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Experiments are revealing a foundation species: a case-study of eastern hemlock (*Tsuga canadensis*)

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Foundation species are species that create and define particular ecosystems; control in large measure the distribution and abundance of associated flora and fauna; and modulate core ecosystem processes, such as energy flux and biogeochemical cycles. However, whether a particular species plays a foundational role in a system is not simply asserted. Rather, it is a hypothesis to be tested, and such tests are best done with large-scale, long-term manipulative experiments. The utility of such experiments is illustrated through a review of the Harvard Forest Hemlock Removal Experiment (HF-HeRE), a multi-decadal, multi-hectare experiment designed to test the foundational role of eastern hemlock, *Tsuga canadensis*, in eastern North American forests. Experimental removal of *T. canadensis* has revealed that after 10 years, this species has pronounced, long-term effects on associated flora and fauna, but shorter-term effects on energy flux and nutrient cycles. We hypothesize that on century-long scales, slower changes in soil microbial associates will further alter ecosystem processes in *T. canadensis* stands. HF-HeRE may indeed continue for > 100 years, but at such time scales, episodic disturbances and changes in regional climate and land cover can be expected to interact in novel ways with these forests and their foundation species.

Introduction

A decade ago, my colleagues and I introduced the concept of a *foundation species* (sensu Dayton [1]) to terrestrial ecologists [2]. At the time, we were focused on the potential for certain tree species to act as foundation species: species that create and define particular ecosystems; control in large measure the distribution and abundance of associated flora and fauna; and modulate core ecosystem processes, including energy flux and biogeochemical cycles [2]. We asserted that the possession of all three of these characteristics distinguish foundation species from other “important” species, such as keystone predators, core species, dominant species, cornerstone species, and ecosystem engineers ([2]; and see below). Although we identified a number of different tree species that we hypothesized were good candidates for foundation species, at the time, many of the participants in the workshop that contributed to [2] were focused on a particular species: *Tsuga canadensis* (L.) Carr., for which decades of observational data (summarized in [3]) had suggested that it possesses the three characteristics associated with a foundation tree species.

First, *T. canadensis* is widespread and abundant. Its range in eastern North America spans more than 10,000 km² from Georgia north into southern Canada and west into Michigan and Wisconsin (Fig. 1). In the cove forests in the southern Appalachian Mountains, in the mixed conifer-hardwood forests of New England, and along riparian corridors throughout its entire range, *T. canadensis* can comprise > 50% of the total basal area in a given stand [4, 5]. Second, it has unique assemblages of associated fauna: particular birds, arthropods, and salamanders live in the *T. canadensis* understory or among its evergreen branches [6–12]. Specialist communities of aquatic invertebrates and fish inhabit streams that flow through *T. canadensis* stands [13, 14].

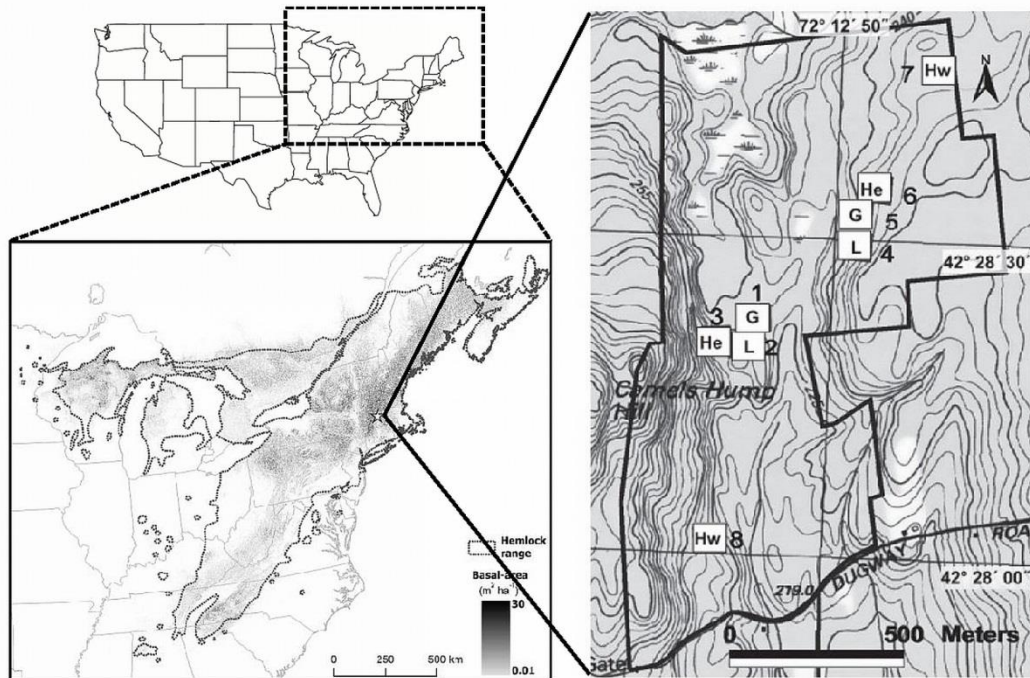


Figure 1 - Distribution (grey shading indicating basal area in m^2/ha) of *Tsuga canadensis* in northeastern North America; location of the Harvard Forest (star in regional map at lower left); and layout of the Harvard Forest Hemlock Removal Experiment. In the right-hand panel, the treatments applied to each 0.81-ha plot are abbreviated: He – Unmanipulated hemlock control; Hw – Unmanipulated hardwood control; G – bark and cambium of all hemlock seedlings, saplings, and trees girdled with chainsaws and knives; L – all merchantable hemlock (≥ 20 cm diameter at breast height [DBH]) and some merchantable hardwoods and white pines (*Pinus strobus*) cut and removed from the site.

Finally, ecosystem dynamics in *T. canadensis* stands differ from surrounding stands of hardwoods or other conifers. The dense canopy of mature *T. canadensis* allows little light to penetrate to the forest floor and the soils beneath this tree are quite cool [15]. The evergreen canopy photosynthesizes whenever air temperatures are above freezing, but photosynthetic rates are slow, water-use efficiency is high, and peak carbon fixation by *T. canadensis* occurs in spring and fall, not in the summer when co-occurring broadleaved, deciduous trees are in full leaf [16]. Because the needles of *T. canadensis* are slower to decompose than all of the other regionally co-occurring trees [17], organic matter accumulates unusually rapidly beneath *T. canadensis* canopies [18] but the soils are acidic and nutrient-poor [19]. Overall, both carbon flux [16, 20–

23] and nutrient cycling [19, 24–26] are much slower in *T. canadensis* stands than in stands dominated either by hardwoods or other conifers.

All of these characteristics fit our notion of how a foundation species should differ from other co-occurring species, but I emphasize that the idea that *T. canadensis* is a foundation species was presented in 2005 as an hypothesis to be tested [2; see also 27–29], not as a foregone conclusion. In this Outlook article, I illustrate the importance of using large-scale field experiments to provide a critical test of this hypothesis.

A natural experiment

In the central and southeastern portion of its range – from southern Vermont, New Hampshire, and Maine south to Georgia – *T. canadensis* is dying from infestations by a nonnative insect, the hemlock woolly adelgid (*Adelges tsugae* Annand). This insect was introduced into the United States from Japan in the early 1950s [30]. Since its initial introduction near Richmond, Virginia, the hemlock woolly adelgid has spread primarily northeast and southwest, but it crossed over to the western side of the Appalachian Mountains sometime in the late 1990s or early 2000s [31–33]. *Tsuga canadensis* has little, if any, resistance to the hemlock woolly adelgid [34] and rarely recovers from chronic infestations [35, 36]. In many infested stands, > 90% of *T. canadensis* dies within 10 years of the arrival of the adelgid [37–39].

Detailed longitudinal studies of *T. canadensis* decline have been underway in southern New England since the adelgid first colonized the region in the 1980s. An expectation of the imminent, rapid death of *T. canadensis* [40] and the subsequent transformation of the forested landscape into early successional habitat, as the adelgid swept through and living trees were preemptive salvaged by landowners intent on extracting economic value from their forests [37, 41,

42], led to the establishment of a network of permanent monitoring plots in Connecticut and Massachusetts in the 1990s [36, 37, 43]. Two decades later, data from this permanent plot network have shown that in Connecticut, where *T. canadensis* is distributed patchily in relatively small stands, tree mortality has been somewhat slower than initially forecast and salvage logging has been less extensive than feared [36]. Faunal change in these small declining stands has been pronounced (e.g. [6, 7]) but carbon storage – one measure of ecosystem function – has proven to be resilient to conversion of *T. canadensis*-dominated stands to early successional hardwoods (*Betula lenta* L., *Acer rubrum* L.). Both models [44] and observations [45] suggest that the distribution, but not the magnitude, of carbon storage is changed across the landscape as *T. canadensis* declines and disappears.

As the adelgid continues to move north, however, it has arrived in a region where *T. canadensis* is more abundant, and dispersal between stands is easier [32, 33]. Climate, especially winter minimum temperature, remains the primary environmental factor limiting the northward spread (Fig. 2; see also [31, 45], overwinter survivorship, and long-term persistence of the hemlock woolly adelgid [36, 47–51].

Although the most recent winter (2013–2014) was unusually cold relative to the last 30 years, the minimum temperature at Harvard Forest, in north-central Massachusetts still did not drop below -20°C ; the last time the temperature at Harvard Forest fell below -25°C was on a single day in January 2011, and before that on three successive January nights in 2004 [52] (Fig. 2). The expectation is that *T. canadensis* will continue to decline relatively rapidly throughout the region, except in colder, high elevation sites, such as in the Adirondack Mountains of New York [36].

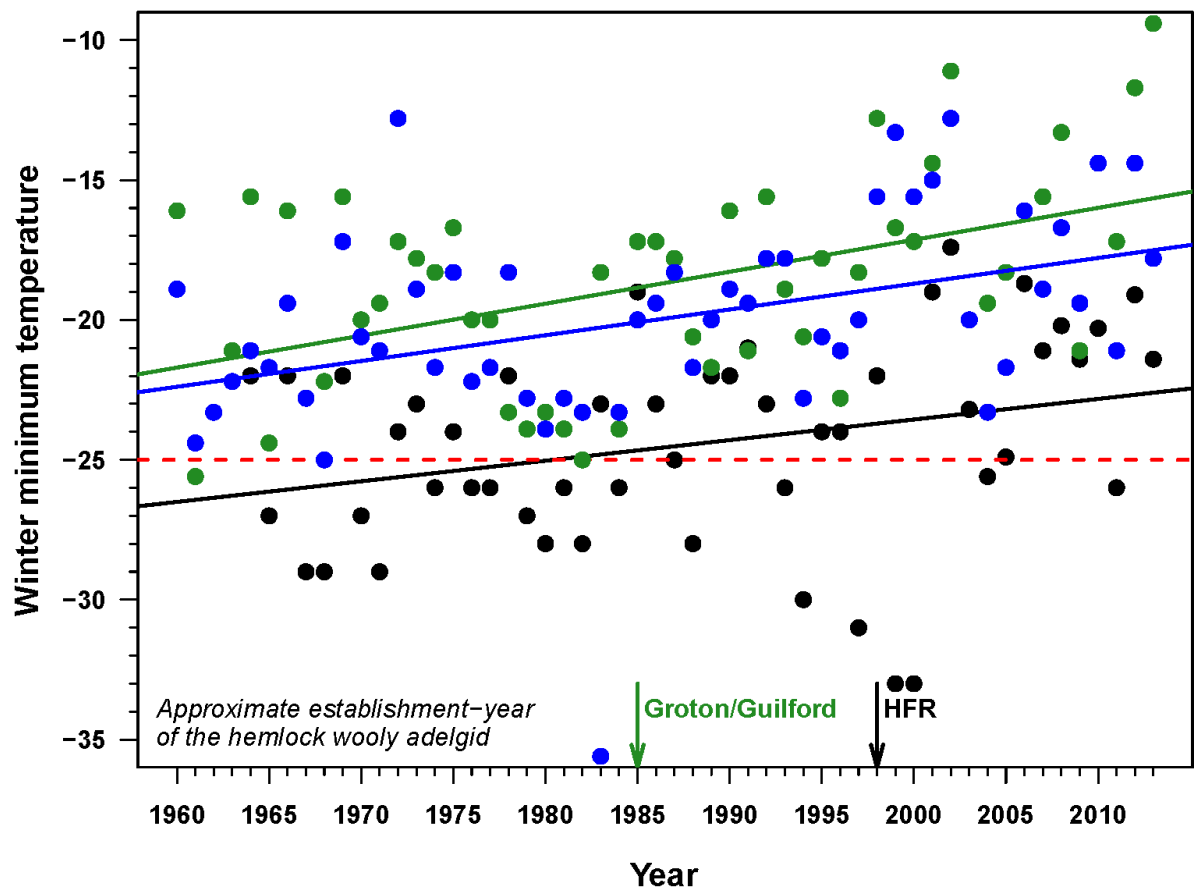


Figure 2 - Winter minimum temperatures (1960-2013) at Groton, Connecticut (41.35 °N, -72.03 °W; green symbols), Storrs, Connecticut (41.81 °N, -72.25 °W; blue symbols), and Harvard Forest (HFR; black symbols) (42.53 °N, -72.19 °W) along with approximate establishment dates of the hemlock woolly adelgid (*Adelges tsugae*) in southern Connecticut and at Harvard Forest (green and black arrows). Solid lines are best-fit linear temperature trends; the dashed red line at -25 °C indicates the LT₅₀ for the hemlock woolly adelgid – the temperature at which 50% mortality of the adelgid is expected (Parker et al. 1998, 1999).

In sum, observational studies have lent some support to the hypothesis that *T. canadensis* is a foundation species in eastern US forests. Where it is abundant, *T. canadensis* acts as a structural species (sensu Huston [53]), creating and defining “hemlock forests” that are recognized not only by ecologists but also by poets, writers, naturalists, and many other non-scientists [3, 27]. *Tsuga canadensis* also supports unique assemblages of associated organisms,

and the most pronounced ecological changes observed following loss of *T. canadensis* have been observed in plant and animal assemblages. The diversity and abundance of understory herbs, shrubs, and saplings, and of birds, salamanders, fish, and invertebrates changes quickly – hemlock specialists disappear and are replaced by more common inhabitants of second-growth hardwood forests – and these changes persist for decades. In many cases, the local (stand-level) species richness increases following *T. canadensis* loss, but the regional (“beta”) diversity declines as the forested landscape becomes more homogeneous. Fewer long-term (years-to-decades) change in ecosystem processes have been observed after *T. canadensis* dies. As hardwoods regrow rapidly, energy and nutrient cycles are restored [19]. Soil characteristics certainly differ between hemlock and hardwood forests. Thus, very long-term (i.e., century-scale) monitoring will be required to determine how soil properties may be changed following loss of *T. canadensis*, and how (or even if) these potential changes will affect faunal diversity and ecosystem processes.

The need for manipulative experiments

Observational studies and manipulative experiments are complementary. Long-term observational studies like the ones described above have documented changes occurring in hemlock forests throughout eastern North America, not only their current decline but also their historical and pre-historical (paleoecological) decline and subsequent recovery (e.g., [54–56]). Such observations have been critical both for developing models of possible future conditions of eastern forests and for testing the accuracy of these models when “hind-casting” past conditions (e.g., [57]). These observations and models also have been used to suggest best practices for local and regional forest management in the face of imminent decline of *T. canadensis* (e.g.,

[58]). But there is little control over the timing and location of observational studies. For example, scientists could not decide when the adelgid colonized a stand, when a logging crew showed up, or compare these “natural” events to various types of forest management on more-or-less equivalent sites at the same time.

Large field experiments address these logistical challenges and improve the strength of the inferences made about how forests respond to loss of *T. canadensis*. Although observational studies have come to dominate large-scale ecological research in recent decades (e.g., [59–61]), it is worth remembering that experiments remain the “gold-standard” for scientific hypothesis testing. Well-designed experiments rapidly identify spurious correlations while reliably identifying cause-and-effect relationships (e.g., [62–65]). Although large-scale field experiments still must account for environmental heterogeneity (e.g., through blocking; [66]), selecting comparable sites where contrasting treatments are applied and untreated “controls” are sited can provide robust power to test hypotheses. In forest stands, collection of extensive data on a wide range of variables and processes *before* the stand is manipulated (i.e., the use of a Before-After-Control-Impact [BACI] design) further accounts for underlying temporal variability while, under appropriate conditions, minimizing temporal pseudoreplication [67, 68]. Finally, when manipulations are applied, the timing, type, and intensity can be specified more precisely.

Ecologists have always looked to manipulative experiments to provide strong and convincing evidence that particular species play disproportionate roles in ecological systems. Paine [69] used removal experiments and exclosures to identify *keystone predators* – those species that enhance species diversity of organisms at lower trophic levels by preferentially preying on competitive dominants. Hanski [70] defined *core species* to be species that are locally abundant and regionally common; he contrasted them with associated satellite species that are

sparse or rare (*sensu* Rabinowitz [71]). Hanski [70] went on to elaborate the core–satellite hypothesis and derived a metapopulation model to explain relationships between the local abundance of an individual species and its distribution on the broader landscape. This hypothesis and the model have been examined extensively in many systems [72], but manipulative experiments testing the core-satellite hypothesis are comparatively uncommon (recent examples include [73, 74]). Numerous other hypothesis, none of which have unequivocal (experimental) support have been proposed to explain observed distributions of common and rare species [75]. Grime [76] characterized *dominant species* that competitively exclude subordinate species by garnering a disproportionate share of resources and contributing most to productivity; many subsequent studies in grasslands have provided experimental support for the functional importance of dominant species in maintaining ecosystem functioning (e.g., [77–79]) and the conservation relevance of dominant species [80].

Holling [81] elaborated on Paine’s definition of a keystone species by hypothesizing that all terrestrial ecosystems are controlled and organized by a small set of “extended keystone” species that share the characteristics of core species, dominant species, and keystone predators. Although the idea of extended keystone species is enticing (and as of April 2014 according to ISI/Web of Science, Holling [81] has been cited nearly 800 times), it is difficult to see how a single species could have characteristics of both keystone predators, which either are uncommon or account for only a small fraction of the biomass in an assemblage, and dominant species that are common and make up most of the biomass in an ecosystem. For example, in the benthic ecosystem at McMurdo Sound, Antarctica that Dayton [1] was studying when he developed the foundation species concept, the sponge *Mycale acerata* Kirkpatrick was the competitive dominant but normally was rare because it was eaten by a specialized predatory sea-star,

Perknaster fuscus antarcticus (Koehler) another example of keystone predation). In contrast, a group of sponges in the family Rosellidae accounted for the majority of the biomass *and* the physical structure of the benthic environment at McMurdo Sound [1, 82] and these foundation species defined the benthic assemblages. It is not clear that any of these taxa would qualify as extended keystone species.

In the mid-1990s, the idea that particular species can create physical structures in the environment, limit or amplify variation in environmental conditions, or provide resources or habitats for other species was independently proposed by Huston [53], who termed such species *structural species*, and Jones et al. [83], who called them *ecosystem engineers*. In the last two decades, hundreds of experimental studies have been used to unravel the effects of ecosystem engineers.

As virtually all species modify their environment to some degree (the process of *niche construction* – [84]), Ellison et al. [2] emphasized that the effects of foundation species on co-occurring species and their environments should be disproportionate to their abundance or biomass, and their actions should occur from within (as by *autogenic* ecosystem engineers of [83]), not from without (as by *allogenic* ecosystem engineers of [83]). But with few exceptions, the key difference between ecosystem engineers and foundation species is their abundance.

Autogenic ecosystem engineers, like *cornerstone species* [85], often are uncommon or rare and exert strong “bottom-up” effects on higher trophic levels. Exceptions are species like cordgrass (*Spartina* species; e.g., [86–89]) and some invasive plants (e.g., [90, 91]). Like these autogenic engineers, foundation tree species should be common, and exert strong bottom-up effects [92].

The Harvard Forest Hemlock Removal Experiment

To determine experimentally the level of support for our hypothesis that *T. canadensis* is a foundation species my colleagues and I have used hectare-scale manipulations at Harvard Forest in Massachusetts. The Harvard Forest Hemlock Removal Experiment (HF-HeRE; [93]) is a multi-hectare, decades-long BACI experiment that complements the regional survey of *T. canadensis* described above. HF-HeRE has overcome many of the logistical and inferential challenges of studying system-wide consequences of loss of this species and has allowed for more focused, yet comprehensive, testing of the hypothesis that *T. canadensis* is a foundation species (Fig. 3).

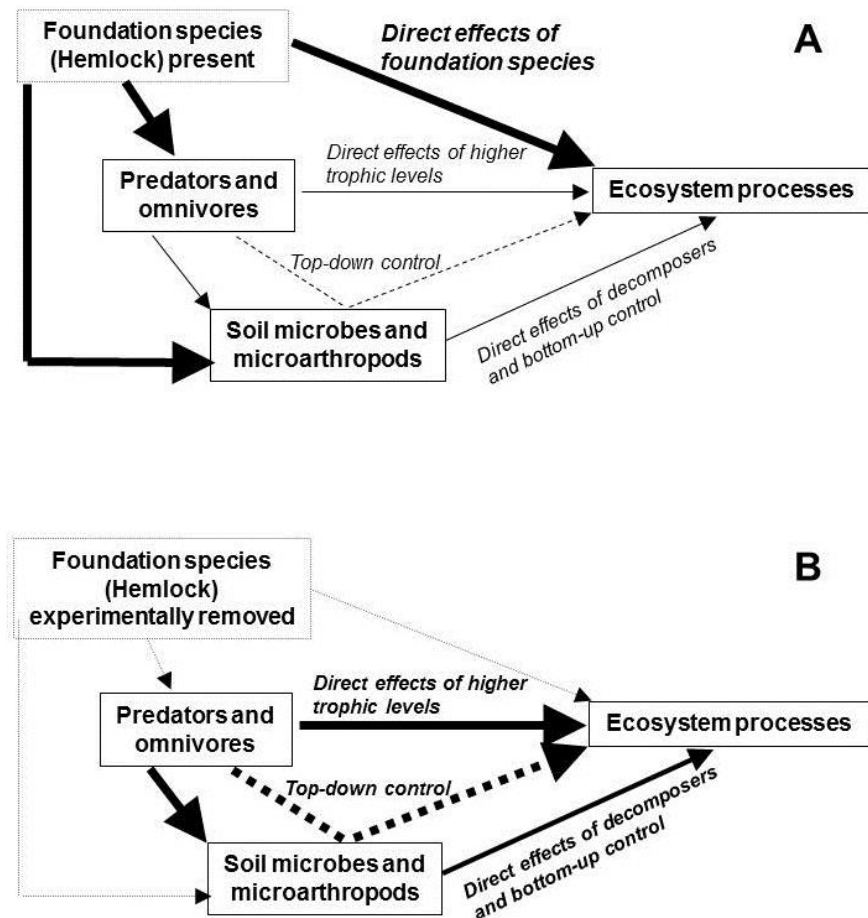


Figure 3 - Conceptual model illustrating the effects of experimentally removing a foundation species from a forested ecosystem. Line width indicates the strength of influence of the foundation species on

ecological processes within the forest; dotted lines indicate indirect effects. Redrawn and modified from [93].

Forest blocks in HF-HeRE includes two removal treatments each applied to $\approx 90 \times 90$ -m (0.81-ha) forested plots (map in Fig. 1, above): girdling of all *T. canadensis* individuals to simulate the progressive death-in-place of trees caused by the adelgid; and logging all *T. canadensis* individuals >20 cm diameter, along with some additional merchantable trees, to simulate a typically intensive level of pre-emptive salvage harvesting [93]. These canopy-manipulation treatments were paired with a hemlock control in which no manipulation occurred and a hardwood control dominated by *B. lenta* and *A. rubrum* that represented what is expected to be the future conditions of most current *T. canadensis* stands in (north)eastern North America [26, 44, 93].

Researchers working on HF-HeRE have studied a wide range of responses to the experimental treatments. These studies have included: changes in microclimate [15]; turnover and succession of plants in the seed bank [94, 95]; shifts in composition and abundance of understory and overstory plants [19]; dynamics of fauna including invertebrates [12], salamanders [9], small rodents (A. Deggrassi, *unpublished data*), white-tailed deer (*Odocoileus virginianus* Miller) and moose (*Alces alces* (L.)) (E. Faison, *unpublished data*); and fluxes and cycles of nitrogen and carbon [19, 45, 96]. All of these changes reflect the relative influence of *T. canadensis*, the adelgid, human activities past and present, and background variability inherent in any ecological system. Disentangling these influences and interpreting our experimental results have been informed not only by region-wide observations discussed above but also by a deep knowledge of the experimental site itself and its history [97], as well as by extensive observational information about how changes in abundance and distribution of *T. canadensis* distribution, past and present, have altered forests across New England.

When HF-HeRE was established in 2003, the adelgid had not yet reached far into the Harvard Forest; the 1998 colonization event (Fig. 2) was confined to a single tree adjacent to the main administration and office building and was thought to have been brought there on the clothing of a researcher. But in 2003, we expected the adelgid to expand into the forest at some point in the near future; in the interim, the experiment was designed to examine the physical loss of *T. canadensis* killed in place (from girdling) to physical loss and removal of this species (from logging) [93]. We first observed the adelgid at low densities in all of the control plots and on remaining *T. canadensis* throughout the experimental plots in 2009 and 2010. Since then, the focus of the experiment has changed from one in which we contrasted the effect of girdling and salvage logging to one in which we now contrast the effects of physical loss of *T. canadensis* (from girdling) to the effects of mortality due to the adelgid (see also [25]).

Forest microclimate

Most of the early responses of the forest to our treatments were consistent with our hypothesis that *T. canadensis* was functioning as a foundation species in these forests. Forests dominated by *T. canadensis* are dark, cool, and moist, but after girdling or logging they became bright, warm, and dry [15]. These changes occurred more rapidly in the logged plots than in the girdled plots, but by 2009, the microclimates in plots subject to these two different canopy-manipulation treatments nearly had converged. Removing the *T. canadensis* canopy also changed the daily and seasonal variance in microclimate. Air temperatures in the logged and girdled plots tended to be warmer during the day and cooler during the night, and warmer during the summer and colder during the winter than air temperatures in either intact hemlock or hardwood control plots. The daily and seasonal extremes were more pronounced early on in the logged plots, but five years

after the treatments had been applied, the variability was similar in both logged and girdled plots. The observed changes in microclimate and canopy cover, induced either by the adelgid or by pre-emptive salvage logging, appeared to have induced a cascade of effects on forest dynamics that began with altered vegetation composition, continued through the animals, and ended in the cycling of nutrients and energy (Fig. 3).

Seed bank and seed rain

Post-treatment seed rain was dominated by *Betula* spp. seeds, with *T. canadensis* cones and seeds running a distant second. Although seeds continually germinate from the seed bank, they are replenished by the seed rain, and species richness in the seed bank was similar before treatments were applied (in 2004; [94]) and five years after (in 2010; [95]). Nonetheless, the understory vegetation – herbs, tree seedlings, and saplings – was not compositionally similar to the seed bank in the hemlock and hardwood control plots because seed germination is suppressed by the dense overstories in those plots. However, following canopy removals either by girdling or logging, the understory vegetation has become more similar to the seed bank as seeds germinated and seedlings established [95].

Vegetation

When HF-HeRE began, the hemlock plots were larger (had more basal area) than the young hardwood plots, and there was a bit more basal area in plots on the ridge than there was in the valley [93]. Four years after logging and girdling, these plots had lost nearly 70% of their basal area and more than 60% of their stems [19]. However, the pace and structure of loss differed between the two treatments. In the logged plots, basal area was lost immediately as trees were

felled, boles were removed from the site, and the remaining dead wood was piled on the forest floor. In the girdled plots, trees died over two years and > 80% of the dead trees (and their wood) is still standing (in early 2014). During this same time interval, the control plots added a 4-6% basal area and lost \approx 10% of their stems to normal mortality and stand thinning.

Suppressed, sub-canopy *B. lenta* and *A. rubrum* trees responded with more rapid growth to removal of *T. canadensis* by logging or girdling than did existing canopy dominants (*Pinus strobus* L. and *Quercus rubra* L.). Similarly, saplings (stems > 1.3 m tall but < 5 cm diameter) and stump sprouts responded rapidly to canopy removal, and by 2011, there were dense thickets of *B. lenta* in both the girdled and the logged plots [19].

The number of herbs and shrubs in the understory has been constant in both hemlock (8 species) and hardwood (20 species) control plots since 2003. In 2003, the logged and girdled plots had similarly low numbers of understory species, but by 2010, the species richness of the understory in these canopy-removal plots had increased by 50% [19, 95]. Many new species in the manipulated plots were early successional opportunists and species with long-lived seed banks, including *Aralia hispida* Vent., *Erechtites hieracifolia* Raf., *Rubus* spp., *Lysimachia quadrifolia* L., and *Dennstaedtia punctilobula* (Michx.) T. Moore [95]. Two invasive species also had colonized the girdled plots by 2007: *Berberis thunbergii* DC. and *Celastrus orbiculatus* Thunb. (A. A. Barker Plotkin and A. M. Ellison, *unpublished data*).

Fauna

The most comprehensive data on faunal responses to loss of *T. canadensis* has come from annual samples of ants in the experimental plots. In parallel with observational data [7], we observed rapid colonization into the girdled and logged plots of large ants – notably *Camponotus* and

Formica species – that are uncommon or absent in the hemlock control plots [12]. Species that favor open habitats, such as *Formica dolosa* Buren, have been collected only in the logged plots. The nearest other known occurrence of this species in the region is approximately 20 km north [98].

We have also sampled beetles and spiders, although not as regularly as ants. The predatory tiger beetle (*Cicindela sexguttata* Fabricius) has colonized the logged plots, while in the girdled plots, populations of web-building spiders have increased dramatically (Fig. 4). In both girdled and logged plots, we hypothesize – as illustrated in Fig. 3 – that as *T. canadensis* has died that the soil food webs have shifted from bottom-up (detrital) controlled in intact hemlock forests to top-down (predator) controlled in the logged plots.

In contrast, red-backed salamanders (*Plethodon cinereus* (Green)) and red-spotted newts (*Notophthalmus viridescens* (Raf.)) were more abundant in intact hemlock forests than in hardwood forests [9]. This pre-manipulation census is currently being replicated in the (post-treatment) canopy manipulation plots (A. A. Hassabelkreem, *unpublished data*).

The adelgid itself was first observed in the HF-HeRE plots at low densities in 2008. Infestation levels were assessed in the canopy manipulation plots and controls in late summer and early fall, 2009. By then, 46% of the *T. canadensis* stems (trees, saplings, seedlings) in the hemlock control plots; 20% of the *T. canadensis* stems in the hardwood controls, and 15% of the few small *T. canadensis* seedlings and saplings left in the logged plots were considered infested by the adelgid (A. A. Barker Plotkin and A. M. Ellison, *unpublished data*). We note that these numbers likely *underestimate* the infestation because the trees were surveyed in the summer, when the presence of adelgid is less obvious than at times when the white woolly is more visible. The adelgid was present in the logged and hardwood plots, but at much lower infestation rates.

The few surviving *T. canadensis* individuals (mostly seedlings) in the girdled plots were not yet infested in 2009. The next adelgid census in the plots is scheduled for summer 2014.



Figure 4 - Webs of *Agelenopsis* spiders on the forest floor of a plot in which all *T. canadensis* individuals were girdled to kill them in place. The average web density $> 5/\text{m}^2$. Photograph by the author.

Ecosystem dynamics

If *T. canadensis* is functioning as a foundation species, then its loss also should lead to change in core ecosystem processes such as carbon flux and nutrient cycles. This prediction was supported most clearly for changes in litterfall, which is one index of aboveground primary productivity [99]. In the girdled treatment plots at HF-HeRE, there was a sharp pulse in litterfall followed by a gradual decline [19]; similar patterns have been observed in other hemlock girdling experiments [22, 39, 100]. This shift reflects only the transient loss of standing biomass as the canopy died; litterfall recovered within four years to pre-manipulation (i.e., control-plot) levels

as understory shrubs (primarily *Rubus* spp.) and seedlings of *Betula* spp. rapidly colonized the girdled plots through seedling recruitment [95]. Not surprisingly, litterfall immediately decreased in the logged plots because trees were cut and removed from the site. Recovery of litterfall rates and quantities was slower in the logged plots than in the girdled plots because the soil scarification caused by, and the residual material left on site from, the logging operation (≈ 1 m of coarse woody debris scattered throughout the plot) slowed colonization of the plots by other species [19]. However, hardwoods cut or damaged during the logging operation re-sprouted, contributing to local hot-spots of litterfall.

In contrast to the significant among-treatment differences in litterfall, *within*-treatment variation in carbon flux (i.e., soil respiration), nitrogen availability, and nitrogen cycling generally was higher than among-treatment variation, and their initial responses to the canopy manipulations were modest, transient, and not statistically significant [19]. The rapid return to pre-treatment levels of nitrogen availability reflected rapid establishment of other plant species following logging (e.g., [41, 96, 100, 101]); this has been observed in stands shortly following adelgid infestation [24, 26]. However, we also found no substantive differences in nitrogen mineralization between the hemlock and hardwood control plots, which may also reflect the generally nutrient-poor, glacially-derived granitic soils at Harvard Forest. It is important to note, however, that changes in soil dynamics resulting from canopy change may take decades to centuries to appear. This is because a dominant driver of soil dynamics is decomposition of large fallen boles and other coarse woody debris. In stands dominated by *T. canadensis*, decomposition is dominated by brown-rot fungi that primarily break down cellulose. In contrast, in hardwood-dominated stands, decomposition is dominated by white-rot fungi that primarily break down lignin [102, 103]. Thus, we hypothesize that over several centuries, soil nutrient

availability in stands formerly dominated by *T. canadensis* will decline significantly only after dead *T. canadensis* boles and smaller coarse woody debris of *T. canadensis* branches and twigs have decomposed and brown-rot fungi are no longer dominant.

Conclusion – is *Tsuga canadensis* a foundation species?

Observational, experimental, and modeling work of the role of *T. canadensis* in eastern North American forests provides one of the best opportunities to test the hypothesis that a single species of tree is a foundation species. Although the distribution and abundance of *T. canadensis* has expanded and contracted since the end of the most recent glaciation (*ca.* 15,000 years ago), when *T. canadensis* recovers and regains its local dominance, hemlock forests are like no other forest types in the region [27]. “Natural” or experimental removal of *T. canadensis* leads to immediate and long-term changes in the distribution and abundance of associated plant and animal species, and these are much more pronounced than when nearby hardwood forests are thinned, logged, or undergo succession. On the other hand, shifts in energy flux and biogeochemical cycles following loss of *T. canadensis* are expressed weakly in the short term; much longer-term experiments may reveal the extent to which *T. canadensis* and its microbial associates control ecosystem processes in hemlock stands.

I emphasize that most of the hemlock stands on the modern-day landscape, and virtually all of the ones in which the role of *T. canadensis* as a foundation species, and the effects of its loss due either to the adelgid or to logging, are relatively young (80–200-year-old) second-growth stands. The few remaining old-growth hemlock stands have very different characteristics from second-growth stands [104, 105], and their effects on forest dynamics have not been studied. In addition, our interpretations of causes and consequences of changes in distribution

and abundance of *T. canadensis* are conditioned on a particular set of historical events that have occurred in the region (e.g., [3, 54, 97]). From a vantage point in 2014, and in light of: the loss of *Castanea dentata* from North American forests in the early twentieth century; ongoing declines of many other forest tree species, including *Fagus grandifolia* Ehrh. and *Acer saccharum* Marsh; land clearance by European colonists from the 1600s through the mid-19th century, and continued logging of *P. strobus*, *Quercus alba* L., *Q. rubra*, and *Carya* spp. from our forests; and the extirpation of many top predators; *Tsuga canadensis* appears to be a foundation species. The permanence of this foundation, however, remains an open avenue for research.

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