



ARTICLE

Climate Ecology

The impact of ice storms on mycorrhizal fungi varies by season and mycorrhizal type in a hardwood forest

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Abstract

Extreme weather events, such as ice storms, are increasing and have potentially large impacts on forests, including belowground structures such as fine roots and mycorrhizal fungi. Many forest trees rely on the mutualistic relationship between mycorrhizal fungi and plants; a relationship that, when disrupted, can negatively impact tree net primary productivity. We took advantage of a large-scale ice storm manipulation in the northeastern United States to test the hypothesis that increasing ice storm intensity and frequency would reduce ectomycorrhizal fungal root tips per unit root length and arbuscular mycorrhizal fungal structures per unit root length, hereafter colonization. We found that ice storm intensity reduced spring ectomycorrhizal fungal and arbuscular mycorrhizal fungal colonization. However, these patterns changed in the fall, where ice storm intensity still reduced ectomycorrhizal fungal root tips, but arbuscular mycorrhizal fungal colonization was higher in ice storm treatments than controls. The amount of ectomycorrhizal fungal root tips and arbuscular mycorrhizal fungal colonization differed seasonally: ectomycorrhizal fungal root tips were 1.7× higher in the spring than in the fall, while arbuscular mycorrhizal fungal colonization was 3× higher in the fall than in the spring. Our results indicate that mycorrhizal fungal colonization responses to ice storm severity vary temporally and by mycorrhizal fungal type. Further, arbuscular mycorrhizal fungi may recover from ice storms relatively quickly, potentially aiding forests in their recovery, whereas ice storms may have a long lasting impact on ectomycorrhizal fungi.

KEYWORDS

climate change, extreme events, Hubbard Brook Experimental Forest (HBEF), Ice Storm Experiment (ISE), plant-fungal mutualisms

INTRODUCTION

Periodic, extreme weather events such as ice storms are expected to increase in frequency and severity in the

northeastern United States as the climate changes (Cheng et al., 2011; Hayhoe et al., 2007; Swaminathan et al., 2018). Such high-impact events may have a greater influence on forest ecosystem structure and function than

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the gradual changes in temperature and precipitation associated with climate change (Arnone et al., 2011; Jentsch et al., 2007). Although relatively rare on an annual timescale, over 1300 ice storms occurred in the northeastern United States between 2000 and 2018 (NCEI, 2019). These storms can substantially damage forest canopies (Fahey et al., 2020; Rhoads et al., 2002; Rustad & Campbell, 2012; Weeks et al., 2009), but below-ground impacts are largely unquantified.

Mycorrhizal fungal associations play a large role in maintaining forest structure and function by increasing plant water and nutrient uptake (Smith & Read, 2008; van der Heijden et al., 1998) in exchange for carbon provided by host plants. Yet, mycorrhizal fungi species and groups vary widely in traits, including root colonization strategy, competitive ability (e.g., Allen et al., 2003; Lilleskov & Bruns, 2003; Talbot & Treseder, 2010), hyphal density, length, and turnover, and nutrient uptake mechanisms and rates (Agerer, 2001; Averill, 2016; Chagnon et al., 2013; Johnson & Gehring, 2007; Peay et al., 2011). This trait variation mediates mycorrhizal ecosystem impacts and responses to disturbances (Bennett & Classen, 2020; Rodriguez-Ramos et al., 2021; van der Heyde et al., 2017), but little is known about how they will respond to ice storms (Gellesch et al., 2013).

Arbuscular mycorrhizal fungi and ectomycorrhizal fungi are two types of mycorrhizal fungi that often co-occur (Bennett & Classen, 2020), but come from different ancestral fungal species, use different physiological structures to obtain soil nutrients (Tinker et al., 1992), and diverge in the benefits they provide to plants (Smith & Read, 2008). Arbuscular mycorrhizal fungi can obtain inorganic nitrogen and amino acids (Govindarajulu et al., 2005; Whiteside et al., 2012), and high levels of arbuscular mycorrhizal fungal colonization correlate with high inorganic nutrient availability and fast nitrogen and carbon cycling rates (Phillips et al., 2013). In contrast, ectomycorrhizal fungi can produce extracellular enzymes to mine soil organic matter for nitrogen (Chalot & Brun, 1998; Courty et al., 2010) and phosphorous, so they have greater access to organic nutrients than arbuscular mycorrhizal fungi (Averill et al., 2014; Turner, 2008). They can also release chelators to weather minerals and mobilize phosphorus and calcium to maintain tree health (van Breemen et al., 2000). Because the different roles played by arbuscular mycorrhizal fungal and ectomycorrhizal fungal impact ecosystem-level nutrient and carbon dynamics (Averill, 2016; Averill et al., 2014; Phillips et al., 2013), if ice storms have different effects on these mycorrhizal fungal types, the biogeochemical and forest production effects could be large over time.

Ice storms damage forest canopies and trees by reducing leaf area and bud formation and breaking twigs, branches, and trunks (Fahey et al., 2020; Rhoads et al., 2002; Weeks et al., 2009). Ice storm damage can therefore change the quantity, quality, and timing of litter deposited on the forest floor, shift the soil microclimate, and reduce growing season photosynthesis pending canopy recovery. For example, canopy gaps formed by the 1998 ice storm at the Hubbard Brook Experimental Forest in the northeastern United States resulted in increased soil temperatures (Likens et al., 2004) and reduced leaf area (Rhoads et al., 2002) for 3 years following the storm. A pilot ice storm simulation at the Hubbard Brook Experimental Forest in 2011 produced a year's worth of fine litter and dramatically increased coarse litter deposition (Rustad & Campbell, 2012). This same pilot study found that as ice storm intensity increased, so did the damage inflicted on trees (Rustad & Campbell, 2012).

Given that ice storms significantly impact forest canopies and soils, mycorrhizal fungal colonization may be positively or negatively impacted for a variety of reasons. First, lower photosynthesis following ice storms reduces carbon availability and thus may reduce mycorrhizal fungi colonization and development (Bücking & Heyser, 2003; Johnson & Gehring, 2007; van der Heyde et al., 2017). Alternatively, the pulse of carbon inputs to soil resulting from canopy damage may immobilize soil nutrients (e.g., within 1 year of wood addition in Homyak et al., 2008; Lajtha, 2020; Piatek, 2011), causing trees to allocate more carbon belowground to access scarce nutrients, thereby increasing support for mycorrhizal fungal associations (Allen et al., 2003; Kivlin et al., 2013; Treseder, 2004). Finally, warmer soils under canopy gaps may increase mycorrhizal fungal colonization (Kivlin et al., 2013).

We studied mycorrhizal fungal colonization responses to ice storms in the large-scale Ice Storm Simulation Experiment at the Hubbard Brook Experimental Forest in the northeastern United States. This large-scale ecosystem experiment simulated four ice storm intensity levels and one level of increased frequency to better understand the impacts of these extreme events on eastern North American deciduous forests (Rustad & Campbell, 2012). Given the potential for ice storms to cause above-ground damage that reduces photosynthesis and thus the availability of carbon for mycorrhizal fungal associations, we hypothesized that increased ice storm intensity would decrease ectomycorrhizal fungal root tips and arbuscular mycorrhizal fungal root colonization. Understanding the effects of ice storms on plant-fungal mutualisms will enhance our ability to predict the consequences of these extreme events for plant productivity and forest nutrient cycles.

METHODS

Study site and experimental design

We conducted this study in the Hubbard Brook Experimental Forest located in North Woodstock, NH, USA (43°56' N, 71°44' W, 500-m elevation). The climate is cool, humid, and continental, with the monthly mean air temperature ranging from -9°C in January to 18°C in July. Average annual precipitation is 1400 mm, with roughly one-third falling as snow. Hubbard Brook lies within the ice belt of the United States. Since the 1800s, Hubbard Brook has experienced a documented 26 major ice storm events and suffered major ecological setbacks due to a 1998 ice storm, which resulted in ice thicknesses ranging from 6 to 14 mm (Rhoads et al., 2002; Rustad & Campbell, 2012).

To investigate the impact of ice storms on forest structure and function, 10 experimental plots (20×30 m each) were created in the Hubbard Brook Experimental Forest near the main branch of the Hubbard Brook in a tract composed of 70–100-year-old northern hardwood tree species. Dominant tree species include sugar maple (*Acer saccharum* Marsh.), red maple (*Acer rubrum* L.), and yellow birch (*Betula alleghaniensis* Ehrh.), with American beech (*Fagus grandifolia* Britt.) predominant in the understory (Rustad & Campbell, 2012). Common understory species include Hobblebush (*Viburnum alnifolium*), *Lycopodium* spp., *Dryopteris intermedia*, and *Maianthemum canadense*. Ice storms were simulated by spraying stream water, pumped from the main branch of Hubbard Brook, over the canopy on below-freezing winter nights so that falling water would freeze on contact with vegetation, closely approximating natural conditions leading to ice accretion (see Campbell et al., 2020; Rustad & Campbell, 2012). Ice accretion was measured using the caliper method on four passive ice collectors that were located within each plot. At the time of application, surface air temperatures ranged from -13 to -4°C . Ten plots, 20×30 m, with a 5 m buffer between plots, were assigned one of five ice severity treatments ($n = 2$). In most parts of the US, ice thicknesses between 6 and 19 mm are considered mild to moderate (return interval of 2–5 years); thicknesses between 19 and 32 mm are considered severe (return intervals of 35–85 years; Changnon, 2003; Irland, 2000; Jones & Mulherin, 1998). Following this classification, ice severity treatments included no ice (control), low ice with a target treatment of 6.4 mm in thickness (6.3 ± 0.3 mm measured), moderate ice with a target of 12.7 mm (8.4 ± 1.1 mm measured), extreme ice with a target treatment of 19 (13.3 ± 1.2 mm measured), or moderate ice for two consecutive years with a target of 12.7 mm per year (moderate $\times 2$; 11.0 ± 1.6 mm measured in year 1 and

11.3 ± 0.2 mm measured in year 2) (Campbell et al., 2020). During the winter of 2016, all treatments received at least one ice event (January 18–19 or February 10–11). During the winter of 2017, the moderate $\times 2$ treatment received an additional ice treatment (January 9–13). Within each plot, three 5×5 m subplots were established for destructive soil sampling. Thus, the ecosystem-scale nature of this experiment, combined with limits placed on destructive sampling (due to a long-term and interdisciplinary sampling plan), limited treatment and sampling replication (more detail below). However, the insights provided by such large-scale, interdisciplinary experiments remain valuable, and some recent work suggests that a gradient approach such as ours can be as effective as extensive replication, particularly for the detection of nonlinear effects (Hanson & Walker, 2020; Kreyling et al., 2018).

Root sampling

We collected 3 soil cores (0–10 cm with diameter of 7.62 cm) within each of the 10 plots on May 12, 2017, and on November 7, 2017, for a total of 6 soil cores per treatment per sampling date (30 cores per sampling; 60 cores total). Our sampling occurred 17 months after the initial ice storm treatments, meaning that mycorrhizal fungal colonization observed in the light, moderate, and extreme treatments had one full growing season in between the treatment and our measurements, and moderate $\times 2$ was measured after the second ice event. Our sampling on May 12 occurred as trees were beginning to leaf out (stage 2 of four stages of leafing out), whereas our November 7 sampling occurred post-leaf fall.

We manually extracted all roots from soil cores to quantify both ectomycorrhizal fungal tips and arbuscular mycorrhizal fungal colonization according to root morphology (note that we did not identify root species). We removed all roots that were less than 0.5 mm from each soil core and washed the extracted roots three times in deionized (DI) water. We analyzed roots where the mantle was intact and that had the characteristic forked appearance for ectomycorrhizal fungal colonization, and roots without forking for arbuscular mycorrhizal fungal colonization. Using a dissecting microscope at $12\times$ magnification, we quantified ectomycorrhizal fungal infection of root tips on ~ 20 cm of fine roots from each soil core (Celestron Professional Stereo Zoom Microscope, Torrance, CA). Following microscopic inspection, we scanned roots using an Epson perfection V39 scanner (model J371A, Seiko Epson Corp., Indonesia) and measured the length using the measurement tool in ImageJ (Schneider et al., 2012). We used exact root length to calculate the number of ectomycorrhizal tips per centimeter of root length.

We quantified arbuscular mycorrhizal fungal colonization using a modified protocol following Brundrett (1991). To lighten root pigments, we bleached fine roots (10-cm length) in 10% KOH for 48 h and then washed them in DI water for 5 min. Next, we acidified roots in a 2% HCl solution for 30 min prior to staining them with 0.05% Trypan Blue solution overnight. We stored the stained roots in a 1:1 acidified glycerol solution in the refrigerator to allow the remaining trypan blue stain to diffuse from the roots. After 2 days, we washed the root samples with DI water, mounted the stained roots on microscope slides using polyvinyl-lacto-glycerol glue (INVAM, 2017), and counted the fungal structures (arbuscules, spores, and vesicles) at 200× with a Nikon Eclipse E600 (Nikon Instruments, Melville, NY) using the intersect method (McGonigle et al., 1990). The arbuscular mycorrhizal fungal “score” was calculated as the number of arbuscular mycorrhizal fungal structures (arbuscules, vesicles, and hyphae) observed per centimeter root length. These counts were summed into one “score number” for arbuscular mycorrhizal fungal structures, expressed as arbuscular mycorrhizal fungal structures per centimeter of root length (Brundrett, 1991; Claassen & Zasoski, 1992; Vierheilig et al., 2005).

Statistical analysis

We used linear mixed-effects models with subplot nested within plot as a random effect to determine statistical significance of experimental ice storm treatment and season on ectomycorrhizal fungal and arbuscular mycorrhizal fungal colonization (nlme package, Pinheiro et al., 2021). Models were inspected for normality and homogeneity of variance by visual inspection of residual and QQ plots. We used a constant variance structure (varIdent) to account for heterogeneity in variance associated with treatment (nlme package, Pinheiro et al., 2021). We log transformed

arbuscular mycorrhizal fungal data to meet normality assumptions. Type 3 ANOVA (car package, Fox & Weisberg, 2011) was completed on the models to determine statistical significance, and we calculated marginal and conditional R^2 values using the piecewiseSEM package (Lefcheck, 2015) to determine model fit. Given that the basal area of arbuscular mycorrhizal and ectomycorrhizal tree species varied across our 10 plots and that the abundance of these tree types impacts the presence and abundance of arbuscular mycorrhizal and ectomycorrhizal fungal colonization and association (respectively; e.g., Eagar et al., 2022; Grünfeld et al., 2020; Rosling et al., 2016), we ran a second analysis, using the statistical model described above, where we corrected for these differences by normalizing the arbuscular mycorrhizal fungal structure and ectomycorrhizal fungal tip data by the basal area of trees in 2017 (measured as in Rustad et al., 2020) associated with arbuscular or ectomycorrhizal fungi (respectively) in each plot (trees were associated with mycorrhizae type based on Chaudhary et al., 2016). We conducted all analyses in R version 3.4.4 (R Core Team, 2016).

RESULTS

Ectomycorrhizal fungal root tips

Ice storm treatments reduced ectomycorrhizal root tips per unit root length relative to control plots, but this effect was larger in the spring than in the fall (significant ice treatment by season interaction, $p < 0.05$; Table 1; Figure 1a,c). These results were sustained even when data were normalized by the basal area of ectomycorrhizal trees that occurred within each plot (Figure 1a,c; Table 1). In the spring, there were the most ectomycorrhizal fungal root tips in the control plots (1.8 ± 0.09 , mean \pm SE; Figure 1a). On average, the low (1.0 ± 0.07) and moderate $\times 2$ (1.1 ± 0.07) ice treatments

TABLE 1 ANOVA results for ectomycorrhiza (ECM) tips and arbuscular mycorrhiza fungal (AMF) structures normalized by the basal area of ECM or AM trees in each plot or not normalized.

Mycorrhizal type	Effect	Not normalized				Normalized			
		R^2	df	χ^2	p	R^2	df	χ^2	p
ECM tips	Treatment		4	7.58	0.1082		4	4.81	0.3071
	Season		1	24.88	<0.0001		1	20.40	<0.0001
	Treatment \times season		4	22.26	0.0002		4	31.18	<0.0001
	Marginal R^2	69%				61%			
AMF structures	Treatment		4	6.87	0.1430		4	7.40	0.1160
	Season		1	29.62	<0.0001		1	27.99	<0.0001
	Treatment \times season		4	46.75	<0.0001		4	51.45	<0.0001
	Marginal R^2	84%				73%			

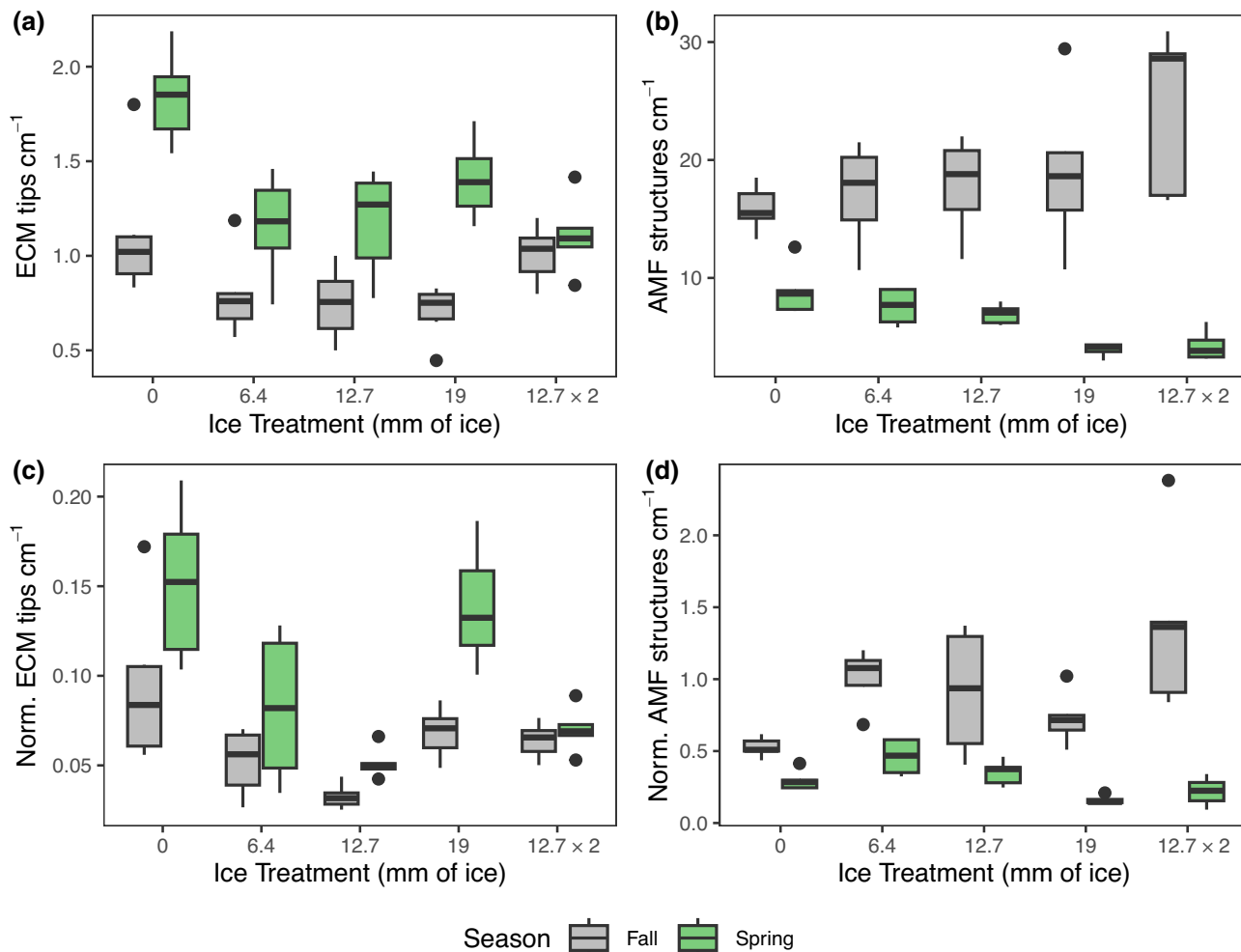


FIGURE 1 Ectomycorrhiza (ECM) tips and arbuscular mycorrhizal fungal (AMF) structures by season and across ice treatments (in millimeters of ice; 12.7 × 2 is 12.7 mm of ice in two consecutive winters). Boxplots of (a) ECM tips per centimeter or (c) ECM tips per centimeter normalized (norm.) by the basal area of ECM trees in each plot for the fall and spring sampling periods. In both cases, there were more (and more variable) ECM tips in the spring than in the fall. Treatment impacts varied by season (significant interaction; Table 1). Boxplots of (b) AMF structures per centimeter or (d) AMF structures normalized by the basal area of AM trees in fall and spring. For both cases, fall colonization was higher and more variable than fall, and ice storm intensity interacted with season to affect colonization (significant interaction; Table 1). In the boxplots, the lower and upper hinges correspond to 25th and 75th percentiles, respectively. The upper whisker extends from the hinge to the largest value no further than 1.5 × inter-quartile range (IQR); the lower extends from the hinge to the smallest value at most 1.5 × IQR. Data beyond the whiskers are outlier points.

decreased ectomycorrhizal fungal root tips by 48% and 40%, respectively, while the moderate (1.4 ± 0.02) and extreme (1.4 ± 0.08) ice treatments only decreased root tips by approximately 24% relative to controls. There were more ectomycorrhizal fungal root tips, on average, in the spring than in the fall, except for in the moderate × 2 treatment, where ectomycorrhizal root tips were similar in the spring and the fall (1.0 ± 0.06 in the fall; Figure 1a). In the fall, the control (1.1 ± 0.13) and moderate × 2 treatments had similar ectomycorrhizal root tips per root length, which were up to 37% higher than ectomycorrhizal root tips measured in the low, moderate, and extreme ice treatments (0.7 ± 0.09 , 0.8 ± 0.05 , and 0.7 ± 0.05 , respectively; Figure 1a). The statistical

model explained 67% of the variation in ectomycorrhizal fungal root tips across our treatments (Table 1).

Arbuscular mycorrhizal fungal colonization

Similar to our ectomycorrhizal results, we found a strong season by treatment interaction with arbuscular mycorrhizal fungal colonization ($p < 0.05$; Table 1), but colonization was greater in the fall than in the spring (Figure 1b,d). Again, these results were similar whether data were normalized by the basal area of arbuscular mycorrhizal trees in each plot or not (Figure 1b,d; Table 1). Arbuscular

mycorrhizal fungal colonization decreased in the spring with increasing ice storm treatment severity and frequency, such that the control (8.9 ± 0.88) and the low (8.3 ± 0.42) ice treatments were comparable and 30%–40% higher than in the moderate treatment (6.3 ± 0.25), which was 50%–60% higher than the extreme (3.9 ± 0.28) and moderate $\times 2$ treatments (4.2 ± 0.45 ; Figure 1b). While arbuscular mycorrhizal fungal colonization decreased with ice storm severity and frequency in the spring, it increased with severity and frequency in the fall (Figure 1b). Control and low ice treatments had similar colonization (15.9 ± 0.65 and 13.9 ± 1.43 , respectively), followed by higher colonization in the moderate (20.9 ± 0.44) and extreme (19.0 ± 2.7) ice treatments, and finally the highest and most variable colonization in the moderate $\times 2$ treatment (24.4 ± 2.81 ; Figure 1b). The statistical model explained 84% of the variation in arbuscular mycorrhizal fungi colonization across all the treatments (Table 1).

Seasonal comparison of ectomycorrhizal and arbuscular mycorrhizal fungal colonization

Across all treatments, ectomycorrhizal and arbuscular mycorrhizal fungal species had different root colonization patterns in the fall and the spring. Arbuscular mycorrhizal fungal colonization was 3 \times higher in the fall than in the spring. In contrast, ectomycorrhizal fungal colonization was 1.7 \times higher in the spring than in the fall. Among all the ice storm treatments and across both types of mycorrhizae, only ectomycorrhizal fungal root tips in the moderate $\times 2$ treatment were similar across seasons (Figure 1). In all other treatments, ectomycorrhizal fungal root tips and arbuscular mycorrhizal fungal colonization varied with season (Table 1).

DISCUSSION

Ice storms are extreme events that damage forest canopies and alter forest inputs and microclimates—changes that may impact the belowground mycorrhizal system. Using a novel, large-scale ice storm experiment that manipulated ice storm intensity and frequency in a mixed deciduous forest, we found that the impact ice storms have on mycorrhizae was different when observing colonization in the fall and in the spring. Ice storm damage decreased both ectomycorrhizal fungal root tips and arbuscular mycorrhizal fungal colonization in the spring, but this pattern only held for ectomycorrhizal fungal root tips in the fall, for all treatments except the moderate $\times 2$ treatment. Arbuscular mycorrhizal fungal

colonization, on the other hand, increased with ice storm severity and frequency in the fall. We also found large differences in mycorrhizal root tips and colonization in the fall and the spring. Ectomycorrhizal fungal root tips were, on average, 1.7 \times greater in the spring than in the fall, whereas arbuscular mycorrhizal fungal colonization was around 3 \times greater in the fall than in the spring.

Both ectomycorrhizal fungal and arbuscular mycorrhizal fungal colonization decreased with ice storm frequency and severity in the spring. The low ice treatment reduced ectomycorrhizal fungal colonization by 52% relative to control. The greatest reduction in arbuscular mycorrhizal fungal colonization was in the extreme ice treatment with an average decrease of 42% (vs. the control). This reduced colonization could indicate that, due to aboveground damage sustained from ice events, plants reduced their belowground allocation of nonstructural carbohydrates, which would also reduce carbon availability for mycorrhizal fungal symbionts. The fact that this trend was detectable in the second spring following ice storm damage suggests that the effects of this punctuated storm may be relatively long-lasting. Further, the mycorrhizal responses to the more frequent, moderate storm were not substantially different from this longer term response (Figure 1). Indeed, previous research found that leaf area was not restored to prestorm values until three years following a moderate-to-severe ice storm event (Rhoads et al., 2002). Such a poststorm lowered photosynthetic potential throughout the growing season and could reduce nonstructural carbohydrate stores with effects across years pending leaf area recovery. This idea is supported by evidence from the ice storm experiment that tree wound closure, which also relies on nonstructural carbohydrates, was reduced with increased crown damage in the ice storm treatment plots (P. Schaberg, personal communication). While speculative, the detrimental impact of ice storm frequency and intensity may have been amplified during our spring sampling because it was conducted prior to full leaf out of deciduous trees. At this time, tree reserves of nonstructural carbohydrates are typically at their lowest point, since reserves are built up during the growing season and depleted throughout the dormant season to meet metabolic demands (Furze et al., 2019). Exploring the plant physiological drivers for our observed patterns would be an exciting area for further ice storm research.

The amount of mycorrhizal fungal root tips and colonization, as well as responses to treatments, varied by mycorrhizal fungi type and season. Ectomycorrhizal fungal root tips per centimeter in the spring and in the fall were lower than the control in all ice treatments except the moderate $\times 2$ treatment in the fall, which was not different from the controls. These results suggest that ice storm severity could depress ectomycorrhizal fungi throughout

the year, but that an increase in ice storm frequency may result in the rapid recovery of ectomycorrhizal fungi. Overall, the moderate $\times 2$ treatment maintained a relatively constant number of ectomycorrhizal fungal root tips per centimeter throughout the growing season, perhaps because annual ice storm disturbances caused this community of ectomycorrhizal fungal to grow more slowly. Unfortunately, the large-scale nature of our experiment limited our ability to further disentangle relationships among ice storm frequency and intensity.

In contrast to the relatively consistent response of ectomycorrhizal fungi to treatments throughout the year, the response of arbuscular mycorrhizal fungal colonization to ice storms was different in the fall than in the spring. In the spring, arbuscular mycorrhizal fungal colonization decreased with increasing ice storm severity and frequency, but in the fall, arbuscular mycorrhizal fungal colonization increased with increasing ice storm severity and frequency. This suggests that, while reduced availability of belowground plant carbon for arbuscular mycorrhizae in the spring may have exacerbated ice storm impacts on arbuscular mycorrhizal fungal colonization, later in the growing season, these same plants may have increased photosynthate allocation belowground and to arbuscular mycorrhizal fungal symbionts with increased ice storm severity and frequency, perhaps due to nutrient limitation resulting from the addition of ice storm-produced woody debris (Homyak et al., 2008; Johnson & Gehring, 2007; Lajtha, 2020; Piatek, 2011). The positive response of arbuscular mycorrhizal fungal colonization to ice storm severity and frequency in the fall could also be a response to enhanced root growth (Giovannetti et al., 1993; Rhoads et al., 2002), but, to date, there have been no significant differences in root growth among the ice storm treatments (T. J. Fahey, personal communication).

Overall and across treatments, we found that ectomycorrhizal and arbuscular mycorrhizal fungi had opposite seasonal trends. There were more ectomycorrhizal fungal root tips in the spring than in the fall, whereas arbuscular mycorrhizal fungal colonization was higher in the fall than in the spring. These results support prior work showing a higher percentage of root area colonized by ectomycorrhizal fungal in the early versus late growing season (Sung et al., 1995). A recent review found that ectomycorrhizal fungi were less sensitive than arbuscular mycorrhizal fungi to temperature (Soudzilovskaia et al., 2015), and ectomycorrhizal fungi may also be less sensitive than arbuscular mycorrhizal fungi to reductions in plant carbon allocation since many ectomycorrhizal fungi can produce extracellular enzymes that degrade soil organic matter (Nicolás et al., 2019; Shah et al., 2016). Thus, ectomycorrhizal fungi may have been less sensitive

than arbuscular mycorrhizal fungi to low early spring temperatures as well as to declines in plant belowground carbon allocation.

We observed higher arbuscular mycorrhizal fungal colonization in the fall than in the early spring, suggesting that more plant photosynthate may be allocated and available belowground for mycorrhizal fungal symbionts later in the growing season than in the winter and early spring when plant nonstructural carbohydrates are depleted. Indeed, carbon allocation to fungal symbionts can increase later in the growing season based on host plant physiology (Brundrett, 1991; Högberg et al., 2010). Further, arbuscular mycorrhizal fungal plant root colonization declines at low temperatures (Brundrett & Kendrick, 1988; Soudzilovskaia et al., 2015). Thus, arbuscular mycorrhizal fungal temperature constraints and host physiology may interact to affect colonization, where host plants that produce roots during the late spring to mid-fall when the soil is warm have more arbuscular mycorrhizal fungal colonization relative to plants that produce roots in the spring when soils are cold (Brundrett & Kendrick, 1988; Santos-González et al., 2007). Finally, arbuscular mycorrhizal fungal hyphae can have relatively short turnover times (days vs. months to years for ectomycorrhizal hyphae; Frey, 2019), and species, diversity, and community dynamics can vary seasonally (Abbott & Robson, 1991; Dumbrell et al., 2011; Santos-González et al., 2007). Thus, the high fall arbuscular mycorrhizal fungal colonization observed in this study may be a result of mycorrhizal succession with faster growing arbuscular mycorrhizal fungal species appearing later in the growing season, tolerant species resuming full growth (Klironomos et al., 2001), seasonally driven plant or arbuscular mycorrhizal fungal community growth, or species turnover due to changing environmental conditions over the season and in response to ice storm severity and frequency.

Overall, our results suggest that arbuscular mycorrhizal fungi may recover from ice storm events relatively quickly, potentially aiding forests in their recovery, while the impacts of ice storms on ectomycorrhizal fungi are longer lasting. While there is substantial trait variation among species of arbuscular and ectomycorrhizal fungi that may impact ecosystem properties and processes (e.g., Agerer, 2001; Chagnon et al., 2013; Johnson & Gehring, 2007), systems dominated by arbuscular mycorrhizal associations are often characterized by fast turnover of inorganic nutrients and carbon, as opposed to the slow cycling and carbon accumulation often prevalent in stands dominated by ectomycorrhizal associations (Averill, 2016; Averill et al., 2014; Jo et al., 2019; Phillips et al., 2013). Thus, the faster recovery of arbuscular mycorrhizal fungi in these forests may result in relatively faster biogeochemical

cycling relative to ectomycorrhizal-dominated forests or forests undamaged by ice storms.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Yancey et al., 2023) are available from the Environmental Data Initiative Data Portal: <https://doi.org/10.6073/pasta/0c2c3eae0f6ba1fceb7ff16913c83712>.

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