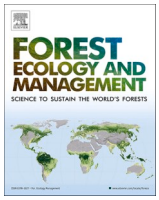
Forest Ecology and Management 600 (2026) 123294



Contents lists available at ScienceDirect

Forest Ecology and Management

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





Oak mortality in combination with deer browse alters understory community composition and increases non-native species abundance in the Northeastern United States

Katherine P. Terlizzi [a,*,1], Calvin B. Heslop [b,1], Benton N. Taylor [b], William S.F. Schuster [a], Matthew I. Palmer [c]

[a] Black Rock Forest, 65 Reservoir Rd., Cornwall, NY, USA
[b] Harvard University, Department of Organismic and Evolutionary Biology, 26 Oxford St., Cambridge, MA, USA
[c] Columbia University, Department of Ecology, Evolution, and Environmental Biology, 1200 Amsterdam Ave, New York, NY, USA

ARTICLE INFO

Keywords:
Mixed hardwood forest
Disturbances
Understory vegetation
Diversity
Herbivory
Invasive species

ABSTRACT

Large-scale pathogen-induced tree mortality alters forest function, community composition, and ecosystem processes. Some combination of plant-herbivore interactions and competition for newly available resources likely dictate the community dynamics of the understory following large-scale tree mortality. To assess how understory plant community dynamics may shift with oak mortality, we established a tree girdling experiment where 100 % oak trees, 50 % oak trees, and all non-oak trees, were girdled to simulate death by pathogens such as oak wilt. To assess how herbivore pressure interacts with oak loss we paired this experiment with browser exclusion fences within each plot. We found a transient increase in understory diversity within one year (particularly in 100 % oak girdled plots), but it was no longer detectable 13 years post-girdling. Impacts on understory community composition were more lasting. Over the 13-year census period, the understories became increasingly oak dominated in all treatments except when all oaks were girdled, where maples dominated. Finally, the combination of oak mortality and browsing increased the abundance of non-native species in the understory which was most apparent in 100 %-oak gridled plots. Our results show that below 50 % oak mortality, the forest understory remains relatively stable, but once 100 % oak mortality is reached the understory experiences long-term shifts in community composition. Browsing pressure can influence understory responses, and the combination of tree mortality and browsing may amplify the proliferation of non-native species. Our data show that if high tree mortality is imminent, reducing herbivore pressure from forests could reduce the expansion of non-native understory species.

1. Introduction

Increasing anthropogenic activity places a variety of pressures on natural ecosystems and the interactions between these pressures can substantially alter ecosystem structure and function, particularly in regions of high human population densities (Breitburg et al., 1998; Crain et al., 2008; Orr et al., 2020). One such pressure is the introduction of novel pests and pathogens which have caused widespread death of a multitude of tree species across all continents (Nahrung and Carnegie, 2020; Thu et al., 2021; Montgomery et al., 2023; Schei et al., 2024). Examples include hemlock wooly adelgid (*Adelgis tsugae*) in Eastern North America (Ellison et al., 2018), ash dieback caused by the fungus (*Hymenoscyphus fraxineus*) in temperate Europe (Schei et al., 2024), and jarrah dieback (*Phytophthora cinnamomic*) in Australia (Shearer and Tippett, 1989).

Two of the most significant factors affecting deciduous forests in North America are the introduction of plant pests and pathogens (Lovett et al., 2006; Crowl et al., 2008) and the overabundance of large herbivore populations (Healy, 1997; Underwood and Porter, 1997; Côte et al., 2004). The introduction of invasive species and plant pathogens can create stand-level disturbances which alter both community composition and ecological processes (Lovett et al., 2006). When coupled with

* Corresponding author.
E-mail address: katie.terlizzi@gmail.com (K.P. Terlizzi).
[1] Co-first authors

https://doi.org/10.1016/j.foreco.2025.123294
Received 29 July 2025; Received in revised form 4 October 2025; Accepted 22 October 2025
Available online 29 October 2025
0378-1127/© 2025 Published by Elsevier B.V.

increased browse pressure from an overabundance of large herbivores such as white-tailed deer (*Odocoileus virginianus*), these changes may persist for years or decades (Pendergast et al., 2016; Kilheffer et al., 2019). How these two factors interact with one another across time has not been studied and therefore it is unknown how communities will respond to future large-scale disturbances or how long it will take forest systems to recover.

Plant pests such as emerald ash borer (*Agrilus planipennus*) and the newly emergent plant pathogen, beech leaf disease (*Litylenchus crenatae mccanii*), have already caused large scale canopy disturbances in the forests of the Northeastern United States (Klooster et al., 2018; Ewing et al., 2019). Additional diseases such as oak wilt (*Bretziella fagacearum*) threaten to exacerbate the deleterious effects of species loss in already stressed forests. Oak wilt is of particular concern as the genus *Quercus* dominates many eastern U.S. forests, often comprising 70 % or more of stand biomass (Cadenasso et al., 2007; Schuster et al., 2008; Abrams and Sands, 2010).

Canopy gaps resulting from the death of multiple canopy trees following pathogen-induced tree mortality have been shown to alter nutrient cycling (Ávila et al., 2021), community composition (Metz et al., 2012; Klooster et al., 2018), and faunal interactions (Klooster et al., 2018; Fleming et al., 2021). These changes can cause a multitude of effects which, depending on a variety of factors such as community resilience, magnitude of initial disturbance, and human intervention, can persist for years. Ash tree (*Fraxinus spp.*) mortality caused by the emerald ash borer (*Agrilus planipennis*) in the eastern U.S. has had varied effects depending on the geographic location and dominance of ash in the region. However, most studies have shown that the canopy gaps created by the loss of ash increase light availability leading to increased cover in the mid- and under-story (Hausman et al., 2010; Davis et al., 2017; Engelken et al., 2020). Similarly in eastern hemlock (*Tsuga canadensis*) dominated forests, high mortality of this foundation species increased understory diversity (Ford et al., 2012) and increased nitrate availability in soil and soil water (Yorks and Dabydeen, 1999; Cessna and Nielsen, 2012). Large herbivores can exacerbate these effects by selectively browsing more palatable native species (Knight et al., 2009; Averill et al., 2018), hampering regeneration and prolonging compositional shifts (Rooney and Waller, 2003; Pendergast et al., 2016; Kilheffer et al., 2019). As deer are selective browsers and have increased in abundance in North America over the last century, they have been found to be a significant driver in changes to community composition often changing relative abundance through selective browsing on native species and avoidance of non-native species (Eschtruth and Battles, 2008). The whole understory community has the potential to be greatly affected by both large-scale canopy mortality produced by plant pests and pathogens and by the overabundance of large herbivores, but it is also of particular interest to understand how non-native species are affected by these two factors as well.

The understory community has long been recognized as a reservoir of forest biodiversity but is disproportionally underrepresented in forest community studies compared to the overstory. Landuyt et al. (2019) outline three important functions of the understory: 1) chemical cycling (*e.g.*, carbon, nutrients, water) 2) filtering overstory regeneration and 3) habitat and food generation for fauna. A diverse understory performs all these functions and has built-in redundancy to buffer against local species loss (Deng et al., 2023). The increase in light (Beaudet et al., 2004) and nutrient availability (Prescott, 2002) following canopy disturbance leads to a higher density and diversity of understory plants and saplings (Ellison et al., 2015; Kermavnar et al., 2018). However, when herbivore abundance is high, understory tree diversity often remains low (Nuttle et al., 2013). Few studies have examined the combined effects of canopy disturbance and herbivore abundance on the understory community and those that have largely focus on regenerating tree species with little to no examination of the herbaceous community (e.g. Eschtruth and Battles, 2008; Forrester et al., 2014).

Complex interactions between multiple factors can be difficult to identify and quantify when studying natural disturbances. Therefore, it can be beneficial to undertake large-scale manipulative experiments to pinpoint the importance of specific variables within the system. As the threat of oak mortality from pathogens increases, it is important to understand how our forests may change with the loss of dominant tree taxa. To better understand the potential impacts of canopy mortality and deer browsing on the understory community we censused the forest floor community in plots exposed to different levels of tree mortality and exposure to deer browsing to ask: 1) How do tree mortality and deer browse impact the diversity of the understory and tree seedling communities, and do these effects differ over time? 2) How do tree mortality and deer browse influence understory community composition? 3) Are particular species associated with different disturbance and browsing treatments, and do certain disturbance regimes tend to promote non-native species?

2. Methods

2.1. Site description

This study took place in Black Rock Forest, a nearly 1600 ha private forest located in the Hudson Highlands region of New York State (41°24′ N, 74°01′ W) which is run by the non-profit organization of the same name. The mean annual air temperature is 9.7 ºC but varies seasonally with mean monthly temperatures ranging from 24 ºC to −2.1 ºC (NOAA, 2020). The mean annual precipitation is 1300 mm yr^{-1} and soils are typically well-draining, shallow, and rocky. This deciduous temperate forest is dominated by oak species, which comprise 70 % of tree biomass (Schuster et al., 2008). The most recent full botanical inventory of the forest, undertaken between 1990 and 1998, documented 688 vascular plant species (Barringer and Clemants, 2003). If previous surveys are included such as the 1938 survey done by Raup (1938), the flora of Black Rock Forest comprises 729 species of vascular plants (Barringer and Clemants, 2003).

Black Rock Forest has monitored the over-wintering white-tailed deer (*O. virginianus*) herd size since 1988 and has managed the population via a hunting program since the 1950s. From the onset of this experiment (2008) until the present, over-wintering deer density has ranged from 4.3 to 8.0 deer km^{-2} with an average deer density of 5.6 deer km^{-2} (Brady, 2021; Schuster et al., 2024a). A study from the US Forest Service found that tree regeneration is likely to occur with deer densities below 6.9 deer km^{-2} (Tilghman, 1989) and therefore deer densities below this threshold are desired to maintain forest communities. Therefore, densities observed in the study area are on the high end of an “acceptable” density and considered moderate for the region.

2.2. Experimental setup

The Future of Oak Forests experiment, established in 2005, consists of twelve 75 m by 75 m experimental plots arranged in a three by four grid on the north slope of Black Rock Mountain (Fig. 1). Treatments were arranged according to a semi-randomized block design grouped by slope position (blocks: low, middle and high). Each treatment was represeted once within each slope position, for a total of three plots per treatment. In 2008, each plot received one of four treatments: 0 % trees girdled (control), 100 % oak trees girdled (OG), 50 % oak trees girdled (O50), and 100 % non-oak trees girdled (NOG) (Fig. 1). The 100 % non-oak girdled treatment was included to isolate the effect of oak loss from that of any species loss. To mimic gradual death by pathogens, notch girdling (Noel, 1970) was performed during the summer of 2008. A chain saw was used to make a 5 cm deep incision around the circumference of the tree, the cut penetrated from the bark through the phloem and the cambium, preserving most of the xylem but blocking the flow of nutrients between roots and leaves (Falxa-Raymond et al., 2012). Girdled trees were left standing if greater than 10 cm in diameter at breast height (DBH) and felled if smaller. Trees that continued to

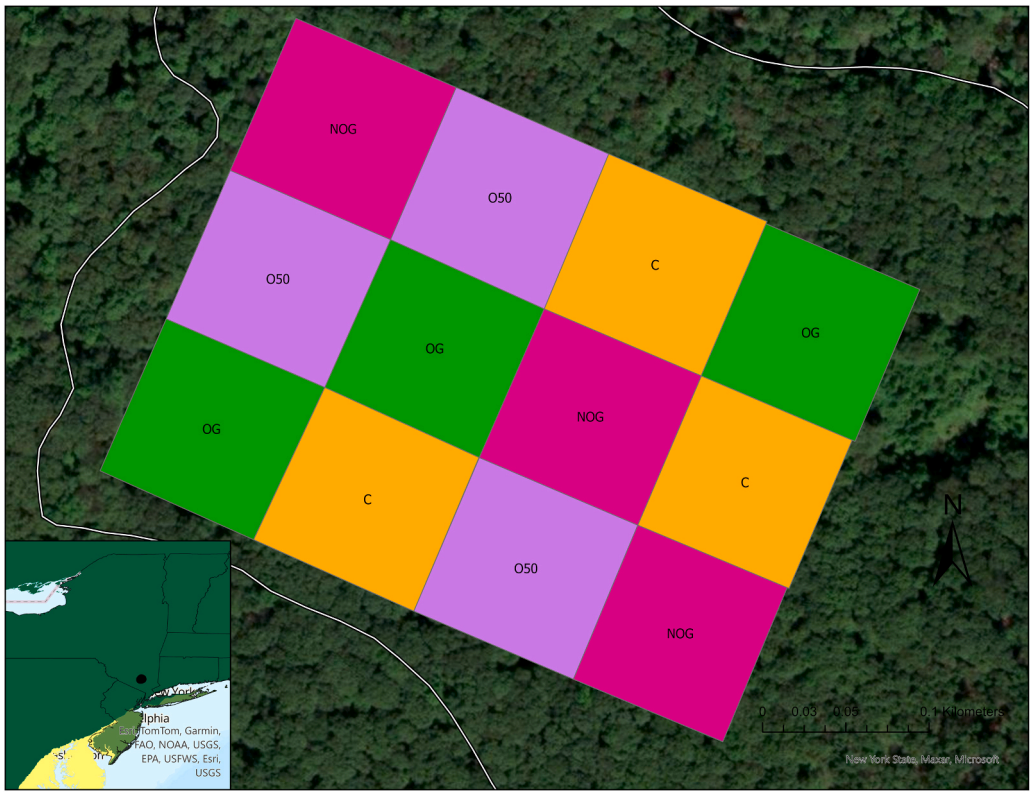


Fig. 1. Treatment layout for the Future of Oak Forests experiment at Black Rock Forest Cornwall, NY. Plots were assigned using a semi-randomized block design using slope position as the blocking factor. Each treatment (C = control; NOG = non-oaks girdled; O50 = half oak girdled; OG = all oak girdled) is represented at each slope position (A = low; B= middle; C = high).

produce leaves were girdled a second time in 2010. Post-treatment, the average fraction of the total basal area girdled in the 100 % oak girdled, 50 % oak girdled, non-oak girdled, and control plots was 78.1 %, 35.5 %, 21.4 %, and 0 %, respectively (McCulloch et al., 2025). This resulted in a 29 % increase in canopy openness in 100 % oak girdled plots compared to control (Taylor et al., 2017).

Each plot was divided into nine, 25 m by 25 m subplots (Figure S1). In the north-central subplot of each treated plot, 1.8 m high deer exclusion fences (henceforth exclosures) were erected in the summer of 2008 with an approximate area of 150 m^2. All exclosures were approximately the same area with slightly different overall dimensions due to topographical and geological conditions at each plot. While fencing was not buried into the soil, no evidence of animals burrowing under the fence was observed. It is assumed the fences exclude any non-volant animal larger than 4 cm width (the mesh size of the fencing material). Fences were maintained throughout the course of the study and re-established when damaged.

In 2006, ten 1 m^2 permanent understory vegetation sampling quadrats were established entirely within the central subplots to reduce potential edge effects from neighboring treatments (Sircely, 2007). Limiting vegetation sampling quadrats to the central subplots provided a minimum 50 m buffer between sampling quadrats of another treatment and a minimum 25 m buffer to treatment edges. Sampling quadrats within a treated plot were spaced with a minimum distance of 5 m. In 2009, an additional ten 1 m^2 permanent vegetation sampling quadrats were established inside each exclosure. Enclosed quadrats were located at a minimum of 2 m from the fence line and spaced approximately 1.5 m from each other. Enclosed quadrats were 12–15 m from treatment edge, a sufficient distance to limit significant edge effects. This design resulted in 20 vegetation sampling quadrats per experimental plot – 10 exposed to the natural herbivore community and 10 inside deer exclosures protected from large herbivore browse for a total of 240 sampling quadrats across the experiment.

2.3. *Understory vegetation surveys*

In 2006 and 2008, before exclosures were erected, pre-treatment surveys were conducted in all unexclosed (n = 120) quadrats. Exact exclosure locations had not been determined and therefore, pre-treatment exclosure surveys were not conducted. Surveys of all 240 understory quadrats were conducted annually in late summer (August to September) from 2009 to 2018 and then again in 2021. At each quadrat, two observers identified all vascular plants to species and assigned each species a percent cover value. All plant nomenclature follows the USDA PLANTS database (Natural Resources Conservation Service 2025). Pre-treatment surveys were conducted by a different set of observers, however all observers were trained and calibrated for percent cover estimates by the same individual (author Schuster). The same pair of observers conducted surveys from 2009 to 2017 and one from that pair continued the surveys for 2018 and 2021. The percent cover of moss was also recorded but moss species were not identified. Counts of tree seedlings and some woody shrubs were also recorded in addition to percent cover values. Saplings 1.3 m tall or taller were not counted (Terlizzi et al., 2025).

2.4. Statistical Analyses

All statistical analyses were performed in R Statistical Software (v4.5.1 R Core Team, 2024). To assess the effects of girdling treatment, deer browsing, and time on total cover, species richness, and Shannon diversity for both tree seedlings and all understory species, we utilized generalized linear mixed effects models using the function *lme* in the R package nlme (Pinheiro et al., 2022). A random intercept of quadrat nested within plot, nested within block was used. Omnibus models were fit that included all interaction effects between girdling treatment, exclosure treatment, and time. A second order orthogonal polynomial was included in the Shannon diversity model to address a non-linear effect of time. Model assumptions were assessed visually using plots of residuals against fitted values and each predictor variable. Normality was assessed using quantile-quantile plots of model residuals. To meet assumptions of equal variance in the all-understory species richness model, a variance structure was specified using the *varIdent* function that modeled variance between girdling treatments (Zuur et al., 2009). Temporal autocorrelation was assessed using Autocorrelation Function (ACF) and partial ACF plots. To account for temporal autocorrelation, correlation structures were fit using an autoregressive moving average function (R function *corARMA*, $p = 1, q = 1$), for all understory Shannon diversity and tree species richness, and a first order autoregressive function (R function *corAR1*) for all understory species richness and tree species Shannon diversity values. After assumptions were assessed, interactions were tested for significance. Non-significant interactions were dropped (unless a higher order interaction was significant) and the models were refit. Pairwise post hoc comparisons were made and p-values corrected using the single step method using the R function *glht* in the *multcomp* package (Hothorn et al., 2008). Pairwise comparisons were made within the first and final post-treatment years (2009 and 2021), except for total cover where comparisons were also made in 2016 when treatment effects peaked. Because of the large number of potential comparisons of which only a subset were of interest, post hoc comparisons only differed by one treatment at a time (*e.g.*, control with deer browsing vs control without deer browsing but not control with deer browsing vs oak girdled without deer browsing).

To assess the effects of girdling treatment, deer browsing, time, and their interactions on all understory and tree seedling community composition as well as abundance of plant functional types we utilized distance-based redundancy analysis (dbRDA) with Bray-Curtis distances using the R package *vegan* (Oksanen et al., 2022). To account for non-independence of quadrats within plots, quadrat level values were averaged by plot. Singleton species (species that occur in only one plot) were removed. Seedling, all understory species, and plant functional type community composition was modeled by girdling treatment, exclosure treatment, time, and their interactions. Models were conditioned on the effect of block. The significance of interactions was assessed and like above, non-significant interactions were dropped and the model refit. Species scores were calculated with the recommended transformation for Bray-Curtis distances (standardized by margin total, and square root divided by two) using the function *sppscores*. Scree plots were used to determine the appropriate number of ordination axes.

To identify individual species that responded strongly to the treatments, the strength of association between each understory species and treatment was assessed by calculating the cosine similarity between the species score and linear constraint matrices of the dbRDA ordination. This represents a scaled measure of the alignment (the cosine of the angle) of each species and linear constraint vector in the ordination space and can be interpreted as the strength of the association between species and treatment levels at each point in time. Cosine similarity values range from 1 to –1 with 1 indicating perfect alignment (species grow more only in that treatment), 0 indicating orthogonality (species do not respond to the treatment), and –1 indicating perfectly negative alignment (species grow less only in that treatment). Significance of cosine similarity values were assessed using a permutation test with 1000 permutations stratified by block. To focus on temporally consistent associations, cosine similarities for each species–treatment combination were only considered significant if $p < 0.05$ in at least 5 of 11 years. This resulted in a Bonferroni-adjusted family-wise error rate < 0.05 based on the binomial probability of at least 5 type I errors in 11 trials.

The same modeling procedure for richness and diversity was used for the frequency of non-native species. However, due to non-native species being relatively rare and to meet assumptions of normality, we averaged the frequency of non-native species within each quadrat across time and applied a square root transformation. As such, models only included girdling treatment, deer browsing, and their interaction as predictor variables with no factor of time included. Additionally, by averaging across time, quadrats were no longer repeatedly measured so only plot nested within block was used as a random effect. To meet assumptions of equal variance, a variance structure was specified that modeled variance between girdling treatments using the function *varIdent*.

3. Results

To ensure that any treatment differences we observed were due to the treatments themselves rather than preexisting differences between plots, we conducted and analyzed pre-treatment censuses in each plot, except for the browsing exclusion treatment where no pre-treatment data was available. There were no significant differences in any of the response variables we assessed between treatment plots prior to the implementation of the treatments in 2008 (Supplemental table S1).

3.1. Total Cover

Total cover of all understory species was significantly affected by both girdling ($p < 0.01$) and browsing ($p < 0.05$) treatments (Fig. 2), but these effects changed over time (Table 1). At the onset of the experiment in 2009 there was no difference in total cover between girdling or browsing treatments (Table 1). The effects of tree mortality on understory cover was strongest 7–9 years post treatment (2015–17; Fig. 2a). In 2016, with browsing, total cover in 100 % oak-girdled (OG) and non-oak girdled (NOG) increased 2.56 and 2.18 times respectively compared to control (C), while with no browsing, cover increased 4.08 (OG) and 3.44 (NOG) times. Total cover in 50 % oak-girdled plots was not statistically different from control regardless of browsing treatment. Additionally, total cover was reduced by half (C and O50) or one third (NOG and OG) in plots exposed to browsing compared to plots protected from browsing ($p < 0.05$) (Fig. 2; Table S2). By 2021, 13 years post treatment, girdling effects on understory cover had largely dissipated, with only marginal differences between girdling treatments ($p > 0.05$ for all comparisons).

3.2. Species richness and diversity

Similar to responses of total cover, understory diversity was influenced by tree mortality, but these effects changed over time (Table 1). In 2009 - only one year post treatment- species richness was 173 % and 98 % higher in 100 % oak girdled (OG) plots compared to control, with and without deer browsing respectively ($p < 0.01$ and $p = .031$; Fig. 3c). Shannon diversity increased by 80 % and 78 % in the 100 % oak girdled (OG) plots compared to control with and without deer browsing respectively compared to control in 2009 (Fig. 3a). Again, by 2021 there were no differences in Shannon diversity for any girdling or

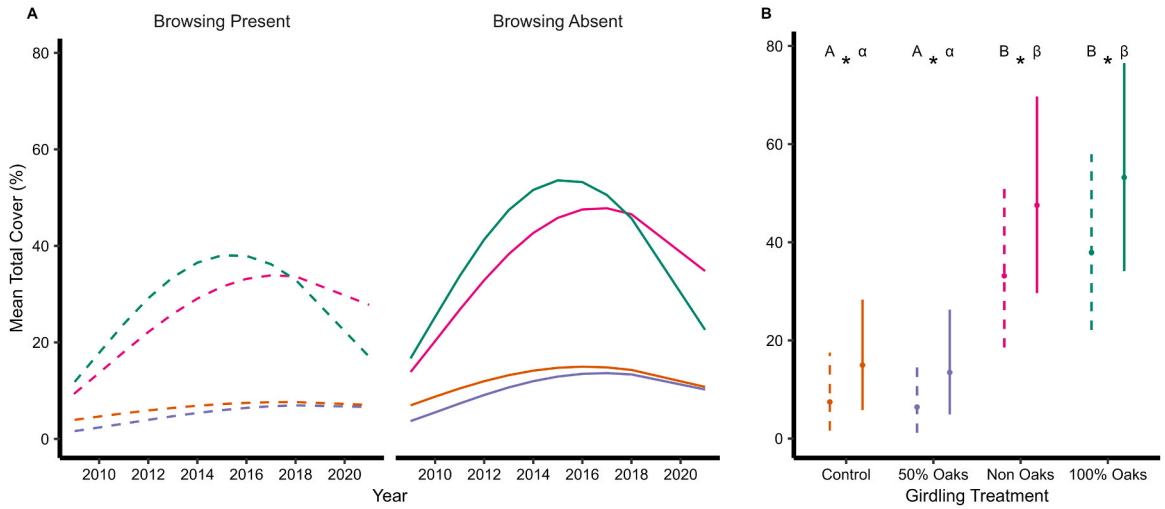


Fig. 2. Modeled total understory vegetation cover in response to girdling and browsing treatments through time (A) and in 2016 (B). Panel A shows predicted total cover through time with deer browsing present (dashed lines) and absent (solid lines). Panel B shows the same but only in 2016 where treatment differences were strongest. Letters represent significant differences between girdling treatments. Latin letters signify differences between girdling treatments with browsing present and Greek letters with browsing absent. Comparisons were not made across browsing and girdling treatments simultaneously (e.g. Control with deer to 100 % Oaks without deer) so Latin and Greek letters should not be compared. Asterisks (*) represent significant differences between deer browsing treatments within a girdling treatment. Lines and points represent predicted total cover, vertical lines are 95 % confidence intervals. Colors represent girdling treatments (control: orange, 50 % oaks: purple, non-oaks: pink, and 100 % oaks: green).

browsing treatments, and the only significant treatment effects for species richness was significantly higher richness (111 % increase) in non-oak girdled (NOG) vs control plots where browsing was present ($p < 0.05$) and a significantly higher species richness (55 %) in 50 % oak girdled plots with browsing excluded compared to when browsing was present ($p < 0.05$).

We also specifically analyzed treatment impacts on abundance of tree seedlings to understand the responses of species that could potentially replace the canopy following oak mortality (Table 1). In 2009, the 100 % oak girdled plots had ~200 % higher Shannon diversity of tree seedlings than control which was significantly higher than all other treatments regardless of browsing exposure ($p < 0.001$ for all; Fig. 3b). Similarly, in 2009, species richness was ~200 % higher in 100 % oak girdled plots compared to control and significantly higher than all other treatments ($p < 0.001$) except the non-oak girdled plots exposed to browsing ($p > 0.05$; Fig. 3d). For comparison, on average, Shannon diversity of canopy trees was 11 % lower in the 100 % oak girdled plots than the control plots in 2009 and 8 % lower in 2021 (Schuster et al., 2024b). By 2021, no treatment effects persisted for either species richness or Shannon diversity in the canopy tree seedling community ($p > 0.1$ for all).

3.3. Community composition

The dbRDA of all understory species cover and plant functional types (trees, shrubs, vines, herbs, graminoids, ferns, moss) showed significant responses to both girdling and enclosure treatments. There were significant two-way interaction effects between girdling treatment, enclosure treatment, and time for both ordinations (Tables 2 and 3). The functional group ordination showed that 100 % oak girdled plots exhibit a weak change in functional type composition over time compared to other treatments (Fig. 4a). Over time all treatments move towards increased tree abundance with the 100 % oak girdled treatment showing a weaker trend. Cosine similarity between all understory species and treatment combinations showed treatment combinations differed markedly in both the number and identify of species with which they were associated (Table 3). While the control plots had only eight significantly positively associated species, the plots with all oaks girdled had 45 significantly associated species, while non-oak girdled and half oaks girdled had 15 and 21 respectively.

The distance-based redundancy analysis used to assess changes in tree seedling community composition over time showed that the tree seedling communities in 100 % oak girdled plots changed along a different trajectory than control, non-oak girdled and 50 % oak girdled plots between 2009 and 2021 (Fig. 4b). Interactions between girdling and exclosure treatments, as well as between girdling treatment and time were significant (Table 2). Over the 13 years following girdling treatments, the control, non-oak and 50 % oak girdled plots all shifted towards tree seedling communities dominated primarily by oak species (Fig. 4c). The 100 % oak girdled plots, however, shifted away from an oak-dominated seedling community towards a seedling community dominated by maples (Fig. 4c). Shifts in tree seedling community composition through time was unaffected by the presence of browsing.

3.4. Non-native species

The frequency of non-native species across all plots was relatively low (average of 6.09 $\pm$ 0.60 % across all observations) but increased under the combination of girdling and browsing. The 100 % oak girdled plots exposed to browsing had 106 times higher frequency of non-native species than browsing-exposed control plots ($p < 0.05$), and within the 100 % oak girdled treatment, non-native species frequency was nearly double (1.9x) in areas exposed to browsing than those where browsers were excluded ($p < 0.001$; Fig. 5). Cosine similarities between species and treatment combinations for the all understory species dbRDA ordination showed all girdling treatments, except control, were significantly positively associated with non-native species. The control was significantly negatively associated with the non-native oriental bittersweet (*Celastrus orbiculatus*). Additionally, non-native species made up 20 % of the species significantly positively associated with the 100 % oak girdled treatment, compared to 11, 7, and 0 % in the half oaks girdled, non-oaks girdled, and control treatments respectively.

Table 1
Summary tables for mixed effects models.

Total Cover		Estimate	Std Error	DF	t-value	p-value
	Intercept	2.512	0.731	2354	3.435	< 0.001
	Half oaks	−0.343	0.967	6	−0.354	0.735
	Non oaks	2.444	0.967	6	2.527	0.045
	All oaks	2.767	0.967	6	2.862	0.029
	Year	10.875	5.017	2354	2.168	0.030
	$Year^2$	−6.636	4.216	2354	−1.574	0.116
	DeerAbsent	0.973	0.203	227	4.798	2.909
	Half oaks:Year	9.757	6.356	2354	1.535	0.125
	Non oaks:Year	25.609	6.344	2354	4.036	< 0.001
	All oaks:Year	6.056	6.349	2354	0.954	0.340
	Half oaks:$Year^2$	−2.786	5.344	2354	−0.521	0.602
	Non oaks:$Year^2$	−19.585	5.329	2354	−3.675	< 0.001
	All oaks:$Year^2$	−36.669	5.337	2354	−6.870	< 0.001
	Year:DeerAbsent	1.135	4.484	2354	0.253	0.800
	$Year^2$:DeerAbsent	−9.349	3.769	2354	−2.481	0.013
	AR ($p = 1$, $\varphi = 0.721$), $R^2_m = 0.328$, $R^2_c = 0.660$					
Shannon		Value	Std Error	DF	t-value	p-value
	Intercept	0.694	0.114	2352	6.067	< 0.001
	Half oaks	0.097	0.144	6	0.672	0.526
	Non oaks	0.305	0.144	6	2.122	0.078
	All oaks	0.492	0.144	6	3.424	0.014
	Year	0.969	1.143	2352	0.847	0.397
	Year2	1.346	0.907	2352	1.484	0.138
	DeerAbsent	0.138	0.046	227	2.994	0.003
	Half oaks:Year	−0.449	1.449	2352	−0.310	0.757
	Non oaks:Year	1.890	1.444	2352	1.309	0.191
	All oaks:Year	−3.446	1.445	2352	−2.385	0.017
	Half oaks:Year2	−0.690	1.152	2352	−0.600	0.549
	Non oaks:Year2	−2.020	1.146	2352	−1.762	0.078
	All oaks:Year2	−0.750	1.149	2352	−0.653	0.514
	Year:DeerAbsent	1.852	1.021	2352	1.813	0.070
	Year2:DeerAbsent	−2.078	0.811	2352	−2.561	0.011
	ARMA ($p = 1$, $\varphi = 0.843$, $q = 1$, $\theta = -0.410$), $R^2_m = 0.147$, $R^2_c = 0.430$					
Richness		Value	Std.Error	DF	t-value	p-value
	Intercept	2.959	1.106	2354	2.676	0.008
	Half oaks	0.615	1.378	6	0.446	0.671
	Non oaks	3.117	1.387	6	2.247	0.066
	All oaks	5.120	1.400	6	3.657	0.011
	DeerAbsent	1.561	0.605	224	2.582	0.010
	Year	0.072	0.023	2354	3.135	0.002
	Half oaks:DeerAbsent	−0.215	0.877	224	−0.245	0.806
	Non oaks:DeerAbsent	−1.920	0.905	224	−2.120	0.035
	All oaks:DeerAbsent	−0.675	0.943	224	−0.716	0.475
	Half oaks:Year	−0.045	0.038	2354	−1.175	0.240
	Non oaks:Year	0.093	0.044	2354	2.114	0.035
	All oaks:Year	−0.077	0.052	2354	−1.484	0.138
	DeerAbsent:Year	0.008	0.033	2354	0.249	0.803
	Half oaks:DeerAbsent:Year	0.058	0.054	2354	1.085	0.278
	Non oaks:DeerAbsent:Year	−0.066	0.062	2354	−1.053	0.293
	All oaks:DeerAbsent:Year	−0.181	0.073	2354	−2.480	0.013
	AR ($p = 1$, $\varphi = 0.471$), $R^2_m = 0.206$, $R^2_c = 0.743$					
Tree Shannon		Value	Std.Error	DF	t-value	p-value
	Intercept	0.192	0.058	1979	3.293	0.001
	Half oaks	0.114	0.075	6	1.517	0.180
	Non oaks	0.169	0.075	6	2.256	0.065
	All oaks	0.497	0.074	6	6.687	0.001
	Year	0.004	0.005	1979	0.870	0.384
	DeerAbsent	0.057	0.031	226	1.820	0.070
	Half oaks:Year	−0.008	0.007	1979	−1.217	0.224
	Non oaks:Year	−0.002	0.007	1979	−0.379	0.705
	All oaks:Year	−0.030	0.007	1979	−4.615	< 0.001
	AR ($p = 1$, $\varphi = 0.332$, $R^2_m = 0.118$, $R^2_c = 0.376$					
Tree Richness		Value	Std.Error	DF	t-value	p-value
	Intercept	0.692	0.229	2355	3.020	0.003
	Half oaks	0.515	0.319	6	1.615	0.157
	Non oaks	0.798	0.319	6	2.503	0.046
	All oaks	1.683	0.318	6	5.289	0.002
	DeerAbsent	0.695	0.284	224	2.448	0.015
	Year	0.054	0.020	2355	2.704	0.007
	Half oaks:DeerAbsent	−0.334	0.401	224	−0.833	0.406
	Non oaks:DeerAbsent	−0.343	0.401	224	−0.857	0.393
	All oaks:DeerAbsent	0.729	0.401	224	1.821	0.070
	Half oaks:Year	−0.019	0.029	2355	−0.658	0.511
	Non oaks:Year	−0.015	0.028	2355	−0.536	0.592

(*continued on next page*)

Table 1 (*continued*)

Total Cover		Estimate	Std Error	DF	t-value	p-value
	All oaks:Year	−0.091	0.028	2355	−3.185	0.001
	DeerAbsent:Year	0.007	0.028	2355	0.231	0.818
	Half oaks:DeerAbsent:Year	−0.015	0.040	2355	−0.378	0.705
	Non oaks:DeerAbsent:Year	−0.007	0.040	2355	−0.162	0.871
	All oaks:DeerAbsent:Year	−0.106	0.040	2355	−2.635	0.008
	ARMA (p = 1, φ = 0.753, q = 1, θ = −0.350), $R^2_m = 0.201$, $R^2_c = 0.484$					
Non-native occurrence		Value	Std.Error	DF	t-value	p-value
	Intercept	0.005	0.680	133	0.007	0.994
	DeerAbsent	−0.002	0.006	133	−0.374	0.709
	Half oaks	0.069	0.962	6	0.072	0.945
	Non oaks	1.142	0.979	6	1.166	0.288
	All oaks	1.586	1.061	6	1.494	0.186
	DeerAbsent:Half oaks	0.014	0.036	133	0.398	0.691
	DeerAbsent:Non oaks	0.295	0.250	133	1.182	0.239
	DeerAbsent:All oaks	−0.791	0.580	133	−1.364	0.175
	$R^2_m = 0.162$, $R^2_c = 0.751$					

4. Discussion

The interactions among oak mortality, browsing, time, and their combined influence on the understory community are complex. The understory of eastern deciduous forests is typically composed of hundreds of species, each potentially responding differently to disturbance. Our results show an initial pulse in diversity and richness which diminishes over a period of 13 years. When disturbance is mild to moderate the forest recovers quickly with no significant shift in community composition. However, when disturbance is large and especially in the presence of herbivory, community composition shifts and recovery takes longer.

4.1. Species richness and diversity

We found that species richness and diversity increased immediately following high tree mortality (100 % oak girdling), regardless of browsing treatment. However, this effect was transient; by 13 years post-treatment, richness and diversity had declined to levels comparable to controls. In contrast, moderate tree mortality (50 % oak girdling and non-oak girdling) maintained elevated richness after 13 years. In the 50 % oak girdling treatment, richness was higher when browsing was excluded than when browsing was present. However, in the non-oak girdling treatment with browsing, richness was significantly higher than control. Non-oak girdled plots also exhibited greater variance in non-native species cover relative to controls and 50 % oak girdled plots, suggesting that establishment of non-native species may underlie the sustained increase in richness outside exclosures. Many of these species (e.g., *Berberis thunbergii*, *Rosa multiflora*, *Celastrus orbiculatus*, *Alliaria petiolata*) are avoided by deer (Averill et al., 2016). While *B. thunbergii*, *R. multiflora*, and *A. petiolata* were present prior to treatment, other non-native species (e.g. *Euonymus alatus*, *C. orbiculatus*, *Rhamnus cathartica*) were not observed in plots before treatment but occurred nearby. These species may have colonized following disturbance and contributed to the sustained increase in richness observed in non-oak girdled plots.

The long-term decline in richness and diversity in the fully girdled plots may be due to increased competition for light in the mid-story. Although we did not analyze the available mid-story vegetation data (1–3 m in height) (Terlizzi et al., 2025), field observations beginning in 2012 indicate that many seedlings had developed into dense sapling layers in these plots. This dense mid-story largely composed of *Betula lenta* and *Liriodendron tulipifera* likely reduced light availability, creating unsuitable conditions for light-demanding herbaceous species (e.g. *Erechtites hieraciifolius*, *Phytolacca americana*) which were abundant in the years immediately following disturbance but disappeared by 2013. Future analyses incorporating mid-story structure would help clarify these dynamics.

4.2. Community composition

Our community composition results mirror the patterns observed for species richness and diversity. Plots with no mortality (controls) or moderate mortality (non-oak and 50 % oak girdled) retained largely similar species composition over time, regardless of browsing. In contrast, 100 % oak girdled plots exposed to browsing exhibited a distinct compositional trajectory. Cosine similarity scores (Table 3) show that species associated with control, non-oak, and 50 % oak girdled plots reflect typical understory flora of northeastern oak forests (Barringer and Clemants, 2003), which favor shaded, moist, slightly acidic to neutral soils (NRCS 2025). Within exclosures, woody seedlings, shrubs, and vines (e.g., *Acer rubrum*, *Vaccinium corymbosum*, *Viburnum prunifolium*, *Vitis labrusca*) represent a higher proportion of the associated flora than herbaceous species, consistent with studies showing deer exclusion promotes woody regeneration with little effect on the herbaceous layer (Habeck and Schultz, 2015).

By contrast, 100 % oak girdled plots were associated with a markedly different suite of species, dominated by shade-intolerant, short-lived pioneer taxa (NRCS 2025). Many of these species also prefer moist to wet soils and tolerate a wide range of soil pH (NRCS 2025). In 100 % oak girdled plots exposed to browsing, non-native species comprised a much greater proportion of the associated flora. In this experiment 100 % oak girdled plots have significantly higher light (Taylor et al., 2017), higher soil nitrogen (Taylor et al., 2017) and higher soil moisture content (Bruner, 2024) compared to other treatments, suggesting that release from competition for these resources has facilitated establishment of early-successional and non-native species producing a shift in community composition.

Our results indicate that when oak mortality remains low to moderate ($\leq$ 50 %), the seedling community continues to be dominated by oak. However, when 100 % of oaks are girdled, we observe a shift in seedling community composition, with maples (*Acer rubrum* and *A. saccharum*) replacing oaks. Because our study focused on the seedling layer, this shift suggests potential long-term changes in canopy composition. Bruner (2024) recently reported from this same experiment that mature *A. saccharum* exhibited the strongest post-girdling growth response and posited that it may become the dominant species in the absence of oaks. These results are consistent with broader regional trends showing that many oak-hickory forests are increasingly being replaced by shade-tolerant maples (Nowacki and Abrams, 1992; Brose et al., 2014). The likely mechanisms driving this shift are mesophication of the soil environment (Lorimer,1998; Nowacki and Abrams, 2008) and seed/seedling predation and mortality (Lorimer,1998). Although soil mesophication has been widely implicated in oak regeneration failure across the northeastern U.S., it is unlikely to explain our results, as oaks persisted even in control plots. If mesophication driven by centuries of fire suppression were the primary cause, we would expect maple

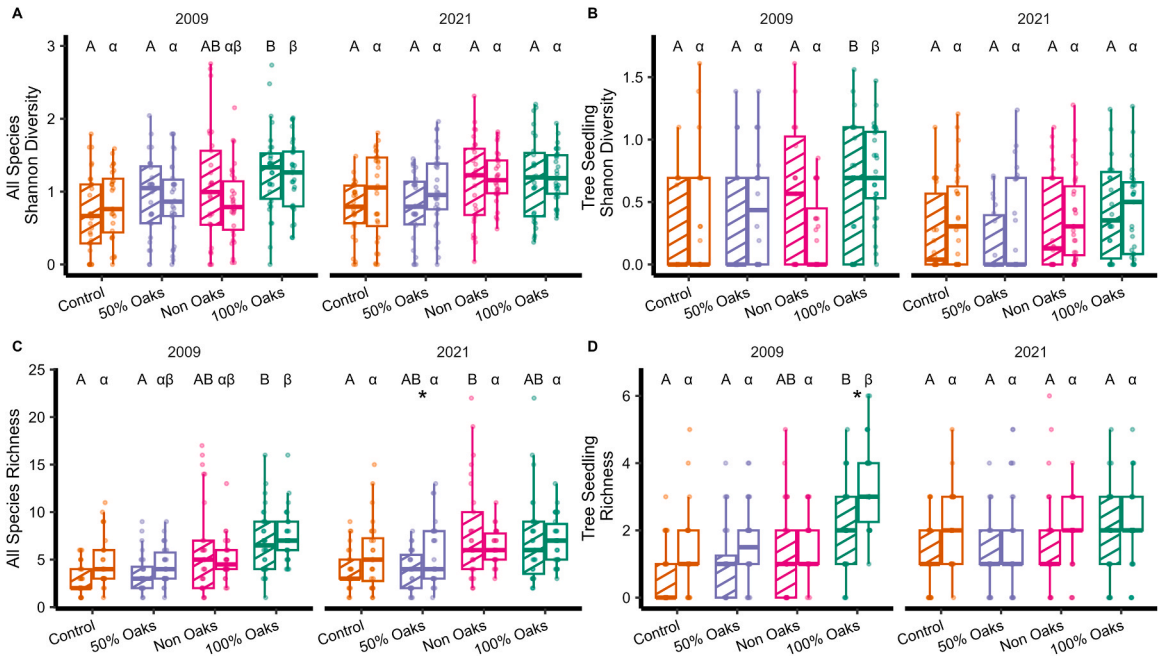


Fig. 3. Shannon Diversity (A and B) and species richness (C and D) in response to girdling and browsing treatments for all understory species (A and C) and canopy tree seedlings only (B and D) in 2009 and 2021. Hashed and solid boxes represent plots with and without browsing, respectively. Within each panel, the left-hand and right-hand sets of boxes are 2009 and 2021, respectively. Pairwise comparisons were made between treatments within years and not between years. Symbols showing pairwise differences are as in Fig. 2. No pairwise differences were significant for Shannon Diversity in 2021.

Table 2
Summary statistics for dbRDA ordinations for tree seedlings, all understory species, and all understory functional types. Interactions up to three way interactions were tested for and removed if not significant.

Model	Variable	DF	SS	F-value	p-value
Tree Seedling	Girdling	3	7.486	16.621	< 0.001
	Enclosure	1	0.525	3.497	< 0.001
	Year	1	2.344	15.613	< 0.001
	Girdling: Enclosure	3	1.933	4.291	< 0.001
	Girdling: Year	3	1.724	3.828	< 0.001
	Residual	250	37.531		
All Understory Species	Girdling	3	13.125	18.774	< 0.001
	Enclosure	1	4.999	17.164	< 0.001
	Year	1	2.062	8.847	< 0.001
	Girdling: Enclosure	3	6.245	8.934	< 0.001
	Girdling: Year	3	1.212	1.734	0.004
	Enclosure: Year	1	0.516	2.216	0.018
	Residual	249	58.025		
Understory Functional Types	Girdling	3	10.935	28.829	< 0.001
	Enclosure	1	2.339	18.503	< 0.001
	Year	1	2.345	18.550	< 0.001
	Girdling: Enclosure	3	3.023	7.969	< 0.001
	Girdling: Year	3	0.760	2.004	0.017
	Enclosure: Year	1	0.293	2.319	0.035
	Residual	249	31.483		

dominance across all treatments. While mesophication may operate as a long-term regional driver, our data suggest that seed-source limitation following mortality is the proximate cause of the observed shift. Because oaks are masting species, with only a subset of trees producing acorns in any given year (Rose et al., 2012), the survival of ≥ 50 % of mature oaks appears sufficient to maintain seed input and ensure persistence over a 13-year period. In contrast, complete oak mortality eliminates the seed source, preventing regeneration and allowing other early-successional species (e.g., *Betula lenta*) and, ultimately, maples to establish dominance.

Once again, our results emphasize the resilience of these forests to disturbance. However, Fralish (2004) highlights the importance of periodic moderate disturbance in maintaining oak dominance, arguing that such disturbance favors shade-intolerant species. Our findings generally support this, as oaks appear more likely to persist under moderate disturbance. However, our data also suggests that oak regeneration can persist even without disturbance, contrary to Fralish's conclusions, though we did not model future scenarios. Fralish cautions that a shift toward maple dominance may reduce forest productivity, diminish understory diversity, and negatively impact wildlife species dependent on acorns, such as small mammals and birds.

Changes in community composition extended beyond trees. Cosine similarity analyses revealed that control plots had the fewest number of significantly associated species. In contrast, plots with complete oak mortality had the highest number of significantly associated species, signifying a shift toward a distinct plant community following oak loss. The 100 % oak girdled treatment also had the most non-native significantly associated species while the control was significantly negatively associated with the non-native oriental bittersweet (*Celastrus orbiculatus*), suggesting that high tree mortality created conditions favorable to invasive species. One change which could potentially explain shifts in community composition is an increase in soil pH. Plots with high oak mortality (100 % oaks and 50 % oaks) were found to have less acidic soil and an increase in fungal soil diversity even 13 years post-girdling (McCulloch et al., 2025). Additionally, in the first two years post-girdling soil nitrogen increased significantly but quickly dissipated (Taylor et al., 2017). These short- and long-term changes in soil properties could explain some of the variation in species composition we have observed.

Table 3
Summary of cosine similarity analysis of the all understory species dbRDA showing species significantly associated with girdling and browsing treatment groups. Non-native species are shown in bold. Similarity is the cosine similarity between the species scores and linear constraints matrices. A cosine similarity of 1 indicates perfect alignment of species abundance with treatments in the dbRDA space; –1 indicates negative alignment, and 0 indicates orthogonality. Mean similarity is averaged over years. Minimum and maximum similarity are shown with their respective years in parentheses. To keep the family wise error rate below 0.05 using Bonferroni corrections, only species that were significant for three or more years are included.

Girdling	Browsing	Species	Functional Type	Mean Similarity	Min Similarity (year)	Max Similarity (year)
Control	Browsing	*Monotropa uniflora*	forb	0.775	0.3 (2021)	0.962 (2011)
		Monotropa hypopitys	forb	0.761	0.499 (2009)	0.885 (2016)
		Viburnum prunifolium	shrub	−0.757	−0.841 (2013)	−0.53 (2021)
	No Browsing	*Viola blanda*	forb	0.917	0.739 (2009)	0.985 (2016)
		Viola sororia	forb	0.847	0.706 (2021)	0.901 (2013)
		Uvularia sessilifolia	forb	0.76	0.656 (2009)	0.805 (2015)
		Carex digitalis	graminoid	0.757	0.618 (2009)	0.81 (2015)
		Acer pensylvanicum	tree	−0.8	−0.919 (2010)	−0.534 (2021)
		Celastrus orbiculatus	**vine**	**−0.802**	**−0.919 (2010)**	**−0.54 (2021)**
Non-oaks	Browsing	*Osmunda cinnamomea*	fern	0.632	−0.128 (2009)	0.99 (2015)
		Ranunculus abortivus	forb	0.584	−0.294 (2009)	0.999 (2015)
		Vaccinium stamineum	shrub	0.528	−0.293 (2009)	0.916 (2015)
		Carex rosea	graminoid	0.494	−0.503 (2009)	0.998 (2017)
		Geranium maculatum	forb	0.47	−0.53 (2009)	0.987 (2017)
		Sisyrinchium angustifolium	forb	0.437	−0.6 (2009)	0.999 (2018)
	No Browsing	*Kalmia latifolia*	shrub	0.929	0.755 (2021)	0.999 (2014)
		Cirsium arvense	**forb**	**0.924**	**0.7 (2021)**	**0.999 (2013)**
		Solidago altissima	forb	0.918	0.763 (2021)	0.987 (2014)
		Osmunda claytoniana	fern	0.838	0.723 (2009)	0.904 (2015)
		Vaccinium corymbosum	shrub	0.781	0.38 (2021)	0.942 (2010)
		Vitis labrusca	vine	0.742	0.393 (2009)	0.957 (2021)
		Carex albicans albicans	graminoid	0.715	0.355 (2021)	0.857 (2010)
		Acer rubrum	tree	0.714	0.445 (2009)	0.86 (2018)
Half Oaks	No Browsing	*Carex albursina*	graminoid	0.869	0.622 (2009)	0.986 (2016)
		Polystichum acrostichoides	fern	0.845	0.575 (2021)	0.945 (2013)
		Carex swanii	graminoid	0.841	0.552 (2021)	0.944 (2013)
		Maianthemum canadense	forb	0.832	0.602 (2021)	0.922 (2013)
		Carex communis	graminoid	0.778	0.607 (2009)	0.87 (2015)
		Carpinus caroliniana	tree	0.736	0.398 (2009)	0.906 (2017)
		Quercus velutina	tree	0.729	0.429 (2009)	0.874 (2017)
		Sassafras albidum	tree	0.713	0.349 (2009)	0.905 (2018)
	No Browsing	*Carex albicans emmonsii*	graminoid	0.908	0.809 (2009)	0.96 (2015)
		Carex laxiflora	graminoid	0.907	0.722 (2009)	0.999 (2017)
		Tilia americana	tree	0.903	0.711 (2009)	0.999 (2018)
		Ilex verticillata	shrub	0.895	0.693 (2009)	0.998 (2018)
		Rhamnus cathartica	**shrub**	**0.888**	**0.724 (2009)**	**0.967 (2017)**
		Ampelopsis brevipedunculata	**vine**	**0.883**	**0.566 (2021)**	**1 (2010)**
		Amphicarpaea bracteata	forb	0.848	0.745 (2009)	0.898 (2016)
		Galium pilosum	forb	0.824	0.471 (2021)	0.976 (2009)
		Trichophorum planifolium	graminoid	0.82	0.709 (2009)	0.873 (2016)
		Tsuga canadensis	tree	0.818	0.652 (2009)	0.899 (2017)
		Viburnum prunifolium	shrub	0.746	0.603 (2009)	0.815 (2017)
All Oaks	Browsing	*Carex scoparia*	graminoid	0.932	0.738 (2021)	0.999 (2014)
		Circaea lutetiana canadensis	forb	0.932	0.742 (2021)	0.999 (2014)
		Rubus occidentalis	shrub	0.932	0.741 (2021)	0.999 (2014)
		Equisetum arvense	forb	0.931	0.803 (2021)	0.998 (2015)
		Carex prasina	graminoid	0.93	0.718 (2021)	0.998 (2014)
		Carex stipata	graminoid	0.93	0.813 (2021)	0.999 (2015)
		Carex laxiculmis	graminoid	0.926	0.797 (2009)	0.999 (2015)
		Epilobium coloratum	forb	0.919	0.644 (2021)	0.999 (2013)
		Althaea officinalis	**forb**	**0.913**	**0.727 (2021)**	**0.979 (2014)**
		Rubus phoenicolasius	**shrub**	**0.911**	**0.765 (2021)**	**0.975 (2014)**
		Alliaria petiolata	**forb**	**0.901**	**0.696 (2021)**	**0.966 (2014)**
		Euthamia caroliniana	forb	0.885	0.663 (2009)	0.999 (2017)
		Onoclea sensibilis	fern	0.885	0.663 (2009)	0.999 (2017)
		Microstegium vimineum	**graminoid**	**0.883**	**0.616 (2021)**	**0.96 (2013)**
		Polygonum hydropiperoides	forb	0.876	0.548 (2021)	0.975 (2012)
		Prenanthes alba	forb	0.875	0.552 (2021)	0.973 (2012)
		Pilea pumila	forb	0.872	0.506 (2021)	0.99 (2011)
		Cardamine impatiens	**forb**	**0.867**	**0.631 (2021)**	**0.938 (2013)**
		Leersia oryzoides	graminoid	0.867	0.619 (2009)	0.998 (2018)
		Dennstaedtia punctilobula	fern	0.866	0.719 (2009)	0.942 (2016)
		Amelanchier canadensis	tree	0.862	0.462 (2021)	0.998 (2011)
		Polygonum sagittatum	forb	0.86	0.477 (2021)	0.987 (2011)
		Polygonum lapathifolium	**forb**	**0.831**	**0.406 (2021)**	**0.989 (2010)**
		Ageratina altissima	forb	0.794	0.616 (2009)	0.883 (2017)
		Carya ovata	tree	0.757	0.549 (2009)	0.865 (2017)
		Acalypha rhomboidea	forb	0.755	0.382 (2021)	0.89 (2010)
		Carex pensylvanica	graminoid	0.753	0.296 (2021)	0.95 (2009)
		Symphyotrichum racemosum	forb	0.74	0.584 (2021)	0.793 (2014)

(*continued on next page*)

Table 3 (*continued*)

Girdling	Browsing	Species	Functional Type	Mean Similarity	Min Similarity (year)	Max Similarity (year)
		Polygonum hydropiper	**forb**	**0.72**	**0.384 (2021)**	**0.836 (2010)**
	No Browsing	*Rubus odoratus*	shrub	0.956	0.869 (2021)	0.997 (2013)
		Ilex opaca	shrub	0.945	0.825 (2021)	0.998 (2012)
		Maianthemum racemosa	forb	0.945	0.78 (2009)	0.998 (2016)
		Toxicodendron radicans	vine	0.918	0.817 (2021)	0.964 (2012)
		Aralia nudicaulis	shrub	0.916	0.693 (2009)	0.998 (2018)
		Prunus virginiana	tree	0.915	0.778 (2021)	0.976 (2011)
		Lonicera japonica	**vine**	**0.887**	**0.827 (2009)**	**0.923 (2013)**
		Mitchella repens	forb	0.853	0.73 (2009)	0.893 (2015)
		Prunus serotina	tree	0.788	0.614 (2009)	0.848 (2017)
		Fraxinus americana	tree	0.783	0.727 (2021)	0.815 (2013)

4.3. Non-native Species

We observed that non-native plant cover increased substantially following high oak mortality, especially with browsing. This finding is consistent with Sabo et al. (2017), who reported that invasive species cover increased with canopy gap size. However, the role of deer exclusion in promoting invasives was less clear in their study as deer exclusion was not found to be a significant factor.

Averill et al. (2018) found that while the proportion of invasive species increased when deer were excluded, the absolute abundance remained unchanged, suggesting that reductions in native species were due to preferential deer browse. Although our study did not absolute abundance, we also found that the proportion of non-native cover increased in the most disturbed plots, and that exclosures mitigated these effects. This also aligns with our community composition findings, where a high proportion of non-native species were strongly associated with the 100 % oak girdling treatment, particularly under deer browse. Our dbRDA results further indicate that the 100 % oak girdled plots are diverging from a tree-dominated community. Because deer preferentially browse woody species (Gill and Beardall, 2001), browsing pressure combined with competition from non-native plants appears to be shifting the understory away from tree recruitment. The non-native species associated with these plots span all functional types examined and are generalist taxa capable of persisting under a wide range of light and soil conditions. In addition, these species appear to benefit from the elevated light and nitrogen availability following canopy loss, which further promotes their establishment and spread. Importantly, our data also show that reducing deer browse mitigates these effects, suggesting that deer management will be critical for sustaining oak regeneration and limiting non-native expansion following large canopy disturbances. This is consistent with other studies showing that under moderate deer pressure and limited canopy disturbance, eliminating herbivory has little effect on understory richness and cover (Wayne, 2014), whereas in regions with higher deer densities, deer management programs have been shown to increase plant diversity over time (Green, 2021).

5. Conclusions

Our findings suggest that there are threshold levels of tree mortality beyond which the understory community undergoes long-term shifts in structure and composition. While moderate tree mortality combined with low to moderate browsing can enhance species richness and maintain oak dominance, high levels of tree mortality, particularly when paired with browsing, resulted in distinct plant comunities with increased non-native species dominance and reduce diversity over time.

These findings underscore the importance of proactive management. When large-scale tree mortality (*e.g.*, from pathogens or climate-related mortality) is anticipated, measures such as the installation of deer exclosures or reduction of herbivory pressure should be considered to mitigate long-term ecological shifts. Careful management, especially of herbivore impacts, may help sustain diverse and functionally resilient oak-hickory ecosystems even in the face of moderate tree mortality.

Funding

The authors would like to thank the following foundations and funds for supporting this work: the Golden Family Foundation, the Ralph E. Ogden Foundation, the Howard Phipps Foundation, the Michael Gellert Trust, the Vetlesen Foundation and the Black Rock Forest David Redden Conservation Science Fund.

CRediT authorship contribution statement

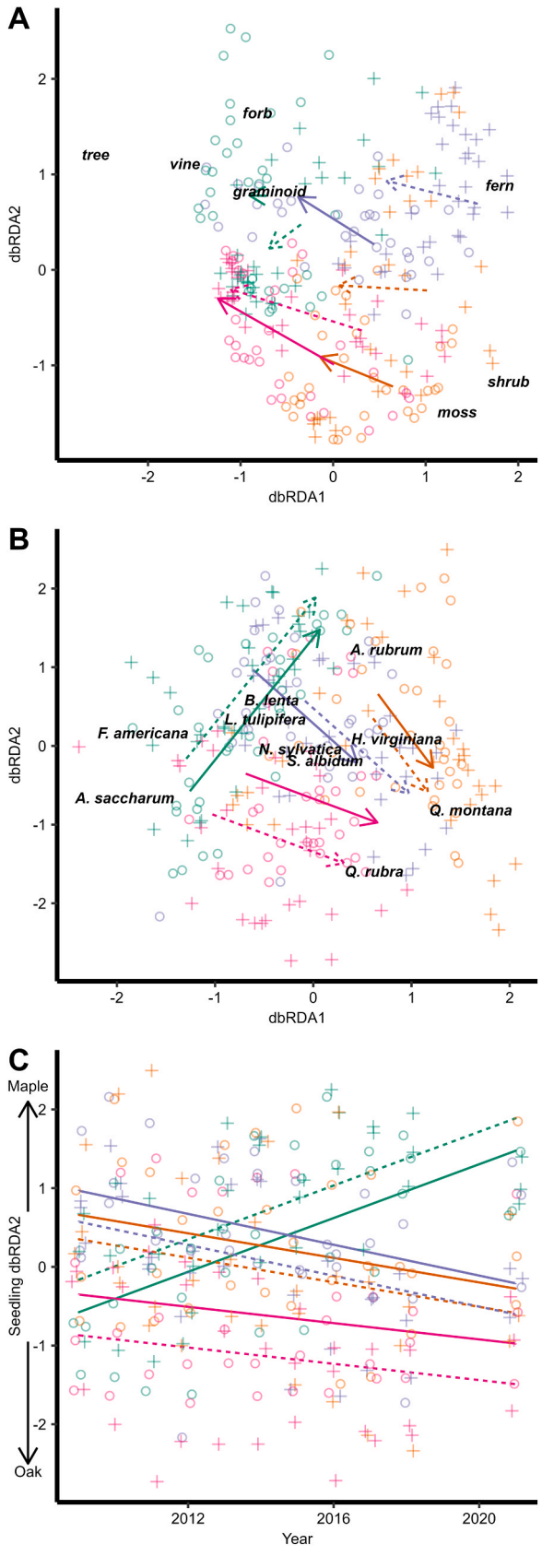
Matthew I. Palmer: Writing – review & editing, Supervision, Resources, Methodology, Investigation, Conceptualization. **Terlizzi Katherine Pavlis:** Writing – review & editing, Writing – original draft, Visualization, Project administration, Investigation, Data curation. **Calvin B. Heslop:** Writing – review & editing, Writing – original draft, Visualization, Investigation, Formal analysis, Data curation. **Benton N. Taylor:** Writing – review & editing, Supervision, Resources, Project administration, Investigation, Funding acquisition. **William S.F. Schuster:** Writing – review & editing, Supervision, Resources, Methodology, Funding acquisition, Conceptualization.

Declaration of Generative AI and AI-assisted technologies in the writing process

During the preparation of this work author Terlizzi used ChatGPT to refine language in the first draft of the Discussion section. After using this tool, all authors reviewed and edited the content as needed and take full responsibility for the content of the publication.

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.



(caption on next column)

Fig. 4. Change in understory tree seedling species composition through time. Panels A and B are biplots of distance-based redundancy analysis (dbRDA) for plant functional types (A) and tree seedlings (B). Arrows show the modeled trend in species composition through time (2009 at the tail and 2021 at the head). Colors represent girdling treatments (control: orange, 50 % oaks: purple, non-oaks: pink, and 100 % oaks: green). Dashed arrows and + symbols represent plots with browsing while solid lines and open circles represent plots without. Species scores of the 10 most common species are shown in black text. Panel C shows temporal shifts in each treatment along the second axis of the tree seedling dbRDA (B). Lower values of dbRDA2 correspond to sites with higher relative abundance of oak seedlings, while larger values have higher relative abundance of maple.

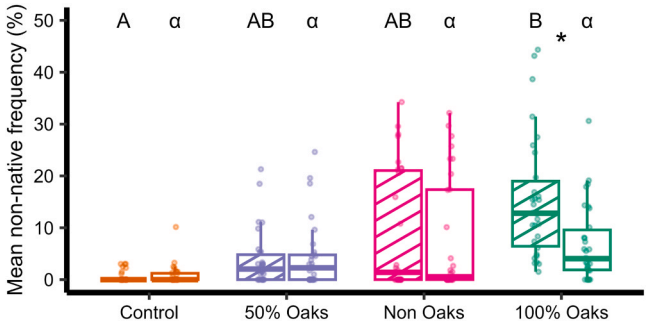


Fig. 5. Mean frequency of non-native species in each treatment averaged across time. Colors and symbols are as in Fig. 2.

Acknowledgements

The authors would like to thank Sara Pace for her 10 years of data collection in the field, Carina Berlingeri, Jeremy Hise and Gary Pavlis in the assistance of data curation and management, Terressa Hollingsworth for her advice on the statistical analysis, and all Black Rock Forest staff for their assistance and maintenance of the experimental plots.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2025.123294.

Data availability

The data used is cited in the text and in the reference list. Available on EDI data portal

References

Abrams, M.D., Sands, B.A., 2010. Oak forest composition on contrasting soil types at the Mohonk Preserve, Eastern New York. North. J. Appl. For. 27 (3), 105–109. https://doi.org/10.1093/njaf/27.3.105.

Averill, K.M., Mortensen, D.A., Smithwick, E.A.H., Post, E., 2016. Deer feeding selectivity for invasive plants. Biol. Invasions 18, 1247–1263. https://doi.org/10.1007/s10530-016-1063-z.

Averill, K.M., Mortensen, D.A., Smithwick, E.A.H., Kalisz, S., McShea, W.J., Bourg, N.A., Parker, J.D., Royo, A.A., Abrams, M.D., Apsley, D.K., Blossey, B., Boucher, D.H., Caraher, K.L., DiTommaso, A., Johnson, S.E., Masson, R., Nuzzo, V.A., 2018. A regional assessment of white-tailed deer effects on plant invasion. plx047 AoB PLANTS 10 (1). https://doi.org/10.1093/aobpla/plx047.

Ávila, J.M., Gallardo, A., Ibáñez, B., et al., 2021. Pathogen-Induced Tree Mortality Modifies Key Components of the C and N Cycles with No Changes on Microbial Functional Diversity. Ecosystems 24, 451–466. https://doi.org/10.1007/s10021-020-00528-1.

Barringer, K., Clemants, S.E., 2003. The vascular flora of Black Rock Forest, Cornwall, New York. J. Torre Bot. Soc. 130 (4), 292–308. https://doi.org/10.2307/3557547.

Beaudet, M., Messier, C., Leduc, A., 2004. Understorey light profiles in temperate deciduous forests: recovery process following selection cutting. J. Ecol. 92 (2), 328–338. https://doi.org/10.1111/j.0022-0477.2004.00869.x.

Brady, J. (2021). "Black Rock Forest internal report: overwinter deer density estimates using post-snow tracking surveys." Available upon request from science@blackrockforest.org.
Breitburg, D.L., Baxter, J.W., Hatfield, C.A., Howarth, R.W., Jones, C.G., Lovett, G.M., et al., 1998. "Understanding effects of multiple stressors: ideas and challenges". In: Pace, M.L., Groffman, P.M. (Eds.), Successes, limitations, and frontiers in ecosystem science. Springer, New York, pp. 416–431.
Brose P.H., Dey, D.C., Waldrop, T.A. (2014). "The fire-oak literature of eastern North America: synthesis and guidelines." General technical report NRS-135. U.S. Department of Agriculture, Forest Service, northern Research Station, Newtown Square, PA.
Bruner, S.G. (2024). Complementarity underlies forest function: diversity as a facet of compensation and stability (Publication No. 31146226) [Doctoral dissertation, Columbia University]. ProQuest Dissertations & Theses. ⟨https://www.proquest.com/openview/3331e66ecd8181d03ebe183c822ec5a1⟩.
Cadenasso, M.L., Pickett, S.T.A., McDonnell, M.J., Pouyat, R.V., 2007. "Forest vegetation along an urban-rural gradient in the New York City metropolitan area: patterns and relationships to ecosystem processes.". Trans. Linna Soc. N. Y. *10*. https://doi.org/10.1007/978-0-387-73412-5_18.
Cessna, J.F., Nielsen, C., 2012. Influences of hemlock woolly adelgid–induced stand-level mortality on nitrogen cycling and stream water nitrogen concentrations in southern Pennsylvania. Castanea 77 (2), 127–135. https://doi.org/10.2179/11-025.
Côte, S.D., Rooney, T.P., Tremblay, J., Dussault, C., Waller, D.M., 2004. Ecological impacts of deer overabundance. Annu. Rev. Ecol. Evol. Syst. 35, 113–147. https://doi.org/10.1146/annurev.ecolsys.35.021103.105725.
Crain, C.M., Kroeker, K., Halpern, B.S., 2008. Interactive and cumulative effects of multiple human stressors in marine systems. Ecol. Lett. 11, 1304–1315.
Crowl, T.A., Crist, T.O., Parmenter, R.R., Belovsky, G., Lugo, A.E., 2008. The spread of invasive species and infectious disease as drivers of ecosystem change. Front. Ecol. Environ. 6, 238–246. https://doi.org/10.1890/070151.
Davis, J.C., Shannon, J.P., Bolton, N.W., Kolka, R.K., Pypker, T.G., 2017. Vegetation responses to simulated emerald ash borer infestation in *Fraxinus nigra* dominated wetlands of Upper Michigan, USA. Can. J. For. Res. 47 (3), 319–330. https://doi.org/10.1139/cjfr-2016-0105.
Deng, J., Fang, S., Fang, X., Jin, Y., Kuang, Y., Lin, F., Liu, J., Ma, J., Nie, Y., Ouyang, S., Ren, J., Tie, L., Tang, S., Tan, X., Wang, X., Fan, Z., Wang, Q.W., Wang, H., Liu, C., 2023. "Forest understory vegetation study: current status and future trends.". For. Research14 3, 6. https://doi.org/10.48130/FR-2023-0006.
Ellison, A.M., Barker Plotkin, A.A., Kahlid, S., 2015. Foundation species loss and biodiversity of the herbaceous layer in New England forests. Forests 7 (1), 9. https://doi.org/10.3390/f7010009.
Ellison, A.M., Orwig, D.A., Fitzpatrick, M.C., Preisser, E.L., 2018. "The past, present, and future of hemlock wooly adelgid (*Adelges tsugae*) and its ecological interactions with Eastern hemlock (*Tsuga canadensis*) forests. Insects 9 (4), 172.
Engelken, P.J., Benbow, M.E., McCullough, D.G., 2020. Legacy effects of emerald ash borer on riparian forest vegetation and structure. For. Ecol. Manag. 457, 117684. https://doi.org/10.1016/j.foreco.2019.117684.
Eschtruth, A.K., Battles, J.J., 2008. Deer herbivory alters forest response to canopy decline caused by an exotic insect pest. Ecol. Appl. 18, 360–376. https://doi.org/10.1890/07-0446.1.
Ewing, C.J., Hausman, C.E., Pogacnik, J., Slot, J., Bonello, P., 2019. Beech leaf disease: An emerging forest epidemic. For. Pathol. 49, e12488. https://doi.org/10.1111/efp.12488.
Falxa-Raymond, N., Patterson, A.E., Schuster, W.S.F., Griffin, K.L., 2012. Oak loss increases foliar nitrogen, δ15N and growth rates of Betula lenta in a northern temperate deciduous forest. Tree Physiol. 32 (9), 1092–1101. https://doi.org/10.1093/treephys/tps068.
Fleming, P.A., Wentzel, J.J., Dundas, S.J., Kreplins, T.L., Craig, M.D., Hardy, G.E.S.J., 2021. Global meta-analysis of tree decline impacts on fauna. Biol. Rev. 96, 1744–1768. https://doi.org/10.1111/brv.12725.
Ford, C.R., Elliott, K.J., Clinton, B.D., Kloeppel, B.D., Vose, J.M., 2012. Forest dynamics following eastern hemlock mortality in the southern Appalachians. Oikos 121 (4), 523–536. https://doi.org/10.1111/j.1600-0706.2011.19622.x.
Forrester, J.A., Lorimer, C.G., Jacob, H.D., Stith, T.G., Mladenoff, D.J., 2014. Response of tree regeneration to experimental gap creation and deer herbivory in north temperate forests. For. Ecol. Manag. 329, 137–147. https://doi.org/10.1016/j.foreco.2014.06.025.
Fralish, J.S., 2004. The keystone role of oak and hickory in the central hardwood forest. In: In Upland Oak Ecology Symposium: History, Current Conditions, and Sustainability, October 7-10, 2002. Southern Research Station, *Fayetteville, Arkansas*, p. 78.
Gill, R.M.A., Beardall, V., 2001. The impact of deer on woodlands: the effects of browsing and seed dispersal on vegetation structure and composition. For. Int. J. For. Res. 74 (3), 209–218. https://doi.org/10.1093/forestry/74.3.209.
Green III, R.H., 2021. White-tailed deer harvest success and its impact on forest understory vegetation: evaluating management program efficacy in Southeastern. Pace University, New York. Master of Science Thesis,.
Habeck, C.W., Schultz, A.K., 2015. Community-level impacts of white-tailed deer on understorey plants in North American forests: a meta-analysis. AoB PLANTS 7, plv119. https://doi.org/10.1093/aobpla/plv119.
Hausman, C.E., Jaeger, J.F., Rocha, O.J., 2010. Impacts of the emerald ash borer (EAB) eradication and tree mortality: potential for a secondary spread of invasive plant species. Biol. Invasions 12 (7), 2013–2023. https://doi.org/10.1007/s10530-009-9604-3.
Healy, W.M., 1997. Influence of deer on the structure and composition of oak forests in central Massachusetts. In: McShea, W.J., Underwood, H.B., Rappole, J.H. (Eds.), The science of overabundance: deer ecology and population management. Smithsonian Books, Washington, D.C., pp. 249–266
Hothorn, T., Bretz, F., Westfall, P., 2008. Simultaneous Inference in General Parametric Models. Biom. J. 50 (3), 346–363.
Kermavnar, J., Eler, K., Marinšek, A., Kutnar, L., 2018. Initial understory vegetation responses following different forest management intensities in Illyrian beech forests. Appl. Veg. Sci. 22 (1), 48–60. https://doi.org/10.1111/avsc.12409.
Kilheffer, C.R., Underwood, H.B., Leopold, D.J., Guerrieri, R., 2019. Evaluating legacy effects of hyperabundant white-tailed deer (Odocoileus virginianus) in forested stands of Harriman and Bear Mountain State Parks, 2019-1116. US Geological Survey, *New York*.
Klooster, W.S., Gandhi, K.J.K., Long, L.C., Perry, K.I., Rice, K.B., Herms, D.A., 2018. Ecological impacts of emerald ash borer in forests at the epicenter of the invasion in North America. Forests 9 (5), 250. https://doi.org/10.3390/f9050250.
Knight, T.M., Dunn, J.L., Smith, L.A., Davis, J., Kalisz, S., 2009. "Deer Facilitate Invasive Plant Success in a Pennsylvania Forest Understory. Nat. Areas J. 29 (2), 110–116. https://doi.org/10.3375/043.029.0202.
Landuyt, D., De Lombaerde, E., Perring, M.P., Hertzog, L.R., Ampoorter, E., Maes, S.L., De Frenne, P., Ma, S., Proesmans, W., Blondeel, H., Sercu, B.K., Wang, B., Wasof, S., Verheyen, K., 2019. The functional role of temperate forest understorey vegetation in a changing world. Glob. Change Biol. 25 (11), 3625–3641. https://doi.org/10.1111/gcb.14756.
Lorimer, C.G. (1998). "Causes of the oak regeneration problem" in Loftis, D.L and McGee, C.E. Oak regeneration: serious problems, ptractical recommendations: Symposium Proceedings. Knoxville, TN September 8-10, 1992 p.14-39.
Lovett, G.M., Canham, C.D., Arthur, M.A., Weathers, K.C., Fitzhugh, R.D., 2006. "Forest ecosystem responses to exotic pests and pathogens in eastern North America. BioScience 56 (5), 395–405. https://doi.org/10.1641/0006-3568(2006)056[0395:FERTEP]2.0.CO;2.
McCulloch, L., Berlingeri, C., Chari, N., Church, L., Prada, C., Schuster, W., Terlizzi, K., Taylor, B., 2025. Loss of dominant tree-mycorrhizal mutualism increases soil fungal diversity and alters community structure. Funct. Ecol. 39, 2425–2436. https://doi.org/10.1111/1365-2435.70126.
Metz, M.R., Frangioso, K.M., Wickland, A.C., Meentemeyer, R.K., Rizzo, D.M., 2012. An emergent disease causes directional changes in forest species composition in coastal California. Ecosphere 3 (10), 86. https://doi.org/10.1890/ES12-00107.1.
Montgomery, K., Walden-Schreiner, C., Saffer, A., Jones, C., Seliger, B.J., Worm, T., Tateosian, L., Shukunobe, M., Kumar, S., Meentemeyer, R.K., 2023. Forecasting Global Spread of Invasive Pests and Pathogens through International Trade. Ecosphere 14 (12), e4740. https://doi.org/10.1002/ecs2.4740.
Nahrung, H.F., Carnegie, A.J., 2020. Non-native forest insects and pathogens in Australia: establishment, spread, and impact. Front. For. Glob. Change 3. https://doi.org/10.3389/ffgc.2020.00037.
National Oceanic and Atmospheric Administration (NOAA). (2020). "Monthly station normals of temperature, precipitation, and heating and cooling degree days". National Climatic Data Center, Asheville, N.C. Available at https:// www.ncdc.noaa.gov/cdo-web/datatools/normals.
Natural Resources Conservation Service (NCRS). PLANTS Database. United States Department of Agriculture. Accessed July 2025, from ⟨https://plants.usda.gov⟩.
Noel, A.R.A., 1970. The girdled tree. Bot. Rev. 36, 162–195. https://doi.org/10.1007/BF02858959.
Nowacki, G.J., Abrams, M.D., 1992. Community, edaphic, and historical analysis of mixed oak forests of the Ridge and Valley Province in central Pennsylvania. Can. J. For. Res. 22 (6), 790–800. https://doi.org/10.1139/x92-108.
Nowacki, G.J., Abrams, M.D., 2008. The demise of fire and 'mesophication' of forests in the eastern United States. BioScience 58 (2), 123–138.
Nuttle, T., Royo, A.A., Adams, M.B., Carson, W.P., 2013. Historic disturbance regimes promote tree diversity only under low browsing regimes in eastern deciduous forest. Ecol. Monogr. 83 (1), 3–17. https://doi.org/10.1890/11-2263.1.
Oksanen J., Simpson G., Blanchet F., Kindt R., Legendre P., Minchin P., O'Hara R., Solymos P., Stevens M., Szoecs E., Wagner H., Barbour M., Bedward M., Bolker B., Borcard D., Borman T., Carvalho G., Chirico M., De Caceres M., Durand S., Evangelista H., FitzJohn R., Friendly M., Furneaux B., Hannigan G., Hill M., Lahti L., McGlinn D., Ouellette M., Ribeiro Cunha E., Smith T., Stier A., Ter Braak C., Weedon J. (2022). vegan: Community Ecology Package. R package version 2.6-4 ⟨https://github.com/vegandevs/vegan⟩, ⟨https://vegandevs.github.io/vegan/⟩.
Orr, J.A., Vinebrooke, R.D., Jackson, M.C., Kroeker, K.J., Kordas, R.L., Mantyka-Pringle, C., et al., 2020. Towards a unified study of multiple stressors: divisions and common goals across research disciplines. Proc. R. Soc. B Biol. Sci. 287, 20200421.
Pendergast, T.H.I.V., Hanlon, S.M., Long, Z.M., Royo, A.A., Carson, W.P., 2016. The legacy of deer overabundance: long-term delays in herbaceous understory recovery. Can. J. For. Res. 46 (3), 362–369. https://doi.org/10.1139/cjfr-2015-0280.
Pinheiro J., Bates D., R.Core Team (2022). nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-160, <⟨https://CRAN.R-project.org/package=nlme⟩>.
Prescott, C.E., 2002. The influence of the forest canopy on nutrient cycling. Tree Physiol. 22 (15–16), 1193–1200. https://doi.org/10.1093/treephys/22.15-16.1193.
R Core Team (2024). R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. ⟨https://www.R-project.org⟩.
Raup, H.M., 1938. Botanical studies in the Black Rock Forest. Bulletin No. 7. Black Rock Forest Bulletin. Cornwall Press, p. 161.
Rooney, T.R., Waller, D.M., 2003. Direct and indirect effects of white-tailed deer in forest ecosystems. For. Ecol. Manag. 181 (1-2), 165–176.
Rose, A.K., Greenberg, C.H., Fearer, T.M., 2012. Acorn production prediction models for five common oak species of the eastern United States. J. Wildl. Manag. 76, 750–758. https://doi.org/10.1002/jwmg.291.

Sabo, A.E., Frerker, K.L., Waller, D.M., Kruger, E.L., 2017. Deer-mediated changes in environment compound the direct impacts of herbivory on understory plant communities. J. Ecol. 105 (5), 1386–1398. https://doi.org/10.1111/1365-2745.12748.

Schei, F.H., Arnberg, M.P., Grytnes, J., Johanesen, M.S., Johansen, J., Milford, A.B., Røynstrand, A., Tollefsrud, M.M., 2024. Ash dieback: A single-species catastrophe or a cascade of ecological effects in the ground flora? For. Ecol. Manag. 572, 122322. https://doi.org/10.1016/j.foreco.2024.122322.

Schuster, W., Culotta, A., Terlizzi, K.P., LaPoint, S., 2024a. "Pellet group surveys of white-tailed deer (Odocoileus virginianus) in Black Rock Forest, Cornwall, NY 2014-2024." ver 1. Environ. Data Initiat. https://doi.org/10.6073/pasta/5e7a903fec190032240912efba4f0223. Accessed 2025-03-24.

Schuster, W.F., Terlizzi, K.P., Griffin, K., Naeem, S., 2024b. "Tree species identity, diameter and qualitative canopy health measurements (full, partial or dead) from 2005 to 2023 on 12 experimental oak loss plots in Black Rock Forest, NY." ver 1. Environ. Data Initiat. https://doi.org/10.6073/pasta/30a243844c2537ef734117a813ce865f. Accessed 2025-03-24.

Schuster, W.S., Griffin, K.L., Roth, H., Turnbull, M.H., Whitehead, D., Tissue, D.T., 2008. Changes in composition, structure and aboveground biomass over seventy-six years (1930–2006) in the Black Rock Forest, Hudson Highlands, southeastern New York State. Tree Physiol. 28 (4), 537–549.

Shearer, B.L., Tippett, J.T., 1989. Jarrah dieback: the dynamics and management of *Phytophthora cinnamomi* in the jarrah (*Eucalyptus marginata*) forest of south-western Australia. Res. Bull. Dep. Conserv. Land Manag. West. Aust. (3), 76.

Sircely, J.A. (2007). The influence of scale on the relationships amond diversity, function, and invasibility [Masters of Art Thesis, Columbia University, New York].

Taylor, B.N., Patterson, A.E., Ajayi, M., Arkebauer, R., Bao, K., Bray, N., Elliott, R.M., Gautheir, P.P.G., Gersony, J., et al., 2017. Growth and Physiology of a Dominant Understory Shrub, Hamamelis virginiana, Following Canopy Disturbance in a Temperate Hardwood Forest. Can. J. For. Res. 47 (2), 193–202. https://doi.org/10.1139/cjfr-2016-0208.

Terlizzi, K., C. Heslop, B. Taylor, W. Schuster, S. Lawrence, and M. Palmer. (2025). "Percent cover of under- and mid-story vegetation and seedling counts in the Future of Oak Forests project at Black Rock Forest, Cornwall, NY." ver 1. Environmental Data Initiative. https://doi.org/10.6073/pasta/d5bd3ef7bd255e6af9da0ae8f49a2057.

Thu, P.Q., Quang, D.N., Chi, N.M., Hung, T.X., Binh, L.V., Dell, B., 2021. New and Emerging Insect Pest and Disease Threats to Forest Plantations in Vietnam. Forests 12 (10), 1301. https://doi.org/10.3390/f12101301.

Tilghman, N., 1989. Impacts of white-tailed deer on forest regeneration in northwestern Pennsylvania. J. Wildl. Manag. 53 (3), 524–532.

Underwood, H.B., Porter, W.F., 1997. Reconsidering paradigms of overpopulation in Ungulates. In: McShea, W.J., Underwood, H.B., Rappole, J.H. (Eds.), The science of overabundance: deer ecology and population management. Smithsonian Books, Washington, D.C., pp. 185–198. ⟨https://archive.org/details/scienceofoverabu0000unse/mode/2up⟩ (Available on the internet archive).

Wayne, J. (2014). Effects of deer exclosure establishment and subsequent removal on vegetation diversity, tree regeneration, and understory biomass at Black Rock Forest. [Undergraduate Thesis, Barnard College].

Yorks, T.E., Dabydeen, S., 1999. Seasonal and successional understory vascular plant diversity in second-growth hardwood clearcuts of western Maryland, USA. For. Ecol. Manag. 119 (1-3), 217–230.

Zuur, A., Ieno, E.N., Walker, N., Saveliev, A.A., & Smith, G.M. (2009). Mixed effects models and extensions in ecology with R (2009th ed.). Springer.