time and space. For example, logging and diseases such as chestnut blight or white pine blister rust have resulted in rapid loss of foundation species over broad areas. This contrasts with the slow death of individuals over decades or partial loss of a species through removal or death of only one age or size class, as in beech bark disease (Griffin *et al.* 2003). Similarly, whether the spatial pattern of individual deaths occurs in mosaic fashion or as an advancing wave influences the timing and magnitude of loss of a foundation species (Holdenreider *et al.* 2004), and perhaps the ultimate outcome. Forest fragmentation often occurs in mosaic patterns across the

landscape (eg Halpern *et al.* 2005), whereas epidemiological models of plant pathogens or species invasions indicate that changes in forest structure occur in wave-like patterns (Johnson *et al.* 2004). Such studies suggest that where complex spatial and temporal patterns of species loss occur, the effects at any particular location are unlikely to be a linear function of area altered or changes in species' dominance. Indeed, threshold responses, including transitions to new types of ecosystems, should be expected where key dependent variables, such as mast production, herbivore or detritivore abundance, or adult survival, result from a complex web of indirect relationships (eg Ebenman and Jonsson in press).

#### ■ Responding to the loss of foundation species

Because foundation tree species tend to be common, abundant, and large, our responses to their loss often come late and are conducted at inappropriate scales. For example, the ongoing attempt to recreate the American chestnut by backcrossing the few remaining fertile individuals with resistant species from Europe and Asia holds out the promise of specimen trees in suburban lawns but is unlikely to reforest four million hectares with hybrid chestnuts. Similarly, chemical control of the hemlock woolly adelgid requires injecting trees annually and can only target isolated single trees or small groves. Biological control of the adelgid using non-native, generalist, predaceous beetles is being explored with uneven regard for the long history of unexpected impacts that can accompany the importation of exotic insects (eg Howarth 1991; Boettner *et al.* 2000). Although several million beetles are released every year, there have been no systematic attempts to determine whether self-sustaining populations have become established or how effective they are at actually controlling the adelgid in the field. Overall, we would be much more likely to conserve foundation species and the systems they create if we set aside very large reserves of intact forests and adopted techniques that preserve ecosys-

tem integrity in managed forest stands (Foster *et al.* 2005).

## ■ Conclusions

There is no sign that the currently increasing rates of resource extraction, climate change, or global movement of pests and pathogens will slow any time soon. Foundation species have disappeared before and they will continue to disappear. Despite nearly half a century of research on foundation species (Panel 1), our understanding of the consequences of their loss is based on a small number of case studies, as we usually identify foundation species only after they have declined dramatically. Our examples illustrate how foundation tree species can control both terrestrial forest processes and the dynamics of aquatic systems within their watersheds. However, detailed information on the importance of foundation species for key ecosystem processes are scarce. Likewise, the impact on water quality from the loss of foundation species could be substantial and merits further study.

Long-term monitoring can reveal how losses of foundation species alter rates and trajectories of succession, leading in some cases to novel forest types (such as black birch forests in New England) with unexpected dynamics. However, monitoring is not enough. Ecologists have long appreciated the complex nature of interactions among species, and we encourage direct, experimental approaches that use current losses of foundation species as an opportunity to determine how the removal of a single species can have immediate and profound effects on other species and ecosystem processes.

The dynamics of communities and ecosystems shaped by foundation species are dominated by a small number of strong interactions (Figure 2). Such systems are relatively fragile and susceptible to switching between alternative stable states following even small perturbations (Dudgeon and Petraitis 2005). At the same time as many forested systems are losing their foundation species, they are simultaneously and synergistically threatened by climate change, atmospheric deposition, drought, and invasion of exotic species, all of which may increase their overall fragility. Temperate-zone forests, such as those we have highlighted here, have few tree species relative to the species-rich tropical forests that garner much attention from ecologists and conservation biologists. When there are only one or two foundation species in a forest, there is little functional redundancy in many important respects, and their loss is likely to lead to rapid, possibly irreversible, shifts in biological diversity and system-wide changes in structure and function (Ebenman and Jonsson in press). Regrettably, the lack of detailed knowledge of the natural history of most species in most forests, and the abandonment of courses and curricula in natural history (Dayton 2003), will leave us unaware of the collapse of the intricate webs of interactions and processes that are lost when foundation species disappear.

These species provide fundamental structure to a system, and thus are by definition irreplaceable. For example, with-

out hemlock, hemlock forests cease to exist, and no other native conifer possesses the same suite of structural and functional characteristics that simultaneously define its position in the system and control system-wide dynamics and processes. Many recognized foundation tree species (Panel 2) that have been identified are conifers, but it remains an open question whether conifers are disproportionately represented among foundation species. We need new research tools, models, and metrics that will allow us to identify foundation species a priori and to anticipate the cascade of immediate, short- and long-term changes in ecosystem structure and function that follow their loss. Community viability analysis (Ebenman and Jonsson in press) may provide some of these tools, but its utility awaits empirical evaluation. Ongoing declines of many foundation species (Panel 2) provide timely, though unfortunate, opportunities to develop such tools and models.

## ■ Acknowledgements

We thank A Barker-Plotkin, P Dayton, E Farnsworth, S Jefts, J Jones, J Malloway, B Mathewson, R McDonald, T Spies, and F Swanson for useful discussion and constructive comments on the manuscript. This work was supported by the Harvard Forest, NSF grants DEB 00–80592, DEB 02–18001, DEB 02–18039, DEB 02–36154, and DEB 02–36897, and the US Forest Service, and is a cross-site contribution of the Andrews, Baltimore, Coweeta, Harvard Forest, Hubbard Brook, and Luquillo Long-Term Ecological Research Programs.

## ■ References

- Anagnostakis SA. 1987. Chestnut blight: the classical problem of an introduced pathogen. *Mycologia* **79**: 23–37.
- Arno SF. 2001. Community types and natural disturbance processes. In: Tomback DF, Arno SF, and Keane RE (Eds). *Whitebark pine communities, ecology and restoration*. Washington, DC: Island Press.
- Bhiry N and Filion L. 1996. Mid-holocene hemlock decline in eastern North America linked with phytophagous insect activity. *Quaternary Res* **45**: 312–20.
- Boettner GH, Elkinton JS, and Boettner CJ. 2000. Effects of a biological control introduction on three nontarget native species of Saturniid moths. *Conserv Biol* **14**: 1789–1806.
- Catovsky S, Holbrook NM, and Bazzaz FA. 2002. Coupling whole-tree transpiration and canopy photosynthesis in coniferous and broad-leaved tree species. *Can J For Res* **32**: 295–309.
- Davison EM and Tay FCS. 1987. The effect of waterlogging on infection of *Eucalyptus marginata* seedlings by *Phytophthora cinnamomi*. *New Phytol* **105**: 585–94.
- Dayton PK. 1972. Toward an understanding of community resilience and the potential effects of enrichments to the benthos at McMurdo Sound, Antarctica. In: Parker BC (Ed). *Proceedings of the colloquium on conservation problems in Antarctica*. Lawrence, KS: Allen Press.
- Dayton PK. 2003. The importance of the natural sciences to conservation. *Am Nat* **162**: 1–13.
- Dudgeon S and Petraitis PS. 2005. First year demography of the foundation species, *Ascophyllum nodosum*, and its community implications. *Oikos* **109**: 405–15.
- Ebenman B and Jonsson T. Using community viability analysis to identify fragile systems and keystone species. *Trends Ecol Evol*

- doi:10.1016/j.tree.2005.06.011. In press.
- Eldridge N. 1998. Life in the balance: humanity and the biodiversity crisis. Princeton, NJ: Princeton University Press.
- Ellison AM and Farnsworth EJ. 2001. Mangrove communities. In: Bertness MD, Gaines SD, and Hay ME (Eds). Marine community ecology. Sunderland, MA: Sinauer Associates.
- Ellison AM, Chen J, Díaz D, *et al.* 2005. Changes in ant community structure and composition associated with hemlock decline in New England. In: Onken B and Reardon R (Eds). Proceedings of the 3rd symposium on hemlock woolly adelgid in the eastern United States. Morgantown, WV: USDA Forest Service.
- Farnes PE. 1990. SNOTEL and snow course data describing the hydrology of whitebark pine ecosystems. In: Schmidt WC and McDonald KJ (Eds). Proceedings of a symposium on whitebark pine ecosystems: ecology and management of a high mountain resource. Ogden, UT: USDA Forest Service Intermountain Research Station.
- Foster DR, Kittredge D, Donahue B, *et al.* 2005. Wildlands and woodlands: a vision for the forests of Massachusetts. Petersham, MA: Harvard Forest.
- Frost R. 1923. Dust of snow. In: New Hampshire: a poem with notes and grace notes. New York, NY: Henry Holt and Co.
- Griffin JM, Lovett GM, Arthur MA, *et al.* 2003. The distribution and severity of beech bark disease in the Catskill Mountains, NY. *Can J For Res* 33: 1754–60.
- Grime JP. 1984. Dominant and subordinate components of plant communities: implications for succession, stability and diversity. In: Gray AJ and Crawley MJ (Eds). Colonization, succession and stability. Oxford, UK: Blackwell.
- Halpern CB, McKenzie D, Evans SA, *et al.* 2005. Initial responses for forest understories to varying levels and patterns of green-tree retention. *Ecol Appl* 15: 175–95.
- Hamburg SP and Cogbill CV. 1988. Historical decline of red spruce populations and climatic warming. *Nature* 331: 428–31.
- Hansen EM, Goheen DJ, Jules ES, *et al.* 2000. Managing Port-Orford cedar and the introduced pathogen *Phytophthora lateralis*. *Plant Dis* 84: 4–10.
- Hanski I. 1982. Dynamics of regional distribution: the core and satellite species hypothesis. *Oikos* 38: 210–21.
- Holdenreider O, Pautasso M, Weisberg PJ, *et al.* 2004. Tree diseases and landscape processes: the challenge of landscape pathology. *Trends Ecol Evol* 19: 446–52.
- Holling CS. 1992. Cross-scale morphology, geometry, and dynamics of ecosystems. *Ecol Monogr* 62: 447–502.
- Hollingsworth RG and Hain FP. 1991. Balsam woolly adelgid (Homoptera: Adelgidae) and spruce-fir decline in the southern Appalachians: assessing pest relevance in a damaged ecosystem. *Florida Entomol* 74: 179–87.
- Howarth FG. 1991. Environmental impacts of classical biological control. *Ann Rev Entomol* 36: 485–509.
- Huston MA. 1994. Biological diversity: the coexistence of species on changing landscapes. Cambridge, UK: Cambridge University Press.
- Jacobs DF and Severeid LR. 2004. Dominance of interplanted American chestnut (*Castanea dentata*) in southwestern Wisconsin, USA. *Forest Ecol Manag* 191: 111–20.
- Jenkins J, Aber JD, and Canham CD. 1999. Hemlock woolly adelgid impacts on community structure and N cycling rates in eastern hemlock forests. *Can J For Res* 29: 630–45.
- Johnson DM, Bjørnstad ON, and Liebhold AM. 2004. Landscape geometry and travelling waves in the larch budmoth. *Ecol Lett* 7: 967–74.
- Jones CG, Lawton JH, and Shachak M. 1994. Organisms as ecosystem engineers. *Oikos* 69: 373–86.
- Kendall KC and Keane RE. 2001. Whitebark pine decline: infection, mortality, and population trends. In: Tomback DF, Arno SF, and Keane RE (Eds). Whitebark pine communities, ecology and restoration. Washington, DC: Island Press.
- Kizilinski ML, Orwig DA, Cobb RC, *et al.* 2002. Direct and indirect ecosystem consequences of an invasive pest on forests dominated by eastern hemlock. *J Biogeogr* 29: 1489–503.
- MacDonald GI and Hoff RJ. 2001. Blister rust: an introduced plague. In: Tomback DF, Arno SF, and Keane RE (Eds). Whitebark pine communities, ecology and restoration. Washington, DC: Island Press.
- MacDonald GM, Cwynar LC, and Whitlock C. 1989. Late quaternary dynamics of pines: northern North America. In: Richardson DM (Ed). Ecology and biogeography of *Pinus*. New York, NY: Cambridge University Press.
- Mattson DJ, Kendall KC, and Reinhart DP. 2001. Whitebark pine, grizzly bears, and red squirrels. In: Tomback DF, Arno SF, and Keane RE (Eds). Whitebark pine communities, ecology and restoration. Washington, DC: Island Press.
- McMartin B. 1992. Hides, hemlocks, and Adirondack history. Utica, NY: North Country Books.
- McWilliams WH and Schmidt TL. 2000. Composition, structure, and sustainability of hemlock ecosystems in eastern North America. In: McManus KA, Shields KS, and Souto DR (Eds). Proceedings: symposium on sustainable management of hemlock ecosystems in eastern North America, June 22–24, 1999. Durham, NH: USDA Forest Service.
- Orwig DA, Foster DR, and Mausel DL. 2002. Landscape patterns of hemlock decline in New England due to the introduced hemlock woolly adelgid. *J Biogeogr* 29: 1475–87.
- Paillet F. 2002. Chestnut: history and ecology of a transformed species. *J Biogeogr* 29: 1517–30.
- Paine RT. 1966. Food web complexity and species diversity. *Am Nat* 100: 65–75.
- Parker GG, Harmon MA, and Lefsky JQ. 2004. Three-dimensional structure of an old-growth *Pseudotsuga tsuga* canopy and its implications for radiation balance, microclimate, and gas exchange. *Ecosystems* 7: 440–53.
- Reid WV, Mooney HA, Cropper A, *et al.* 2005. Millennium ecosystem assessment synthesis report. Washington, DC: Millennium Assessment and World Resources Institute.
- Sharitz R and Mitsch WJ. 1993. Southern floodplain forests. In: Echternacht AC (Ed). Biodiversity of the southeastern United States: lowland terrestrial communities. New York, NY: John Wiley and Sons.
- Smock LA and MacGregor CM. 1988. Impact of the American chestnut blight on aquatic shredding macroinvertebrates. *J N Am Benthol Soc* 7: 212–21.
- Snyder CD, Young JA, Smith D, *et al.* 2002. Influence of eastern hemlock (*Tsuga canadensis*) forests on aquatic invertebrate assemblages in headwater streams. *Can J Fish Aquat Sci* 59: 262–75.
- Sun G, McNulty SG, Shepard JP, *et al.* 2001. Effects of timber management on the hydrology of wetland forests in the southern United States. *Forest Ecol Manag* 143: 227–36.
- Tingley MW, Orwig DA, Field R, *et al.* 2002. Avian response to removal of a forest dominant: consequences of hemlock woolly adelgid infestations. *J Biogeogr* 29: 1505–16.
- Vandermaast DB, Van Lear DH, and Clinton BD. 2002. American chestnut as an allelopath in the southern Appalachians. *Forest Ecol Manag* 165: 173–81.
- Wallace JB, Webster JR, Eggert SL, *et al.* 2001. Large woody debris in a headwater stream: long-term legacies of forest disturbance. *Int Rev Hydrobiol* 86: 501–13.
- Wills RT. 1992. The ecological impact of *Phytophthora cinnamomi* in the Stirling Range National Park, Western Australia. *Aust J Ecol* 17: 145–59.
- Wills RT and Keighery GJ. 1994. Ecological impact of plant disease on plant communities. *J Roy Soc W Aust* 77: 127–31.