Forest Ecology and Management 600 (2026) 123304

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

# The speed of eastern hemlock loss alters the persistence of microbial legacies following hemlock woolly adelgid infestation

Corey A. Palmer[a,b,*], Audrey Barker Plotkin[c], Ashley D. Keiser[a]

[a] Stockbridge School of Agriculture, University of Massachusetts Amherst, Amherst, MA 01003, United States
[b] Division of Natural Science and Mathematics, Keuka College, Keuka Park, NY 14478, United States
[c] Harvard Forest, Harvard University, Petersham, MA 01366, United States

ARTICLE INFO

*Keywords:*
Decomposition
Disturbance
Carbon
Nitrogen
Home-field advantage
Functional legacy
Non-native insect pest

ABSTRACT

In eastern North America, invasive hemlock woolly adelgid (*Adelges tsugae*, HWA) is causing widespread hemlock (*Tsuga canadensis*) decline, leading a transition to black birch (*Betula lenta* L.) and other deciduous forest canopies. The rate of hemlock mortality varies geographically, with rapid decline observed in the southern U.S. (within years) and gradual loss in the Northeast (over decades). To investigate how forest transition speed impacts litter decomposition and forest carbon and nitrogen cycling, we worked within a hemlock manipulation experiment at the Harvard Forest, Petersham, MA, USA, across three forest types: a reference hemlock plot experiencing natural HWA infestation and slow decline, a girdled plot simulating rapid hemlock mortality, and a hardwood plot representing a potential post-HWA state. Litter decomposition varied by litter and forest type, with patterns consistent with home-field advantage (HFA): faster decomposition on the soil of origin. Hemlock litter exhibited positive HFA in the hemlock reference plot, but neutral HFA in the girdled plot where birch had positive HFA. Litter mass loss did not differ among species in the girdled forest type, suggesting a weakening of hemlock functional legacy after rapid hemlock loss. In contrast and despite increased plant species richness, soil carbon and nitrogen cycling remained similar between the girdled and hemlock reference forest types. Pest-driven forest transitions are common in forests globally and vary in their pace. The results from this study suggest that the rate of change can alter the persistence of microbial legacies and result in distinct trajectories for forest carbon and nitrogen cycling.

## 1. Introduction

Two of the major threats to temperate forests across the U.S. are invasive pests (Brockerhoff et al.2011; Finley and Chhin, 2016; Klapwijk et al., 2016) and climate change (Keenan, 2015; Kaarakka et al., 2021). In Northeastern U.S. forests, warmer winters associated with climate change enhance the overwintering survival of invasive insects, while global trade continues to introduce novel pests (Tobin et al., 2014; Fei et al., 2019). Insect-driven tree mortality has led to large-scale shifts in canopy composition, forest biomass, and nutrient cycling, with cascading effects on soil carbon (C) and nitrogen (N) dynamics (Ellison et al., 2005; Fei et al., 2019; Woodman et al., 2021). Examples include the rapid loss of ash from emerald ash borer (EAB; Herms and McCullough, 2014), gradual decline of American beech due to beech bark disease (Houston, 1994), and regional oak mortality associated with oak wilt (Juzwik et al., 2011). Though varying in the speed of host decline, these outbreaks eventually eliminate host species and drive structural and functional ecosystem changes (Youngquist et al., 2017). Salvage or preemptive logging can accelerate stand transitions (Orwig et al., 2002; Brooks, 2004; Barker Plotkin et al., 2024), further compounding disturbance impacts. However, it remains unclear how the pace of host decline interacts with belowground processes, particularly the capacity of soil microbial communities to buffer or amplify ecological change.

Litter decomposition is a fundamental ecosystem process linking above- and belowground nutrient cycling and dynamics. Because litter decomposition helps govern soil fertility and contributes to long-term C storage, understanding how disturbances impact litter breakdown is key to forecasting changes in forest ecosystem function. As tree species are lost and replaced, shifts in litter quality and canopy cover can alter decomposition rates and the rate at which nutrients are returned to the soil. However, microbial responses to disturbance are not always immediate. Soil microbial communities responsible for litter

---

* Corresponding author at: Division of Natural Science and Mathematics, Keuka College, Keuka Park, NY 14478, United States.
*E-mail address:* cpalmer@keuka.edu (C.A. Palmer).

https://doi.org/10.1016/j.foreco.2025.123304
Received 30 July 2025; Received in revised form 26 October 2025; Accepted 27 October 2025

decomposition and nutrient cycling can retain functional legacies, maintaining these traits shaped by past environments that can persist even for decades (Keiser et al., (2011), (2014); Bond-Lamberty et al., (2016); Veen et al.,

2018). These microbial legacies can be expressed through phenomena such as "Home-Field Advantage" (HFA), where litter decomposes faster in its plot of origin due to microbial specialization (Hunt et al., 1988; Gholz et al., 2000; Austin et al., 2014; Fanin et al., 2021), or as "functional breadth," in which decomposer communities from systems with chemically complex litter exhibit generalist capacities to decompose a wide range of substrates (Van Der Heijden et al., 2008; Strickland et al., 2009; Keiser et al., 2011; Fanin, Fromin and Bertrand, 2016). In addition to these legacy-driven effects, soil microbial communities may also differ in overall functional ability, an intrinsic capacity to decompose litter regardless of origin, which can reflect historical resource conditions or selection for generalist decomposers (Keiser et al., 2014; Veen et al., 2018). Functional breadth and ability may buffer decomposition against environmental change. However, it remains unclear whether legacy persistence is affected by the rate of change in litter inputs driven by forest transition, from gradual transitions over decades to rapid disturbance such as insect-driven canopy loss.

Eastern hemlock (*Tsuga canadensis* L., hereafter "hemlock") forests are increasingly threatened by the invasive hemlock woolly adelgid (*Adelges tsugae*, henceforth "HWA"), an aphid-like insect that feeds on nutrients in the hemlock twigs, ultimately causing tree decline and mortality (McClure, 1990; Ellison et al., 2018). The progression of HWA infestation varies geographically, largely due to climate-mediated differences in insect survival and host stress (Orwig and Foster, 1998; Evans and Gregoire, 2007). In the warmer southern U.S., mortality occurs rapidly, often within four to ten years of infestation (Evans and Gregoire, 2007; Nuckolls et al., 2009). In contrast, infested hemlocks in New England can persist for decades (Orwig and Foster, 1998; Parker et al., 1998, 1999; Skinner et al., 2003; Evans and Gregoire, 2007; Costa et al., 2008), likely due to colder winter temperatures that limit adelgid survival (Costa et al., 2008; Paradis et al., 2008). However, warming New England winters may accelerate hemlock loss in the future (Fei et al., 2019). Some land managers preempt this loss through salvage logging (Orwig et al., 2002; Brooks, 2004), which rapidly shifts forest composition in areas otherwise undergoing gradual decline.

Hemlock mortality opens canopy gaps that facilitate recruitment of species such as tulip poplar (*Liriodendron tulipifera*) and red maple (*Acer rubrum*) in the southern range (Brantley, Ford and Vose, 2013), and black birch (*Betula lenta* L., hereafter "birch") in New England (Orwig and Foster, 1998; Ellison et al., 2018). As a result, the canopy is transitioning from lignin-rich hemlock foliage with a waxy cuticle (Cornelissen, 1996; Chae et al., 2019) to more chemically labile deciduous litter (Coûteaux, et al., 1995; Wardle, Bonner and Barker, 2002). These canopy shifts also alter forest microclimate including increased soil temperatures and decreased soil moisture under open canopies, which can accelerate critical components of litter decomposition rates (Cobb and Orwig, 2002; Wardle et al., 2002; Fierer et al., 2005; Ayres et al., 2009a; Cobb, 2010). How microbial functional legacies interact with this shift in litter quality and the pace of canopy transition remains poorly understood. Hemlock-associated microbial communities may retain greater functional breadth, allowing them to decompose diverse litter types efficiently. This legacy, shaped by exposure to recalcitrant litter, may buffer changes in decomposition and nutrient cycling even after species turnover (Strickland et al., 2009; Keiser et al., 2014; Fanin et al., 2016). However, the persistence of functional breadth under rapid versus gradual hemlock decline remains an open question.

To evaluate whether the pace of forest compositional change alters decomposition and microbial legacies, we used a long-term hemlock removal experiment at Harvard Forest (MA, USA), which contrasts three forest conditions: a reference hemlock forest type experiencing natural HWA infestation, a girdled forest type simulating rapid hemlock mortality, and a nearby hardwood forest type representing a potential post-HWA state. Girdling has been used as an effective method to mimic abrupt tree mortality, killing trees within 2 years (Nuckolls et al., 2009; Ellison et al., 2010). Working in the experimental forest types 17 years after girdling and 13 years after the arrival of HWA into the reference hemlock forest type, we asked whether rapid vs. gradual hemlock loss altered litter decomposition and soil nutrient cycling. We hypothesized that (H1) litter decomposition in the girdled forest type will begin to resemble that of the adjacent hardwood forest type. Rapid hemlock loss and a subsequent shift to a birch-dominated overstory will induce a loss of the functional legacy and a shift in ecosystem biogeochemical cycling in the girdled forest type that resembles the nearby hardwood stand. In contrast, we further hypothesized (H2) that gradual hemlock mortality and minimal shifts in litter inputs observed in the hemlock reference, typical of New England hemlock decline, will maintain soil microbial functional legacies for decades after HWA infestation. By comparing forest types that vary in disturbance rate and contemporary overstory composition, this study examines whether the speed of disturbances alters microbial and biogeochemical legacies in transitioning forests.

## 2. Methods

### 2.1. Experimental design

We worked within the Harvard Forest Hemlock Removal Experiment (HF-HeRE, Ellison et al., 2010). The HF-HeRE is located within the 121-ha Simes Tract (42.47–42.48 N; 72.22–72.21 W) at the Harvard Forest Long-Term Ecological Research Site (Petersham, MA, USA). The soils are predominantly coarse loamy, mixed, active, mesic Typic Dystrudepts in the Charlton Series (USDA Soil Survey Staff, n. d.).

The HF-HeRE was established in 2003 within a single, contiguous hemlock stand (Ellison et al., 2010) to test ecosystem consequences of tree species loss. The HF-HeRE study delineated two, 90 × 90 (0.81 ha) plots within the hemlock stand as hemlock treatments: a hemlock reference forest type, which was unmanipulated but became subsequently infested with regional HWA spread in 2009, and a girdled forest type in which all hemlocks had a ring of bank and cambium removed (girdled) over a two-day treatment in 2005, causing hemlock mortality within two years (for more details see Ellison et al., 2010). To provide a comparison with a common successional endpoint of hemlock decline, we established a third forest type: an adjacent hardwood stand dominated by black birch to match birch dominance in declining Northeastern US hemlock stands (Fig. 1).

Number per hectare of live and dead hemlock at the hemlock reference and girdled forest types were counted in 2004 (pre-treatment), 2019, and 2024 (Supplemental Fig. S1). Understory species richness was sampled in the hemlock reference and girdled forest types by calculating the number of tree species $< 1.3$ m tall, as well as herbs, shrubs, ferns, and grasses in the center of a 30 m × 30 m area. Understory percent vegetation cover was based on ten 1 $m^2$ quadrats within the center of the hemlock reference, girdled, and hardwood forest types.

### 2.2. Litter bag assembly and deployment

Three litter species were collected in fall 2022: hemlock, birch, and tulip poplar (*Liriodendron tulipifera*). The three litters were chosen as analogs for the past, present, and potential future respectively of hemlock stands as they transition and are influenced by climate change. While tulip poplar was not present within the experimental forest types, it is predicted to expand northward due to climate change (U.S. Forest Service n.d.), has been found at transitioning hemlock sites near the Massachusetts-Connecticut border (Palmer et al., 2025), and may act as an analog for a potential future species coming into HWA-affected stands. Hemlock and birch litter were collected at Harvard Forest (Petersham, MA, USA). Recently senesced birch leaves were collected from the forest floor by hand. Given that hemlock does not drop needles in a discrete time frame, hemlock twigs were cut from trees at Harvard

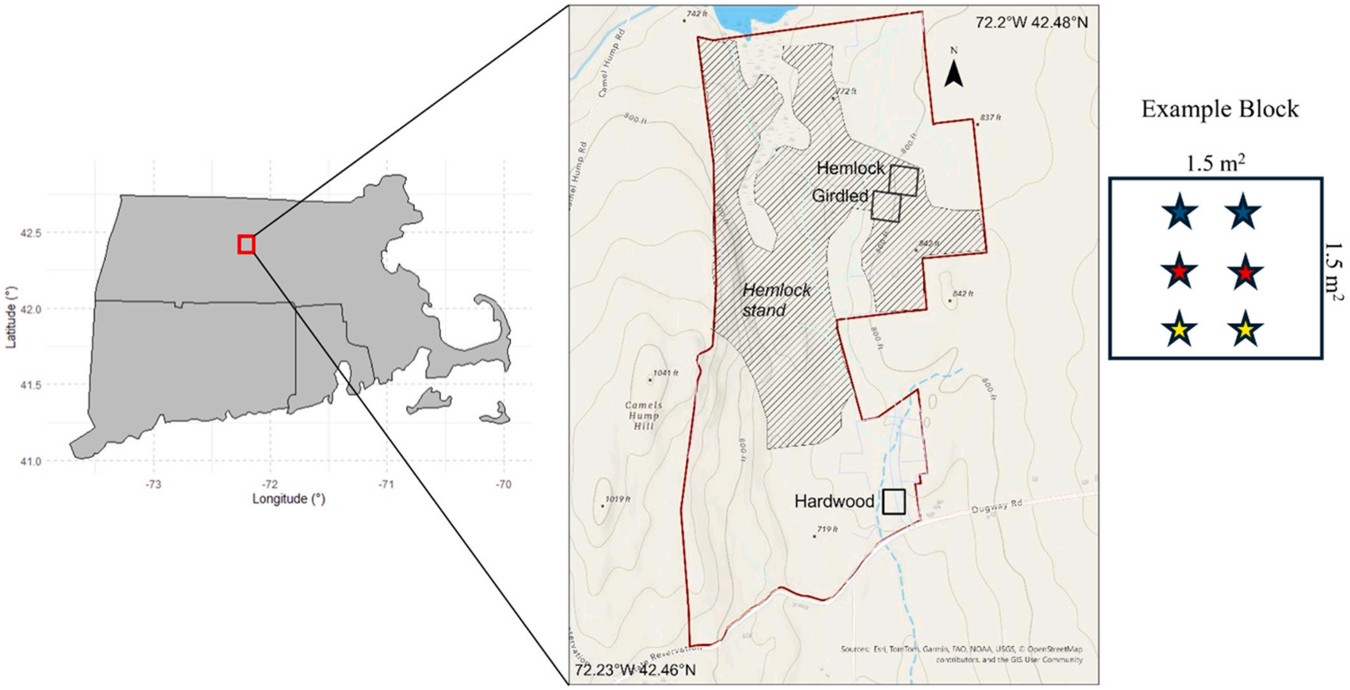

**Fig. 1.** Study location within the Harvard Forest, Petersham, MA, USA and the experimental design. Forest types (black outline) are located within the Simes Tract of Harvard Forest (red outline). The hemlock reference and girdled forest types are both within a large hemlock-dominated stand (hatched area), while the hardwood forest type is adjacent. At each forest type, we established three replicate blocks (1.5 $m^2$) running parallel to slope (8-13%). A schematic of a representative block illustrates the arrangement of six litter bags, with colors denoting different litter types.

Forest within the same geographic area. Once brought to the lab and air dried, the hemlock needles were easily separated from the woody twig. As tulip poplar is not established at Harvard Forest, recently senesced tulip poplar leaves were collected at the University of Massachusetts Amherst (Amherst, MA, USA), ~ 33 km from HF-HeRE. The lawn area surrounding the tulip poplar trees received turf fertilizer on an annual basis. For all species, leaves that appeared free of herbivory or fungal colonization were returned to the lab and air dried. The 19 $cm^2$ litter bags were assembled using 1 mm nylon mesh on the top, allowing access by mesofauna such as microarthropods, and a 53 μm polyester mesh on the bottom, which permits entry by microbes and some microfauna (e.g., nematodes) while minimizing litter loss and excluding larger soil fauna such as earthworms. Each litter bag type received a total of 3 g of either hemlock, black birch, or tulip poplar litter.

Litterbags were deployed across the three forest types in December 2022 prior to soil freezing. At each forest type, we established three replicate blocks (1.5 $m^2$) running parallel to slope (8–13 %) to account for landscape heterogeneity (sensu Keiser et al., 2017). All three litter species were represented within each block. Each litter species occupied one row (20 cm apart, random order). To account for two collection dates, two replicate bags per litter type were placed side-by side (20 cm apart) within a row. This design resulted in 54 experimental bags in total (3 forest types × 3 blocks × 3 litter types × 2 collection dates). All bags were pinned to the forest floor below the year's senesced leaves. At deployment, three additional "travel bags" of each litter type were deployed and then immediately collected to account for mass loss due to deployment and collection of the bags.

### 2.3. Litter bag collections and analyses

Litter bags were collected at 9 and 18 months (September 2023 & June 2024, respectively) after deployment (December 2022). These times were chosen to account for the initial fast phase of decomposition (September 2023) and the second, slower phase of decomposition (June 2024) (Adair et al., 2008). For each collection, a litter bag of each bag type was randomly selected from each block and returned to the lab on ice for further analysis (n = 27). Litter bags were air dried at room temperature for at least four weeks. Once dry, any foreign material, including fine roots and soil particles, was removed from the litter before weighing. Mass loss was calculated by dividing the final weight of each litter bag over the initial weight and converting to a percentage (relative mass loss).

We followed the equation in Lu et al., (2021) to determine home-field advantage for hemlock and birch litter in a variety of "home" and "away" forest type combinations using the following equation (Eq. 1):

$$\text{HFA } (\%) = (RML_{home} - RML_{away}) \;/\; RML_{away} \times 100 \qquad (1)$$

where HFA (%) represents how much faster the hemlock or birch litter decomposed at the designated "home" and "away" forest types, with $RML_{home}$ representing the relative mass loss (RML) at the "home" forest types and $RML_{away}$ representing the relative mass loss at the "away" forest types. There were a total of four forest type combinations, with two per litter. For hemlock, the combinations were: hemlock reference (home) v. girdled (away) and girdled (home) v. hardwood (away). For birch, the combinations were: girdled (home) v. hemlock reference (away) and hardwood (home) v. hemlock reference (away). Tulip poplar was not included as it is not present at Harvard Forest and therefore does not have a "home" forest type. The HFA percentages are compared relative to each other and evaluated on whether they are greater than (positive HFA) or less than (no HFA) zero (Ayres et al. 2009b).

Roughly 3 mg of litter was milled (SPEX mixer mill, Cole-Parmer, NJ USA) for C and N analysis at the Kansas State University using an Elementar EA Vario Pyrocube (Elementar

Americas Inc., Ronkonkoma, NY, USA). Milled litter samples were analyzed using Fourier

Transform Infrared-Attenuated Total Reflectance (FTIR-ATR, Perkin-Elmer Spectrum One, Shelton, CT, USA) spectroscopy to detect changes in leaf litter functional groups, such as cellulose, proteins, lignin, and aromatic rings, over time. Milled litter samples were analyzed for infrared absorbance spectra over a 20-second period. Absorbance values for wavelengths associated with functional groups, including saccharides, amides, and lignin, were identified using established reference peaks (Keiluweit et al., 2015). Preliminary examination indicated minimal forest type-level divergence in absorbance profiles, and further sample splitting by forest type would have reduced sample replication per category, limiting interpretability. Thus, FTIR analysis was focused on compositional shifts among litter types as decomposition progressed.

### 2.4. Soil collections and analyses

At litter bag deployment, initial soil samples were collected for baseline soil chemical and physical measurements within each block. Ten soil cores (2.5 cm diameter, 15 cm depth) were taken across each block and homogenized. The soils were returned to the lab on ice for further analysis. At each litterbag collection, soil was collected to a depth of 15 cm from beneath each bag. All soils were returned to the lab on ice for further analysis. At each sample time

(deployment and litterbag collections), we recorded soil temperature within each block to a depth of 10 cm using a Traceable soil temperature probe allowing the temperature to stabilize across 1 min (Traceable, Webster, TX, USA).

At the lab, all soils were sieved to 2 mm before determining field moisture content [subsample dried at 105°C for 24 hrs] and water holding capacity [fully saturated subsample, drained for 2 hrs, dried at 105°C for 24 hrs] (Bradford et al., 2008; Keiser et al., 2016). Soil pH was determined at each collection using a 1:1 soil-water solution by volume (Allen, 1989). To estimate the readily available C resources of the soil, a 30-day soil incubation at 20 °C and 65 % water holding capacity, was set up after each collection, as described in Fierer et al., (2005) and Bradford et al. (2008). Briefly, soil samples incubated in 50 mL centrifuge tubes with lids modified for gas analysis were repeatedly measured for $CO_2$ efflux using a Li-7000 infrared injection gas analyzer (LiCOR, Lincoln, NB, USA) across 30 days (mg C g dry weight soil$^{-1}$). Active microbial biomass was estimated through substrate-induced respiration (SIR) (West and Sparling, 1986; Bradford, Fierer and Reynolds, 2008). Chloroform fumigation extraction (CFE) was used to measure total microbial biomass C and total N as followed by Fierer and Schimel (2003), and samples were run on a Shimadzu TOC-L (Shimadzu, Maryland, USA). Ammonium-N (NH4$^+$-N) and nitrate-N ($NO_3^-$-N) concentrations were determined using a BioTek Synergy HTX multi-mode plate reader aft a 28-day KCl extraction (method modified from Doane and Horwáth, 2003). Net N mineralization was calculated as $NH_4^+$ and $NO_3^-$ at day 28 minus $NH_4^+$ and $NO_3^-$ at day 0. Net nitrification was calculated as $NO_3^-$ at day 28 minus $NO_3^-$ at day 0 (Goodale and Aber, 2001). These measurements reflect microbial processes influenced by resource availability, often driven by the quality of decomposing litter. Air dried soils were analyzed for soil texture (deployment soils only) and soil C and N content. Roughly 8 mg of dried soil was milled (SPEX mixer mill) and sent for C and N analysis at the Kansas State University using a NA 1500 CHN Analyzer (Carlo Erba Stumentazione, Milan, Italy).

### 2.5. Statistical analysis

All statistical analyses were conducted in R Studio version 4.3.0 (R Core Team, 2022). We used linear mixed-effect models (LMMs) with Satterthwaite denominator degrees of freedom to account for small and uneven sample sizes and random-effects variance. Models for the soil analyses (temperature, pH, microbial biomass C, active microbial biomass C, soil labile C, and soil inorganic N rates) included forest type, date (deployment and the two collection dates), and their interaction as fixed effects, with block as the random intercept nested within forest type Litter mass loss was analyzed at the final collection date (June 2024) with a lme model that included fixed effects for litter, forest type, and their interaction, again with block as a random effect nested within forest type.

We examined the average percent differences in mass loss among hemlock, birch, and tulip poplar within a forest type as a measure of microbial perception of differences in the litter (sensu Keiser et al., 2014). For each forest type, we calculated the absolute percentage differences between all pairwise combinations (i.e. |Birch – Hemlock| / Hemlock), and then averaged these values across replicates within a block.

Changes in litter chemistry (%C, %N, and C:N) were evaluated as differences from initial, non-decomposed values, with models including fixed effects of litter, forest type, and date, and block as a random intercept. To identify the strongest predictors of decomposition, additional LMMs were constructed with mass loss as the response variable and candidate predictors including soil and litter chemistry (C, N, C:N), microbial activity (active microbial biomass, labile C, nitrification, net N mineralization, MBC), and environmental factors (forest temperature, pH). Post-hoc contrasts for all analyses used estimated marginal means with Tukey adjustments. Statistical assumptions (e.g., normality, homogeneity of variance) were checked using residual plots.

Because our experiment included three forest types (hemlock reference and girdled within the HF-HeRE and an adjacent hardwood stand outside of HF-HeRE, our “forest types” (hemlock reference, girdled, and hardwood) could be viewed as large-scale units without replication at the stand level. This is a common issue in experimental manipulations that require large-scale treatment areas for realistic ecological responses (Schindler, 1998; Davies and Gray, 2015). To avoid pseudoreplication (Hurlbert 1984), all statistical inference was conducted using blocks ($n = 3$ per forest type) as the replicates. Forest and litter type were treated as fixed effects, and block was modeled as a random effect nested within forest type. Thus, our analyses test for consistent differences across replicated blocks within each forest type, rather than relying solely on a single mean from each forest type. Accordingly, our results should be interpreted as strong within-stand contrasts among disturbance trajectories, rather than broad landscape-level generalizations. Our block design provides replicated litter and soil measurements within each experimental treatment (i.e. Bond-Lamberty et al., 2016; Keiser and Bradford, 2017; Hawkes et al., 2017) and a nested structure consistent with other large-scale ecological manipulation experiments (e.g., Davies and Gray, 2015; Schindler, 1998), which often lack true stand-level replication (Barker Plotkin et al., 2013).

## 3. Results

### 3.1. Forest type conditions and decomposition dynamics

The ratio of live:dead hemlock in the hemlock reference and girdled forest types decreased from 2004 to 2024. In the hemlock reference, live:dead hemlock slowly declined from 26.7 in 2004–2.8 in 2024. The girdled forest type saw more rapid hemlock mortality; a live:dead hemlock ratio of 38.1 in 2004 abruptly decreased to 0.006 in 2009, and remained < 0.2 through 2024 (Supplemental Fig. S1). Understory species richness was greater in the girdled forest type (30) than in the hemlock reference (26) in 2023 (Supplemental Fig. S2). Average soil temperature did not vary across forest type ($F_{2,96} = 0.0929$, $p = 0.91$), with a mean temperature across forest types of 14.5 °C, though it did vary across dates ($F_{1,\ 93} = 164.5$, $p < 0.001$), with December 2022 temperatures being the lowest (5.39 ± 0.18 °C) and similar between September 2023 and June 2024 (14.01 ± 0.03 °C and 15.1 ± 0.03 °C, respectively). In contrast, soil pH did vary significantly across forest type ($F_{2,96} = 198.03$, $p < 0.001$), with the hardwood forest type having higher pH (5.17) than both the hemlock reference (4.31) and the girdled forest types (4.34). Soil pH was not significantly different between the hemlock reference and the girdled forest types ($p = 0.92$).

Decomposition patterns varied by forest and litter type, with inverse patterns among litter species at the hemlock reference compared to the hardwood forest type (Fig. 2). A linear mixed-effects model revealed a litter × forest type interaction ($F_{4,16} = 14.24$, $p < 0.0001$). In the

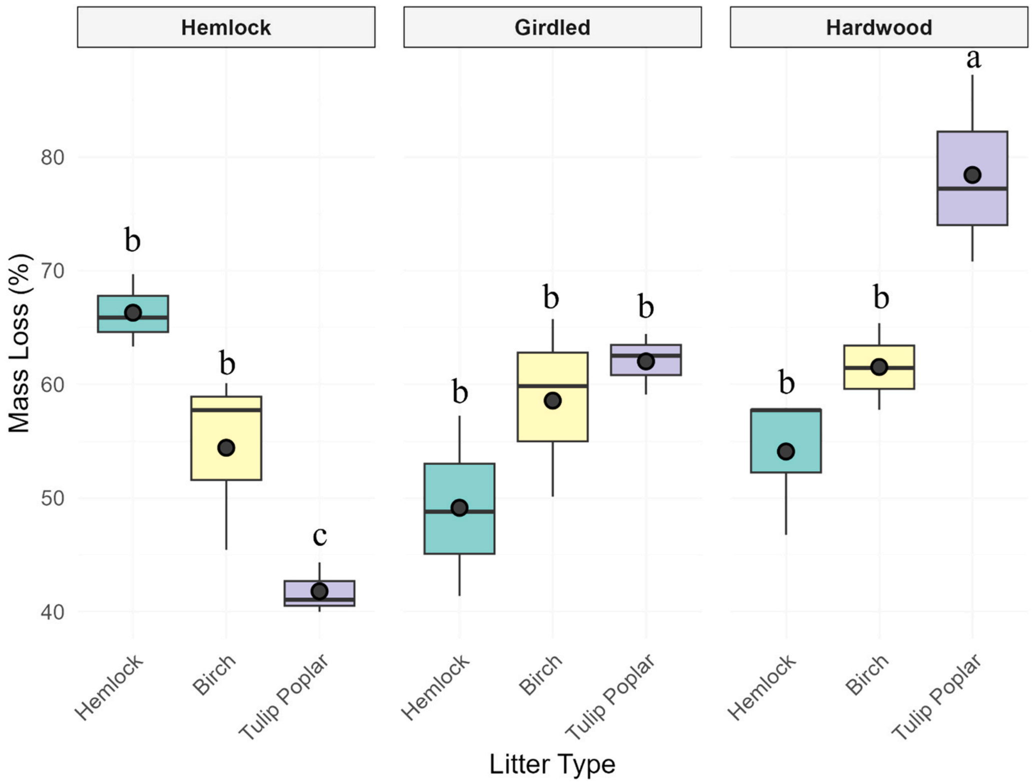

**Fig. 2.** Percent mass loss after 1.5 years (June 2024) for each litter bag type across the three forest types. Black circles indicate average mass loss for each litter type at each site. Letters denote significant differences across litters × forest types ($p < 0.05$).

hemlock reference, hemlock litter decomposed significantly more than tulip poplar litter (hemlock: 66.3 ± 1.8 %; tulip poplar: 41.8 ± 1.3 %; $p = 0.0029$) and did not differ from birch litter (birch litter 54.4 ± 4.5 %; $p = 0.32$). No significant differences in mass loss were observed among the litter types in the girdled forest type despite a biological trend of increasing mass loss from hemlock to birch and tulip poplar. In the hardwood forest type, tulip poplar decomposed significantly more than both birch (tulip poplar: 78.4 ± 4.8 %; birch: 61.5 ± 2.2 %; $p = 0.0035$) and hemlock (54.1 ± 3.7 %, $p = 0.0031$), but hemlock and birch did not differ significantly from each other. Tulip poplar in the hardwood forest type exhibited the greatest mass loss of any litter × forest type combination (78.4 ± 4.8 %), while tulip poplar in the hemlock reference exhibited the lowest mass loss (41.8 ± 1.3 %).

Home-field advantage (HFA) analyses for birch and hemlock litter showed differences by litter and forest type (Fig. 3). The HFA value provides the percent difference in decomposition at “home” versus “away” and is relative within a study. Hemlock litter exhibited a positive HFA % when hemlock litter was home in the hemlock reference and away at the girdled forest type (38 ± 16.7 %), but no HFA when hemlock litter was home in the girdled and away at the hardwood forest type

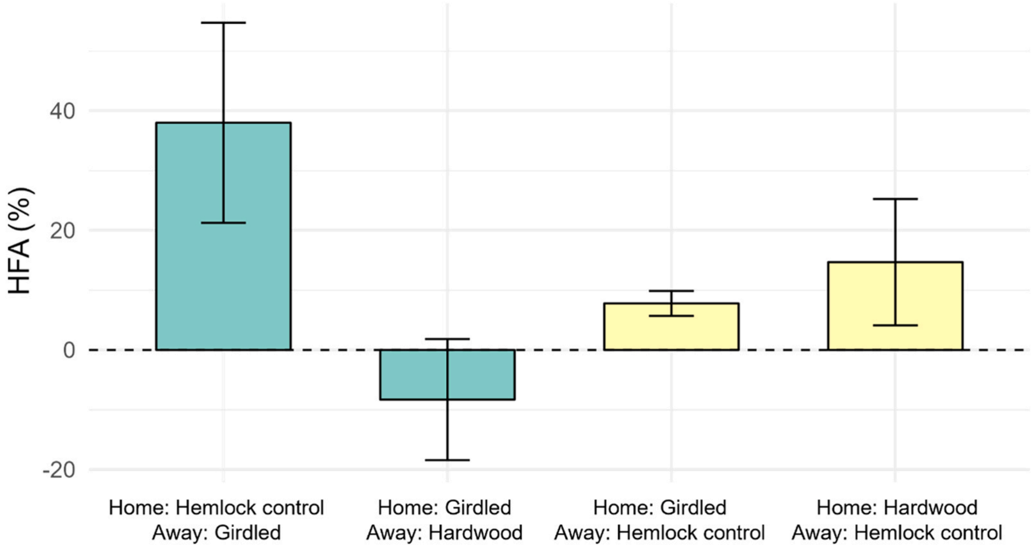

**Fig. 3.** Percent of home-field advantage experienced by hemlock and birch litters based on Lu, Kotze and Setälä (2021). Error bars are ± SE. Color denotes litter type, where green = hemlock, and yellow = birch.

(-8.3 ± 10.1 %). These results suggest that hemlock litter in the girdled forest type has lost a home advantage since rapid loss of this canopy species. Birch exhibited positive HFA when the girdled (7.8 ± 2.1 %) or hardwood (14.7 ± 10.6 %) forest types were designated as "home", and the hemlock reference forest type was designated as "away." Additionally, the average % difference values (Fig. 4) decreased from the hemlock reference (0.45 ± 0.16 %) to girdled (0.28 ± 0.13 %) to hardwood forest type (0.25 ± 0.07 %).

### 3.2. Litter chemical quality

Litter type and date drove differences in litter quality over the course of the experiment (Table 1). Changes in %C varied by both litter and time, with a significant litter × date interaction ($F_{2,34} = 3.79$, $p = 0.0328$) and a forest type × date interaction ($F_{2,34} = 3.58$, $p = 0.0389$). Tulip poplar %C significantly increased over time ($p = 0.0054$), while birch and hemlock did not differ from initial values. Litter %N increased significantly for all litters by the end of the experiment relative to initial values ($p < 0.01$ for all litters), but the magnitude of increase differed among litters ($F_{2,36} = 37.00$, $p < 0.0001$). Similar to %C, C:N ratios varied by both litter ($F_{2,34} = 675.99$, $p < 0.0001$) and date ($F_{1,34} = 5.44$, $p = 0.0257$). The C:N ratio for all litters significantly decreased over time ($p < 0.01$ for all litters), reflecting the increase in %N.

FTIR-ATR spectra revealed shifts in litter chemistry over time, particularly in the saccharide, amide, and lignin regions (Fig. 5, Table S1). As there were minimal discernible differences between forest types, FTIR analysis was focused on compositional shifts among litter types as decomposition progressed, and data was averaged among forest type for each litter. In the saccharide region (950–1100 $cm^{-1}$), absorbance declined from baseline (deployment, December 2022) to September 2023, reflecting microbial consumption. Hemlock litter, which had the highest saccharide absorbance at baseline, declined sharply and then stabilized, suggesting early microbial processing and possible stabilization of recalcitrant compounds. In the amide region (1550–1650 $cm^{-1}$), absorbance declined for hemlock and tulip poplar, but not birch. In the lignin region (1500–1520 $cm^{-1}$, 1220–1275 $cm^{-1}$), hemlock retained high lignin absorbance, consistent with its recalcitrant nature.

### 3.3. Soil nutrient analysis

Soil %C, %N, and the C:N ratio varied strongly among forest types (Table 2). Across all dates, the girdled forest type consistently had higher %C and %N than the hemlock reference and hardwood forest types ($p < 0.001$), while %C and %N in the hemlock reference were intermediate and sometimes significantly greater than hardwood (e.g., %C in June 2024, $p = 0.043$). Although %C and %N did not change significantly over time ($p > 0.3$ for all), C:N ratios showed a significant forest type × date ($F_{2,60} = 4.96$, $p < 0.02$), with hardwood soils maintaining consistently lower values (11.4 – 14.9) compared to both the hemlock reference (18.6 – 19.2) and girdled soils (22.6 – 23.0) ($p < 0.01$ for all pairwise comparisons). All forest types saw an increase in C:N ratios from December 2022 to September 2023, while the differences in C:N ratios were subtle between September 2023 and June 2024 (Table 2).

Soil microbial biomass C (MBC) showed a strong forest type × date interaction ($F_{4,90} = 10.318$, $p < 0.001$), with values significantly lower in the hardwood forest type than both the hemlock reference ($p = 0.016$ in September 2023; $p < 0.0001$ in June 2024) and girdled forest types ($p < 0.0001$ at both dates), while values did not differ consistently between hemlock and girdled forest types (Table 2). Active microbial biomass (SIR) varied significantly by forest type and date (forest type × date: $F_{2,58} = 4.98$, $p = 0.010$), increasing over time in the girdled and hemlock reference to levels greater than the hardwood forest type (Table 2). In contrast, net nitrification rates were strongly elevated in the hardwood forest type compared to the other forest types, reflected in significant interaction between forest type × date ($F_{2,58} = 16.0$, $p < 0.001$) (Table 2). Soil labile C exhibited a significant forest type × litter interaction ($F_{8,58} = 2.16$, $p = 0.044$; Table 3). Across litter types, labile C values were consistently lower in the hardwood soils compared to the girdled and hemlock reference forests, which did not differ significantly from each other. Net N mineralization increased significantly from Sept. 2023 to June 2024 ($F_{1,58} = 11.5$, $p = 0.0012$; Table 4), but showed no consistent differences among forest types or litter types.

## 4. Discussion

Working in the Hemlock Removal Experiment at the Harvard Forest, we examined how contrasting rates of hemlock loss and subsequent forest transition impacts decomposition dynamics and soil biogeochemical properties. We observed a difference in litter mass loss patterns between the hemlock and hardwood forest types whereby total mass loss decreased from hemlock and birch to tulip poplar litter in the hemlock reference while mass loss increased from hemlock and birch to tulip poplar at the hardwood forest type. Litter mass loss was not significantly different among litter species in the girdled forest type showing a transition away from mass loss dynamics in the hemlock reference, in partial support of H1. Trends in soil microbial activity and nutrient

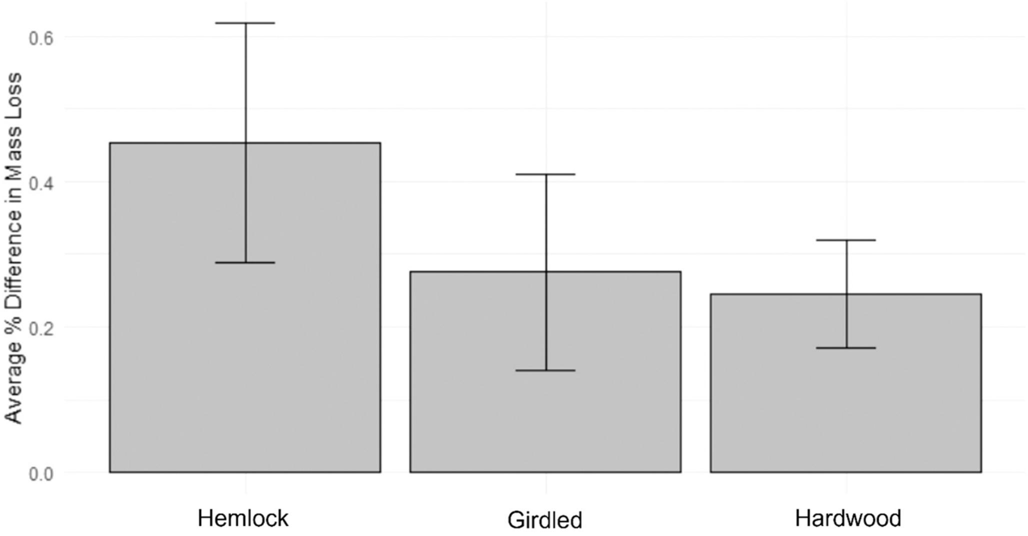

**Fig. 4.** Difference in decomposition among hemlock, birch, and tulip poplar litters within a forest type (mean ± SE).

**Table 1**

Initial (deployment) and final litter chemistry (%C, %N, C:N) for birch, hemlock, and tulip poplar. Values are mean ± SE. Letters indicate significant differences among litter types ($p < 0.05$) within a column. Asterisks (*) denote significant differences between litter initial and final values for each analysis (%C, %N, C:N; $p < 0.05$).

| Litter | %C Initial | %C Final | %N Initial | %N Final | C:N Initial | C:N Final |
|---|---|---|---|---|---|---|
| Birch | $46.97 \pm 0.05^{a}$ | $49.06 \pm 1.10^{a}$ | $1.04 \pm 0.00^{b}$ | $2.06 \pm 0.17^{a*}$ | $45.05 \pm 0.04^{b}$ | 24.94 ± 1.72a* |
| Hemlock | $47.02 \pm 0.02^{a}$ | $49.21 \pm 1.31^{a}$ | $1.46 \pm 0.00^{a}$ | $1.83 \pm 0.10^{a*}$ | $32.19 \pm 0.06^{c}$ | $27.47 \pm 1.38^{a*}$ |
| Tulip poplar | $41.26 \pm 0.03^{b}$ | $46.83 \pm 0.52^{b*}$ | $0.52 \pm 0.00^{c}$ | $1.82 \pm 0.13^{a*}$ | $78.76 \pm 0.06^{a}$ | $26.58 \pm 1.56^{a*}$ |

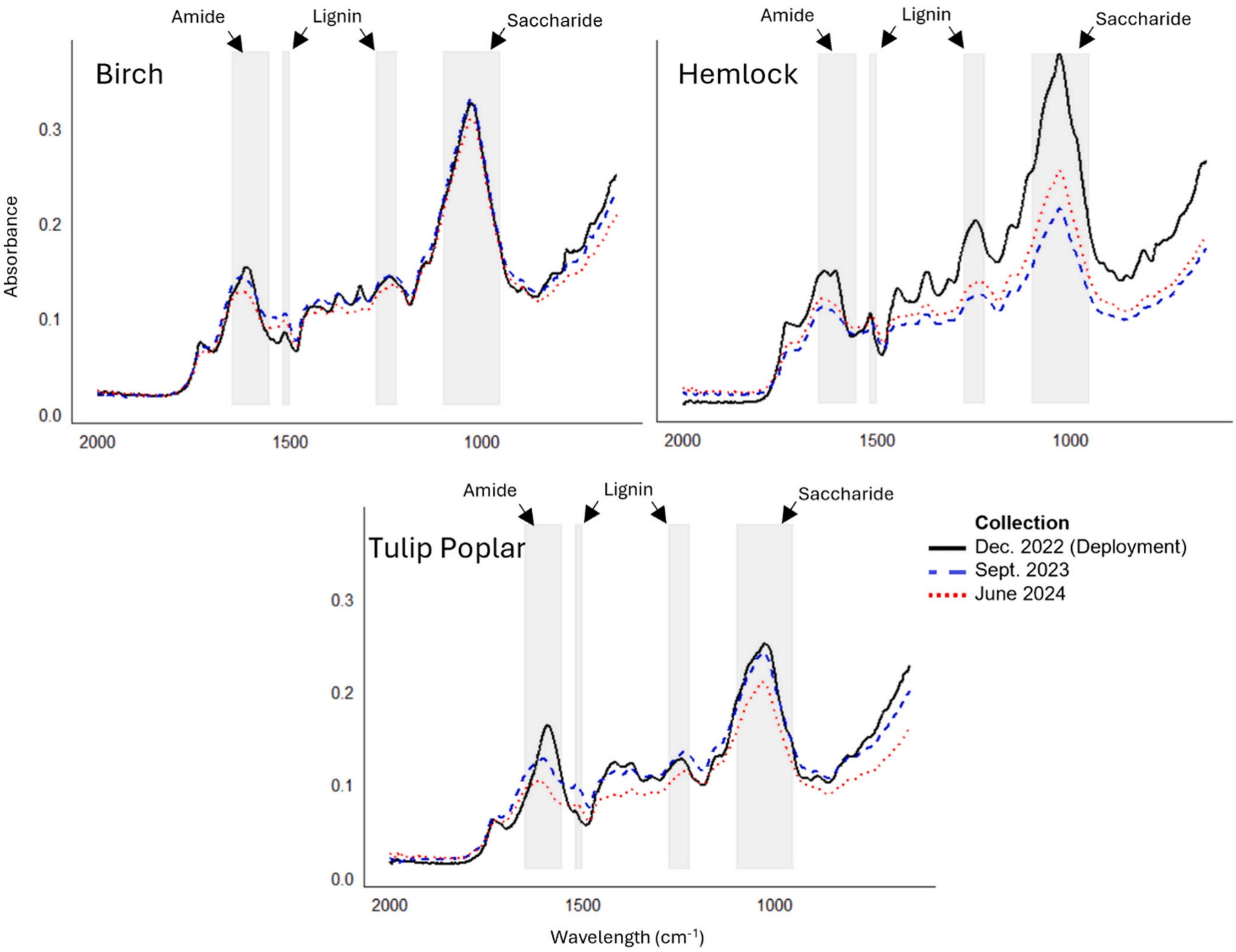

**Fig. 5.** FTIR-ATR spectra for each litter, averaged among forest types. Shaded regions denote amide, lignin, and saccharide wavelength regions.

cycling in the girdled forest type remained more similar to the hemlock reference, indicating that belowground legacies can persist despite rapid canopy shifts. These findings suggest that while litter decomposition processes respond relatively quickly to rapid shifts in canopy composition, underlying microbial functions related to C and N cycling may remain resilient over decadal timescales, even following abrupt forest transitions.

Litter decomposition is partially determined by functional legacies, or the relationship between the soil community and its historical litter input (Keiser et al., 2011; Fanin, Fromin and Bertrand, 2016; Schroeter et al., 2022). Legacies can be driven by home field advantage whereby microbial communities are more efficient at processing litter types they have historically encountered (Gholz et al., 2000; Fanin et al., 2021). The occurrence of HFA was dependent on the forest type and litter species. Hemlock had a positive HFA effect at the hemlock forest type (following the paired HFA method of Lu et al., (2021), supporting H2, but had lost an HFA effect at the girdled forest type becoming neutral (Fig. 3), again partially supporting H1. Birch litter had a positive HFA effect at the hardwood forest type where it is a dominant overstory species, albeit smaller than the hemlock HFA in the hemlock reference (Fig. 3). The hemlock microbial community may have a greater overall functional ability to decompose the more complex hemlock litter (Keiser et al., 2014; 2017), resulting in the most positive HFA percentage. Birch also had a positive HFA in the girdled forest type (Fig. 3), indicating that in the 19 years since girdling, the soil microbial community shifted from a positive hemlock HFA to a positive birch HFA which now dominates the plot. A shift in the microbial perception of litter inputs, which reflects microbial functional ability (Strickland et al., 2009; Keiser et al., 2013), was reflected in a narrower percent difference in mass loss among litters between girdled and hardwood forest types (Fig. 4). The HFA and microbial perception data suggest that a rapid canopy transition in the girdled forest type and a concomitant shift in litter inputs has removed a

**Table 2**
Soil %C, %N, C:N, microbial biomass C (MBC), active microbial biomass C, and net nitrification rates (mean ± SE) by forest type and collection date. Values are averaged across litter types. Superscript letters within a column indicate significant differences among forest types only within a soil analysis and specific date [within column comparisons] ($p < 0.05$).

| Soil Analysis | Forest Type | December 2022 (deployment) | September 2023 (Collection 1) | June 2024 (Collection 2) |
|---|---|---|---|---|
| **%C** | Hemlock | 7.98 ± 0.72$^{b}$ | 7.91 ± 0.72$^{b}$ | 7.89 ± 0.72$^{b}$ |
| | Girdled | 9.33 ± 0.72$^{a}$ | 11.92 ± 0.72$^{a}$ | 11.83 ± 0.72$^{a}$ |
| | Hardwood | 4.19 ± 0.72$^{c}$ | 4.29 ± 0.72$^{c}$ | 6.03 ± 0.72$^{c}$ |
| **%N** | Hemlock | 0.52 ± 0.034$^{ab}$ | 0.412 ± 0.034$^{b}$ | 0.431 ± 0.034$^{b}$ |
| | Girdled | 0.55 ± 0.034$^{a}$ | 0.528 ± 0.034$^{a}$ | 0.527 ± 0.034$^{a}$ |
| | Hardwood | 0.32 ± 0.034$^{b}$ | 0.376 ± 0.034$^{b}$ | 0.389 ± 0.034$^{b}$ |
| **C:N** | Hemlock | 15.6 ± 0.7$^{b}$ | 19.2 ± 0.7$^{b}$ | 18.6 ± 0.7$^{b}$ |
| | Girdled | 15.0 ± 0.7$^{a}$ | 22.6 ± 0.7$^{a}$ | 23.0 ± 0.7$^{a}$ |
| | Hardwood | 10.0 ± 0.7$^{c}$ | 11.4 ± 0.7$^{c}$ | 14.9 ± 0.7$^{c}$ |
| **MBC** μg C g$^{-1}$ dry soil | Hemlock | 62.3 ± 84.8$^{a}$ | 261.0 ± 37.9$^{a}$ | 680.6 ± 37.9$^{a}$ |
| | Girdled | 67.0 ± 84.8$^{a}$ | 462.4 ± 37.9$^{a}$ | 838.6 ± 37.9$^{a}$ |
| | Hardwood | 56.4 ± 84.8$^{a}$ | 100.5 ± 37.9$^{b}$ | 173.4 ± 37.9$^{b}$ |
| **Active microbial biomass C** μg C g$^{-1}$ soil | Hemlock | 2.5 ± 4.8$^{a}$ | 4.7 ± 2.6$^{a}$ | 11.4 ± 2.6$^{a}$ |
| | Girdled | 1.4 ± 4.8$^{a}$ | 3.6 ± 2.6$^{a}$ | 16.8 ± 2.6$^{a}$ |
| | Hardwood | 1.8 ± 4.8$^{a}$ | 1.9 ± 2.6$^{b}$ | 1.7 ± 2.6$^{b}$ |
| **Net nitrification** mg N g$^{-1}$ soil per 28 d | Hemlock | −0.004 ± 0.003$^{b}$ | 0.001 ± 0.002$^{b}$ | 0.004 ± 0.002$^{b}$ |
| | Girdled | −0.003 ± 0.003$^{b}$ | −0.001 ± 0.002$^{b}$ | 0.001 ± 0.002$^{b}$ |
| | Hardwood | 0.001 ± 0.003$^{a}$ | 0.024 ± 0.002$^{a}$ | 0.038 ± 0.002$^{a}$ |

**Table 3**
Soil labile C (cumulative $CO_2$, μg C g$^{-1}$ dry soil). Values are mean ± SE (n = 3). Superscript letters denote significant differences among forest types within each litter type ($p < 0.05$).

| | Litter | | |
|---|---|---|---|
| **Forest Type** | **Hemlock** | **Birch** | **Tulip Poplar** |
| Hemlock Reference | 42.60 ± 11.90$^{b}$ | 30.64 ± 3.70$^{b}$ | 49.02 ± 13.64$^{a}$ |
| Girdled | 66.83 ± 17.19$^{a}$ | 78.02 ± 21.21$^{a}$ | 46.87 ± 11.69$^{a}$ |
| Hardwood | 22.97 ± 3.40$^{c}$ | 19.37 ± 2.90$^{c}$ | 20.00 ± 6.46$^{b}$ |

**Table 4**
Net N mineralization rates (mg N g$^{-1}$ dry soil per 28 d). Values are mean ± SE (n = 9, averaged across forest types and litter). Superscript letters denote significant differences among dates ($p < 0.05$).

| Date | Net N mineralization (mg N g$^{-1}$ soil per 28 d) |
|---|---|
| Dec. 2022 | 0.00 ± 0.00$^{a}$ |
| Sept. 2023 | 0.02 ± 0.00$^{b}$ |
| June 2024 | 0.04 ± 0.00$^{c}$ |

hemlock functional legacy 17 years after rapid loss of the hemlock overstory. In contrast, and in support of H2, a slow transition in the hemlock canopy, as found in the hemlock reference, retains HFA 15 years after HWA infestation.

Litter decomposition in the gridled forest type was still distinct from that found in the hardwood reference suggesting that microbial functional shifts following disturbance do not immediately mirror aboveground vegetation changes (Bradford et al., 2014; Liu et al., 2023). Notably, tulip poplar, which does not yet grow at the Harvard Forest but is expected to expand its range with climate change (U.S. Forest Service), had significantly greater mass loss in the hardwood forest type with decreasing mass loss in the girdled and hemlock reference forest types. A decrease in tulip poplar mass loss (hardwood > girdled > hemlock reference) is also consistent with microbial functional breadth, or the ability of decomposers to break down litters with a range of chemical complexity at similar rates (Keiser et al., 2014; Fanin et al., 2016; Veen et al., 2018). Litter chemistry was reflected in the FTIR data with tulip poplar and birch exhibiting greater lignin degradation, suggesting faster breakdown of lignin during decomposition (Meentemeyer, 1978; Melillo et al., 1982; Laishram and Yadava, 1988), whereas hemlock retained more lignin (Fig. 5). The girdled forest type, which now has a functional history of chemically recalcitrant hemlock and more chemically labile birch was able to decompose all three litters at more similar rates, supporting a wider functional ability despite losing hemlock HFA.

A rapid shift in the overstory species at the girdled forest type and subsequent loss of an HFA legacy for litter decomposition did not extend to whole ecosystem dynamics. Soil biogeochemical cycling, a critical determinant of site fertility and what plants can grow at a site (Smith et al., 2015), remained similar between the hemlock reference and girdled forest types (Tables 2–4). The hemlock reference and girdled forest types had higher measures of soil C and slower N cycling than the hardwood, indicating potential material legacies of the hemlock needles in the girdled forest type despite new birch inputs. This aligns with research showing that shifts in microbial function lags aboveground shifts (Bradford et al., 2014; Fanin et al., 2016). Nitrification rates, for example, were significantly higher in the hardwood forest type, reinforcing the link between higher nitrogen availability and faster decomposition enabled by a long-term history of hardwood species (Fierer et al., 2005; Cobb, 2010). Higher soil C in the girdled treatment compared to the other two forest types may reflect a stand still in transition belowground (Table 2) with dense overstory growth and more labile litter increasing total soil C. Microbial community function, particularly nitrification and C mineralization, appears to lag behind vegetation change, showing a decoupling in functional legacies between litter decomposition and biogeochemical cycling when hemlock decline and stand transition occurs within a few years (girdling) as opposed to multiple decades (natural HWA infection).

Altogether, the findings from our study within a single hemlock stand divided into experimental manipulations underscore the lag between vegetation shifts and microbial functional adaptation, reinforcing that microbial responses to disturbance can depend on the speed of forest disturbance: a quick transition or slow decline (Kostenko et al., 2012; Jongen et al., 2021, Palmer et al., 2025). The girdled forest type may serve as a proxy for how hemlock forests will respond if climate change increases the speed of hemlock decline in New England (Nuckolls et al., 2009) or if salvage logging efforts increase (Orwig et al., 2002; Brooks, 2004). Our findings suggest that such rapid transitions could disrupt microbial specialization and alter decomposition pathways in a shorter timescale than current rates of hemlock decline. Future work should aim to determine the tipping point at which belowground processes realign with aboveground vegetation, and how this timing varies across disturbance trajectories to accurately estimate C cycling. Given the contrasting shift in microbial functional legacies depending on the speed of transition in eastern hemlock stands (few years v. multi-decade), it is imperative to understand how long these soil legacies persist and when potential functional convergence with hardwood ecosystems occurs. This work reinforces the importance of understanding microbial functional legacies in forests under pressure from non-native pests to accurately quantify short-and long-term C and N cycling in North American forest ecosystems.

## Author contributions

CAP and ADK lead the research design. CAP collected and analyzed data with guidance from ABP and ADK. CAP wrote the first drafts of the manuscript. ABP and ADK helped with revisions to the manuscript.

## Funding

This research was funded by USDA Forest Service Evaluation Monitoring grant 22-DG11094200–204, as well as LTER grant NSF-DEB-1832210. This research was also supported by the University of Massachusetts Amherst.

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Acknowledgements

The authors thank the Harvard Forest for use of the HF-HeRE site and the LTER Network. The authors would also like to thank two anonymous reviewers whose feedback significantly improved this manuscript.

## Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2025.123304.

## Data availability

Data will be made available on request.

## References

Adair, E.C., et al., 2008. Simple three-pool model accurately describes patterns of long-term litter decomposition in diverse climates (Available at:). Glob. Change Biol. 14 (11), 2636–2660. https://doi.org/10.1111/J.1365-2486.2008.01674.X.

Allen, S.E., 1989. Chemical Analysis of Ecological Materials, 2nd edn. Blackwell Science, Oxford.

Austin, A.T., et al., 2014. There's no place like home? An exploration of the mechanisms behind plant litter–decomposer affinity in terrestrial ecosystems (Available at:). N. Phytol. 204 (2), 307–314. https://doi.org/10.1111/NPH.12959.

Ayres, E., et al., 2009a. Soil biota accelerate decomposition in high-elevation forests by specializing in the breakdown of litter produced by the plant species above them (Available at:). J. Ecol. 97 (5), 901–912. https://doi.org/10.1111/j.1365-2745.2009.01539.x.

Ayres, E., et al., 2009b. 'Home-field advantage accelerates leaf litter decomposition in forests. Soil Biol. Biochem. 41, 606–610.

Barker Plotkin, A., et al., 2013. Survivors, not invaders, control forest development following simulated hurricane. Ecology 94 (2), 414–423.

Barker Plotkin, A., et al., 2024. Logging response alters trajectories of reorganization after loss of a foundation tree species (Available at:). Ecol. Appl. 34 (3), e2957. https://doi.org/10.1002/EAP.2957.

Bond-Lamberty, B., et al., 2016. Soil Respiration and Bacterial Structure and Function after 17 Years of a Reciprocal Soil Transplant Experiment (Available at:). PLOS ONE 11 (3), e0150599. https://doi.org/10.1371/JOURNAL.PONE.0150599.

Bradford, M.A., et al., 2008. Thermal adaptation of soil microbial respiration to elevated temperature (Available at:). Ecol. Lett. 11 (12), 1316–1327. https://doi.org/10.1111/J.1461-0248.2008.01251.X.

Bradford, M.A., et al., 2014. Discontinuity in the responses of ecosystem processes and multifunctionality to altered soil community composition' (Available at:). Proc. Natl. Acad. Sci. USA 111 (40), 14478–14483. https://doi.org/10.1073/PNAS.1413707111/SUPPL_FILE/PNAS.201413707SI.PDF.

Bradford, M.A., Fierer, N., Reynolds, J.F., 2008. Soil carbon stocks in experimental mesocosms are dependent on the rate of labile carbon, nitrogen and phosphorus inputs to soils' (Available at:). Funct. Ecol. 22 (6), 964–974. https://doi.org/10.1111/j.13652435.2008.01404.x.

Brantley, S., Ford, C.R., Vose, J.M., 2013. Future species composition will affect forest water use after loss of eastern hemlock from southern Appalachian forests'. Ecol. Appl. 23 (4), 777–790.

Brockerhoff, E.G., Liebhold, A.M. and Jactel, H. (2011) 'The ecology of forest insect invasions and advances in their management', https://doi.org/10.1139/x06-013, 36 (2), pp. 263–268. Available at: https://doi.org/10.1139/X06-013.

Brooks, R.T., 2004. Early regeneration following the presalvage cutting of hemlock from hemlock-dominated stands (Available at:). North. J. Appl. For. 21 (1), 12–18. https://doi.org/10.1093/NJAF/21.1.12.

Chae, H.M., et al., 2019. Effect of litter quality on needle decomposition for four pine species in Korea (Available at:). Forests 10 (371). https://doi.org/10.3390/f10050371.

Cobb, R.C., 2010. Species shift drives decomposition rates following invasion by hemlock woolly adelgid (Available at:). Oikos 119 (8), 1291–1298. https://doi.org/10.1111/j.1600-0706.2009.18308.x.

Cobb, R.C., Orwig, D.A., 2002. Impacts of Hemlock Woolly Adelgid infestation on decomposition'. In: Reardon, R.C., Onken, B.P., Lashomb, L. (Eds.), Symposium on the Hemlock Woolly Adelgid in Eastern North America. New Jersey Ag. Exp, Sta., New Brunswick, NJ, pp. 317–323.

Cornelissen, J.H.C., 1996. An experimental comparison of leaf decomposition rates in a wide range of temperate plant species and types'. J. Ecol. 84 (4), 573–582.

Costa, S.D. *et al.* (2008) 'Low Temperature in the Hemlock Woolly Adelgid System', in *Fourth Symposium on Hemlock Woolly Adelgid in the Eastern United States*.

Coûteaux, M.-M., Bottner, P., Berg, B., 1995. 'Litter decomposition, climate and litter quality'. Trends Ecol. Evol. 10 (2), 63–66.

Davies, G.M., Gray, A., 2015. Don't let spurious accusations of pseudoreplication limit our ability to learn from natural experiments (and other messy kinds of ecological monitoring). Ecol. Evol. 5, 5295–5304. https://doi.org/10.1002/ece3.1782.

Doane, T.A., Horwáth, W.R., 2003. Spectrophotometric determination of nitrate with a single reagent (Available at:). Anal. Lett. 36 (12), 2713–2722. https://doi.org/10.1081/AL-120024647.

Ellison, A.M., et al., 2005. Loss of foundation species: consequences for the structure and dynamics of forested ecosystems' (Available at:). Front. Ecol. Environ. 3, 479–486. https://doi.org/10.1890/1540-9295.

Ellison, A.M., et al., 2010. Experimentally testing the role of foundation species in forests: the Harvard Forest Hemlock Removal Experiment (Available at:). Methods Ecol. Evol. 1 (2), 168–179. https://doi.org/10.1111/j.2041-210x.2010.00025.x.

Ellison, A.M., et al., 2018. The past, present, and future of the Hemlock Woolly Adelgid (Adelges tsugae) and its ecological interactions with eastern Hemlock (Tsuga canadensis) forests (Available at:). Insects MDPI AG. https://doi.org/10.3390/insects9040172.

Evans, A.M., Gregoire, T.G., 2007. A geographically variable model of hemlock woolly adelgid spread' (Available at:). Biol. Invasions 9 (4), 369–382. https://doi.org/10.1007/S10530-006-9039-Z/METRICS.

Fanin, N., et al., 2021. Home-field advantage of litter decomposition: from the phyllosphere to the soil (Available at:). N. Phytol. 231 (4), 1353–1358. https://doi.org/10.1111/NPH.17475.

Fanin, N., Fromin, N., Bertrand, I., 2016. Functional breadth and home-field advantage generate functional differences among soil microbial decomposers (Available at:). Ecology 97 (4), 1023–1037. https://doi.org/10.1890/15-1263.1.

Fei, S., et al., 2019. Biomass losses resulting from insect and disease invasions in US forests' (Available at:). Proc. Natl. Acad. Sci. USA 116 (35), 17371–17376. https://doi.org/10.1073/PNAS.1820601116/SUPPL_FILE/PNAS.1820601116.SD01.XLSX.

Fierer, N., et al., 2005. Litter quality and the temperature sensitivity of decomposition (Available at:). Ecology 86 (2), 320–326. https://doi.org/10.1890/04-1254.

Fierer, N., Schimel, J.P., 2003. A Proposed Mechanism for the Pulse in Carbon Dioxide Production Commonly Observed Following the Rapid Rewetting of a Dry Soil (Available at:). Soil Sci. Soc. Am. J. 67 (3), 798–805. https://doi.org/10.2136/sssaj2003.7980.

Finley, K., Chhin, S., 2016. Forest Health Management and Detection of Invasive Forest Insects. Resources 5 (2), 18, 2016, Vol. 5, Page 18.

Gholz, H.L., et al., 2000. Long-term dynamics of pine and hardwood litter in contrasting environments: toward a global model of decomposition'. Glob. Change Biol. 6, 751–765.

Goodale, C.L., Aber, J.D., 2001. The long-term effects of land-use history on nitrogen cycling in northern hardwood forests'. Ecol. Appl. 11 (1), 253–267.

Hawkes, C.V., Waring, B.G., Rocca, J.D., Kivlin, S.N., 2017. Historical climate controls soil respiration responses to current soil moisture. Proc. Natl. Acad. Sci. 114, 6322–6327.

Herms, D.A., McCullough, D.G., 2014. Emerald ash borer invasion of north america: History, biology, ecology, impacts, and management' (Available at:). Annu. Rev. Entomol. 59, 13–30. https://doi.org/10.1146/ANNUREV-ENTO-011613162051/CITE/REFWORKS.

Houston, D.R., 1994. Major new tree disease epidemics: Beech bark disease' (Available at:). Annu. Rev. Phytopathol. 32, 75–87. https://doi.org/10.1146/ANNUREV.PY.32.090194.000451/CITE/REFWORKS.

Hunt, H.W., et al., 1988. Nitrogen Limitation of Production and Decomposition in Prairie, Mountain Meadow, and Pine Forest'. Ecology 69 (4), 1009–1016.

Jongen, R., et al., 2021. Plant community legacy effects on nutrient cycling, fungal decomposer communities and decomposition in a temperate grassland (Available at:). Soil Biol. Biochem. 163. https://doi.org/10.1016/J.SOILBIO.2021.108450.

Juzwik, J., et al., 2011. Challenges and successes in managing oak wilt in the United States' (Available at:). Plant Dis. 95 (8), 888–900. https://doi.org/10.1094/PDIS12-10-0944.

Kaarakka, L., et al., 2021. Improved forest management as a natural climate solution: a review' (Available at:). Ecol. Solut. Evid. 2 (3), e12090. https://doi.org/10.1002/26888319.12090.

Keenan, R.J., 2015. Climate change impacts and adaptation in forest management: a review' (Available at:). Ann. For. Sci. 72 (2), 145–167. https://doi.org/10.1007/S13595-0140446-5/TABLES/2.

Keiluweit, M., et al., 2015. Long-term litter decomposition controlled by manganese redox cycling'. Proc. Natl. Acad. Sci. USA 112 (38), E5253–E5260. Available at: https://doi.org/10.1073/PNAS.1508945112//DCSUPPLEMENTAL/PNAS.201508945SI.PDF.

Keiser, A.D., et al., 2011. The effect of resource history on the functioning of soil microbial communities is maintained across time (Available at:). Biogeosciences 8 (6), 1477–1486. https://doi.org/10.5194/bg-8-1477-2011.

Keiser, A.D., et al., 2014. Disentangling the mechanisms underlying functional differences among decomposer communities (Available at:). J. Ecol. 102 (3), 603–609. https://doi.org/10.1111/1365-2745.12220.

Keiser, A.D., Bradford, M.A., 2017. Climate masks decomposer influence in a cross-site litter decomposition study'. Soil Biol. Biochem. 107, 180–187.

Keiser, A.D., Knoepp, J.D., Bradford, M.A., 2013. Microbial communities may modify how litter quality affects potential decomposition rates as tree species migrate. Plant Soil 372 (1), 167–176.

Keiser, A.D., Knoepp, J.D., Bradford, M.A., 2016. Disturbance Decouples Biogeochemical Cycles Across Forests of the Southeastern US (Available at:). Ecosystems 19, 50–61. https://doi.org/10.1007/s10021-015-9917-2.

Klapwijk, M.J., et al., 2016. Forest management and natural biocontrol of insect pests (Available at:). For. Int. J. For. Res. 89 (3), 253–262. https://doi.org/10.1093/FORESTRY/CPW019.

Kostenko, O., et al., 2012. Legacy effects of aboveground-belowground interactions (Available at:). Ecol. Lett. 15, 813–821. https://doi.org/10.1111/j.1461-0248.2012.01801.x.

Laishram, I.D., Yadava, P.S., 1988. Lignin and nitrogen in the decomposition of leaf litter in a sub-tropical forest ecosystem at Shiroy hills in north-eastern India'. Plant Soil 106 (1), 59–64.

Liu, Y., et al., 2023. Dynamics of litter decomposition rate and soil organic carbon sequestration following vegetation succession on the Loess Plateau, China (Available at:). Catena 229, 107225. https://doi.org/10.1016/J.CATENA.2023.107225.

Lu, C., Kotze, D.J., Setälä, H.M., 2021. Evergreen trees stimulate carbon accumulation in urban soils via high root production and slow litter decomposition (Available at:). Sci. Total Environ. 774, 145129. https://doi.org/10.1016/J.SCITOTENV.2021.145129.

McClure, M.S., 1990. Role of Wind, Birds, Deer, and Humans in the Dispersal of Hemlock Woolly Adelgid (Homoptera: Adelgidae). Environ. Entomol. 19 (1), 36–43. Available at: ⟨https://academic.oup.com/ee/article/19/1/36/377032⟩.

Meentemeyer, V., 1978. Macroclimate and lignin control of litter decomposition rates'. Ecology 59 (3), 465–472.

Melillo, J.M., Aber, J.D., Muratore, J.F., 1982. Nitrogen and Lignin Control of Hardwood Leaf Litter Decomposition Dynamics'. Source. Ecol. 63 (3), 621–626.

Nuckolls, A.E., et al., 2009. Hemlock declines rapidly with hemlock woolly adelgid infestation: Impacts on the carbon cycle of southern appalachian forests' (Available at:). Ecosystems 12 (2), 179–190. https://doi.org/10.1007/S10021-008-9215-3/FIGURES/5.

Orwig, D.A., et al., 2002. Landscape patterns of hemlock decline in New England due to the introduced hemlock woolly adelgid'. J. Biogeogr. 29, 1475–1487.

Orwig, D.A., Foster, D.R., 1998. Forest Response to the Introduced Hemlock Woolly Adelgid in Southern New England, USA. J. Torre Bot. Soc. 125 (1), 60–73 (Available at: https://about.jstor.org/terms).

Palmer, C.A., Orwig, D.A., McIntire, C.D., Keiser, A.D., 2025. Decomposer functional breadth maintains litter decomposition patterns three decades after Eastern Hemlock decline. Soil Biol. Biochem. 210. https://doi.org/10.1016/j.soilbio.2025.109943.

Paradis, A., et al., 2008. Role of winter temperature and climate change on the survival and future range expansion of the hemlock woolly adelgid (Adelges tsugae) in eastern North America (Available at:). Mitig. Adapt. Strateg. Glob. Change 13 (5–6), 541–554. https://doi.org/10.1007/S11027-007-9127-0/FIGURES/6.

Parker, B.L., et al., 1998. Survival of Hemlock Woolly Adelgid (Homoptera: Adelgidae) at Low Temperatures. For. Sci. 44 (3).

Parker, B.L., et al., 1999. Low Lethal Temperature for Hemlock Woolly Adelgid (Homoptera: Adelgidae)'. Popul. Ecol. 28 (6), 1085–1091. Available at: ⟨https://academic.oup.com/ee/article-abstract/28/6/1085/449344⟩.

R Core Team, 2022. 'R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Schindler, David W., 1998. 'Replication verus realism: the need for ecosystem-scale experiments'. Ecosystems 1, 323–334.

Schroeter, S.A., et al., 2022. Microbial community functioning during plant litter decomposition' (Available at:). Sci. Rep. 12 (1), 7451. https://doi.org/10.1038/s41598022-11485-1.

Skinner, M., et al., 2003. 'Regional Responses of Hemlock Woolly Adelgid (Homoptera: Adelgidae) to Low Temperatures'. Popul. Ecol. 32 (3), 523–528.

Smith, P., Cotrufo, M.F., Rumpel, C., Paustian, K., Kuikman, P.J., Elliott, J.A., McDowell, R., Griffiths, R.I., Asakawa, S., Bustamante, M., House, J.I., Sobocká, J., Harper, R., Pan, G., West, P.C., Gerber, J.S., Clark, J.M., Adhya, T., Scholes, R.J., Scholes, M.C., 2015. Biogeochemical cycles and biodiversity as key drivers of ecosystem services provided by soils. SOIL 1, 665–685. https://doi.org/10.5194/soil-1-665-2015.

Strickland, M.S., et al., 2009. Testing the functional significance of microbial community composition. Ecology 90 (2), 441–451. Available at: ⟨http://www.psb.ugent.be/rRNA/index.htmli⟩.

Tobin, P.C., Parry, D., Aukema, B.H., 2014. The Influence of Climate Change on Insect Invasions in Temperate Forest Ecosystems. In: Fenning, T. (Ed.), Challenges and Opportunities for the World's Forests in the 21st Century. Springer, Dordrecht, pp. 267–293. https://doi.org/10.1007/978-94-007-7076-8_12.

U.S. Forest Service (no date) *Climate Change Atlas: Liriodendron tulipifera (Yellow-poplar)*, *Northern Research Station [online]*. Available at: ⟨https://www.fs.usda.gov/nrs/atlas/tree/v4/modals/summary-change.php?spp=621⟩ (Accessed: 30 April 2025).

USDA Soil Survey Staff(no date) Official Soil Series Descriptions, Natural Resources Conservation Service, United States Department of Agriculture.

Van Der Heijden, M.G.A., Bardgett, R.D., Van Straalen, N.M., 2008. The unseen majority: soil microbes as drivers of plant diversity and productivity in terrestrial ecosystems (Available at:). Ecol. Lett. 11 (3), 296–310. https://doi.org/10.1111/J.1461-0248.2007.01139.X.

Veen, G.F. (Ciska) *et al.* (2018) 'Variation in home-field advantage and ability in leaf litter decomposition across successional gradients', *Functional Ecology*. Edited by M. Hart, 32(6), pp. 1563–1574. Available at: https://doi.org/10.1111/1365-2435.13107.

Wardle, D.A., Bonner, K.I., Barker, G.M., 2002. Linkages between plant litter decomposition, litter quality, and vegetation responses to herbivores (Available at:). Funct. Ecol. 16 (5), 585–595. https://doi.org/10.1046/J.1365-2435.2002.00659.X.

West, A.W., Sparling, G.P., 1986. Modifications to the substrate-induced respiration method to permit measurement of microbial biomass in soils of differing water contents. J. Microbiol. Methods.

Woodman, S.G., et al., 2021. Forest defoliator outbreaks alter nutrient cycling in northern waters' (Available at:). Nat. Commun. 12 (1), 1–8. https://doi.org/10.1038/s41467021-26666-1.

Youngquist, M.B., et al., 2017. Potential effects of foundation species loss on wetland communities: a case study of black ash wetlands threatened by emerald ash borer (Available at:). Wetlands 37 (4), 787–799. https://doi.org/10.1007/S13157-017-0908-2.