

Trajectories of forest composition, structure, and productivity following an experimental ice storm disturbance

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Abstract

Disturbance creates structural legacies that are important drivers of functional and compositional stabilities in forested ecosystems. We used an experimental ice storm disturbance to evaluate effects of disturbance severity on structural legacies and their functional consequences. We evaluated canopy structural characteristics (height, density, openness, and complexity) before and after disturbance using data from terrestrial LiDAR. We compared trajectories of structural characteristics and functional outcomes (composition, mortality, and productivity) among treatments and relative to controls. We found significant post-disturbance change for all canopy structural characteristics especially at higher severity levels, with persistent legacy effects on mean canopy height and canopy complexity. There were limited changes in biomass, productivity, and composition, and mortality did not vary significantly among treatments. There was limited evidence for linkages between structural and functional responses, but plots that retained greater complexity had higher stability of net primary productivity. Our findings indicate persistent structural legacies associated with ice storm disturbance, but declining structural legacies over time may affect interactions with subsequent disturbance or stressors. Improved understanding of these trajectories could help with predicting outcomes of changing disturbance regimes associated with global change.

Key words: moderate disturbance, legacy effects, global change, interactions, ice storms

Introduction

Disturbance is a primary driver of forest structure and functioning, resulting in both near-term direct impacts and long-term legacy effects associated with ecosystem response and reorganization (Seidl and Turner 2022). Near-term outcomes and longer-term legacies of disturbance can be structural, compositional, or functional in nature and these characteristics often interact with each other to influence ecosystem response and stability following disturbance (Seidl et al. 2014; Johnstone et al. 2016; Scheuermann et al. 2018). For example, changes in forest canopy structure immediately following disturbance (i.e., structural legacies) have been shown to strongly affect productivity resistance, but shifts in structure cannot be easily separated from changing composition and diversity (Gough et al. 2021a). These interrelated legacies of disturbance are also likely to be primary drivers of longer-term stability and reorganization of forests following disturbance, but the specific effect of structural legacies on these trajectories is not generally well understood (Seidl and Turner 2022).

Canopy structure has been shown to be a strong driver of ecosystem functioning and disturbance response in forest ecosystems (Ishii et al. 2004; Hardiman et al. 2011; Fahey et al. 2019a). The structure and complexity of the canopy affects a wide variety of forest ecosystem processes and characteristics including microclimate, water use and cycling, light capture and transmittance, and light use efficiency (Ehbrecht et al. 2017; Gough et al. 2019; LaRue et al. 2023). Relationships between canopy structure and ecosystem functions are both responsive to disturbance and an important driver of forest ecosystem response to disturbance (Niedermaier et al. 2022). For example, light capture by the canopy is often negatively affected by disturbance, but the efficiency by which leaf area drives productivity can be increased following disturbance (Haber et al. 2020). Near-term canopy structural outcomes following disturbance have been associated with disturbance characteristics such as mechanism, severity, vertical and horizontal patterning, and timing (Atkins et al. 2020; Choi et al. 2023). However, structural responses and reorganization following disturbance are driven by complex

interactions between these disturbance characteristics and the compositional and structural legacies that they produce (Fotis et al. 2018; Gough et al. 2022).

Disturbance severity and type are recognized as important drivers of both near-term outcomes and longer-term response trajectories (Reyes et al. 2010; Stuart-Haëntjens et al. 2015; Halpin and Lorimer 2016). In particular, moderate severity disturbances by definition leave biological legacies in the form of residual vegetation and have been shown to impart legacies of complexity and diversity on forest ecosystems that can persist for long time periods (Frelich 2002). However, the legacy effects of moderate severity disturbance are likely to be particularly responsive to variation in source and pattern of disturbance, because of the differential structural and compositional outcomes imparted by these disturbances (Meigs and Keeton 2018). For example, the species-specific pest emerald ash borer (*Agrilus planipennis*) reduces functional diversity in northern hardwood forests and has a largely top-down impact on canopy structure (Flower and Gonzalez-Meler 2015). Other disturbance sources, such as fire or wind, can have variable structural and compositional impacts that are strongly associated with the intensity of the disturbance (Reyes et al. 2010).

One common source of moderate disturbance in temperate forests is ice and snow storms, which can lead to substantial effects on forest canopy structure and functioning (Ireland 2000; Nagel et al. 2016). The effects of ice storms on forest canopy structure are largely top-down in directionality, but substantial differences in post-storm outcomes can result from variation in intensity (i.e., ice thickness and duration; Duguay et al. 2001; Rhoads et al. 2002; Arie and Lechowicz 2007; Takahashi et al. 2007; Weeks et al. 2009; Fahey et al. 2019b). The structural impact of ice disturbance can also be affected by characteristics of the pre-disturbance forest (Jones et al. 2001; Turcotte et al. 2012; Nock et al. 2016). For example, successional stage or age of the forest and variable species composition can affect damage from equivalent ice loading (Jones et al. 2001; Rhoads et al. 2002; Arie and Lechowicz 2007; Beaudet et al. 2007; Kraemer and Nyland 2010; Klopčič et al. 2020). However, assessment of structural reorganization of forests following ice disturbance and separating the effect of ice loading intensity from that of pre-disturbance forest composition and structure has not previously been possible (Rustad and Campbell 2012).

Manipulative ecosystem-scale experiments are an avenue to understanding the structural and functional outcomes of disturbance and identifying the role of variable disturbance characteristics in these outcomes (Fayle et al. 2015; Song et al. 2019). Long-term monitoring of ecosystems after they have undergone experimental disturbance can also illustrate trajectories of structural and functional response (Gough et al. 2021b). In studies that have been designed in a controlled experimental framework, the effects of the disturbance and its characteristics can further be separated from pre-disturbance conditions and subsequent disturbance or stressors. Such experiments have produced foundational knowledge in ecosystem science on topics such as carbon dioxide enrichment (Norby and Zak 2011), drought stress (Beier et al. 2012), wind

and pest disturbance (Barker Plotkin et al. 2013; Zimmerman et al. 2014), and acidification and calcium depletion (Huggett et al. 2007).

In this study, we utilize monitoring data associated with the Hubbard Brook Ice Storm Experiment (ISE) to characterize trajectories of forest canopy structure composition, and aboveground productivity following experimental ice storm disturbance. In particular, we focused on the specific effects of variable disturbance intensity and repeated disturbance on these trajectories. We addressed the following specific research questions: (1) Were there shifts in tree species dominance in response to variable intensities of experimental ice storm disturbance?, (2) How has canopy structure and complexity reorganized over time following initial changes associated with direct disturbance impacts?, (3) How has aboveground biomass (AGB) and primary productivity been affected by variable intensities of experimental ice storm disturbance?, and (4) Is the response trajectory of productivity following ice storm disturbance related to response and stability of canopy structure? Our findings are relevant to understanding how ice storms can affect forest composition, structure, and function and add to a growing base of knowledge on the effects of moderate severity disturbance on linkages between forest canopy structure and ecosystem functioning.

Methods

Study site and experimental design

The Hubbard Brook ISE is situated within the Hubbard Brook Experimental Forest (HBEF), which is an ~3200 ha northern hardwood forest forming part of the White Mountain National Forest, New Hampshire, USA (43°56'N, 71°45'W). HBEF has a cold continental climate with mean air temperatures of −9 °C in January and 18 °C in July, and mean annual precipitation of ~1400 mm year^{−1}. HBEF was impacted by the 1998 ice storm and establishment of the ISE was partially motivated by observational research documenting the ecosystem consequences and variable impacts (related to topography, environmental conditions, and stand structure and composition) of the 1998 ice storm (Rhoads et al. 2002; Houlton et al. 2003).

The ISE treatment plots were established in summer 2015 within a 70–100-year-old mixed northern hardwood stand dominated by American beech (*Fagus grandifolia*), sugar maple (*Acer saccharum*), red maple (*Acer rubrum*), and yellow birch (*Betula alleghaniensis*), with a minor conifer component comprised of red spruce (*Picea rubens*) and balsam fir (*Abies balsamea*; Rustad et al. 2020). Ten 20 × 30 m plots were established and two plots were randomly assigned to each of five treatments with variable ice intensity targets (as radial ice accretion) and frequency: (1) Control; no experimental icing applied, i.e., 0 mm; (2) Light; 6.4 mm of ice in year 1 only; (3) Moderate; 12.7 mm of ice in year 1 only; (4) Double; 12.7 mm of ice in years 1 and 2; and (5) High; 19.0 mm of ice in year 1 only. Treatments generally approximated the ice accretion targets based on caliper and water volume measurement on canopy dowels (Rustad et al. 2020). Although these levels represent substantial ice accumulation, which can be associated

with significant damage to trees and infrastructure, they do not represent the most extreme levels of accretion in natural ice storms (Irland 1998). The targeted amounts of ice accretion were chosen to be relevant to National Weather Service Ice Storm Warnings in the Northeast US, which occur at 6.4 mm (0.25 in.) in the mid-Atlantic region and 12.7 mm (0.5 in.) in New York and New England.

Ice treatments were implemented during subfreezing conditions in 2016 and 2017 (“Double” treatment plots only). To create ice accretion, water was sprayed vertically through gaps in the canopy using fire hoses and allowed to fall as a fine mist onto the canopy (Rustad et al. 2020). Ice accretion was quantified using caliper measurements on wooden dowel “ornaments” suspended in the canopy (Rustad and Campbell 2012; Rustad et al. 2020). Accretion levels differed significantly among treatments and were qualitatively close to targets and thus used as an indicator of disturbance intensity. Additionally, fine woody debris (FWD) mass produced by treatments was sampled using litter traps installed in each treatment plot and used as an indicator of disturbance severity. Fine litter (woody material < 2 cm and foliar litter; hereafter FWD) was collected in plastic baskets (52 L × 37 W × 27 H cm) approximately 2–3 weeks after icing treatments and at the end of subsequent summer (Rustad et al. 2020). After sorting and subsampling for leaf area (see below), litter was oven-dried at 60 °C for 48 h (or constant weight) and weighed to estimate total mass of treatment-associated FWD and this mass was used as an indicator of treatment disturbance severity (Table 1).

Measurement and quantification of canopy structure and light transmission

We quantified canopy structure in each plot prior to the ISE treatments in August 2015 and on an annual basis thereafter through 2022. We quantified canopy cover, arrangement, and complexity using a ground-based, portable canopy LiDAR (PCL) system (Parker et al. 2004; Hardiman et al. 2011). Data were collected along five permanently marked 30 m transects per plot (Fahey et al. 2019b). Raw PCL data were processed using the *forestr* package in R (Atkins et al. 2018a). In the *forestr* algorithm, PCL returns are binned into 1 m² bins with light saturation corrections made based on LiDAR return density. A suite of canopy structure metrics are then calculated, which describe the density, distribution, and variance of LiDAR returns along the horizontal and vertical axes of the 2D plane that transects the canopy (Hardiman et al. 2013; Atkins et al. 2018a). Many expressions of canopy structure can be derived from LiDAR, we selected metrics that describe five different aspects of canopy structure (Atkins et al. 2018a). The metrics included in this analysis were: (1) *canopy height*—assessed based on mean and maximum vegetation height; (2) *canopy density*—assessed based on vegetation area index (VAI); (3) *canopy arrangement*—assessed based on the clumping index (Ω), which describes internal canopy architecture; (4) *canopy cover*—assessed based on gap fraction (θ); and (5) *canopy complexity*—assessed based on canopy rugosity (R_C) and effective number of layers, which describe three-dimension variability in vegetation

Table 1. Characteristics of treatment plots in the Hubbard Brook Ice Storm Experiment.

Plot	Treatment	Treatment FWD (g)	AGB_2015 (Mg ha ⁻¹)	AGB_2021 (Mg ha ⁻¹)	ANPP (kg ha ⁻¹ year ⁻¹)	ΔANPP (kg ha ⁻¹ year ⁻¹)	ANPPrt	ANPPst	ANPPrv	Annual mortality (%)	ΔRugosity	ΔOpenness
1	Double	839.9	188.6	198.5	5297.2	25.8	0.45	0.52	-0.13	0.93	7.6	6.8
2	Light	275.9	165.7	173.1	4872.2	65.5	0.40	0.51	-0.21	1.30	5.1	0.2
3	Moderate	673.7	243.3	223.5	6866.7	-234.0	1.63	0.23	0.13	3.44	10.0	46.1
4	Control	176.6	213.9	232.5	5407.8	234.7	0.63	0.43	-0.11	1.11	4.6	2.0
5	Heavy	537.3	189.7	187.5	4778.3	116.7	0.46	0.50	-0.23	1.71	15.2	12.2
6	Light	365.2	170.8	162.7	3403.9	-154.4	0.69	0.29	-0.57	2.38	3.5	18.2
7	Control	217.0	281.7	263.6	6642.2	-189.8	1.37	0.33	0.10	1.03	0.6	8.4
8	Double	831.0	268.6	286.1	6486.9	-118.2	1.55	0.29	0.07	1.59	10.7	33.6
9	Heavy	592.0	240.0	227.0	4287.2	-45.1	0.71	0.17	-0.34	2.52	12.2	31.4
10	Moderate	374.2	256.5	278.0	6198.6	51.6	1.00	0.09	0.03	0.93	8.7	3.3

Note: “Treatment FWD” refers to fine woody debris collected in litter traps during the treatment application. “AGB” is estimated aboveground biomass based on allometry. “NPP” is net primary productivity based on the biomass increment of surviving trees in each annual increment. “ANPPrt” is resistance, “ANPPst” is stability, “ANPPrv” is recovery, and “Annual mortality” is the average annual percent of stems that died. ANPP, aboveground net primary productivity.

arrangement. Details on derivation of these metrics can be found in Atkins et al. (2018a).

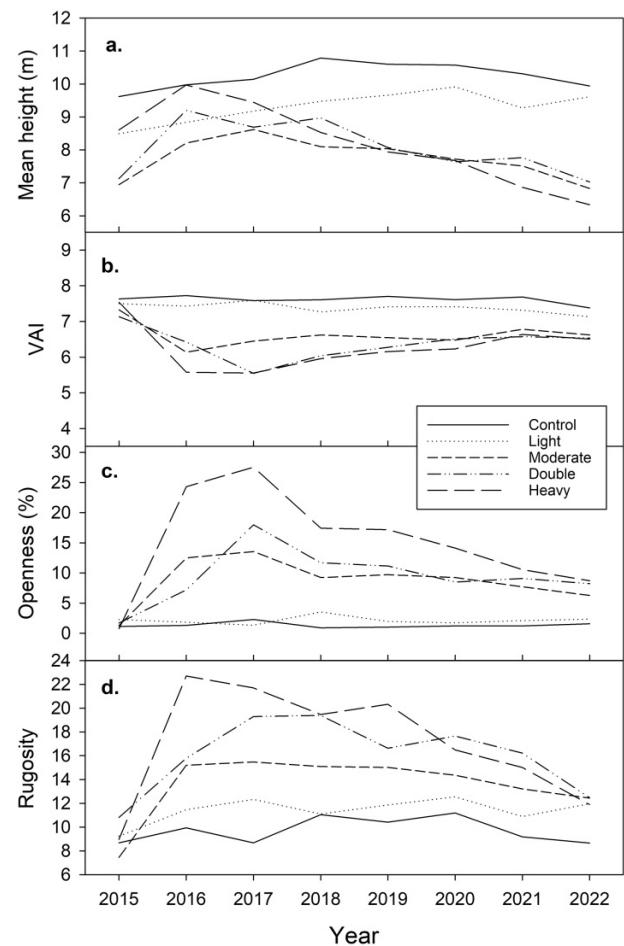
Species composition and aboveground biomass production

Trajectories in forest composition and AGB were assessed based on annual remeasurement of the ISE permanent plots and individually tagged trees ≥ 5 cm diameter at breast height (DBH) in these plots. For each tree DBH was measured in each year directly above the tree tag. Diameters were converted into estimates of AGB using allometries specifically developed for the Hubbard Brook Ecosystem Study (Rutherford and Battles 2024). AGB was calculated for each live tree in each year and summed as an estimate of total AGB at the plot level. For each annual interval in the census period biomass of mortality (of trees alive at the beginning of the census period, including ingrowth) and biomass production of surviving trees were estimated at the plot level. Changes in species composition were assessed based on trajectories of relative dominance assessed as the proportion of AGB at the plot level by species.

Data analysis

To assess trajectories in canopy structural metrics and forest biomass and productivity across the study period, we characterized the multidimensional stability of these factors in response to the disturbance based on the framework of Mathes et al. (2021) as described below. For canopy structural variables and AGB, we compared post-disturbance values to pre-disturbance conditions assessed in 2015. For above-ground NPP, we compared post-disturbance values in treated plots to control plots because we did not have multiple years of pre-disturbance stand measurements with which to calculate NPP. The disturbance response metrics (Mathes et al. 2021) that we calculated included: (1) *resistance* as the log response ratio of immediate post-disturbance (2016 for single treatments and 2017 for Double treatment plots) values relative to pre-disturbance condition (or control for NPP), (2) *stability* as the coefficient of variation across the study period (2015–2021), and (3) *recovery* as the log response ratio of post-disturbance values at the end of the study period relative to pre-disturbance conditions (or control for NPP). We compared stability metrics for each structural and productivity response variable among treatments using Analysis of variance using the *aov* function in R v. 4.4.2 (R Core Team 2024). For structural and biomass response variables, we conducted linear contrasts comparing treatments to Control values. For productivity and mortality responses, we conducted comparisons among the treatments and corrected for multiple comparisons using the Tukey–Kramer adjustment. To assess relationships among canopy structure, productivity and mortality responses, we evaluated individual pairwise relationships with linear models using the *glm* function in R v. 4.4.2 (R Core Team 2024). We did not attempt to use multivariate linear models to assess relationships between canopy structure metrics and productivity response because of high degrees of collinearity among the canopy structural variables.

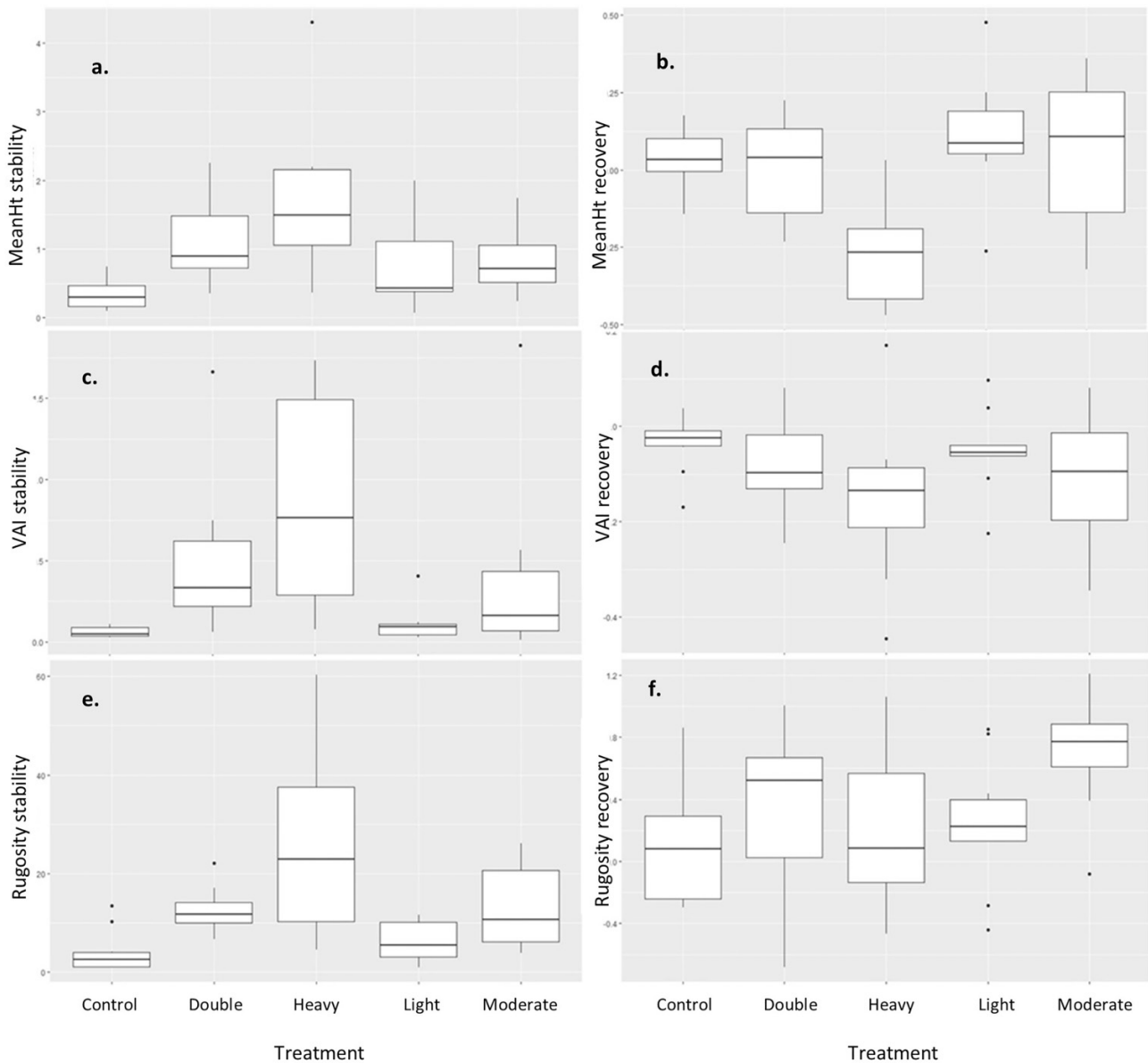
Fig. 1. Trajectories of canopy structural characteristics for pre-disturbance (2015) and 7 years post-disturbance based on terrestrial LiDAR data. Mean height is meters above ground level, vegetation area index (VAI) is meters of vegetation per unit ground area, openness is percent of ground area.



Results

There were differences in structural trajectories among the treatments that generally aligned with disturbance severity as defined by the treatments (Fig. 1). For each structural metric studied, the Light treatment was most similar to the Control throughout the study period and the more intense treatments had greater differentiation that decreased over the study period but was maintained throughout. All of the structural parameters had strong treatment-related responses, and generally did not return entirely to pre-disturbance levels by the end of the monitoring period (Fig. 1). Mean vegetation height initially increased slightly in the moderate and high treatments, which may have been associated with subcanopy damage. However, there was a subsequent subcanopy response that led to reductions in mean vegetation height and increasing differentiation from the Control across the study period (Fig. 1a). In contrast, the other structural parameters showed very strong initial impacts from treatment, but consistently became less differentiated from the Control over the study period. Canopy density and cover were reduced

Fig. 2. Box plots illustrating stability (coefficient of variation) and recovery (log response ratio of pre- vs. post-disturbance values) for three canopy structural metrics by treatment over the 2015–2022 study period in the ice storm experiment plots. (a) Mean canopy height stability, (b) mean canopy height recovery, (c) vegetation area index (VAI) stability, (d) VAI recovery, (e) canopy rugosity stability, and (f) canopy rugosity recovery.



by the treatments, as VAI declined and Canopy Openness increased, especially in the more intense treatments (Fig. 1c). At the same time, canopy complexity (as Canopy Rugosity) was strongly increased by treatment, and this difference was maintained to some degree throughout the study period (Fig. 1d). There were significant differences among the treatments in stability for all of the structural metrics, but recovery only differed among treatments for mean vegetation height and canopy rugosity (Table 1; Fig. 2).

Trajectories of AGB did not differ substantially among treatments and there was no consistent pattern of aboveground net primary productivity (ANPP) variation across the study period (Fig. 3). Change in AGB and total ANPP did not differ among treatments and there were a variety of responses in change in ANPP, with individual plots showing both pos-

itive and negative responses (Table 1). Trajectories in these factors did not appear to follow a resilience-response trajectory (Fig. 3). Resistance, stability, and response for both AGB and ANPP varied substantially among plots but did not differ consistently among treatments or relative to the control (Table 1). There were minimal changes in species composition over the course of the study period, with only minor shifts in relative biomass dominance (Fig. 4).

There was no mortality response associated with the treatments as neither total biomass mortality nor annual mortality rate differed among the treatments (Table 1). There was no pulse of mortality following the treatment, instead a large pulse of mortality occurred in 2018, but was actually most pronounced in the Control (Fig. 5). The common species with the highest mortality rates were red spruce and American

Fig. 3. Trajectories of aboveground biomass and aboveground net primary productivity (ANPP) estimated based on allometric equations converting tree diameter at breast height to biomass.

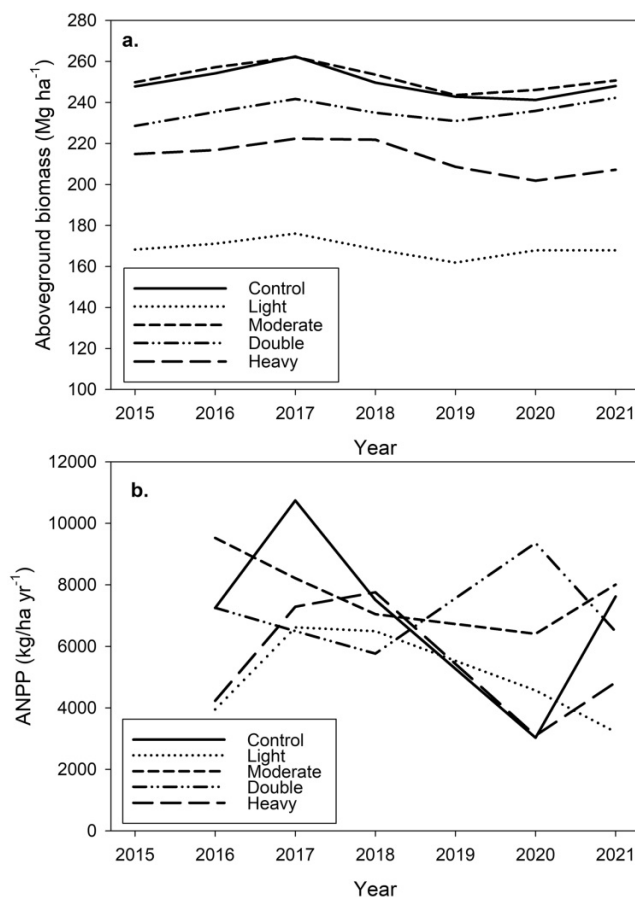


Fig. 4. Trajectories of species composition across all ice storm experiment plots based on relative biomass (percent of total biomass), mortality patterns did not differ among treatments (see Table 1). ABBA = *Abies balsamea*, ACPE = *Acer pensylvanicum*, ACRU = *Acer rubrum*, ACSA = *Acer saccharum*, BEAL = *Betula alleghaniensis*, BEPA = *Betula papyrifera*, FAGR = *Fagus grandifolia*, FRAM = *Fraxinus americana*, PIRU = *Picea rubens*, POGR = *Populus grandidentata*.

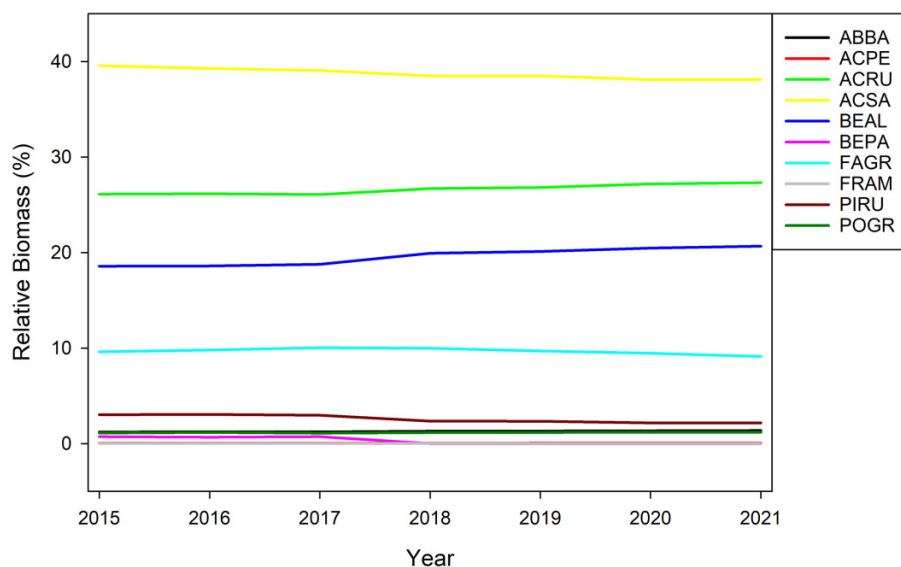
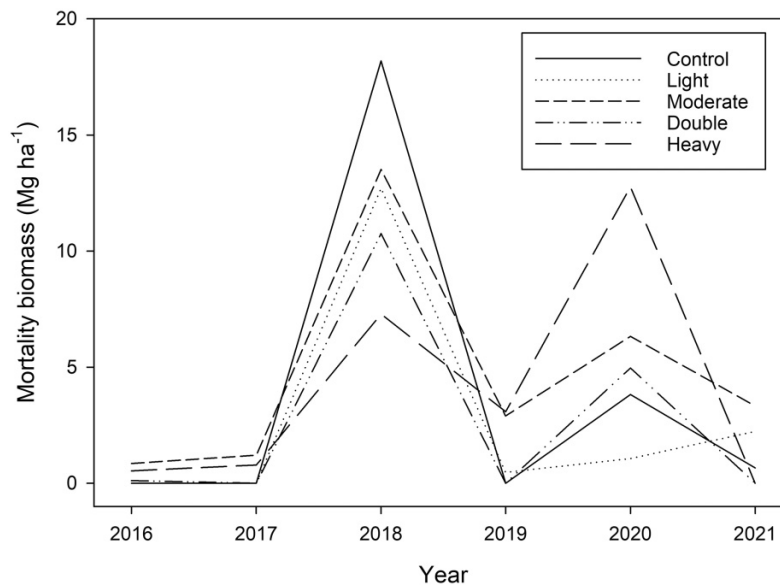


Fig. 5. Trajectories of mortality based on estimated aboveground biomass of trees that died in each year during the study period following the ice storm experiment treatment in winter 2015.



beech (Table 2), but these differences did not affect relative dominance among the species that made up the community (Fig. 5).

The only significant relationship between change in AGB and structural response variables were significant relationships between VAI and gap fraction recovery and Δ AGB ($R^2 = 0.41$, $p = 0.047$; $R^2 = 0.46$, $p = 0.032$, respectively), where plots that had greater increase in AGB were those that recovered more in canopy density and closure (Fig. 6). For stability of ANPP, the only significant relationship was with recovery in Canopy Rugosity ($R^2 = 0.43$, $p = 0.039$), where plots that had higher ending R_c relative to their starting point had greater productivity stability (Fig. 6).

Discussion

Structural trajectories and legacies

Structural legacies of disturbance are an important driver of ecosystem stability and response to global change stressors such as climate change and invasive pests and pathogens (Johnstone et al. 2016). Understanding the magnitude and longevity of these legacies is essential to forecasting the outcomes of disturbance for ecosystem functioning (LaRue et al. 2023). In this study, we found that the structural outcomes of experimental ice storm disturbance were somewhat persistent over the 6–7-year period covered during this study. Canopy density and complexity were initially strongly altered by the disturbance and, although these differences decreased over time, these structural characteristics remained somewhat distinct from pre-disturbance and control conditions at the end of the study period. Differentiation of these canopy characteristics continued to be outside the range of pre-disturbance conditions for most of the studied factors, but absolute recovery only differed among the treatments for complexity and canopy height (Table 3). The time needed for

these structural features to fully recover following the disturbance is unknown and could depend on interaction with subsequent disturbance (Weeks et al. 2009), but based on our work, these signatures could persist for many years. The effect of these changes on ecosystem processes and resource distribution is hard to fully quantify, but the actual biological differences were not especially large for most of these structural features.

The one structural feature for which there was an especially substantial shift was mean vegetation height, which was significantly lower for the three more intense treatments than the control. This response trajectory for this feature of the canopy also differed from the other treatments in that it was delayed and appeared to be continuing to deviate from the Control at the end of the sampling period. The shift to a shorter, more bottom-heavy canopy has implications for ecosystem processes such as light capture, microclimatic conditions and related processes (e.g., relative humidity and evapotranspiration), and community processes such as tree regeneration and ground layer plant diversity (Ehbrecht et al. 2017; Atkins et al. 2018b). In addition, this shift is predominantly associated with response in the subcanopy and formation of a dense understory American beech layer (Weeks et al. 2009), which will likely be susceptible to the effects of Beech Leaf Disease (Ewing et al. 2019) as well as stress associated with increasing drought severity and frequency expected with climate change (Mathes et al. 2024). The susceptibility of this layer to these looming threats could lead to future disturbance and could be a case where the legacy of the original disturbance affects the probability and potential severity of impacts from a future disturbance (Buma 2015).

Canopy complexity and structural change as a legacy of disturbance can be affected by severity and generally have a nonlinear relationship across the broad spectrum of severity, peaking at moderate levels of severity (Haber et al. 2020). This

Table 2. Species composition and mortality based on total aboveground biomass (AGB) and biomass mortality across all plots in the ice storm experiment.

Species	Live AGB (Mg ha ⁻¹)	Mortality AGB (Mg ha ⁻¹)	% Mortality
<i>Abies balsamea</i>	2.7	<0.1	0.3
<i>Acer pensylvanicum</i>	0.1	0.0	0.0
<i>Acer rubrum</i>	55.6	2.4	4.1
<i>Acer saccharum</i>	79.1	8.9	10.1
<i>Betula alleghaniensis</i>	40.8	0.5	1.2
<i>Betula papyrifera</i>	1.6	1.6	50.0
<i>Fagus grandifolia</i>	15.5	5.8	27.4
<i>Fraxinus americana</i>	<0.1	0.0	0.0
<i>Picea rubens</i>	4.4	2.3	34.3
<i>Populus grandidentata</i>	2.4	0.0	0.0

study focused on low–moderate severity disturbance where there was very low stem mortality and biomass removal, but significant reductions in leaf area (Fig. 1; Rustad et al. 2020). These low–moderate severity treatments promoted canopy complexity, matching results of prior work on the subject (Fahey et al. 2015; Meigs et al. 2017). Across the limited spectrum of severity reflected in these treatments, changes in canopy structure were more pronounced and persistent at the higher (but still low–moderate) levels of disturbance (Figs. 1 and 2).

Ice storms largely result in partial crown and branch loss and bending of trees under ice loads, which can predispose trees to future mortality associated with stressors such as drought or pests (Smith 2000; Kraemer and Nyland 2010). These features of ice storms may have affected the structural trajectories evident in this study, which were somewhat transient in the case of canopy density, but more persistent for canopy height (Fig. 1). These differences also likely account for differences in structural impacts and trajectories relative to other moderate severity disturbances such as wind or vascular disruption that lead to substantial direct tree mortality (Fahey et al. 2015; Meigs and Keeton 2018). In addition, the top-down and horizontally dispersed effects of ice storm disturbance may have a distinct structural signature and legacy relative to more bottom-up or patchy disturbance mechanisms (Atkins et al. 2020).

Biomass, mortality, and compositional change

Moderate severity disturbances often produce shifts in forest AGB and can stimulate net primary productivity (Fahey et al. 2019a; Gough et al. 2021a). In this study, we found that experimental ice storm disturbance led to very limited changes in AGB and net primary productivity, and no substantial variation in the responses with differing disturbance treatment severity (Fig. 3). This finding is likely associated with the relatively limited mortality associated with the treatments and the lack of differences among treatments in mortality rates (Table 1). Other results at ISE indicate that differences in radial growth were more evident when tree-specific crown damage rather than plot treatment levels were considered (Schaberg et al. 2024). With this approach, it was

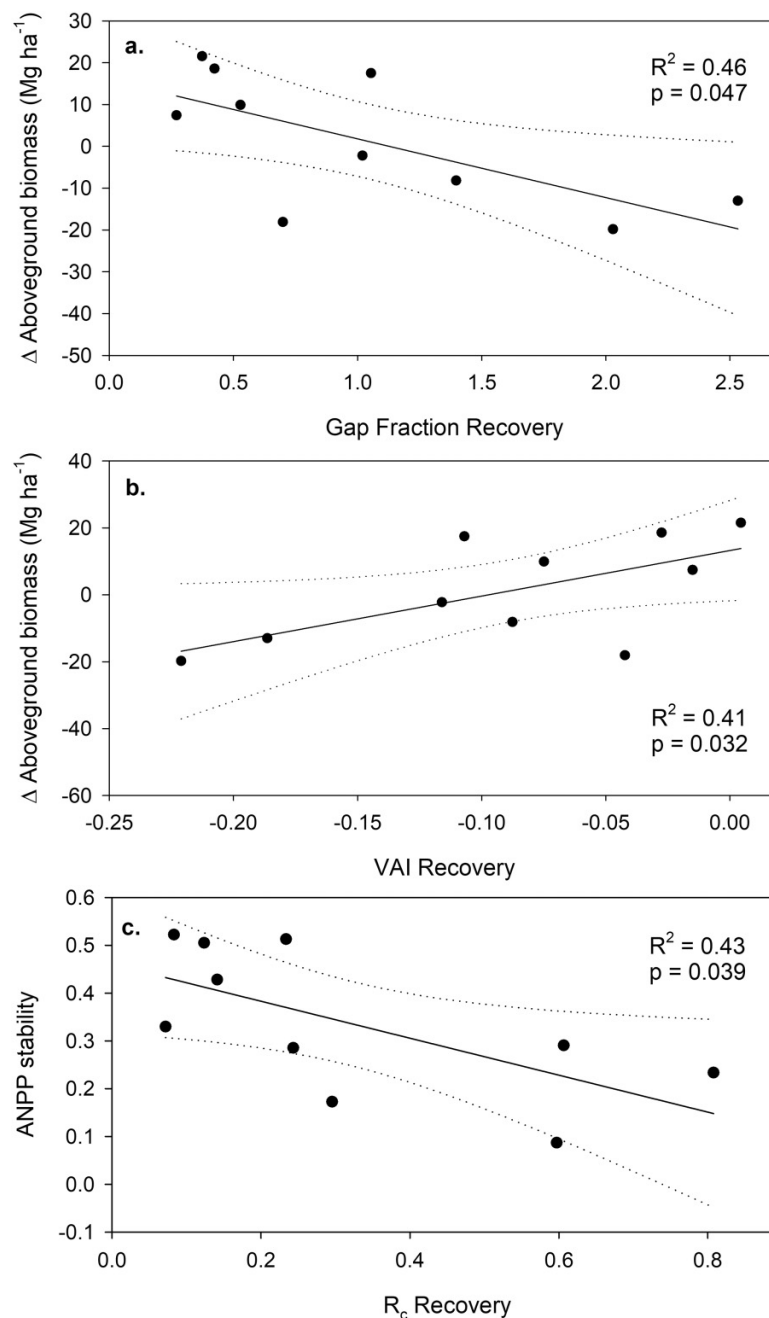
found that red maples with moderate (<50%) and high (≥50%) damage showed gradually declining growth over 4 years post treatment, whereas sugar maples with high damage showed ~80% reduction in growth the first year after injury (Schaberg et al. 2024). Although the ice storm disturbance resulted in substantial reductions in canopy density, this effect did not appear to be related to the loss of trees to mortality. There was a pulse of mortality in 2018, but this was also apparent in the Control and may have been associated with drought rather than the icing treatments. The reductions in canopy density may have been more related to crown damage and individual branch loss. This effect likely limited the potential for redistribution of limiting resources other than light (Fotis et al. 2018), restricting the stimulation of productivity illustrated in other experimental disturbance studies (Gough et al. 2021b). The lack of a biomass response could also be related to allocational patterns, where resources are distributed to regrowth of canopy elements and away from radial stem growth (Nock et al. 2016), which was what was assessed here.

Forest community composition can also be strongly affected by some forms of moderate severity disturbance (Frelich and Reich 1999; Haber et al. 2020). However, neither tree species composition nor relative dominance were substantially altered by this experimental ice storm disturbance (Fig. 4). This outcome is likely associated with the relative low levels of mortality associated with the disturbance. The loss of branches and leaf area from the canopy would not be reflected as much in wood biomass as in species-level leaf area changes, which were not analyzed here. However, the relatively low species specificity of ice storms also probably limited the potential for compositional shifts (Ireland 2000; Duguay et al. 2001). In addition, the overstory-focused data analyzed here may have masked some changes in the seedling and sapling layer that could have important implications for future composition, but are not reflected in biomass dominance.

Conclusion

An improved understanding of potential trajectories of structure and function following disturbance and the

Fig. 6. Relationships between change in aboveground biomass and (a) recovery in canopy gap fraction and (b) recovery in canopy vegetation area index (VAI) and (c) stability in aboveground net primary productivity (ANPP) in relation to recovery in canopy rugosity based on results of generalized linear modeling.



magnitude and longevity of disturbance legacies could be highly valuable for forecasting the outcomes and consequences of changing disturbance regimes (Turner and Seidl 2023). Our findings indicate some degree of persistent structural legacies associated with ice storm disturbance, but also showed that the strength of these legacies somewhat declined over time (Weeks et al. 2009). The degradation of structural legacies over time may affect their interaction with subsequent disturbance or stressors, and information on these trajectories could help with prediction of the consequences of interacting disturbances (Buma 2015). Although these tra-

jectories are likely to be highly site and forest type specific (Foster et al. 1998), the experimental aspect of this study allows for assessment of structural and functional outcomes and patterns while controlling for characteristics of the initiating disturbance (e.g., severity). Continued monitoring of these experimental plots could allow for assessment of the effects of global change stressors and novel disturbances on structure and function in this system. In addition, more observational, experimental, and modeling research is needed to evaluate the potential generality of the patterns and relationships illustrated in this study.

Table 3. Results of Analysis of variance comparing stability and recovery of structural characteristics among treatments.

Variable	Stability		Recovery	
	$F_{[4,45]}$	p	$F_{[4,45]}$	p
Mean vegetation height	5.40	<0.01	7.68	<0.01
Mean outer canopy height	6.65	<0.01	1.94	0.12
Vegetation area index	5.46	<0.01	1.63	0.18
Gap fraction	5.04	<0.01	1.15	0.35
Clumping index	2.71	0.04	0.96	0.44
Effective number of layers	9.16	<0.01	0.90	0.48
Canopy rugosity	7.64	<0.01	2.81	0.04

Significant p -values at $p < 0.05$ indicated in bold.

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This paper is part of a collection celebrating Tim Fahey’s career and contributions to forest ecology.

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Data availability

Data generated or analyzed during this study are available in the Hubbard Brook Data Repository, <https://hubbardbrook.org/data-catalog/>. Canopy structure data: Fahey, R.T. 2021. Ice storm experiment (ISE) canopy structure data, 2015–present ver 1. Environmental data initiative. <https://doi.org/10.6073/pasta/834eb91736ed5f4a5e080494622354a3> (accessed 14 February 2025). Plot inventory data: Rustad, L. and

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Competing interests

The authors declare there are no competing interests.

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