379

Interactions between wind and fire disturbance in forests: Competing amplifying and buffering effects

Jeffery B. Cannon[a,*], Suzanne K. Henderson[b], Michael H. Bailey[b], Chris J. Peterson[b]

[a] Colorado Forest Restoration Institute, Department of Forest and Rangeland Stewardship, Colorado State University, 1472 Campus Delivery, Fort Collins, CO 80523, USA
[b] Department of Plant Biology, University of Georgia, Athens, GA 30602, USA

A B S T R A C T

Many studies of ecological disturbance highlight the unexpected impact that compounded disturbances have on communities. One of the well-studied mechanisms by which forest wind and fire disturbances interact is that wind damage increases flammable fuels—amplifying the effects of fire—leading to unexpected changes in vegetation composition. However, wind disturbance may also buffer the effects of fire through mechanisms such as disrupting fuel continuity. The extent to which wind and fire disturbances buffer, or reduce, the magnitude of ecological change has been less well studied. In this study, we winched trees in a *Pinus taeda* L. forest to simulate wind damage in experimental plots and combined this treatment with prescribed fire. This design allowed investigation of how forest regeneration responds to combinations of wind and fire disturbance, with particular emphasis on whether disturbance interactions were amplifying or buffering. We also tested for evidence of two mechanisms of disturbance interaction that are expected to buffer the cumulative ecological impact of wind and fire disturbances, testing (1) whether wind damage increased resprouting response following fire and (2) whether seedlings on tip-up mounds were protected from fire. We identified evidence for a combination of disturbance interactions occurring in both an amplifying direction (e.g., rapid recruitment and establishment of *Rhus copallinum*) as well as interactions occurring in a buffering direction (e.g., increased resilience in resprouting saplings in winched plots). Such varying responses may lead to a heterogeneous mixture of amplifying and buffering effects following compounded disturbances, such that at the stand scale, the aggregate regeneration response of two disturbances is the net effect of these individual interaction mechanisms. The results of this study highlight that mechanisms of disturbance interactions may vary spatially and temporally and may be best understood by considering factors such as disturbance severity, species life history traits, and timing between disturbances.

1. Introduction

Disturbances have long been studied as important drivers of ecological processes in communities (e.g., Cowles, 1899). Some recent studies of disturbance highlight the profound impact of compounded disturbances, particularly when ecosystems are affected by multiple disturbances in rapid succession (Buma, 2015; Cannon et al., 2014; Frelich, 2002; Paine, 1966; Scheffer et al., 2001). In these cases, the impacts of multiple disturbances may be multiplicative rather than additive, leading to drastic, unexpected, or non-linear changes in ecosystem structure, composition, or diversity (Buma and Wessman, 2011; Frelich and Reich, 1999; Paine et al., 1998; Scheffer et al., 2001). Through a variety of mechanisms, compounded disturbances may interact such that the occurrence of the first disturbance increases the

likelihood, intensity, or severity of a second disturbance (Buma, 2015; Cannon et al., 2017; Folt et al., 1999). One striking illustration of compounded disturbances that interact in an amplifying direction includes the observation that catastrophic fires often follow severe hurricanes in coastal forests. By increasing surface fuels (e.g., downed woody debris), hurricanes can amplify the effect of subsequent wildfires and lead to unexpected change in overstory composition and structure (Liu et al., 2008; Myers and Van Lear, 1998).

Research on disturbance interaction mechanisms often emphasizes catastrophic scenarios; however, a growing body of recent evidence suggests that in many cases, disturbances can also reduce the probability, intensity, or severity of subsequent disturbances and instead interact in a buffering direction (Cannon et al., 2017; *sensu* Folt et al., 1999). Early studies of interactions between insect outbreaks and

---

* Corresponding author.
  E-mail address: jbcannon.pubs@gmail.com (J.B. Cannon).

subsequent fires hypothesized that outbreaks may increase fire severity (Amman and Schmitz, 1988); yet later studies revealed that insect outbreaks may instead reduce fire likelihood or severity in many cases (Harvey et al., 2014; Meigs et al., 2016,2015). Because of the complexity of disturbance interactions, it is critical to understand the mechanisms that drive individual interactions to improve predictions of how ecosystems respond to compounded disturbances (Johnson and Miyanishi, 2007).

We focus on interactions between two disturbances common to eastern U.S. forests—wind damage and prescribed fire. Forest wind disturbance is widespread with profound impacts on vegetation structure and landscape dynamics (Beatty, 1984; Cannon et al., 2016; Chambers et al., 2007; Dahal et al., 2014; Dale et al., 2001; Peterson and Pickett, 1995; Ulanova, 2000). Prescribed fire is a common forest management tool in both eastern and western U.S. forests to manage wildfire hazard, wildlife, and restore rare ecosystems (Addington et al., 2015; Agee and Skinner, 2005; Cannon and Brewer, 2013; Glitzenstein et al., 1995; Main and Richardson, 2002; Melvin, 2012). Canopy removing disturbances such as wind damage can increase the probability, intensity, or severity of subsequent fires by increasing woody or herbaceous surface fuels. They may also delay recovery from fire via removal of propagule sources leading to amplifying effects (Buma and Wessman, 2011; Chambers et al., 2016; D'Amato et al., 2011; Foster, 1988; Holzmueller and Jose, 2011; Kulakowski and Veblen, 2007; Liu et al., 2008; Myers and Van Lear, 1998; Turner et al., 1994). However, in some cases, wind damage may act in a buffering direction, instead reducing the probability, intensity, or severity of subsequent fire. The large woody debris produced by windstorms (Busing et al., 2009) may not be available for combustion during cool-season prescribed fires, which suggests that interactions between wind and fire may depend, in part, on exogenous factors such as weather conditions or internal factors such as size distribution of woody debris (Cannon et al., 2017, 2014). Lack of leaf litter input from sparse overstory trees may disrupt fuel continuity, further decreasing fire severity and extent (Cannon et al., 2014; O'Brien et al., 2008; Ross et al., 2009). Besides interactions involving fuel, other buffering interaction mechanisms may play a role in shaping ecosystem response to wind damage and fire.

At least two additional buffering interaction mechanisms related to treefall mound microsites and resprouting may decrease fire impacts as a result of prior wind disturbance and influence recovery following compounded disturbances. First, prescribed fire frequently kills the aboveground portions of many hardwoods which can generally recover rapidly through basal sprouting, made possible by utilizing belowground carbohydrate reserves (Hodgkins, 1958; Robertson and Ostertag, 2009). Increased light availability following wind damage may accelerate sapling recovery following fire compared to recovery without concomitant overstory removal, potentially facilitating a buffering interaction mechanism. Second, a prominent legacy of forest blowdowns are large tip-up mounds formed when trees are uprooted. Tip up mounds are elevated above the intact forest floor and are characterized by a distinct microclimate and plant species composition (Beatty, 1984; Betras et al., in press; Peterson et al., 1990; Sobhani et al., 2014; Ulanova, 2000). This slight micro-elevation of woody seedlings above the forest floor has been previously observed to protect seedlings from herbivory (Krueger and Peterson, 2006; Long et al., 1998), as well as provide refuge from competition with dense understory vegetation (Betras et al., in press; Nakashizuka, 1989). Analogously, mound microsites may protect established plants from prescribed fire as radiative energy decreases with height above the flame (Cruz et al., 2011).

Given that disturbance interactions can occur through diverse mechanisms, a recent review of wind and fire interactions posits that disturbance interactions may act in both amplifying and buffering directions in the same pair of disturbances; it may be inappropriate to consider compounded disturbances to be wholly synergistic or antagonistic when multiple mechanisms drive the interaction (Cannon et al.,

2017). This parallels earlier examples where initial application of succession concepts was monolithic, but was followed by the realization that the net effect is a spatial or temporal composite of mechanisms. Connell and Slatyer's (1977) classification of successional interactions into inhibition, tolerance, and facilitation could not wholly describe oldfield succession (Armesto and Pickett, 1986; Hils and Vankat, 1982); later consideration revealed these mechanisms operated simultaneously (Pickett et al., 1987; Werner and Harbeck, 1982).

Here, we test the hypothesis that amplifying and buffering interaction mechanisms co-occur, and examine how the coupling of wind damage and prescribed fire affect woody understory structure, composition, and diversity. In this study, we winched trees to simulate severe wind damage in experimental plots and crossed this treatment with prescribed fire using a factorial design. We measured the response of woody understory plants to disturbance combinations to identify amplifying effects, buffering effects, or a combination of effects. We also evaluated evidence for two specific mechanisms of wind–fire disturbance interactions, testing whether (1) basal resprouting from saplings after fire is more rapid when burning is preceded by wind damage, and whether (2) tree seedlings established on mounds are less vulnerable to fire. We expect species to respond to wind, fire, or combinations of disturbance according to species-specific life history traits and structural characteristics, leading to a heterogeneous mixture of interaction mechanisms that act in both amplifying and buffering directions.

2. Methods

2.1. Experimental design and approach

The Piedmont National Wildlife Refuge (PNWR) is located in central Georgia (33.11°, –83.68°). The study area within the PNWR was dominated by 80 + year old *Pinus taeda* L. trees with a mixed-hardwood sapling understory consisting primarily of *Liquidambar styraciflua* L. and *Acer rubrum* L. saplings and a seedling layer largely consisting of *P. taeda*. Soils in the study area are well drained, consisting of Davidson series loams on broad ridge tops and clay loams on rounded ridges and hillsides adjacent to streams (Payne, 1976). We established twelve 0.125 ha plots (Fig. 1) within a single burn unit which received prescribed fires in 2004, 2006, and 2009 (Carl Schmidt, US Fish and Wildlife Service, personal communication). The selected plots had a standing tree (> 5 cm dbh) basal area of 17–34 m^2 ha^{-1} and tree densities ranged from 130 to 580 stems ha^{-1}. To investigate the interactive effects of wind and fire disturbance, we used a 2 × 2 factorial design with four combinations of simulated wind disturbance and prescribed fire. In 2012, we treated six plots with simulated wind disturbance, and in 2013, the wind disturbance treatments were crossed with a cool season prescribed fire—resulting in combinations winched and burned plots, burned only plots, winched only plots, and control plots with three replicates (Fig. 1).

In order to impose realistic changes in forest structure and light levels, we simulated wind disturbance in the six winched plots by using static winching to pull down approximately 80% of basal area starting with the largest trees (Figs. 1 and 2). We applied tension to target trees using a system of nylon straps, a snatch block pulley, and a steel cable until trees snapped or uprooted (Cannon et al., 2015, 2014). To simulate typical tornado outcomes, we winched trees northward (Peterson, 2007), and winched between March and May, when significant tornado disturbance occurs in the region (Peterson, 2000). We created 40 m diameter gaps (0.125 ha) as this was the maximum size we could practically implement with replication. Because this size is on the lower end of typical gap sizes created by tornados (Zenoble and Peterson, 2017), we created circular gaps to minimize edge effects. We mimicked many aspects of a natural windstorm, but some effects such as heavy rain and stripping of leaves by wind could not be adequately simulated (Cooper-Ellis et al., 1999). Approximately one year after winching (9 April 2013), the PNWR staff and volunteers implemented a prescribed
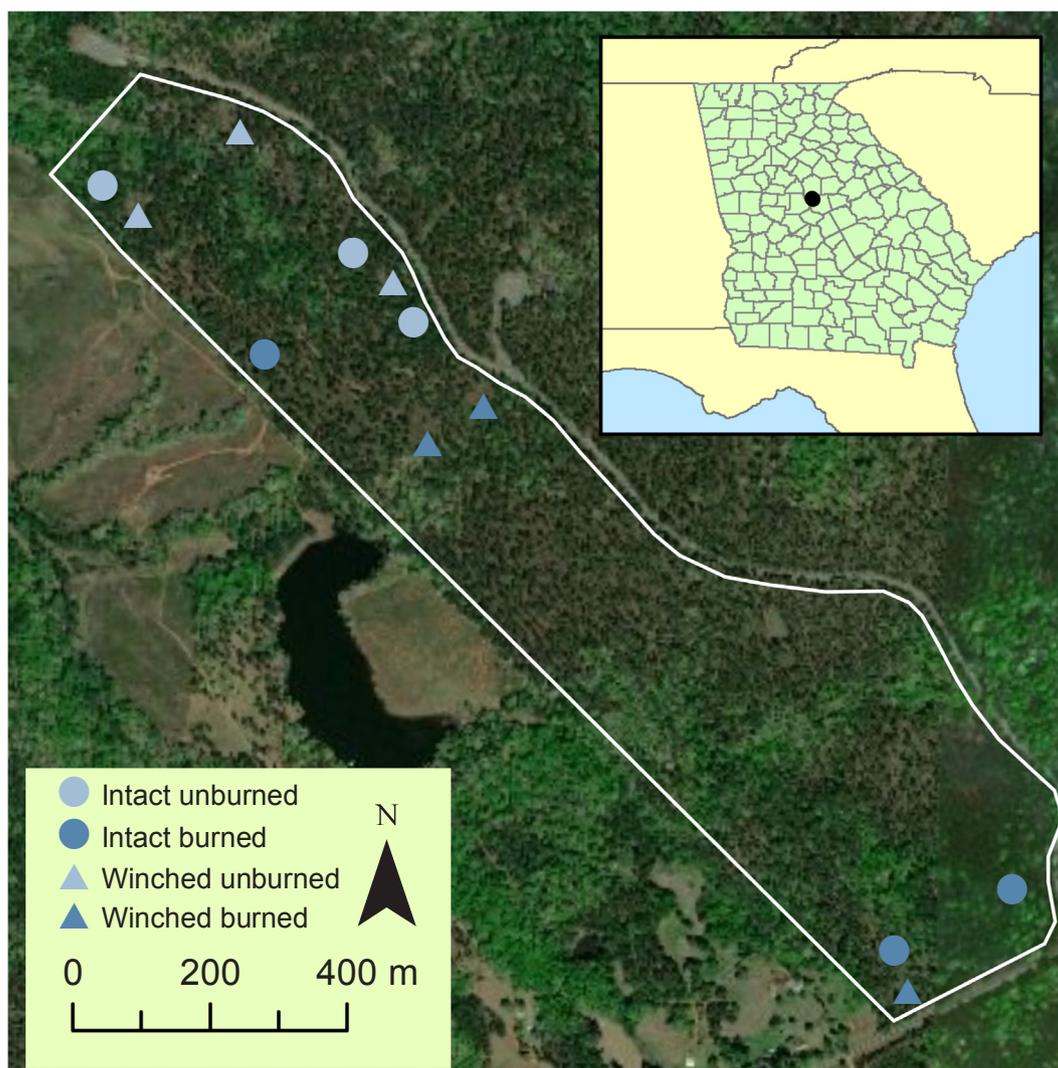
Fig. 1. Map of study area within the Piedmont National Wildlife Refuge illustrating locations of twelve 0.125 ha plots. Intact plots are indicated by circles and winched plots are indicated by triangles. Burned plots (light blue) and unburned (dark blue) plots are indicated. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

fire in half of the study plots with the objective to remove understory competition from hardwoods (Fig. 1). Ambient air temperatures during the burn ranged from 26 to 27 °C, and relative humidity decreased from 52 to 40% over the course of the fire. Flame lengths ranged from < 0.5 m for backing fires to 2.5–3.5 m for heading fires. Although fuel accumulation was higher in winched plots, available fuel was similar and extreme fire characteristics in winched plots were limited to the relatively small area within downed tree crowns (Cannon et al., 2014). Further details on fuel conditions and fire characteristics can be found in Cannon et al. (2014).

We used two approaches to investigate interactive effects of wind damage and fire on understory structure and composition. First, we conducted surveys of woody understory vegetation and used linear mixed models to test for differences in density, size, composition, and species diversity of regeneration among the four treatment combinations. We complemented these analyses with an ordination of species composition to aid in interpretation of interactive effects on regeneration composition. Second, we established two additional experiments to test for evidence of specific buffering interaction mechanisms including testing whether wind damage may ameliorate the impacts of burning by (1) increasing vigor of resprouts or (2) providing fire refugia for seedlings that are established on tree tip-up mounds. We discuss the sampling and statistical analyses for each of these approaches below.

2.2. Interactive effects on understory structure, composition, and diversity

To capture overall changes in woody understory vegetation due to disturbance combinations, we surveyed woody saplings (≥ 1.37 m tall and < 5 cm dbh) and seedlings (< 1.37 m tall). We did not measure sprouting response of overstory trees, as we expected them to be minimally affected by low-intensity prescribed fire. We established eight $9 \, \text{m}^2$ sampling quadrats within each plot (96 total). Within quadrats, we tagged and identified all living saplings to species and measured sapling height to the nearest 1 cm and diameter at breast height (dbh) and diameter at root collar (drc) to the nearest 0.1 cm. We re-measured saplings for growth and survival from 2011 to 2014, including a pre-disturbance survey (2011), a survey between winching and fire disturbances (2012), and two post-fire surveys (2013–2014). Similarly, we established four $1 \, \text{m}^2$ seedling quadrats within each plot (48 total). In seedling plots, we tagged and identified each living seedling to species and measured plant height to the nearest 1 cm. We monitored seedlings from 2011 to 2013, including a pre-disturbance survey (2011), a survey between winching and fire disturbances (2012), and one post-fire survey (2013). The understory survey resulted in a database of approximately 1100 saplings and 1200 seedlings present in plots during at least one sampling period.

To interpret changes in sapling and seedling density and size in

Fig. 2. Aerial photograph plot with experimental wind gaps. This plot is the northernmost winched and burn plot depicted in Fig. 1. Photo courtesy of USDA Forest Service, Southern Research Station, Center for Forest Disturbance Science.

terms of aboveground biomass we developed allometric equations for dominant sapling (≥ 1.37 m) and seedling species (< 1.37 m) in the plots. The three most common sapling species during our 2011 survey included *L. styraciflua* (43%), *A. rubrum* (29%), and *Rhus copallinum* L. (15%). The most common seedling species were *Pinus taeda* (54%) and *L. styraciflua* (8%). We harvested aboveground portions of individuals of *L. styraciflua* (n = 23), *A. rubrum* (n = 23), and *R. copallinum* (n = 18) outside of plots across the range of sizes found in understory surveys (i.e., 1.37–4.5 m). For seedlings, we collected individuals of *P. taeda* (n = 35) and *L. styraciflua* (n = 19) with heights ranging from 3 to 40 cm and 10–137 cm, respectively. We identified all individuals to species and recorded height to the nearest 1 cm. For saplings, we also recorded diameter at breast height (dbh) and diameter at root collar (drc) to the nearest 1 mm. We dried plants in a drying oven for 72 h at 70 °C, and measured total biomass (leaves and stems) of each sapling to the nearest 1 g. For the three dominant sapling species, we developed allometric equations for instances where height, dbh, and drc were all known (Eq. (1)). For instances when sapling diameter measurements were missing, we also developed allometric equations using height only for saplings (Eq. (2)). For the two dominant seedling species, we developed allometric equations using seedling height (Eq. (2)).

$$\log_e(bm) = a\log_e(h) + b\log_e(dbh) + c\log_e(drc) + i \tag{1}$$

$$\log_e(bm) = a\log_e(h) + i \tag{2}$$

where *bm* is aboveground biomass measured in kg, *h* is the sapling or seedling height (in m), and *dbh* and *drc* represent sapling diameter at breast height and diameter at root collar (in mm) for saplings. To estimate biomass in non-dominant species, we also developed composite allometric equations using pooled data from all saplings and seedlings respectively.

To evaluate whether combinations of winching and burning exhibited interactive effects (winch × burn) on woody understory structure, composition, and diversity, we derived a dataset of changes in understory structure, composition, and diversity for both saplings and seedlings (Table 2). The dataset included differences in each

characteristic for sapling or seedling quadrat including total density, total aboveground biomass, and mean height. We derived species-specific changes in density and biomass for the dominant sapling and seedling species, and we calculated changes in diversity metrics including species richness and evenness index ($E_H = H'/H'_{max}$; Pielou, 1966; Shannon and Weaver, 1963). We used linear mixed models to test for interactive effects of winching and burning on each response variable in Table 2 using the lmerTest package in R. The model included main effects for winching, burning, and a winch × burn interactive effect, and a random effect of plot to account for within plot variability of subsampled quadrats. We applied a $\log(x + \varepsilon)$ transformation to all density and biomass response variables to reduce heteroscedasticity, where ε is a small number so that $\log(x + \varepsilon)$ is defined for all x (ε equaled 2 kg and 0.06 kg for saplings and seedlings respectively). Because we evaluated interaction coefficients for 26 variables (Table 2), we used a sequential Bonferroni correction (Holm, 1979) to test for significance of interaction effects, although this is likely conservative for the multiple correlated variables tested. We further qualified each interactive effect as occurring in either an amplifying or buffering direction. An interaction between winching and fire implies that the presence of winching alters the effect of fire. Thus, we classified interactions as occurring in an amplifying direction when the coefficient of a significant interaction was in the same direction as the burn coefficient or as buffering if they were in opposite directions. In other words, interactions occur in an amplifying direction when they increase the magnitude of the fire-effect or buffering when they decrease the magnitude of the fire effect.

After finding evidence for interactive effects on composition for saplings, we generated an ordination of sapling composition using non-metric multi-dimensional scaling (NMS). We used the woody understory survey data to build species by understory plot matrices for all years surveyed. The species matrices for saplings consisted of the estimated biomass of 27 species for 96 understory plots over 4 years (resulting in 384 composition points in ordination space). We applied a log $(x + \varepsilon)$ transformation to biomass estimates and included a single dummy species to allow calculation of Bray–Curtis distance matrix

between all samples. We used the metaMDS function in the vegan package (Minchin, 1987; Oksanen et al., 2016) in R to reduce dimensionality to three axes using 10,000 random starts, we selected a 3 dimensional solution with stress of 11.5%, as we noted diminishing reductions in stress for 4 and 5 dimensional solutions as recommended by McCune and Grace (2002). We averaged NMS axis scores for each treatment and year combination to illustrate overall changes in sapling composition.

2.3. Testing specific interaction mechanisms

In addition to the sampling above exploring overall interactive effects on woody understory vegetation, we conducted two additional analyses to test for evidence of specific interactions mechanisms acting in a buffering direction, where the presence of prior wind damage reduced fire impacts. First, we tested whether basal sprouting from fire-damaged saplings differed between burned-only plots relative to burned plots with previous winching disturbance. We quantified basal sprouting from fire-damaged saplings in the year following winching (2013) for saplings present prior to the prescribed fire (n = 199). For each fire-damaged sapling, we noted the number of basal sprouts (if any) occurring at the base of each sapling, as well as the height of each sprout. To test whether survival and resprouting differed between fire-damaged saplings in burned-only plots versus those in winched and burned plots, we calculated the percentage of resprouting saplings for both burned-only plots and winch + burn plots. We tested for differences in occurrence of resprouting using a binomial logistic regression including winching as a main effect. Among resprouting saplings (n = 167), we applied allometric equations (Eqs. (1) and (2)) to estimate the biomass of each sapling and its associated resprouts. We tested whether saplings in winch + burn areas exhibited greater resprouting productivity by modeling total sprout biomass using a linear mixed model and including sapling biomass, winching treatment, and biomass × winch interaction. Measures of sapling and resprout biomass were both log-transformed to minimize heteroscedasticity.

We conducted an additional analysis of disturbance interaction mechanisms occurring in a buffering direction, testing whether seedlings that established higher on tip-up mounds following winching were less vulnerable to mortality from fire. We surveyed woody understory plants established on mounds following winching disturbance in fall 2012 and fall 2013. We surveyed 8 mounds within burned plots (prior to burning) and 14 mounds within unburned plots including 154 seedlings on mounds in burned plots and 99 seedlings on mounds in unburned plots. We tagged all seedlings and recorded seedling elevation above ground level to the nearest 1 cm. Following the April 2013 fire, we recorded survival of each tagged seedling. To test whether seedlings established on elevated portions of mounds had higher survival following fire, we modeled individual seedling survival using multiple logistic regression. We included main effects for burn treatment and elevation of seedlings relative to the ground. To test whether mounds buffered seedlings from mortality by fire by providing elevational refugia, we included a burn × elevation interaction effect and we included individual mounds as a random effect to account for correlation in survival among seedlings on the same mound.

3. Results

3.1. Interactive effects on overall woody understory structure, composition, and richness

Allometric equations showed strong relationships between biomass and size parameters (Fig. 3) with r^2 values between 0.84 and 0.94 and all p < 0.0001 for saplings and r^2 values between 0.95 and 0.98 and all p < 0.0001 for seedlings (Table 1). For sapling allometry, inclusion of diameter measurements (dbh and drc) increased r^2 values and lowered AIC-scores relative to equations that did not include diameter

measurements. We report coefficients and intercepts of allometric equations based on height, dbh, and drc (saplings) and height only (saplings and seedlings) (Table 1).

Both winching and burning had large effects on woody understory structure; however, we focus on interactive effects where the effect of fire was altered by the previous winching disturbance. We found no evidence of significant interactive effects on seedlings (Table 3). However, the combination of winching and burning interactively affected species composition of saplings. We also noticed potential (though non-significant) interactive effects on saplings that occurred in a buffering direction. Among the interactive effects occurring in an amplifying direction, where wind damage increased the burn impacts, we found significant amplifying interactive effects of winching and burning for both biomass and density of *R. copallinum* (Table 3, Fig. 4). Across all plots, *R. copallinum* biomass averaged 0.01 kg m^{-2} before disturbances and increased to an average of 0.03 kg m^{-2} in singly-disturbed plots (fire only, winch only, Table 4). However in winch + burn plots, the two disturbances interact. We found that *R. copallinum* biomass increased to 0.09 kg m^{-2}, representing a much larger change in biomass than expected if the single disturbance interacted additively (Fig. 4A, Table 4). Similarly, *R. copallinum* density averaged approximately 0.11 m^{-2} before disturbances, rose to 0.21 m^{-2} in singly-disturbed plots, and increased to 0.44 m^{-2} in winch + burn plots (Table 4, Fig. 4D). The NMS ordination aids in illustrating interactive changes in sapling composition (Fig. 5). As expected, compositional change in intact, unburned plots showed a small directional change in sapling composition but slightly increased along NMS1 toward increasing dominance of *L. styraciflua*. Similarly, winch-only plots showed increased dominance of *L. styraciflua* though the directional change appeared greater. The burn-only plots shifted lower along NMS1 following prescribed fire, as dominant sapling species were reduced, and recovered toward the initial composition. However, when winching and burning were combined, the compositional change increased along NMS1, NMS2, and NMS3 axes indicating increases in *L. styraciflua* as well as increased representation of *R. copallinum* that was not observed in either of the singly-disturbed trajectories (Fig. 5).

In addition to the amplifying interactive effects of *R. copallinum* sapling biomass and density, our results suggested the potential presence of several interaction effects on sapling density and diversity that occurred in a buffering direction where prior wind damage reduced the impacts of subsequent fire (Table 3). These interactive effects were not significant at the α = 0.05 level using a sequential Bonferroni correction; however, we discuss these here with cautious inference as our resprouting analyses (discussed below) supported a similar trend and limited information on buffering mechanisms and their effects are presently available. Overall changes in total sapling density suggest potential interactive effects that buffered the impact of fire (Fig. 4C and D). In control plots, sapling density increased 51% over the course of the study (from 1.32 to 1.99 m^{-2}; Table 4), but the effect of single disturbances on sapling density differed. In winched-only plots, sapling density increased 94% (from 0.54 to 1.05 m^{-2}); whereas in burn-only plots, sapling density actually decreased 6% (from 0.71 to 0.67 m^{-2}). This decrease likely occurred because recovery in burned plots was delayed due to top-kill of saplings. However, despite also recovering from top-kill, density increased 176% in the winch + burn plots (from 0.41 to 1.13 m^{-2}) over the course of the study (Fig. 4C; Table 4). Thus the expected decrease in sapling density expected after burning was offset when combined with winching. We found that the dominant species *A. rubrum* showed a parallel pattern where, despite declines in biomass and density following burning, potential biomass losses were offset when burning was combined with winching (Fig. 4D; Table 4). Similarly, we found burning led to reductions in species richness and evenness; however, when combined with winching, these losses in species diversity were ameliorated (Fig. 4E and F; Table 4).
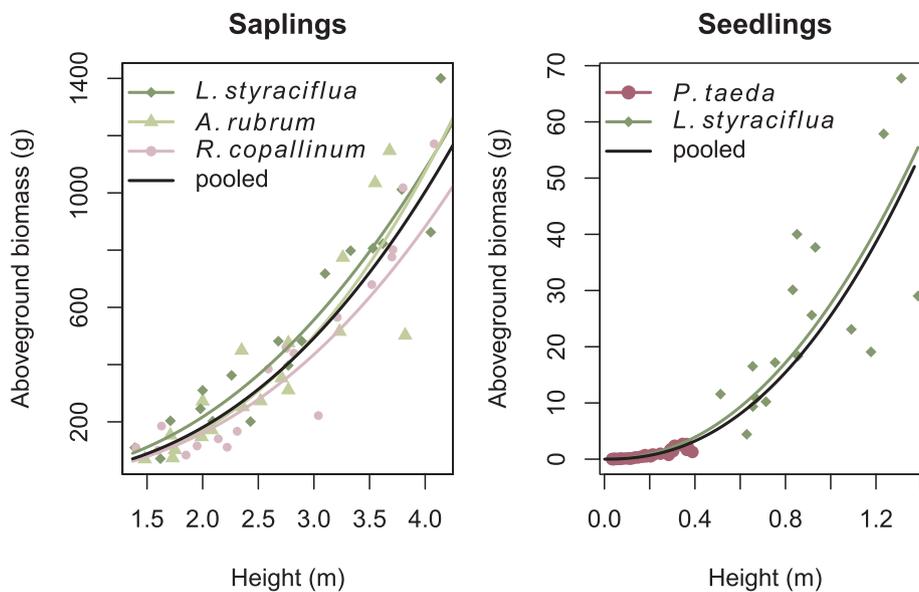
Fig. 3. Aboveground biomass of dominant sapling and seedling species across the range of heights observed at the study site. Height only allometric equations (Eq. (2)) are shown.

3.2. Specific interaction mechanisms

Tip-up mounds in winched plots did not appear to serve as refugia from fire as we found no significant difference in survival of seedlings higher on mounds (p = 0.365), nor did we find a significant burn × elevation interaction (p = 0.430). In fact, survival patterns were in the opposite direction than expected (Fig. 6). Overall, seedling survival was much lower in burned areas (9.0%) compared to unburned areas (55.5%, p = 0.352). On unburned mounds, survival of seedlings was similar for seedlings in lower elevations and higher elevations (57 vs 54%, respectively); yet on mounds in burned plots, seedling survival was 12% on lower elevations and 0% on higher elevations, although this interactive effect was not significant (Fig. 6).

We found that resprouting exhibited a buffering effect in winched and burned plots (Fig. 7). We found no differences in tendency to resprout following top-kill after fire between saplings in winched and unwinched plots (p = 0.556), and approximately 84% of saplings survived and resprouted following fire in both winched and unwinched plots. However, we did find evidence that greater resprout growth in winched plots likely leads to a buffering effect. In general, sprout biomasses from top-killed saplings in winch + burn plots were 2–2.5 times greater than sprouts from burn-only saplings of a similar size (Fig. 7). We found that the biomass of sprouts increased with the biomass of associated parent saplings (p < 0.0001), and sprout biomass was

greater for a given sapling size in winch + burn plots relative to burn-only plots (p = 0.0001; Fig. 7), representing a significant interaction that can buffer the effect of subsequent fires whereby prior winching enhances sapling growth and recovery from top kill.

4. Discussion

4.1. Evidence of amplifying and buffering effects

The results of this study support the idea that wind and fire disturbances, like other compounded perturbations, can interactively affect understory communities in ways not easily predicted by the individual disturbances themselves (Buma and Wessman, 2012; Liu et al., 2008; Myers and Van Lear, 1998). We found that compounded wind and fire disturbances can interact in both amplifying and buffering directions through a variety of mechanisms in a single combination of disturbances depending on the response variable of interest. Diverse species-specific responses may drive differences in interaction mechanisms following compounded disturbances and aid in predicting ecosystem trajectories following disturbance. Further, because ecosystem responses such as plant density, biomass, and species diversity are often related, interactions in some variables can drive similar or opposite interactions in other responses.

The changes in composition of saplings following wind and fire

Table 1
Allometric parameters for dominant sapling and seedling species based on diameter at breast height (dbh, in mm) and diameter at root collar (drc, in mm) across the range of heights (h, in m) observed. Sapling aboveground biomass (bm, in kg) is given by $\log_e(bm) = a\log_e(h) + b\log_e(dbh) + c\log_e(drc) + i$ when dbh and drc are known. When only height is known and for seedlings, biomass is given by $\log_e(bm) = a\log_e(h) + i$. Overall model p < 0.0001 for all models.

Size class	Species	a	b	c	i	n	r^2	Height range (m)
Sapling	A. rubrum	0.6642	0.0073	0.0727	3.3072	18	0.976	1.48–3.82
		2.6579	–	–	3.2951	18	0.861	1.48–3.82
	L. styraciflua	0.7419	0.0271	0.0443	3.6429	18	0.955	1.39–4.14
		2.3191	–	–	3.7731	18	0.893	1.39–4.14
	R. copallinum	0.2263	0.065	0.0442	3.5591	18	0.953	1.4–4.08
		2.4536	–	–	3.3808	18	0.829	1.4–4.08
	Species pooled	0.6508	0.0317	0.051	3.494	54	0.957	1.39–4.14
		2.4757	–	–	3.4803	54	0.844	1.39–4.14
Seedling	L. styraciflua	2.1338	–	–	3.319	19	0.911	0.09–1.39
	P. taeda	2.1278	–	–	2.9187	35	0.973	0.03–0.39
	Species pooled	2.2595	–	–	3.2411	54	0.977	0.03–1.39

Table 2

Vegetation response variables calculated for sapling and seedlings.

Vegetation characteristic		Saplings (2011–2014)	Seedlings (2011–2013)
Structure		Δ total sapling density (m^{-2})	Δ total seedling density (m^{-2})
		Δ total sapling biomass (kg m^{-2})	Δ total seedling biomass (g m^{-2})
		Δ mean sapling height (m)	Δ mean seedling height (mm)
Composition		Δ sapling aboveground biomass by species (kg m^{-2})	Δ seedling aboveground biomass by species (g m^{-2})
		L. styraciflua	*P. taeda*
		A. rubrum	*L. styraciflua*
		R. copallinum	*R. copallinum*
		All other saplings	All other seedlings
		Δ sapling density by species (m^{-2})	Δ seedling density by species (m^{-2})
		L. styraciflua	*P. taeda*
		A. rubrum	*L. styraciflua*
		R. copallinum	*R. copallinum*
		All other saplings	All other seedlings
Diversity		Δ sapling richness (per 9 m^2)	Δ seedling richness (per 1 m^2)
		Δ sapling evenness (per 9 m^2)	Δ seedling evenness (per 1 m^2)

Table 3

P-values of univariate linear mixed models showing significance of winching, burning, and winch × burn interactive effects. [†]Interaction direction is indicated as amplifying + (A) or buffering − (B) if the interaction coefficient is in the same or opposite direction of the burn coefficient. [‡]We determined significance of interaction effects using a sequential Bonferroni correction (familywise α = 0.05) and significant interaction effects are indicated by an asterisk (*).

Size class	Vegetation characteristic			*p*-value			Interaction	
				Winch	Burn	W × B	Direction‡	Signif. †
Saplings	Structure		Total density	0.2084	0.0607	0.0066	− (B)	
			Total biomass	0.0131	0.0724	0.5615	− (B)	
			Mean height	< 0.0001	0.0077	0.4469	− (B)	
	Composition	Biomass	*L. styraciflua*	0.5617	0.2062	0.8813	+ (A)	
			A. rubrum	0.1907	0.4227	0.0413	− (B)	
			R. copallinum	0.0063	0.0249	0.0008	+ (A)	*
			Other saplings	0.0137	0.0083	0.7008	− (B)	
		Density	*L. styraciflua*	0.0368	0.1928	0.3904	+ (A)	
			A. rubrum	0.1270	0.2522	0.0331	− (B)	
			R. copallinum	0.0101	0.0042	0.0006	+ (A)	*
			Other saplings	0.0492	0.0446	0.6655	+ (A)	
	Diversity		Richness	0.2084	0.0077	0.0196	− (B)	
			Evenness	0.4245	0.0011	0.0133	− (B)	
Seedlings	Structure		Total density	0.7420	0.5801	0.4336	− (B)	
			Total biomass	0.3862	0.1833	0.8468	− (B)	
			Mean height	0.5138	0.0920	0.9615	+ (A)	
	Composition	Biomass	*P. taeda*	0.0745	0.6742	0.7897	− (B)	
			L. styraciflua	0.0148	0.0890	0.2735	− (B)	
			R. copallinum	0.0020	0.2265	0.3437	+ (A)	
			Other seedlings	0.0009	0.9860	0.2051	+ (A)	
		Density	*P. taeda*	0.2643	0.3513	0.3415	+ (A)	
			L. styraciflua	0.3397	0.3067	0.3014	− (B)	
			R. copallinum	0.3044	0.3044	0.2990	− (B)	
			Other seedlings	0.5798	0.9427	0.8640	− (B)	
	Diversity		Richness	0.0427	0.9161	0.1581	+ (A)	
			Evenness	0.1393	0.7389	0.2700	+ (A)	

disturbances found in this study illustrate an interaction occurring in an amplifying direction, with more change in species composition than expected from either individual disturbance (Figs. 4 and 5). The most notable compositional change we observed was a large increase in *R. copallinum* following disturbance from wind and fire that was not evident after either single disturbance (Figs. 4 and 5). Although *R. copallinum* exhibited an interactive effect, we found that many understory characteristics respond in an additive manner (i.e., no significant interaction; Table 4). Although our overall woody understory survey did not detect any interactive effects in a buffering direction that were significant at the α = 0.05 level, we did observe changes in overall sapling density, especially for species such as *A. rubrum*, and measures of species diversity that are suggestive of buffering interactive effects. Rapid growth of resprouts from saplings in winch + burn plots led to less change in sapling density than expected from winching and burning alone (see discussion of sprouting analysis below), thus leading to

buffering in density of species such as *A. rubrum* and diversity metrics.

In addition to overall changes in woody understory vegetation, we examined evidence of two specific interactive mechanisms where prior wind damage may reduce the impact of fire. We found strong evidence that resprouting saplings mediate an important interaction between wind damage and fire with much greater resprout growth following fire in winched plots relative to controls (Fig. 7), allowing rapid recovery of saplings following fire. Faster growth in basal sprouts in winched plots following fire could simply be the result of increased light and decreased competition with adult trees for soil resources. However, many hardwood saplings often have substantial underground carbohydrate reserves (Hodgkins, 1958; Robertson and Ostertag, 2009). High light availability in winched plots may allow increased investment in belowground tissues of some saplings prior to fire that allow more rapid regrowth and recovery following fire. Although we expected tip-up mounds created by wind damage to serve as refugia from subsequent
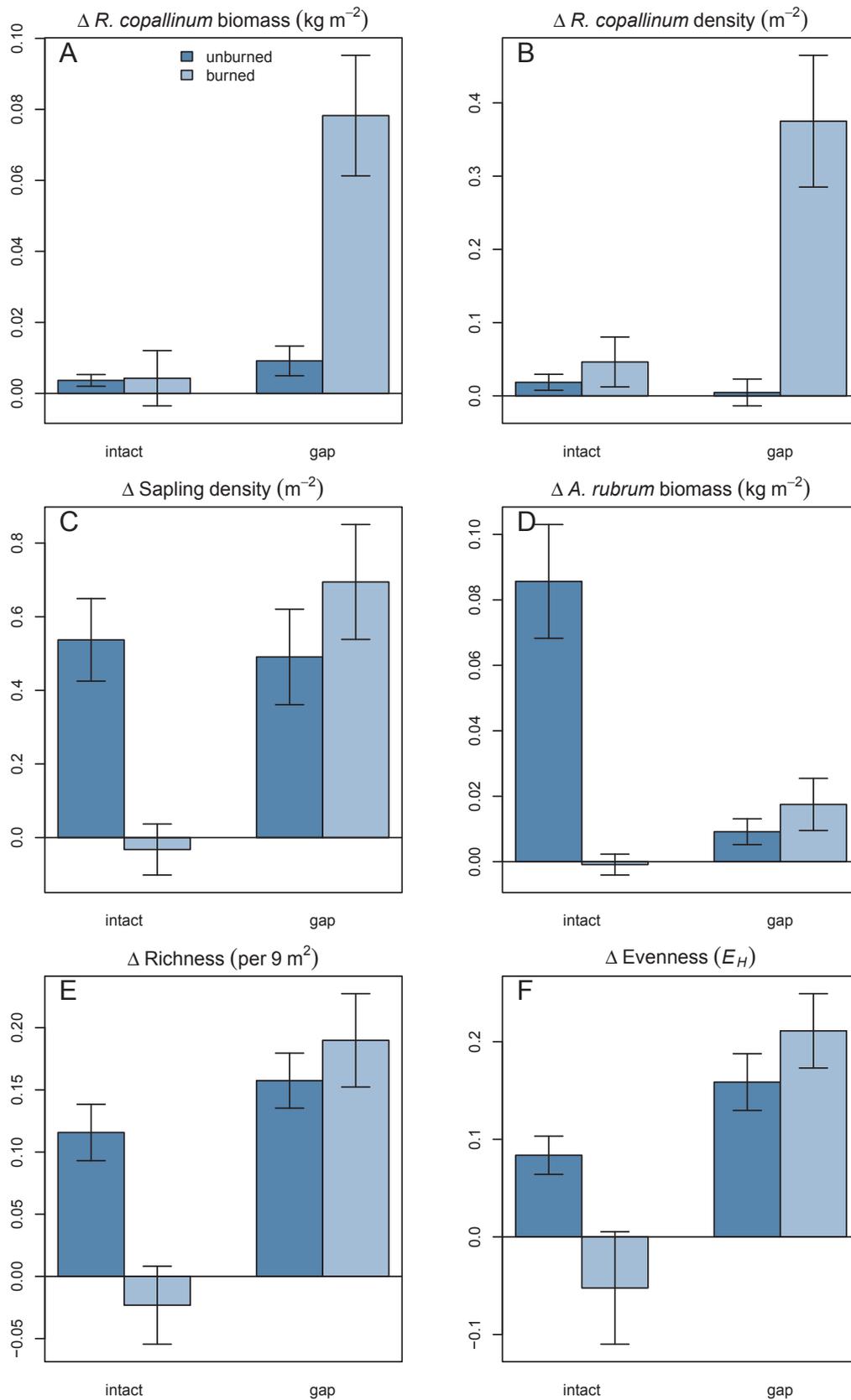
Fig. 4. Changes in sapling characteristics between 2011 and 2014 following combinations of winching and prescribed burning indicating amplifying and buffering interactive effects on (A) biomass and (B) density of *R. copallinum*, (C) density of all saplings, (D) biomass of *A. rubrum*, (E) species richness, and (F) evenness index (E_H).

Table 4
Changes in sapling structure, composition and diversity for combinations of winching and burning including start (2011) and end (2014) dates of sapling survey. Values represent mean (s.d.) of 96 quadrats across 12 plots.

			Intact				Winched			
			Unburned		Burned		Unburned		Burned	
Vegetation characteristic			2011	2014	2011	2014	2011	2014	2011	2014
Structure		Total density (m^{-2})	1.32 (1.00)	1.99 (1.12)	0.71 (0.78)	0.67 (0.6)	0.54 (0.59)	1.05 (0.92)	0.41 (0.42)	1.13 (0.92)
		Total biomass (kg m^{-2})	0.21 (0.21)	0.46 (0.36)	0.12 (0.15)	0.11 (0.12)	0.11 (0.14)	0.46 (0.49)	0.06 (0.07)	0.22 (0.15)
		Mean height (m)	1.85 (0.26)	2.16 (0.44)	1.84 (0.24)	1.79 (0.30)	1.95 (0.26)	2.28 (0.58)	1.77 (0.24)	1.97 (0.35)
Composition	Biomass	L. styraciflua (kg m^{-2})	0.11 (0.16)	0.22 (0.31)	0.07 (0.09)	0.06 (0.10)	0.09 (0.13)	0.33 (0.46)	0.04 (0.07)	0.06 (0.10)
		A. rubrum (kg m^{-2})	0.08 (0.08)	0.19 (0.15)	0.01 (0.01)	0.00 (0.01)	0.00 (0.01)	0.01 (0.03)	0.01 (0.03)	0.03 (0.07)
		R. copallinum (kg m^{-2})	0.00 (0.01)	0.01 (0.02)	0.03 (0.10)	0.04 (0.07)	0.01 (0.03)	0.02 (0.04)	0.00 (0.01)	0.09 (0.09)
		Other saplings (kg m^{-2})	0.01 (0.02)	0.04 (0.03)	0.02 (0.02)	0.01 (0.01)	0.01 (0.02)	0.09 (0.11)	0.01 (0.03)	0.04 (0.05)
	Density	L. styraciflua (m^{-2})	0.43 (0.57)	0.43 (0.56)	0.30 (0.39)	0.30 (0.39)	0.31 (0.45)	0.37 (0.49)	0.21 (0.39)	0.24 (0.42)
		A. rubrum (m^{-2})	0.78 (0.07)	1.26 (0.98)	0.04 (0.08)	0.04 (0.09)	0.03 (0.12)	0.09 (0.19)	0.06 (0.23)	0.19 (0.56)
		R. copallinum (m^{-2})	0.03 (0.06)	0.05 (0.10)	0.22 (0.53)	0.28 (0.05)	0.14 (0.26)	0.14 (0.23)	0.05 (0.15)	0.44 (0.48)
		Other saplings (m^{-2})	0.08 (0.17)	0.25 (0.19)	0.15 (0.23)	0.06 (0.16)	0.06 (0.15)	0.45 (0.69)	0.09 (0.15)	0.26 (0.28)
Diversity		Richness (per 9 m^2)	0.22 (0.14)	0.36 (0.14)	0.19 (0.16)	0.16 (0.12)	0.14 (0.13)	0.30 (0.19)	0.14 (0.12)	0.34 (0.18)
		Evenness	0.16 (0.11)	0.23 (0.12)	0.13 (0.16)	0.12 (0.13)	0.15 (0.11)	0.21 (0.16)	0.06 (0.12)	0.25 (0.15)

fire, we found no evidence for this mechanism, and contrarily found some trends suggesting that seedlings higher on mounds may have even lower survival than those nearer to the forest floor. This finding is opposite what we expected based on other findings that for some species, mounds can serve as refugia from competition or browsing (Betras et al., in press; Krueger and Peterson, 2006; Long et al., 1998; Nakashizuka, 1989). Size of tip-up mounds typically increase with tree size (Sobhani et al., 2014), yet the highest mounds in our study (1.5 m) were not high enough to protect seedlings from fire. In addition, it is possible that at upper portions of mounds seedlings may be exposed to fire while also being vulnerable to increased erosion, as soil dynamics can differ in various positions of pit–mound complexes (Peterson et al., 1990).

4.2. Drivers of interaction mechanisms

Because of the labor requirements that constrain studies using static

winching, this study was somewhat limited in replication. However, the results reveal that wind damage can (1) amplify the effects of a previous fire through large increases in *R. copallinum* following compounded disturbances, and (2) buffer the effects of subsequent fire with less reduction in sapling density and species richness than expected due to enhanced resprouting in winched plots. This finding suggests that rather than considering disturbance interactions as wholly amplifying or buffering, conceptual frameworks that recognize the variety of mechanisms through which interactions occur may improve predictions of compounded disturbances (Cannon et al., 2017; Johnson and Miyanishi, 2007). In addition, several generalizations emerge from this study regarding what factors predict when interaction mechanisms may be amplifying or buffering that warrant further investigation in other disturbance combinations and forest types.

First, individual species differences in life history traits underlie many differences in responses we observed. *R. copallinum* is a fast-growing and short-lived early pioneer shrub species which has been

Sapling compositional change (NMS)

Legend:
- ● Intact unburned
- ● Intact burned
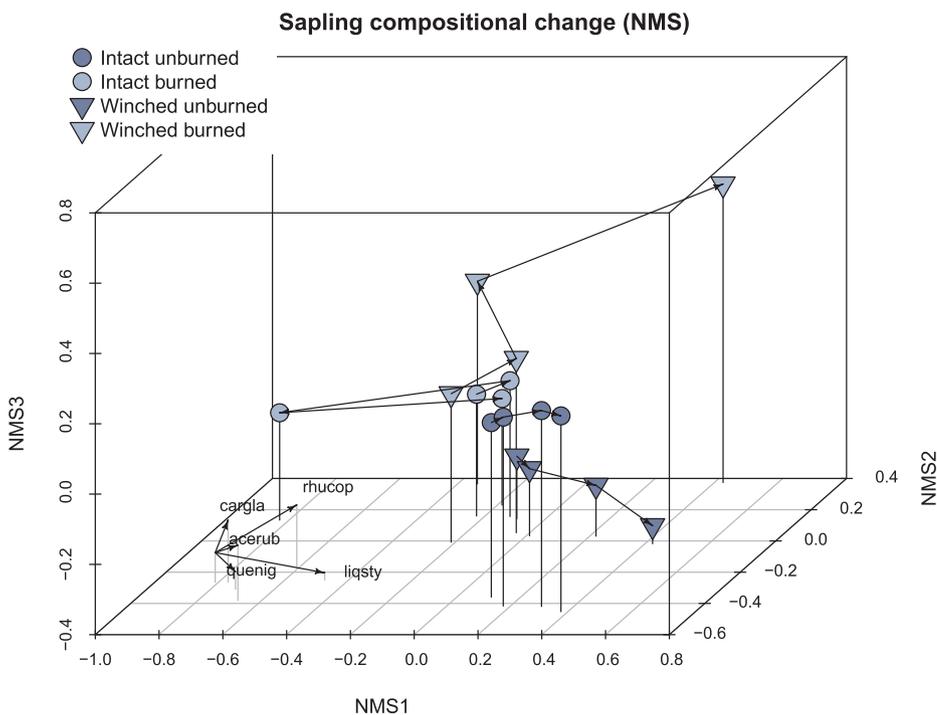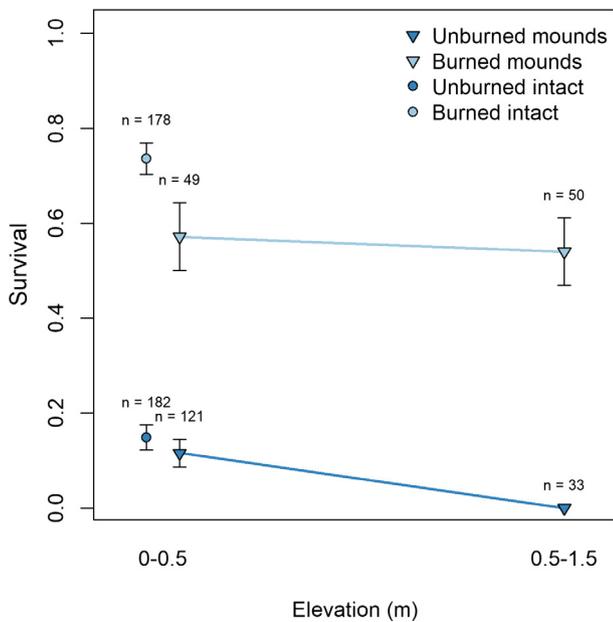- ▼ Winched unburned
- ▽ Winched burned

Fig. 5. Three-dimensional ordination of sapling composition using non-metric multi-dimensional scaling (NMS) based on sapling biomass. Species loading arrows in the bottom-left corner show the five strongest correlations with NMS axes (liqsty = *Liquidambar styraciflua*, acerub = *Acer rubrum*, rhucop = *Rhus copallinum*, cargla = *Carya glabra*, and quenig = *Quercus nigra*).

Fig. 6. Mean seedling survival for burned (dark blue) and unburned (light blue) seedlings on tip-up mounds (triangles). Data from seedling observations in winched plots from the seedling survey (circles) are shown to illustrate survival of seedlings on intact soil in winched areas. Seedlings on tip-up mounds are classified by elevation class to illustrate effect of elevation on seedling survival. Error bars represent one standard error of mean survival. Note that survival of high elevation seedlings on burned mounds was 0%, thus no error bars are displayed for this treatment combination. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)
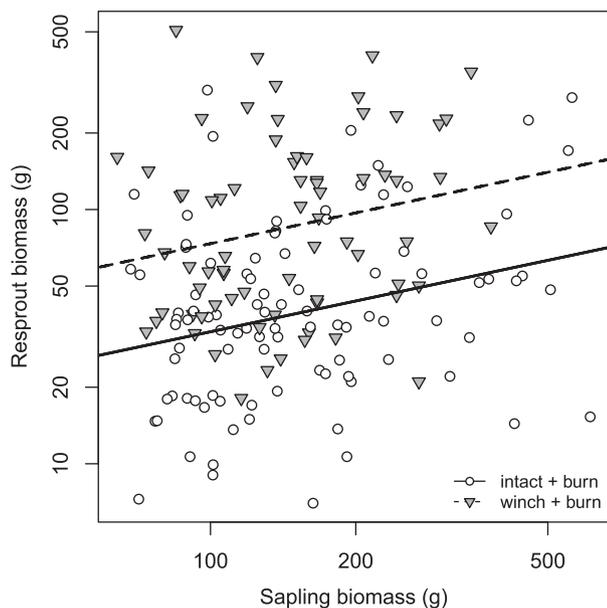
Fig. 7. Relationship of sapling biomass of resprouting saplings and the total biomass of basal sprouts from individual damaged saplings in winched (grey triangles) and intact (white circles) plots, indicating higher sprout productivity from saplings in winched and burned plots. Note both axes show log-transformed biomass in grams.

shown to exhibit a fire-stimulated clonal sprout response and seed germination (Cain and Shelton, 2003; Duncan and Duncan, 1988; Taylor and Herndon, 1981). The large increase in *R. copallinum* following wind and fire disturbance indicates that generalist reproductive strategies may exhibit greater resilience following compounded

disturbances than specialist strategies. Gagnon and Platt (2008) found that giant cane (*Arundinaria gigantea* (Walter) Muhl.) responded similarly to combinations of windstorm and fire, and exhibited rapid clonal growth when given adequate light. Species such as *Populus tremuloides* Michx. (quaking aspen) can regenerate by seed as well as through asexual sprouting. This species has been shown to recover more rapidly following blowdown and fire disturbance relative to specialist species like *Pinus banksiana* Lamb. (jack pine) and *Pinus contorta* Douglas ex Loudon (lodgepole pine) which rely on serotinous cones, making these species sensitive to removal of adults after blowdown (Buma and Wessman, 2012; D'Amato et al., 2011; Gill et al., 2017). Likewise, the resprouting responses responsible for interactive effects occurring in a buffering direction likely differ according to species. *Acer rubrum* is generally classified as shade tolerant, but also sprouts prolifically following damage to the main stem (Burns and Honkala, 1990). In our study, buffering interactive effects resulted mainly from increased sprouting responses among hardwood species. Sprouting responses to fire damage are common in many hardwood species, but can vary considerably among species. Many species of *Quercus* L. (oak species) saplings, for example, are known for higher investment of photosynthate into belowground tissues, compared to other hardwood species (Johnson et al., 2002), allowing rapid resprouting and recovery of *Quercus* spp. following fire relative to some other species (Cannon and Brewer, 2013). Pelz and Smith (2012) found increased representation of the fire resilient species *P. tremuloides* in the overstory and regeneration strata 30 years following mountain pine beetle outbreaks in *P. contorta* forests. Thus, other disturbances that increase light availability and promote resprouting hardwood species may display similar interactive effects in a buffering direction.

Second, the timing between disturbances can likely change interactive effects on the woody understory. Brose and Van Lear (1998) examined regeneration of *A. rubrum* after a canopy thinning followed two years later by a prescribed fire. They found that regeneration of *A. rubrum* was greatly reduced following disturbance combinations, whereas in our study, canopy disturbance lessened the reduction in *A. rubrum* following fire. Saplings of *A. rubrum* included in our study were larger (1.76 ± 0.35 m tall) relative to those from Brose and Van Lear (1998) study (1.25 ± 0.8 m tall). Despite the fact that 100% of the saplings in burned plots in our study were top-killed by fire, rapid resprouting and regrowth in gap plots allowed for rapid recovery of sapling density. Thus, we expect that given longer time between wind and fire disturbances, resilience through resprouting ability may become greater and lead to stronger interactive effects where prior wind damage buffers the impact of fire.

Third, this study highlights that in some cases, interactive effects on some vegetation responses may drive opposite interactions in other vegetation responses. For example, the amplification effect leading to increased density of *R. copallinum* strengthened buffering effects in other vegetation responses such as sapling density. Although resprouting played a role in recovering sapling densities in burned plots, sapling density increased in winch + burn plots primarily through recruitment of *R. copallinum*, which accounted for over 54% of the increased sapling density in that treatment. In singly-disturbed plots, recruitment of *R. copallinum* was relatively low (ranging from 0% to 70% increases), but was much higher in winch + burn plots (> 800% increase).

4.3. Conclusions and management implications

Undoubtedly, severe windthrow can amplify wildfire intensity and induce changes in fire behavior and plant composition (e.g., Buma and Wessman, 2011; Cannon et al., 2014; Frelich, 2002; Liu et al., 2008; Urquhart, 2009). However, these interactive effects where wind damage amplifies the intensity or severity of fire are not inevitable. Instead, the nature of disturbance interactions may differ when the interacting disturbances are of lower severity. For example, increases in

fire intensity may not manifest following windthrow if weather conditions are not extreme enough to cause consumption of additional fuels (Cannon et al., 2014). Interactive effects acting in a buffering direction may be more common when fire disturbances are of lower-intensity, such as in frequent-fire systems including oak-pine systems or *Pinus palustris* Mill. (longleaf pine) forests. Disturbance interactions occurring in an amplifying directions have also been shown to be less important when the disturbances are of lower severity. For example, some of the negative interactive effects of wind damage and subsequent salvage logging (Foster et al., 1997), may not occur when disturbance combinations are of lower severity (Peterson and Leach, 2008; Royo et al., 2016). The severity of wildfire can be extremely spatially heterogeneous (Turner et al., 1994), and forest wind damage from tornadoes can be similarly heterogeneous in severity (Cannon et al., 2016). Thus, when wind damage and fire interact in forests, a range of severities of each disturbance are likely to co-occur and interact, resulting in a complex mixture of different interaction mechanisms. The interaction between wind damage and fire is thus a net result of multiple co-occurring interaction mechanisms driving understory recovery that may amplify the effect of fire in some cases and buffer the effect of fire in others. Disturbance interactions depend on a host of factors including the severity and timing of the disturbances, individual species responses, and the ecosystem responses considered. Moving toward a more mechanistic and comprehensive understanding of interactions can help predict how multiple co-occurring disturbance interactions can drive overall response to disturbances at larger scales and provide guidance on management response to these disturbances.

Acknowledgments

References

Addington, R.N., Hudson, S.J., Hiers, J.K., Hurteau, M.D., Hutcherson, T.F., Matusick, G., Parker, J.M., 2015. Relationships among wildfire, prescribed fire, and drought in a fire-prone landscape in the south-eastern United States. Int. J. Wildl. Fire 24, 778–783.

Agee, J.K., Skinner, C.N., 2005. Basic principles of forest fuel reduction treatments. For. Ecol. Manage. 211, 83–96. https://doi.org/10.1016/j.foreco.2005.01.034.

Amman, G.D., Schmitz, R.F., 1988. Mountain pine beetle: lodgepole pine interactions and strategies for reducing tree losses. Ambio 17, 62–68. https://doi.org/10.2307/4313420.

Armesto, J.J., Pickett, S.T.A., 1986. Removal experiments to test mechanisms of plant succession in oldfields. Vegetatio 66, 85–93. https://doi.org/10.1007/BF00045498.

Beatty, S.W., 1984. Influence of microtopography and canopy species on spatial patterns of forest understory plants. Ecology 65, 1406–1419. https://doi.org/10.2307/1939121.

Betras, T., Diggans, T., Jaunzems, M., Kuebbing, S., Carson, W., n.d. Do novel plant communities develop rapidly on tree tip-up mounds?: A review and two case studies from northern Michigan. Can. J. For. Res.

Brose, P.H., Van Lear, D.H., 1998. Responses of hardwood advance regeneration to seasonal prescribed fires in oak-dominated shelterwood stands. Can. J. For. Res. 28, 331–339. https://doi.org/10.1139/x97-218.

Buma, B., 2015. Disturbance interactions: characterization, prediction, and the potential for cascading effects. Ecosphere 6, 1–15.

Buma, B., Wessman, C.A., 2012. Differential species responses to compounded perturbations and implications for landscape heterogeneity and resilience. For. Ecol. Manage. 266, 25–33. https://doi.org/10.1016/j.foreco.2011.10.040.

Buma, B., Wessman, C.A., 2011. Disturbance interactions can impact resilience mechanisms of forests. Ecosphere 2, art64. doi:10.1890/ES11-00038.1.

Burns, R.M., Honkala, B.H. (Eds.), 1990. Silvics of North America: 2. Hardwoods. Agriculture Handbook 654. U.S. Department of Agriculture, Forest Service, Washington, D.C.

Busing, R.T., White, R.D., Harmon, M.E., White, P.S., 2009. Hurricane disturbance in a temperate deciduous forest: patch dynamics, tree mortality, and coarse woody detritus. Plant Ecol. 201, 351–363. https://doi.org/10.1007/978-90-481-2795-5_26.

Cain, M.D., Shelton, M.G., 2003. Fire effects on germination of seeds from Rhus and Rubus: competitors to pine during natural regeneration. New For. 26, 51–64. https://doi.org/10.1023/A:1024406209842.

Cannon, J.B., Barrett, M.E., Peterson, C.J., 2015. The effect of species, size, failure mode, and fire-scarring on tree stability. For. Ecol. Manage. 356, 196–203. https://doi.org/10.1016/j.foreco.2015.07.014.

Cannon, J.B., Brewer, J.S., 2013. Effects of tornado damage, prescribed fire, and salvage logging on natural oak (Quercus spp.) regeneration in a xeric southern USA coastal plain oak and pine forest. Nat. Areas J. 33, 39–49. https://doi.org/10.3375/043.033.0105.

Cannon, J.B., Hepinstall-Cymerman, J., Godfrey, C.M., Peterson, C.J., 2016. Landscape-scale characteristics of forest tornado damage in mountainous terrain. Landsc. Ecol. 31, 2097–2114. https://doi.org/10.1007/s10980-016-0384-8.

Cannon, J.B., O'Brien, J.J., Loudermilk, E.L., Dickinson, M.B., Peterson, C.J., 2014. The influence of experimental wind disturbance on forest fuels and fire characteristics. For. Ecol. Manage. 330, 294–303. https://doi.org/10.1016/j.foreco.2014.07.021.

Cannon, J.B., Peterson, C.J., O'Brien, J.J., Brewer, J.S., 2017. A review and classification of interactions between forest disturbance from wind and fire. For. Ecol. Manage. 406, 381–390. https://doi.org/10.1016/J.FORECO.2017.07.035.

Chambers, J.Q., Fisher, J.I., Zeng, H., Chapman, E.L., Baker, D.B., Hurtt, G.C., 2007. Hurricane Katrina's carbon footprint. Science (80-.), 318, 2. doi:10.1126/science.1148913.

Chambers, M.E., Fornwalt, P.J., Malone, S.L., Battaglia, M.A., 2016. Patterns of conifer regeneration following high severity wildfire in ponderosa pine – dominated forests of the Colorado Front Range. For. Ecol. Manage. 378, 57–67. https://doi.org/10.1016/j.foreco.2016.07.001.

Connell, J.H., Slatyer, R.O., 1977. Mechanisms of succession in natural communities and their role in community stability and organization. Am. Soc. Nat. 111, 1119–1144. https://doi.org/10.1086/521238.

Cooper-Ellis, S., Foster, D.R., Carlton, G., Lezberg, A., 1999. Forest response to catastrophic wind: results from an experimental hurricane. Ecology 80, 2683–2696 10.1890/0012-9658(1999) 080[2683:FRTCWR]2.0.CO;2.

Cowles, H.C., 1899. The ecological relations of the vegetation on the sand dunes of Lake. Michigan. Bot. Gaz. 27 97–117, 167–902, 281–308, 361–391.

Cruz, M.G., Butler, B.W., Viegas, D.X., Palheiro, P., 2011. Characterization of flame radiosity in shrubland fires. Combust. Flame 158, 1970–1976. https://doi.org/10.1016/j.combustflame.2011.03.002.

D'Amato, A.W., Fraver, S., Palik, B.J., Bradford, J.B., Patty, L., 2011. Singular and interactive effects of blowdown, salvage logging, and wildfire in sub-boreal pine systems. For. Ecol. Manage. 262, 2070–2078. https://doi.org/10.1016/j.foreco.2011.09.003.

Dahal, D., Liu, S., Oeding, J., 2014. The carbon cycle and hurricanes in the United States between 1900 and 2011. Sci. Rep. 4, 5197. https://doi.org/10.1038/srep05197.

Dale, V.H., Joyce, L.A., McNulty, S., Neilson, R.P., Ayres, M.P., Flannigan, M.D., Hanson, P.J., Irland, L.C., Lugo, A.E., Peterson, C.J., Simberloff, D., Swanson, F.J., Stocks, B.J., Wotton, B.M., 2001. Climate change and forest disturbances. Bioscience 51, 723.

Duncan, W.H., Duncan, M.B., 1988. Trees of the Southeastern United States. The University of Georgia Press, Athens, GA.

Folt, C.L., Chen, C.Y., Moore, M.V., Burnaford, J., 1999. Synergism and antagonism among multiple stressors. Limnol. Oceanogr. 44, 864–877. https://doi.org/10.4319/lo.1999.44.3_part_2.0864.

Foster, D.R., 1988. Disturbance history, community organization and vegetation dynamics of the old-growth Pisgah Forest, South-Western New Hampshire, U.S.A. J. Ecol. 76, 105–134. https://doi.org/10.2307/2260457.

Foster, D.R., Aber, J.D., Melillo, J.M., Bowden, R.D., Bazzaz, F.A., 1997. Forest response to disturbance and anthropogenic stress. Bioscience 47, 437–445. https://doi.org/10.2307/1313059.

Frelich, L.E., 2002. Forest Dynamics and Disturbance Regimes: Studies from Temperate Evergreen-Deciduous Forests. Cambridge Studies in Ecology, Cambridge University Press.

Frelich, L.E., Reich, P.B., 1999. Neighborhood effects, disturbance severity, and community stability in forests. Ecosystems 2, 151–166.

Gagnon, P.R., Platt, W.J., 2008. Multiple disturbances accelerate clonal growth in a potentially monodominant bamboo. Ecology 89, 612–618. https://doi.org/10.1890/07-1255.1.

Gill, N.S., Sangermano, F., Buma, B., Kulakowski, D., 2017. Populus tremuloides seedling establishment: an underexplored vector for forest type conversion after multiple disturbances. For. Ecol. Manage. 404, 156–164. https://doi.org/10.1016/j.foreco.2017.08.008.

Glitzenstein, J.S., Platt, W.J., Streng, D.R., 1995. Effects of fire regime and habitat on tree dynamics in north Florida longleaf pine savannas. Ecol. Monogr. 65, 441–476. https://doi.org/10.2307/2963498.

Harvey, B.J., Donato, D.C., Romme, W.H., Turner, M.G., 2014. Fire severity and tree

regeneration following bark beetle outbreaks: the role of outbreak stage and burning conditions. Ecol. Appl. 24, 1608–1625. https://doi.org/10.1890/13-1851.1.

Hils, M.H., Vankat, J.L., 1982. Species removals from a first-year old-field plant community. Ecology 63, 705–711. https://doi.org/10.2307/1936791.

Hodgkins, E.J., 1958. Effects of fire on undergrowth vegetation in upland southern pine forests. Ecology 39, 36–46. https://doi.org/10.2307/1929965.

Holm, S., 1979. A simple sequentially rejective multiple test procedure author(s): scand. J. Stat. 6, 65–70. https://doi.org/10.2307/4615733.

Holzmueller, E.J., Jose, S., 2011. Invasion success of cogongrass, an alien C4 perennial grass, in the Southeastern United States: exploration of the ecological basis. Biol. Invas. 13, 435–442. https://doi.org/10.1007/s10530-010-9837-1.

Johnson, E.A., Miyanishi, K., 2007. Plant Disturbance Ecology: The Process and the Response. Elsevier/Academic Press.

Krueger, L., Peterson, C., 2006. Effects of White-tailed Deer on *Tsuga canadensis* regeneration: evidence of microsites as refugia from browsing. Am. Midl. Nat. 156, 353–362 10.1674/0003-0031(2006) 156[353:EOWDOT]2.0.CO;2.

Kulakowski, D., Veblen, T.T., 2007. Effect of prior disturbances on the extent and severity of wildfire in Colorado subalpine forests. Ecology 88, 759–769. https://doi.org/10.1890/06-0124.

Liu, K., Lu, H., Shen, C., 2008. A 1200-year proxy record of hurricanes and fires from the Gulf of Mexico coast: testing the hypothesis of hurricane–fire interactions. Quat. Res. 69, 29–41. https://doi.org/10.1016/j.yqres.2007.10.011.

Long, Z.T., Carson, W.P., Peterson, C.J., 1998. Can disturbance create refugia from herbivores: an example with hemlock regeneration on treefall mounds. J. Torrey Bot. Soc. 125, 165–168.

Main, M.B., Richardson, L.W., 2002. Response of wildlife to prescribed fire southwest Florida flatwoods. Wildl. Soc. Bull. 30, 213–221.

McCune, B., Grace, J.B., 2002. Analysis of Ecological Communities. Mjm Software Design.

Meigs, G.W., Campbell, J.L., Zald, H.S.J., Bailey, J.D., Shaw, D.C., Kennedy, R.E., 2015. Does wildfire likelihood increase following insect outbreaks in conifer forests? Ecosphere 6, 1–24.

Meigs, G.W., Zald, H.S.J., Campbell, J.L., Keeton, W.S., Kennedy, R.E., 2016. Do insect outbreaks reduce the severity of subsequent forest fires? Environ. Res. Lett. 11, 045008.

Melvin, M.A., 2012. 2012 National Prescribed Fire Use Survey Report. Coalition of Prescribed Fire Councils, Inc.

Minchin, P.R., 1987. An evaluation of the relative robustness of techniques for ecological ordination. Vegetatio 69, 89–107. https://doi.org/10.1007/BF00038690.

Myers, R.K., Van Lear, D.H., 1998. Hurricane–fire interactions in coastal forests of the south: a review and hypothesis. For. Ecol. Manage. 103, 265–276. https://doi.org/10.1016/S0378-1127(97)00223-5.

Nakashizuka, T., 1989. Role of uprooting in composition and dynamics of an old-growth forest in Japan. Ecology 70, 1273–1278. https://doi.org/10.2307/1938186.

O'Brien, J.J., Hiers, J.K., Callaham, A.J. Mac, Mitchell, R.J., Jack, S.B., 2008. Interactions among overstory structure, seedling life-history traits, and fire in frequently burned neotropical pine forests. Ambio 37, 542–547. https://doi.org/10.1579/0044-7447-37.7.542.

Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Szoecs, E., Wagner, H., 2016. Vegan: Community Ecology Package. R Package Version 2.4-1.

Paine, R.T., 1966. Food web complexity and species diversity. Am. Nat. 100, 65. https://doi.org/10.1086/282400.

Paine, R.T., Tegner, M.J., Johnson, E.A., 1998. Compounded perturbations yield ecological surprises. Ecosystems 1, 535–545. https://doi.org/10.1007/s100219900049.

Payne, H.H., 1976. Soil survey of Baldwin, Jones, and Putnam Counties. Georgia, United States Department of Agriculture, Soil Conservation Service and Forest Service.

Pelz, K.A., Smith, F.W., 2012. Thirty year change in lodgepole and lodgepole/mixed conifer forest structure following 1980s mountain pine beetle outbreak in western Colorado, USA. For. Ecol. Manage. 280, 93–102. https://doi.org/10.1016/j.foreco.2012.05.032.

Peterson, C.J., 2007. Consistent influence of tree diameter and species on damage in nine eastern North America tornado blowdowns. For. Ecol. Manage. 250, 96–108. https://doi.org/10.1016/j.foreco.2007.03.013.

Peterson, C.J., 2000. Catastrophic wind damage to North American forests and the potential impact of climate change. Sci. Total Environ. 262, 287–311. https://doi.org/10.1016/S0048-9697(00)00529-5.

Peterson, C.J., Carson, W.P., McCarthy, B.C., Pickett, S.T.A., 1990. Microsite variation and soil dynamics within newly created treefall pits and mounds. Oikos 58, 39–46. https://doi.org/10.2307/3565358.

Peterson, C.J., Leach, A.D., 2008. Limited salvage logging effects on forest regeneration after moderate-severity windthrow. Ecol. Appl. 18, 407–420. https://doi.org/10.1890/07-0603.1.

Peterson, C.J., Pickett, S.T.A., 1995. Forest reorganization: a case study in an old-growth forest catastrophic blowdown. Ecology 76, 763–774.

Pickett, S.T.A., Collins, S.L., Armesto, J.J., 1987. Models, mechanisms and pathways of succession. Bot. Rev. 53 (3), 355–371.

Pielou, E.C., 1966. The measurement of diversity in different types of biological collections. J. Theor. Biol. 13, 131–144. https://doi.org/10.1016/0022-5193(66)90013-0.

Robertson, K.M., Ostertag, T.E., 2009. Biomass equations for hardwood resprouts in fire-maintained pinelands in the southeastern United States. South. J. Appl. For. 33, 121–128.

Ross, M.S., O'Brien, J.J., Ford, R.G., Zhang, K., Morkill, A., 2009. Disturbance and the rising tide: the challenge of biodiversity management on low-island ecosystems. Front. Ecol. Environ. 7, 471–478. https://doi.org/10.1890/070221.

Royo, A.A., Peterson, C.J., Stanovick, J.S., Carson, W.P., 2016. Evaluating the ecological impacts of salvage logging: can natural and anthropogenic disturbances promote coexistence? Ecology 97, 1566–1582. https://doi.org/10.1890/15-1093.1.

Scheffer, M., Carpenter, S., Foley, J.A., Folke, C., Walker, B., 2001. Catastrophic shifts in ecosystems. Nature 413, 591–596. https://doi.org/10.1038/35098000.

Shannon, C.E., Weaver, W., 1963. The Mathematical Theory of Communication. University of Illinois Press, Urbana.

Sobhani, V.M., Barrett, M., Peterson, C.J., 2014. Robust prediction of treefall pit and mound sizes from tree size across 10 forest blowdowns in eastern North America. Ecosystems 17, 837–850. https://doi.org/10.1007/s10021-014-9762-8.

Taylor, D.L., Herndon, A., 1981. Impact of 22 years of fire on understory hardwood shrubs in slash pine communities within Everglades National Park. Report T-640. Homestead, FL.

Turner, M.G., Hargrove, W.W., Gardner, R.H., Romme, W.H., 1994. Effects of fire on landscape heterogeneity in Yellowstone National Park, Wyoming. J. Veg. Sci. 5, 731–742. https://doi.org/10.2307/3235886.

Ulanova, N.G., 2000. The effects of windthrow on forests at different spatial scales: a review. For. Ecol. Manage. 135, 155–167. https://doi.org/10.1016/S0378-1127(00)00307-8.

Urquhart, G.R., 2009. Paleoecological record of hurricane disturbance and forest regeneration in Nicaragua. Quat. Int. 195, 88–97. https://doi.org/10.1016/j.quaint.2008.05.012.

Werner, P.A., Harbeck, A.L., 1982. The pattern of tree seedling establishment relative to staghorn sumac cover in michigan old fields. Am. Midl. Nat. 108, 124–132.

Zenoble, M.D., Peterson, C.J., 2017. Remotely visible width and discontinuity of 50 tornado damage paths through forested landscapes. Electron. J. Sev. Storms Meteorol. 12, 1–21.