



Understory plant growth forms respond independently to combined natural and anthropogenic disturbances

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ABSTRACT

Natural disturbances can maintain forest diversity by creating a heterogeneous resource landscape, which can contribute to coexistence of early- and late-successional species. However, almost all forested ecosystems are also subject to multiple anthropogenic stressors, which could inhibit plant diversity and forest recovery after natural disturbances. Here, we present the first large-scale replicated field experiment testing the interactions among two natural and two anthropogenic disturbances in a mature secondary temperate forest. Specifically, we test the extent to which: 1. a natural windthrow (tornado), 2. deer browsing, 3. salvage logging, a common forestry practice to generate revenue after natural disturbances, and 4. mechanical removal of the understory, drive subsequent plant community assembly, diversity, and abundance. Our results have two clear messages. First, the combined disturbances, especially salvage logging, increased plant species richness and abundance; we found 65 more species in 0.1 ha of the disturbed areas versus the same area of reference forest. Second, we found that it was critical to analyze plant growth forms separately; each major plant growth form responded to the disturbances differently. Surprisingly, salvage logging, browsing, and vegetation removal had negligible effects on the diversity and abundance of *tree* seedlings or saplings. In contrast, salvaging increased herb richness by 30% (six extra species per 36 m² plot), and shrubs were twice as abundant in salvaged versus unsalvaged plots. The combined disturbances created unique plant communities in comparison to adjacent undisturbed reference sites, but plant growth forms differed in which combination of disturbances shifted community composition the most. We did not find that non-native invasive species substantially increased in abundance in response to the disturbances, nor were invasive species unique to the salvaged areas. Together, our results demonstrate that a patchwork of combined natural and anthropogenic disturbances can promote plant diversity in a human-modified temperate forest. In particular, the combination of a natural wind disturbance and salvage logging benefited native herbaceous species, the plant group that represents the vast majority of vascular plant species (~80%) in temperate forests across the world.

1. Introduction

Natural disturbances typically promote diversity and have long been a central focus of ecology (Connell, 1978; Pickett and White, 1985; Tilman, 1990). In forests, overstory disturbances at various spatial scales such as windthrows, insect outbreaks, and ice storms, can promote long-term coexistence of both light-demanding early successional species and shade-tolerant late successional species (Fischer et al., 2013; Grime, 1973; Roberts and Gilliam, 2014; Schnitzer and Carson, 2001). However, where natural and anthropogenic disturbances co-occur, they can

reduce biodiversity, facilitate the invasion and spread of exotic species, and reduce forest resilience to subsequent perturbations (reviewed in Burton et al., 2020; Cowles et al., 2021; Ibáñez et al., 2019; Chazdon, 2003; Johnstone et al., 2016; Lindenmayer et al., 2017). Temperate forests across the world are characterized by centuries of simultaneous anthropogenic pressures, including repeated logging, overabundant deer, fire suppression, and the near extirpation of apex predators. Despite decades of research, the consequences of these chronic changes for forest diversity and resilience remain poorly understood (Foster et al., 1998; Nowacki and Abrams, 2008; Nuttle et al., 2013). Moreover,

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climate change models predict that the frequency and intensity of catastrophic natural disturbances will increase in the future, potentially further eroding forest resilience (Anderson-Teixeira et al., 2013; Dale et al., 2001; Easterling et al., 2000). Thus, understanding forest recovery processes after combined natural and anthropogenic disturbances is a priority for forest ecologists and land management practitioners (Leverkus et al., 2018).

Salvage logging commonly occurs in forests worldwide as a means to recover lost revenue and to mitigate risk from subsequent natural forest disturbances, including fire, insect outbreaks, and ice and wind storms (Leverkus et al., 2018; Royo et al., 2016; Thorn et al., 2018). Even though salvaging is a widespread practice, the ecological consequences of salvage logging remain ambiguous and controversial. On one hand, salvaging can decrease seedling regeneration by up to 71% (Donato et al., 2006) and can delay or redirect forest community recovery, often down impoverished successional pathways (Bowd et al., 2018; Hernández-Hernández et al., 2017; Santoro and D'Amato, 2019). Salvaging can homogenize large swaths of land by reducing or nearly eliminating structural heterogeneity, particularly coarse woody debris and tip-up mounds (Bottero et al., 2013; Lindenmayer et al., 2017; Russell et al., 2006; Santoro and D'Amato, 2019; Waldron et al., 2013, but see Donato et al., 2006; Spicer et al., 2018). These structural alterations may remove browse refugia and create unfavorable regeneration microsites (Bottero et al., 2013; Krueger and Peterson, 2006; Long et al., 1998; Waldron et al., 2013). On the other hand, evidence is growing that salvage logging has either negligible or positive impacts on forest diversity and regeneration (e.g., Leverkus et al., 2021). For example, salvaged and unsalvaged sites often have similar patterns of tree species composition and diversity, both immediately after logging and more than a decade later (from less than five years to 10–30 years; Kleinman et al., 2020; Kramer et al., 2014; Peterson and Leach, 2008a; Royo et al., 2016; Snyder et al., 2020). Studies that quantify salvaging effects on the broader vascular plant community show that non-tree species, in particular herbaceous plants, respond positively to salvage logging (Kärklipa et al., 2020; Kurulok and Macdonald, 2007; Lang et al., 2009; Suzuki et al., 2021). These conflicting results may be due to differences unique to each disturbance (e.g., intensity, type, site; Kramer et al., 2014; Taerøe et al., 2019), time elapsed since the disturbance, or perhaps most likely, additional biotic processes that mediate the effects of salvage logging on forest regeneration. The interactions among natural and anthropogenic disturbances should thus be studied with other key ecological processes that operate across the landscape.

Ungulate browsers also strongly mediate understory forest dynamics. Selective browsers such as deer or moose cause widespread shifts in plant and animal communities where they are abundant, and can lead to alternate successional trajectories (De Vriendt et al., 2021; Heikkilä et al., 2003; Kouki et al., 2004; Putman, 1996; Roberts and Gilliam, 2014; Rooney, 2001; Suzuki et al., 2021; Vázquez, 2002). Heavy browsing pressure can indirectly depress understory diversity by creating dense layers of few browse-tolerant species and promoting non-native species (Bourg et al., 2017; Eschtruth and Battles, 2009; Royo and Carson, 2006; Suzuki et al., 2008; Waller, 2014). However, the combination of moderate browsing and disturbance can also promote understory native plant diversity (Boulanger et al., 2018; Faison et al., 2016; Royo et al., 2010a). In eastern North America, white-tailed deer (*Odocoileus virginianus*) have been overabundant for nearly a century, causing biodiversity declines of over 80% across large swaths of deciduous and coniferous forest (Côté et al., 2004; Habeck and Schultz, 2015; Nuttle et al., 2013; Waller, 2014). Over-browsing threatens forest diversity in this region because deer target herbs and shrubs, which together constitute greater than 90% of the vascular plant species (Gilliam, 2007; Spicer et al., 2020). Further, the depauperate understories and near monocultures of browse-tolerant species that remain persist for decades, even when deer have been removed from the landscape or returned to low historic densities (Nuttle et al., 2014; Pendergast et al., 2016; Royo et al., 2010b; Tanentzap et al., 2012). Thus, our classical expectations of

“healthy” forest regeneration after natural disturbance, or after anthropogenic disturbances like salvage logging, are likely unrealistic in the context of decades of deer overabundance (Nuttle et al., 2013; Sabo et al., 2019).

Mechanical or chemical removal of the understory is a frequently used management technique to reduce competition from recalcitrant herbs and thus promote regeneration of tree species of interest (reviewed in De Lombaerde et al., 2021). Although these removals can be effective in enhancing tree recruitment in temperate forests (De La Cretaz and Kelty, 1999; De La Cretaz and Kelty, 2006; De Lombaerde et al., 2021; Hupperts et al., 2022), the impact on overall plant diversity is less well understood (De Lombaerde et al., 2021; Duguid et al., 2013; Landuyt et al., 2019; Ristau et al., 2011). Reducing dominant herbaceous species could also increase the diversity of herbs and shrubs by releasing rare species from heavy competition (De La Cretaz and Kelty, 1999; Fei et al., 2010), and could shift resource availability for overstory species (Elliott et al., 2015). Alternatively, physical understory disturbance could provide an opportunity for non-native invasive species to enter or spread in forested landscapes, by creating trails, spreading propagules, and making available potentially new resources or niche space (e.g., Bonanomi et al., 2018; Brewer et al., 2015). The impact of these management techniques on forest biodiversity are yet unresolved in part because few studies focus on the response of non-trees to understory removals (e.g., Spicer et al., 2020).

Here, we present a large-scale, replicated field experiment explicitly testing the interactions among four key processes governing understory diversity and successional dynamics. Specifically, we evaluate the degree to which a tornado blowdown, salvage logging, deer browsing, and understory removal act independently and in concert to drive subsequent forest regeneration. Because we are interested in diversity of the whole community of vascular plants, we include all plant growth forms in our definition of forest regeneration and recovery, not just trees. Using a unique opportunity, where a single tornado created four separate blowdowns, we set up an experiment in which we could nest disturbance manipulations within multiple sites caused by the same storm. By comparing the plant communities in our experimental disturbance matrix to undisturbed reference forest areas, we can parse apart the combined effects of multiple natural and anthropogenic processes that operate simultaneously across forested landscapes. Because salvage logging, deer overabundance, and understory competition have been shown to cause sharp declines in plant diversity in our study region (e.g., Goetsch et al., 2011), we predicted that the combination of these factors would delay regeneration and reduce diversity.

2. Materials and methods

2.1. Study site

Our study took place at the Powdermill Nature Reserve in Westmoreland County, Pennsylvania (40.16°N, −79.27°W; Fig. 1E). The bulk of the reserve is 900 ha of mature 80–120-year-old mesophytic forest; common overstory tree species include maples (*Acer rubrum*, *A. saccharum*), tulip poplar (*Liriodendron tulipifera*), American beech (*Fagus grandifolia*), oaks (*Quercus rubra*, *Quercus montana*, *Quercus alba*), black cherry (*Prunus serotina*), and sweet birch (*Betula lenta*). Temperatures range from −20 to 33 °C and mean annual precipitation is approximately 1100 mm (Murphy et al., 2015; Spicer et al., 2018). We located our experiment within four large blowdowns caused by an EF-1 tornado that occurred on June 1st, 2012. We refer to these four blowdowns as *sites*. More information about the land use history, overstory community, and details of the windstorm can be found in Spicer et al. (2018), Curtze et al. (2018), and Snyder et al. (2020).

The entire region, including urban and rural areas, have had high deer densities for decades (Adams and Villareal, 2020; Carson et al., 2014; Redding, 1995; Rushing et al., 2020). Because deer management in Pennsylvania is based off the number of deer tags filled by hunters and

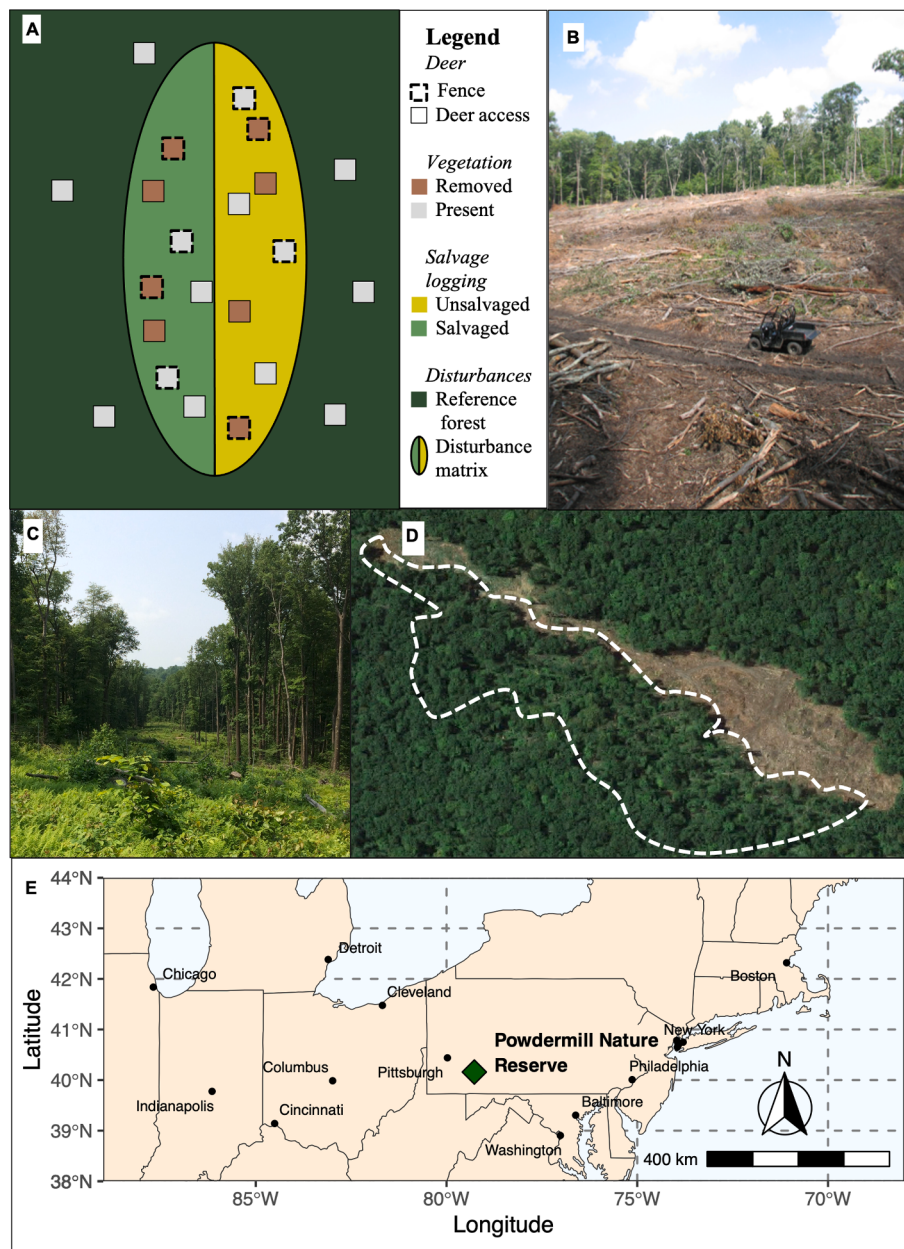


Fig. 1. Experimental design, photos, and map of the study area. A. Illustration of experimental design of one blowdown site (of four total). The 16 experimental plots and six reference plots per site are represented by squares, with colors and outlines corresponding to experimental treatments. B. Photo of a blowdown that was intensively salvaged logged, shortly after the logging operation was completed. C. Photo of regrowing vegetation in salvaged site, two growing seasons after the logging operation. The blowdown site is to the right in this photo. Note the many standing trees that were not toppled by the tornado. D. An aerial view of one randomly selected half of a blowdown that was salvaged. The unsalvaged portion of the blowdown is outlined in white; salvaged and unsalvaged areas were approximately the same, but look different due to drone camera angle and ground contours. E. Map of the region with study site labeled as green diamond.

reported to the Game Commission, no direct measure of deer abundance exists for Powdermill. However, previous research on plant responses to deer exclusion show that browsing pressure throughout the Powdermill Nature Reserve is heavy; [Murphy and Comita \(2021\)](#) found that browsing reduced the growth and survivorship of multiple tree species. Furthermore, several species of unpalatable ferns dominate the understory in much of the closed-canopy forest (e.g., *Dennstaedtia punctilobula*, *Dryopteris intermedia*); see [Table S1](#) for the top ten understory species in our study.

2.2. Experimental design

We designed a 2x2x2 blocked, split-plot field experiment to examine the independent and interacting effects on forest re-assembly of 1) salvage logging, 2) deer browsing, and 3) the reduction of the above ground biomass of the understory community. We salvage logged a randomly selected half of each of the four blowdown sites and left the other half unsalvaged during the winter of 2013–2014, following the

tornado in June of 2012. The salvage logging operation harvested both downed and standing live trees, effectively removing all large trees from each site and often damaging advance regeneration and shrubs ([Fig. 1B](#)). This intensity of logging is commonly used across many deciduous and boreal forests, particularly on private land ([Leverkus et al. 2018](#)). Removing all trees also avoided creating inter-site differences in the amount of standing trees left, which occurs with variable-intensity salvaging operations. Details and a map of the salvage logged blowdowns are in [Slyder et al. \(2020\)](#), and are depicted in [Fig. 1](#). To test how deer browsing drives forest understory re-assembly, we set up 32, 8x8x2.4 m fences during the summer and fall of 2014. We placed the fences in a randomized blocked design throughout each of the four blowdown sites (four fences in the salvaged half, and four in the unsalvaged half in each of the four blowdown sites). We also set up 32, 8x8 m control plots (unfenced), marking the corners with the same metal poles that support the fences. To account for possible seed dispersal effects from birds perching on fences, we ran a metal wire around the border of the control plots at a height of 2 m. We refer to

these 64, 64 m² areas (whether fenced or unfenced) as *plots*, and they are the primary unit of replication for this study.

To evaluate whether competition from the understory plant community drives forest regeneration, we used hand shears and a gasoline-powered string trimmer to cut all vegetation to ground level within 32 of the 64 plots in the summer of 2015 (selected randomly within-block). This vegetation consisted of advance regeneration present prior to the blowdown and salvaging, as well as species that colonized from the seed bank, from below-ground roots and rhizomes, and from newly dispersed propagules. Importantly, this treatment allowed us to target one potential difference between the effects of a tornado versus salvaging: the understory is heavily disturbed by salvaging but to a much lesser degree by a windstorm alone. Treatments were blocked within each of the four blowdowns such that each half of the blowdown area (salvage logged or unsalvaged) contained four plots where the above-ground initial community was removed, and four plots where it was left present. Thus, we had a blocked, split-plot experimental design with 8 replicate plots of each of the experimental treatment combinations: salvage logging (Unsalvaged/Salvaged), deer access (Deer/Fenced), and removal of the understory layer (Present/Removed); two replicates of each combination were at each site (Fig. 1; see also Fig. 1 in [Slyder et al., 2020](#)). We refer to the naturally disturbed blowdown area as the *disturbance matrix*. The disturbance matrix encompassed all 64 experimental plots, including the “control plots” that experienced only the natural disturbance (no other experimental treatments) as well as plots experiencing the combined natural and added anthropogenic disturbances (our additional experimental treatments described above).

We also established 5–7 36 m² *reference plots* near each blowdown site, within the area of the forest that was not affected by the tornado (and was not experimentally manipulated). The reference plots were placed to avoid recent gaps and were located at least 30 m away from the edge of each blowdown, to characterize the forest community adjacent to each site. These 24 total reference plots represent the undisturbed deciduous forest with no large light gaps, ambient deer densities, and a legacy of at least several decades of abundant deer ([Carson et al., 2014](#); [Murphy and Comita, 2021](#); [Rushing et al., 2020](#)).

2.3. Data collection

In the summer of 2017 (five years after the tornado, four years after the salvaging, three years after the fences were erected, and two years after the vegetation removal), we surveyed all 64 experimental plots within the disturbance matrix as well as the 24 reference plots. We collected both presence/absence data with timed meander surveys and quantitative cover estimate data on all plants. Meander surveys were done with daily rotating two- or three-person subsets of the same five-person team, and times were scaled accordingly (10 min for a two-person team or 7 min for a three-person team). We identified and included all live vegetation under 1 m, including leaves from plants that were taller than 1 m overall. To avoid edge effects, we left a 1 m buffer around the border of each experimental plot, surveying only the center 36 m². Meander surveys for presence/absence were done throughout this entire 36 m² zone, but cover data were collected in four 1x1 m *quadrats* located at the four corners of each 36 m². Plant traits and growth forms were determined by referencing the USDA PLANTS database and [Rhoads & Block \(2007\)](#).

2.4. Statistical analyses

We calculated species richness from the whole species list, including all species found in the 36 m² meander survey as well as the four 1x1 m cover estimate quadrats. We calculated total mean vegetative cover (per plot) as the sum of the mean per-species cover estimates (per quadrat). We used cover estimates to calculate Shannon Diversity Index (hereafter, diversity) and used presence-absence matrices to perform community analyses.

We first compared overall mean species richness, diversity, and total cover among the reference plots (“reference”, outside the disturbed area), the control plots (“natural”, which experienced only the wind disturbance, but no additional anthropogenic disturbances), and the natural and anthropogenic disturbance plots (“anthropogenic”, tornado and additional experimental disturbances). We ran type-II ANOVAs on the raw metrics (non-normalized) and included disturbance type (reference, natural, or natural and anthropogenic), a site effect, and their interaction in the model. We complemented this overall analysis with species accumulation curves to quantify how the total number of species, rather than mean species per plot, varied among the disturbance types. We compared species accumulation curves between the disturbance matrix and the reference forest. We also broke the disturbance matrix into salvaged and unsalvaged sides of the blowdown and compared these species accumulation curves to the adjacent reference forest. Because these tests are unbalanced (e.g. the disturbance types have large differences in sample size), we checked that the results do not change with a random balanced design of eight plots per disturbance type.

Our main plot-scale analyses focused on the interacting effects of the anthropogenic disturbances within the context of the tornado; that is, including only the nested disturbance matrix plots (64 total, excluding the reference plots). Our linear models included the main effects of effects of logging (salvaged or unsalvaged), deer (deer access or fenced), and understory vegetation removal treatment (removed or present), as well as their 2- and 3-way interactions. Because environmental context is important for plant communities at the regional and local scale (e.g., [Kärklina et al., 2020](#); [Kramer et al., 2014](#)), and because preliminary analyses showed differences in plant diversity among sites ([Figure S1](#), [Table S2](#)), we also incorporated site effects (i.e., the effect of location of each of the four blowdowns) into our models by normalizing the responses to each reference site. We calculated each plot-level response variable as the measured value minus the site-level reference forest mean, and divided this difference by the total for that reference site. Therefore, the final response variables represent the site-specific effect of the experimental treatment in comparison to the reference forest. We ran each set of three models (species richness, diversity, and total cover) first for the whole plant community and then separately for each of the four major plant growth forms (trees, herbs, shrubs, and vines) to elucidate growth-form differences.

In addition, we explored the main effects of site, the tornado, salvage logging, browsing, and vegetation removal, and the two- and three-way experimental interactions on the plant community compositions with PERMANOVAs of a multivariate presence-absence community matrix using Bray-Curtis distances ([Oksanen, 2010](#)). Like the diversity analyses above, we first analyzed the full community dataset with all plant growth forms and all plots (including reference sites) to test whether disturbance type (reference, natural disturbance, and combined natural and anthropogenic disturbances) differed in community composition, and then tested differences among experimental treatments within the disturbance matrix (excluding reference plots). We ran the disturbance matrix analyses separately for trees, herbs, shrubs, and vines to compare across plant growth forms. For this analysis we blocked the plots within site and visualized these community differences with NMDS ordinations. Because rare species can be overweighted in nonmetric multidimensional analyses, we removed species that occurred in less than five percent of plots ([McCune and Grace, 2002](#); [Slyder et al., 2020](#)). Next, we explored the species-specific responses of plants to the tornado, salvage logging, deer, and vegetation removal by running four separate indicator species analyses on the full community matrix with all species ([De Cáceres et al., 2012](#); [Dufréne and Legendre, 1997](#)). To encompass the possible important effects of the disturbances on rare species, we included the species that occurred in < 5% of the plots in the indicator species analyses ([Dufréne and Legendre, 1997](#); [Thorn et al., 2020](#)). Because of the complex and iterative nature of the indicator species analysis, we could only test the main effects of the experimental

treatments and only report species that were associated with single experimental treatments. To account for non-independence of these three tests, we interpreted our indicator species analyses using a Bonferroni-corrected alpha (Cabin and Mitchell, 2010; Holm, 1979).

All response variables were modeled with a normal distribution in linear mixed models, and their residual distributions were checked with qq plots (Zuur et al., 2009). Analyses were run in R version 3.6.0 (R Core Team 2019). Diversity estimates and species-accumulation curves were calculated with the vegan package (Oksanen et al., 2019). We used linear models constructed with the lme4 package to test whether salvage logging, browsing, or understory mowing drive changes in plant diversity and abundance (Bates et al., 2014). We first interpreted the results with a Type III ANOVA in the car package, and then re-ran the tests as stronger Type II ANOVAs if there were no significant interactions (Fox and Weisberg, 2019). Indicator species analyses were run with the indicspecies package (De Cáceres, 2013).

3. Results

3.1. Overall comparisons of disturbed and reference forest

We identified a total of 264 species: 40 trees, 190 herbs, 15 shrubs, and 17 vines, and two of unknown growth form. 253 species were found within the four blowdown sites (the disturbance matrix), while 123 species were found within the reference forest (Fig. 2A). Within the same area, the disturbance matrix harbored 188 species while the reference forest had 123. Species accumulation curves began to asymptote, indicating that we achieved sufficient sampling (Fig. 2). The unsalvaged natural blowdown areas accumulated 49 more species than the reference forest community outside of the tornado blowdown (Fig. 2B), indicating some positive effect of the natural disturbance on forest species richness. Salvage logging added another 53 species for a total of 225 species, 102 more than the reference forest (Fig. 2B). The combined natural and anthropogenic disturbances caused an increase of approximately 10 species per 36 m² and a 34% increase in diversity versus the adjacent undisturbed reference forest (Fig. 3, Table S2). The natural

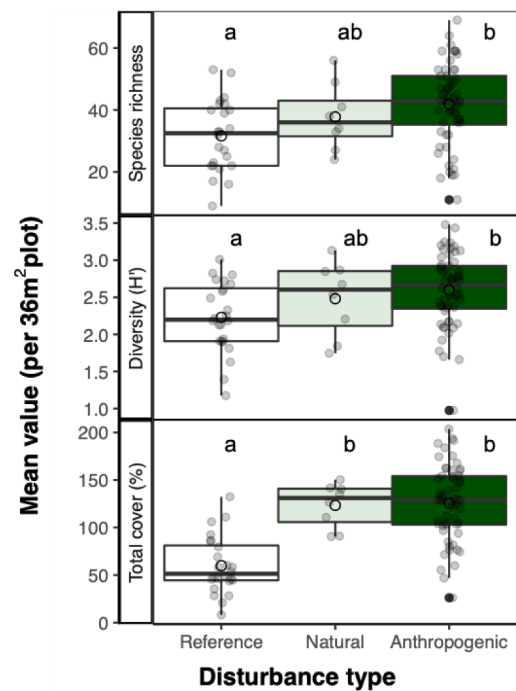


Fig. 3. Comparison of overall mean species richness, diversity, and total cover in the 24 reference forest plots (forest outside of the tornado blowdowns), versus the eight 36 m² plots within the blowdown areas that only experienced the natural disturbance (*natural*), versus the 56 *anthropogenic* plots within the disturbance matrix (wind plus anthropogenic disturbances). Natural disturbance alone did not change plant species richness or diversity, but increased cover by over 100%.

disturbance caused the total cover on average per plot to double; there was no additional increase in cover due to the added anthropogenic disturbances (Fig. 3, Table S2).

3.2. Differing effects of natural and anthropogenic disturbances among plant growth forms

Each plant growth form (trees, herbs, shrubs, and vines) responded differently to the independent and combined natural and anthropogenic disturbances. Surprisingly, deer alone (main effect) never caused any significant changes for any response variable or plant growth form. For trees, none of the disturbances caused any significant changes in species richness, diversity, or total cover (Fig. 4A, Table S3). This, however, was not the case for the three other growth forms. Salvage logging caused a 30% increase in *herbaceous* species richness, or, on average, an increase of six more herbaceous species in each relatively small 36 m² plot (Fig. 4B, Table S3). Removing the understory caused an increase of 23% in mean herbaceous cover (Fig. 4B, Table S3). For shrubs, salvaging almost tripled mean cover (13% cover in unsalvaged versus 36% in salvaged plots), but caused no significant changes in species richness or diversity (Fig. 4C, Table S3). Excluding deer caused a 14% decline in shrub cover in plots where we left the initial community present, however, excluding deer caused 67% increase in shrub cover in plots where we removed the initial community (significant deer by vegetation removal interaction, Fig. 4C, Table S3). Vine cover responded complexly to the combined natural and anthropogenic disturbances (significant three-way interaction among all three experimental treatments, Fig. 4D, Table S3).

The natural and anthropogenic disturbances created distinct plant community compositions from the reference forest, and community composition varied by site (PERMANOVA Disturbance type: $p = 0.042$; Site: $p < 0.0001$, Fig. 5A, 5B, Table S4). When we classified species by

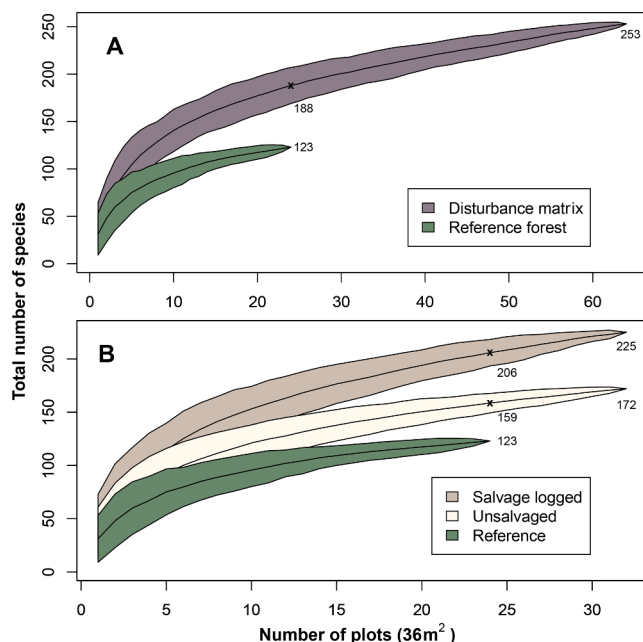


Fig. 2. Species-accumulation curves. A. Disturbance matrix plots versus reference forest plots (outside of the tornado path); this included the meander surveys. B. Disturbance matrix with and without salvage logging, versus reference forest plots. Note that the number of plots (x-axis) differs between A and B.

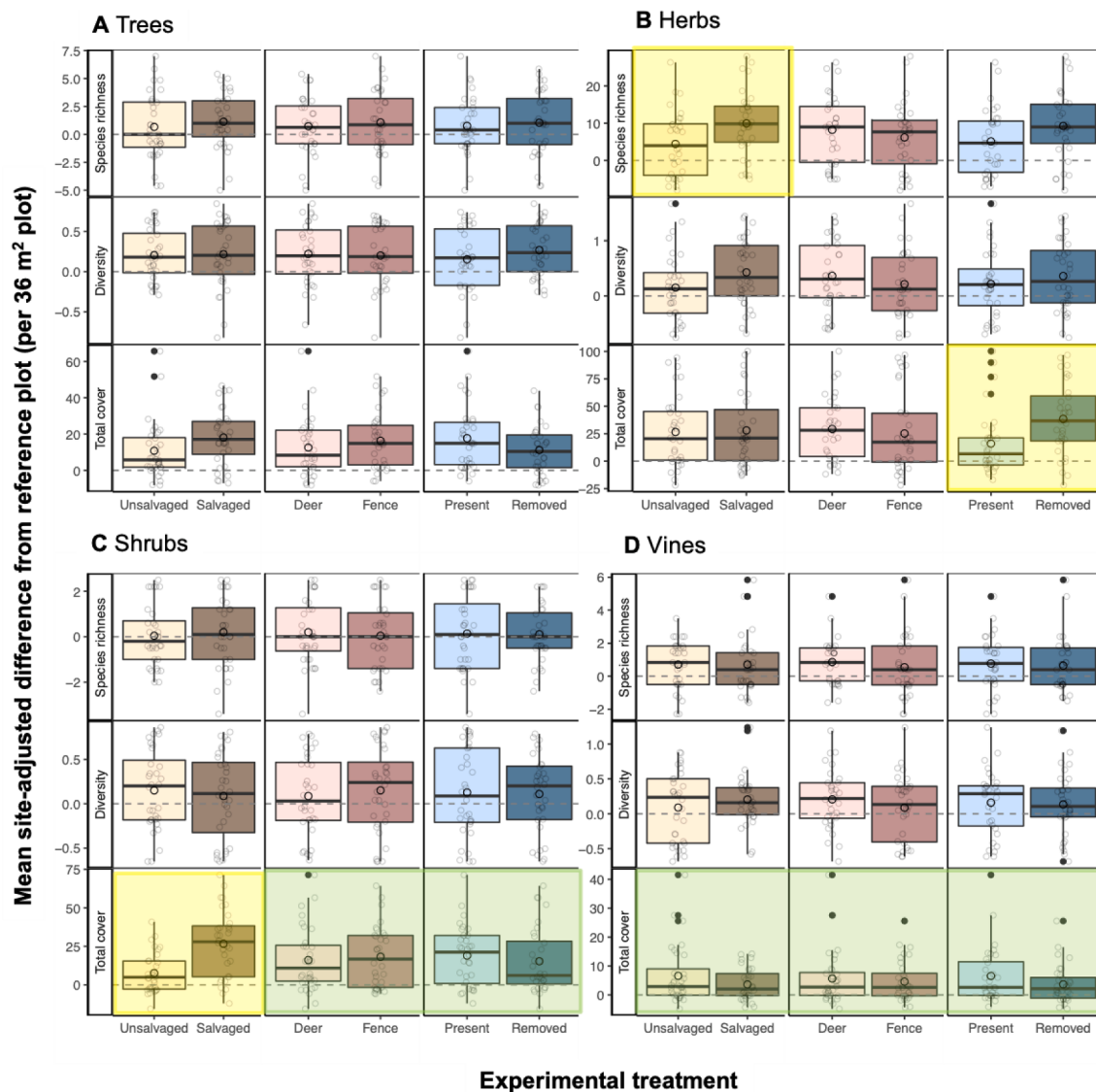


Fig. 4. Windthrown forest understory responses to salvaging, deer, and mowing, separated by plant growth form. Response variables shown are mean differences from site-adjusted reference forest plots. **A.** Anthropogenic disturbances had no detectable effects on **tree** species richness, diversity, or abundance. **B.** Salvaging increased mean **herbaceous** species richness by 30% (six species per plot), and vegetation removal increased total herb cover by 23% in comparison to plots where the initial community was present. **C.** Salvaging doubled mean total **shrub** cover in comparison to unlogged plots, and deer and mowing had interacting effects on shrub cover. **D.** Salvaging, deer access, and vegetation removal had interacting effects on mean total **vine** cover. Panel shaded colors correspond to main effects and interacting effects: yellow = main effect at $\alpha < 0.05$; green = interacting effects effect at $\alpha < 0.05$.

growth form within the disturbance matrix, we found again that each plant growth form responded to different drivers (or combinations of drivers). Tree community composition did not significantly differ across any of the measured treatment groups (Fig. 5C, Table S4). Herbaceous community composition (Fig. 5D) responded to the interaction between salvaging and deer exclusions within the disturbance matrix (Salvage*Deer $p = 0.048$). Shrub community composition (Fig. 5E), on the other hand, was relatively consistent across all plots. Vine community composition (Fig. 5F) responded to the interacting effects of salvaging and vegetation removal in the disturbance matrix (Salvage*Removal $p = 0.019$).

When comparing across the disturbance types in the whole forest, our species indicator analyses resulted in six native species associated with the unmanipulated reference forest (*Thelypteris noveboracensis* (L.) S.E.Fawc. & A.R.Sm., *Trillium* sp. L., *Viola pubescens* Aiton, *Geum canadense* Jacq., *Eutrochium purpureum* (L.) E.E. Lamont, and *Quercus montana* Willd.; Table S5). Within the disturbance matrix, our species indicator analyses resulted in one native species associated with areas

where vegetation was left intact (*Trillium* sp. L.), and one native plant associated with the vegetation removal plots (*Poa* sp. L.) (Table S5). Ten unique species (species only found once in the dataset) were present in single-treatment plots, including 8 in the reference forest, and two in the natural-disturbance only plots (Table S6). An additional 7 unique species were found in plots that had combined disturbances. Although a full trait analysis remains for future research, we did not observe any major shifts in browse-tolerant species in our deer-exclusion plots. Among all treatment groups, most species were native herbaceous forest species, 7% were introduced species, and 3.5% (9 species) are listed as invasive in Pennsylvania (Table 1).

4. Discussion

4.1. Enhanced diversity following combined anthropogenic and natural disturbances

We predicted that severe anthropogenic disturbances layered on top

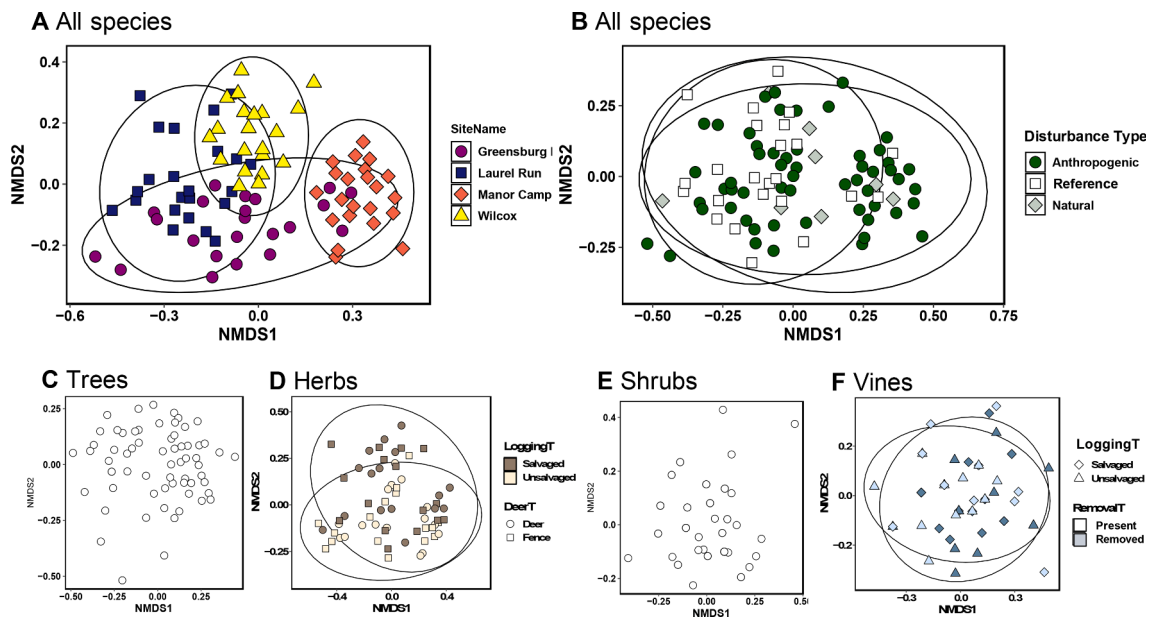


Fig. 5. Plant community composition differed among the four blowdowns (sites), as well as between reference and disturbed plots. A. Overall plant community composition differed among sites, represented by the four polygons and colors. B. The natural wind disturbance and added anthropogenic disturbances also created distinct plant communities from the reference forest. C. Tree species composition did not significantly differ across experimental treatments within the disturbance matrix. D. Herbaceous plant community composition was similar across sites, but differed among interacting combinations of salvage and deer treatments. E. Shrub species composition was consistent across all sites and disturbances. F. Vine composition differed among interacting combinations of salvage and vegetation removal treatments. Colors for sites (yellow, orange, blue, and purple) correspond to Figure S1, and colors for disturbance types (dark green, light green, and white) correspond to Fig. 3. Ellipses represent 95% confidence intervals of each treatment group; absent ellipses indicate no significant differences in community compositions among treatment groups.

Table 1

Comparison of traits of the communities of each experimental forest group, as a percent of total group species richness (N). Percentages may not total to 100% due to species with unknown traits (not shown in table).

CATEGORY	TRAIT	All species N = 264		Reference forest N = 123		Disturbance N = 253		Salvaged N = 225		Fenced N = 192		Removed N = 211	
		SR	%	SR	%	SR	%	SR	%	SR	%	SR	%
Woody	Herbaceous	196	74.2	89	72.4	186	73.5	166	73.8	135	70.3	157	74.4
	Woody	66	25.0	35	28.5	65	25.7	58	25.8	55	28.6	53	25.1
Origin	Introduced	18	6.8	6	4.9	18	7.1	16	7.1	11	5.7	15	7.1
	Native	184	69.7	100	81.3	176	69.6	160	71.1	148	77.1	151	71.6
Habitat	Edge	39	14.7	10	8.1	40	15.8	36	16	25	13	36	17.1
	Field	45	17.0	14	11.4	43	17	42	18.7	25	13	36	17.5
	Forest	157	59.5	96	78	150	59.3	131	58.2	128	66.7	124	58.8
	Generalist	4	1.5	3	2.4	5	2.0	5	2.2	5	2.6	5	2.4

of a natural windthrow would alter community dynamics in regenerating forest patches (Brewer et al., 2012; Leverkus et al., 2018). In particular, because salvage logging and deer overabundance have caused substantial declines in tree diversity, we expected at least one, or a combination of these factors, to delay community recovery strongly and reduce diversity in comparison to naturally disturbed forests (Côté et al., 2004; Lindenmayer et al., 2017; Nagel et al., 2015; Pendergast et al., 2016; Rooney, 2001; Rojo and Carson, 2006; Thorn et al., 2014; Waller, 2014). Our results showed the opposite; the combination of natural and anthropogenic disturbance had no effect on tree species diversity or abundance, whereas it substantially enhanced herbaceous species richness and shrub cover. Ultimately, the disturbance matrix supported *more than 100 additional plant species* than the undisturbed reference forest. Not only could a higher total number of species increase the resilience or stability to the system, but each of these species could potentially contribute unique ecological functions and species interactions opportunities (e.g., Bunnell et al., 2004; Curtze et al., 2018; Nuttle et al., 2011). When accounting for site differences, the natural wind disturbance alone doubled total vegetative cover; salvaging also independently increased mean total cover by 51% (Fig. 3). Thus, the

combination of the natural wind disturbance and salvage logging had the greatest impact on the plant community overall, and each plant growth form responded differently to the disturbances. Below, we parse out and expand upon these major findings in greater detail.

4.2. Native herbs and shrubs benefited the most from salvaging

Across the Eastern Deciduous Forest Biome non-tree species comprise 93% of vascular plant species richness (Spicer et al., 2020), and make up 84% of the species in our dataset. Although salvaging had a negligible impact on trees, it enhanced herb species richness and doubled shrub abundance. In results similar to ours from a boreal forest, Pykälä (2004) found 81 additional herbaceous species following a clear-cut logging operation in comparison to nearby uncut mature forests. This positive effect of a gap-forming land management technique on herbaceous diversity has also been reported in Rumbaitis del Rio (2006), Kärklä et al. (2020), Orczewska et al. (2019), and Suzuki et al. (2021). For the most part, non-tree species seem to respond positively, and more strongly, to the combined natural and anthropogenic disturbances than the tree community does. This is an important distinction that has not

been heavily emphasized in the literature, and has implications for forest management (see discussion in Spicer et al., 2022, and *Mechanisms* section below).

Importantly, non-native invasive species were only a minor component of the disturbed plant community in our study. The vast majority of species in our whole study area were native plants (Table 1). Nine of the 19 non-native species present in our dataset are known to be invasive in Pennsylvania (DCNR, 2019; Rhoads and Block, 2007), however, these nine species were relatively uncommon and were never in high abundance. In addition, the proportion of non-native species was very similar between the salvaged area and the reference forest (salvaged: 16/225 species (7%); reference: 6/123 (5%); Table 1), so their presence was not unique to the disturbances or salvage logging. No invasive species were statistically significant indicators of any disturbance, but we did note that *Berberis thunbergii* DC., an invasive species in PA, was associated with the disturbed areas more than the intact areas. Although a previous study in Powdermill did find higher associations of invasive species with land-use history of disturbance, in particular mining and agriculture (Calinger et al., 2015), we did not find that the logging operation strongly promoted invasive species.

Many of the early successional species found in our disturbance matrix typically do not persist over 50 years in the understory as the tree canopy matures and begins to cast deeper shade (Burns and Honkala, 1990; Vankat and Snyder, 1991). It is therefore unlikely that these short-statured herbaceous plants, or short-lived trees, would halt succession and suppress diversity in this area, as has been suggested as a possible consequence of salvaging (Lindenmayer et al., 2017; Michalová et al., 2017; Thorn et al., 2018). Instead, the salvage logging operation almost certainly created an opportunity for many species to flourish via vegetative reproduction, emergence from the seedbank, and dispersal from nearby seed sources (outlined as mechanisms for post-disturbance herbaceous recovery in Roberts and Gilliam, 2014). Seedbank replenishment could effectively contribute to the storage effect and the maintenance of plant diversity in the long-term (Chesson and Warner, 1981; Pake and Venable, 1996; Plue et al., 2010; Pykälä, 2004; Warner and Chesson, 1985; Olmsted et al., unpublished data). The majority of the species that occurred across our treatments likely form persistent seed banks, although long-term seedbank studies for many herbaceous species do not exist (Baskin & Baskin, 1998; Olmsted et al., unpublished data). For example, *Rubus* species (blackberries) were very abundant in many of our disturbed plots; they are fast growing early successional species that form persistent seed banks (Peterson and Carson, 1996; Swanson et al., 2011; USDA, 2019). The emergence and rapid growth of *Rubus* spp. likely explains the increase in shrub cover after salvaging (Fig. 4C). Propagules of some plant species may also have been carried on the salvaging machinery, in particular on tire treads (Bajwa et al., 2018; Buckley et al., 2003; Marinissen and van den Bosch, 1992; Mausel and Bartkowiak, 2019; Rew et al., 2018; Veldman and Putz, 2010; Zenner and Berger, 2008). The equipment used in salvage logging upturns soil, which may have further stimulated germination of some seed banking species (Bjorkbom and Walters, 1986; Nyland et al., 2007; Peterson and Leach, 2008b; Pykälä, 2004). Soil scarification associated with salvaging also compacts soil and crushes the vegetation that survived the storm, potentially mitigating the negative impacts of recalcitrant understory layers. These soil dynamics may have contributed to the success of native herbs, most of which likely invest in clonal growth (Wyatt and Silman, 2014), and the lack of strong effects of recalcitrant deer-resistant understory species (described below). Overall, our findings suggest that we currently underestimate the role seed banks and propagule availability play in the long-term maintenance of temperate forest plant diversity via the storage effect. More research on the mechanisms of herbaceous layer recovery after disturbance (e.g., Roberts and Gilliam, 2014) would greatly advance the field.

4.3. No direct effect of deer browsing on understory diversity

Throughout much of the world, and in particular in eastern North America, ungulate browsing often causes substantial declines in plant species diversity (Russell et al. 2001, Rooney 2001, Côté et al. 2004, Nuttle et al. 2013, Carson et al. 2014, Pendergast et al. 2016), and leads to the formation of wide-spread recalcitrant understory layers (*sensu* Royo & Carson 2006). Thus, we predicted that excluding browsers and removing the above-ground portion of the initial plant community would strongly mediate community reassembly, increase plant species richness, and redirect succession. To our surprise, for the most part, this did not occur (*cf.* Nuttle et al. 2013): we did not detect any *direct* effect of excluding deer on plant diversity or abundance in the time span of this study.

Notably, deer instead had interactive effects on several response variables. Deer mediated the effect of initial community removals on shrub cover, mediated the effect of salvaging and removals on vine cover, and interacted with salvaging to shift herb community composition. While speculative, we suggest our vegetation removal stimulated abundant *Rubus* regrowth, which was then heavily browsed by deer in unprotected areas, but not where we excluded deer, explaining part of these interactions. *Rubus* spp. are well-known disturbance-adapted species that grow rapidly after natural canopy gaps as well as logging operations (Donoso and Nyland, 2006). Deer browse fresh *Rubus* regrowth, which may have been particularly abundant in salvaged and mowed areas. However, in areas where we did not remove initial vegetation, deer may have avoided dense, older *Rubus* thickets (e.g., Royo and Stanovick 2019). A few other studies have demonstrated *Rubus* to have facilitative effects on seedling regeneration via protection from deer browse (e.g., Harmer et al. 2010). The rapid growth rate of *Rubus* and formation of dense thickets can outpace the browsing effects of deer for 5–10 years, even protecting other species from browse pressure via associational resistance (Barbosa et al., 2009; Harmer et al., 2010; Horsley et al., 2003). Kraft et al. (2004) also found only subtle effects of deer on plant communities in a disturbed forest; moderate forest thinning increased species richness and herb cover, while protecting plants from deer led to higher growth and reproduction of herbs. In the undisturbed reference forest of Powdermill, (Murphy and Comita, 2021) found strong survival and growth benefits of fencing, but fencing did not increase rarefied species richness or evenness. Our study contributes to the growing literature that show ungulate browsers as important but hard-to-predict drivers of plant community change, often with context-dependent effects.

4.4. Applicability of this study to other systems

We want to be careful to place our conclusions within their proper context. The first one is scale; the tornado knocked over four large patches of forest within a larger, relatively intact continuous forest stand. Our results will likely not scale up to logging vast areas of continuous forest with no intact forest nearby, though this would depend, at least in part, on whether the disturbed forest had a healthy seed bank. Nonetheless, in our case and others (Roxburgh et al., 2004; Woods, 2004), the nearby reference forest, combined with large-scale highly disturbed forest patches, favored the establishment of a highly diverse regenerating community. Notably, even though salvaging removed all marketable fallen and standing trees, unmarketable trees and tree crowns were left on the forest floor (Fig. 1B). The presence of some coarse and fine woody debris likely contributed to understory regeneration and seed dispersal by providing refugia from browsing, unlike in post-fire salvaging operations in western coniferous forests or more heavily cleared boreal forests (Keyser et al., 2009; Santoro and D'Amato, 2019; Waldrón et al., 2013; but see Vander Yacht et al., 2020).

We expect that our results would not apply to forest areas in which propagules have been drastically depleted by previous human land-use or repeated catastrophic disturbances such as canopy fire (Leverkus

et al., 2018; Lindenmayer et al., 2017; Thorn et al., 2018), or in which the forest is even more threatened by non-native species (Burnham and Lee, 2010). A widespread and dense understory of multiple non-native species can create invasional meltdowns and a lasting depauperate stable state, in particular when in combination with invaders in higher trophic levels such as earthworms (Ackerman et al., 2014; Kuebbing et al., 2014; Simberloff, 2006; Yelenik and Antonio, 2013). Although non-native invasive species do exist in the surrounding areas of the Powdermill Nature Reserve (Calinger et al., 2015), the native plant community in the mature forest does not yet seem to be seriously threatened by non-native plant species, even after experiencing combined natural and anthropogenic disturbances. The understory community in our study likely re-assembled via all four mechanisms named in Roberts and Gilliam (2014).

We also note that our survey happened after an asynchronous series of disturbances; the tornado occurred in 2012, salvaging and fences were placed in 2013–2014, and the understory was removed in 2015. Although these complex asynchronous dynamics are typical in managed forests, it does limit our ability to expand our results. Repeated surveys across seasons or years would have captured a more thorough response of the understory community, especially herbaceous plants that grow quickly and senesce within a growing season (e.g., Sokol et al., 2017). Time-lags in management and plant response are common, but several methodological challenges remain in quantifying longitudinal herbaceous understory community dynamics (discussed in Spicer et al., 2022).

5. Conclusions

Here, we experimentally tested the extent to which salvage logging, deer browsing, and understory removals interact to mediate post-windthrow forest regeneration. Contrary to our predictions, we found that the patchwork combination of natural and intense anthropogenic disturbance facilitated very high diversity and abundance of understory plants, in particular herbaceous species. Our results have several important implications for forest ecology and management. First, the combination of natural windthrow and salvage logging had the greatest positive impact on understory plant communities, so, at the proper spatial scale, salvage logging could be used as a strategy for enhanced regeneration of diverse forest communities. Moreover, excluding deer had no measurable direct effect on re-assembling plant communities. Although perhaps important in other contexts, deer and understory management strategies *alone or in combination* were not effective in promoting post-windthrow understory diversity in this time frame. Finally, the *herbaceous* plant species were the major driver of our community regeneration patterns; tree species were largely unaffected by the intense disturbances. Our results highlight the need for more explicit consideration of non-tree growth forms in forest ecology and management, in particular for the conservation of plant diversity (e.g., Spicer et al., 2022). Our understanding of the mechanisms underlying the diversity and abundance of herbaceous plants lag far behind those of trees (e.g., Gilliam, 2014), even though herbs make up the vast majority of temperate vascular plant species (e.g., Spicer et al., 2020). In summary, our research contributes an important experimental field test to forest disturbance theory as well as shifts the perspective of effective eastern deciduous forest management practices to include herbs, shrubs, and vines.

CRedit authorship contribution statement

Michelle Elise Spicer: Conceptualization, Formal analysis, Investigation, Data curation, Writing – original draft, Writing – review & editing, Visualization, Project administration, Funding acquisition. **Alejandro A. Royo:** Conceptualization, Methodology, Investigation, Writing – review & editing. **John W. Wenzel:** Conceptualization, Methodology, Investigation, Writing – review & editing, Funding acquisition, Project administration. **Walter P. Carson:**

Conceptualization, Methodology, Investigation, Writing – review & editing, Supervision, Funding acquisition.

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.

Data availability

All data are available on Dryad at the link: doi: 10.5061/dryad.dz08kprx9.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2023.121077>.

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