The relative contributions of seed bank, seed rain, and understory vegetation dynamics to the reorganization of *Tsuga canadensis* forests after loss due to logging or simulated attack by *Adelges tsugae*

Elizabeth J. Farnsworth, Audrey A. Barker Plotkin, and Aaron M. Ellison

Abstract: Profound changes are occurring in forests as native insects, nonnative insects, or pathogens irrupt on foundation tree species; comprehensive models of vegetation responses are needed to predict future forest composition. We experimentally simulated hemlock woolly adelgid (*Adelges tsugae* Annand) infestation (by girdling trees) and preemptive logging of eastern hemlock (*Tsuga canadensis* (L.) Carrière) and compared vegetation dynamics in replicate 90 m × 90 m treatment plots and intact hemlock stands from 2004 to 2010. Using Chao–Sørensen abundance-based similarity indices, we assessed compositional similarities of trees, shrubs, forbs, and graminoids among the seed bank, seed rain, and standing vegetation over time and among treatments. Post-treatment seed rain, similar among treatments, closely reflected canopy tree composition. Species richness of the seed bank was similar in 2004 and 2010. Standing vegetation in the hemlock controls remained dissimilar from the seed bank, reflecting suppressed germination. Recruits from the seed rain and seed bank dominated standing vegetation in the logged treatment, whereas regeneration of vegetation from the seed bank and seed rain was slowed due to shading by dying hemlocks in the girdled treatment. Our approach uniquely integrates multiple regeneration components through time and provides a method for predicting forest dynamics following loss of foundation tree species.

Résumé : Les forêts subissent de profonds changements à mesure que les insectes indigènes, les insectes exotiques et les pathogènes envahissent les espèces arborescentes fondamentales. Des modèles détaillés des réactions de la végétation sont nécessaires pour prédire la composition future des forêts. Nous avons expérimentalement simulé une infestation du puceron lanigère de la pruche (*Adelges tsugae* Annand) en annelant les arbres et nous avons pratiqué une coupe préventive de la pruche du Canada (*Tsuga canadensis* (L.) Carrière). Nous avons ensuite comparé la dynamique de la végétation dans des placettes répliquées de 90 m × 90 m et des peuplements intacts de pruche de 2004 à 2010. À l'aide des indices de similarité basés sur l'abondance de Chao–Sørensen, nous avons évalué la similitude de la composition en espèces d'arbres, d'arbustes, de plantes herbacées non graminoïdes et de graminées dans la banque de semences, la pluie de semences et la végétation sur pied dans le temps et parmi les traitements. Après le traitement, la pluie de semences qui était semblable parmi les traitements reflétait étroitement la composition en espèces d'arbres qui formaient le couvert. La richesse en espèces de la banque de semences était semblable en 2004 et 2010. La végétation sur pied dans les placettes témoins de pruche demeurait différente de la banque de semences, reflétant le fait que la germination était inhibée. Les recrues provenant de la pluie de semences et de la banque de semences dominaient la végétation sur pied dans les placettes où les arbres avaient été coupés tandis que la régénération de la végétation provenant de la banque de semences et de la pluie de semences était ralentie par l'ombrage des pruches mourantes dans les placettes où les arbres avaient été annelés. Notre approche intègre de façon originale les multiples composantes de la régénération dans le temps et fournit une méthode pour prédire la dynamique forestière à la suite de la perte des espèces arborescentes fondamentales.

[Traduit par la Rédaction]

Introduction

A key aim of forest ecology is to elucidate factors that influence transitions of plants from the seed to the canopy under a range of management conditions. Changes in forest species composition through time are driven by several factors, including recruitment from the seed bank, inputs from seed rain, interactions with standing vegetation, variable edaphic and climatic conditions, and a range of mortality agents including insects and pathogens (Lovett et al. 2006; Burton et al. 2011). Long-term, integrative studies of these ecological factors are needed to predict the species composi-

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E.J. Farnsworth. New England Wild Flower Society, 180 Hemenway Road, Framingham, MA 01701, USA.
A.A. Barker Plotkin and A.M. Ellison. Harvard Forest, Harvard University, 324 North Main Street, Petersham, MA 01366, USA.

Corresponding author: Aaron M. Ellison (e-mail: aellison@fas.harvard.edu).

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tion of future forests, especially as herbivores irrupt and pathogens become more prevalent. Pathogens and insects can damage or eliminate dominant and foundation tree species (sensu Ellison et al. 2005), rapidly and radically altering the composition of forest stands. Silvicultural practices and preemptive measures such as logging, undertaken to remove vulnerable and (or) economically valuable tree species before an infestation or infection occurs, also affect seed-banking, regeneration, and forest dynamics (Graae and Sunde 2000; Decocq et al. 2004).

Eastern hemlock (*Tsuga canadensis* (L.) Carrière) forests provide a model system in which to examine these dynamics, specifically comparing responses to preemptive hemlock logging or infestation by the hemlock woolly adelgid (*Adelges tsugae* Annand). Intact, mature hemlock forests tend to be stable and long-lived, with depauperate understories suppressed by a very shady microenvironment and acidic needle litter (Catovsky and Bazzaz 2000; D'Amato et al. 2009). Palynological data illustrate that hemlock forests underwent a region-wide decline ~5400 years ago caused by a combination of insect-driven defoliation and climatic change, but they recovered to their current extent after 300–1200 years (Foster et al. 2006).

A similar process has been unfolding in the last 30 years. The hemlock woolly adelgid has been spreading rapidly since the 1980s, defoliating trees and causing more than 95% mortality in parts of its range (Orwig et al. 2008). Preemptive salvage logging has occurred in many hemlock stands to extract economic value before the adelgid infests and kills the trees (Foster and Orwig 2006). Slow loss of living hemlock due to the adelgid acts as a gradually changing filter on vegetation recruitment, progressively suffusing the understory with light, stimulating seed germination, and creating opportunities for plant colonization. For example, Yorks et al. (2003) documented gradually increasing abundance of *Betula*, *Acer*, and four monilophyte species in the 5 years following a hemlock girdling treatment.

In contrast, logging removes the canopy suddenly, greatly increasing light availability at the forest floor in a single pulse (Krasny and Whitmore 1992). Logging also often leaves a large amount of slowly decomposing slash that initially suppresses regeneration, and effects of rutting, scarification, and other disturbances can persist in second-growth hemlock stands (Smith 1986). In either case, the composition of the forest eventually increases in species richness, with new broad-leaved tree species coming to predominate in even-aged stands (Orwig and Foster 1998). However, the near-term composition of the recovering forest is difficult to predict; stochastic dynamics, coupled with a warming climate that favors increased herbivory or recruitment of plant species adapted to warmer climate conditions (Paradis et al. 2008), may cause novel assemblages to form (e.g., Spaulding and Rieske 2010).

In this paper, we present results of a 7-year study that documents species present in the seed bank, seed rain, and tree, sapling, seedling, and herbaceous vegetation before and after hemlock-dominated stands were subjected to three experimental treatments: (*i*) simulated attack by *A. tsugae*, (*ii*) preemptive logging, and (*iii*) intact control. We ask four specific questions.

(1) To what extent are the initial compositions of the seed bank, seed rain, canopy, and existing forest floor species similar? Comparative studies frequently report disparities among the plant species compositions of the seed bank, seed rain, and standing vegetation (Hopfensperger 2007). Such disparities pose challenges for predicting future forest composition, but can also indicate the most important ecological filters operating on particular species, life forms, and life stages (Myers and Harms 2011). Based on previous studies, we expected to find little concordance in species composition among these regeneration components.

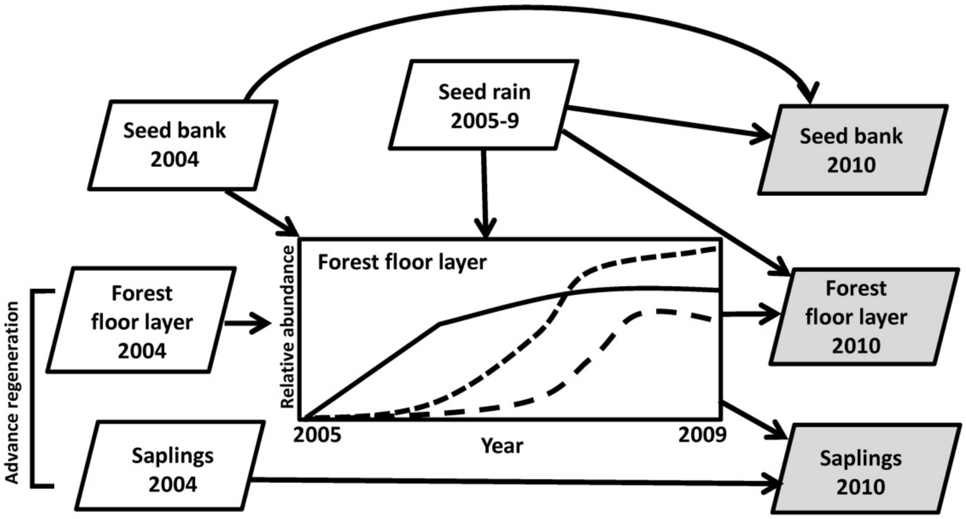
(2) Do the compositions of the seed bank, seed rain, canopy, sapling, seedling, and herbaceous vegetation diverge or converge in similarity over time or among treatments? We hypothesized that the composition of the developing forest floor vegetation would more closely reflect the inputs of seed rain and the seed bank as the girdled canopy gradually ceased acting as a strong filter on germination and establishment of seedlings. We also expected the 2010 seed bank to diverge in composition from the 2004 seed bank in the logged treatment as new seed sources became available and the existing bank became depleted as seeds germinated and recruited to the seedling layer.

(3) Does the vegetation composition differ between stands undergoing mortality due to simulated adelgid attack versus logging, and how does post-disturbance composition compare with intact stands? We predicted that seed rain would continue to supply new recruits as the canopy slowly died in the girdled treatment, while the upper layer (0–10 cm depth) of the forest seed bank would contribute most of the new recruits in newly logged stands, as it would be most responsive to scarification during skidder activity. We also expected the composition of the vegetation on the forest floor to remain stable and dominated by shade-tolerant *T. canadensis* in the heavily shaded hemlock control treatment (Catovsky and Bazzaz 2002).

(4) Can we use these data to predict stand composition as post-hemlock succession proceeds? The advance regeneration afforded by sapling, shrub, and herbaceous layers, plus ongoing seed rain, should dominate the vegetation that develops in post-treatment years. Figure 1 depicts a simple, conceptual null model in which these inputs contribute equally to outcomes in stand composition. Observed departures from this model, reflected in different treatment responses, would reflect contrasting ecological filters imposed by processes such as insect or pathogen damage and logging. Although we anticipated that the composition of the standing vegetation would differ between adelgid-impacted and logged stands during early phases of stand regeneration, over much longer terms, standing vegetation may converge in similarity.

Prior studies of regeneration in logged or adelgid-infested hemlock stands separately have documented changes in plant species composition (Orwig et al. 2008), provided baseline data on seed bank and understory vegetation (Catovsky and Bazzaz 2000; Yorks et al. 2000; Sullivan and Ellison 2006), or used successional data to inform predictive models of tree species abundance (Spaulding and Rieske 2010); ours is the first to integrate all of these types of data with information on temporal dynamics of seed bank and seed rain compositions in an experimental context. Most previous plot-based studies have tended to focus on single guilds, such as forest floor herbs (Burton et al. 2011), or examined ecosystems other than temperate forests (e.g., Drake 1998); we document the emergence of both herbaceous and woody vegetation to present a comprehensive profile of changing assemblages of forest plants.

Fig. 1. Conceptual model illustrating how seed banks (including spores and other propagules), seed rain (also including spores and other propagules), and advance regeneration contribute to plant species abundance in a recovering forest stand over time. The middle panel shows temporal trends in relative abundance of species colonizing the forest floor following canopy manipulations in 2005; the different line types illustrate relative abundances of different taxa. Diagonal open parallelograms on the left show inputs; shaded parallelograms on the right show outcomes.



Methods

Harvard Forest Hemlock Removal Experiment

This study took place in the Harvard Forest Hemlock Removal Experiment (HF-HeRE) plots located within the 121 ha Simes Tract at the Harvard Forest Long-Term Ecological Research Site in Petersham, Massachusetts, USA (42.47–42.48°N, 72.22–72.21° W; elevation 215–300 m above sea level). The Harvard Forest lies within the hemlock – hardwood – white pine transition forest region of eastern North America, and the Simes Tract itself is classified as “hemlock–hardwoods” (Kernan 1980). The soils are predominantly coarse-loamy, mixed, active, mesic Typic Dystrudepts in the Charlton Series that are derived from glacial till (US Department of Agriculture, no date). Prior to the experimental treatments described below, eastern hemlock comprised 50%–69% of the (on average) 50 $m^2{\cdot}ha^{-1}$ (mean) basal area and 55%–70% of the mean 875 $stems{\cdot}ha^{-1}$ (Sullivan and Ellison 2006). Other species that comprised >10% of the initial basal area in any of the plots included white pine (*Pinus strobus* L.), black birch (*Betula lenta* L.), red oak (*Quercus rubra* L.), and red maple (*Acer rubrum* L.).

Full methods and diagrams of the HF-HeRE are given in Ellison et al. (2010); salient details are presented here. Canopy-level manipulations were performed in two 90 m × 90 m (0.81 ha) plots in each of two blocks; an additional 0.81 ha plot in each block served as a control. Blocks were chosen based on their size and capacity to accommodate three large treatment plots without edge effects. The “valley” block is in undulating terrain bordered on its northern edge by a *Sphagnum*-dominated wetland, whereas the “ridge” block is on a forested ridge (see site map in Ellison et al. 2010). Blocks and plots were sited and established in 2003. Within each block, the two treatment plots and the intact control plot were located within 300 m of each other, with similar topography and aspect. In 2003, *A. tsugae* was not present in any of the blocks; as of 2010, the insect was gradually colonizing hemlock stands at the Harvard Forest and was present throughout the Simes Tract, but not yet causing hemlock mortality.

The first canopy manipulation, girdling, was designed to induce the gradual physical decline (i.e., defoliation, biomass loss) caused by *A. tsugae* infestation. In this treatment, *all* hemlock seedlings, saplings, and mature trees were girdled using knives or chainsaws over a 2-day period in early May 2005. The girdled hemlocks died over the course of the next 2 years and since have been slowly disintegrating in a pattern quite analogous to that observed following heavy *A. tsugae* infestations (see also Yorks et al. 2003).

The second treatment, logging, was designed to mimic the effects of a commercial hemlock-salvage operation involving removal of merchantable timber, pulp, and cordwood of hemlock and other species (e.g., *P. strobus* and *Q. rubra*). We applied a fixed-diameter-limit cut. Between 65% and 70% of the stand basal area, including all *T. canadensis* trees >20 cm diameter at breast height (DBH) (1.3 m) and at least half of the merchantable white pine and hardwoods (maple, birch, oaks), was harvested by chainsaw and removed from the two plots using a rubber-tired skidder between February and April 2005 when the ground was frozen. The third plot in each block was left intact to serve as a *T. canadensis* control.

In this paper, we focus on species composition and abundance before treatments were applied in 2005 and vegetation regeneration and reorganization for 5 years following the hemlock removal treatments. Data on microclimate, stand structure, litterfall, coarse woody debris, distribution and abundance of ants, beetles, and spiders, and fluxes of carbon and nitrogen also were collected for 2 years prior to the 2005 treatment and are reported elsewhere (Sackett et al. 2011; Lustenhouwer et al. 2012; D.A. Orwig et al., unpublished data). Overall, changes in these variables in the girdled treatment have been similar in pace and magnitude to those resulting from adelgid invasion throughout New England. For example, light availability increased gradually over time in the girdled treatment (as in Yorks et al. 2003) but abruptly in the logged treatment (Lustenhouwer et al. 2012). Average daily soil and air temperatures in the logged and girdled treatments are 2–4 °C warmer in summer and cooler in winter relative to the hemlock control plots, and both diurnal and seasonal variances in temperatures are highest in the logged treatment (Lustenhouwer et al. 2012). Decline and loss of eastern hemlock in the logged and girdled treatments at HF-HeRE also have led to reductions in overstory densities and basal area comparable with those seen in sites long infested by the adelgid (Orwig and Foster 1998; Orwig et al. 2002) or that have been salvage-logged (Kizlinski et al. 2002).

Composition of the seed rain

To characterize the composition of the seed rain, seeds were manually removed from litter collected in five litterfall baskets that were placed at random coordinates throughout each 90 m × 90 m plot. Baskets (40.6 cm long × 33 cm wide × 25.4 cm deep) were constructed of Sterilite plastic with vent and drainage holes and lined with no-see-um cloth (0.25 mm mesh) that was fastened to the edges with clips and suspended slightly above the bottom of the basket to keep the litter dry. Replicate baskets were placed in the field at the beginning of September 2005, and material was collected quarterly in early April, mid-June, mid-October, and early December of each year. Samples were air-dried and seeds separated. Seeds were identified to species (when possible; to genus when not) using dichotomous keys in Montgomery (1977); vouchers are stored in the Harvard Forest Herbarium. Representative individual seeds of each species were weighed, and numbers of seeds in each sample were determined from the mass of total samples (Greene and Johnson 1994).

Composition of the seed bank

In June 2004, we marked five randomly chosen points in the center 30 m × 30 m subplot of each of the experimental treatment plots (to avoid edge effects) and collected a single 60 cm × 60 cm × 20 cm deep soil monolith at each point (Sullivan and Ellison 2006). In May 2010, we returned to the same points, chose a new sample location within 2 m of the original location, and collected a single 15 cm × 15 cm × 20 cm deep soil core at each point. In both years, we returned the soil cores within 5 h to the laboratory for planting. In both 2004 and 2010, all cores were trimmed to 10 cm × 10 cm × 20 cm deep blocks and then sliced into 2 cm depth increments. These samples were placed into separate 7.5 cm × 7.5 cm cells in a divided potting tray, each cell first lined with a 1 cm deep layer of milled sphagnum to facilitate drainage. One replicate reference cell for each of the cores was filled entirely with milled sphagnum and monitored for recruitment of “weedy” species present in the greenhouse seed rain. All trays were placed in the Harvard Forest greenhouse at full light, watered twice daily, and fertilized once during each growing season with 1.7 $g \cdot L^{-1}$ of 20–20–20 fertilizer (J.R. Peters, Inc., Allentown, Pennsylvania). Trays were randomly repositioned twice during each growing season.

Seed bank composition was assessed using the direct germination method, without prior sieving. Opinions differ in the literature about the relative merits of direct germination versus seed extraction by suspension and filtering of seeds in water for characterizing the seed bank. Studies comparing these methods have indicated that seed extraction can be ineffective for detecting small-seeded species and overestimates the viable seed bank because it does not distinguish nonviable seeds (Price et al. 2010). With the caveat that the direct germination approach also can discriminate against seeds not adapted for greenhouse conditions, we selected this method as a more reliable estimator of seeds available for regeneration in the field treatment plots. Trays were monitored on a weekly to biweekly basis from June to September in both 2004 and 2010; after September, no new germination occurred and existing seedlings were senescing. Most newly emerging seedlings were removed to prevent competition with later-emerging plants, except where removal would disturb existing, as-yet-unidentified seedlings. Unidentified specimens were outplanted to larger pots in September of year 1 (2004 or 2010) to ensure that root binding would not cause death or affect their growth in year 2 (2005 or 2011). Specimens still unidentified at the end of the first growing season were hardened off and watered biweekly from November to April, during which time greenhouse temperatures were kept at 4 °C. Surviving seedlings were monitored throughout the second growing season (i.e., summers of 2005 and 2011) until reproduction occurred or until plants were mature enough to identify unambiguously. Haines (2011) was used for identifications and nomenclature, and Jenkins et al. (2008) provided confirmation on species presence at Harvard Forest. Vouchers are stored in the Harvard Forest Herbarium.

Composition of the standing vegetation

In 2003, two 30 m transects were established, running through the center 30 m × 30 m of each plot, for the purposes of sampling the forest floor vegetation. Five 1 m^2 subplots were spaced evenly along each transect. Transects were permanently marked with stakes, and subplots were marked at the northwest corner with flags. Percent covers of herbaceous species, shrubs, and tree seedlings (<1.3 m tall) were estimated, and numbers of tree seedlings were counted in each subplot in July of each year. Saplings, defined as trees >1.3 m tall but with DBH $<$ 5 cm, were identified to species, and all saplings in the 30 m × 30 m central plot were counted in 2004, 2007, and 2009. Canopy trees (minimum size 5 cm DBH) in the entire 90 m × 90 m plot were identified, mapped, and labeled with numbered aluminum tags. Size (DBH) and status (living/dead) were recorded in 2004 and 2009. Additional observations of plants within 3 m of the seed bank core locations were made in May and August 2010. These species occurrences were added to our list of taxa present in each treatment (Table 1) but were not used for calculating relative abundances.

Statistical analyses

Data from all subsamples taken within an individual 90 m × 90 m treatment plot, i.e., individual depth strata within seed bank cores, individual vegetation subplots, or individual litter baskets, were pooled (normally averaged; summed in the case of seed rain) to yield a single value for each variable for each plot. This pooling avoids pseudoreplication and inflation of degrees of freedom and probability of Type I statistical errors (Gotelli and Ellison 2012). Except in the multivariate analysis

Table 1. Species found in the seed rain (R), seed bank (B), understory vegetation (V), and canopy (C) samples (excluding intermediate and suppressed trees in the canopy) within each of the three eastern hemlock (*Tsuga canadensis*) canopy manipulation treatments from 2005 to 2010.

	Canopy treatment		
Species	Hemlock control	Hemlocks girdled	Hemlocks logged
Trees (including seedlings, saplings, and canopy)			
Acer rubrum L.	R, V, C	R, V, C	R, V, C
Betula alleghaniensis Britt.*	C	V	
Betula lenta L.	R, B, C	R, B, V, C	R, B, V, C
Betula papyrifera Marsh.	B, V	B, V, C	V
Carya sp. Nutt.	V, C	V	V
Fraxinus americana L.	R, C		
Fraxinus nigra Marsh.		C	
Nyssa sylvatica Marsh.	R		
Ostrya virginiana (P. Mill.) K. Koch			R
Pinus strobus L.	R, V, C	R, V, C	R, B, V, C
Populus grandidentata Michx.			B
Prunus pensylvanica L.f. var. *pensylvanica*		V	V
Prunus serotina Ehrh. var. *serotina*	V, C	V	V
Quercus alba L.	C	V, C	V, C
Quercus bicolor Willd.		C	
Quercus rubra L.	V, C	V, C	R, V, C
Quercus velutina Lam.			V
Tsuga canadensis (L.) Carrière	R, B, V, C	R, V, C	R, V, C
Shrubs			
Amelanchier sp. Medik.		V	
Berberis thunbergii DC.		V	
Celastrus orbiculatus Thunb.		V	
Comptonia peregrina (L.) Coult.		B	V
Corylus cornuta Marsh. subsp. *cornuta*		V	
Crataegus sp. L.		V	V
Diervilla lonicera P. Mill.			V
Gaultheria cf. *hispidula* (L.) Muhl. ex Bigelow		B	B
Gaultheria procumbens L.*		V	V
Ilex mucronata (L.) M. Powell, Savol. & S. Andrews			V
Ilex verticillata (L.) Gray		V	V
Mitchella repens L.	V	V	B, V
Myrica gale L.			V
Rhododendron periclymenoides (Michx.) Shinners		V	
Rhus copallinum L. var. *latifolia* Engl.		V	V
Rhus hirta (L.) Sudworth	R		
Rubus allegheniensis Porter	B	V	B, V
Rubus flagellaris Willd.	B	B, V	B, V
Rubus hispidus L.	B	B, V	B, V
Rubus idaeus L. subsp. *ideaus*		V	V
Rubus occidentalis L.	B	B, V	B, V
Sambucus racemosa L.		V	V
Sassafras albidum (Nutt.) Nees			V
Sorbus americana Marsh.		V	
Swida alternifolia (L.f.) Small	R	R	
Vaccinium angustifolium Ait.*		V	R, V
Vaccinium corymbosum L.			V
Viburnum nudum L. var. *cassinoides* (Torr.) A. Gray	B	V	B
Vitis sp. L.		V	V
Forbs			
Aralia hispida Vent.		V	B, V
Aralia nudicaulis L.	V		

Table 1 (*concluded*).

	Canopy treatment		
Species	Hemlock control	Hemlocks girdled	Hemlocks logged
Chimaphila maculata (L.) Pursh		V	
Coptis trifolia (L.) Salisb.		V	
Epigaea repens L.		V	
Erichtites hieraciifolius (L.) Raf. ex DC. (s.l.)		V	V
Eurybia cf. *divaricata*	B	B	B
Euthamia graminifolia (L.) Nutt.			B
Goodyera tesselata Lodd.		V	
Hypopitys monotropa Crantz	V	V	
Lobelia inflata L.	B		
Lysimachia borealis (Raf.) U. Manns & A. Anderb.	V	V	V
Lysimachia quadrifolia L.		B, V	B, V
Maianthemum canadense Desf.	B, V		
Medeola virginiana L.	V	V	
Mollugo verticillata L.		B	B
Monotropa uniflora L.	V	V	V
Phytolacca americana L. var. *americana*		B, V	
Polygonatum biflorum (Walt.) Ell.	R		
Pyrola sp. L.		V	
Solidago sp. L.		V	
Taraxacum officinale G.H. Weber ex Wiggers			B
Trifolium repens L.			B
Trillium erectum L.	V		
Viola labradorica Schrank	B		
Viola sororia Willd. var. *novae angliae* Duchesne	B	B	B
Graminoids			
Agrostis hyemalis (Walt.) B.S.P.	B		
Brachyeletrum erectum (Schreb.) Beauv.			V
Carex cf. *ovales* group	B	B	R, B, V
Carex debilis Michx. var. *rudgei* Bailey	B	B	
Carex deweyana Schweinitz		B	
Carex laxiflora L.	B		B
Carex pensylvanica Lam.	B	B, V	B, V
Dichanthelium acuminatum (Sw. Gould) C.A. Clark var. *fasciculatum* (Torr.) Freckmann	B		B
Dichanthelium clandestinum (L.) Gould	B		
Digitaria ischaemum (Schreb.) Muhl.	B	B	B
Juncus brevicaudatus (Engelm.) Fern.	B		
Juncus tenuis Willd.	B	B	B
Scirpus cyperinus (L.) Kunth		B	
Monilophytes and lycophytes			
Dendroycopodium obscurum (L.) A. Haines	V	V	V
Dennstaedtia punctilobula (Michx.) T. Moore	V	V	V
Dryopteris carthusiana (Vill.) H.P. Fuchs	V	V	V
Dryopteris intermedia (Muhl. ex Willd.) Gray		V	V
Huperzia lucidula (Michx.) Trevisan	V		
Osmundastrum cinnamomeum (L.) C. Presl	V	V	
Polypodium virginianum L.	V		
Polystichum acrostichoides (Michx.) Schott	V		

Note: Asterisks indicate species that were detected in the 2004 seed bank samples (Sullivan and Ellison 2006) but not in the 2010 seed bank samples.

described at the end of this section, seed rain data were pooled for the 5 years (2005–2009).

To standardize data across regeneration inputs (Fig. 1), we calculated the relative abundances of each species in the seed bank, seed rain, and herbaceous and sapling layers as the sum of all occurrences within each input — percent covers, numbers of seeds, or numbers of germinating recruits — divided by the total number of all occurrences. Because the majority of species were very rare (<1% relative abundance), relative abundances were computed only for the 14 most frequent genera observed in the combination of seed bank, seed rain, and field plots (*Acer*, *Betula*, *Pinus*, *Prunus*, *Quercus*, *Tsuga*, *Mitchella*, *Rubus*, *Viburnum*, *Aralia*, *Lysimachia*, *Maianthemum*, *Carex*, and *Juncus*; see Results). Although monilophytes and lycophytes comprised a significant portion of the regenerating flora, they were largely undetected in the seed bank (except for one species, *Dennstaedtia punctilobula* (Michx.) T. Moore, that could not be ruled out as a weedy greenhouse recruit) and thus were excluded from the analysis. When multiple species were recorded in a given genus (i.e., *Betula*, *Rubus*, *Carex*, *Juncus*, *Aralia*, and *Viburnum*), species were summed within that genus because they were very similar in physiognomy, successional status, and shade tolerance (with a possible exception of *Aralia hispida* Vent. and *Aralia nudicaulis* L.).

Initial analyses of block and treatment effects on germination were done using linear mixed models in which block was considered a random effect and treatment a fixed effect; *F* ratios for treatment effects were adjusted for the block term (Gotelli and Ellison 2012, p. 304). Comparisons of total numbers of seeds germinating in the three treatments were done using a χ^2 test. Kolmogorov–Smirnov tests were used to compare shapes of relative abundance distributions among the three canopy manipulation treatments. Kendall's coefficient of concordance was used to determine whether the rank abundance distributions of species in the seed rain differed among the three canopy manipulation treatments. Pairwise Chao–Sørensen abundance-based similarities (Chao et al. 2006) were computed among all possible pairings of species compositions of the seed bank, seed rain, herbs, and saplings. The two abundances of any pairwise comparison were considered significantly dissimilar if the bootstrapped 95% confidence interval on the similarity index did not include 1.0.

In addition to exploring and analyzing the responses of individual species, we assessed community-level responses using ordination and permutational multivariate analysis of variance (PERMANOVA) (Anderson 2001). We first computed a Bray–Curtis dissimilarity matrix from the data consisting of the relative abundance of the 14 most abundant genera in the seed bank, seed rain, herbaceous layer, and saplings from each treatment plot. We then modeled changes in the dissimilarity as a function of regeneration component and canopy treatment (both of which entered as fixed factors) and the continuous covariate was the time since treatment. The block effect entered the PERMANOVA model as a "stratum" that constrained the permutations. Significance tests were based on *F* tests from sequential sums-of-squares from 1000 permutations of the raw data.

Linear modeling was done with the lme function in the nlme library of the R statistical software, version 2.12.2 (R Development Core Team 2007). Chi-square tests were done with the chisq.test function in R's stats library, Kolmogorov–Smirnov tests that adjust for ties were done using the ks.boot function in R's Matching library, and concordance of ranked abundances of seed rain data among treatments was computed with the kendall function in R's irr library. Computations of Chao–Sørensen similarities and bootstrapped confidence intervals were done using EstimateS version 8.20 (Colwell 2006). Ordinations and PERMANOVA were done, respectively, using the cca and adonis functions in R's vegan library. For clarity of presentation, only means of the two replicate plots of each treatment are plotted for 2004 and 2010 seed bank and forest vegetation data and for the seed rain data; within-treatment standard deviations are included only for time series of herbaceous layer relative abundances. All raw data are available from the Harvard Forest data archive (http://harvardforest.fas.harvard.edu/data/archive.html), data sets HF-105 (seed bank and seed rain data), HF-106 (vegetation including herbs, shrubs, and trees), and HF-126 (canopy tree data).

Results

Composition of the seed rain

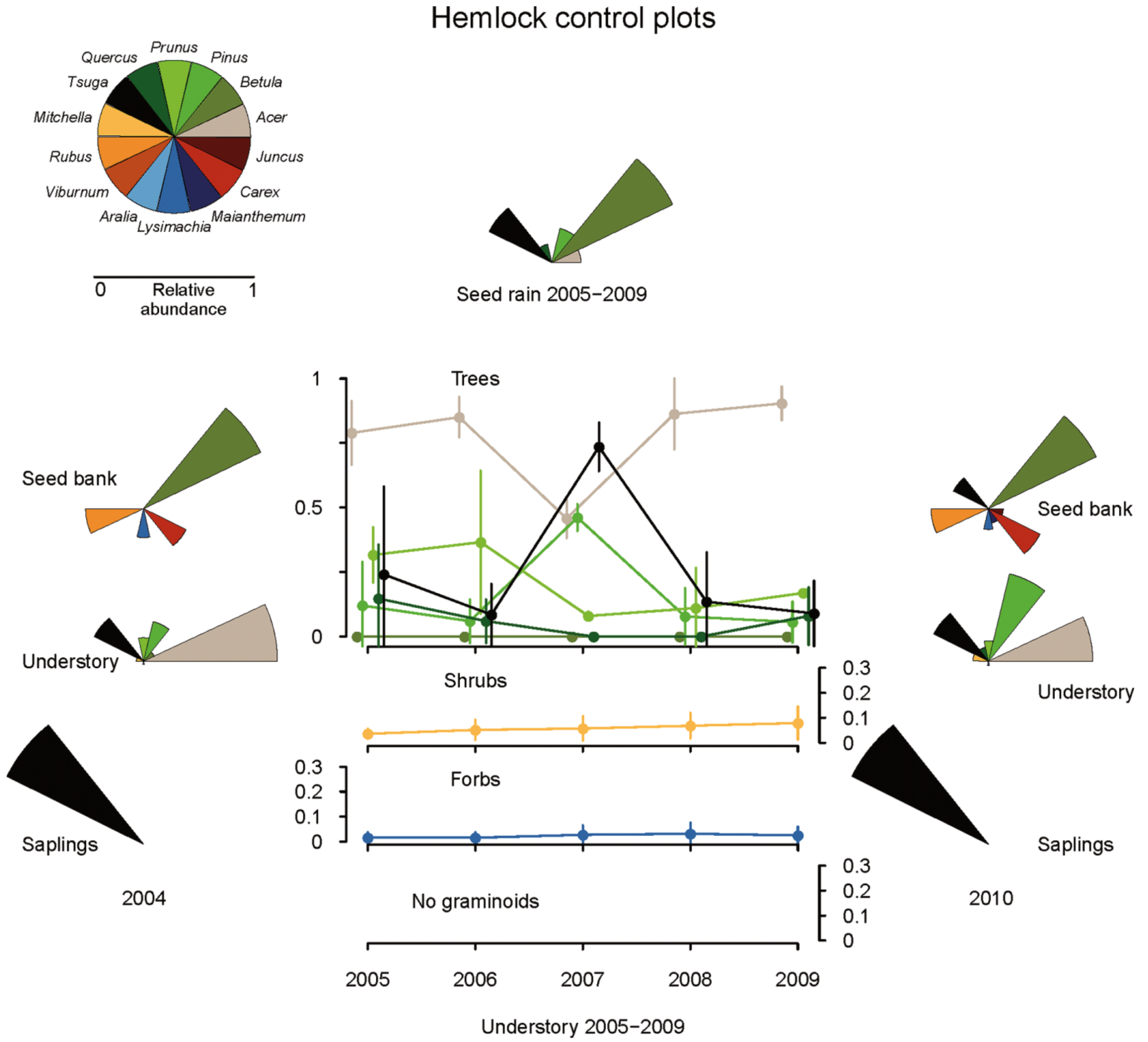
Seed rain composition from 2005 to 2009 was similar among all three treatments (compare graphs at the top of Figs. 2, 3, and 4; inset of Fig. 5). Although rank abundances shifted among a few of the rarer species among the treatments (Kendall's $W = 0.848$, df = 5, $p = 0.026$), there were no significant pairwise differences in the shapes of the relative abundance distributions between treatments (two-sample Kolmogorov–Smirnov test: hemlock control versus girdled, $D = 0.17$, $p = 1$; hemlock control versus logged, $D = 0.33$, $p = 0.93$; girdled versus logged, $D = 0.33$, $p = 0.93$), and Chao–Sørensen indices ranged from 0.99 to 1.00. The seed rain consisted primarily of *Betula* species (particularly *B. lenta*, relative abundance range 0.71–0.91), with much smaller proportions (0.04–0.09) of *T. canadensis* (top graphs in Figs. 2, 3, and 4; inset of Fig. 5). *Pinus strobus, Q. rubra*, and *A. rubrum* also appeared in multiple seed rain samples but at very low relative abundances: 0.02–0.06, 0.002–0.01, and 0.01–0.03, respectively. Spikes in seed production by *B. lenta*, reflected in absolute increases in seeds per quarter, occurred in 2006 and 2009, coinciding with more modest spikes in the same years by *T. canadensis* (data not shown). The other, much rarer taxa found in the seed rain were *Swida alternifolia* (L.f.) Small, *Fraxinus americana* L., *Nyssa sylvatica* Marsh., *Ostrya virginiana* (P. Mill.) K. Koch, *Polygonatum biflorum* (Walt.) Ell., *Rhus hirta* (L.) Sudworth, *Carex* sp., and *Vaccinium* sp.

Considering the common canopy tree species in our top 14 taxa, the similarity of the relative abundances of canopy species (2006–2009) to the relative abundances of species in the seed rain over the same period ranged from 0.998 to 1, so the relative abundance of seeds in the seed rain could be considered to be a reasonable proxy for the composition of species in the canopy (see also Table 1). *Quercus alba* L. and *Quercus bicolor* Willd. were rare members of the canopy that were not found in the seed rain, seed bank, or forest floor vegetation. *Fraxinus americana*, *N. sylvatica*, and *O. virginiana* were present in the seed rain (Table 1), but *N. sylvatica* was never found in any of the treatment plots.

Composition of the seed bank

Thirty-seven taxa germinated in the seed trays during 2010, of which two immature plants (*Gaultheria* cf. *hispidula* (L.) Muhl. ex Bigelow and *Carex* cf. *ovales* group) could only be identified definitively to genus (Fig. 6). Although the total species richness of the seed bank in 2010 (37 taxa) was greater than the 30 taxa recorded in 2004, the average per-treatment species richness (24 in the hemlock control, 21 in the girdled treatment, and 23 in the logged treatment) was nearly identical to those estimated by rarefaction for the pre-treatment control

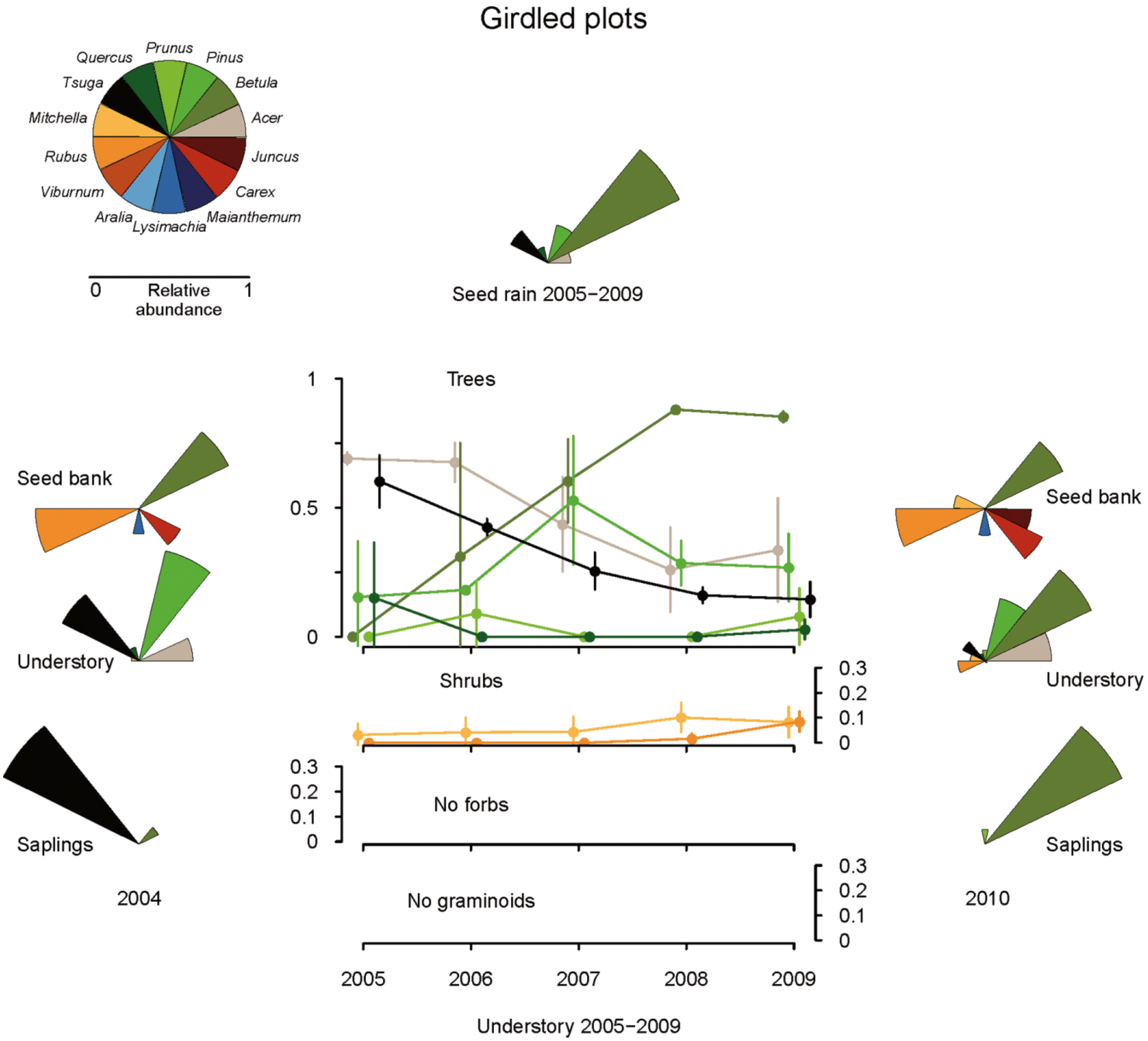
Fig. 2. Composition and relative abundances of the seed rain, seed banks in 2004 and 2010, understory layers and sapling layers in 2004 and 2010, and dynamics of forest understory species between 2005 and 2009 in the eastern hemlock (*Tsuga canadensis*) control treatment. Star plots depict relative abundances of the 14 most common genera in 2004 and 2010; seed rain relative abundances are summed over 2005–2009. Taxa are color coded by genus and life form (trees in greens, shrubs in oranges, forbs in blues, and graminoids in reds); see the color wheel legend at the upper left. For the purposes of visualizing rare taxa clearly, all relative abundances were square root transformed prior to plotting; note that this transformation disproportionately magnifies the relative abundance of rare species. The scale bar at the upper left indicates the length of a radius corresponding to 100% composition of a given species (relative abundance = 1). Note that no graminoids appeared in the understory between 2005 and 2009. Graphs in the center illustrate mean relative abundances (±1 SD) of the 14 most common genera in the two replicate plots within each treatment. Although all treatment plots were censused yearly at approximately the same time, the mean points are shown here slightly offset to allow the points and error bars to be distinguished. Taxa are grouped by life form (trees, shrubs, forbs, and graminoids) and color coding is as shown in the color wheel legend.



plots (24 species) in 2004. Species richness of germinants did not differ significantly among the three treatments in 2010 ($\chi^2 = 0.2$, df = 2, $p = 0.9$).

A total of 529 seedlings emerged in the seed bank trays in 2010; a linear mixed-effects model on log-transformed total germinants (+1) yielded a significant effect of block ($F = 5.01$, df = 1, 56, $p = 0.03$) but no effect of treatment ($F = 2.01$, df = 2, 56, $p = 0.14$). Germination totals were similar between 2010 and 2004 ($\chi^2 = 6.0$, df = 2, $p = 0.19$), with 195 seedlings in the girdled treatment (versus 162 in 2004), 143 in

Fig. 3. Composition and relative abundances of the seed rain, seed banks in 2004 and 2010, understory layers and sapling layers in 2004 and 2010, and dynamics of forest understory species between 2005 and 2009 in the girdled treatment. Species codes, scales, and legends are as in Fig. 2.

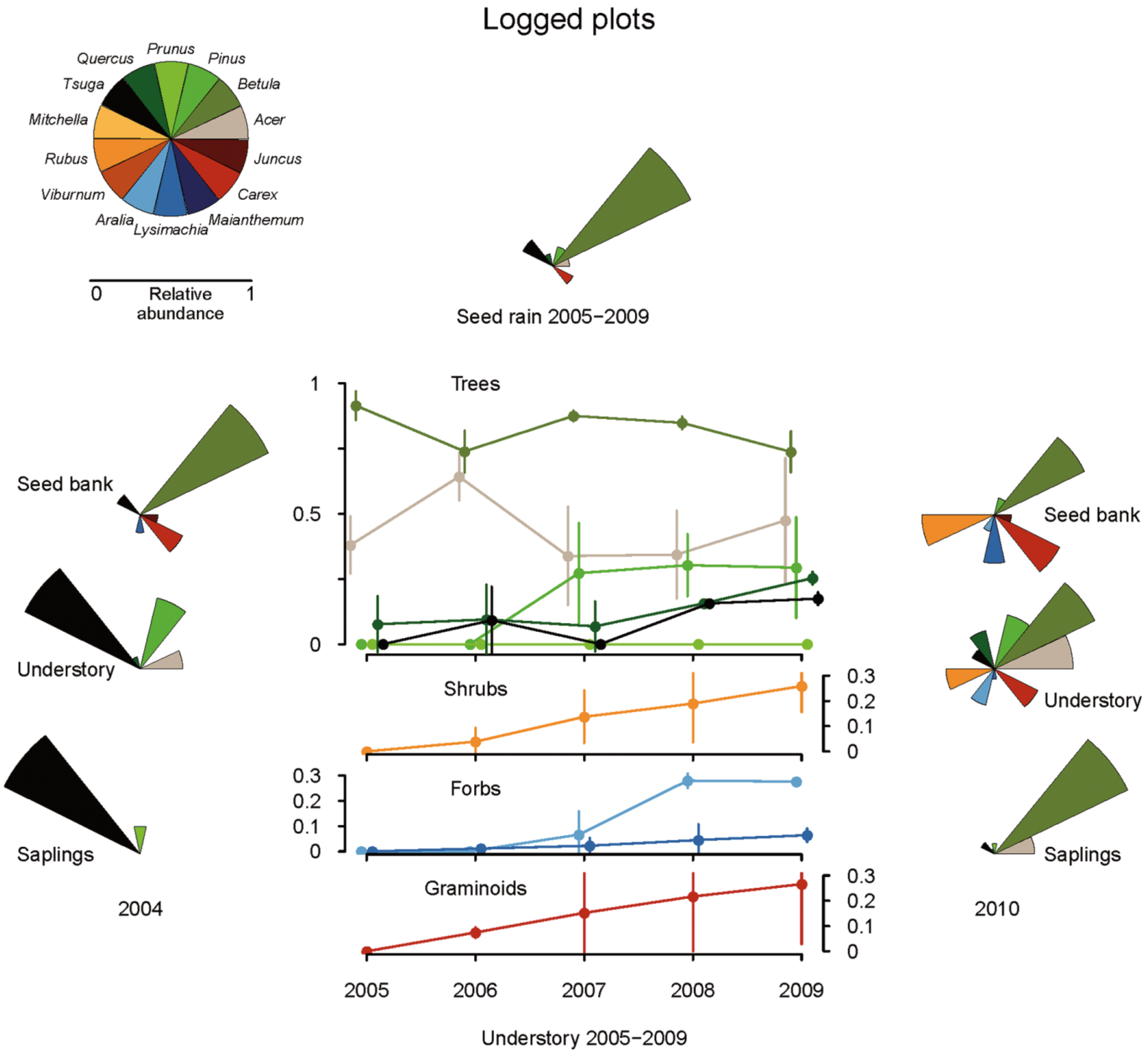


the logged treatment (versus 147), and 191 in the hemlock control treatment (versus 138). For the most common 14 genera identified among all of the regeneration input groups, the rank abundance distributions did not differ significantly between 2004 and 2010 in any of the treatments (hemlock control, $D = 0.21$, $p = 0.69$; girdled treatment, $D = 0.21$, $p = 0.58$; logged treatment, $D = 0.21$, $p = 0.68$). When we compared the composition of the seed bank in 2004 with the composition of the seed bank in 2010 in the control and each of the two canopy manipulation treatments, the seed banks of 2004 and 2010 were most similar in the hemlock control and least similar in the logged treatment (Table 2).

Seventeen species were observed in the seed bank in both 2004 and 2010. Of these, 13 were comparatively common and abundant throughout all of the samples (Fig. 6). Nine “new” species appeared in the 2010 control samples, eight in the samples from the girdled treatment, and 14 in samples from the logged treatment (Table 1). These recent arrivals in the seed bank were infrequent germinants that were also rarely documented from the standing vegetation, with the exceptions of *Phytolacca americana* L. (detected in one of the two girdled plots), *Rubus occidentalis* L. (in all treatments), and *Viburnum nudum* L. var. *cassinoides* (Torr.) A. Gray (in the logged and control treatments).

To test our hypothesis that shallow seed bank layers would contribute more substantially to standing vegetation than the deeper layers, we next compared the numbers and types of germinants emerging from the upper 0–10 cm strata (roughly corresponding to the O+A horizons) of each core with those emerging in the lower 10–20 cm deep stratum (roughly cor-

Fig. 4. Composition and relative abundances of the seed rain, seed banks in 2004 and 2010, understory layers and sapling layers in 2004 and 2010, and dynamics of forest understory species between 2005 and 2009 in the logged treatment. Species codes, scales, and legends are as in Fig. 2.



responding to the B horizon) (Fig. 6). The majority (57%) of the dominant taxa were present in both strata, including *B. lenta*, *Rubus* spp., *Lysimachia quadrifolia* L., *Carex pensylvanica* Lam., and *Juncus tenuis* Willd. However, several other forb and graminoid taxa emerged only from the 10–20 cm layer (Fig. 6), likely reflecting the agricultural past of these ±70-year-old hemlock stands (Kernan 1980; Bettmann-Kerson 2007). Similar species had germinated from the seed bank in 2004 (Sullivan and Ellison 2006); however, none of these taxa was observed in the standing vegetation of the treatment plots between 2004 and 2010 (Table 1). We also detected no significant differences in the rank abundance distributions of the most common 14 genera between the upper and lower strata (hemlock control, $D = 0.21$, $p = 0.69$; girdled treatment, $D = 0.14$, $p = 0.94$; logged treatment, $D = 0.14$, $p = 0.91$), and Chao–Sørensen similarities ranged from 0.652 (±0.300 SD) to 0.965 (±0.057), so we concluded that the upper horizons captured the most important species also found in the lower layer. We thus used data on species composition from the upper stratum in subsequent analyses of relative abundance. Examining the rank abundances of the top 14 genera germinating from the upper horizons, we found no significant differences in the rank abundance distributions between 2004 and 2010 (hemlock controls, $D = 0.43$, $p = 0.42$; girdled treatment, $D = 0.50$, $p = 0.36$; logged treatment, $D = 0.38$, $p = 0.48$). As with the full taxon pool, a linear mixed-effects model yielded a significant effect of block ($F = 7.6$, df = 1, 56, $p = 0.008$) but no effect of treatment ($F = 2.8$,

Fig. 5. Ordination biplot of the changes in the seed bank (2004 versus 2010) and trajectories of the seed rain, understory vegetation, and saplings (2004–2010) (replicates pooled across blocks). The different colors represent the different treatments: blue, eastern hemlock (*Tsuga canadensis*) control; dark yellow, girdled treatment; red, logged treatment, and the start and end of each trajectory are identified. Broken lines indicate seed dynamics (seed rain, seed bank) and solid lines indicate standing vegetation. The inset plot expands the lower right corner of the main biplot to more clearly show the trajectories of the saplings and seed rain, which otherwise overlap extensively in the main biplot. Species whose loadings are >0.1 are shown along the *x*- and *y*-axes.

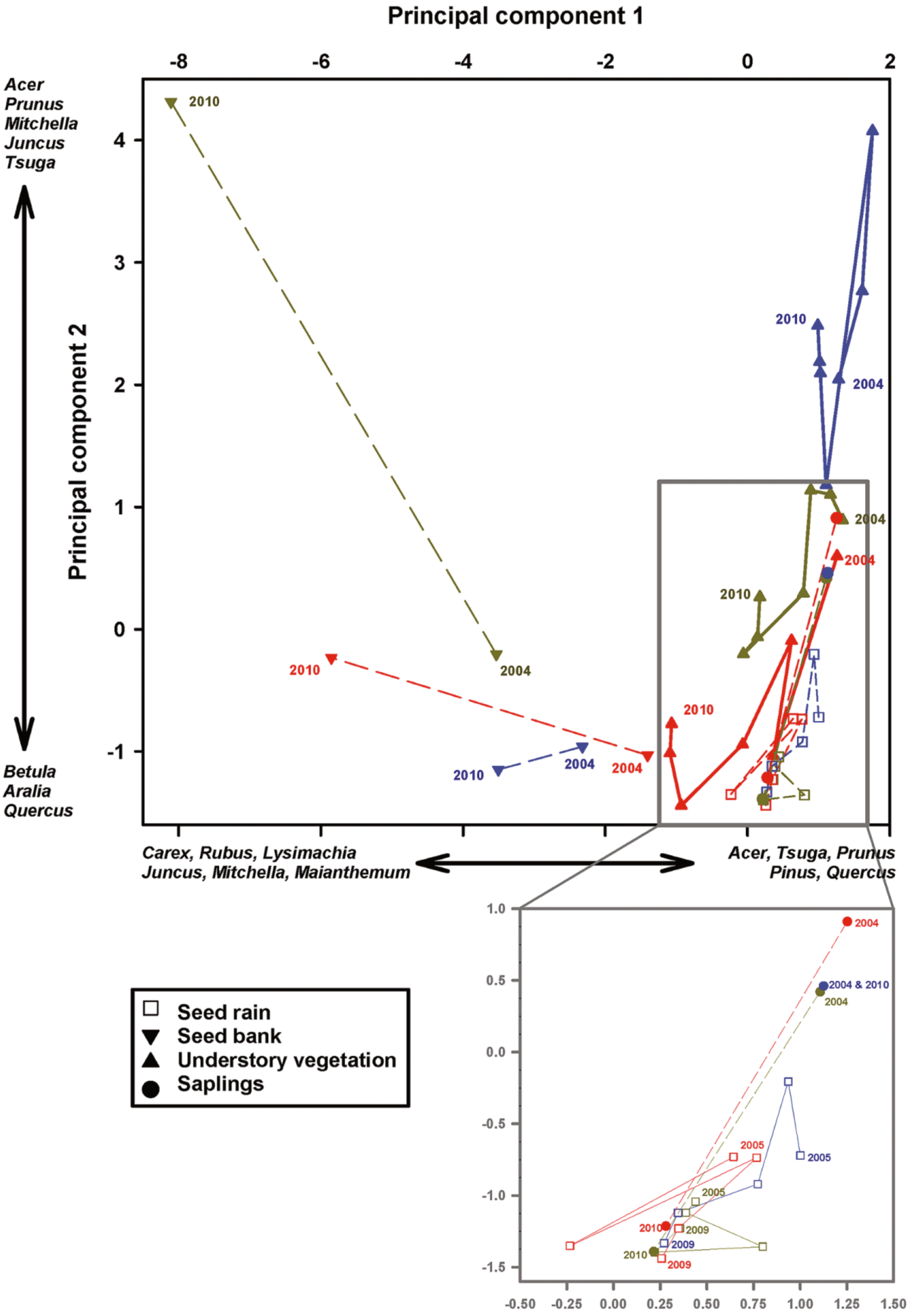
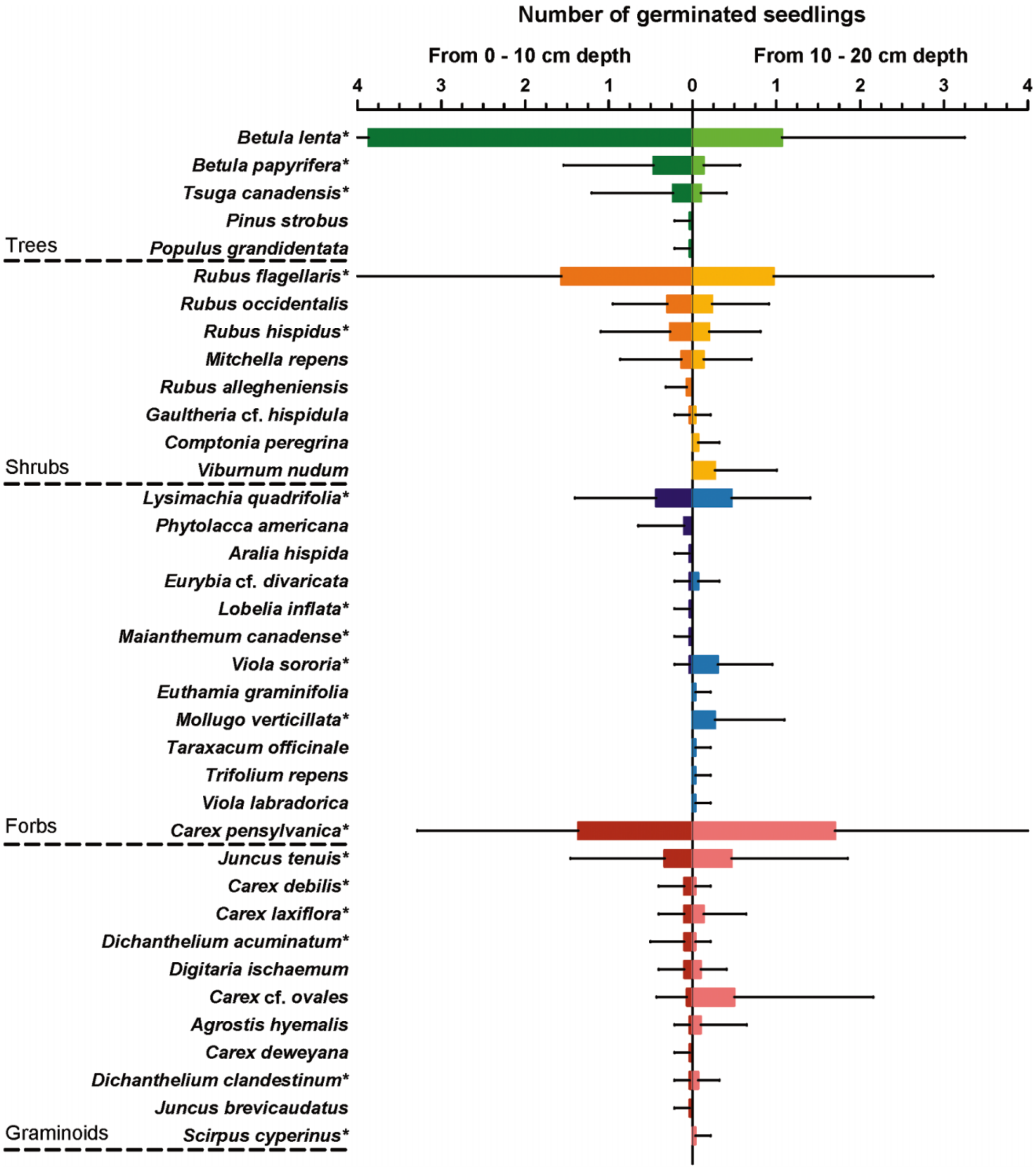


Fig. 6. Mean numbers of germinating seedlings (±1 SD) in the upper (0–10 cm depth) and lower (10–20 cm depth) soil strata in the 2010 seed bank trial pooled across all treatment types and replicates. Means on the left show the plants emerging from the upper 10 cm of the core; those on the right show those emerging from the 10–20 cm depth. Taxa are grouped by trees (greens), shrubs (oranges), forbs (blues), and graminoids (reds) and ordered within groups from most to least abundant in the upper stratum. Asterisks indicate taxa that were identified in both the 2004 and 2010 seed banks.



df = 2, 56, p = 0.064) on total germinants in the upper layer.

Composition of the standing vegetation

The hemlock control treatment contained the fewest overall numbers of forest floor species (21 recorded over the 6-year period), approximately half the species found in the girdled treatment (50) and the logged treatment (42) (Table 1). The three treatments did, however, share some species, including *A. rubrum* seedlings, *Mitchella repens* L., *Betula papyrifera* Marsh., *Q. rubra*, *Lysimachia borealis* (Raf.) U. Manns & A. Anderb., *Monotropa uniflora* L., and several monilophyte species (Table 1). The girdled treatment was most similar in species composition to the logged treatment (Chao–Sørensen index of similarity on species presence–absence S = 0.696) and least similar to the hemlock control treatment (S = 0.413); the logged and control treatments shared just under half of the species present (S = 0.438).

Changes in vegetation composition from 2004 to 2010

Star plots and time-series graphs of the relative abundances of the 14 common taxa in the seed bank, seed rain, herbaceous

Table 2. Pairwise similarities of seed bank composition (upper 10 cm stratum) in 2004 and 2010, forest floor vegetation and saplings in 2004 and 2010, seed rain from 2005 to 2009.

	Seed bank 2010	Understory 2010	Saplings 2010
Eastern hemlock (*Tsuga canadensis*) control treatment			
Seed rain 2005–2009	0.76	0.43	**0.32**
Seed bank 2004	0.94	**0.07**	**0.00**
Understory 2004	**0.42**	1.00	**0.14**
Saplings 2004	**0.13**	**0.24**	0.97
Girdled treatment			
Seed rain 2005–2009	0.46	0.93	0.91
Seed bank 2004	0.93	0.75	0.59
Understory 2004	**0.08**	0.78	**0.00**
Saplings 2004	**0.07**	0.88	**0.07**
Logged treatment			
Seed rain 2005–2009	0.77	0.63	0.98
Seed bank 2004	0.86	0.67	0.87
Understory 2004	**0.05**	**0.20**	**0.25**
Saplings 2004	**0.00**	**0.06**	**0.03**

Note: Seed bank and understory vegetation data were averaged across samples within treatment plots, and seed rain was summed across years within treatment plots so as to avoid pseudoreplication and achieve an appropriate Type I statistical error rate (Gotelli and Ellison 2012). Values are Chao–Sørensen abundance-based similarities (Chao et al. 2006) for the given pair. Values in bold are significantly different from 1.00; pairs were significantly dissimilar at the $\alpha = 0.05$ level based on computation of bootstrapped 95% confidence intervals.

layer, and sapling cohort illustrate the shifts in forest composition occurring in the control and two canopy manipulation treatments (Figs. 2, 3, and 4).

In the intact hemlock stands (Fig. 3), the forest floor vegetation remained stable through time and was very similar in 2004 and 2010 (Table 2). *Acer rubrum* predominated, along with slightly increasing proportions of *P. strobus* and occasional seedlings of *T. canadensis* and *Q. rubra*. A few *T. canadensis* saplings were observed in 2004 and 2010; no other species were present as saplings (Fig. 3). The vegetation in the control hemlock treatment in 2010 reflected a moderate influence of the seed rain (similarity = 0.43) (Table 2), which contained *T. canadensis* seeds (produced by the canopy) as well as *P. strobus*, *A. rubrum*, and *Q. rubra*. Although a large proportion of wind-dispersed *Betula* seeds were present in the seed rain (Fig. 2), the majority joined the seed bank but did not emerge as seedlings in the heavily shaded understory. The seed bank showed little similarity with the understory vegetation (similarity = 0.07) (Fig. 2; Table 2); light-demanding genera such as *Carex* and *Rubus*, although present in the seed bank, never appeared under the dense *T. canadensis* canopy in the control treatment.

In the girdling treatment, the pre-treatment 2004 understory was composed of *T. canadensis* seedlings, *P. strobus*, a lesser proportion of *A. rubrum*, and a small amount of *Q. rubra* and *M. repens* (Fig. 3). A few *Betula* saplings were also present in 2004 (Fig. 3); the 49 *T. canadensis* saplings initially present in the two treatment plots were killed by girdling. Although the composition of the seed rain recorded in the girdling treatment was very similar to that of the hemlock control (compare Figs. 2 and 3), the proportion of *T. canadensis* seed declined as the canopy trees gradually died. As in the hemlock control, the seed bank in the girdled treatment bore little resemblance to the forest floor vegetation in 2004 (Fig. 3) and also reflected minimal influence of the seed rain, except for the preponderance of *Betula*. By 2010, however, the seed bank may have contributed to the emergence of a small proportion of *Rubus* species and was much more similar to the forest floor composition overall (similarity = 0.75) (Table 2; Fig. 3). As the canopy gradually opened, *B. lenta* seedlings became more prominent in the regenerating vegetation as they germinated from the seed bank, joining *P. strobus*, *A. rubrum*, and *T. canadensis* seedlings produced by the dying canopy trees. *Betula lenta* comprised the majority of the sapling layer, with a small proportion of *Prunus* spp. recruiting (Fig. 3).

The logged treatment showed a dramatic increase in vegetation between 2004 and 2010, reflecting the sudden and nearly complete opening of the canopy (Fig. 4). Recruitment of new species commenced in 2006, 1 year after the two plots in this treatment had been logged, and accelerated in 2007. Before logging, the understory had comprised the same species as the other two treatment types, dominated by *T. canadensis*, with lesser proportions of *P. strobus*, *A. rubrum*, and *Q. rubra*. Seed rain over time, disproportionately dominated by *Betula*, was similar to that observed in the hemlock and girdled treatments, with the exception of a small amount of *Carex* spp. seed arriving in 2007, possibly transported by birds or wind. By 2010, the forest floor vegetation bore little resemblance to its former 2004 composition (similarity = 0.20) (Table 2; Fig. 4). The relative abundance distribution of the seed bank became increasingly even from 2004 to 2010 and more similar to the regenerating vegetation, as *Rubus*, *Carex*, *Aralia*, and *Lysimachia* became more prevalent over time (Fig. 4). Although *Prunus serotina* Ehrh. var. *serotina* and *T. canadensis* were the only sapling species found in the logged treatment in 2004 (Fig. 4), and these persisted after logging, they were quickly joined by an influx of *B. lenta* saplings and some *A. rubrum*. Thus, the 2010 sapling layer was highly dissimilar to the 2004 sapling profile (similarity = 0.03) (Table 2; Fig. 4). Overall, recruitment of new species, especially forbs and graminoids, took place much more rapidly in the logged treatment than in the girdled treatment.

Multivariate analyses

Canonical correspondence analysis (Fig. 5) revealed similar patterns to those observed in Figs. 2, 3, and 4. After 6 years, the seed bank of the girdled and logged treatments showed increased dominance of graminoids and forbs but was essentially unchanged in the hemlock control treatment. Similarly, vegetation trajectories in girdled and logged treatments moved towards assemblages dominated by forbs, herbs, and early-successional trees. The understory vegetation in the control treatment was similar in 2004 and 2010 but in the intervening years had moved around ordination space because of year-to-year variability in seedling recruitment and mortality. The first two axes of the ordination accounted for 43% of the variance in the data. PERMANOVA (with permutations constrained by blocks) of these data identified significant differences through time ($p = 0.001$) among regeneration inputs ($p = 0.001$), canopy manipulation treatment ($p = 0.001$), and the regeneration input × canopy treatment interaction ($p = 0.001$) (Table 3).

Table 3. Summary table of the results of the permutational multivariate analysis of variance (PERMANOVA) with permutations constrained by block.

Parameter	df	SS	MS	F (model)	r^2	p (> F)
Regeneration component	3	8.1	2.70	20.66	0.32	0.001
Canopy manipulation treatment	2	1.9	0.96	7.36	0.08	0.001
Year	1	1.6	1.60	12.22	0.06	0.001
Regeneration component × treatment	6	2.7	0.46	3.49	0.11	0.001
Residuals	83	10.9	0.13		0.43	
Total	95	25.2				

Note: This analysis models community-level responses (as a Bray–Curtis dissimilarity matrix) of the 14 most abundant genera in the seed bank, seed rain, herbaceous layer, and saplings in each treatment. Regeneration component is one of seed bank, seed rain, understory, or saplings, canopy manipulation is one of girdled, logged, or eastern hemlock (*Tsuga canadensis*) control, and year is one of 2004, 2005, 2006, 2007, 2008, 2009, or 2010; the block effect constrains the permutations in the PERMANOVA by entering the model as a “stratum”.

Discussion

We have demonstrated here an approach that can be used to create a conceptual model (Fig. 1) of the responses of a widespread temperate forest type to disturbances such as defoliation, irrupting insects, pathogens, or salvage logging. We have shown that reorganization of the herb, shrub, and sapling layers has taken place more slowly in the girdled treatment, exhibiting the gradual dieback typical of adelgid-infested stands, than in the logged treatment, where conditions changed abruptly. Our findings parallel those of other long-term studies of declining hemlock stands (Small et al. 2005; Eschtruth et al. 2006; Spaulding and Rieske 2010) and accord with Kizlinski et al. (2002) and Orwig et al. (2008), who found that logging resulted in faster and denser colonization by *B. lenta* than gradual mortality of the overstory due to the adelgid. Observations from the girdled treatment will continue to provide predictions of the responses of intact hemlock stands as the adelgid begins to infest them in coming years (Yorks et al. 2003; Ellison et al. 2010).

Before the onset of treatments in 2005, all hemlock plots, regardless of block, were very similar in species composition (Fig. 5). The canopy and understory both were dominated by *T. canadensis* and most other understory species were absent or suppressed. Following the treatments, we asked if and how the current vegetation differed between logged and girdled stands. By 2010, plots in the girdled and logged treatments were broadly similar in species composition but differed in two important respects. First, because all seedlings, saplings, and mature hemlocks were girdled, they slowly declined and by 2010, they comprised a negligible part of the vegetation in the girdled treatment. Plots in the logged treatment gained a small number of *T. canadensis* recruits, possibly contributed by seed rain from unharvested (<20 cm diameter) but reproductive trees or from trees just outside the treatment plots. Second, the abundance and species richness of forbs and graminoids increased in the logged treatment quite rapidly, beginning in earnest in 2007 (Figs. 4 and 5). In contrast, the slowly declining canopy of hemlocks in the girdled treatment suppressed recruitment of forbs and graminoids; even shrub recruitment was comparatively low but was accelerating as of 2010 (Figs. 3 and 5).

Next, we explored whether the initial compositions of the seed bank, seed rain, canopy, and forest floor vegetation were similar within and among treatments and observed whether the composition of these regeneration components diverged through time or among treatments. The seed bank composition in 2004 was dominated strongly by *Betula* spp. and bore little similarity to the standing vegetation composition. The composition and richness of the 2010 seed bank remained similar to the 2004 seed bank (Table 2), with some turnover in rare species and singletons (species represented by only a single seedling). The 2010 seed bank continued to differ in composition from the understory in the hemlock control treatment (Figs. 2 and 5). Studies comparing the composition of the seed bank and standing vegetation in intact forests usually find little correspondence, with Chao–Sørensen similarities typically <0.6 (reviewed by Hopfensperger 2007), and our data from our hemlock control treatment are no exception (Table 2; Figs. 2 and 5). Such disparities have been noted in previous studies of dense-canopy conifer forests dominated by *T. canadensis* (Catovsky and Bazzaz 2000) or other species (e.g., Berger et al. 2004; Eycott et al. 2006).

In the logged and girdled treatments, however, the composition of the standing vegetation became more similar over time to the seed banks of 2004 (Table 2) and 2010 (Figs. 3 and 4) as more species were able to establish under the open canopy. As disturbances create new opportunities for recruitment from the persistent seed bank, and the changing vegetation contributes increasingly to the seed bank in turn, similarities between the seed bank and the forest floor vegetation increase, as we observed in the girdled and logged treatments (Figs. 3 and 4). The preponderance of *B. lenta* seeds, plus the relative rarity of other taxa, led to higher similarity in the seed banks of all treatments between 2004 and 2010 (Table 2) than inspection of the relative abundance plots might suggest (Figs. 3 and 4). Nevertheless, the dissimilarity between 2004 and 2010 in the seed banks of the logged treatment was greater than in either the control or girdled treatments (Table 2). This finding was consonant with our predictions and leads to the further prediction that the future seed bank will continue to diverge in composition from the pre-treatment seed bank. In the long term, the seed bank composition of the girdled treatment should eventually come to resemble that of the logged treatment. Likewise, the more speciose standing vegetation in these two treatments will comprise a greater diversity of life forms than in intact hemlock stands as forbs, shrubs, and graminoids become more important. We also predicted, and observed, that the upper layers of the seed bank (0–10 cm depth) contributed more germinants and showed higher similarity to the regenerating vegetation than the lower depths.

A closed hemlock canopy suppresses regeneration from seed rain, whereas newly opened forests are conducive to regeneration from seed rain, especially if a few canopy trees or maturing saplings remain. We predicted, and observed, that similarity between the seed rain and the standing vegetation would increase as the canopy became a less important ecological filter, with the seed rain more strongly influencing the vegetation when a partial canopy remains and woody debris accumulates slowly (as in the girdled treatment). Overall, seed rain remained the predominant factor contributing to regeneration in the girdled treatment, whereas both the seed rain and the seed bank contributed recruits in the logged treatment. As the last girdled or adelgid-attacked hemlocks die, it will become more important to understand the composition of both seed rain and seed banks to make predictions about future forest composition. Likewise, we need to better understand the sources of recruiting monilophytes that can become very common in newly opened stands (Yorks et al. 2003); propagules of these species were generally undetected in the seed rain or seed bank.

Because we used consistent methods to measure the compositions of the seed bank, seed rain, and standing vegetation among years, our data on these different inputs could be tracked and compared through time to inform a general model of forest regeneration (Fig. 1). We caution that integrated studies such as this one are challenging to undertake and to interpret. The timing and frequency of monitoring of different vegetation pools in the HF-HeRE differed somewhat; for example, seed rain monitoring did not commence until after treatments were imposed, whereas before-and-after data were available for both the seed bank and the standing vegetation. Standing vegetation was censused annually, but seed bank composition was assessed at a 6-year interval — insufficiently frequent to permit development of a path analysis linking inputs and outputs (cf. Caballero et al. 2008). Finally, sampling took place at different spatial scales within treatment plots, from randomly located small soil cores for seed banks and litter baskets for seed rain to transects of 1 m × 1 m subplots for seedlings and herbaceous vegetation and larger 30 m × 30 m subplots for sapling counts. However, these sampling methods were appropriate for yielding accurate estimates of relative abundances and species composition of each vegetation component. Ideally, integrated long-term studies should be tightly coordinated in time and space to permit more rigorous quantitative comparisons and development of path models. Such coordination also will allow for species responses to be more mechanistically related to broader ecosystem responses (Yorks et al. 2003).

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