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ARTICLE

Logging response alters trajectories of reorganization after loss of a foundation tree species

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Abstract

Forest insect outbreaks cause large changes in ecosystem structure, composition, and function. Humans often respond to insect outbreaks by conducting salvage logging, which can amplify the immediate effects, but it is unclear whether logging will result in lasting differences in forest structure and dynamics when compared with forests affected only by insect outbreaks. We used 15 years of data from an experimental removal of *Tsuga canadensis* (L.) Carr. (Eastern hemlock), a foundation tree species within eastern North American forests, and contrasted the rate, magnitude, and persistence of response trajectories between girdling (emulating mortality from insect outbreak) and timber harvest treatments. Girdling and logging were equally likely to lead to large changes in forest structure and dynamics, but logging resulted in faster rates of change. Understory light increases and community composition changes were larger and more rapid in the logged plots. Tree seedling and understory vegetation abundance increased more in the girdled plots; this likely occurred because seedlings grew rapidly into the sapling- and tree-size classes after logging and quickly shaded out plants on the forest floor. Downed deadwood pools increased more after logging but standing deadwood pools increased dramatically after girdling. Understory light levels remained elevated for a longer time after girdling. Perhaps because the window of opportunity for understory species to establish was longer in the girdled plots, total species richness increased more in the girdled than logged plots. Despite the potential for greater diversity in the girdled plots, *Betula lenta* L. (black birch) was the most abundant tree species recruited into the sapling- and tree-size classes in both the girdled and logged plots and is poised to dominate the new forest canopy. The largest difference between the girdling and logging treatments—deadwood structure and quantity—will persist and continue to bolster aboveground carbon storage and structural and habitat diversity in the girdled plots. Human responses to insect outbreaks hasten forest reorganization and remove structural resources that may further alter forest response to ongoing climate stress and future disturbances.

KEYWORDS
Adelges tsugae, forest reorganization, forest structure, foundation species, invasive insects, salvage logging, *Tsuga canadensis*

INTRODUCTION

Human activity is accelerating ecosystem stressors and disturbances, which in turn are changing the dynamics of forests and their ability to respond to future stressors and disturbances (McDowell et al., 2020). For example, climate change and globalization move insects to new areas (Liebhold et al., 2012). Some insects cause changes in forest type by eliminating specific tree species (Lovett et al., 2016). Human responses to insect outbreaks may amplify their effects, as many landowners choose to harvest forests threatened by insects (Foster & Orwig, 2006; Holt et al., 2020). Logging may result in larger changes to forest structure and composition, and greater aboveground carbon loss than insect damage alone, as timber harvests result in more abrupt mortality, remove large logs rather than leaving dead trees on-site, remove additional nonhost tree species, and can cause disturbance to the forest floor (MacLean et al., 2020; Markowski-Lindsay et al., 2020).

In the eastern United States, loss of *Tsuga canadensis* (L.) Carr. (Eastern hemlock) is a striking example of ecological transformation by the combination of a rapidly expanding population of a nonnative insect (the hemlock woolly adelgid *Adelges tsugae* Annand, hereafter "HWA") and subsequent human activity. When *T. canadensis*, a foundation tree species (sensu Ellison, 2019), is killed by HWA in southern New England, forests dominated by these evergreen coniferous trees reorganize into deciduous hardwood forests dominated by *Betula lenta* L. (black birch) (Orwig et al., 2002). Salvage logging hastens this transition by accelerating canopy loss, tree regeneration, and nutrient cycling (Kizlinski et al., 2002). This compound disturbance (insect + logging) is prevalent; for example, ~25% of the almost 9000 ha of hemlock stands in the southern Connecticut River Valley of New England, USA were harvested as HWA spread into the area (Orwig et al., 2002).

However, it is unclear whether logging will result in lasting differences in forest structure and dynamics when compared with forests affected only by HWA. To address this question, in 2003 we initiated the Harvard Forest hemlock removal experiment (HF-HeRE; Ellison et al., 2010). This hectare-scale replicated study contrasts the standing death of hemlock by girdling (simulating loss of hemlock to HWA) with loss and removal of hemlock by timber harvest (simulating pre-emptive salvage logging). The experiment also includes unmanipulated hemlock and hardwood forest reference plots (Ellison et al., 2010). Although HWA colonized the study area in 2010, so far we have seen only early signs of hemlock decline in the hemlock reference plots, including modest increases in understory light and ant abundance (Kendrick et al., 2015). Understory species composition has changed little as yet in the hemlock reference plots in contrast with dramatic changes in the girdled and logged plots (Ellison et al., 2016) and ant species composition remained distinct in the hemlock reference plots compared to the logged and girdled treatments (Record et al., 2018). In this region, hemlock trees decline slowly after HWA infestation (Case et al., 2017; Orwig et al., 2012b) and the reference sites have very little mortality, so we cannot yet evaluate whether girdling is a good proxy for hemlock death from HWA. However, a girdling experiment in the southern Appalachians, where HWA killed hemlocks rapidly, showed identical responses in stands killed by HWA or by girdling (Ford et al., 2012; Nuckolls et al., 2009), suggesting that girdling is a reasonable simulation of hemlock death from HWA. As hemlock mortality proceeds over the next decade, we will evaluate similarities and differences between the girdling treatment and hemlock mortality from HWA in our experiment.

Therefore, the focus of this paper is to contrast trajectories of change between the girdling and logging treatments, each of which resulted in the removal of ≈70% of the overstory basal area (Orwig et al., 2013). When we established HF-HeRE, we hypothesized that there would be larger magnitudes and faster rates of change in forest structure, composition, and function in the logged than the girdled treatment as the forest reorganized. Although we expected that many of the metrics of change would converge through time, we hypothesized that the longer window of reorganization and greater deadwood legacies in the girdled plots would lead to some persistent differences in forest structure, composition, and function between the two treatments. We tested these hypotheses with the first 15 years of HF-HeRE data (2004–2019). The differences between the treatments that are still present after 15 years set the stage for, and constrain how, these forests will continue to reorganize and respond to additional stressors and disturbances over the next several decades.

MATERIALS AND METHODS

Here, we succinctly present only the key elements of the experimental design, treatments, and measurements of

HF-HeRE. Methodological details are given in Appendix S1 and in Ellison et al. (2010). Data and code are publicly available from the Environmental Data Initiative (Barker Plotkin, 2023; Barker Plotkin et al., 2024; Ellison, 2023; Ellison & Barker Plotkin, 2021, 2023a, 2023b; Orwig & Foster, 2021).

Site description

The HF-HeRE is located in Petersham, Massachusetts, USA (42.5° N; 72.2° W). As in much of the surrounding region, the current forest was established on lands cleared for agriculture through the mid-1800s by European colonists and subsequent abandonment in the late 1800s of large-scale agricultural activities in the region. Trees in HF-HeRE are <150 years old; *T. canadensis* attained its current dominance beginning in the 1920s (Ellison et al., 2014). The soils are mainly acidic (pH 3.0–4.0) coarse-loamy, mixed, active, mesic Typic Dystrudepts in the Charlton Series that are derived from glacial till. Along with *T. canadensis*, other common species in the HF-HeRE plots include *Pinus strobus* L. (eastern white pine), *Acer rubrum* L. and *A. saccharum* Marsh. (red and sugar maple), *Betula lenta*, and *Quercus rubra* L. and *Q. alba* L. (red and white oak).

Experimental design and treatments

The plots comprising this experiment were grouped into two blocks. The "valley" block is in undulating terrain bordered on its northern edge by a *Sphagnum*-dominated wetland. The "ridge" block is on a drier west-facing ridge. For each plot, we established a 30-m × 30-m core area, surrounded by an approximately 30-m-wide buffer of the same treatment. We established the plots in 2003 and sampled most response variables for 1–2 growing seasons prior to applying girdling or logging treatments. The girdled and logged plots were initially dominated (>50% basal area) by *T. canadensis*. Each block also includes unmanipulated hemlock and hardwood forest reference plots, described in Appendix S1, but the focus here is to contrast trajectories of change between the girdling and logging treatments. Within each block, we sited the logged plot south of the girdled plot. We sited the unmanipulated hemlock to the north (ridge block) or west (valley block) to fit the differing terrain of the two blocks, and we located the hardwood reference plots in the nearby hardwood-dominated forest within each block (details in Ellison et al., 2010).

In the girdled plots ($n = 2$), we cut through the bark and cambium of all hemlock trees and saplings using chainsaws or knives in May 2005. Girdled trees died over a 2-year period (Ellison et al., 2010) and were left standing in place to simulate the physical decline and mortality of hemlock resulting from HWA. Between February and April 2005, we used a chainsaw and skidder to fell and remove all hemlock of ≥20 cm diameter at breast height (dbh; measured 1.3 m above ground) in the corresponding logged plots ($n = 2$). We also harvested about 50% of the other species to generate sawlogs and firewood and left the remainder to provide seed and stand structure. This logging treatment was comparable with timber harvest records of intensive hemlock salvage in the region (Kittredge et al., 2009; Kizlinski et al., 2002). Logging and girdling resulted in similar total dead biomass and numbers of trees. However, girdling killed nearly all hemlocks, whereas logging retained small live hemlocks and removed additional trees that were not hemlock (~35% of the harvested stems were not hemlock; Appendix S1: Table S1).

Summary of measurements and statistical analyses

We assessed trajectories of change in forest structure, composition, and function in response to girdling or logging (Table 1). For most response variables, we collected 1 or 2 years of pretreatment data; however, we began some measurements once treatments were imposed. Standing and down deadwood were first sampled in the summer 2005, when the logging was completed, but the girdled trees were still living. Litterfall collection began in fall 2005, so the first full "litterfall year" was May 2006 through April 2007. We collected one hemispherical photograph from the center of each plot in August 2003 but the first full set of 25 hemispherical photos in each plot was collected in September 2005, after the treatments were completed.

We analyzed whether the rate (years to maximum change), magnitude (total change), and persistence of change (years different from pretreatment) was greater in response to logging or girdling for each response variable. We focused on post-treatment (i.e., mortality) trajectories of response but included pretreatment data (2003 and/or 2004) as a reference in the figures. For deadwood, "post-treatment" is after the girdled trees have died. The girdled treatment also showed a very high pulse of needle-fall as the trees died throughout 2006, so the post-treatment trajectories for litterfall were modeled starting with the 2007 data. For most response variables, we used a generalized linear mixed modeling approach implemented in R with the package *glmmTMB* (Brooks et al., 2017). Treatment (logging or girdling) and number

TABLE 1 Response variables measured in the hemlock removal experiment.

Response	Metric(s)	Measurement	Type	Years sampled
Understory light	Global site factor (GSF)	Hemispherical canopy photos taken when leaves of deciduous trees absent or present	Structure	2004–2017; 2019
Tree density and composition	Tree density and dominance of *Betula lenta* + *B. alleghaniensis*	Tree counts (stems ha^{-1}) and proportion of trees that were *B. lenta* + *B. alleghaniensis*	Structure (density); composition (birch dominance)	
	Trees ≥5 cm dbh	Full plot		2004, 2009, 2014, 2019
	Saplings >1.3 m tall & <5 cm dbh	Center 30-m × 30-m per plot		2004, 2007, 2009, 2011, 2013, 2015, 2019
	Seedlings <1.3 m tall	10 1-m^2 quadrats per plot		2003–2019
Understory vegetation community	Abundance, richness, and community composition	% cover by species in 10 1-m^2 quadrats per plot	Structure (abundance)	Abundance and composition: 2003–2019
	Species richness	Species list for center 30-m × 30-m per plot	Composition (richness; ordination)	Richness: 2003; 2005–2019
Aboveground carbon distribution and stocks	Live trees	Tree diameters on full plot; carbon content calculated from species-specific allometries	Structure + function	2004, 2009, 2014, 2019
	Standing deadwood (snags and stumps); coarse downed wood (>7.5 cm diameter); Fine downed wood (0.6–7.5 cm diameter); Large snags (>50 cm diameter at the base and >3 m tall)	Carbon content of deadwood and its distribution among standing (subplots), coarse and fine downed wood (line-intercept transects)	Structure + function	2005, 2007, 2009, 2011, 2013, 2015, 2017, 2021
	Wood products	C content of wood products estimated using Massachusetts variant of the harvested wood products (HWP) model	Structure + function	Modeled estimates annually since 2005
Litterfall production	Foliar + woody (<0.6 cm diameter) mass	Five baskets per plot collected quarterly	Function	2006–2019
Nitrogen availability	NO_4^+; NO_3^-	Resin bags deployed for growing season and overwinter periods	Function	2004–2009; 2013–2019

Abbreviation: dbh, diameter at breast height.

of years after disturbance were fixed effects, and block was a random effect. We also included a quadratic number of years since disturbance term. We chose distributions and link functions that were appropriate for the data (e.g., a Poisson distribution with a log link was used when modeling counts of species richness, whereas a beta distribution with a logit link was used when modeling proportional data such as understory cover). We visualized and analyzed log-transformed tree densities because densities per hectare among layers spanned six orders of magnitude. We log-transformed live and dead carbon stock data, and nitrogen resin data to meet Gaussian model assumptions. We used *AICmodavg* (Mazerolle, 2020) for model selection, evaluated the models using the *DHARMa* package (Hartig, 2020), and visualized the models using the *ggplot2* and *ggpubr* packages (Kassambara, 2023; Wickham, 2016). Tables listing model parameters (estimates, SE of estimates, and *p*-values) and

AIC model selection tables for each response variable are included in Appendix S2: Tables S1–S28.

To visualize changes in the composition of the understory vegetation community, we used nonmetric multidimensional scaling (NMDS) implemented in the *vegan* package (Minchin et al., 2020). We summarized species abundance from the quadrats by treatment. We then excluded species that were present in <5% of the treatment-year combinations for the NMDS analysis. Based on a scree plot, we chose $k = 3$ dimensions as the most appropriate for this NMDS. To compare the total stored aboveground carbon in these two treatments, we combined estimates of carbon density in standing live and dead, and downed dead from our site measurements, with modeled estimates of carbon in wood products sold or used on-site from the logged wood (more information in Appendix S1).

RESULTS

Forest structure

As expected, the rate of change in the logged plots was faster than in the girdled plots, starting with microclimate. Understory light was very low before we implemented the treatments; global site factor (GSF), the estimated proportion of solar radiation reaching the understory, was <0.1, indicating that <10% of the light reached the understory (Figure 1a). Logging resulted in significantly brighter understory light conditions than girdling, rising to GSF >0.4 during the growing season (“leaf-on”). Understory light increased more slowly and only to ~0.25 GSF in the girdled plots but persisted at this brighter level longer than in the logged plots. Trajectories of mean GSF before deciduous trees leafed out in the spring (“leaf-off”) season were similar (Appendix S2: Figure S1). Spatial heterogeneity of understory light also peaked earlier in the logged plots but persisted longer in the girdled plots (Figure 1b). Overall, the understory light environment was not significantly more variable after girdling than logging (Appendix S2: Table S1).

Increased understory light spurred tree regeneration. Pretreatment seedling densities were highly variable, as the density of first-year germinants fluctuated from year to year. The numbers of seedlings increased rapidly in response to girdling, and then declined as some grew into the sapling size class while others died (Figure 2a; seedlings transitioning to saplings indicated by arrows connecting the boxes). Seedling numbers remained steady in the logged plots as seedlings transitioned rapidly to the sapling layer (Figure 2b).

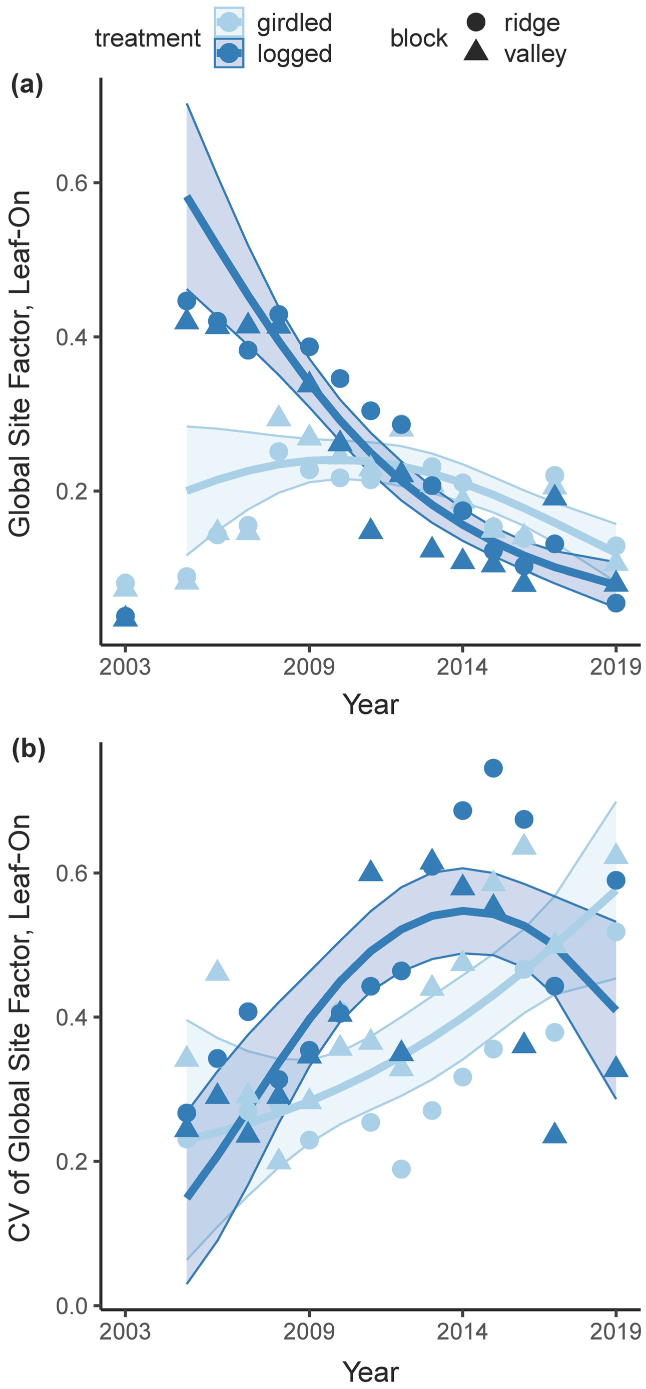

FIGURE 1 Mean (a) and spatial heterogeneity (coefficient of variation [CV]) (b) of understory light in the logged and girdled plots over time, measured using 25 hemispherical photographs taken during August–September (“leaf-on”) in each plot. Global site factor (GSF) is the estimated proportion of direct plus diffuse solar radiation reaching the camera (Lustenhouwer et al., 2012; Rich, 1989). Lines and shading show modeled trajectories with 95% confidence intervals (CI). We collected one pretreatment hemispherical photograph from the center of each plot in August 2003 (2003 data in panel a) but the first full set of 25 hemispherical photos in each plot was collected in September 2005, after the treatments were completed; therefore, no pretreatment CV for understory light is available.

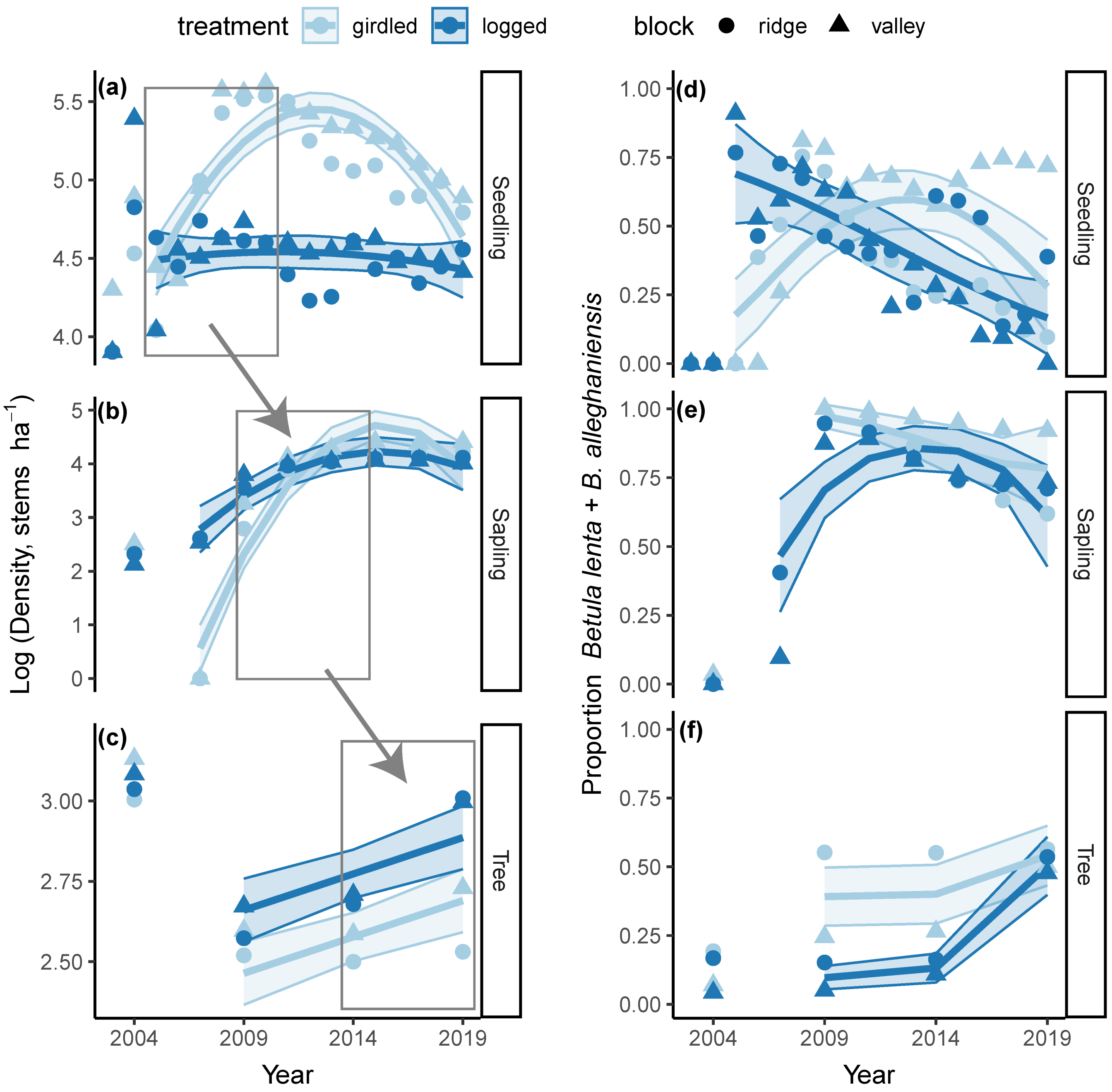

FIGURE 2 Tree density (a–c, all species) and *Betula lenta* + *B. alleghaniensis* dominance (d–f) for the seedling (trees <1.3 m tall), sapling (trees >1.3 m tall but <5 cm dbh), and tree (trees ≥5 cm dbh) strata of the forest. Lines and shading show modeled trajectories with 95% CI. Boxes and arrows in panels a–c indicate the trajectory of trees growing from the seedling size class to saplings, and then from saplings to trees. Pretreatment data are shown from 2003 and 2004 (panels a and d) or 2004 (panels b, c, e, and f).

Sapling numbers dropped to zero after girdling, because all saplings in the girdled plots were *T. canadensis* and were girdled. In contrast, saplings were left uncut in the logged treatment. With mortality from the logging and girdling treatments, trees ≥5 cm dbh declined sharply (Figure 2c) and then rebounded as saplings transitioned to the tree-size class (again, indicated by arrows connecting the boxes). Tree density was greater in the logged than in girdled plots. By 2019, tree density had nearly recovered to pretreatment numbers in the logged plots but remained at <40% of pretreatment densities in the girdled plots.

Similarly, understory vegetation abundance increased dramatically from near-zero pretreatment (Figure 3a). Percent cover of understory herbs, shrubs, and seedlings peaked in ca. 2012 at a maximum of about 40% in the logged plots, and in ca. 2014 with a maximum of ca. 60% cover in the girdled plots. Although the rate of change

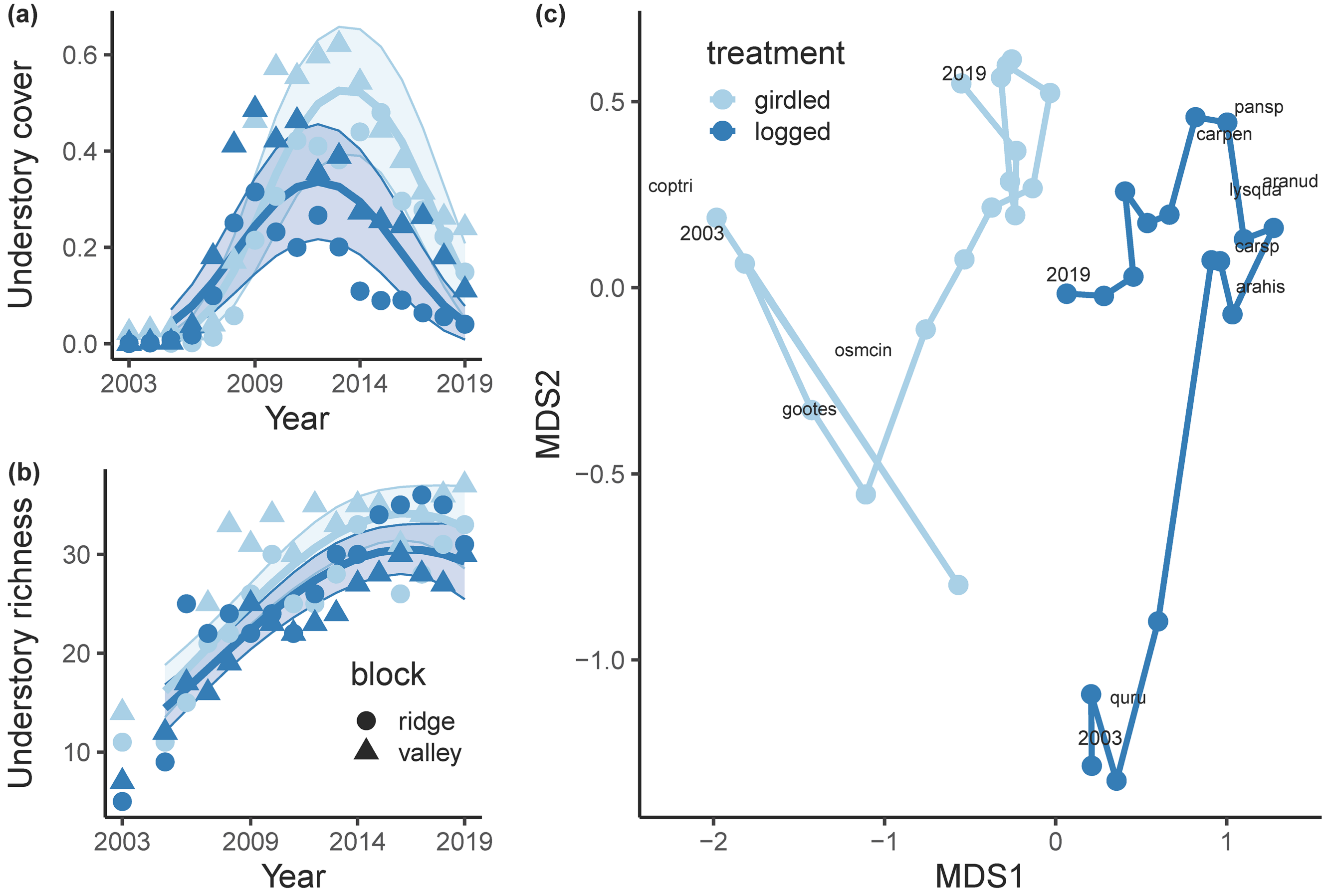

FIGURE 3 Understory vegetation species cover (a proxy for abundance) (a), species richness (b), and community composition (c). Note that species richness was based on a full species list in each plot, whereas abundance and community composition was based on the presence and abundance of understory species in 10 quadrats in each plot. For abundance and richness, lines and shading show modeled trajectories with 95% CI. For the nonmetric multidimensional scaling (NMDS) visualization of the understory vascular plant community (c), lines connect the years as the composition shifts within the ordination space (labeled at the endpoints of 2003 and 2019). The NMDS used three dimensions ($k = 3$, of which axes 1 and 2 are displayed; MDS1 and MDS2 are how these dimensions are labelled when using the *vegan* package). This resulted in low stress (0.074), where stress is a measure of goodness-of-fit and values less than 0.1 typically indicate good fit (McCune & Grace, 2002). Species present in fewer than 5% of the treatment-year combinations were excluded. Species scores for species with absolute MDS1 (axis 1) or MDS2 (axis 2) values of >1 are plotted and labeled using the first three letters of the genus and first three letters of the species (*Aralia hispida* Vent.; *Aralia nudicaulis* L.; *Carex pensylvanica* Lam.; *Carex* spp.; *Coptis trifolia* (L.) Salisb.; *Goodyeara tesselata* Lodd.; *Lysimachia quadrifolia* L.; *Osmundastrum cinnamomeum* (L.) C. Presl; *Panicum* spp.; *Q. rubra*). These species are associated with the site/year points that are in the same ordination space. Pretreatment data are shown for 2003 (panel b) or 2003 and 2004 (panels a and c).

was faster in the logged plots, the magnitude and persistence of change were greater in the girdled plots.

The most prominent change in forest structure was the massive transfer of live trees to standing and downed deadwood pools. Logging and girdling treatments followed the same trajectory of losing >60% of initial aboveground live carbon stocks, with a modest recovery by 2019 (Figure 4a). In the girdled plots, about half the initial aboveground live carbon moved into the standing dead pool (Figure 4b); as the standing dead hemlock trees decayed over time, the downed deadwood increased (Figure 4c,d). In the logged plots, most of the cut stems were removed from the site for saw timber, firewood, and pulpwood (Appendix S1: Table S2), but there was a pulse of downed wood in both the coarse (>7.5 cm diameter) and fine (0.6–7.5 cm diameter) classes post-treatment (Figure 4c,d). Over time, the downed deadwood pool declined as the initial pulse of deadwood from logging decomposed. Overall, the girdled plots had more than an order of magnitude larger, and more persistent, quantity of standing and downed deadwood than the logged plots.

Girdling resulted in a high abundance of large snags (>50 cm diameter at the base and >3 m tall). Both girdled plots had ~35 large snags per hectare that persisted to 2019. In contrast, there were no large snags in the logged plot transects.

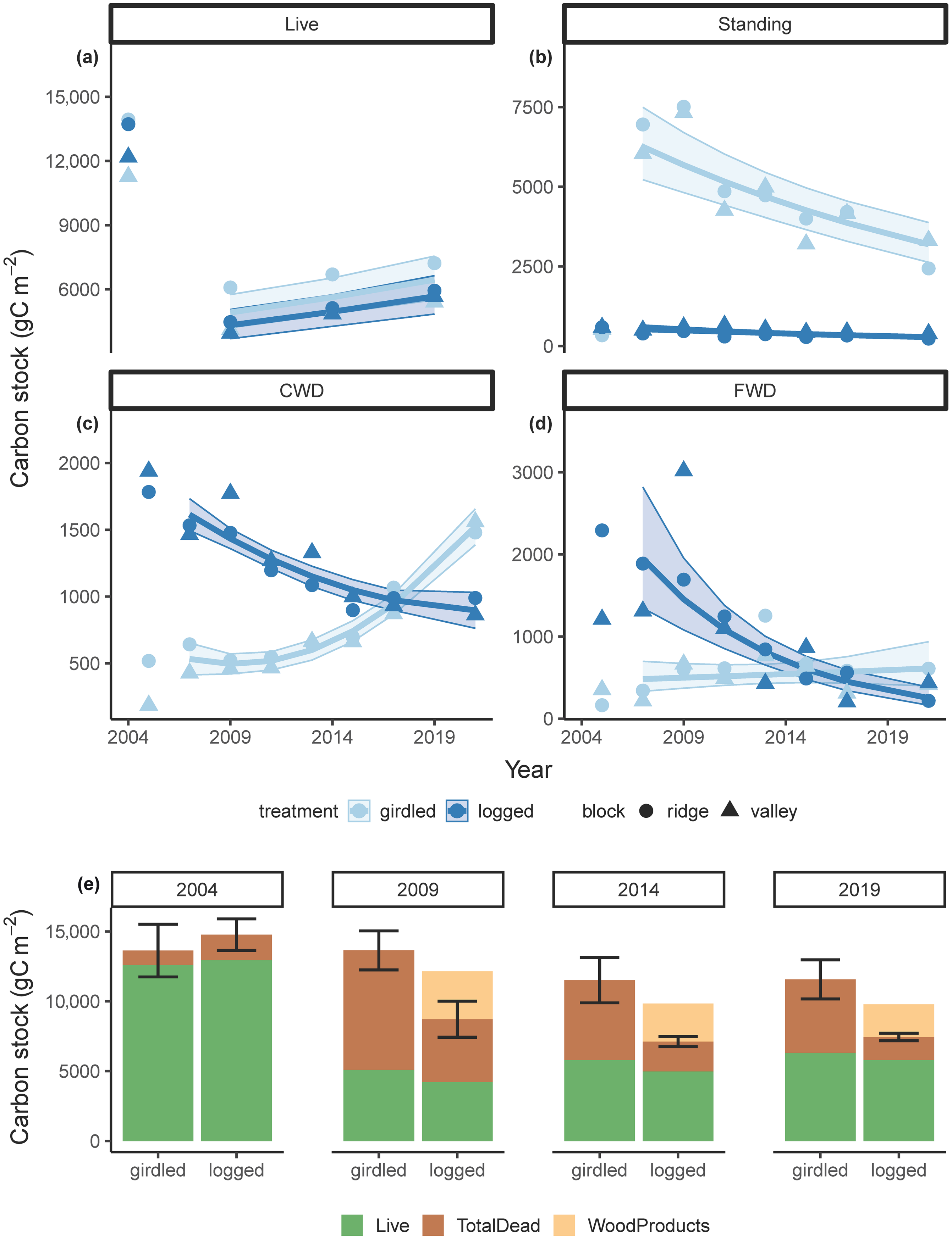

FIGURE 4 Legend on next page.

Composition

Betula was nearly absent in the seedling and sapling layers before logging and girdling. Trajectories of *Betula* seedling dominance (mostly *B. lenta* but also *B. alleghaniensis* Britt. in the valley girdled plot) differed between logged and girdled plots (Figure 2d), with high but declining *Betula* dominance in the logged plots (from nearly 75% of all seedlings soon after logging but declining to <25%), in contrast to fluctuating *Betula* dominance in the girdled plots. *Betula* sapling dominance was significantly greater in the girdled plots (Figure 2e; Appendix S2: Table S9). *Betula* was still the dominant sapling species in 2019, but *P. strobus*, *A. rubrum*, and *T. canadensis* also contributed to the sapling layer. *Betula* dominance in the tree-sized layer increased from <20% pretreatment to ~50% by 2019 in both treatments (Figure 2f). *Betula* dominance in the tree-sized layer increased quickly in the girdled plots because all the hemlocks were killed, thus raising the relative proportions of surviving species. In contrast, ca. 50% of the *B. lenta* stems were cut in the logged plot, and proportional increases in *Betula* trees between 2014 and 2019 were primarily from the recruitment of saplings into the tree-sized class.

Tree regeneration of all species in the girdled plots was entirely from seeds germinating after the treatment. In the logged plots, seed germination also dominated tree regeneration, but there were some cut trees that sprouted (mainly *A. rubrum*) and a few saplings that survived logging. There was high interannual variation in *Betula* dominance of the seedling layer (Figure 2d), but in most years, other species comprised at least one-third of the seedlings. Despite this potential diversity in tree regeneration, most of the trees that were recruited into the sapling and tree layers were *B. lenta*.

Understory species richness in both treatments more than tripled over time (Figure 3b) and leveled off by 2019. The shape of the trajectory was shared between the logging and girdling treatments, but species richness remained greater in the girdled than the logged treatment after 15 years (Appendix S2: Table S13). There was no clear pattern in the identity of the species present in the girdled versus the logged plots, except that two of three nonnative woody shrubs that colonized the treated plots were only found in the girdled treatment (*Berberis thunbergia* DC. and *Frangula alnus* P. Mill.). Understory community composition (Figure 3c) in the logged treatment diverged from pretreatment composition sooner (2007) than in the girdled treatment (2009–2010), and a suite of early-successional species was associated with the logged treatment for a few years after the treatment (e.g., *Aralia hispida*, *Carex pennsylvanicum*, *Carex* spp., *Lysimachia quadrifolia*, *Panicum* spp.). By 2019 however, the understory community composition of the logged and girdled treatments occupied similar ordination space.

Function

Carbon storage in live trees declined by more than half after logging or girdling, but total carbon loss was mitigated by persistent deadwood pools in the girdled plots, and lasting wood products in the logged plots (Figure 4e). Between 2014 and 2019, total carbon storage remained steady in each treatment, as the growth of surviving trees and recruitment of new trees balanced the decay of deadwood on-site or in wood products. Initial carbon storage in live trees was similar in both treatments, although it was more variable in the girdled plots than in the logged plots (Figure 4a). However, by 2019 the girdled sites stored 18% more total aboveground carbon in 2019 than the logged sites, even after accounting for the carbon stored in harvested wood products.

There was a large pulse of needles that abscized and fell in 2006 as the girdled hemlock trees died (Figure 5). Thereafter, foliar litterfall production did not differ between treatments. For both treatments, foliar litterfall increased and then leveled off by 10 years after the treatments were imposed. Total litterfall, including fine twigs and bark, remained elevated in the girdled plots (Appendix S2: Figure S2), probably because the standing dead trees shed fine twigs and bark as they decayed.

FIGURE 4 Carbon stocks of live trees (a), standing deadwood (b, snags and stumps), coarse (>7.5 cm diameter) downed wood (c), and fine (0.6–7.5 cm diameter) downed wood (d). Lines and shading show modeled trajectories with 95% CI. The distribution and total amount of carbon in live trees, deadwood, and wood products differed between the girdled and logged treatments (e). "Live" is the aboveground live carbon content of live trees, "TotalDead" is the sum of standing and coarse + fine downed wood, and "WoodProducts" are modeled estimates of the carbon in harvested wood products that remained at each date, based on the volume of different timber products harvested. The error bars in (e) show combined standard deviation of live and deadwood for each treatment and year. We could not include wood products in the error because the wood products from the two logged plots were not separated on the landing. Data from 2004 are pretreatment for live trees. For deadwood, the girdled trees were still alive during the first measurement in 2005, so we modeled 'post-treatment' data starting with the next measurement of deadwood in 2007.

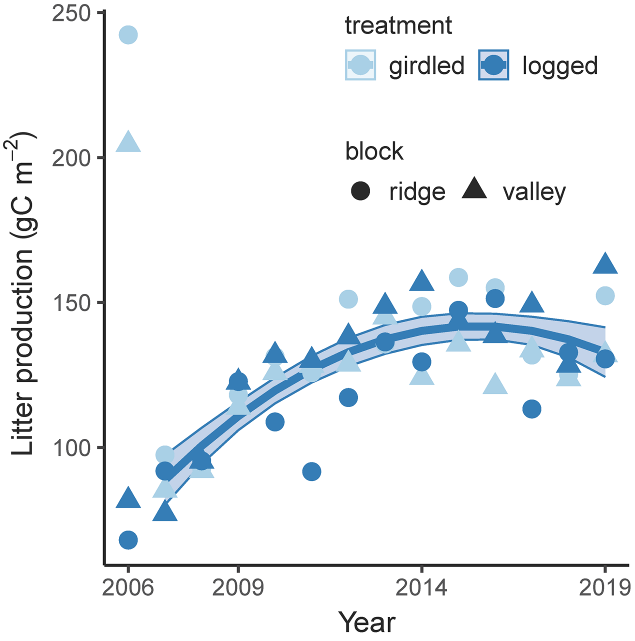

FIGURE 5 Production of foliar litterfall (in grams of carbon per square meter per year) over time. Lines and shading show modeled trajectories with 95% CI. Litterfall collection began in fall 2005, so the first full "litterfall year" was May 2006 through April 2007. The girdled treatment showed a very high pulse of needle-fall as the trees died throughout 2006, so the post-treatment trajectories for litterfall were modeled starting with the 2007 data.

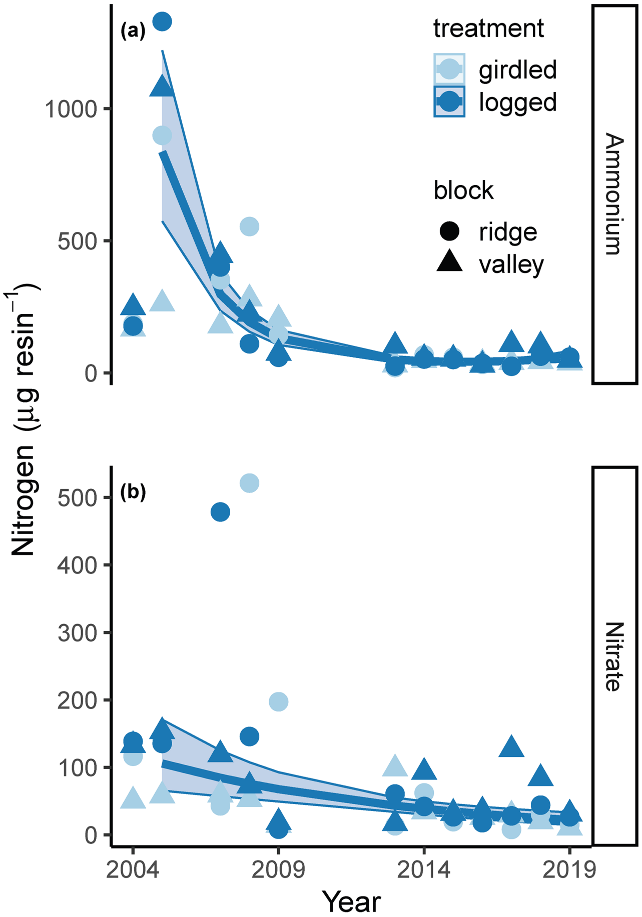

FIGURE 6 Ammonium (a) and nitrate (b) availability (annual totals) over time. Lines and shading show modeled trajectories with 95% CIs. Data from 2004 are pretreatment.

Freely available nitrogen, measured by capture of ammonium and nitrate on resin bags, was elevated after logging or girdling, but decreased to low levels (<110 μg resin year^{-1} for ammonium and <130 μg resin year^{-1} for nitrate) within a few years (Figure 6). Neither ammonium nor nitrate availability differed between treatments (Appendix S2: Table S26). In the first 2 years after treatments were imposed, we measured a few very high spikes in ammonium (>700 μg resin year^{-1}) and nitrate (~500 μg resin year^{-1}).

Overall trends in the rate, magnitude, and persistence of trajectories of change

We summarized differences in the rate, magnitude, and persistence of change between the logged and girdled treatments for 11 major response variables (Table 2). As expected, the rate of change in the logged plots was faster than in the girdled plots (five of 11 responses; the other six showed no difference between the treatments). Logging resulted in an immediate increase in available light and growing space, leading to a rapid increase in understory vegetation cover and a change in understory species composition. Because the trees declined and died over a 2-year period after girdling, light increased in those plots more slowly. The understory vegetation changed more slowly and therefore had a longer window of reorganization in the girdled plots than in the logged plots.

Contrary to our prediction that the magnitude of change would be larger in the logged than in the girdled plots, the magnitude of change in vegetation and ecosystem function was just as likely to be larger in the girdled plots as the logged plots. The logged plots showed a greater magnitude of response for four of 11 variables and the girdled plots had a greater magnitude of response for five of 11 variables; the remaining two responses showed no difference between the treatments. The abundant standing dead trees in the girdled plots led to a less dramatic increase in understory light levels. Maximum seedling density and understory vegetation abundance were greater in the girdled plots than in the logged plots. After logging, a new cohort of trees quickly recruited into the sapling and tree-sized classes and filled the available growing space, therefore limiting seedling and understory vegetation abundance. Perhaps because the window of

TABLE 2 Summary of differences in the rate, magnitude, and persistence of change between the girdled and logged plots over 15 years.

Response	Rate	Magnitude	Persistence	Type	Figure
Understory light	**L > G**	**L > G**	***G > L***	Structure	Figure 1
Tree density	**...**	***G > L (seedling gain & tree loss)***	***G > L (seedlings)***	Structure	Figure 2a–c
Betula **dominance**	**...**	***G > L (saplings)***	**...**	Composition	Figure 2d–f
Understory veg cover	**L > G**	***G > L***	***G > L***	Structure	Figure 3a
Understory veg richness	**...**	***G > L***	***G > L***	Composition	Figure 3b
Understory veg composition	**L > G**	**L > G**	**...**	Composition	Figure 3c
Standing deadwood	**...**	***G > L***	***G > L***	Structure	Figure 4b
Downed deadwood	**L > G**	**L > G**	***G > L***	Structure	Figure 4c, d
Aboveground C stock loss	**L > G**	**L > G**	**L > G**	Function	Figure 4e
Litterfall production	**...**	**...**	**...**	Function	Figure 5
Nitrogen availability	**...**	**...**	**...**	Function	Figure 6

Note: **Boldface type** indicates that the response to logging was greater than the response to girdling, ***boldface italic type*** indicates that the response to girdling was greater than the response to logging, and **ellipses (...)** indicates no significant difference between the two treatments.

opportunity for understory species to establish was longer in the girdled plots, total species richness increased more in the girdled plots than in the logged plots. In the first decade after treatment, community composition diverged more after logging than girdling and featured more early-successional herbaceous species; likely due to the greater amount of light availability, along with soil disturbance from the logging equipment.

Changes were more persistent in the girdled plots (six of 11 responses; one response was more persistent in the logged plots and the other four showed no difference between the treatments). Although initially divergent, the community composition of the logged and girdled plots was more similar after 15 years than pretreatment, likely because the magnitude of canopy disturbance erased idiosyncratic differences in the sparse understory vegetation among plots prior to treatments. Understory light, tree seedling density, understory vegetation abundance and richness, deadwood quantity and structure, and total aboveground woody carbon storage remained greater in the girdled plots 15 years after treatments. Based on the modeled trajectories of change, light, tree seedling density, and understory vegetation, abundance likely will converge within the next decade. However, the modeled trajectories suggest that understory vegetation richness, deadwood structure and quantity, and aboveground woody carbon storage will remain greater in the girdled treatments.

DISCUSSION

The girdled treatment lost hemlock more slowly than the logged treatment, resulting in a longer window of opportunity for reorganization (Seidl & Turner, 2022). However, many differences between the treatments either converged within 15 years or are projected to converge within the next decade, with notable exceptions of understory species richness, deadwood quantity, and aboveground carbon stocks. The differences that persist provide the girdled plots with greater biodiversity and deadwood microhabitats, and thus a potentially greater capacity for resilience to ongoing and future stressors and disturbances. Human responses to insect outbreaks, such as logging, hasten forest reorganization and remove structural resources that may further alter forest response to ongoing climate stress and future disturbances.

Persistent differences in canopy tree loss by simulated insect attack versus pre-emptive logging

Earlier work from HF-HeRE supported the hypothesis that *T. canadensis* is a foundation species (Ellison & Degrassi, 2017; Orwig et al., 2013). Girdling and logging both resulted in a transformation from a deeply shaded evergreen coniferous forest with a sparse understory, to a deciduous hardwood forest with greater understory species abundance and richness (Orwig et al., 2013). This regime shift had cascading effects on salamanders (Ochs & Siddig, 2017; Siddig et al., 2016), moose and deer (Faison et al., 2016), small mammals (Degrassi, 2016), ants (Record et al., 2018), and macroarthropods (Sackett et al., 2011). Soil carbon storage and soil CO_2 efflux changed surprisingly little after hemlock loss (Finzi et al., 2014; Raymer et al., 2013), in contrast with findings of lower soil CO_2 efflux in the southern Appalachians after hemlock loss by HWA or girdling (Nuckolls et al., 2009). However, the loss of hemlock reduced carbon stored in fine roots both at HF-HeRE and in the southern Appalachians (Nuckolls et al., 2009; Raymer et al., 2013).

In this paper, we showed that the trajectories of change from killing *T. canadensis* and leaving it standing, compared with logging and removal, differed in rate and magnitude of response, but converged over time for most variables considered. However, the largest difference between the girdled and logged treatments—deadwood structure and quantity—will persist for decades, with important implications for forest biodiversity, structure, and function. Deadwood levels are much lower in second-growth forests compared with old-growth forests (Barker Plotkin et al., 2017; D'Amato et al., 2008), so the large mass of deadwood and the presence of large snags provides a resource that is lacking across most of the northeastern United States forest. Standing and downed deadwood perform critical functions in ecosystems. Many wildlife and microbial species depend on deadwood (DeGraaf & Yamasaki, 2001; Mathewson, 2009) and it is a major component of nutrient cycles (Harmon et al., 1986). The abundant deadwood likely provided a greater variety of microsites and may have contributed to the persistently greater understory species richness in the girdled plots. The large amount of carbon stored in slowly decomposing deadwood also drove another persistent difference between the treatments, greater carbon storage in the girdled plots.

Differences between HWA and logging may be larger than the girdling treatment we used to simulate HWA decline in this experiment. *T. canadensis* in the northeastern United States typically take at least a decade to die from HWA (Orwig et al., 2012a), in contrast with the 2 years it took them to die from girdling in this experiment. A longer window of opportunity for reorganization could prompt larger divergence in understory light, tree regeneration, understory vegetation composition, and nitrogen availability between HWA and logging. The pace of mortality from the girdling treatment in this experiment was similar to that observed in the southern Appalachian region of the United States (Ford et al., 2012; Nuckolls et al., 2009).

Salvage logging is also more likely to amplify disturbance in systems in which the host tree species is less abundant. For example, Holt et al. (2022) found that timber harvest intensity was greater in forests infested with the rapidly expanding borer insect *Agrilus planipennis* Fairmaire (emerald ash borer, EAB). Further, about half of the total harvest, on average, was from species other than *Fraxinus*, which is EAB's host. Another example comes from the 1972–1986 *Choristoneura fumiferana* Clemens (spruce budworm) outbreak in Maine, USA. Landowners dramatically increased clearcut harvesting in response to the outbreak, intensifying this disturbance and prompting a shift from evergreen coniferous to deciduous hardwood forest (Irland et al., 1988).

Should managers eschew salvage harvest in declining *T. canadensis* stands, given the richer structure and composition of the unharvested plots? "Doing nothing" (Foster & Orwig, 2006; Kittredge & Kittredge, 1998) is a solid management option. However, carefully designed silviculture (Orwig & Kittredge, 2005) with attention to retention of large snags, creating a diversity of microsite conditions, and focusing on long-lasting wood products from harvested wood could lead to similar outcomes to allowing the trees to die standing from HWA.

Betula lenta: A novel canopy dominant

Although the longer window for tree seedling establishment in the girdled plots provided a potentially greater diversity of germination conditions and seed rain, *B. lenta* strongly dominated sapling and tree recruitment in both the logged and girdled treatments. Will *B. lenta* continue to dominate the new cohort? *B. lenta* is part of the deciduous forests in this region, but is not considered a dominant species (Thompson et al., 2013). It remains uncommon in the unmanipulated hemlock reference plots of this experiment and other undisturbed forests at the Harvard Forest (Finzi et al., 2020; Orwig et al., 2013). Modeling studies of forest composition change after *T. canadensis* loss, using the Ecosystem Demography and SORTIE models (Albani et al., 2010; Case et al., 2017), predicted dominance by *P. strobus* along with lesser amounts of *B. lenta* and *Fagus grandifolia* (Ehrh.). Similarly, in the southern Appalachians, Dharmadi et al. (2019) found the highest post-HWA growth rate in *B. lenta* and another *Pinus* species (*P. rigida*) trees. Brown et al. (2018) also showed that *P. strobus* thrives under highly variable partial harvest regimes. Conversion of *T. canadensis* to *P. strobus* (both evergreen conifers) would be a less dramatic ecosystem shift than conversion to a *Betula*-dominated forest. However, post-HWA sites in southern Connecticut, USA, showed continuing *B. lenta* dominance after two decades (Orwig et al., 2002; Raymer et al., 2013). Farnsworth et al. (2012) showed that *Betula* overwhelmingly dominated seed rain in the logged and girdled plots from 2005 to 2009. Recruitment from the sapling- to the tree-size class is still ongoing after 15 years, especially in the girdled plots, so the window for determining canopy composition is not yet closed. *Acer rubrum* and *P. strobus* will contribute to the emerging canopy, and *P. strobus* will likely grow taller than the other species, adding structural diversity

(Hibbs, 1982). However, the strong recruitment of *B. lenta* in this site, along with its persistent dominance in other disturbance experiments and following regeneration after timber harvest in the region (Barker Plotkin et al., 2013; McDonald et al., 2008), suggest that *B. lenta* will continue to dominate the new cohort of trees for many decades.

Post-HWA tree regeneration dynamics differ in other parts of the range of *T. canadensis*. In the southern Appalachians, the evergreen shrub *Rhododendron maximum* dramatically increased after *T. canadensis* mortality (Ford et al., 2012). Tree seedling density increased for a few years, but after a decade there was no recruitment of new trees in these forests (Dharmadi et al., 2019). Loss of *T. canadensis* results in a major ecosystem transition in both regions. In southern New England, the evergreen coniferous forest transforms into a deciduous broadleaf forest, whereas in the southern Appalachians, the transition is toward a dominant evergreen shrub.

Compounding disturbances in a changing world

Superimposed on the experimental treatments in the HF-HeRE are other disturbances and global change stressors that may interact differently with girdling and logging. For example, nonnative invasive plants often establish after canopy disturbance and have major effects on ecosystem function (Lopez et al., 2022). In this study, the plots were embedded in an intact forest (plots were >450 m from a field or road edge) and nonnative plants were rare. Three nonnative taxa, all woody shrubs or small trees (*B. thunbergia*, *Celastrus orbiculatus* Thunb., and *F. alnus*) appeared in the manipulated plots after the treatments were applied. None was widespread enough to make strong inferences about patterns of their establishment, but all three appeared only or first in girdled plots and all three have fleshy fruits that are dispersed by birds, suggesting that the standing dead trees may have provided perch sites for birds that dispersed these species into the plot (Gosper et al., 2005).

Climate change is accelerating the pace of disturbance (McDowell et al., 2020; Seidl & Turner, 2022) and the persistent differences between the girdling and logging treatments may result in differing responses to compounding changes. The girdled plots have compositional and structural resources that the logged plots do not, which may provide the girdled plots with a greater capacity to respond to future stressors and disturbances (i.e., resilience). For example, standing and downed deadwood provide forest structural diversity and structural diversity interacts with disturbance, which can influence forest resilience (Mitchell et al., 2023). The girdled plots also have a greater capacity for biodiversity with more understory species and large deadwood (Franklin et al., 2002; Gilliam, 2007). As we continue to document trajectories of change in the HF-HeRE, the differences between the treatments that persist after 15 years set the stage for and constrain how these forests will continue to reorganize and respond to additional stressors and disturbances over the next several decades.

AUTHOR CONTRIBUTIONS

Audrey Barker Plotkin, Aaron Ellison, Meghan Graham MacLean, and David Orwig conceived the ideas and designed the methodology. Audrey Barker Plotkin, Aaron Ellison, and David Orwig collected the data. Audrey Barker Plotkin and Meghan Graham MacLean analyzed the data. Audrey Barker Plotkin led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data are available in the Environmental Data Initiative data repository as follows: Barker Plotkin (2023), https://

doi.org/10.6073/pasta/673669500a2330d787ed98019a4da4af; Barker Plotkin et al. (2024), https://doi.org/10.6073/pasta/e962581f8bd1d8f2628abf5f0a54e7c8; Ellison (2023), https://doi.org/10.6073/pasta/e9b8d52836d95b0e66d3dc38d5269757; Ellison and Barker Plotkin (2021), https://doi.org/10.6073/pasta/e3b82eaa04198d7889d3e5bfd3667db4; Ellison and Barker Plotkin (2023a), https://doi.org/10.6073/pasta/388e50cef2708d3428fe2859fea98c57; Ellison and Barker Plotkin (2023b), https://doi.org/10.6073/pasta/1536414d201687a39748f05d970dc437; Orwig and Foster (2021), https://doi.org/10.6073/pasta/b4d322afca7f024a95e535f4353e0119.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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