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Differential responses of tree species to a severe ice storm and their implications to forest composition in the southeast United States

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ABSTRACT

The unique terrain, geography, and climate patterns of the eastern United States encourage periodic occurrences of catastrophic ice storms capable of large-scale damage or destruction of forests. However, the pervasive and persistent effects of these glaze events on regional forest distribution and composition have rarely been studied. In the southeastern US, ice storm frequency and intensity increase with increasing latitude and along the complex gradients from the coast (low, flat, sediment controlled and temperature moderated near the ocean) to the interior (high, rugged, bedrock controlled, distant from warming ocean). To investigate the potential influence of this disturbance gradient on regional forest composition, we studied the differential responses of trees (canopy position, lifeform group, and species group) to a particularly severe ice storm. Our results indicated that tree mortality and damage (canopy damage, bent bole, snapped bole, and uprooted) varied significantly between overstory and understory trees, and among species and lifeform groups. Overstory trees were more prone to glaze damage than understory trees, and evergreen broadleaf species were the most susceptible to glaze damage, while deciduous species were the least susceptible. Among the pine species studied, slash pine (*Pinus elliottii* Engelm.) and longleaf pine (*P. palustris* Mill.) suffered more severe damage and mortality than loblolly pine (*P. taeda* L.). Further, ice damage was correlated with distribution-based differences in injury susceptibility among pine and deciduous tree species. The most ice storm-tolerant pine species, loblolly pine, had the most northerly distribution (39.51°N), while the least resistant species were those with more southerly distribution (e.g., 33.29°N for slash pine). These results support hypotheses that the distributions of evergreen tree species are regulated by periodic catastrophic ice storms. Therefore, predicting future distributions of tree species in response to climate change should consider the role of ice storms in shaping the forest composition.

1. Introduction

Understanding the abundance and distribution of species is fundamental to ecology (Krebs, 2008). Through more than a century of studies, ecologists generally agree that climate, specifically temperature and precipitation, drive global or regional species pools, while topo-edaphic factors and biological interactions are important for defining species occurrence on the landscape (Oliver and Larson, 1990; Whittaker, 1962). However, when species are moved out of their native range, extreme weather events often decide the success of naturalization (Bradley et al., 2010), suggesting that disturbance events are also influential drivers of plant distribution (Adams et al., 2009; Zimmermann et al., 2009). Indeed, natural disturbances such as fire and extreme weather may drive the abundance and distribution of tree species by acting as an ecological filter that shapes the composition and structure of forest communities (Irland, 2000; Allen et al., 2010; Clark et al., 2016). For example, the historical dominance of longleaf pine (*P. palustris*) in the coastal plains of the southeastern US was largely controlled by a prevailing frequent surface fire regime (Wahlenberg, 1960). Low-temperature extremes ("hard" frosts) during bud-break in the eastern US have been shown to limit the elevational and latitudinal distribution of hardwoods (Booth, 2012; Kollas et al., 2014).

The influence of natural disturbances on forests has attracted considerable attention over the last several decades (Attiwill, 1994; Irland, 2000; Nagel et al., 2017; Pickett and White, 1985; White, 1979). However, most studies have focused on the short-term effects of only a

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few disturbance types (such as fire or wind) on forested ecosystems. Despite their major impact on both the short-term growth and long-term survival of tree species, disturbances have seldom been studied explicitly as a driver of tree species distribution (Barnes, 2009). This shortcoming limits the ability of researchers to understand biogeographical patterns across ecologically and commercially important forested regions such as the southeastern US, which is experiencing widespread pressures from human population growth, landscape fragmentation, forest type conversion, and climate change (Wear and Greis, 2013). The ability to explain how perturbations influence forest patterns in this region is critical because the southeastern US is affected by multiple large-scale disturbances including fires (Flannigan et al., 2000), hurricanes (Batista and Platt, 2003), droughts (Addington et al., 2015), insect outbreaks (Janousek et al., 2019), and ice storms (Bragg et al., 2003).

Ice storms are among the most frequent and injurious to temperate forests (Irland, 2000; Smith, 2000) yet remain perhaps the most poorly understood ecologically. Meteorologically, ice storms have been defined by the U.S. National Weather Service as an occurrence of freezing precipitation (also called "glaze") that either results in structural damage or deposits at least 6.3 mm of ice (Hauer et al., 2006). Climatologically, eastern North America experiences the most ice storms in the temperate forests throughout the world because its winter weather patterns, coastline, and terrain configuration periodically encourage freezing rain (Changnon and Karl, 2003). This results in a "glaze belt" that extends from north Texas to southern New England and eastern Canada, where ice storms are expected once every three years (Bennett, 1959). Although less frequent (once every 10 to 15 years), major ice storms also periodically strike the southeastern US beyond the glaze belt (Bragg et al., 2003; Changnon and Karl, 2003). The general conditions that produce ice storms in the southeastern U.S. have been described elsewhere (e.g., Gay and Davis, 1993; Degelia et al., 2016), and will not be further reviewed. Rather, we will consider the role of ice storms on large scale forest patterns in the southeastern US.

Most studies to date on ice damage to forests in the southeastern US have been largely limited to ad-hoc assessments of timber loss, usually focusing on a few commercially important tree species (Bragg, 2016; Nicholas and Zedaker, 1989; Shepard, 1978). This focus means that little is known regarding the response of most tree species to ice storms. Given that species-specific differences in ice storm injury or mortality rates have been observed in other regions (Foster et al., 1998; Lemon, 1961; Lafon, 2004; 2006; Seischab et al., 1993), such differences should also be expected in southeastern forests. When coupled with the frequent, widespread, and sometimes extreme nature of ice storms, glazing has the potential to significantly influence the historical range and abundance of individual tree species, thereby helping to control regional forest composition.

Indeed, many studies in North America have provided evidence that periodic ice storms favor ice-resistant tree species, thereby affecting species distributions and forest composition (Bragg et al., 2003; Irland, 2000). For example, canopy status has been associated with the species-based probability and nature of ice damage in the understory of a mature Douglas-fir [*Pseudotsuga menziesii* (Mirb.) Franco] forest (Priebe et al. 2018). Ice storms may contribute to the northerly limits of loblolly pine (*Pinus taeda* L.) (Fowells, 1965; Wahlenberg, 1960). Further, eastern hemlock [*Tsuga canadensis* (L.) Carriére], with strong resistance to crown ice damage, may increase its dominance in mixed stands of less glaze resistant species such as red maple (*Acer rubrum* L.), yellow birch (*Betula alleghaniensis* Britton), and eastern white pine (*Pinus strobus* L.) (Irland, 2000). Further, in the southern Appalachian Mountains, periodic ice storms are thought to help maintain the dominance of chestnut oak (*Quercus montana* Willd.), release abundant red maple from the understory, and restrict pitch pine (*Pinus rigida* Mill.) and Table Mountain pine (*P. pungens* Lamb) to west-facing slopes and other sheltered sites (Lafon, 2006; Wonkka et al., 2013). In many storm events, southern pine species experience higher mortality rates than hardwoods due to the inability of these pines to resprout if their bole breaks below their live crown (Bragg et al., 2003).

The differences in tree species resistance or tolerance of ice damage noted by others (e.g., Lemon, 1961; Seischab et al., 1993; Foster et al., 1998; Lafon, 2006) are likely due to differences in rooting depth, wood density, and decay resistance, tree stature (canopy position), crown architecture, and winter phenology and leaf traits (Bruederle and Stearns, 1985; Hauer et al., 2006; Priebe et al., 2018; Warrillow and Mou, 1999), as well as the interaction of these factors. For example, in purely deciduous forests, species with weaker wood, finer branches, and larger canopy surface areas are particularly susceptible to ice damage (Warrillow and Mou, 1999). Even clonal loblolly ideotypes representing different branches and stem morphologies vary in their response to glaze (Pile et al., 2016). The multi-forked and bare branches of most deciduous hardwoods tend to break once their ice load-bearing threshold has been exceeded (Lafon, 2006), thereby allowing the tree to shed more accumulated ice load, while the less branched, more foliated conifers and evergreen hardwoods continue to add load. This factor, canopy surface area, is critical in determining the degree and severity of glaze damage as it is directly related to the amount of ice accumulation that occurs. Although notable exceptions do occur, deciduous hardwood species typically shed their foliage prior to the onset of the period of the year (late fall to early spring) when ice storms are most likely to occur. Not surprisingly, then, when compared to pines, deciduous broadleaf species typically suffer less ice damage (Whitney and Johnson, 1984). However, few studies have examined the response of marcescent (i.e., species with foliage that dies and withers but is largely retained on the tree during the dormant season), such as many *Quercus* and evergreen broadleaf species to ice storms (Ge et al., 2015). For these species, more severe ice damage is expected due to their persistent (senesced or living) leaves.

While many studies have demonstrated that species characteristics often determine the immediate and short-term impacts of glazing, little is known about how differential species response to ice storms would affect species distribution and forest composition. Considering most evergreen broadleaf species in the southeastern US are confined to areas close to the Atlantic Ocean or the Gulf of Mexico where ice storms are rare, we hypothesize (H1) that periodic ice storms contribute significantly to the lack of evergreen broadleaf species in interior southeastern forests. Therefore, we predict (P1) that evergreen broadleaf species are more sensitive to ice storms and would suffer greater damage and mortality than species that are either deciduous broadleaf or evergreen coniferous. In the southeastern US, evergreen conifer forests distribute near the south and dominate the coastal plains while deciduous forests distribute in the north and dominate the piedmont and mountain ecoregions. Furthermore, southern pine species with natural distributions extending into the piedmont and mountains generally have shorter needles and more flexible branches than those species restricted to the coastal plains. Therefore, we hypothesize (H2) that periodic ice storms help determine the southern boundary of deciduous broadleaf forests and the northern boundary of southern pine forests. Based on H2, we predict (P2) that evergreen coniferous species are more prone to ice damage than deciduous broadleaf species, and southern pines with more northern and interior distributions are less prone to ice damage than pines with more southerly and coastal distributions. Within the coastal plain region, pine forests tend to occupy uplands, while deciduous broadleaf forests tend to occur on lowlands. The abrupt transition between the two forest types may be attributed to winter flooding in the lowlands, but periodic ice storms may also contribute to this abrupt transition. Previous studies reported that the damage patterns were related to tree species, ice thickness, and soil characteristics (Lafon, 2006; Nagel et al., 2016). Trees growing in shallow soils, especially on steep slopes, were more prone to uprooting during severe ice storms (Lafon, 2006; Warrillow and Mou, 1999). Therefore, we hypothesize (H3) that ice storms help define this abrupt transition because evergreenness as a lifeform trait and wet winter soils

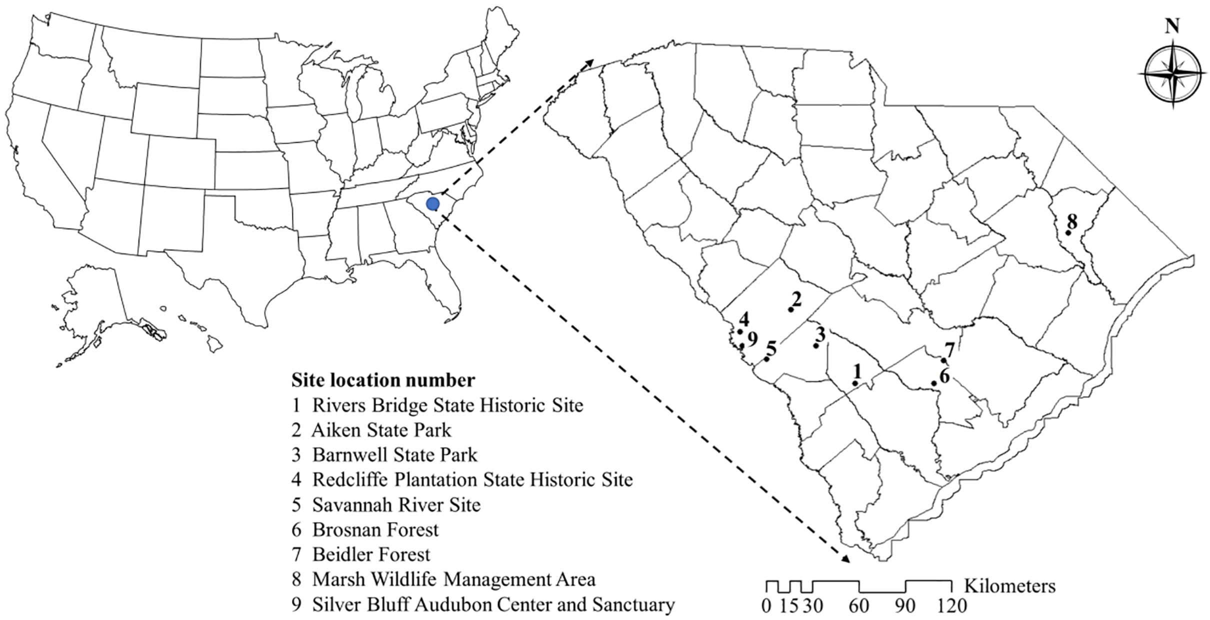

Fig. 1. The location of the nine study areas within South Carolina.

as an edaphic site condition could be a particularly lethal combination to ice damage from ice accumulation and unstable soils resulting in greater potential for uprooting. Based on H3, we predict (P3) that ice damage and mortality of evergreen broadleaf and pines are significantly higher on wetter sites (bottomlands) than on drier sites (uplands).

The objectives of this study were to investigate (1) how a major ice storm affected a wide range of tree species differently and (2) how these differential responses to ice storm might affect species distribution and forest composition in the southeastern US based on data collected from a number of sample locations in the Coastal Plain of South Carolina (Fig. 1). To achieve the first objective, we assessed tree damage sustained from a major ice storm and related the observed ice storm damage to species characteristics, canopy status, and stand/site conditions. To achieve the second objective, we tested the three hypotheses by verifying their corresponding predictions.

2. Materials and methods

2.1. The ice storm event and study areas

Starting on February 11, 2014, in Georgia and ending two days later in North Carolina, the ice storm we studied deposited its greatest ice accumulations (from 25.4 to 38.1 mm) from eastern Georgia to southwestern South Carolina. The direct economic loss from timber damage caused by the ice storm in South Carolina alone was estimated at over US$360 million (https://www.state.sc.us/forest/2014winter-storm.htm). Based on post-storm aerial and ground surveys conducted by the South Carolina Forestry Commission (SCFC), we selected nine study areas in South Carolina that experienced substantial ice impact (> 6 mm ice accumulation) from the storm (Fig. 1; Table 1). The study areas covered both public and private lands, including Marsh Wildlife Management Area, Brosnan Forest, Beidler Forest, Savannah River Site, Silver Bluff Audubon Center and Sanctuary, Aiken State Park, Barnwell State Park, Redcliff Plantation State Historic Site, and Rivers Bridge State Historic Site (Table 1).

2.2. Field sampling design

Fieldwork started in August and ended in November 2014, when the ice damage from this event was still distinguishable. We used subjective criteria during the stand selection. Within each study area, forest stands of different species compositions were identified based on remote sensing data and preliminary ground surveys. Based on observation, only those stands that sustained severe damage from the ice storm were selected for sampling (Zhu et al., 2006). For a given stand type or species, ice damage may be linked to stand density, age, and forest management history (Bragg et al., 2003). Therefore, we limited our sampling to naturally regenerated or unmanaged forest stands that were mature (i.e., past the stem exclusion stage of stand development). While efforts were made to sample a range of forest types across the region, some types were selected more than others. In each area, efforts were also made to ensure that tree species of the different lifeform groups of interest (deciduous, marcescent, evergreen coniferous, or evergreen broadleaf) were present.

In each selected stand, we established one 30 × 30 m plot in the central area of the stand with the help of a GPS, and the plot edge was at least 150 m from the stand edge, which could avoid potential edge effects. Depending on the number of stands selected and the size of the study site, a variable number of plots were sampled in each area. As a result, 107 plots were sampled across the nine study areas, with 3 to 25 plots measured at each site (Table 1). We recorded general information for each plot, including stand type, site type, and amount of ice accumulation based on geospatial information provided by SCFC (Table 1). Each sampled stand was later assigned into one of the four forest types based on species composition (relative basal areas of pines and hardwoods) and topographical location: upland pine (PINE), upland hardwood (UHW), upland pine-hardwood (UPH), or bottomland hardwood (BHW). Upland pine stands contained > 75% pines; upland and bottomland hardwood stands consisted of > 75% hardwoods, and upland pine-hardwood (mixed wood) stands contained between 25% and 75% of pines or hardwoods.

In each plot, stems were assigned into one of the three size classes: tree seedlings (> 5 cm but < 1.4 m tall), understory trees (≥ 1.4 m tall but < 10 cm DBH), and overstory trees (≥ 10 cm DBH). Based on our observations in the field months after the event, seedlings rarely showed observable evidence of damage from the ice storm; hence, they were not assessed for canopy status or damage type. Every tree—including those killed or damaged by the ice storm—at least 1.4 m tall was identified to species, and its DBH measured to the nearest 0.1 cm. For each overstory tree, its pre-ice storm status in the canopy was classified as dominant, co-dominant, intermediate, or suppressed. Further, the status of each under- and over-story tree was recorded as

Table 1
A summary of estimated ice accumulation, the number of plots (30 × 30 m) sampled, and plot distribution by forest type in each study area. PINE: upland pine, UHW: upland hardwood, UPH: upland pine-hardwood, BHW: bottomland hardwood.

Location	Estimated ice accumulation (mm)	Number of Plots	Forest type			
			PINE	UHW	UPH	BHW
Marsh Wildlife Management Area	6.1–9.7	12	8	1	3	0
Brosnan Forest	9.9–13.2	18	12	4	0	2
Beidler Forest	9.9–19.6	25	11	0	0	14
Savannah River Site	20.3–26.7	16	14	0	1	1
Silver Bluff Audubon Center and Sanctuary	20.3–26.7	9	2	2	1	4
Aiken State Park	23.4–26.7	8	1	0	4	3
Barnwell State Park	23.4–26.7	9	0	5	4	0
Redcliffe Plantation State Historic Site	23.4–26.7	3	0	2	1	0
Rivers Bridge State Historic Site	23.4–26.7	7	0	0	6	1
All	**6.1–26.7**	**107**	**48**	**14**	**20**	**25**

either living and not damaged (ND), living and damaged (LD), or damaged and dead (DD) (trees were considered dead when there were no living buds or foliage, with the exception of stump sprouts). For those stems injured (i.e., LD) or killed (i.e., DD) by the ice storm, each was assigned into one of the following categories:

(1) Crown Damage (CD), the live crown removed or partially broken; with crown loss percentage visually estimated in 5% increments (up to 90% crown loss);
(2) Bent Bole (BB), the stem noticeably bent; the vertical distance from treetop to the ground was measured;
(3) Snapped Bole (SB), the main stem was snapped with > 90% of the live crown lost; the height from the ground to the snapping point was recorded; and
(4) Uprooted (UR), the main stem was partially or entirely uprooted.

For our analysis, a tree that sustained multiple types of damage was assigned to the most severe category. For example, an uprooted tree with some broken branches would be classified as UR. Since we started the investigation half a year after the ice storm event, the damages from the ice storm could still be distinguished from others. There were apparent injury signs, such as wet roots of the uprooted stems, fresh surfaces of the snapped boles, and freshly fallen branches, twigs, and leaves from the damaged crowns.

2.3. Species attribute data collection

In addition to data collected from field sampling, we also gathered species attribute data (lifeform, crown architecture, native distribution, growth rate, breakage, and woody density) from the available literature (see Appendix A). Lifeform and crown architecture were classified according to Harlow (1957), Sargent (1965), Miller and Miller (2005), Nelson (2006), and Kirkman et al. (2007). We classified each species into one of four lifeform groups representing deciduous, marcescent, evergreen coniferous, and evergreen broadleaf species according to their leaf traits and winter phenology. The crown architecture was classified into irregular or symmetrical according to crown uniformity, and into open, moderate, or dense according to crown density. We also collected species distribution information from the US Geological Survey (https://www.sciencebase.gov/catalog/item/5540e3fce4b0a658d79395fe). Information on growth rate (fast, moderate, or slow) and breakage potential (susceptible or resistant) were obtained from the US Department of Agriculture Plants database (http://plants.usda.gov/java/characteristics), while wood densities were obtained from Chave et al. (2009) and Miles and Smith (2009).

2.4. Data analysis

To achieve the first objective, we assessed tree damage sustained from the major ice storm and related the observed ice storm damage to species characteristics and stand conditions using a number of sample locations in the Coastal Plain of South Carolina (Fig. 1). First, we evaluated the living or dead trees for any differences between canopy position (overstory versus understory) and damage condition (ND, LD, DD). Since it was evident that canopy trees were more susceptible to the ice storm than understory trees, we evaluated canopy and understory trees separately in most of our analyses, with a focus on canopy trees. Because tree size varied from plot to plot among canopy trees, we also calculated a relative diameter (diameter of each stem was divided by the largest diameter in the plot) for each stem within the plot. Assuming a positive and linear relationship of tree diameter to tree height, we used relative diameter for direct comparison among plots because trees with large relative diameter would shelter trees with smaller relative diameters regardless of plot identity.

We also looked for significant differences between canopy positions and types of injury for all trees that sustained damage (i.e., ND trees were not evaluated). We examined differences in damage categories between tree attributes using Chi-square tests. However, a preliminary analysis identified that heavily skewed distributions existed amongst the four damage categories. To account for this, we conducted our analyses on two separate categorical groupings: (1) the original types (CD, BB, SB, and UR); and (2) reclassified groups into two categories with the three most severe damage types combined (CD and BB + SB + UR). The reclassification helped avoid complications with Chi-square analyses as a small proportion of trees were either SB or UR, whereas most were categorized as CD.

To test H1, we used Chi-square tests to determine if tree mortality and damage category differed between evergreen broadleaf and any other lifeform group (i.e., evergreen coniferous, marcescent, and deciduous species). Further, ANOVAs were used to test differences in the percentage of crown loss between evergreen broadleaf and the other lifeform groups with plot number as a random factor. To test H2, we used Chi-square tests to determine if tree mortality and damage category differed between evergreen coniferous and any other lifeform group (i.e., marcescent and deciduous species), between marcescent and deciduous species, and among pine species. ANOVAs were used to test differences in the percentage of crown loss between evergreen coniferous and the other lifeform groups, between marcescent and deciduous species, and among pine species with plot number as a random factor. Among the five pine species sampled in our study, shortleaf pine (*P. echinata*) and spruce pine (*P. glabra*) were excluded from analyses due to the small sample size (only 16 and 18 overstory stems for each). As a result, we compared three southern pine species: loblolly pine, longleaf pine, and slash pine (*P. ellittii*). To test H3, we used Chi-square tests to determine if tree mortality and damage category differed among the four forest types for evergreen coniferous and evergreen broadleaf lifeform groups. ANOVAs were used to test differences in crown damage among the four forest types for evergreen coniferous and evergreen broadleaf lifeform groups with plot number as a random factor. All the

ANOVAs were conducted using the sampling plots as the minimum analytic units.

Post-hoc pairwise Chi-square tests (with fdr method for adjusting p-value) were conducted to compare all differences between groups using rcompanion package (Mangiafico, 2019). ANOVAs were conducted to examine differences among treatments using nlme package (Pinheiro et al., 2018). Tukey's post hoc tests were conducted to compare all differences between groups after ANOVAs using lsmeans package (Lenth, 2016). To meet the assumptions of hypothesis testing, we checked normality and homogeneity of data prior to conducting ANOVAs. Log transformations were used when needed. A p-value < 0.05 was regarded as statistically significant. All the analyses were conducted in R statistical package (Version 3.3.2, R Core Team, 2016).

3. Results

Our study sampled a total of 12,958 stems from 73 tree species in the 107 plots established in the nine study areas (see Appendix B for a more detailed summary). More trees were sampled in the understory (7,569 stems) than in the overstory (5,389 stems), with most evergreen coniferous trees (86.0%) found in the overstory and most evergreen broadleaf (88.7%), marcescent (70.3%), and deciduous (71.2%) trees in the understory (Table 2).

3.1. The injury and mortality rates by canopy positions and damage types

About 56% of all over and understory stems were injured in the ice storm (Table 2). Damage (LD and DD) occurred in over 90% of overstory trees, but only about 30% of the understory trees, with a small proportion of all damaged trees (3.7%) dead after one growing season (Table 2). Overstory trees had higher mortality ($p < 0.001$) and were more susceptible to ice storm damage ($p < 0.001$) than the understory trees. The mortality of overstory trees (6.3%) was almost four times as much as that of understory trees (1.8%).

The type of ice storm damage to trees also proved important. For example, regardless of canopy status, most damages from the ice storm were in the form of crown damage. Of the 4,986 overstory and 2,258 understory trees damage by this glaze event, 91.6% and 75.7%, respectively, were primarily impacted by crown damage (Table 3). Understory trees were noticeably more likely to be bent than overstory trees (18.5% versus 2.5%), with little difference in the rates of bole snapping and uprooting between canopy positions.

Mortality patterns also differed by damage type. While most trees were affected by the crown loss, the vast tree mortality (83.8%) came from snapped boles (398 trees), bent boles (41 trees), and uprooting (27 trees) (Table 4). The relative lethality of injury type was also significant: 100% of uprooted trees or trees with snapped boles died, while only 7.6% of trees with bent boles and 0.1% trees with crown damage died after one growing season (Table 4).

3.2. The ice storm influences on the species lifeform, forest composition, and distribution

Regardless of canopy status, tree mortality and damage category differed significantly among the lifeform groups ($p < 0.001$; Tables 2 and 3). Mortality and damage severity patterns of overstory trees followed a consistent order: evergreen broadleaf > evergreen coniferous > marcescent > deciduous (Fig. 2a and c). However, evergreen conifers in the understory suffered much higher mortality and damage severity (i.e., BB, SB, and UR) than other lifeform groups (Fig. 2b and d). For trees that suffered CD, lifeform group affected percent crown loss for overstory trees ($p < 0.001$) but not for understory trees ($p = 0.544$). Crown loss in the overstory ranked as follows: evergreen broadleaf > marcescent > evergreen coniferous > deciduous (Fig. 3).

Significant differences in tree mortality were found among the three pine species ($p < 0.05$). Overstory mortality was higher for longleaf pine (9.6%) when compared to loblolly pine (6.2%), while understory mortality was the highest for loblolly (11.6%), followed by longleaf (4.4%) and slash pine (0.0%) (Fig. 4a and b). Similarly, significant differences in damage type were found among the three pine species ($p < 0.001$). Severe damage (i.e., BB, SB, and UR) was the highest for slash pine (20.6% overstory and 90.9% understory), followed by longleaf (14.0% overstory and 54.6% understory) and loblolly pine (7.1% overstory and 37.8% understory) (Fig. 4c and d). For those stems that suffered CD, overstory trees (25.1%) lost more crown than understory trees (10.3%) ($p < 0.001$, Fig. 5). Moreover, slash pine (35.5%) lost more crown than longleaf (19.4%) or loblolly pine (20.4%) in the overstory ($p < 0.01$, Fig. 5).

The mortality of pine and evergreen broadleaf trees in the overstory differed among the four forest types ($p < 0.01$). Pine trees had the highest mortality rate in the PINE (8.2%) forest type, followed by UHW (5.9%), BHW (3.7%), and UPH (1.5%) forest types (Fig. 6a). Evergreen broadleaf trees had the highest mortality in BHW (31.0%) forest type, followed by UHW (14.7%), PINE (11.1%), and UPH (10.1%) forest types (Fig. 6a). The type of damage sustained to overstory pine and evergreen broadleaf trees from the ice storm also differed among the four forest types ($p < 0.001$). Pine trees suffered more severe damage (i.e., BB, SB, and UR) in the PINE (10.6%) forest type, followed by UHW (6.4%), BHW (5.0%) and UPH (2.1%) forest types (Fig. 6b). Evergreen broadleaf trees suffered more severe damage in BHW (31.8%) forest type, followed by PINE (20.8%), UHW (20.7%) and UPH (14.8%) forest types (Fig. 6b). For those trees that suffered CD, pine trees in UHW (35.0%) forest type lost more crown than those in PINE, UPH, and BHW forest types ($p < 0.05$). However, evergreen broadleaf trees did not differ in their percentage of crown loss among the four forest types

Table 2
Status (ND, DL, and DD) of the sampled stems one growing season after the ice storm by the lifeform groups in the overstory and understory. Values represent numbers of stems with the percentage in parentheses (totals may not add to 100% due to rounding errors). Comparisons were conducted separately for the two canopy positions. Different letters indicate significant differences in the stem status ($p < 0.05$) among the four lifeform groups.

Classification	No damage (ND)	Damaged but alive (DL)	Damaged but dead (DD)	Total
Overstory	**403 (7.5)**	**4644 (86.2)**	**342 (6.3)**	**5389 (100.0)**
[c]Deciduous	253 (17.3)	1163 (79.7)	44 (3.0)	1460 (100.0)
[b]Marcescent	29 (4.8)	540 (89.3)	36 (5.9)	605 (100.0)
[b]Evergreen coniferous	94 (3.1)	2750 (89.8)	219 (7.1)	3063 (100.0)
[a]Evergreen broadleaf	27 (10.3)	191 (73.2)	43 (16.5)	261 (100.0)
Understory	**5311 (70.2)**	**2125 (28.0)**	**133 (1.8)**	**7569 (100.0)**
[d]Deciduous	2766 (77.0)	803 (22.4)	20 (0.6)	3589 (100.0)
[c]Marcescent	873 (60.9)	532 (37.1)	28 (2.0)	1433 (100.0)
[b]Evergreen coniferous	173 (34.6)	285 (57.0)	42 (8.4)	500 (100.0)
[a]Evergreen broadleaf	1499 (73.2)	505 (24.7)	43 (2.1)	2047 (100.0)
Total	**5714 (44.1)**	**6769 (52.2)**	**475 (3.7)**	**12,958 (100.0)**

Table 3
Ice storm damage types (CD, BB, SB, and UR) to the sampled stems by the lifeform groups in the overstory and understory. Values represent numbers of damaged stems with the percentage in parentheses (totals may not add to 100% due to rounding errors). Comparisons were conducted separately for the two canopy positions. Different letters indicate significant differences in damage types ($p < 0.05$) among the four lifeform groups.

Classification	Crown damage (CD)	Bent bole (BB)	Snapped bole (SB)	Uprooted (UR)	Total
Overstory	**4569 (91.6)**	**122 (2.5)**	**279 (5.6)**	**16 (0.3)**	**4986 (100.0)**
[c]Deciduous	1155 (95.6)	19 (1.6)	24 (2.0)	9 (0.8)	1207 (100.0)
[b]Marcescent	533 (92.5)	16 (2.8)	26 (4.5)	1 (0.2)	576 (100.0)
[b]Evergreen coniferous	2696 (90.8)	72 (2.4)	196 (6.6)	5 (0.2)	2969 (100.0)
[a]Evergreen broadleaf	185 (79.1)	15 (6.4)	33 (14.1)	1 (0.3)	234 (100.0)
Understory	**1710 (75.7)**	**418 (18.5)**	**119 (5.3)**	**11 (0.5)**	**2258 (100.0)**
[d]Deciduous	691 (84.0)	113 (13.7)	18 (2.2)	1 (0.1)	823 (100.0)
[c]Marcescent	438 (78.2)	95 (17.0)	27 (4.8)	0 (0.0)	560 (100.0)
[b]Evergreen coniferous	177 (54.1)	109 (33.3)	39 (11.9)	2 (0.6)	327 (100.0)
[a]Evergreen broadleaf	404 (73.7)	101 (18.4)	35 (6.4)	8 (1.5)	548 (100.0)
Total	**6279 (86.7)**	**540 (7.4)**	**398 (5.5)**	**27 (0.4)**	**7244 (100.0)**

($p = 0.656$, Fig. 7a).

Based on data in Appendix A, significant differences in the northern-most distribution were found among the lifeform groups ($p < 0.01$). As expected, the northern-most distribution of deciduous species exceeded that of evergreen coniferous ($p < 0.05$) or evergreen broadleaf ($p < 0.01$) species. But there was no significant difference between the northern-most distribution of deciduous species and that of marcescent species ($p = 0.710$).

4. Discussion

Given ice storms are among the most frequent and injurious disturbances in temperate forests (Irland, 2000; Smith, 2000), it is likely that ice storms have played a significant role in influencing the forest composition and distribution of the southeastern US. This appeared to be especially true in southern and coastal regions, where forests often have mixed species and lifeform composition. To better understand these influences, we considered the varying factors involved in the ecological processes.

4.1. The ice storm damages to trees

The 2014 ice storm event caused significant damage to forest trees in the nine study areas in South Carolina. Although tree mortality was low, ice storm injury was extensive, especially among overstory trees. The most common type of ice storm damage we observed was the crown loss, which also likely had the least impact on long-term survival (Lafon, 2004; Nagel et al., 2016). The frequency and degree of crown loss in this study were not surprising, given that our study areas experienced accumulations of between 12.7 and 25.4 mm. Typically, ice accumulations from 6.4 mm to 12.7 mm would remove small or faulty branches, while accumulations from 12.7 mm to 25.4 mm would produce conspicuous breakage (Lemon, 1961). Ice loading is not the only factor to consider, however, when determining the magnitude of tree damage. For example, major ice storms are often accompanied by strong winds. This combination can exacerbate damage over large areas, with up to 40% tree mortality and up to 80% canopy loss (Irland, 2000; Bragg et al., 2003), and may result in the loss of whole cohorts of unsheltered regeneration (Carvell et al., 1957; Halverson and Guldin, 1995).

In the 2014 ice storm event, the other three damage types (i.e., snapped boles, bent boles, and uprooted) were much less common than the crown loss type but resulted in most tree mortality following one growing season. The canopy trees that snapped or uprooted were immediately removed from the forest canopy, making their long-term survival much less likely. Canopy trees that bent in response to ice accumulation were also likely withdrawn from the canopy, but their fate is less certain, depending on the degree of injury as well as the indirect effect of light competition. Bent trees usually survive if they recover to an upright position, which is primarily related to tree size and age (Bragg et al., 2003). A number of studies have reported that small diameter trees in the understory are more likely to recover from bent boles due to their more flexible stems (Bragg and Shelton, 2010; Priebe et al., 2018). When compared with overstory trees, trees in the understory suffered less ice storm damage, especially severe damage and mortality. This result is expected as overstory trees are more exposed to wind with greater accumulations of glaze, whereas understory trees would have reduced accumulation due to a sheltering effect.

Table 4
Mortality patterns caused by different damage types (CD, BB, SB, and UR) after the ice storm by the lifeform groups in the overstory and understory. Values represent numbers of dead stems with the percentage in parentheses (totals may not add to 100% due to rounding errors). Comparisons were conducted separately for the two canopy positions. Different letters indicate significant differences in mortality patterns caused by the four damage types ($p < 0.05$) among the four lifeform groups.

Classification	Crown damage (CD)	Bent bole (BB)	Snapped bole (SB)	Uprooted (UR)	Total
Overstory	**7 (2.0)**	**40 (11.7)**	**279 (81.6)**	**16 (4.7)**	**342 (100.0)**
[c]Deciduous	0 (0.0)	11 (25.0)	24 (54.5)	9 (20.5)	44 (100.0)
[ac]Marcescent	1 (2.8)	8 (22.2)	26 (72.2)	1 (2.8)	36 (100.0)
[b]Evergreen coniferous	5 (2.3)	13 (5.9)	196 (89.5)	5 (2.3)	219 (100.0)
[a]Evergreen broadleaf	1 (2.3)	8 (18.6)	33 (76.7)	1 (2.3)	43 (100.0)
Understory	**2 (1.5)**	**1 (0.8)**	**119 (89.5)**	**11 (8.3)**	**133 (100.0)**
[a]Deciduous	1 (5.0)	0 (0.0)	18 (90.0)	1 (5.0)	20 (100.0)
[a]Marcescent	1 (3.6)	0 (0.0)	27 (96.4)	0 (0.0)	28 (100.0)
[a]Evergreen coniferous	0 (0.0)	1 (2.4)	39 (92.9)	2 (4.8)	42 (100.0)
[a]Evergreen broadleaf	0 (0.0)	0 (0.0)	35 (81.4)	8 (18.6)	43 (100.0)
Total	**9 (1.9)**	**41 (8.6)**	**398 (83.8)**	**27 (5.7)**	**475 (100.0)**

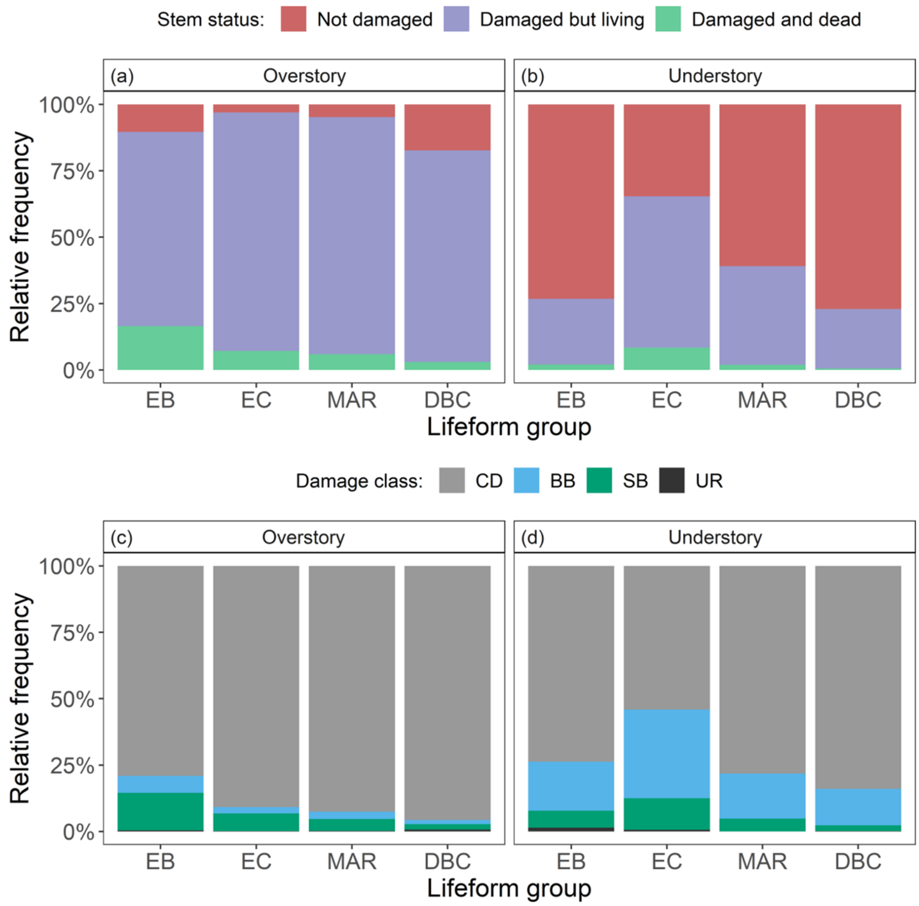

Fig. 2. Mortality and damage severity of four lifeform groups. EB: evergreen broadleaf, EC: evergreen coniferous, MAR: marcescent, DBC: deciduous. CD: canopy damage, BB: bent bole, SB: snapped bole, UR: uprooted.

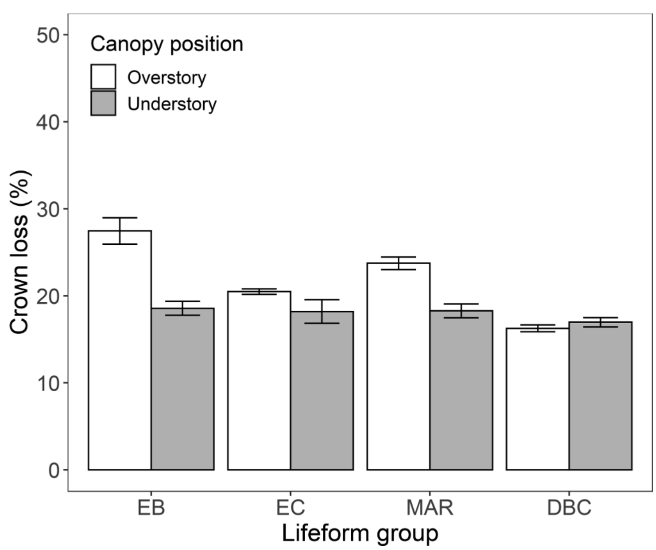

Fig. 3. Crown loss percentage of four lifeform groups. EB: evergreen broadleaf, EC: evergreen coniferous, MAR: marcescent, DBC: deciduous.

4.2. The ice storm influences on the regional forest composition and distribution

Considering that eastern North America experiences the most ice storms among temperate regions in the world (Changnon and Karl, 2003), we believe that ice storms can be an ecological factor limiting the regional distributions of certain tree lifeforms (and, hence, species). Based on our findings, evergreen broadleaf trees are the most susceptible lifeform to ice storms, with higher mortality and damage than other species in the forest overstory. This differential response expresses itself in the taxonomic composition of the stands we evaluated. Among the 11 evergreen broadleaf species, only five species were found in the overstory and of those evergreen broadleaf overstory trees, only 25% were classified as dominant or co-dominant. Thus, species that are sensitive to glaze damage may be able to survive as an understory component but seldom become a part of the canopy (Cao and Peters, 1997). Furthermore, some of the species included in this lifeform (e.g., *Magnolia virginiana*) are documented as trees in their most southerly distribution and shrubs in their northern limits (Priester, 1990). This disparity further supports a previous study by Cao and Peters (1997), who reported that ice storms have prevented canopy dominance by evergreen broadleaf species and favored deciduous forests.

These findings provide evidence to support what has been reconstructed from the paleorecord and other investigations that forest distribution patterns over multiple scales are in part, defined by disturbance patterns, including ice storms. Previous studies showed that the southeastern US was once dominated by evergreen broadleaf forests prior to the Late Cretaceous and Cenozoic (Graham, 1999). However, when the development of extensive ice sheets and the ice-covered Arctic Ocean permitted the invasion of cold waves from the Arctic as intense as at present, these geologically abnormal cold waves gradually eliminated broadleaved evergreen species while leaving broadleaved deciduous trees (Wolfe, 1979). Today, the southeastern US is dominated by deciduous broadleaf or evergreen coniferous forests (Powell et al., 1993) while southeastern China is dominated by evergreen broadleaf forests (Cao and Peters, 1997) despite both regions have the same humid and warm temperate with a hot summer as described by

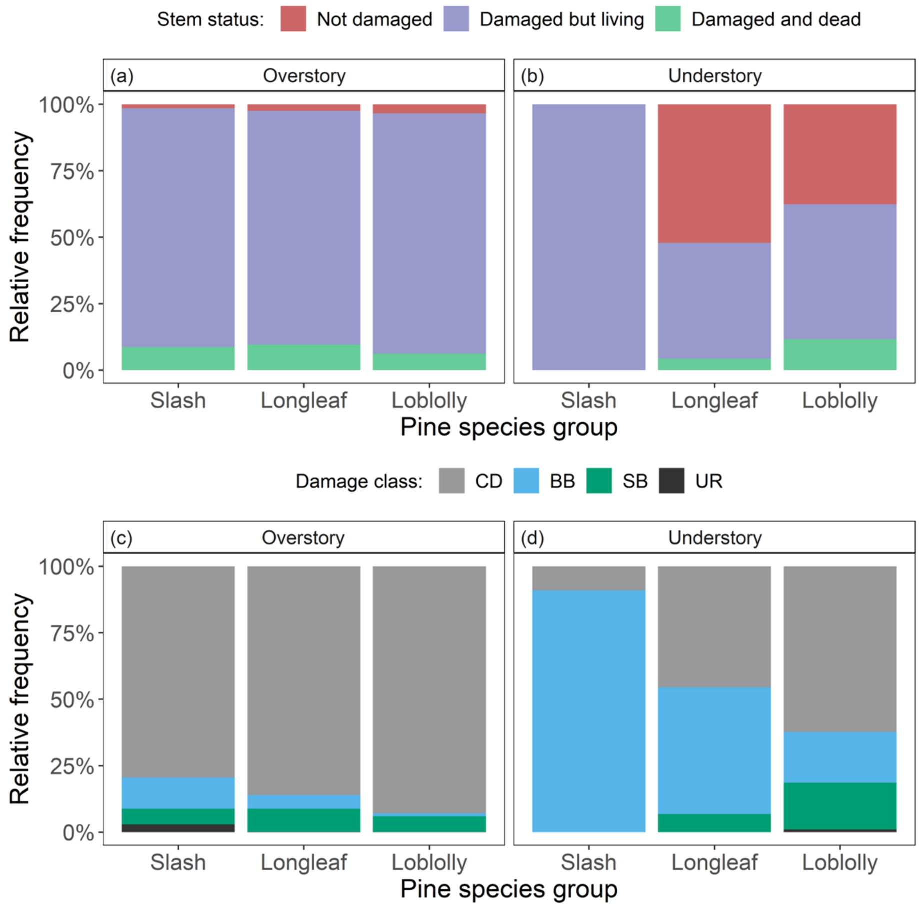

Fig. 4. Mortality and damage severity of three pine species groups. CD: canopy damage, BB: bent bole, SB: snapped bole, UR: uprooted.

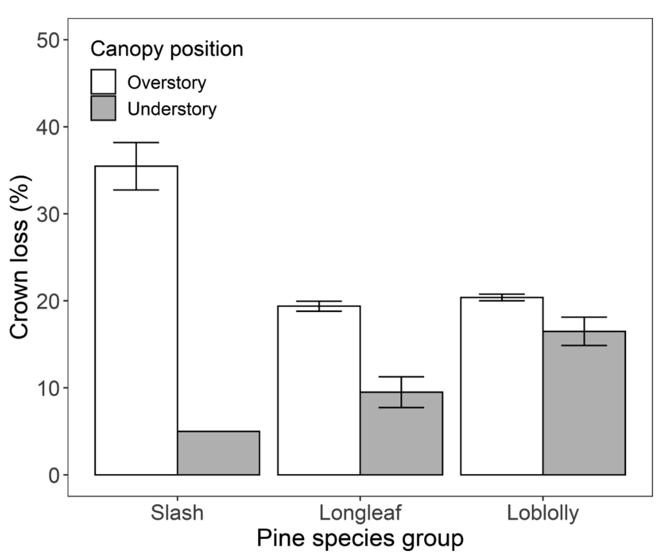

Fig. 5. Crown loss percentage of the three pine species groups. Only one slash pine suffered crown damage in the understory (no error bar).

Köppen's (1884) classification. This observed difference in forest type suggests that factors other than climate may contribute to forest composition in the southeastern US.

Another supporting line of evidence that ice storms can help determine regional species distributions comes from the differences in response among the three pine species. Because the frequency and intensity of ice storms increase with increasing latitude and along the gradients from the Atlantic coast to the piedmont to the Appalachian Mountains in the southeastern US, forest community composition must reflect a range of effects. Corresponding with these gradients, we found that evergreen coniferous trees (slash pine, longleaf pine, and loblolly pine) were much more susceptible to severe damage and mortality from the ice storm than deciduous trees both in the overstory and understory. This consistent with the work of McCarthy et al. (2006) who reported loblolly pine to be several times more likely to be killed by ice storms than deciduous tree species. Such susceptibility could contribute to the limits of our studied pine species and would help explain the increasing dominance of deciduous species from the coast to the mountains (with increasing elevation as a proxy for increasing latitude). The order of the northern geographic borders for the three pine species were loblolly pine (39.51° N), longleaf pine (36.85° N), and slash pine (33.29° N), respectively. Among the three pine species, slash pine suffered more severe damage than longleaf pine, and longleaf pine suffered more severe damage than loblolly pine, which matched with their most northerly distributions. These results support the hypothesis that the northerly distribution of southern pine species can also be related to their resistance to (or tolerance of) ice storm damage.

Finally, we explored possible effects of stand conditions on the susceptibility of evergreen species to ice storms using forest type as a surrogate. Our findings indicated that evergreen broadleaf trees in the overstory suffered the highest mortality and severe damage in bottomland forests. Wetter soils coupled with more ice accumulation on evergreen leaves likely caused elevated mortality and damage. However, pine trees had the highest mortality and severe damage in upland forest types, which contradicted the expected results supported by evergreen broadleaf trees. Most of the sampled pines were distributed in uplands rather than bottomlands. For example, the total number of pines in pine forest types (2,491 stems) was > 30 times of that in bottomland hardwood forest types (81 stems). Fewer pines in

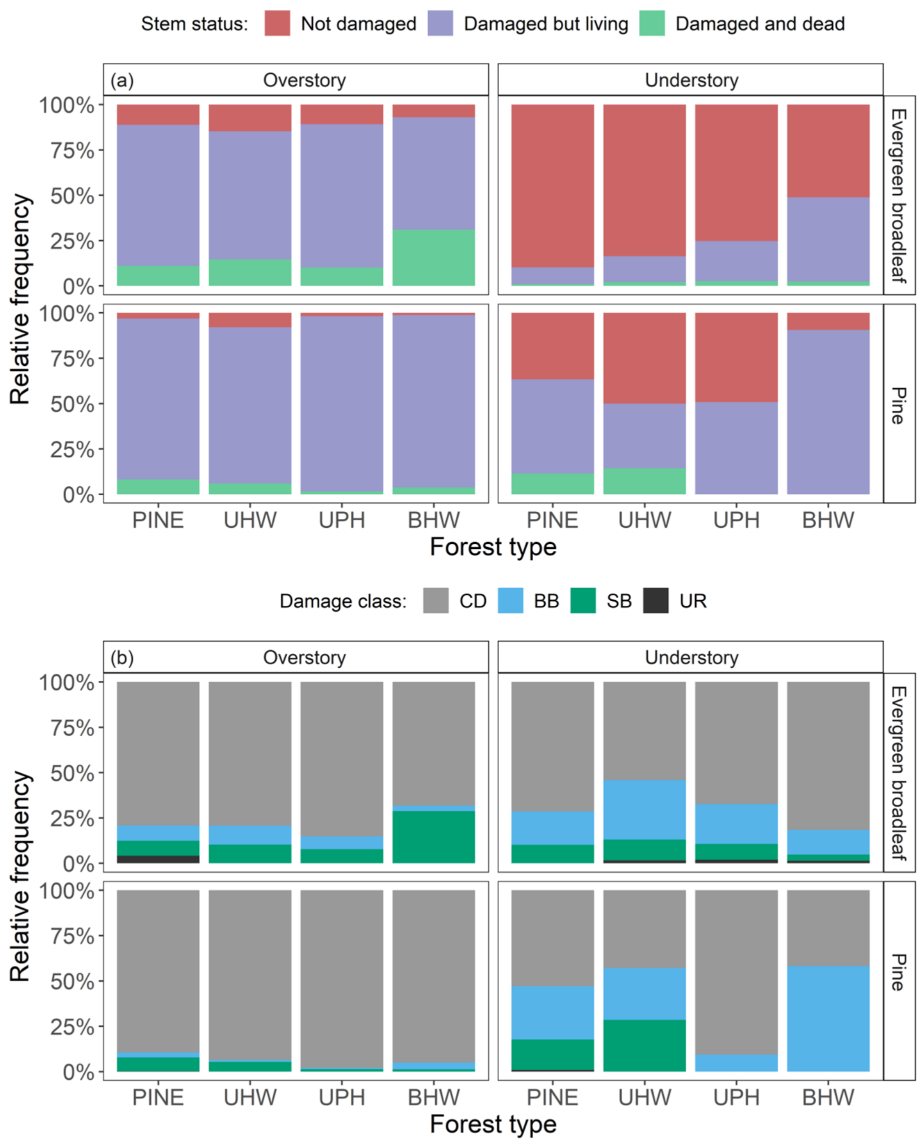

Fig. 6. Mortality and damage severity of pine and evergreen broadleaf species. CD: canopy damage, BB: bent bole, SB: snapped bole, UR: uprooted. PINE: upland pine, UHW: upland hardwood, UPH: mixed upland pine and hardwood, BHW: bottomland hardwood.

the bottomland hardwood plots might only reflect species-level differences but not stand-scale effects.

The current study mainly evaluated the potential influence of the ice storm on tree species distribution but we did not consider other climatic factors such as the winter minimum temperature or the late spring frost. Previous studies indicated that cold events were probably one key factor determining the distribution range of many woody species (Sakai and Weiser, 1973; Daly et al., 2012; Muffler et al., 2016). The earlier start of the growing season during recent decades owing to global warming further increases the risk of cold event damage (Hufkens et al., 2012). For example, a severe late frost event that occurred in spring 2007 in the eastern US caused extensive woody species damage in the form of withered or shed foliage and shoots (Gu et al., 2008). Muffler et al. (2016) linked the spatial distribution of 170 woody species to their damage conditions after an extreme late frost event occurred in May 2011 in Germany and found that the northern distribution limits could be explained by their late frost sensitivity. The US Department of Agriculture Plant Hardiness Zone Map provided the relationships among climatic factors and plant distribution patterns, which is an important reference for determining the distribution ranges of tree species in the US under extreme cold events (Daly et al., 2012). Since ice storms are stronger extreme climatic events and share some features of cold events, understanding the influence of ice storms may also provide opportunities to refine the plant hardiness zone map.

Scientific understanding of how ice storms may change in intensity, frequency, and spatial or temporal distribution in response to global warming is limited (Klima and Morgan, 2015; Groisman et al., 2016). Climate change may affect ice storms in the following ways: (1) a poleward shift and season shortening with the increase in temperature; (2) in areas where an increase in precipitation is likely, ice storms may become more frequent and intense; and (3) while climate change will affect continental trends in precipitation patterns, local characteristics such as mountainous topography can supersede larger effects (Klima and Morgan, 2015). Furthering our knowledge of species-specific response to ice storms will only aid in predicting future forest composition when coupled with environmental data. According to our findings, broadleaf evergreen species, southern coastal pine species, and marcescent species may benefit from poleward shifts in ice storms with climate change. Further, based on biological and abiotic considerations, species such as longleaf pine, slash pine, loblolly pine, southern magnolia, live oak (*Q. virginiana*), laurel oak (*Q. laurifolia*), and American hornbeam (*Carpinus caroliniana*) are expected to gain in abundance

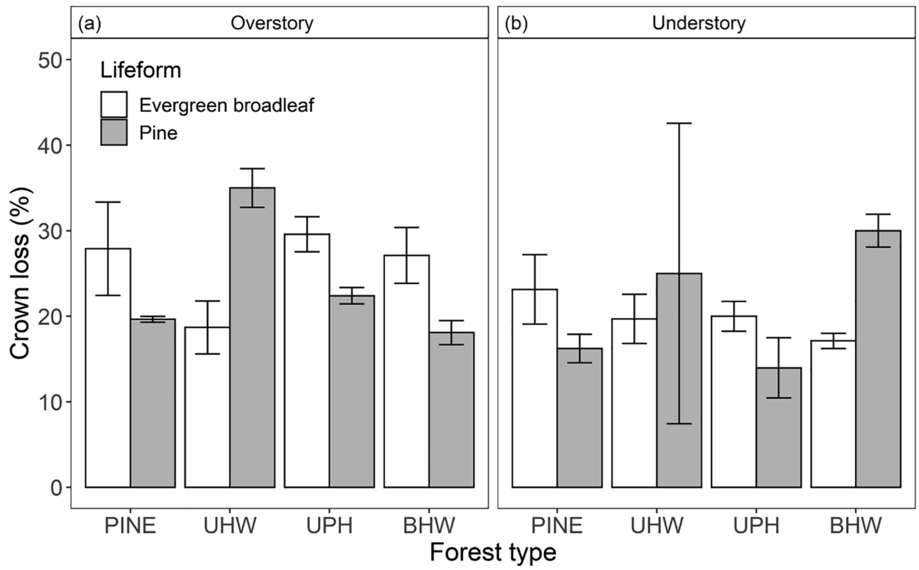

Fig. 7. Crown loss percentage of pine and evergreen broadleaf species. PINE: upland pine, UHW: upland hardwood, UPH: mixed upland pine and hardwood, BHW: bottomland hardwood.

even under the worst climate change model scenarios (Prasad et al., 2014). However, if the unique terrain of the southeastern US continues to influence the spatial pattern of ice storms, the expansion of these species north and westward to the piedmont interior may be limited.

5. Conclusions

Unlike most previous studies, which focused solely on deciduous broadleaf tree species (Abell, 1934; Carvell et al., 1957; Rhoades, 1999; Whitney and Johnson, 1984) or commercial conifer plantations (Amateis and Burkhart, 1996; Belanger et al., 1996; McKellar, 1942), we evaluated four major lifeform groups for any possible differential responses to catastrophic glazing. We found that tree mortality and damage varied significantly between overstory and understory trees, among four major lifeform groups, and among tree species with the same life form. Compared with understory trees, overstory trees are more prone to damage and suffered higher mortality. Evergreen broadleaf species, which have coastal and southerly distributions, sustain more severe damage than deciduous trees. Among the studied pine species, loblolly pine had fewer stems suffer severe damage and mortality than slash pine and longleaf pine, which agreed with their northern range limits. When combined, our results suggest that the periodic occurrence of injurious ice storms can greatly influence the abundance and distribution of tree species.

At the regional scale, it is well-documented that forests in the eastern US have been strongly influenced by several major and reoccurring disturbances such as fires, hurricanes, and ice storms. While our results provide only limited evidence that frequent ice storms in eastern North America can limit the dominance of evergreen broadleaf or coniferous species in the canopy, the fact that this region has the most ice storms in temperate zones (Changnon and Karl, 2003) offers a mechanism upon which more specific testing is possible.

Given that ice storm-related mortality can remain high for years following a single event (e.g., Bragg and Shelton, 2010), additional monitoring is warranted to determine the long-term fate of damaged trees. Further, monitoring should include measures of tree health as stress from ice damage can result in highly susceptible host material for secondary attacks from insects and pathogens (de Groot et al., 2018). To further explore the role of ice storms as a factor regulating tree species distribution, future research should also conduct cross-continental comparisons (e.g., between eastern North America and eastern China) to elucidate the linkage between ice storms and forest composition and distribution.

CRediT authorstship contribution statement

Deliang Lu: Data curation, Formal analysis, Methodology, Writing - original draft. **Lauren S. Pile:** Data curation, Methodology, Supervision of field data collection, writing - review & editing. **Dapao Yu:** Data curation, Methodology, Writing - review & editing. **Jiaojun Zhu:** Writing - review & editing. **Don C. Bragg:** Writing - review & editing. **G. Geoff Wang:** Conceptualization, Funding acquisition, Methodology, Project administration, Writing - review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2020.118177.

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