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Effects of an experimental ice storm on forest canopy structure

Robert T. Fahey, Jeff W. Atkins, John L. Campbell, Lindsey E. Rustad, Meghan Duffy, Charles T. Driscoll, Timothy J. Fahey, and Paul G. Schaberg

Abstract: Intermediate disturbances are an important component of many forest disturbance regimes, with effects on canopy structure and related functions that are highly dependent on the nature and intensity of the perturbation. Ice storms are an important disturbance mechanism in temperate forests that often result in moderate-severity, diffuse canopy damage. However, it has not previously been possible to distinguish the specific effect of ice storm intensity (as ice accretion) from predisturbance stand characteristics and physiographic factors. In this study, we utilized a novel experimental ice storm treatment to evaluate the effects of variable ice accretion levels on forest canopy structure. Our results verified significant impacts of ice storm disturbance on near-term canopy structural reorganization. Canopy openness, light transmission, and complexity increased significantly relative to predisturbance baselines and undisturbed controls. We documented variable impacts with disturbance intensity, as significant canopy changes largely occurred with ice accretion levels of ≥12.7 mm. Repeated ice storm disturbance (two consecutive years) had marginal, rather than compounding, effects on forest canopy structure. Our findings are relevant to understanding how ice storms can affect near-term forest canopy structural reorganization and ecosystem processes and add to a growing base of knowledge on the effects of intermediate disturbances on canopy structure.

Key words: intermediate disturbance, canopy structure, complexity, ecosystem function.

Résumé : Les perturbations intermédiaires sont une composante importante de plusieurs régimes de perturbation des forêts qui ont des effets sur la structure du couvert forestier et les fonctions qui y sont reliées lesquels dépendent fortement de la nature et de l'intensité de la perturbation. Les tempêtes de verglas qui causent des dommages diffus et modérément sévères dans le couvert forestier constituent un mécanisme important de perturbation dans les forêts tempérées. Cependant, il n'a pas précédemment été possible de distinguer l'effet spécifique de l'intensité d'une tempête de verglas (sous forme d'accumulation de glace) des facteurs physiographiques et des caractéristiques du peuplement avant d'être perturbé. Dans cette étude, nous avons utilisé un nouveau traitement expérimental qui reproduit une tempête de verglas pour évaluer les effets de différents niveaux d'accumulation de verglas sur la structure du couvert forestier. Nos résultats ont permis de constater les impacts importants de la perturbation due à une tempête de verglas sur la réorganisation structurale à court terme du couvert forestier. L'ouverture, la transmission de la lumière et la complexité du couvert forestier ont significativement augmenté par rapport à la situation antérieure à la perturbation et aux témoins non perturbés. Nous avons observé des impacts variables selon l'intensité de la perturbation alors que des changements importants dans le couvert forestier sont surtout survenus avec des niveaux d'accumulation de verglas ≥ 12,7 mm. Des perturbations répétées (deux années consécutives) dues à une tempête de verglas ont eu des effets marginaux plutôt que conjugués sur la structure du couvert forestier. Nos résultats sont pertinents pour comprendre de quelle façon les tempêtes de verglas peuvent avoir un impact à court terme sur la réorganisation structurale du couvert forestier et altérer les processus de l'écosystème. Ils contribuent au développement de la base de connaissances sur la structure du couvert forestier. [Traduit par la Rédaction]

Mots-clés : perturbation intermédiaire, structure du couvert forestier, complexité, fonction de l'écosystème.

Introduction

Moderate-severity disturbances are an important driver of ecosystem functioning, structural development, and successional change in forest ecosystems (Frelich 2002; Cohen et al. 2016). Disturbances that result in damage to the existing vegetation community can strongly affect canopy structure and related patterns of light transmission and absorption, microclimate, and competitive interactions among individuals or cohorts (Hanson and Lorimer 2007; Gough et al. 2013; Fahey et al. 2016). Very high- and low-severity disturbances (i.e., stand-replacing events and gap-phase disturbance regimes) can result in simplification of stand structure and composition (Foster et al. 1998; Reyes et al. 2010; Halpin and Lorimer 2016). In contrast, intermediate-severity dis-

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R.T. Fahey. Department of Natural Resources and the Environment, University of Connecticut, Storrs, CT 06269-4087, USA; Center for Environmental Science and Engineering, University of Connecticut, Storrs, CT 06269-4210, USA.
J.W. Atkins. Department of Biology, Virginia Commonwealth University, Richmond, VA 23284-2012, USA.
J.L. Campbell and L.E. Rustad. USDA Forest Service, Northern Research Station, Durham, NH 03824, USA.
M. Duffy. Colgate University, Hamilton, NY 13346, USA.
C.T. Driscoll. Department of Civil and Environmental Engineering, Syracuse University, Syracuse, NY 13244, USA.
T.J. Fahey.* Department of Natural Resources, Cornell University, Ithaca, NY 14853, USA.
P.G. Schaberg. USDA Forest Service, Northern Research Station, Burlington, VT 05403, USA.
Corresponding author: Robert T. Fahey (email: robert.fahey@uconn.edu).

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turbances frequently increase the structural and functional complexity of forests (Woods 2004; Fahey et al. 2015; Stuart-Haëntjens et al. 2015; Halpin and Lorimer 2016). Structural complexity is increased through incorporation of horizontal patchiness and vertical differentiation. Structural reorganization is often associated with heterogeneity in resource environments and population processes (e.g., regeneration) that can lead to increases in the diversity of species and functional group composition (Cooper-Ellis et al. 1999; Fahey et al. 2016) and also strongly affect ecosystem functioning (Amiro et al. 2010; Nave et al. 2011; Flower and Gonzalez-Meler 2015; Gough et al. 2016). For example, light transmittance and light-use efficiency of the canopy can be impacted by disturbance, with implications for forest productivity (Stuart-Haëntjens et al. 2015).

The effects of intermediate disturbance on canopy structure and related functions are highly dependent on the causal agent of disturbance, the severity of disturbance, and the characteristics of the forest prior to disturbance (Peterson 2007; Reyes and Kneeshaw 2008; Reyes et al. 2010; Fahey et al. 2015; Stuart-Haëntjens et al. 2015; Gough et al. 2016). Characteristics of the underlying disturbance mechanism — in terms of agent, intensity, and timing — can have substantial effects on forest structural outcomes. For example, fire and windstorm disturbances have, for the most part, inherently different directionality, with fire largely having bottom-up impacts and wind having top-down impacts (Stephens et al. 2009; Mitchell 2013). In addition, for most disturbance agents, the intensity and timing of the disturbance also affects impacts on canopy structure. For example, high-intensity wind and fire both lead to mortality across a broader range of size classes, lessening the differences in directionality and creating more homogenous impacts on structure (Turner and Romme 1994; Peterson 2000). In addition, the composition and structure of the forest at the time of the disturbance interacts with causal agent and intensity to affect severity and structural impacts. For example, wind disturbance has less of an impact on young forests with low-complexity canopies across a wide range of wind intensities (Woods 2004; Peterson 2007).

Ice storms are a common source of intermediate disturbance in forests for which a large body of research exists, with much of it focused on (or motivated by) the intense ice storm event that affected southeastern Canada and the northeastern United States (USA) in 1998 (Irland 2000; Gyakum and Roebber 2001). Ice storms can have variable effects on forest structure and dynamics, resulting largely from differences in storm intensity (i.e., ice thickness and duration), as the directionality of the disturbance is largely fixed (Duguay et al. 2001; Rhoads et al. 2002; Arii and Lechowicz 2007). Ice storm intensity is associated with total ice accretion and the interactive effects of topography, microclimate, and weather conditions (e.g., wind and temperatures) during and immediately after the storm (Irland 2000; Millward and Kraft 2004; Kraemer and Nyland 2010; Nagel et al. 2016). However, the ultimate severity and structural impact of the ice disturbance can also be affected by characteristics of the predisturbance trees and forest (Jones et al. 2001; Turcotte et al. 2012; Nock et al. 2016). For example, successional stage or age of the forest has been shown to strongly affect damage from equivalent ice loading (Rhoads et al. 2002), and species composition is also likely to affect impacts (Jones et al. 2001; Kraemer and Nyland 2010). There have been many assessments of forest structure and canopy conditions after ice storms (Duguay et al. 2001; Rhoads et al. 2002; Takahashi et al. 2007; Weeks et al. 2009), including a few studies that opportunistically collected data after ice storms from existing plots with predisturbance canopy structure data (Arii and Lechowicz 2007; Beaudet et al. 2007). However, it has not previously been possible to separate the specific effect of ice loading intensity from that of predisturbance forest composition and structure (Rustad and Campbell 2012).

We evaluated the near-term impact of a novel experimental ice storm disturbance on forest canopy structure and assessed the specific effects of variable disturbance intensity and repeated disturbance on canopy structure. We addressed the following specific research questions.

(*i*) How does ice storm damage affect canopy leaf area, density, complexity in arrangement of canopy elements, and light transmission?

(*ii*) How do increasing ice storm disturbance intensity and repeated disturbance affect near-term reorganization of canopy structure?

Our findings are relevant to understanding how ice storms can affect forest canopy structure and processes and add to a growing base of knowledge on the effects of intermediate disturbance on forest structure and functioning.

Methods

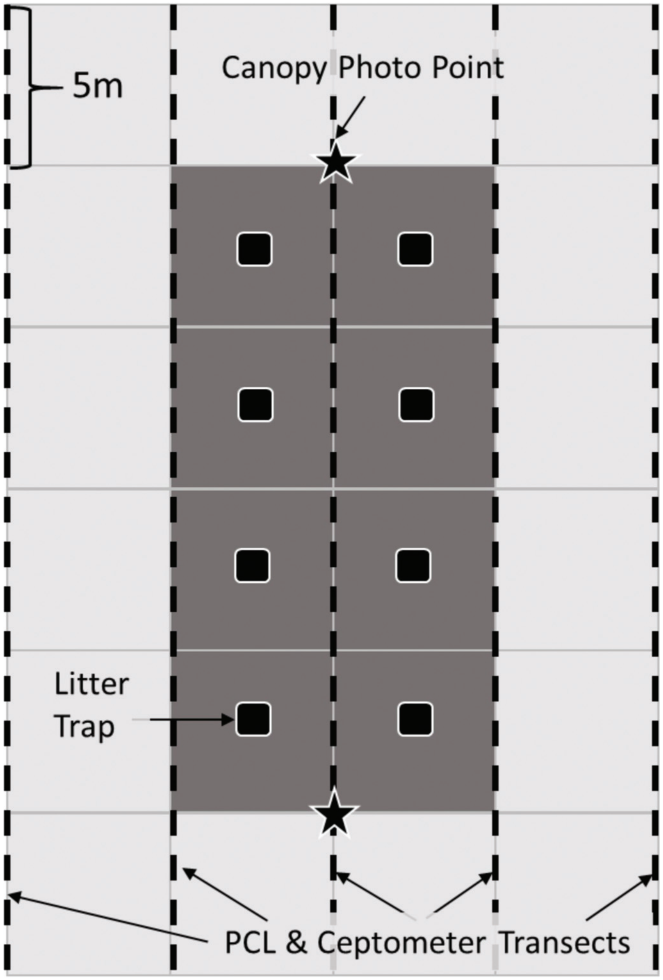
Study site and experimental design

The study was conducted within the Hubbard Brook Ice Storm Experiment (ISE), which was initiated in 2015 at the Hubbard Brook Experimental Forest (HBEF) in New Hampshire, USA. The HBEF is a ~3200 ha northern hardwood forest situated in the southern part of the White Mountain National Forest (43°56′N, 71°45′W). The 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. The 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 was established in a mixed-hardwood stand aged 70–100 years dominated by American beech (*Fagus grandifolia* Ehrh.), sugar maple (*Acer saccharum* Marsh.), red maple (*Acer rubrum* L.), and yellow birch (*Betula alleghaniensis* Britton). Ten 20 m × 30 m plots were established in summer 2015, and pretreatment measurements were initiated. Two plots were randomly assigned to each of five treatments with variable ice intensity targets and frequency: (*i*) Control, no experimental icing applied (i.e., 0 mm); (*ii*) Low, 6.4 mm of ice in year 1 only; (*iii*) Mid, 12.7 mm of ice in year 1 only; (*iv*) Midx2, 12.7 mm of ice in years 1 and 2; and (*v*) High, 19.0 mm of ice in year 1 only. The targeted amounts of ice accretion were chosen to be relevant to the National Weather Service Ice Storm Warnings in northeastern USA, which occur at 6.4 mm (0.25 inches) in the mid-Atlantic region and 12.7 mm (0.5 inches) in New York and New England.

Ice treatments were implemented during subfreezing conditions in 2016 (year 1; across five different dates: 18 January, 27–29 January, and 2 February) and 2017 (year 2; on 14 January). Ice addition targeted the entire 20 m × 30 m plot, but biogeochemical measurements were restricted to the inner 10 m × 20 m, leaving a 5 m buffer (Fig. 1). Ice accretion was quantified using caliper measurements on wooden dowel "ornaments" suspended in the canopy (Rustad and Campbell 2012). Accretion levels differed significantly among treatments and were qualitatively close to those targeted (generally within 2 mm, except for the High treatment, which was within 5 mm; L. Rustad, unpublished data); thus, the treatment designations were 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 referred to as FWD) was collected in plastic baskets (52 cm length × 37 cm width × 27 cm height) that were placed in the center of each of the eight interior subplots (5 m × 5 m) in both treatment and control plots (Fig. 1). Litter collections used to estimate treatment

Fig. 1. Map of nested plot layout indicating locations of measurements of canopy structural variables. The entire plot received the ice treatment, but intensive sampling of biogeochemical response variables was limited to the interior 10 m × 20 m of subplots. PCL, portable canopy light detection and ranging (LiDAR).



disturbance severity were made in each winter (approximately 2–3 weeks after icing treatments) and at the end of summer. In addition, litter was collected in early November following leaf fall and used to estimate leaf area index (see the following section). In instances where fallen branches lay on the litter baskets, twigs < 2 cm were clipped around the perimeter of the basket and included as part of the sample. After sorting and subsampling for leaf area (see the following section), litter was oven-dried at 60 °C for 48 h (or until constant mass) and weighed to estimated total mass of FWD.

Measurement and quantification of canopy structure and light transmission

We quantified canopy structure and light transmission in each plot before and following ISE treatments using a variety of methods and metrics. We placed particular emphasis on four response variables that describe different aspects of canopy structure: leaf area index (LAI), gap light index (GLI; Canham 1988), canopy rugosity (Rc; Hardiman et al. 2011), and the fraction of photosynthetically active radiation (PAR) absorbed by the canopy (fPAR; Atkins et al. 2018*b*). Specific methods used to collect data and derive these metrics are detailed in this section. Unless indicated otherwise, all methods included sampling during summer or fall before the initial treatment in 2015, during summer or fall before the second treatment in 2016, and again during summer or fall of 2017 after all treatments were completed.

Plot-level LAI was quantified based on measurements of leaf litter mass for each species in each year: 2015 (pretreatment) and 2016 and 2017 (posttreatment). Leaf litter from each litter trap was sorted by species (American beech, sugar maple, red maple, and yellow birch). For each species and plot, a subsample of about 30 leaves was carefully collected and stored in leaf presses. The area of each individual leaf was measured to ±1 mm^2 on an LAI-2000 leaf area meter (LI-COR Biosciences, Lincoln, Nebr., USA). The subsamples of each species and plot were dried to constant mass at 60 °C and weighed to determine the ratio of area to dry mass. The ratio of plot-level area to mass was multiplied by the total leaf litter mass for each species in each litter trap in each plot and divided by trap collection area to estimate LAI. The standard errors for LAI in Table 1 represent within-plot variation among eight traps for the sum of the four species.

We used hemispherical canopy imaging to estimate canopy openness, optically derived LAI, and modeled light transmittance. Images were collected in two locations in each plot (northern and southern edges of the "interior" plot; Fig. 1) at a height of 1.5 m above the ground. A north-facing, leveled Nikon D3200 camera (Nikon, Tokyo, Japan) outfitted with a 5.8 mm 180° circular fisheye lens was used to collect images under uniform, diffuse sky conditions. Images were analyzed with Gap Light Analyzer (Hardy et al. 2004) to quantify canopy openness, effective LAI between zenith angles 0°–60° (to minimize error from nearby canopies outside plots), and percent direct and diffuse transmitted radiation (based on modeled sun path throughout the growing season). The estimated percentage of total above-canopy radiation transmitted through the canopy was used to derive the GLI (Canham 1988).

fPAR to a height of 1 m was estimated using an AccuPAR LP-80 handheld ceptometer paired with an open-canopy (unobstructed by vegetation, also collected at a height of 1 m ~600 m away in a road-associated opening) PAR sensor and data logger (Decagon Devices, Pullman, Wash., USA). Below-canopy PAR (bPAR) at a height of 1 m was recorded every 2 m along three 20 m long transects running along the edges and central axis of the interior intensive plot (Fig. 1). Transect-level means of bPAR were then calculated from the mean of all values along each transect. Above-canopy PAR (aPAR) was estimated as the mean of all readings logged on the open-canopy PAR sensor during the time that the below-canopy readings were being collected (based on time stamps on both instruments). fPAR for each transect was calculated by dividing the difference between aPAR and bPAR by aPAR. Data on fPAR were collected only in 2017 on two dates (July and September); means and standard errors in Table 1 represent treatment-level averages of all transects and both sampling dates.

We quantified canopy arrangement and complexity using a ground-based, portable canopy light detection and ranging (LiDAR) system (Parker et al. 2004; Hardiman et al. 2011). Data were collected in each year (2015–2017) along five permanently marked 30 m transects per plot (Fig. 1). Raw portable canopy LiDAR (PCL) data were processed using the forestr package in R (Atkins et al. 2018*a*). In the forestr algorithm, PCL returns are binned into 1 m^2 bins, with light saturation corrections made based on LiDAR return density. A suite of canopy structure metrics is then calculated that describes a variety of canopy structure metrics focused on the density, distribution, and variance of LiDAR returns along the horizontal and vertical axes of the two-dimensional plane that transects the canopy (Hardiman et al. 2013; Atkins et al. 2018*a*). Many expressions of canopy structure can be derived from LiDAR. We utilized a set of 24 metrics that describe five different aspects of canopy structure (Atkins et al. 2018*a*): (*i*) height variables such as mean leaf height that describe the vertical height distribution of vegetation within a canopy; (*ii*) density variables such as vegetation area index (VAI) that summarize vegetation volume, area,

Table 1. Treatment-related fine woody debris (FWD) mass (an indicator of disturbance severity) and canopy structural metrics for all available combinations of treatments and year, including pretreatment (2015) and posttreatment (2016 and 2017) values.

	FWD (g)			LAI			GLI (%)			Rc (m)			fPAR
Treatment	2016	2017	Total	2015	2016	2017	2015	2016	2017	2015	2016	2017	2017
Control	186.2 (0.6)	207.4 (1.6)	393.6 (0.7)	5.8 (0.3)	4.6 (0.1)	5.1 (0.1)	3.8 (0.7)	3.4 (0.6)	3.1 (0.3)	8.6 (1.1)	9.5 (0.6)	8.7 (0.6)	0.963 (0.004)
Low	365.6 (2.0)	275.5 (1.9)	641.1 (1.4)	6.7 (0.1)	4.9 (0.1)	4.9 (0.5)	3.7 (0.5)	4.3 (0.4)	3.9 (0.8)	9.6 (1.1)	12.5 (0.8)	12.8 (0.6)	0.957 (0.008)
Mid	798.2 (4.9)	249.8 (1.5)	1048.0 (3.1)	4.9 (0.2)	3.7 (1.2)	4.2 (1.1)	4.5 (0.9)	11.6 (4.2)	8.4 (3.0)	7.1 (0.6)	13.0 (1.5)	13.4 (1.6)	0.940 (0.013)
Midx2	583.8 (2.5)	1087.1 (10.4)	1670.9 (4.6)	6.1 (0.1)	4.6 (0.1)	4.2 (0.1)	2.7 (0.6)	5.9 (0.5)	6.7 (0.9)	10.3 (1.8)	14.9 (1.0)	17.3 (1.5)	0.917 (0.009)
High	910.6 (6.0)	218.7 (1.5)	1129.3 (3.7)	5.5 (1.2)	3.2 (0.4)	3.4 (0.5)	4.3 (0.6)	12.9 (2.1)	13.4 (2.5)	10.1 (0.5)	20.5 (1.5)	19.4 (2.1)	0.899 (0.011)

Note: Values are means, with standards errors in parentheses. LAI, leaf area index; GLI, gap light index; Rc, canopy rugosity; fPAR, fraction of above-canopy photosynthetically active radiation intercepted by the canopy.

and density; (*iii*) arrangement variables such as clumping index (Ω) that describe internal canopy architecture; (*iv*) cover and openness variables such as gap fraction (θ) that indicate the extent and distribution of canopy gaps; and (*v*) variability variables such as Rc that describe vegetation arrangement and variability. In the analysis, we placed special emphasis on Rc because of evidence from previous studies that this metric is indicative of variation among canopies that can be related to intermediate disturbance (Fahey et al. 2015) and represents useful functional information (Atkins et al. 2018*b*; Gough et al. 2019). In addition to a univariate focus on Rc, we also utilized the full suite of LiDAR-derived canopy structural metrics as traits that describe multivariate characteristics of the forest canopy (Fahey et al. 2019).

Data analysis

We analyzed the influence of ice storm treatments using linear mixed-effects models, with models setup differently depending on the collection protocol for the data. We compared each of the primary canopy structure response variables (LAI, GLI, Rc, and fPAR) among treatments and in relation to treatment severity (based on FWD production). We analyzed treatment outcomes for posttreatment data (2017) for all four response variables. For this analysis, we conducted mixed-model analysis of variance (ANOVA) with plot and transect (for fPAR and Rc) or subplot (for LAI and GLI) as random effects nested within treatments. We also assessed treatment effects for response variables with yearly data (LAI, Rc, and GLI) using repeated measures mixed-effects ANOVA with plot and transect (for Rc) or subplot (for LAI and GLI) as random effects nested within treatments and unstructured variance for the repeated measurements on individual transects or subplots. All ANOVA analyses were conducted using PROC MIXED in SAS version 9.4 (SAS Institute, Cary, N.C., USA).

The effect of disturbance severity (as total FWD mass) on canopy structure was analyzed using simple linear regression. Plot-level means and proportional changes from pretreatment condition for LAI, GLI, and Rc in 2016 were regressed against treatment-related FWD mass (collected in spring and summer 2016 following the initial winter 2016 treatment). Plot-level means and proportional changes from pretreatment condition for 2017 were regressed against overall disturbance severity (as the sum of 2016 and 2017 treatment-related FWD mass) for all response variables (but only plot mean for fPAR). All simple regression analyses were conducted using PROC GLM in SAS version 9.4.

To assess relationships between different aspects of canopy structure and measured light transmittance after the treatments in 2017, we evaluated the relationship between fPAR and different canopy structure characterizations (GLI, Rc, and LAI). We used multiple regression in an information-theoretic model selection framework to identify the combination of canopy structure variables that most strongly predicted plot-level fPAR. Models incorporating all combinations of the three predictors were ranked based on Akaike's information criterion corrected for small sample size (AIC_c). Multiple regression modeling was conducted using PROC GLM.

Finally, to evaluate the effect of treatments on overall canopy structure as measured by the broad suite of metrics derived from the PCL using the forestr package, we utilized multivariate analysis methods. Ordination was conducted on a matrix of all 24 PCL-derived metrics (relativized to the maximum value for each metric to scale all metrics equivalently) using nonmetric multidimensional scaling (NMS) in PC-ORD version 5.31 (McCune and Mefford 2006) with Sorensen's distance measure and the "slow and thorough" autopilot setting, using 250 runs of real data and 250 Monte Carlo randomizations to assess the robustness of the solution. We tested for differences among treatments (blocked by year) in multivariate suites of complexity metrics using permutational multivariate analysis of variance (PERMANOVA) with Sorensen's distance measure in PC-ORD. To evaluate whether ice storm treatments had differential effects on multivariate canopy structure, we connected plots in the ordination space with transition vectors representing change in canopy structure through time and compared the length and direction of these vectors among treatments using multivariate analysis of variance (MANOVA; using PROC GLM).

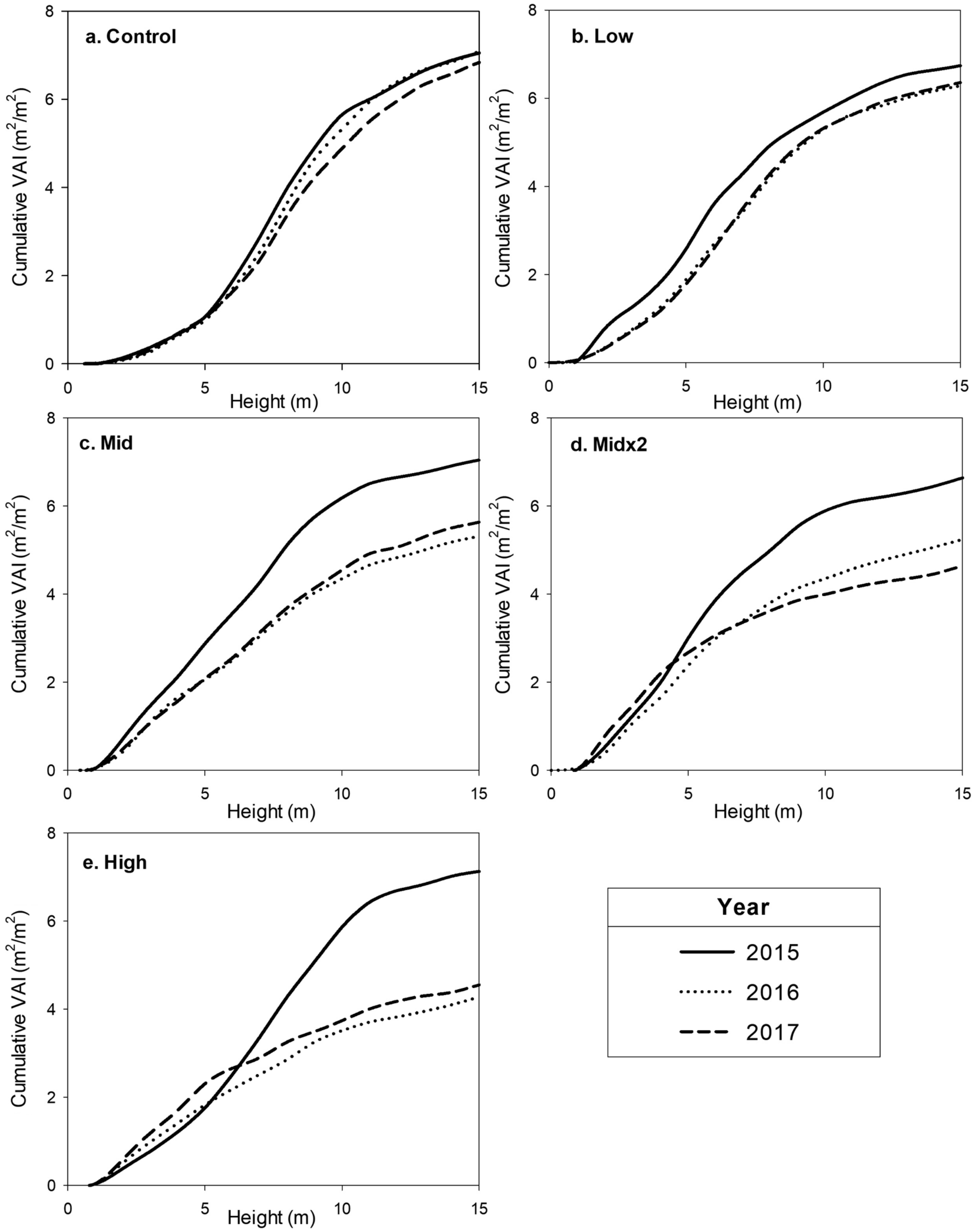
Results

FWD mass following ice application did not differ among treatments for 2016 alone (ANOVA, $F_{[4,5]} = 3.50$, $p = 0.100$) but did differ for a contrast of the control vs. treatment plots ($F_{[4,5]} = 7.13$, $p = 0.044$). FWD mass differed very strongly among treatments for 2016 and 2017 combined ($F_{[4,5]} = 11.76$, $p = 0.009$). The level of FWD mass produced by the treatments was strongly related to ice thickness targets (in millimetres) for the treatments (simple linear regression: 2016 FWD and ice addition, $R^2 = 0.68$; total (2016 and 2017) FWD and total ice addition, $R^2 = 0.87$). This finding indicates that ice treatment severity (as FWD produced) was strongly related to ice treatment intensity (as ice load applied). We therefore used FWD mass, in addition to treatment designations, as a predictor of canopy structural changes related to ice treatments.

Vertical profiles of VAI from terrestrial LiDAR illustrated shifts in vertical canopy structure in response to treatment. Cumulative VAI profiles were similar among years in the Control but showed substantial shifts in treatment plots following the ice storm (Fig. 2). In particular, a higher proportion of VAI was observed in the lower canopy in the ice treatments. In addition, the pattern of response to treatments differed with treatment intensity and timing. In the Low and Mid ice treatments, VAI accumulation with height decreased in a relatively uniform manner across the vertical canopy profile (Figs. 2*b* and 2*c*). The same was true of the initial (2016) ice application in the Midx2 treatment (Fig. 2*d*). However, in both the High treatment and following the second (2017) ice application in the Midx2 treatment, the accumulation rate of VAI was much greater in the lower part of the canopy (~0–5 m) compared with that of the pretreatment condition (Figs. 2*d* and 2*e*).

LAI estimated by litter traps differed strongly among years ($F_{[2,10]} = 37.87$, $p < 0.001$), and there was a significant interaction between treatment and year ($F_{[8,10]} = 5.07$, $p = 0.010$). LAI differed among years in the Low, Midx2, and High treatments (Fig. 3), with

Fig. 2. Cumulative vegetation area index (VAI) by height above the ground for each treatment across the 3 years as measured using terrestrial LiDAR (Atkins et al. 2018*a*).



pretreatment values (2015) differing significantly from both posttreatment values (2016 and 2017) in each case. Mean LAI in 2017 declined by 27% in the Low treatment, 31% in the Midx2 treatment, and 37% in the High treatment relative to pretreatment LAI values (Table 1). Annual variation in litter trap LAI was also observed in the Control (despite apparent constancy in total VAI; Fig. 2), but differences among years were not significant (Fig. 3). Litter trap LAI was strongly correlated with hemispherical photograph-based LAI estimates following treatments in 2016 and 2017 but not in the 2015 pretreatment analysis (see Supplementary data, Supplementary Fig. S1[1]). Total LAI and LAI change relative to pretreatment conditions were strongly significantly related to FWD mass in 2016, but only total LAI was related to FWD mass in 2017 (Table 2).

GLI differed significantly among years ($F_{[2,10]}$ = 15.57, p < 0.001) and treatments ($F_{[4,10]}$ = 3.64, p = 0.044), and there was also a strong interaction between treatment and year ($F_{[8,10]}$ = 3.97, p = 0.023). GLI differed among years for the Mid and High treatments (Fig. 4), with pretreatment values differing from immediate posttreatment values (2016) for the Mid treatment and both posttreatment values (2016 and 2017) for the High treatment. GLI increased

[1]Supplementary data are available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/cjfr-2019-0276.

Fig. 3. Leaf area index (LAI) as estimated from litter trap sampling across years and treatments. LAI differed among treatments and years based on analysis of variance (ANOVA) (treatment × year interaction: $F_{[8,10]} = 5.07$, $p = 0.010$). Letters above bars indicate significant differences among years for those treatments that illustrated a significant effect of year on LAI.

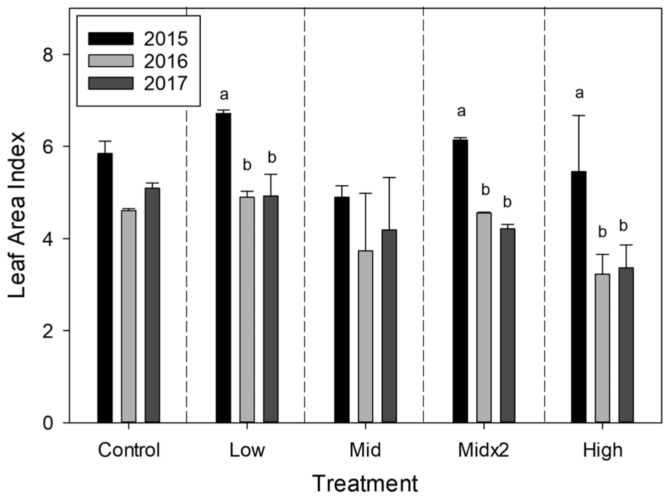


Table 2. Regression results relating canopy structural characteristics to disturbance severity (as fine woody debris (FWD) mass).

Variable	2016 R^2	2016 p	2017 R^2	2017 p
LAI	**0.76**	**0.001**	**0.43**	**0.040**
ΔLAI	**0.48**	**0.027**	0.36	0.069
GLI	**0.88**	**<0.001**	0.30	0.104
ΔGLI	**0.70**	**0.002**	**0.66**	**0.005**
Rc	**0.44**	**0.037**	0.39	0.056
ΔRc	**0.64**	**0.005**	0.33	0.083
fPAR	—	—	**0.60**	**0.009**

Note: Only 2016 data were used for comparison with 2016 canopy structure. The sum of 2016 and 2017 data was used for comparison with 2017 canopy structure. Boldface type indicates parameters or years that are statistically significant at $p \leq 0.05$. LAI, leaf area index; GLI, gap light index; Rc, canopy rugosity; fPAR, fraction of above-canopy photosynthetically active radiation intercepted by the canopy.

Fig. 4. Gap light index (GLI; Canham 1988) across years and treatments calculated as percentage of total above-canopy radiation transmitted through the canopy as estimated from hemispherical canopy photographs. GLI differed among treatments and years based on ANOVA (treatment × year interaction: $F_{[8,10]} = 3.97$, $p = 0.023$). Letters above bars indicate significant differences among years for those treatments that illustrated a significant effect of year on GLI.

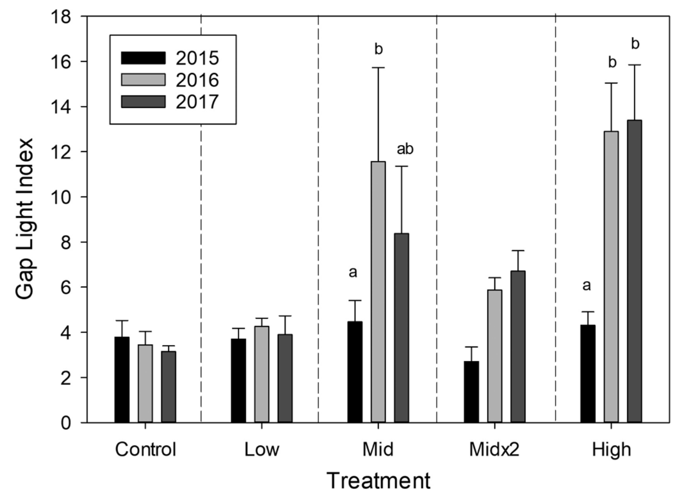
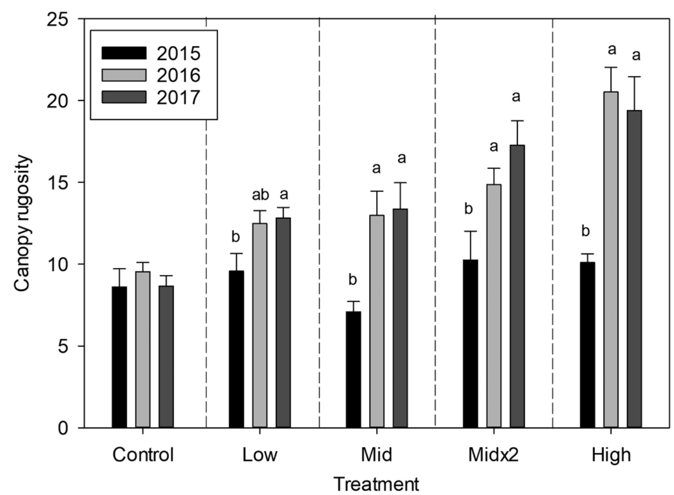


Fig. 5. Canopy rugosity (Rc) sampled using terrestrial LiDAR (Atkins et al. 2018*a*) across years and treatments. Rc differed among treatments and years based on ANOVA (treatment × year interaction: $F_{[8,10]} = 22.72$, $p < 0.001$). Letters above bars indicate significant differences among years for those treatments that illustrated a significant effect of year on Rc.



by >200% in 2017 relative to pretreatment values in the High treatment. GLI was very strongly related to FWD mass in 2016, and change in GLI relative to pretreatment was significantly related to FWD mass in both 2016 and 2017 (vs. total treatment-related FWD; Table 2).

Rc differed strongly among years ($F_{[2,10]} = 187.14$, $p < 0.001$) and treatments ($F_{[4,10]} = 10.45$, $p = 0.001$), and there was also a highly significant interaction between treatment and year ($F_{[8,10]} = 22.72$, $p < 0.001$). Rc differed among years for each of the treatments except Control, with increased complexity following disturbance for each level of treatment (Fig. 5). Following the initial ice treatment, Rc was ~100%, 80%, and 30% higher than predisturbance level in High ice accretion plots, Mid plots, and Low plots, respectively. The second ice treatment in Midx2 increased mean Rc by an additional 25%, but there was not a statistically significant difference between 2016 and 2017 in this (or any other) treatment. Both 2016 Rc and change in Rc from 2015 to 2016 were significantly related to 2016 FWD mass, but neither relationship was significant in 2017 (Table 2).

fPAR differed significantly among treatments in 2017 ($F_{[4,18]} = 6.40$, $p = 0.002$), with the High and Midx2 treatments exhibiting significantly greater light transmittance than the Control (Fig. 6). Light transmittance by the canopy in 2017 was strongly positively related to total FWD mass (2016 and 2017; Table 2). Multiple regression analysis illustrated that 2017 fPAR was most strongly predicted by a model that included both 2017 LAI and 2017 Rc, which very strongly explained variance in canopy light absorption ($R^2 = 0.89$; Table 3).

Multivariate analysis of canopy structural metrics illustrated substantial shifts in overall canopy structure that varied among treatments in directionality and magnitude (Fig. 7). The NMS ordination of multivariate canopy structure for the full data set had a two-dimensional solution and explained 97.5% of the variance in the original data matrix (Fig. 7). The first axis explained the majority of the variation in the data set (73.8%) and was strongly related to effective number of layers ($r = 0.926$), whereas the second axis explained 23.7% of the variance and was related to

Fig. 6. Posttreatment (2017) fraction of photosynthetically active radiation (PAR) absorbed by the canopy (fPAR) by treatment as estimated from ceptometer measurements. fPAR differed among treatments based on ANOVA results ($F_{[4,18]} = 6.40$, $p = 0.002$). Letters above bars indicate significant differences among treatments after adjustment for multiple comparisons.

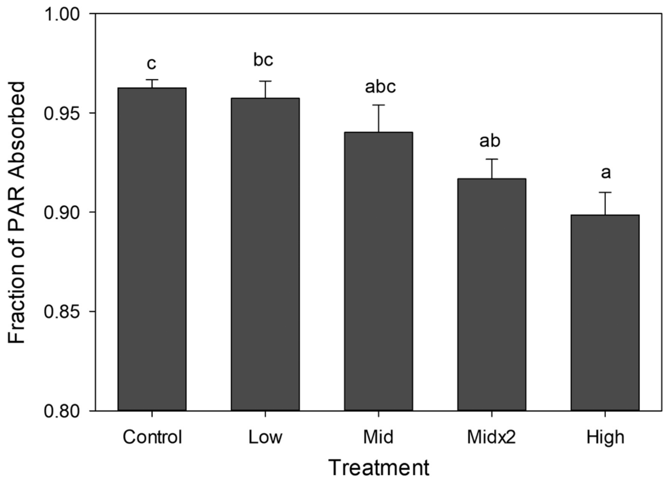


Table 3. Results of multiple regression model selection for predicting fraction of above-canopy photosynthetically active radiation intercepted by the canopy (fPAR) in 2017 based on canopy structural characteristics.

Model	*k*	AIC$_c$	Δ
LAI2017 Rc2017	4	−49.0	0.0000
LAI2017	3	−46.9	2.1414
GLI2017 Rc2017	4	−42.2	6.8506
GLI2017	3	−41.9	7.1415
LAI2017 GLI2017	4	−41.5	7.5483
LAI2017 GLI2017 Rc2017	5	−41.1	7.9605
Rc2017	3	−38.8	10.2227
Null	2	−37.0	12.0142

Note: LAI, leaf area index; Rc, canopy rugosity; GLI, gap light index; AIC$_c$, Akaike's information criterion corrected for small sample size; *k*, number of parameters in the model.

variance in mean canopy height ($r = 0.932$). In general, canopy complexity and height variance increased with treatment intensity, whereas vegetation density decreased with treatment intensity. Treatments differed significantly from each other in suites of canopy structure traits based on PERMANOVA in both 2016 ($F_{[4,45]} = 7.48$, $p < 0.001$) and 2017 ($F_{[4,45]} = 8.44$, $p < 0.001$), with significant pairwise differences for all comparisons except Control vs. Low, Control vs. Mid, and Low vs. Mid. There was a significant difference among treatments in the direction and magnitude of change in multivariate canopy structure in 2016 (Wilks' lambda: $F_{[8,8]} = 3.74$, $p = 0.04$), but not in 2017 (Wilks' lambda: $F_{[8,8]} = 1.34$, $p = 0.34$), based on analysis of change vectors using MANOVA.

Discussion

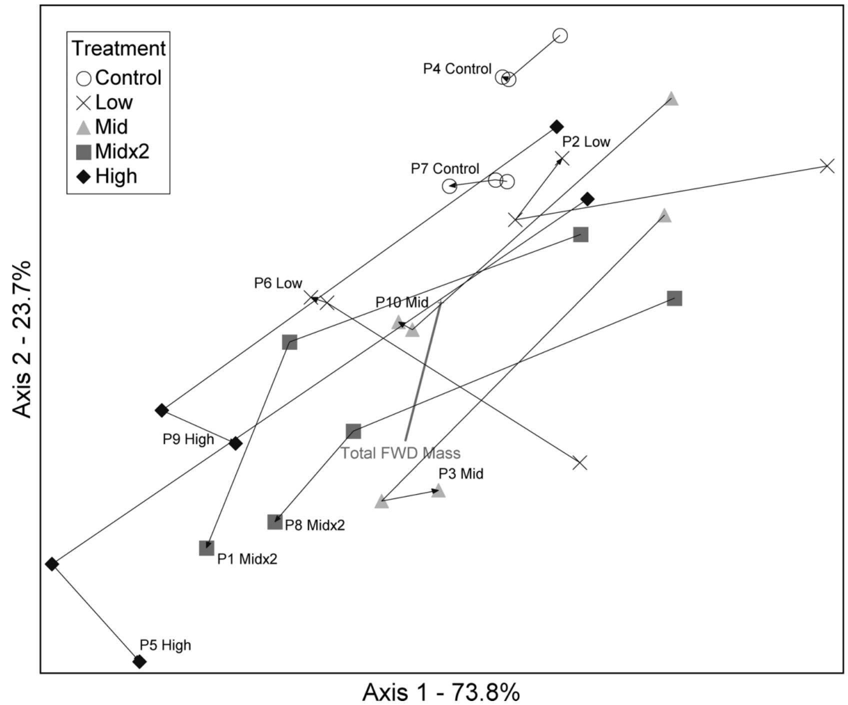
Intermediate disturbance is increasingly recognized as an important factor in temperate forest dynamics and is commonly used as the basis for ecological silviculture practices (Hanson and Lorimer 2007); however, the impact of intermediate disturbance on forest ecosystems is strongly related to the pattern and intensity of effects on canopy structure and processes that are mediated by the canopy (Gough et al. 2013). The ice storm disturbance analyzed here had a substantial effect on canopy structure and light interception that was largely aligned with expectations based on the characteristics of the disturbance and prior work on the topic (Irland 2000; Rhoads et al. 2002; Arii and Lechowicz 2007; Beaudet et al. 2007). However, our experimental results also illustrate the substantial variation that disturbance intensity (as ice accretion) and timing (single vs. repeat disturbance) can impart on canopy structural outcomes. The alteration of canopy structure in a broad, multitrait sense was also substantial and may represent disturbance-mediated shifts in generalized canopy structural type caused by ice storms (Fahey et al. 2019).

Ice storm disturbance directionality is generally characterized as top-down, with shifts in vegetation area to lower levels of the canopy (Weeks et al. 2009). Our results support such characterizations, with a relative shift in vegetation area from upper to lower levels of the canopy (Fig. 2). Our findings also indicate that the canopy vertical dislocation illustrated in prior studies is related to both immediate, within-season structural changes and long-term canopy architecture and subcanopy tree response to increased resource availability (Beaudet et al. 2007; Weeks et al. 2009). This immediate shift in vertical structure is likely related to the combination of physical dislocation of tree crowns through bending and breaking (Duguay et al. 2001), the response of existing buds and leaves to increased light availability (Fotis et al. 2018), and the removal of the upper canopy (leading to increased relative density in the lower canopy; Beaudet et al. 2007). The direct transfer of material among layers may be highly characteristic of (but not limited to) ice storms as a disturbance type and places this type of disturbance somewhat outside existing frameworks of disturbance impact (Roberts 2007). There was fine-scale horizontal variability in vertical canopy reorganization, which had the effect of increasing horizontal heterogeneity in canopy height and vertical layering within the canopy volume, despite decreased overall canopy height, which is often positively associated with these factors (Ehbrecht et al. 2016; Atkins et al. 2018*b*). Increased canopy vertical layering is important to many ecosystem functions, including photosynthesis, gas exchange, and wildlife habitat value (MacArthur and Horn 1969; Reich et al. 1990; Ellsworth and Reich 1993; Parker and Brown 2000; Lesak et al. 2011).

Although vertical canopy reorganization was an important component of the near-term response of canopy structure to ice storm disturbance, there were also substantial (and linked) shifts in overall leaf area, canopy openness, and horizontal heterogeneity in canopy density. Natural ice storms have been shown to reduce overall leaf area and increase canopy openness as a result of ice damage (Duguay et al. 2001; Rhoads et al. 2002; Olthof et al. 2003; Weeks et al. 2009). The 20%–30% (or greater) posttreatment declines in LAI and two- to threefold increase in canopy openness estimated in our moderate- to high-intensity treatment plots generally align with findings from stands affected by intense natural ice storms. Combined shifts in vertical and horizontal canopy density and arrangement also produced an overall near-term increase in the complexity of the canopy, which is reflected in the positive response of integrative metrics, including Rc, that describe canopy complexity. These metrics have been related to potentially important ecosystem functions such as primary productivity, light capture and light-use efficiency, and habitat value (Lesak et al. 2011; Ehbrecht et al. 2017; Atkins et al. 2018*a*; Gough et al. 2019).

Although there were shifts in canopy structure in all treatment plots (relative to both predisturbance conditions and Control plots), there was substantial variation among treatments that appeared to be strongly related to disturbance intensity (e.g., Figs. 2 and 7). Intensity of intermediate disturbance is often an important factor in canopy structural response, especially when comparing different instances of the same type of disturbance (Reyes et al. 2010; Fahey et al. 2015; Stuart-Haëntjens et al. 2015). We utilized two different metrics (representing disturbance intensity and severity) as predictors, and both were strongly related to the degree of disturbance impact on canopy structural characteristics. Direct measurements of ice accretion are a common indicator of ice storm intensity and are used in predicting and

Fig. 7. Ordination of canopy structure metrics, with plot points connected by successional vectors illustrating shifts in canopy structure through time. The starting points of the vectors indicate pretreatment conditions (2015), and the arrowheads indicate condition in 2017. Treatments differed significantly from each other in suites of canopy structure traits based on permutational multivariate analysis of variance (PERMANOVA) in both 2016 ($F_{[4,45]} = 7.48$, $p < 0.001$) and 2017 ($F_{[4,45]} = 8.44$, $p < 0.001$). Biplot overlay results indicate that total treatment-produced fine woody debris (FWD) was associated with the ordination solution and was strongly related to axis 2. P, plot.



classifying storm impacts (L. Rustad, unpublished data). Such measurements formed the basis for treatment designations in this study (based on preliminary work and validated by field measurements; Rustad and Campbell 2012), and the treatment differences evident here validate the relationship between ice accretion and disturbance impacts. FWD mass as an indicator of disturbance severity also showed a strong relationship with shifts in canopy structure (and predicted variation among treatments; L. Rustad, unpublished data). This finding is noteworthy, as measurement of FWD is easier to implement than a direct measure of ice accretion and can be performed in any location with existing litter traps (including National Ecological Observatory Network sites and other long-term study plots). There may be some evidence for a threshold in disturbance impacts related to intensity (Frelich and Reich 1999), as low-intensity treatments generally had less impact on response variables than moderate- to high-intensity treatments; however, this was not true for all variables, and the strength of differences with disturbance intensity varied among canopy structural characteristics.

Repeated or interacting disturbances often have compounding effects on ecosystem structure and functioning that manifest as additive, or even multiplicative, impacts on structural or functional features (Buma 2015; Cannon et al. 2017). In this study, repeated moderate-intensity ice storm disturbance exhibited additional impacts on canopy structure beyond that of a single disturbance of equivalent intensity. However, in contrast to some studies of repeated disturbance (Buma and Wessman 2011; Lucash et al. 2018; Cannon et al. 2019), the effects of consecutive ice storm disturbance generally had a marginal, rather than additive or multiplicative, effect. Canopy structural changes related to repeated disturbance were not consistently greater than those related to single moderate- or high-intensity disturbance, but these plots were the only ones that showed additional structural changes in the second year. This included changes to the vertical VAI profile that resulted in a shift from a pattern more consistent with the initial Mid disturbance to a more "bottom-heavy" pattern associated with the High treatment (Fig. 2). Interestingly, disturbance severity in terms of FWD mass produced was equivalent or even higher in the second application than the in first application, indicating that the effect on the canopy may have, in some respects, been exacerbated by the second disturbance. However, the overall structural changes resulting from the first disturbance were consistently greater than those from the subsequent disturbance, indicating a potential saturating response or even some degree of resistance to further structural change related to the initial disturbance (Buma and Wessman 2011; Johnstone et al. 2016). These results are likely associated with the fact that the two disturbances were essentially equivalent in terms of agent, directionality, and intensity; the potential for compounding effects related to repeat disturbance may be greater when the disturbances are less similar (Buma 2015). Although the near-term structural response to repeat disturbance did not consistently illustrate compounding impacts, there may be long-term effects (especially considering the FWD results). An evaluation of whether repeat disturbance lowered resilience to disturbance (e.g., in terms of LAI recovery or net primary production (NPP)) would be of particular interest.

Moderate-severity disturbances can have significant impacts on ecosystem processes and function, including light capture, productivity, and nutrient and water cycling (Gough et al. 2013). Although it is premature to evaluate the response of forest productivity to the experimental ice storm, the treatments did have a substantial effect on light interception and transmittance. Prior ice storm studies have also found increased heterogeneity in light availability (Beaudet et al. 2007). Such an effect was apparent in our study (based on greater variance in fPAR) but was limited to moderate- and high-intensity disturbance treatments. Altered postdisturbance light transmittance was most strongly related to the combined effect of leaf area and complexity in canopy arrangement (as Rc, based on multiple regression; Table 3), which matched prior work in undisturbed (Atkins et al. 2018*a*) and partially disturbed forest ecosystems (Stuart-Haëntjens et al. 2015). In other studies, the effect of increased canopy complexity was manifested not only in altered light capture, but also increased light-use efficiency (productivity per unit light captured), which appeared to be related to changes in leaf traits and their position within the canopy volume or light environment (but could also be related to light quality or scattering within the canopy volume; Gough et al. 2016). The effects of altered light conditions on leaf area, morphology, and physiology are not likely to have been fully manifested (Fotis et al. 2018), so light environments within treated plots are unlikely to be static in coming years. A recovery of LAI to predisturbance levels was not observed during this initial study period, which matches results from the 1998 ice storm (Rhoads et al. 2002; Weeks et al. 2009). Continued monitoring will be needed to evaluate treatment effects on light-use efficiency over time and effects of canopy reorganization on other ecosystem functions such as nutrient and water cycling (Scheuermann et al. 2018).

Conclusion

Ice storm intensity may increase in the future within northern hardwood-dominated forests of northeastern USA and southeastern Canada as a result of global climate change (Cheng et al. 2011; Swaminathan et al. 2018). The results of this study illustrate the variable impacts that ice storms can have on forest canopy structure and suggest potential functional effects that may be associated with these shifts. The general relationships illustrated here between ice storm intensity and severity (as ice accretion thickness and FWD production) and the degree of impacts on various aspects of forest canopy structure should allow for improved modeling and prediction of the effects of ice storms (and potential increased intensity and frequency of these events) on ecosystem structure and function. Further work is needed to validate these experimental results, either through additional experimentation or monitoring of plots affected by ice storms using permanently installed litter traps with FWD mass as a metric of ice storm intensity. Continued monitoring of the ISE plots will allow for assessment of ice storm effects on forest productivity and other ecosystem functions and relationships between long-term ecosystem resilience and the intensity, severity, and frequency of disturbance (Curtis and Gough 2018).

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