forests

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Foundation Species Loss and Biodiversity of the Herbaceous Layer in New England Forests

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Received: 4 November 2015; Accepted: 21 December 2015; Published: 25 December 2015
Academic Editor: Diana F. Tomback

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Abstract: Eastern hemlock (*Tsuga canadensis*) is a foundation species in eastern North American forests. Because eastern hemlock is a foundation species, it often is assumed that the diversity of associated species is high. However, the herbaceous layer of eastern hemlock stands generally is sparse, species-poor, and lacks unique species or floristic assemblages. The rapidly spreading, nonnative hemlock woolly adelgid (*Adelges tusgae*) is causing widespread death of eastern hemlock. Loss of individual hemlock trees or whole stands rapidly leads to increases in species richness and cover of shrubs, herbs, graminoids, ferns, and fern-allies. Naively, one could conclude that the loss of eastern hemlock has a net positive effect on biodiversity. What is lost besides hemlock, however, is landscape-scale variability in the structure and composition of the herbaceous layer. In the Harvard Forest Hemlock Removal Experiment, removal of hemlock by either girdling (simulating adelgid infestation) or logging led to a proliferation of early-successional and disturbance-dependent understory species. In other declining hemlock stands, nonnative plant species expand and homogenize the flora. While local richness increases in former eastern hemlock stands, between-site and regional species diversity will be further diminished as this iconic foundation species of eastern North America succumbs to hemlock woolly adelgid.

Keywords: *Adelges tsugae*; flora; Harvard Forest; herbaceous layer; species diversity; species richness; *Tsuga canadensis*; understory

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1. Introduction

Foundation species (*sensu* [1,2]) create and define ecological communities and ecosystems. In general, foundation species are found at the base of food webs [3] and exert bottom-up control on the distribution and abundance of associated biota [4]. Characteristics of foundation species include those of core species [5], dominant species [6], structural species [7], and autogenic ecosystem engineers [8], but none of the latter possesses all of the characteristics of a foundation species [2]. Because of these characteristics, the loss of a foundation species from an ecosystem can have dramatic, cascading effects on other species in the system; on ecosystem stability, resilience, and functioning; and can change our perception of the landscape itself [2].

There is no explicit or implicit magnitude or directionality of the effect of a foundation species on the ecosystem it creates. For example, assemblages of forest understory species in a system dominated by the foundation species *Agathis australis* (D.Don) Lindl. Ex Loudon (Auricariaceae; a.k.a. New Zealand kauri) are different from, but neither more nor less speciose, than forest understory assemblages in systems dominated by other conifers [9]. Alternatively, richness of associated species in an ecosystem defined by a particular foundation species can be greater or less than that of other ecosystems, and the loss of the foundation species could lead either to increased or decreased species richness of the entire associated assemblage [3]. Such variable effects have been found for alpine cushion plants, which have higher alpha (within-cushion) diversity than adjacent, open microhabitats [10–12] but lower beta (between-cushion) diversity [13]. These contrasting effects are thought to arise from creation of "safe sites" for stress-intolerant plants through the local amelioration of stress by cushion plants that simultaneously lead to more homogeneous assemblages on them [13]. In contrast, some perennial kelp species that create complex habitats and provide structure for associated epiphytes have locally negative effects on biodiversity in high stress environments, locally positive effects on biodiversity in less stressful environments, and overall negative effects on biodiversity at larger spatial scales [14].

Eastern hemlock (*Tsuga canadensis* (L.) Càrr.; Pinaceae) is a foundation species of eastern North American forests [2]. The herbaceous understory flora (*sensu* [15]) of hemlock forests is usually thought of as species poor [16–18], but this perception may be due to the much lower understory species richness in the more common second-growth hemlock forests relative to the higher-diversity understory of rare old-growth hemlock forests [19]. However, second-growth hemlock forests dominate the range of the species [20], and the foundation species in these forests is declining and dying rapidly as trees are infested and killed by the nonnative hemlock woolly adelgid (*Adelges tsugae* Annand) [20–22].

In this paper, we describe the effects of loss of eastern hemlock on the local and regional species richness and diversity of the associated forest understory flora. We focus on changes in understory species richness and diversity following experimental removal of the hemlock canopy in central Massachusetts, but place the work in the context of the broad geographic range of eastern hemlock in eastern North America. The impetus for this work came from two directions. First, we were interested in determining whether any rare plant species occur only in the understory of eastern hemlocks or if the loss of eastern hemlock resulted in new habitats for other rare plant species. Second, many of our students and colleagues seeing eastern hemlock forests for the first time are surprised by their species-poor understory. Their implicit expectation is that systems structured by foundation species should be more diverse than systems not structured by foundation species. Thus, we also aim here to provide a more nuanced picture of the interplay between a widespread foundation species and associated diversity at the local and landscape scales.

2. Materials and Methods

2.1. Eastern Hemlock

Tsuga canadensis (eastern hemlock; Pinaceae) is an abundant and widespread late-successional coniferous tree. It grows throughout eastern North America from Georgia north into southern Canada and west into Michigan and Wisconsin [17,20]. In forest stands of the cove forests in the southern part of its range, in mixed forests of New England and southern Canada, and along riparian corridors throughout its >10,000 km^2 range, eastern hemlock can account for >50% of the total basal area [17,23]; see [2,24–26] for detailed discussions of the foundational role of eastern hemlock in stands where it is the dominant species. The forest floor beneath the eastern hemlock canopy is cool and dark [16,27], and the slowly decomposing hemlock needles give rise to a deep organic layer, which is very acidic and low in nutrients [28]. Unique faunal assemblages, including groups of birds [29], arthropods [30–32], and salamanders [33] live in eastern hemlock stands. Fungal diversity in eastern hemlock stands rarely have been studied, but in general is at best equal to, and generally lower than, that in deciduous forests [34–36]. Similarly, both plant diversity and abundance of the species in the herbaceous layer of hemlock understories are low. However, the seed bank and the few established seedlings and saplings respond rapidly to loss of eastern hemlock from disturbances ranging from individual tree falls to wholesale death or removal of entire stands [16,18,25,37–39].

2.2. The Harvard Forest Hemlock Removal Experiment

As part of a long-term, multi-hectare experiment aimed at identifying the effect of loss of eastern hemlock [24], we have documented the response of the herbaceous layer to two different mechanisms of hemlock loss. This Harvard Forest Hemlock Removal Experiment (HF-HeRE) is described in detail in [24]; key details are reiterated here.

HF-HeRE is located in the ≈150-ha Simes Tract (42.47°–42.48° N, 72.22°–72.21° W; 215–300 m above sea level) at the Harvard Forest Long Term Ecological Research Site in Petersham, Massachusetts (complete site description is in [40]). The experiment consists of two blocks, each of which has four ≈ 90 × 90-m (≈0.81-ha) plots. The treatments applied to each plot include: girdling all eastern hemlock individuals (from seedlings to mature trees) to simulate the progressive death-in-place of trees caused by the hemlock woolly adelgid; logging all eastern hemlock individuals ⩾20 cm diameter at breast height (DBH, measured 1.3 m above ground), along with some additional merchantable cordwood (black birch: *Betula lenta* L.; red maple: *Acer rubrum* L.) and sawtimber (red oak: *Quercus rubra* L.; white pine: *Pinus strobus* L.), to simulate a typically intensive level of pre-emptive salvage harvesting; and unmanipulated hemlock controls. Each block also includes a hardwood control dominated by black birch (*Betula lenta* L.) and red maple (*Acer rubrum* L.) that represents the young stands expected to replace eastern hemlock as it is lost from the forests of northeastern North America [41].

When HF-HeRE was established in 2003, the hemlock woolly adelgid had not yet colonized the forest interior at Harvard Forest. As we expected it to eventually colonize our hemlock control plots, HF-HeRE was designed explicitly to contrast the effects on these forests from physically disintegrating trees (resulting from girding them) with removal of them from the site (following logging). Since the adelgid colonized the hemlock controls—which occurred in 2009 and 2010—we have been able to contrast the effects of physical disintegration of eastern hemlock (in the girdled plots) with the effects of the adelgid (in the hemlock control plots), which includes not only physical disintegration but also changes caused by the adelgid directly, including, e.g., nitrogen inputs [42,43].

2.3. The Herbaceous Layer

In 2003, prior to canopy manipulations, we established two transects running through the central 30 × 30 m of each canopy manipulation plot and the associated hemlock and hardwood control plots to quantify understory richness, cover, and density. Five 1-m^2 subplots were spaced evenly along each transect and have been sampled annually since 2003. In each subplot, percent cover of herbs, shrubs, ferns and grasses was estimated to the nearest one percent. Grasses and sedges were identified only to genus as most lacked flowers or fruits necessary for accurate species-level identification. Each year, we also noted all understory species occurring in the entire central 30 × 30-m area of each plot; these incidence-level data encompass not only relatively common species enumerated along our sample transects but also the more uncommon species. Nomenclature follows [44]. Data reported herein were collected at HF-HeRE from 2003 through 2014.

We estimated species diversity in the different treatments from the incidence data (*i.e.*, presence-absence data in the entire 30 × 30-m central area of each plot) using Hill numbers [45]; comparisons among plots used previously published methods [46,47]. Changes in similarity and composition of herbaceous assemblages were examined using principal components analysis on centered and standardized percent cover data (collected along the two transects within each plot). All analyses were done using the R statistical software system [48], version 3.2.2 and routines within the *SpadeR* package [49] for diversity calculations, prcomp within the *stats* library for principal components analysis; and aov and TukeyHSD within the *stats* library for repeated-measures (random-effects) analysis of variance. Data and code are available from the Harvard Forest Data Archive, dataset HF106 [50].

3. Results and Discussion

3.1. The Response of the Herbaceous Layer to Experimental Removal of Eastern Hemlock

In total and across all years, we found 73 shrub, herb, graminoid, and fern/fern-ally species growing in the eight experimental plots (complete list of species is in [50]). Observed species richness in the herbaceous layer (pooled across all years) was highest in the girdled and hardwood control plots, and lowest in the hemlock control plots (Table 1). Estimated diversity (as Hill numbers of richness, Shannon diversity, and Simpson's diversity) was significantly lower in the hemlock controls than in the other three canopy-manipulation treatments (Table 1). Mean pairwise similarity between canopy manipulation treatments of the herbaceous layer averaged 0.55 (Figure 1). The herbaceous layers of the girdled and logged treatments were most similar (Jost's D = 0.824), whereas, they were the least similar between the hemlock control and the logged plots (D = 0.383). Although the number of shared species (bracketed numbers in Figure 1) varied four-fold among pairs of treatments, pairwise similarities were related neither to the total number of understory species (Table 1) nor to the numbers of shared species (Figure 1).

Table 1. Species richness (all years pooled) in the Harvard Forest Hemlock Removal Experiment. Values given are number of incidences (occurrences of species in both plots of each canopy manipulation treatment), number of species observed (S_{obs}), and estimated Hill numbers (95% confidence intervals) for species richness (${}^0q$), Shannon diversity (${}^1q$), and Simpson's diversity (${}^2q$).

	Incidences	S_{obs}	${}^0q$	${}^1q$	${}^2q$
Hemlock control	188	18	19.9 (16.9, 23.0)	15.9 (14.8, 17.1)	14.9 (13.4, 16.8)
Girdled	388	53	54.2 (45.0, 63.5)	42.8 (39.5, 46.0)	36.7 (33.3, 40.0)
Logged	305	38	50.2 (17.7, 82.8)	30.4 (27.2, 33.5)	25.9 (23.1, 28.7)
Hardwood control	616	51	52.6 (40.0, 65.2)	41.1 (39.1, 43.1)	37.2 (35.0, 39.4)
All treatments pooled	1497	73	73.5 (73.0, 81.4)	53.8 (50.2, 54.9)	43.2 (39.3, 44.6)

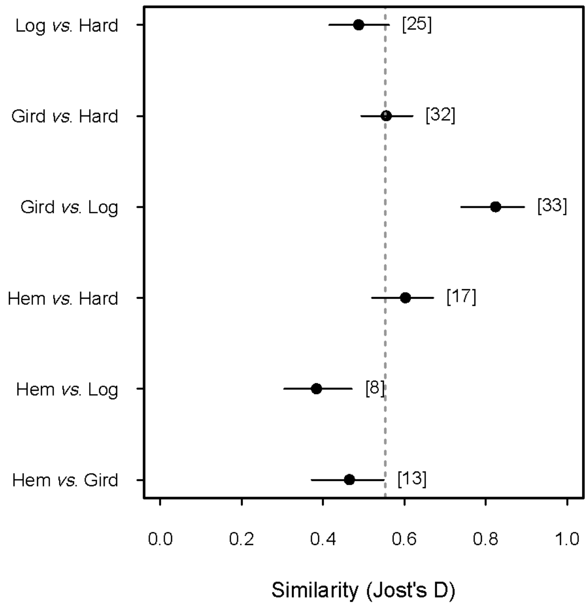

Figure 1. Pairwise similarities in understory species composition (with 95% confidence intervals) between the canopy manipulation treatments in the Harvard Forest Hemlock Removal Experiment. Abbreviations for treatments are: Hem—Hemlock controls; Gird—Hemlocks girdled; Log—Hemlocks cut and removed; Hard—Hardwood controls. Numbers in brackets are the total number of shared species for each pairwise comparison, and the grey dashed line is the average overall pairwise similarity.

The vegetation composition in the herbaceous layer varied substantially among the four canopy manipulation treatments and through time (Figure 2). The first three principal axes accounted for 50% of the variance in vegetation composition, and visual examination of the scree plot suggested that subsequent axes were uninformative. Of the 49 shrub, herb, graminoid, fern, and fern-ally species identified in the sampled transects across all plots, only 18 loaded heavily on the first three principal axes (absolute value of their loading $\geqslant 0.25$), and these "important" taxa segregated cleanly among them (Table 2). In Figure 2, principal axis 1 emphasizes understory herbs that are common in all plots, including hemlock-dominated ones, whereas principal axes 2 and 3 have taxa that are more common in early- to mid-successional mixed forests stands (e.g., *Epigaea repens*, *Rhododendron periclymenoides*, *Dyropteris carthusiana*, and *Carex* spp.) or commonly recruit after disturbance (such as the two *Rubus* species, *Panicum* sp., and the nonnative *Berberis thunbergii*) (Table 2). No state-listed rare, threatened, or endangered taxa were found in any of the plots.

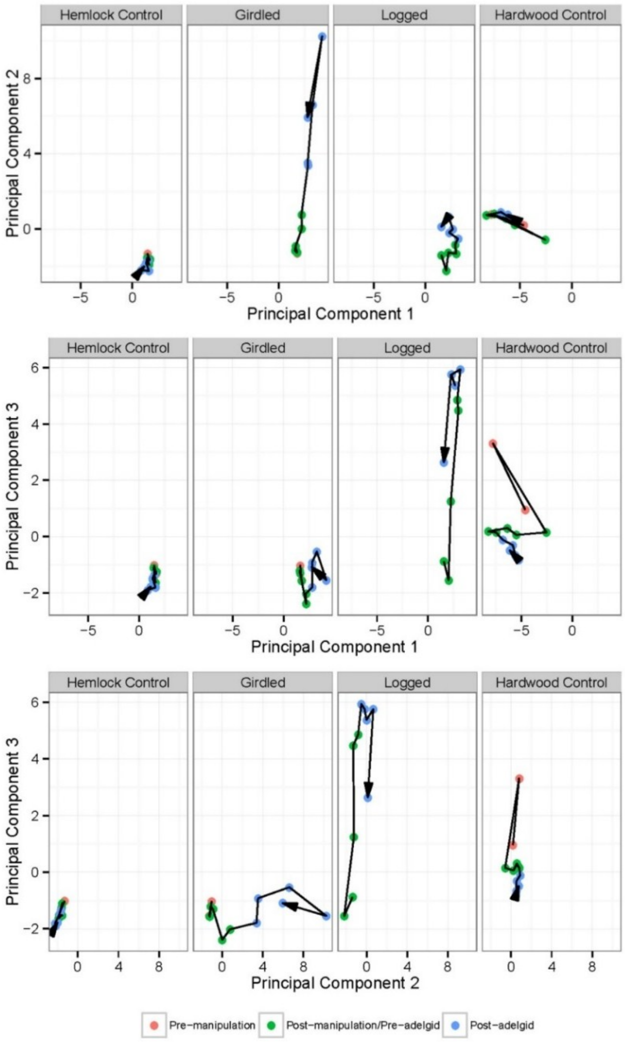

Figure 2. Temporal trajectories of understory vegetation composition in principal components space in the Harvard Forest Hemlock Removal Experiment. Each point represents the vegetation composition in a given year, and the line traces the trajectory through time from before canopy manipulations (2003–2004: red points), after manipulations but prior to adelgid colonization of the plots (2005–2009: green points), and after the adelgid had colonized the plots (2010–2014: blue points). In four of the panels (PC1 *vs.* PC2 for the girdled plots, and all three panels for the logged plots), the 2003–2004 vegetation composition was not distinguishable from the 2005 data and so the red symbols are not visible.

Table 2. Loadings of species on each of the three principal components axes illustrated in Figure 2. Only species for which the absolute value of the loading ⩾0.25 are shown.

Species	PC-1	PC-2	PC-3
Aralia nudicaulis L.	−0.26		
Dendrolycopodium obscurum (L). A. Haines	−0.26		
Lysimachia borealis (Raf.) U. Manns & A. Anderb.	−0.25		
Berberis thunbergii DC.		0.36	
Lonicera canadensis Bartr. Ex Marsh.		0.36	
Dryopteris carthusiana (Vill.) H.P. Fuchs		0.32	
Ilex verticillata (L.) Gray		0.32	
Osmundastrum cinnamomeum (L.) C. Presl		0.31	
Epigaea repens L.		0.31	
Viburnum acerifolium L.		0.31	
Rhododendron periclymenoides (Michx.) Shinners		0.26	
Lysimachia quadrifolia L.			0.38
Carex sp.			0.34
Rubusallegheniensis Porter			0.31
Araliahispida Veng.			0.30
Rubusidaeus L.			0.28
Carex cf. *pennsylvanica* Lam.			0.28
Panicum sp.			0.27

The overall impression from Figure 2 is that the understory of the hemlock control plots has been relatively stable through time, a result that is attributable primarily to its low species richness and the sparseness of what is there. We expect this to change as the overstory declines in coming years. The young hardwood control stands, in contrast, exhibit more temporal changes, both because the understory has more species and more cover to begin with, and because of the interaction of canopy closure as the trees grow and new gap creation from treefalls.

Repeated-measures analysis of variance (with pre-manipulation, post-manipulation/pre-adelgid infestation, and post-adelgid as the repeating groups or "temporal strata") revealed that principal axis 1 scores differed among the canopy manipulation treatments (Table 3). The first principal axis scores of the hardwood controls were significantly lower ($p \leqslant 0.05$, all pairwise comparisons using Tukey's HSD test) than the other three canopy manipulation treatments (Hemlock Control = Girdled = Logged < Hardwood Control) and these comparisons did not change after treatments were applied or the adelgid colonized the plot (Table 3). In contrast, principal axis 2 scores were significantly different for all four canopy manipulation treatments (Girdled > Hardwood Control > Hemlock Control = Logged), and differed significantly after the adelgid had colonized the plots relative to the preceding 7 years (Pre-treatment = Post-treatment/pre-adelgid < Post-adelgid). Finally, there were significant differences among canopy manipulation treatments for principal axis 3 (Logged > Hardwood Control > Girdled = Hemlock Control). The differences in PC-2 and PC-3 between canopy manipulation treatments were most dramatic in pairwise comparisons between treatments after the adelgid had colonized the plots relative to the previous two temporal strata (Figures 3 and 4; nested terms in Table 3).

These experimental results support earlier results that showed a rapid increase in seedling germination [38,39], density [18,25] and diversity [18,25,37] as hemlock dies and light levels at the forest floor increase [27]. Unexpectedly, however, the composition of the herbaceous layer shifted further after the adelgid colonized the plots, albeit unevenly across treatments (*i.e.*, the significant term representing canopy manipulation treatment nested within temporal stratum). The difference in interaction terms observed in PC-2 (Figure 3) most likely reflects a rapid decline in light levels of the understory in the girdled plots as birch saplings are growing exponentially [25]. This growth is occurring concomitantly with adelgid infestation in the hemlock controls. Although we have observed steady increases in light in the hemlock control plots as the adelgid increased in abundance [51], this is not yet strongly affecting understory vegetation in the hemlock controls. We expect that in coming years, additional nonlinear changes in soil N in the hemlock control plots as a function of the adelgid, as suggested by [42,43] and observed by [51] may affect understory composition. Soil N initially increases because carbon sloughing off from the waxy coating of the adelgid provides additional energy for microbial N immobilization of the relatively N-rich needles of infested trees [42]. Consequently, Nitrogen fluxes initially decrease with infestation, but later rise as hemlock declines and is replaced by deciduous trees, whose litter has a higher percentage of N [42]. The differences in interaction terms for PC-3 (Figure 4) suggest increased rate of succession following logging, as the small hemlocks that were not removed during the logging operation have not yet succumbed to the adelgid.

Table 3. Results of repeated-measures ANOVA on the first three principal axis scores of vegetation composition in the Harvard Forest Hemlock Removal Experiment. Factors include three temporal strata (pre-manipulation (2003–2004); post-manipulation but prior to adelgid colonization (2005–2009); and after the adelgid had colonized the plots (2010–2014)) and four canopy manipulation treatments (hemlock control, girdled, logged, and hardwood control). To account for the repeated measures, canopy manipulation treatments are nested within temporal strata.

Response	Factor	df	MS	F	*P*
PC-1	Temporal stratum	2	1.05	1.21	0.31
	Treatment	3	196.21	226.23	<0.001
	Treatment within stratum	6	0.76	0.88	0.52
	Residual	36	0.87		
PC-2	Temporal stratum	2	22.95	21.68	<0.001
	Treatment	3	33.31	31.47	<0.001
	Treatment within stratum	6	14.87	14.05	<0.001
	Residual	36	1.06		
PC-3	Temporal stratum	2	3.40	2.53	0.09
	Treatment	3	44.97	33.44	<0.001
	Treatment within stratum	6	10.66	7.93	<0.001
	Residual	36	1.34		

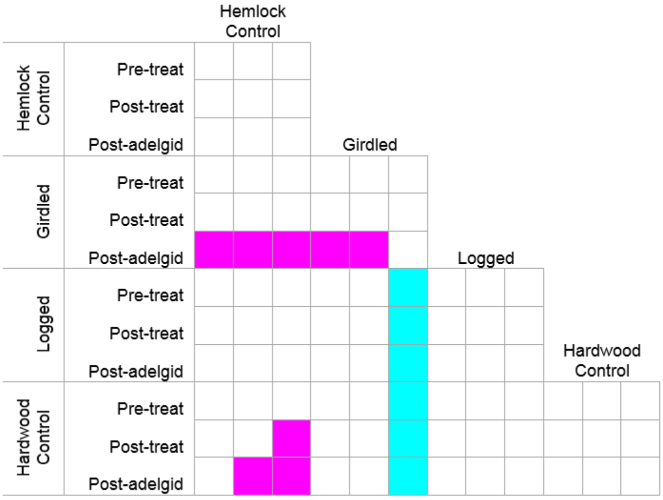

Figure 3. *Post-hoc*, pair-wise comparisons (Tukey's Honest Significant Difference Test) of the response (principal axis 2) to canopy manipulation treatments (hemlock control, girdled, logged, and hardwood control) repeated within temporal strata (pre-manipulation (2003–2004); post-manipulation but prior to adelgid colonization (2005–2009); and after the adelgid had colonized the plots (2010–2014)). For each pair-wise comparison, differences between PC-2 of a given row and PC-2 of a given column are significantly greater than (magenta) or less than (blue) zero ($p \leqslant 0.05$).

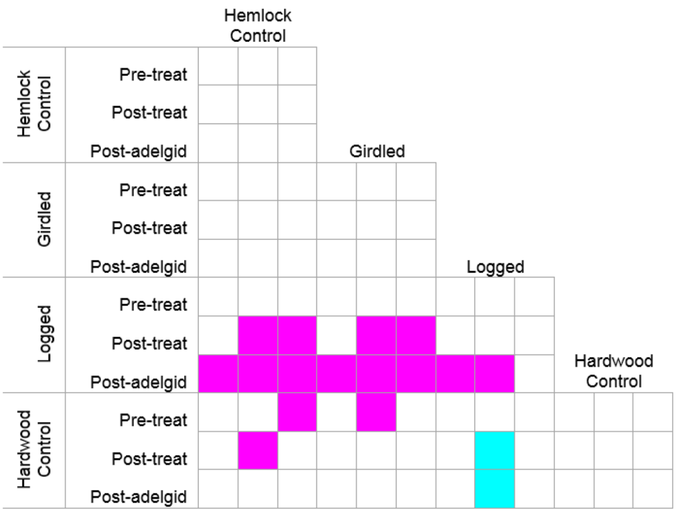

Figure 4. *Post-hoc*, pair-wise comparisons (Tukey's Honest Significant Difference Test) of the response (principal axis 3) to canopy manipulation treatments (hemlock control, girdled, logged, and hardwood control) repeated within temporal strata (pre-manipulation (2003–2004); post-manipulation but prior to adelgid colonization (2005–2009); and after the adelgid had colonized the plots (2010–2014)). For each pair-wise comparison, differences between PC-3 of a given row and PC-3 of a given column are significantly greater than (magenta) or less than (blue) zero ($p \leqslant 0.05$).

3.2. The Herbaceous Layer in Other Eastern Hemlock Stands

Substantial differences in the herbaceous flora of eastern hemlock stands relative to nearby stands dominated by other conifers or mixed hardwood have been documented repeatedly [16–19,52–54]. In Indiana, Daubenmire placed 25 1-m^2 quadrats in hemlock forest and found only one species of herb (*Monotropa uniflora* L.), no shrubs, and three trees [16]. In nearby beech-maple forests, however, he found 14 species of herbs, four shrubs, and seven trees. He also noted that *Monotropa* growing in the forest understory "was as dominant in the Hemlock as Sugar Maple was in the Beech-Maple" [16]. Likewise, under hemlocks growing in southeast Ohio, the ground-layer was >80% bare ground, and herbaceous species richness was correspondingly low [54].

Although the herbaceous flora in hemlock stands of southeast North America is much richer than that in the northeastern part of hemlock's range, it also is species poor relative to nearby hardwood stands. Unlike in the northeast, however, the herbaceous layer of southeast hemlock forests has been found repeatedly to be distinctive [52,53,55]. In the southeast, *Rhododendron maximum* L. can grow in dense thickets, and the shrub *Leucothoe fontanesiana* (Steud.) Sleumer, the ground-creeping *Mitchella repens* L. and the herb *Hexastylis shuttleworthii* (Britten and Baker f.) Small are predictably associated with hemlock stands [17,20].

Prior to the arrival in the 1980s of the hemlock woolly adelgid in northeast North America [21], intact hemlock stands from Wisconsin (USA) to Nova Scotia (Canada) had an average percent cover in the herbaceous layer of ≈5% and consisted primarily of common species [17]. Furthermore, these stands had no compositionally distinctive groups of understory species. Rather, all herbaceous-layer species growing in these hemlock stands also were found in northern mixed hardwood stands [17]. In contrast, many herbaceous species common in mixed hardwood stands were rare in hemlock-dominated stands [17].

When individual eastern hemlock trees die, fall, and form gaps, species richness of the herbaceous layer increases rapidly [16,18,34]. Early studies of the herbaceous flora of hemlock forests were done in what were thought to be "climax" [16], "old-growth" [18] or "virgin" [52,53] stands. Gap creation in old-growth stands in Wisconsin led to increases in richness and cover of herbaceous species in gaps relative to intact forest [18]. This result was echoed by those of D'Amato *et al.* [19]

in relict old-growth stands in Massachusetts (USA). Although these old-growth hemlock stands supported twice the number of understory species and had four times the understory vegetation cover as nearby second-growth hemlock stands [19], these differences were attributable to small-scale disturbances (treefall gaps, self-thinning), leading to lower density canopies and more light reaching the forest floor. Such gap dynamics also alter understory diversity in hardwood-dominated stands (Figure 2).

Similar responses occur when entire stands of hemlock are killed by the hemlock woolly adelgid. For example, between 1994 and 2006, up to 42% of individuals died from adelgid infestation in hemlock stands in the Delaware Water Gap National Recreation Area [56]. During this interval, species richness and cover of bryophytes (mosses and liverworts) more than doubled, in large part because of the amount of new habitat (dead and fallen branches and boles) and higher light availability on streambanks. In the same plots, all understory ferns, herbs (except for *Streptopus amplexifolius* (L.) DC), shrubs, and trees increased in occurrence and abundance as hemlock declined [57]. At the same time, there was a large increase—further accelerated by increasing density of deer—in abundance of nonnative species, including *Ailanthus altissima* (P.Mill.) Swingle, *Alliaria petiolata* (M. Bieb) Cavara and Grande, *Berberis thunbergii*, *Microstegium vimineum* (Trin.) A.Camus, and *Rosa multiflora* Thunb. ex Murray [58].

4. Conclusions

In sum, observational and experimental data illustrate that the herbaceous layer of eastern hemlock stands generally is sparse and species-poor. With few exceptions, hemlock stands have not been found to have a unique set of associated understory species. Rather, species that are common in the hemlock understory also are common in mixed hardwood stands, whereas other species that are common in mixed hardwoods are uncommon in hemlock stands. Death of individual hemlock trees or of whole stands routinely leads to rapid increases in species richness and percent cover of shrubs, herbs, graminoids, ferns, and fern-allies.

What is lost besides hemlock, however, is variability in the structure and composition of the herbaceous layer. In the Harvard Forest Hemlock Removal Experiment, initial removal of hemlock by either girdling or logging, and subsequently by the hemlock woolly adelgid led to a proliferation of early-successional and disturbance-dependent understory species. In other declining hemlock stands, nonnative species expand and homogenize the flora. While local richness increases, between-site and regional species diversity can be expected to decline further as eastern hemlock—an iconic foundation species of eastern North America—is lost from many forest stands.

Acknowledgments: We thank Diana Tomback for inviting us to prepare this contribution. A.M.E. and A.A.B.P.'s work on hemlock forests is part of the Harvard Forest Long Term Ecological Research (LTER) program, supported by grants 06-20443 and 12-37491 from the US National Science Foundation. S.K. was supported by a scholarship from the Higher Education Commission of Pakistan. Ally Degrassi pointed us to useful background references, and Simon Smart and two anonymous reviewers provided helpful comments on the initial submission. This paper is a contribution of the Harvard Forest LTER program.

Author Contributions: A.M.E. and A.A.B.P. conceived of the study, did data analysis, and co-wrote the paper. A.A.B.P. and S.K. collected and organized the data, and co-wrote the paper.

Conflicts of Interest: The authors declare no conflict of interest.

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