Forest Ecology and Management 481 (2021) 118724

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Tree, stand, and landscape factors contributing to hurricane damage in a coastal plain forest: Post-hurricane assessment in a longleaf pine landscape

Brandon T. Rutledge [a,*], Jeffery B. Cannon [a], R. Kevin McIntyre [a], Angela M. Holland [b], Steven B. Jack [c]

[a] The Jones Center at Ichauway, 3988 Jones Center Dr., Newton, GA 39870, United States
[b] University of Delaware, 531 S College Ave., Newark, DE 19716, United States
[c] Boggy Slough Conservation Area, T.L.L. Temple Foundation, 204 Champions Drive, Lufkin, TX 75901, United States

ARTICLE INFO

Keywords:
Tropical cyclones
Hurricane Michael
Hurricane damage
Forest resilience
Timber management
Longleaf pine

ABSTRACT

Hurricanes occur regularly along the Atlantic and Gulf Coasts of the southern United States and can have intense ecological and economic impacts on forests. Frequent low-intensity fire plays a well-known role in many coastal plain upland forests, including longleaf pine (*Pinus palustris*). Hurricanes may also play a critical role in shaping these communities. Field studies investigating wind susceptibility of coastal tree species often rank longleaf pine among the most wind-resistant species. This assertion is usually based on analyses that evaluate whether the fraction of downed trees is greater than expected by chance. However, tree species' associations with different soil types and landforms, and differences in tree size and spatial distribution can confound inferences. Accounting for tree, stand, and landscape factors can improve estimates of species differences in probability of wind damage. Following Hurricane Michael in 2018, we used observations from more than 3000 trees and generalized linear mixed models to investigate how tree-level factors (species and DBH), stand-level factors (stand density and soil type), and landscape-level factors (wind exposure and landscape configuration) affect tree vulnerability to hurricane winds in a longleaf pine-dominated landscape. Probability of damage varied between species, was dependent on soil type, and increased with increasing diameter for all species. Longleaf pine was in the lower range of treefall probability for all soil types and showed the lowest variability in wind susceptibility, confirming findings from other studies. However, we observed important interactions between species and soil types. Oak (*Quercus* spp.) species were more susceptible to treefall on drier soils, while pine (*Pinus* spp.) species were more resistant, suggesting that hurricanes, along with frequent fire, may play a role in shaping the landscape-scale structure of southeastern pine systems. Understanding the role of hurricanes in disturbance-prone forests can provide insight on the ecological processes structuring diverse coastal forest systems while informing activities critical for their management and conservation. Additionally, multi-aged silvicultural approaches may serve to increase the hurricane resilience of forests.

1. Introduction

Natural disturbances shape forest structure and function across the globe (Pickett and White, 1985). Tropical cyclones are perhaps the most significant source of meteorological forest disturbance due to their combined scale and severity (Stanturf et al., 2007). Hurricanes (>33 m s^{-1} wind speed) impact 1.2 million ha annually in the U.S. (Dale et al., 2001) and can have intense ecological and economic impacts on forests. Often perceived as locally rare events, tropical cyclones recur regularly along the southeastern U.S. Atlantic and Gulf coasts. The historical return period for all hurricanes (Saffir-Simpson Wind Scale Categories 1–5) averages 13 years from 33 locations between the states of North Carolina and Texas, and 58 years for major (>49 m s^{-1} wind speed; Saffir-Simpson Wind Scale Categories 3–5) hurricanes (Keim et al., 2007). Moreover, there is general agreement among climate models that the number of tropical cyclones reaching major hurricane strength will likely increase in the future (Bender et al., 2010; Pielke et al., 2005).

Wind damage associated with hurricanes can have substantial impacts on forests at multiple scales. Mortality from wind alters forest structure, affecting the composition of tree species and distribution as

* Corresponding author.
E-mail address: brandon.rutledge@jonesctr.org (B.T. Rutledge).

https://doi.org/10.1016/j.foreco.2020.118724
Received 31 August 2020; Received in revised form 14 October 2020; Accepted 16 October 2020
Available online 4 November 2020
0378-1127/

well as shrub and herbaceous communities (Beatty, 1984; Cooper-Ellis et al., 1999; Foster et al., 1997; Peterson and Pickett, 1995; Ulanova, 2000). Wind damage can amplify or buffer the effects of other disturbances such as herbivory or fire (Cannon et al., 2017; Krueger and Peterson, 2006; Shinoda and Akasaka, 2020). At the landscape scale, wind damage can be extremely variable in space and intensity, driving patch dynamics and generating a range of gaps varying in size and damage severity (Cannon et al., 2016; Pickett and White, 1985; Xi et al., 2008). Severe hurricane events can be extensive and are known to impact carbon dynamics at a regional level (Chambers et al., 2007; Dahal et al., 2014).

Fire plays a well-known role in shaping many hurricane-prone upland forests such as longleaf pine (*Pinus palustris*), but hurricanes may also affect the structure of these forests. Historically, frequent fire favored fire-resistant longleaf pine in upland areas and maintained open conditions suitable for a diverse assemblage of endemic plants and animals (Noss et al., 1995). In the absence of frequent fire, fire-sensitive hardwood species typically restricted to lower, wetter portions of the landscape (e.g., laurel oak, *Quercus laurifolia*; live oak, *Quercus virginiana*; water oak, *Quercus nigra*) can encroach into pine-dominated uplands (Frost, 2007). Once these species are established, low intensity fire is less effective at causing mortality, particularly in larger diameter individuals (Rebertus et al., 1989) and especially those that produce voluminous fire impeding leaf litter (Kreye et al., 2013; Nowacki and Abrams, 2008). Susceptibility of tree species to wind damage varies considerably and is governed, in part, by tree size and species (Everham and Brokaw, 1996; Peterson, 2007). Studies on the role of wind damage in fire-adapted forests often focused on indirect effects that alter fuel and regeneration conditions (Cannon et al., 2017; Gilliam et al., 2006; Myers and Van Lear, 1998; O'Brien et al., 2008). However, if wind affects species differentially across landscape settings, it may play a reinforcing role, alongside frequent fire, in shaping the structure and composition of southeastern forests.

Beyond their ecological effects, tropical cyclones pose a significant economic threat to forest management in terms of foregone revenue and timber loss in wind-prone areas (Prestemon and Holmes, 2010). The recognition of these impacts has spurred an interest in strategies to manage for wind resilient forests (Stanturf et al., 2007). Between 1870 and 1930, heavy harvest of longleaf pine forests led to loblolly pine (*Pinus taeda*) and slash pine (*Pinus elliottii*) becoming the preferred species for forest management as they were more easily established, grew more quickly, and were suited as feedstock for the nascent pulp and paper industry that proliferated after World War II (Carter et al. 2015, Oswalt et al. 2012, Van Lear et al. 2005). By the 1970s, southern pine silviculture was dominated by plantations of faster-growing southern pine species, and longleaf pine was relegated to a minor component of the region's forests. Some observations of southern pine wind damage have suggested that longleaf pine is more wind-firm than other pine species, particularly loblolly pine (Hook et al., 1991; Johnsen et al., 2009; Touliatos and Roth 1971). A foundational aspect of managing forests for tropical cyclone resilience is to understand what factors drive susceptibility to wind across tree species.

Potential mechanisms for differences in species vulnerability to wind damage include variation in stem properties (e.g., modulus of elasticity, wood strength, and stiffness) or structural differences (e.g., crown shape, branching patterns, and leaf area) (Garms and Dean, 2019; Hedden et al., 1995; Peterson, 2007). However, two issues arise when thinking about how and why trees are affected by windstorms. First, studies often use proportional analysis (i.e., contingency tables) to evaluate whether the fraction of downed trees is greater than expected based on each species' sample abundance (Derr and Enghardt, 1957; Duryea et al., 2007; Oswalt and Oswalt, 2008). Because large trees are generally more susceptible to wind, differences in size structure among species populations can confound inferences related to the susceptibility of each species. Studies that use logistic regression to estimate the probability of wind damage instead can remove the confounding effects of size structure (e.g., Harcombe et al., 2009). A second issue is that spatial dependence among observations in most field studies limits the ability to separate tree-scale factors (e.g., species and size) from stand- and landscape-scale factors (e.g., soils, structure, edge effects) if spatial autocorrelation among observations is not explicitly considered (Zuur et al., 2009). For example, if trees rooted in poorly drained soil are more vulnerable, then unequal distribution of species across soil types obscures species variation in susceptibility. Likewise, other factors such as stand density, soil type, elevation, and topographic position (Cannon et al., 2016; Lindemann and Baker, 2002; Wang and Xu, 2009) have been shown to affect impacts from extreme winds and may confound individual tree-level differences.

In our study, we use generalized linear mixed models in addition to basic proportional analyses to examine factors driving tree susceptibility to wind at multiple scales, while accounting for effects of spatial and size structure that are inherent to natural forest populations. Using observations from more than 3000 trees, we investigated how tree-level factors (species and size), stand-level factors (stand density and soil type) and landscape-level factors (wind exposure and landscape configuration) affect tree vulnerability to hurricane winds in a longleaf pine-dominated landscape.

2. Methods

2.1. Study site and Hurricane Michael

This study was conducted at Ichauway, the 11,741 ha research site of the Jones Center in Baker County, Georgia. Approximately 7300 ha of Ichauway consists of second-growth longleaf pine woodlands (~100 years old), with about 4400 ha containing a diverse native ground cover dominated by wiregrass (*Aristida stricta* Michx.). Prescribed fire is the primary management tool used to restore and maintain an open forest structure with an herbaceous understory. The majority of Ichauway is managed on a 2-year prescribed burn rotation with 4000–4900 ha burned annually, and a history of frequent fire (≤2 years) dating back to at least the 1920s. During timber harvests, modified individual tree selection is used for forest management throughout the property to promote and maintain a stand-level, multiple age-class structure (McIntyre et al., 2008). In addition to longleaf pine woodlands, some portions of forest contain loblolly pine (906 ha), slash pine (800 ha), or shortleaf pine (*Pinus echinata*, 415 ha) as a dominant or component species. Oaks (e.g., *Q. falcata, Q. incana, Q. laevis, Q. laurifolia, Q. nigra, Q. stellata,* and *Q. virginiana*) are scattered throughout the uplands as individual trees or in small isolated patches within the pine matrix. Hardwood-dominated forests occur in association with streams and drainages, and in fire shadows around roads and some isolated wetlands. Additional hardwood species include: *Carya* spp., *Cornus florida*, *Diospyros virginiana*, *Fraxinus* spp., *Nyssa* spp., *Taxodium* spp., and *Ulmus* spp.

On October 10, 2018 Hurricane Michael made landfall in the southeastern U.S. near the Florida panhandle city of Mexico Beach (NOAA, 2020). According to the National Hurricane Center, maximum sustained winds were 257 km h^{-1} at landfall, making it the third-most intense recorded hurricane to strike the continental United States, and only the fourth Category 5 storm (on the Saffir-Simpson scale) to have done so (NOAA, 2019). The eye of Hurricane Michael passed within ~10 km of the study area (Fig. 1); anemometers failed early in the storm, while on-site weather stations recorded a minimum atmospheric pressure of 970 mbar at 1900 EDT. Although modern Saffir-Simpson hurricane categories are based on wind speed without regard to pressure, the minimum pressures observed at the study site during Hurricane Michael have historically been associated with strong Category 2 storms (SECOORA, 2020).

2.2. Field methods and tree-level variables

In 2001, a long-term forest monitoring program was established in

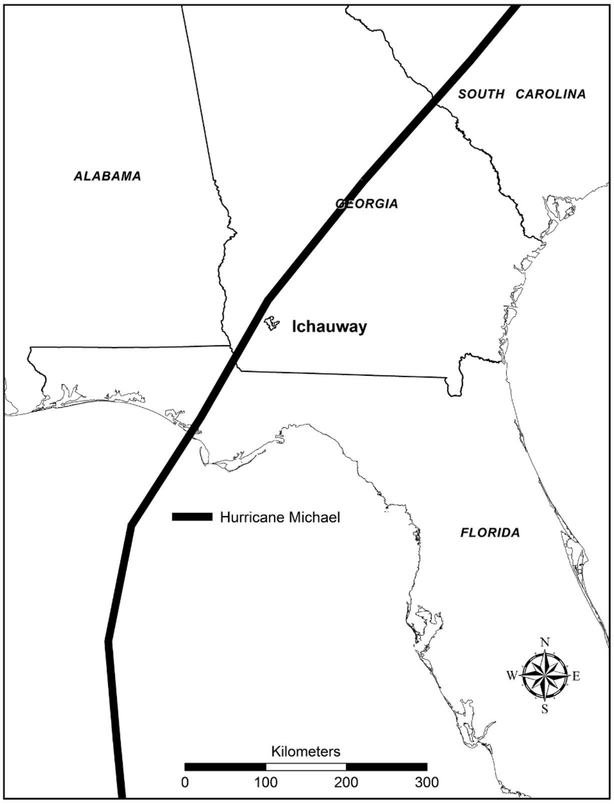

Fig. 1. Storm path of Hurricane Michael that made landfall on October 10, 2018 and the location of Ichauway, Baker County, Georgia USA.

the study area to monitor changes in vegetation structure and composition through time and with active management (Holland et al., 2019). Using a Random Tessellation Stratified design with hierarchical randomization (Stevens, 1997), 864 1.0 ha plots were selected for long-term monitoring within eight ecological communities (i.e., dry terrace, fire intolerant depression, fire tolerant depression, flatwoods, floodplain, fluvial terrace, sand ridge, and upland). In 0.10 ha subplots within each plot, all trees were mapped and standard forestry measurements for trees ≥ 10 cm in diameter at breast height (DBH) were recorded over four year intervals [DBH, tree height, tree defect, tree history (i.e. live tree, standing dead tree, fallen dead tree, harvested tree)]. A full description of the monitoring program and associated ecological communities is presented in Holland et al., 2019.

We revisited 268 long-term forest monitoring plots from December 2018 through February 2019 to assess forest impacts due to Hurricane Michael (Fig. 2). Plots were chosen within ecological communities most likely to be salvage logged (i.e., dry terrace, flatwoods, fluvial terrace, sand ridge, and upland) to allow storm damage assessment prior to logging. Additionally, we limited sampling to those plots previously sampled ≤ 18 months before Hurricane Michael to minimize uncertain causes of tree damage or mortality. Tree damage was assessed by the following criteria: no damage, uprooted, severe lean (>45°), leaning (≤45°), visual estimate of crown damage (damage to 1/3, 2/3, or >2/3 of crown), snapped (base, stem, or crown), and unknown (salvaged before plot visit). To assess probability of treefall, we further classified trees as 'down' or 'fallen' if they were severely leaning, had broken crowns (≥2/3), snapped, uprooted, or unknown (Table 1). Unknown trees were salvage logged before sampling. In these cases, we could not assess their damage, but they were considered fallen based on salvage logging criteria. Tree species and DBH were determined using the most recent measurement (≤18 months) from the long-term forest monitoring program.

2.3. Stand- and landscape-level variables

Stand density was calculated for each plot using Reineke's Stand Density Index (SDI, Reineke, 1933). We determined soil drainage class for each plot using data from the USDA Soil Survey Geographic (SSURGO) database (SSURGO, 2020). SSURGO drainage classes were then numerically coded: (1) excessively drained, (2) somewhat excessively drained, (3) well drained, (4) moderately well drained, (5) somewhat poorly drained, and (6) poorly drained. We calculated an index of local wind sheltering (Plattner et al., 2006) at the landscape scale using topographic attributes calculated site-wide (Fig. 3). Using a 30 m resolution digital elevation model (U.S. Geological Survey, 2015) we calculated wind exposure using the RSAGA package (Brenning, 2013) within a 254 ha moving window (radius of 30 pixels) using a wind

Table 1
Post-hurricane tree damage assessment, and treefall classification used for trees in the study.

Tree damage assessment	Description	Treefall (binary classification)
No damage	Intact tree, no visual damage	0
Leaning	Leaning ≤ 45°	0
Minor crown damage	Crown damage ~ 33%	0
Severely leaning	Leaning > 45°	1
Crown broken	Crown damage ~ 66%	1
Trunk snapped		1
Uprooted		1
Unknown	Salvage logged prior to sampling	1

Fig. 2. Damage from Hurricane Michael in a longleaf pine (*Pinus palustris* Mill.) dominated forest with wiregrass (*Aristida stricta*) understory at the Jones Center at Ichauway illustrating diversity of damage types including blown over, snapped, broken crowns, and leaning trees. Photo Credit R.T. Bryant.

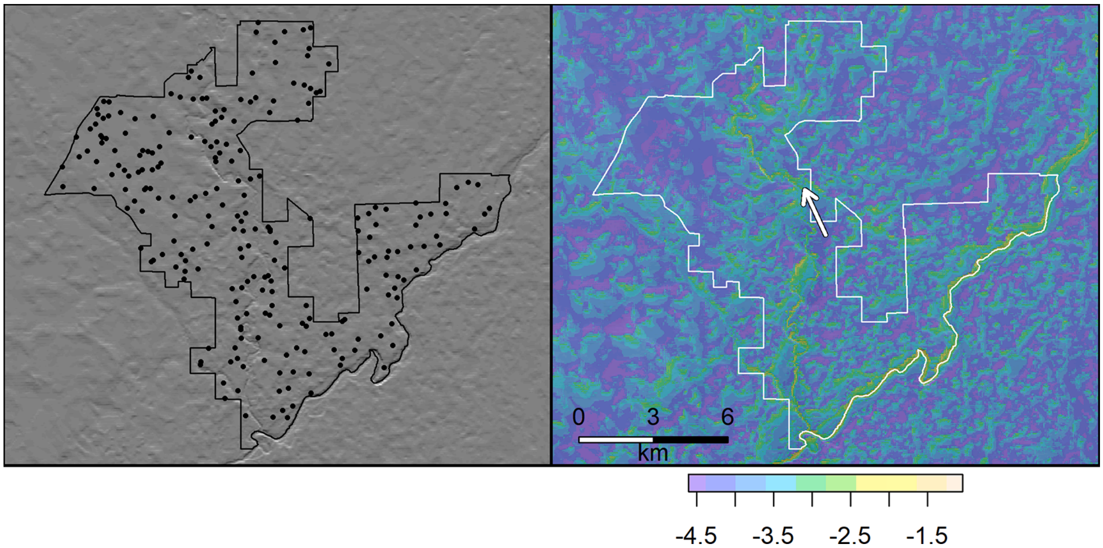

Fig. 3. (left) Digital elevation model (30 m) of study site with plot locations and hill shade relief, and (right) output of natural log transformed wind exposure index (Plattner et al., 2006) calculated within a 254 ha moving window and a wind direction of 335° (white vector). Areas with a larger (less negative) wind exposure index represent more wind-exposed topographies whereas smaller (more negative) value represents more leeward topographies.

direction of 335° based on the direction of maximum wind intensity observed from local meteorological stations (S. Brantley, unpublished data) and aerial observation of downed tree direction (Jones Center, unpublished data). Using ArcGIS (ESRI, 2014), we determined the perpendicular distance from each plot to the path of Hurricane Michael (NOAA, 2020). The Jones Center's land cover database was used to determine the distance of each plot from open areas (e.g., non-forested areas not including rivers, streams, or roads) greater than 1 ha in size.

2.4. Analysis of treefall probability

Field data collection and GIS processing led to a dataset of 3697 trees within 268 unique plots. This large dataset presented several analytical challenges including a binary response variable (fallen or intact, Table 1) and a hierarchical design with some measurements taken at the scale of individual trees (i.e., tree damage, species, and DBH) and other variables measured at the plot scale (e.g., soil type, SDI, wind exposure index, distance from hurricane, and distance from opening).

We modeled probability of treefall based on tree-, stand-, and landscape-scale predictors, following suggestions in Zuur et al. (2009) for testing and validating generalized linear mixed effects models using R (R Core Team, 2017). To ensure homogeneity, we removed outliers from the binary dataset including (1) trees larger than 80 cm (n = 14) which occurred only in *Quercus* spp.; (2) trees in one plot with a stand density index > 250 (n = 184) which occurred only in a planted stand of slash pine; and (3) non-oak hardwood species which were usually represented by fewer than 10 individuals in the sample (n = 84). To maintain statistical power needed to make ecological and management inferences about *Quercus* spp., we classified oaks into either mesic oaks (*Q. laurifolia*, laurel oak; *Q. nigra*, water oak; and *Q. virginiana,* live oak) or xeric oaks (*Q. falcata*, southern red oak; *Q. laevis*, turkey oak; *Q. margaretta*, sand post oak; *Q. incana*, bluejack oak; and *Q. stellata*, post oak) based on existing classifications (Cavender-Bares et al., 2004). We removed individuals identified as sand live oak (*Quercus geminata*) which were uncommon (n = 11), can be considered a variety of live oak, and may be difficult to distinguish in the field (Kirkman et al., 2007). The resulting dataset contained 3404 individual trees in 235 plots. Our check for collinearity among predictor variables showed only weak correlations (all $|r| < 0.3$ and variance inflation factors < 1.2). We z-transformed all continuous predictor variables prior to modeling to improve model convergence.

Because observations of damage to individual trees within plots are non-independent, we constructed variograms using a beyond optimal model including all predictor variables and two-way interactions as recommended by Zuur et al. (2009). The variogram indicated that spatial auto-correlation did not increase beyond approximately 10 m with no evidence of anisotropy. Given that the minimum distance between plots was 55 m, we modeled each plot with a random intercept, thus treating each plot as an independent set of observations. We modeled probability of treefall by specifying a generalized linear model using a binomial distribution with a complementary log-log link as recommended over the more common logit link for binomial datasets when there are unequal numbers of zeros and ones. We specified the model as follows:

$$p(\text{treefall})^{\sim}\ \text{dbh} \times \text{species} + \text{soil drainage class} \times \text{species} + \text{SDI} + \text{distance from path} \times \text{wind exposure index} + \text{distance from openings}$$

We calculated marginal and conditional pseudo-r^2 values using the method presented in Nakagawa and Schielzeth (2013) with the MuMIn package in R (Barton, 2019).

2.5. Analysis of tree damage type

Although we used a multiple regression approach to model tree damage across the dataset (treefall vs. intact), the ability to use multiple regression to model damage type (i.e., leaning, minor crown damage, uprooted) for individual tree, stand, and landscape-scale predictors was limited. Despite the large sample size of trees included in this study (n = 3404), and that 20.5% of trees sustained some level of damage, sample sizes for particular damage types across species and soil types were sparse in many cases. When separated by species, size, and soil type, all species except *Quercus* spp. exhibited fewer than three observations of leaning and severely leaning trees. Among longleaf pine, over one-third of crosstab cells of damage type and soil type contained three or fewer observations. Thus, we limited our analysis of tree damage type to summary statistics across tree- and stand-scale factors important in the treefall model. We included only the three most abundant species categories (longleaf pine, slash pine, and mesic oaks) in our sample to examine the interactive effects of tree size and soil type across species on damage type. We excluded 45 plots from the analysis, which contained some individual trees that had been salvage logged prior to sampling

Table 2
Tree-level summary data indicating sample size (*n*), study site-wide density, percent treefall, and percent trees damaged in bins of 20 cm. Percent trees damaged includes all damage types, including treefall. Data from all 3686 individuals in the dataset, including 282 removed to meet assumptions of generalized linear models, are shown. Species of interest included mesic oaks (*Q. laurifolia*, laurel oak, QULA; *Q. nigra*, water oak, QUNI; and *Q. virginiana,* live oak, QUVI), xeric oaks (*Q. falcata*, southern red oak, QUFA; *Q. laevis*, turkey oak, QULV; *Q. margaretta*, sand post oak, QUMA; *Q. incana*, bluejack oak, QUIN; and *Q. stellata*, post oak, QUST), *Pinus echinata* (shortleaf pine), *P. elliotti* (slash pine), *P. palustris* (longleaf pine), *P. taeda* (loblolly pine), and other (*Acer rubrum*, red maple; *Carya tomentosa*, mockernut hickory; *Carya glabra*, pignut hickory; *Carya ovata*, shagbark hickory; *Celtis laevigata*, sugarberry; *Crataegus viridis*, hawthorne; *Diospyros virginiana*, persimmon; *Juniperus virginiana*, eastern red cedar; *Liquidambar styraciflua*, sweetgum; *Nyssa sylvatica*, black gum; *Prunus angustifolia*, Chickasaw plum; *Prunus serotina*, black cherry; *Prunus umbellata*, hog plum; *Taxodium ascendens*, pond cypress; and *Ulmus alata*, winged elm).

Species category	Species	dbh (cm)	n	Density (ha^{-1})	% treefall	% trees damaged
mesic oak	QULA	10–30	50	1.87	20.0%	24.0%
		30–50	9	0.34	44.4%	66.7%
		50–70	3	0.11	33.3%	66.7%
	QUNI	10–30	70	2.62	30.0%	35.7%
		30–50	9	0.34	11.1%	66.7%
		50–70	2	0.07	50.0%	50.0%
	QUVI	10–30	30	1.12	10.0%	16.7%
		30–50	22	0.82	13.6%	36.4%
		50–70	24	0.90	4.2%	20.8%
		70–90	11	0.41	27.3%	54.5%
		90–110	4	0.15	25.0%	75.0%
		110–130	2	0.07	0.0%	0.0%
	pooled		236	8.85	20.8%	33.5%
xeric oak	QUFA	10–30	31	1.16	0.0%	0.0%
		30–50	18	0.67	50.0%	66.7%
		50–70	14	0.52	50.0%	71.4%
		70–90	7	0.26	42.9%	71.4%
		90–110	1	0.04	100.0%	100.0%
		110–130	1	0.04	100.0%	100.0%
	QUIN	10–30	8	0.30	12.5%	25.0%
		30–50	1	0.04	0.0%	0.0%
	QULV	10–30	20	0.75	15.0%	25.0%
		50–70	1	0.04	100.0%	100.0%
	QUMA	10–30	15	0.56	6.7%	6.7%
		30–50	3	0.11	66.7%	66.7%
	QUST	10–30	42	1.57	21.4%	21.4%
		30–50	22	0.82	45.5%	68.2%
		50–70	2	0.07	0.0%	0.0%
		70–90	1	0.04	0.0%	100.0%
	pooled		187	7.01	25.7%	34.8%
P. echinata		10–30	51	1.91	31.4%	31.4%
		30–50	34	1.27	32.4%	32.4%
		50–70	12	0.45	83.3%	91.7%
		70–90	1	0.04	100.0%	100.0%
	pooled		98	3.67	38.8%	39.8%
P. elliottii		10–30	430	16.12	25.8%	27.4%
		30–50	122	4.57	26.2%	27.0%
		50–70	31	1.16	29.0%	41.9%
	pooled		583	21.86	26.1%	28.1%
P. palustris		10–30	1393	52.23	10.6%	11.2%
		30–50	705	26.44	14.5%	17.6%
		50–70	235	8.81	18.3%	26.8%
		70–90	3	0.11	33.3%	100.0%
	pooled		2336	87.59	12.5%	14.8%
P. taeda		10–30	77	2.89	14.3%	16.9%
		30–50	59	2.21	23.7%	27.1%
		50–70	25	0.94	12.0%	36.0%
		70–90	1	0.04	100.0%	100.0%
	pooled		162	6.07	17.9%	24.1%
Other		10–30	81	3.04	14.8%	23.5%
		30–50	3	0.11	100.0%	100.0%
	pooled		84	3.15	17.9%	26.2%
Total			3686	138.22	16.9%	20.5%

Table 3
ANOVA table from generalized linear mixed effects model of tree including *p* values calculated using Type II sum of squares (Zuur et al., 2009).

Variable		df	Pr(>χ2)
dbh	13.52	1	0.0002
Species	33.74	5	0.0000
Soil drainage class	4.78	1	0.0288
SDI	1.28	1	0.2584
Dist. from hurricane	0.08	1	0.7813
Wind exposure index	1.40	1	0.2374
Dist. from opening	0.00	1	0.9778
dbh × species	13.36	5	0.0203
Soil drain. × species	23.41	5	0.0003
Hurricane dist. × wind exp.	1.70	1	0.1929

and contained trees whose primary damage type could not be confirmed.

3. Results

Based on proportional data among tree species groups, rates of damage varied across species: longleaf pine (14.8%), loblolly pine (24.1%), slash pine (28.1%), mesic oak (33.5%), xeric oak (34.8%), and shortleaf pine (39.8%) (Table 2). Overall, we found that both individual tree and landscape scale factors influenced probability of treefall following Hurricane Michael. Approximately 16.9% (n = 624) of trees ≥ 10 cm DBH were downed, accounting for 20.9% of the study-wide basal area prior to the storm. Generally, treefall frequency increased with increasing DBH for most species, and the range of severity varied across species and size classes (Table 2). The treefall model suggested that treefall was explained by a combination of significant tree-level factors (DBH and species category), and landscape-scale factors (soil drainage class), and interactions between these factors (all $p < 0.03$; Table 3). Stand density index, which ranged from 3.5 to 237.6 with a mean of 86.6 study-wide, and other landscape-level factors (distance from hurricane, openings, and wind exposure index) were not significant predictors of probability of treefall (Table 3). Overall explanatory power of the fixed effects in the model was relatively low (marginal pseudo $r^2 = 0.099$ and conditional pseudo $r^2 = 0.037$).

The probability of treefall increased with tree size for most species, but a significant species × DBH interaction suggests that the strength of this relationship varied among species (Table 3; Fig. 4; Fig. 5). Xeric oaks and shortleaf pine both showed strong size sensitivity, with greater increases in treefall susceptibility among larger size classes (Fig. 4B-C). Other southern pines, including slash pine, longleaf pine, and loblolly

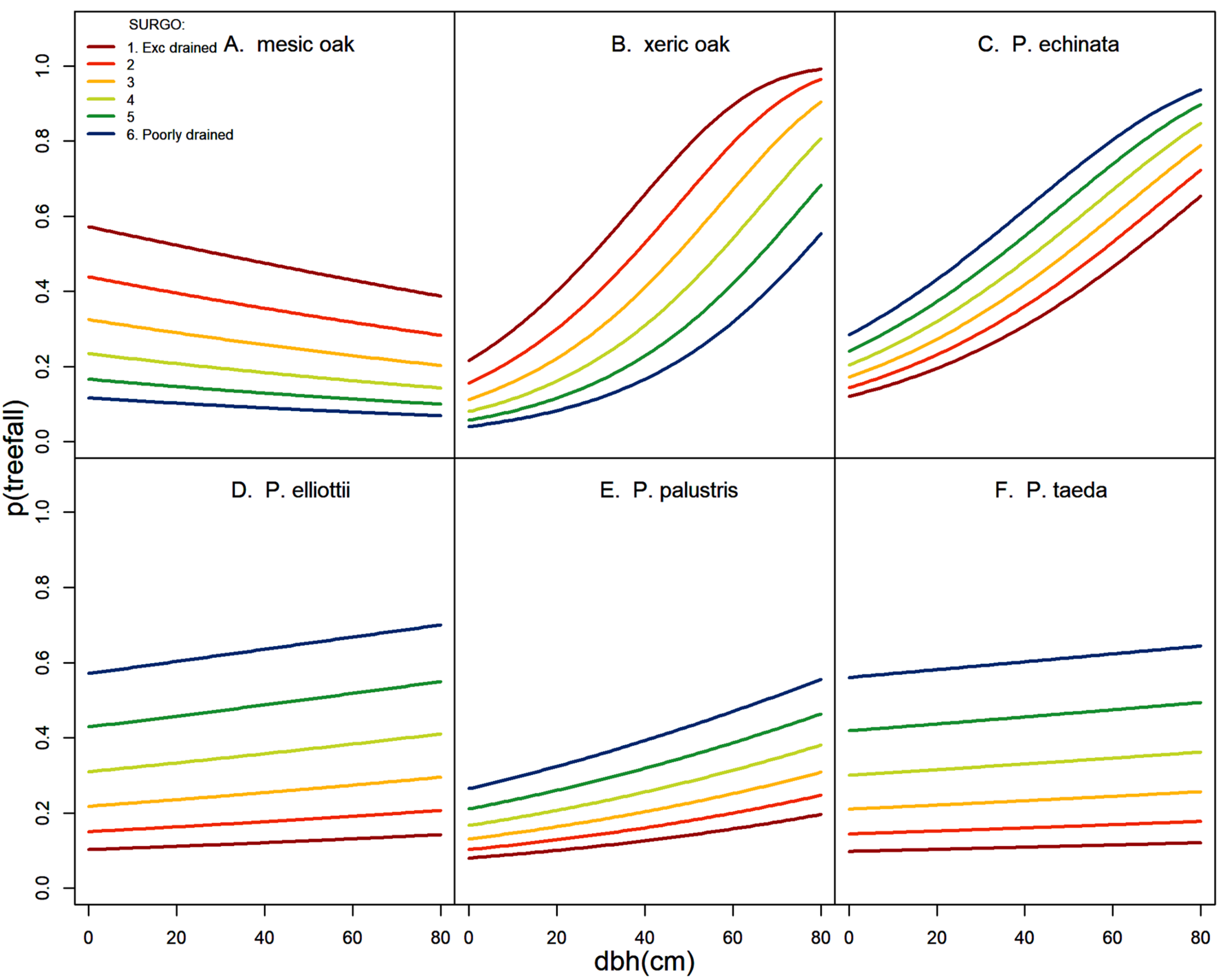

Fig. 4. Model prediction indicating the relationship between tree size (DBH) and estimated probability of treefall across six soil types for four pine species and two *Quercus* species groups. Soil types include excessively drained (drainage class 1) to very poorly-drained (drainage class 6). To simplify interpretation, model predictions were run using site-level averages for non-significant parameters (Table 3) and a random plot intercept of 0.

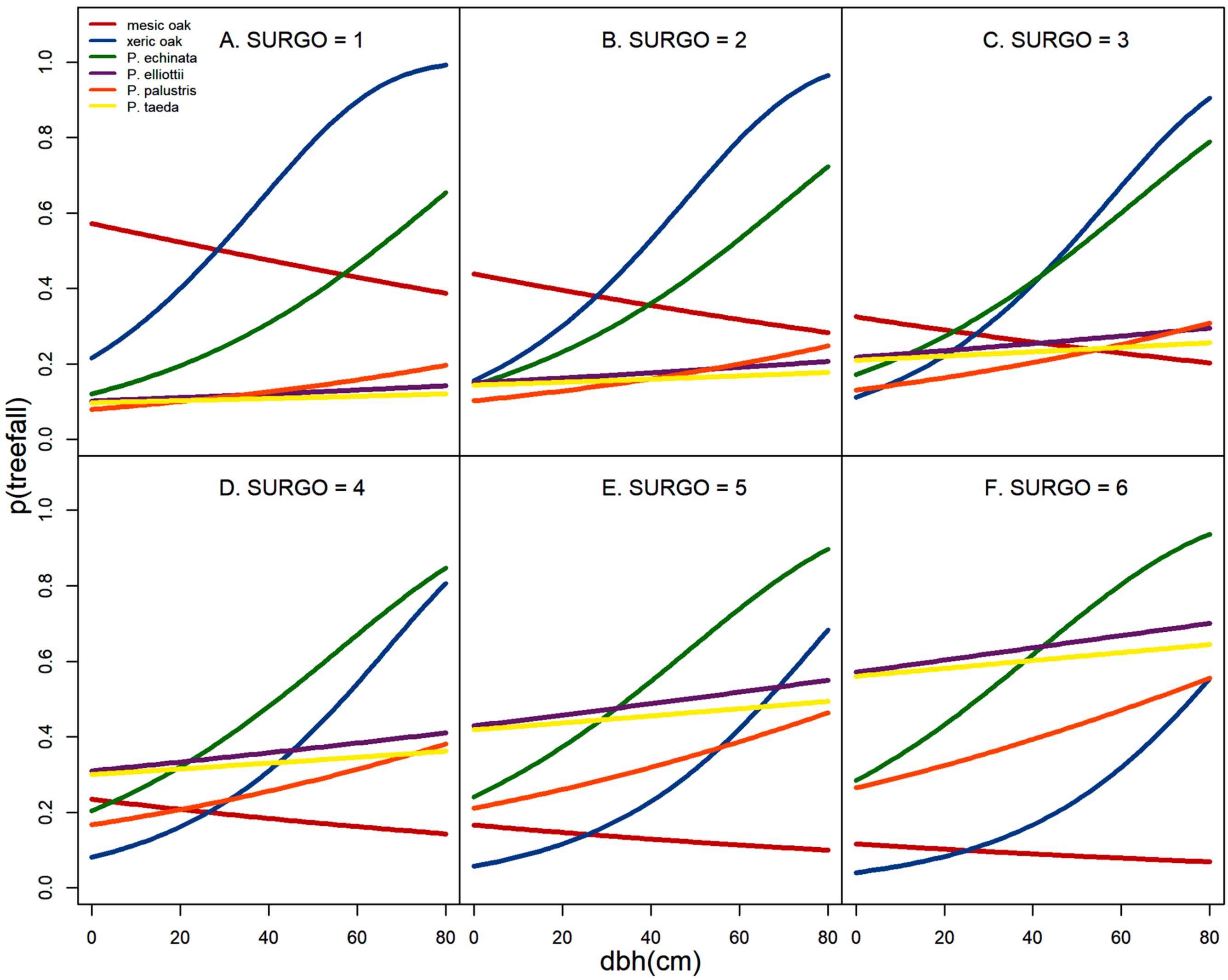

Fig. 5. Model prediction indicating the relationship between tree size (DBH) and estimated probability of treefall across five species and six soil types ranging from excessively drained (SURGO 1) to very poorly drained (SURGO 6). To simplify interpretation, model predictions were run using site-level averages for non-significant parameters (Table 3) and a random plot intercept of 0.

pine also increased in susceptibility among larger size classes (Fig. 4D-F). Mesic oaks, by exception, showed no increase in treefall susceptibility with size, and even reduced susceptibility in the largest size classes (Fig. 4A).

Soil drainage class influenced treefall susceptibility differently among pines and oaks (Fig. 4; Fig. 5). For both mesic oaks and xeric oaks, treefall was highest in well-drained soil, and was lowest in poorly drained soil (Fig. 4A-B). Conversely, for pines, treefall susceptibility increased in poorly-drained soil types and was lowest in well-drained soils (Fig. 4C-F). Slash pine and loblolly pine were most sensitive to soil moisture with treefall probability increasing from approximately 0.1 in well drained soils up to 0.7 in poorly drained soils for the largest trees (Fig. 4D, F). Longleaf pine, by contrast, showed less sensitivity to soil type with treefall probability increasing from 0.2 to 0.6 in poorly drained soils (Fig. 4E).

The ranking of species' treefall susceptibility to hurricane winds was dependent on soil type. Well-drained soils (drainage class 3) were the most common soils represented in the dataset (57% of plots). In these soil types, xeric oaks and shortleaf pine were most susceptible to treefall, especially in larger size classes (>40 cm DBH; Fig. 5C). Wind susceptibility of other pines was relatively similar in well-drained soils (Fig. 5C). In the driest soil types (drainage class 1–2), treefall susceptibility of both mesic and xeric oaks increased, whereas susceptibility of pine species decreased (Fig. 5A-B). In the wetter soil types (drainage class 4–6), treefall susceptibility of mesic and xeric oaks decreased, while susceptibility of pines increased and was most pronounced among slash pine and loblolly pine (Fig. 5D-F).

Among damaged trees, where damage type was known ($n = 450$), the most common types of damage observed were snapped (35.5%) and uprooted (23.3%), followed by trees with minor crown damage (<2/3 crown damage, 18.7%) or leaning > 45° (16.4%). We found relatively rare instances of broken crowns (≥2/3 crown damage, 3.8%) and trees leaning < 45° (2.2%). Despite the large number of damaged trees in our study, particular combinations of damage type across species, size, and soil classes were relatively sparse. Nevertheless, we cautiously summarize the major trends across the factors important in determining treefall. Among the most abundant species types in our sample (longleaf pine and mesic oaks), we found similar rates of uprooting, yet longleaf pine had greater instances of snapped and leaning trees, while mesic oaks had higher instances of minor crown damage and broken crowns (Fig. 6A). Slash pine had the highest instance of uprooting (Fig. 6A). With increasing tree size, we noted increased rates of both uprooting and minor crown damage while other types of damage generally became less frequent (Fig. 6B). Severely leaning trees (>45°) were notably present in

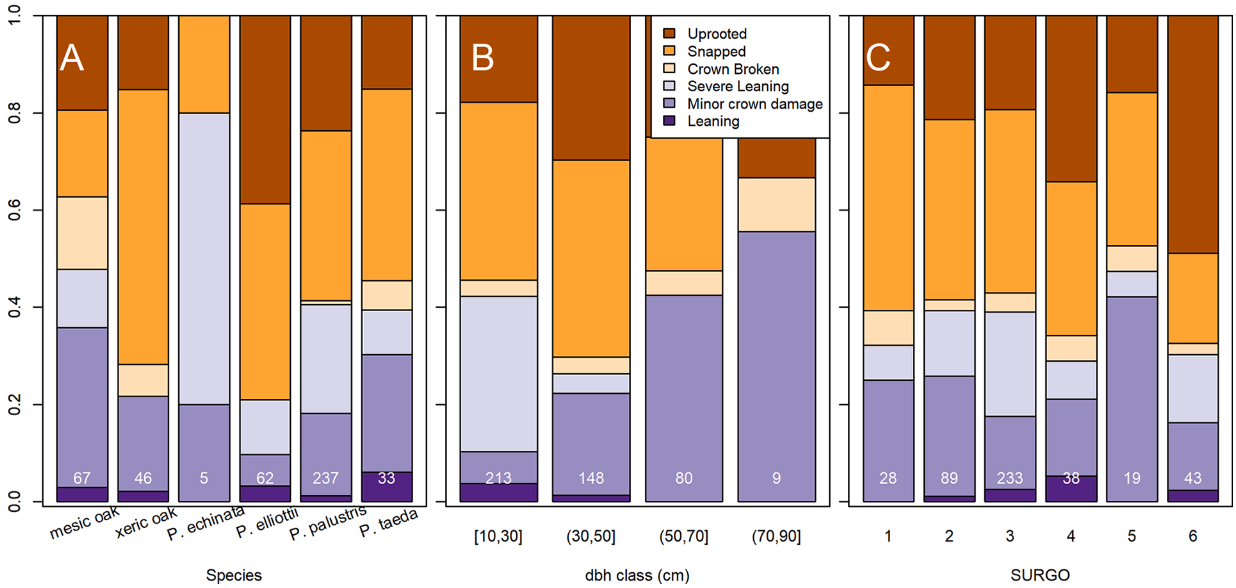

Fig. 6. Proportional bar plots summarizing type of damage by (A) species, (B) DBH in centimeters, and (C) soil drainage type (1 = excessively well drained soil, 6 = very poorly drained soils). Numbers in white indicate total sample size included in each bar.

only the smallest tree size classes. Across soil drainage types, rates of severe damage (snapping and uprooting) were relatively consistent (approximately 60%), yet more poorly drained soils (classes 4–6), exhibited greater uprooting, while more well drained soils exhibited greater snapping (Fig. 6C).

Factors driving tree damage type differed among the most abundant species. Mesic oaks showed many damage types among trees in the 10–30 cm size class. Among larger individuals (>30 cm DBH) minor crown damage was the dominant failure mode (Fig. 7A). The most abundant pine species (longleaf pine and slash pine), showed increased uprooting and minor crown damage as tree size increased, with a concomitant reduction in other damage types (Fig. 7B-C). As with tree size, relationships between soil type and damage type varied among species (Fig. 7D-F). For mesic oaks, sub-lethal forms of damage such as minor crown damage and leaning were common in poorly drained soils, whereas lethal forms of damage (uprooting and snapping) were most common in well drained soils (Fig. 7D). For slash pine, sample sizes were sparse for many soil types, yet the data available for soil types with adequate sample size indicate a drastic increase in uprooting and decrease in snapping for slash pine in the least well drained soils (Fig. 7E). Lastly, for longleaf pine, instances of uprooting and minor crown damage decreased in poorly drained soils and severe leaning became more common (Fig. 7F).

4. Discussion

4.1. Factors driving tree fall susceptibility

The results from this study are generally consistent with several other studies showing that the primary drivers of treefall susceptibility were tree size, species differences, and soil types (Table 3). While many other studies did not explicitly consider large-scale effects, or found them to have either low or no significance (Derr and Enghardt, 1957; Gresham et al., 1991; Johnsen et al., 2009; Oswalt and Oswalt, 2008), our study accounts for stand- and landscape-level effects, which can confound tree-scale effects and add rigor to quantification of differences in wind vulnerability among tree species. As with previous studies, we found that treefall susceptibility increases with tree size (Peterson, 2007), and found important differences among species susceptibility to treefall. After Hurricane Camille in 1969, a qualitative ranking of resistance was developed in which longleaf pine was reported to have less damage than other southern pines, though no quantitative analysis was given (Touliatos and Roth, 1971). Hook et al. (1991) used proportional analyses to assess damage between species and at different distances from Hurricane Hugo (1986). At the Santee Experimental Forest (within the eyewall) approximately 90% of all stems of longleaf pine, loblolly pine, and bottomland hardwood species were either broken or uprooted, although longleaf experienced less breakage and greater uprooting. Significant differences were found between pines, with 17% of longleaf broken or uprooted compared to 52% of loblolly, on the Hobcaw Forest (~50 km east of the eyewall) (Hook et al. 1991). An analysis of impacts of Hurricane Katrina (2005) in southeastern Mississippi showed tree height, plot density, and diameter/height had only minor impacts on species variation in tree mortality with mortality lower in longleaf (7%) than slash (14%) and loblolly (26%) pines (Johnsen et al., 2009). Longleaf pine also showed equal mortality from broken stems and uprooting, while mortality of other species was primarily (75%) from broken stems (Johnsen et al., 2009). Similarly, the proportional data from our study indicates that slash pine mortality (26.1%) was approximately twice that of longleaf pine (12.5%) (Table 2). However, because tree size and soil type also influenced susceptibility, these overall summaries should be interpreted with respect to these factors in order to avoid misleading inferences. For example, for a 30 cm tree in poorly drained soil, longleaf pine susceptibility was 0.35 compared to 0.6 in slash pine, indicating longleaf pine is more wind resistant in this setting (Fig. 5F). However, in excessively drained soils, susceptibility of both species was approximately equal (~0.1, Fig. 5A).

Our study also found that treefall susceptibility varies across soil types, and that soils interact with species, adding further complexity to patterns of treefall susceptibility. In general, treefall susceptibility increased in poorly drained soils for all pine species. For longleaf pine, treefall susceptibility was somewhat stable across a range of soil moisture, while susceptibility varied widely across soil type for other pine species examined (Fig. 4). In contrast, treefall susceptibility decreased in *Quercus* spp. in wetter soils. *Quercus* spp. were generally more susceptible to treefall relative to pines in well-drained soils, but were less susceptible to treefall in poorly drained soils. It is important to note that larger diameter trees (>30 cm DBH) for both the mesic and xeric oak species categories in our study were largely represented by two species, live oak (73.2% of large mesic oaks) and southern red oak (57.8% of large xeric oaks). While we were unable to analyze these species

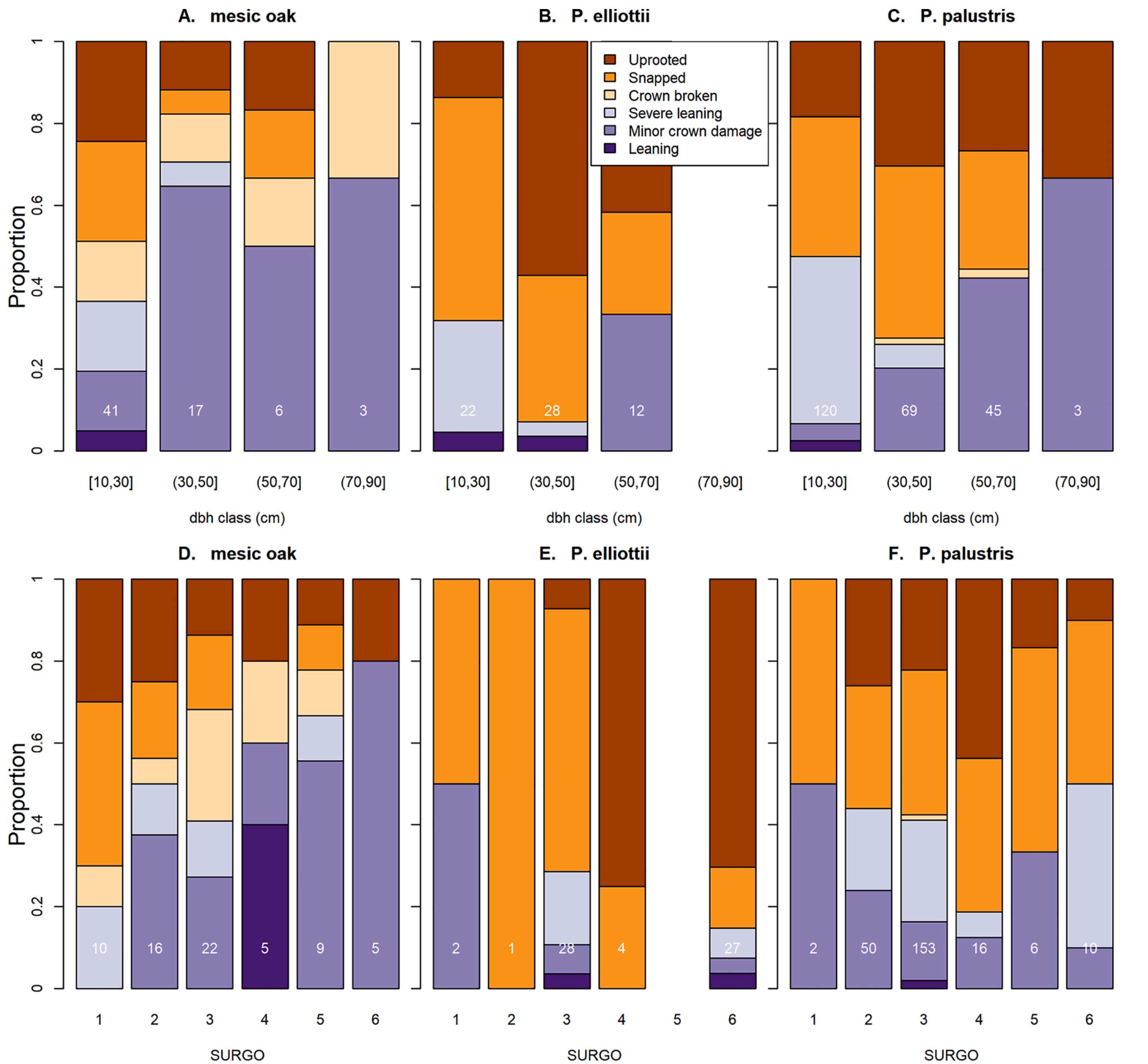

Fig. 7. Proportional bar plots summarizing damage type by diameter at breast height (A-C) and soil drainage type (D-F) for each of the most common species in the dataset. Numbers in white indicate the total sample size included in each bar.

independently, they could be influencing treefall patterns of oak species groups and warrant further investigation. Direct comparisons between studies can be problematic due to differences in objective and methodologies (Everham and Brokaw, 1996; Peterson, 2007). Notwithstanding, Harcombe et al. (2009) found that loblolly pine was more vulnerable on a mesic site relative to a dry site, and that susceptibility of water oak was lower on a wet site than a mesic site, corroborating our finding of opposite influences of soil moisture on pine and oak species.

The finding that longleaf pine, and other pines, were less susceptible to wind damage in well-drained soils relative to *Quercus* spp. suggests that wind damage may interact with frequent fire and play a role in shaping the landscape-scale structure of southeastern pine systems. Frequent low intensity fire is needed to maintain open conditions important for dominance of upland sites by longleaf pine (Noss et al., 1995). Disruptions to fire regimes can allow encroachment of mesic species into otherwise pine-dominated regions (Frost, 2007; Gilliam and Platt, 1999). The fire-impeding leaf litter of mesic species may provide further suppression of fire and reinforce encroachment of mesic tree species into drier uplands (Kreye et al., 2013; Nowacki and Abrams, 2008; Rebertus et al., 1989). Wind damage represents a mechanism to disrupt and reverse this feedback by disproportionately removing mesic oak species in uplands, as we found that probability of treefall of mesic oaks increased six-fold in well-drained soils relative to poorly drained soils. Previous studies suggest that disturbances such as wind damage can interact with fire to shape community dynamics in frequent fire forests, by increasing fuel loadings or disrupting fuel continuity (Cannon et al., 2017, 2014; Myers and Van Lear, 1998) and altering fire behavior. Together, our findings suggest that wind damage from hurricanes along with fire may affect landscape-scale patterns in wind- and fire-prone coastal plain forests.

4.2. Factors driving type of damage sustained

We found similar results to previous studies showing that tree-level factors such as tree size and species are associated with the type of damage that trees sustain (Peterson, 2007). Large trees in our study exhibited more minor crown damage or uprooting relative to smaller trees across species examined. We found greater uprooting in wetter soils, but this may be confounded with other factors such as size structure, vertical heterogeneity, species spatial distribution, or variation in tree rooting patterns with soil moisture (Nicoll et al. 2006; Fan et al. 2017). One interesting pattern is that longleaf pine (which was somewhat wind resistant to treefall in all soil types) and mesic oak (which was wind resistant to treefall in wetter soil types) both showed a relatively high diversity of damage types, with higher rates of minor crown damage, especially apparent in larger trees (Fig. 7). Higher branch fragility in larger trees was also noted by Duryea et al. (2007) using proportional analysis. Differences in wood properties among species such as elasticity may, in part, account for patterns of tree damage especially to the tree bole (Cannon et al., 2015; Garms and Dean, 2019; Ribeiro et al., 2016). However, crown architecture exerts considerable influence on converting forces from wind into torque on the bole, and crown area is an important factor in explaining tree mortality and damage according to wind simulation models (Peterson et al., 2019). Using simulation modeling, Hedden et al. (1995) showed that bending and breaking occurring in crowns under a wind load can drastically reduce the tree mortality with only 25% crown loss, thereby reducing mortality by more than 50% at wind speeds up to 220 km h^{-1}. Live oak has been noted to be less susceptible to hurricane damage than other mesic oaks and this may be related to its canopy shape and wood strength (Gresham et al., 1991; Touliatos and Roth, 1971). The broad sprawling crowns of coastal species such as live oak, which made up 37% of the mesic oaks in our dataset (73.2% of mesic oaks $\geq$ 30 cm DBH) and the high rate of minor crown damage in larger trees may also be part of a wind-resistance syndrome (sensu Batista and Platt, 2003) in mesic oaks where crown fragility may ultimately promote survival in areas subjected to frequent extreme winds.

4.3. Limitations and future research

This study confirmed important trends relative to treefall susceptibility using generalized linear models that considered tree-, stand-, and landscape-scale factors to examine how variability in tree size, species, and soil types affect treefall susceptibility. However, despite this uncommonly large dataset, we were unable to use hierarchical models to examine tree damage types, revealing some drawbacks to the use of large-scale empirical studies to examine factors important to predicting forest wind damage. Despite the large sample size included in our study, once observations of damage type were divided among damage classes and explanatory factors (i.e., species, soil types, sizes, etc.), few observations remained within each factor-level combination, leading to low statistical power to detect fundamental trends. Variation in size structure and spatial structure (e.g., associations between species and soil types) exacerbates this issue. Second, our study used generalized linear mixed modeling to account for variation in size and spatial structure inherent to forests. Although our results give insight into how wind susceptibility varies among southeastern tree species and soil types, the predictive power of our treefall model was somewhat low with a marginal pseudo-r^2 of only 0.10 suggesting that the fixed effects (e.g., species, size, soil type) explain only a small amount of the variation, while more variability is captured by random effects (among plot variability). This is not unexpected given the very large spatial variability inherent in many types of windstorms (Cannon et al., 2016; Foster and Boose, 1992; Lindemann and Baker, 2001; Webb, 1989).

Compared to large-scale empirical studies, mechanistic studies of forest wind damage such as those employing static winching and/or wind simulation experiments (Cannon et al., 2015; Peterson et al., 2019) may offer a more efficient means of developing a mechanistic understanding of interactions between species and soil types across a range of tree sizes. Several stand-scale factors, such as the phenomenon of susceptibility of emergent trees (Harcombe et al., 1998) or wind speed reduction in denser stands (Gardiner et al., 1997) may best be addressed using mechanistic wind models (Peltola, 2006). Wind damage has been simulated for managed stands at landscape-scales in simple terrain but models of forest wind damage in complex terrain and natural systems is not well-studied (Zeng et al., 2007). Wind movement through rugged terrain has been integrated in many models of forest wildfire (Hoffman et al., 2016; Sanjuan et al., 2014) but these tools have yet to be incorporated for use in large-scale mechanistic models of wind damage.

5. Conclusions and management implications

Like other studies, we found that pine species showed increased treefall susceptibility in wetter soils, while hardwoods showed the opposite trend. Considering that the direct economic impacts from hurricane damage to forests in the 30 years since Hurricane Hugo total almost 9 billion in 2018 dollars (Prestemon and Holmes, 2010; Brody, 2019) and climate models suggest there will be increasing intensity of tropical cyclones (Bender et al., 2010; Pielke et al., 2005), consideration of how forest landowners might mitigate risk is warranted (Stanturf et al., 2007). Landscape-scale risk models in hurricane-prone areas that incorporate actuarial analyses of damage risk for forests could be useful for developing wind risk mitigation strategies. Empirical studies focused on determining tree characteristics (e.g., species, size, trunk characteristics, and crown area) that reduce wind risk will help in the development of these models, along with prediction for landscape- and stand-level variables affecting wind velocities.

Other results of this study highlight opportunities to manage for more resilient forests in hurricane-prone areas, in terms of both ecological and economic resilience. We define ecological resilience as the ability of a forest to absorb disturbances and re-organize under change to maintain similar function and structure (Holling, 1973; Scheffer, 2009). Two years after the storm the forest seems to have met those criteria, with adequate fuels to carry prescribed fire, flourishing wildlife populations, and net ecosystem exchange and productivity returning to pre-storm levels (Brantley, unpublished data). Increasingly, approaches to forest management seek to incorporate or mimic natural disturbance processes to increase resilience and maintain function of natural systems (Franklin et al., 2007, 2002; Mitchell et al., 2009).

A more management oriented definition of resilience, based on the concept of adaptive management (Walters, 1986; Walters and Holling, 1990), suggests resilience can be captured in the sustainable management of forests that maintains their biodiversity, productivity, regeneration capacity, vitality, and their potential to fulfill, now and in the future, relevant ecological, economic and social functions (Wilkie et al., 2003). In addition to greater resistance to damage across a range of soil types, longleaf pine showed high percentages of leaning trees and trees that only suffered minor crown damage in larger size classes. This effectively increases the value of the stems available for salvage, since these trees can still be merchandized as sawlogs. The lower amounts of damage to smaller diameter trees indicate that a multi-aged approach to management may increase forests' economic resilience to hurricanes. Employing selection-based silviculture, or the use of irregular shelterwoods to achieve a multiple age-class structure, may provide this greater resilience by balancing merchantability and value of older, large trees with the wind-resistance of smaller diameter trees (Brockway and Outcalt, 2017; Jack and McIntyre, 2017; McIntyre et al., 2017, Mitchell et al., 2006). Additionally, heterogeneity of vertical structure has also been suggested as a hedge against disturbances associated with changing climatic conditions (Guldin, 2019). For ownerships that place greater emphasis on the production of timber, the resilience of multi-aged forests can be incorporated in careful management planning that maintains a mosaic of different age classes of even-aged stands across the landscape.

Aside from increased economic value, the presence of large trees provides many ecological benefits in spite of any elevated risk of treefall or wind damage. Large, old trees have been described as keystone structures storing large quantities of carbon, providing distinct microenvironments, and playing a local role in hydrology that cannot be produced by younger, small trees (Lindenmayer et al., 2012). Additionally, they provide critical habitat for many sensitive (i.e., red-cockaded woodpecker, *Leuconotopicus borealis*; Sherman's fox squirrel, *Sciurus niger* Shermani) and common (i.e., eastern rat snake, *Pantherophis alleghaniensis*) wildlife species (Conner et al., 1991; Engstrom and Sanders, 1997; Howze et al., 2019; Jackson and Jackson, 1986; Landers and Boyer, 1999; Perkins and Conner, 2004; Walters et al., 2002; Zwicker and Walters, 1999). McIntyre et al. (2019) reported that basal area of pine trees > 35.5 cm DBH was an important predictor of quality habitat for multiple wildlife species associated with open pine woodlands. In particular, larger longleaf pine trees are an important source of natural regeneration and fuels needed to maintain frequent prescribed fire (Croker and Boyer, 1976; Jack and McIntyre, 2017; Mitchell et al., 2009).

Finally, we found wind damage differentially affected pines and oaks based on soil type, indicating relatively frequent hurricanes, along with frequent fire may reinforce historical tree species distributions of longleaf pine-dominated uplands. Understanding the role of hurricanes on disturbance-prone forests can provide insight on the ecological processes shaping diverse coastal forest systems while informing processes critical for their management and conservation. Utilizing spatially explicit planning, management and restoration decisions should consider tree species relative to topographic and edaphic factors in order to maintain a diversity of stand structures and help mitigate impacts of future hurricanes.

CRediT authorship contribution statement

Brandon T. Rutledge: Conceptualization, Methodology, Investigation, Writing - original draft, Writing - review & editing, Project administration, Supervision. **Jeffery B. Cannon:** Formal analysis, Investigation, Writing - original draft, Writing - review & editing, Visualization. **R. Kevin McIntyre:** Writing - original draft, Writing - review & editing, Visualization. **Angela M. Holland:** Conceptualization, Methodology, Writing - review & editing, Formal analysis, Investigation, Data curation. **Steven B. Jack:** Conceptualization, Methodology, Writing - review & editing, Project administration.

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.

Acknowledgements

We would like to thank B. W. Smith and J. A. Van Wyk for field data collection associated with this study and J. C. Brock for assistance with figures. Financial support for this project was provided by The Jones Center at Ichauway and the Robert W. Woodruff Foundation, United States. The funding source had no involvement with the study design, the collection, analysis and interpretation of data, in the writing of the report, and in the decision to submit the article for publication.

References

Barton, K., 2019. MuMIn: Multi-Model Inference v. 1.43.15.

Batista, W.B., Platt, W.J., 2003. Tree population response to hurricane disturbance: syndromes in a south-eastern USA old-growth forest. J. Ecol. 91, 197–212. https://doi.org/10.2307/3599755.

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.

Bender, M.A., Knutson, T.R., Tuleya, R.E., Sirutis, J.J., Vecchi, G.A., Garner, S.T., Held, I. M., 2010. Modeled impact of anthropogenic warming on the frequency of Atlantic hurricanes. Science 327 (5964), 454–458. https://doi.org/10.1126/science.1180568.

Brenning, A., 2013. SAGA Geoprocessing and Terrain Analysis in R v. 1.3.0. Comprehensive R Archive Network (CRAN). https://CRAN.R-project.org/package=RSAGA.

Brockway, D.G., Outcalt, K.W., 2017. Influence of reproduction cutting methods on structure, growth and regeneration of longleaf pine forests in flatwoods and uplands. For. Ecol. Manage. 389, 249–259. https://doi.org/10.1016/j.foreco.2017.01.002.

Brody, Anne R. April 2019. Weathering the Storm: Assessing the Agricultural Impact of Hurricane Michael. Southern Legislative Conference Regional Resource, Southern Office of the Council of State Governments. [Accessed 2020, August 24] http: https://www.slcatlanta.org/Publications/AgRD/Hurricane_Michael.pdf.

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., 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.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.

Carter, M.C., Kellinson, R.C., Wallinger, R.S., 2015. Forestry in the U.S. South: A History. Louisiana State University Press, Louisiana.

Cavender-Bares, J., Kitajima, K., Bazzaz, F.A., 2004. Multiple trait associations in relation to habitat differentiation among 17 Floridian oak species. Ecol. Monogr. 74, 635–662. https://doi.org/10.1890/03-4007.

Chambers, J.Q., Fisher, J.I., Zeng, H., Chapman, E.L., Baker, D.B., Hurtt, G.C., 2007. Hurricane Katrina's carbon footprint on U.S. Gulf Coast forests. Science 318 (5853), 1107. https://doi.org/10.1126/science.1148913.

Conner, R.N., Snow, A.E., O'Halloran, K.A., 1991. Red-cockaded woodpecker use of seed-tree/shelterwood cuts in eastern Texas. Wildlife Soc. Bull. 19, 67–73.

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. https://doi.org/10.1890/0012-9658(1999)080[2683:FRTCWR]2.0.CO;2.

Croker Jr., T.C., Boyer, W.D., 1976. Regenerating longleaf pine naturally. US Forest Service Research Paper (SO-112).

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.

Derr, H.J., Enghardt, H., 1957. Some forestry lessons from Hurricane Audrey. South. Lumberm. 195, 142–144.

Duryea, M.L., Kampf, E., Littell, R.C., Rodríguez-Pedraza, C.D., 2007. Hurricanes and the urban forest: II. Effects on tropical and subtropical tree species. Arboric. Urban For. 33, 98–112.

Engstrom, R.T., Sanders, F.J., 1997. Red-cockaded woodpecker foraging ecology in an old growth longleaf pine forest. Wilson Bulletin 109, 203–217.

ESRI, 2014. ArcGIS Desktop Release 10.3 Environmental Systems Research Institute.

Everham, E.M., Brokaw, N.V.L., 1996. Forest damage and recovery from catastrophic wind. Bot. Rev. 62, 113–185. https://doi.org/10.1007/BF02857920.

Fan, Y., Miguez-Macho, G., Jobbagy, E.G., Jackson, R.B., Otero-Casal, C., 2017. Hydrologic regulation of plant rooting depth. PNAS 114 (40), 10572–10577. https://doi.org/10.1073/pnas.1712381114.

Foster, D., Boose, E., 1992. Patterns of forest damage resulting from catastrophic wind in central New England. USA. J. Ecol. 80, 79–98.

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.

Franklin, J.F., Lindenmayer, D., Thornburgh, D., Pelt, R.V., Chen, J., Spies, T.A., Carey, A.B., Shaw, D.C., Berg, D.R., Harmon, M.E., Keeton, W.S., Bible, K., 2002. Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. For. Ecol. Manage. 155, 399–423. https://doi.org/10.1016/S0378-1127(01)00575-8.

Franklin, J.F., Mitchell, R.J., Palik, B.J., 2007. Natural disturbance and stand development principles for ecological forestry. Gen. Tech. Rep. NRS-19 44.

Frost, C., 2007. History and future of the longleaf pine ecosystem. Longleaf Pine Ecosyst. 9–48. https://doi.org/10.1007/978-0-387-30687-2_2.

Gardiner, B.A., Stagey, G.R., Belcher, R.E., Wood, C.J., 1997. Field and wind tunnel assessments of the implications of respacing and thinning for tree stability. Forestry 70, 233–252. https://doi.org/10.1093/forestry/70.3.233.

Garms, C., Dean, T.J., 2019. Relative resistance to breaking of Pinus taeda and Pinus palustris. For. An Int. J. For. Res. 92, 417–424. https://doi.org/10.1093/forestry/cpy038.

Gilliam, F.S., Platt, W.J., 1999. Effects of long-term fire exclusion on tree species composition and stand structure in old-growth *Pinus palustris* (longleaf pine) forest. Plant Ecol. 140, 15–26.

Gilliam, F.S., Platt, W.J., Peet, R.K., 2006. Natural disturbances and the physiognomy of pine savannas: a phenomenological model. Appl. Veg. Sci. 9, 83–96. https://doi.org/10.1658/1402-2001(2006)9[83:NDATPO]2.0.CO;2.

Gresham, C.A., Williams, T.M., Lipscomb, D.J., 1991. Hurricane Hugo Wind Damage to Southeastern U.S. Coastal Forest Tree Species. Biotropica 23, 420. https://doi.org/10.2307/2388261.

Guldin, J.M., 2019. Silvicultural options in forests of the southern United States under changing climatic conditions. New Forests 50 (1), 71–87. https://doi.org/10.1007/s11056-018-9656-2.
Harcombe, P.A., Hall, R.W., Glitzenstein, J.S., Cook, E.S., Krusic, P., Fulton, M., Streng, D.R., 1998. Sensitivity of Gulf Coast forests to climate change, in: Vulnerability of Coastal Wetlands in the Southeastern United States: Climate Change Research Results. pp. 47–66. U.S. Geological Survey, Biological Resources Division. Lafayette, LAUSGS/BRD/BSR-1998-0002.
Harcombe, P.A., Mann Leipzig, L.E., Elsik, I.S., 2009. Effects of Hurricane Rita on three long-term forest study plots in East Texas, USA. Wetlands 29, 88–100. https://doi.org/10.1672/08-64.1.
Hedden, R.L., Fredericksen, T.S., Williams, S.A., 1995. Modeling the effect of crown shedding and streamlining on the survival of loblolly pine exposed to acute wind. Can. J. For. Res. 25, 704–712. https://doi.org/10.1139/x95-078.
Hoffman, C.M., Ziegler, J., Canfield, J., Linn, R.R., Mell, W., Sieg, C.H., Pimont, F., 2016. Evaluating crown fire rate of spread predictions from physics-based models. Fire Technol. 52, 221–237. https://doi.org/10.1007/s10694-019-00856-2.
Holland, A.M., Rutledge, B.T., Jack, S.B., Stober, J.M., 2019. The longleaf pine forest: long-term monitoring and restoration of a management dependent ecosystem. J. Nat. Conserv. 47, 38–50.
Holling, C.S., 1973. Resilience and stability of ecological systems. Ann. Rev. Ecol. Systematics 4, 1–23.
Hook, D.D., Buford, M.A., Williams, T.M., 1991. Impact of Hurricane Hugo on the South Carolina coastal plain forest. J. Coastal Res. Special Issue No. 8 291–300 www.jstor.org/stable/25735422.
Howze, J.M., Sash, K.J., Carroll, J.P., Smith, L.L., 2019. A regional scale assessment of habitat selection and home range of the eastern rat snake in pine-dominated forests. Forest Ecol. Manage. 432, 225–230.
Jack, S.B., McIntyre, R.K., 2017. Restoring and managing the overstory: an ecological forestry approach. In: Kirkman, L.K., Jack, S.B. (Eds.), Ecological Restoration and Management of Longleaf Pine Forests. CRC Press, Boca Raton, Florida, pp. 175–205.
Jackson, J.A., Jackson, B.J.S., 1986. Why do red-cockaded woodpeckers need old trees? Wildlife Soc. Bull. 14, 318–322.
Johnsen, K.H., Butnor, J.R., Kush, J.S., Schmidtling, R.C., Nelson, C.D., 2009. Hurricane Katrina winds damaged longleaf pine less than loblolly pine. Southern J. Appl. Forestry 33 (4), 178–181.
Keim, B.D., Muller, R.A., Stone, G.W., 2007. Spatiotemporal patterns and return periods of tropical storm and hurricane strikes from Texas to Maine. J. Clim. 20 (14), 3498–3509.
Kirkman, L.K., Brown, C.L., Leopold, D.J., 2007. Native trees of the Southeast. Timber Press.
Kreye, J.K., Varner, J.M., Hiers, J.K., Mola, J., 2013. Toward a mechanism for eastern North American forest mesophication: differential litter drying across 17 species. Ecol. Appl. 23, 1976–1986. https://doi.org/10.1890/13-0503.1.
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. https://doi.org/10.1674/0003-0031(2006)156[353:EOWDOT]2.0.CO;2.
Landers, J.L., Boyer, W.D., 1999. An old growth definition for upland longleaf and south Florida slash pine forests, woodlands, and savannas. USDA Forest Service General Technical Report SRS-29.
Lindemann, J., Baker, W., 2001. Attributes of blowdown patches from a severe wind event in the Southern Rocky Mountains. USA. Landsc. Ecol. 16, 313–325.
Lindemann, J.D., Baker, W.L., 2002. Using GIS to analyse a severe forest blowdown in the Southern Rocky Mountains. Int. J. Geogr. Inf. Sci. 16, 377–399. https://doi.org/10.1080/13658810210136069.
Lindenmayer, D.B., Laurance, W.F., Franklin, J.F., 2012. Global decline in large old trees. Science 338, 1305–1306. https://doi.org/10.1126/science.1231070.
McIntyre, R.K., Conner, L.M., Jack, S.B., Schlimm, E.M., Smith, L.L., 2019. Wildlife habitat condition in open pine woodlands: field data to refine management targets. J. Forest Ecol. Manage. 437, 282–294.
McIntyre, R.K., Jack, S.B., Mitchell, R.J., Hiers, J.K., Neel, W.L., 2008. Multiple Value Management: The Stoddard-Neel Approach to Ecological Forestry. Newton, Georgia: Joseph W. Jones Ecological Research Center: 31pp.
McIntyre, R.K., McCall, B.B., Wear, D.N., 2017. The social and economic drivers of the southeastern forest landscape. In: Kirkman, L.K., Jack, S.B. (Eds.), Ecological Restoration and Management of Longleaf Pine Forests. CRC Press, Boca Raton, Florida, pp. 39–67.
Mitchell, R.J., Hiers, J.K., O'Brien, J.J., Jack, S.B., Engstrom, R.T., 2006. Silviculture that sustains: the nexus between silviculture, frequent prescribed fire, and conservation of biodiversity in longleaf pine forests of the southeastern United States. Can. J. Forest Res. 36, 2724–2736.
Mitchell, R., Hiers, J., O'Brien, J., Starr, G., 2009. Ecological forestry in the southeast: understanding the ecology of fuels. J. For. 107, 391–397.
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.
Nakagawa, S., Schielzeth, H., 2013. A general and simple method for obtaining R2 from generalized linear mixed-effects models. Methods Ecol. Evol. 4, 133–142. https://doi.org/10.1111/j.2041-210x.2012.00261.x.
National Oceanic and Atmospheric Administration (NOAA), 2019. The National Hurricane Center's Tropical Cyclone Reports. Accessed August 17, 2020. https://www.nhc.noaa.gov/data/tcr/index.php?season=2018&basin=atl.
National Oceanic and Atmospheric Administration (NOAA), 2020. NOAA Historical Hurricane Tracks. Accessed August 17, 2020. https://oceanservice.noaa.gov/news/historical-hurricanes/.
Nicoll, B.C., Gardiner, B.A., Rayner, B., Peace, A.J., 2006. Anchorage of coniferous trees in relation to species, soil type, and rooting depth. Can. J. Forest Res. 36 (7), 1871–1873. https://doi.org/10.1139/x06-072.
Noss, R.F., Laroe, E.T., Scott, J.M., 1995. Endangered ecosystems of the United States: a preliminary assessment of loss and degradation. Biol. Rep. - US Dep. Inter. Natl. Biol. Serv. 28 https://doi.org/10.3368/er.14.1.95.
Nowacki, G.J., Abrams, M.D., 2008. The demise of fire and "mesophication" of forests in the eastern United States. Bioscience 58, 123–138.
O'Brien, J.J., Hiers, J.K., Callaham, Mac A., 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.
Oswalt, C. M., Cooper, J.A., Brockway, D.G., Brooks, H.W., Walker, J.L., Connor, K.F., Oswalt, S.N., Conner, R.C., 2012. History and current condition of longleaf pine in the Southern United States. Gen. Tech. Rep. SRS-166. Asheville, NC: U.S. Department of Agriculture Forest Service, Southern Research Station. 51p.
Oswalt, S.N., Oswalt, C.M., 2008. Relationships between common forest metrics and realized impacts of Hurricane Katrina on forest resources in Mississippi. For. Ecol. Manage. 255, 1692–1700. https://doi.org/10.1016/j.foreco.2007.11.029.
Peltola, H.M., 2006. Mechanical stability of trees under static loads. Am. J. Bot. 93, 1501–1511. https://doi.org/10.3732/ajb.93.10.1501.
Perkins, M.W., Conner, L.M., 2004. Habitat use of fox squirrels in southwestern Georgia. J. Wildlife Manage. 68, 509–513.
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., Pickett, S.T.A., 1995. Forest reorganization: a case study in an old-growth forest catastrophic blowdown. Ecology 76, 763–774.
Peterson, C.J., Ribeiro, G.H.P. de M., Negrón-Juárez, R., Marra, D.M., Chambers, J.Q., Higuchi, N., Lima, A., Cannon, J.B., 2019. Critical wind speeds suggest wind could be an important disturbance agent in Amazonian forests. For. An Int. J. For. Res. 92, 444–459. https://doi.org/10.1093/forestry/cpz025.
Pickett, S.T.A., White, P.S., 1985. The Ecology of Natural Disturbance and Patch Dynamics. In: The Ecology of Natural Disturbance and Patch Dynamics. Academic Press Inc, Orlando, FL, pp. 3–13. https://doi.org/10.1016/B978-0-12-554520-4.50006-X.
Pielke Jr, R.A., Landsea, C., Mayfield, M., Layer, J., Pasch, R., 2005. Hurricanes and global warming. Bull. Am. Meteorol. Soc. 86 (11), 1571–1576.
Plattner, B.C., Braun, L.N., Brenning, A., 2006. Spatial variability of snow accumulation on Vernagtferner, Austrian Alps, in Winter 2003/2004. Zeitschrift für Gletscherkunde und Glazialgeologie, 39 (2003-2004), 43-57, 1.
Prestemon, Jeffrey P. and Thomas P. Holmes. 2010. In: Pye, John M.; Rauscher, H. Michael; Sands, Yasmeen; Lee, Danny C.; Beatty, Jerome S., tech. eds. 2010. Advances in threat assessment and their application to forest and rangeland management. Gen. Tech. Rep. PNW-GTR-802. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest and Southern Research Stations: 207-221.
R Core Team, 2017. R: A language and environment for statistical computing.
Rebertus, A., Williamson, G., Moser, E., 1989. Longleaf pine pyrogenicity and turkey oak mortality in Florida xeric sandhills. Ecology 70, 60–70.
Reineke, L.H., 1933. Perfecting a stand-density index for even-aged forests. J. Agric. Res. 46, 627–638.
Ribeiro, G.H.P.M.G., Chambers, J.Q.J., Peterson, C.J.C., Trumbore, S.E.S., Magnabosco Marra, D., Wirth, C., Cannon, J.J.B., Negrón-Juárez, R., Lima, A.J.N.A., de Paula, E., dos Santos, J., Higuchi, N., Négron-Juárez, R.I., Lima, A.J.N.A., de Paula, E.V.C.M., dos Santos, J., Higuchi, N., 2016. Mechanical vulnerability and resistance to snapping and uprooting for Central Amazon tree species. For. Ecol. Manage. 380, 1–10. https://doi.org/10.1016/j.foreco.2016.08.039.
Sanjuan, G., Brun, C., Margalef, T., Cortés, A., 2014. Wind field uncertainty in forest fire propagation prediction. In: Procedia Computer Science. Elsevier, pp. 1535–1545. https://doi.org/10.1016/j.procs.2014.05.139.
Scheffer, M., 2009. Critical Transitions in Nature and Society. Princeton University Press, Princeton, NJ.
Shinoda, Y., Akasaka, M., 2020. Interaction exposure effects of multiple disturbances: plant population resilience to ungulate grazing is reduced by creation of canopy gaps. Sci. Rep. 10 https://doi.org/10.1038/s41598-020-58672-6.
Soil Survey Staff, Natural Resources Conservation Service, United States Department of Agriculture. Soil Survey Geographic (SSURGO) Database for [Baker County, Georgia]. https://sdmdataaccess.sc.egov.usda.gov. Accessed August 17, 2020.
Southeast Coastal Ocean Observing Regional Association. Accessed August 17, 2020. https://secoora.org/education-outreach/hurricanes/hurricane-glossary/.
Stanturf, J.A., Goodrick, S.L., Outcalt, K.W., 2007. Disturbance and coastal forests: a strategic approach to forest management in hurricane impact zones. For. Ecol. Manage. 250, 119–135. https://doi.org/10.1016/j.foreco.2007.03.015.
Stevens, D.L., 1997. Variable density grid-based sampling designs for continuous spatial populations. Environmetrics 8 (3), 167–195.
Touliatos, P., Roth, E., 1971. Hurricanes and Trees: Ten Lessons from Camille. J. For. 69, 285–289. https://doi.org/10.1093/jof/69.5.285.
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.
U.S. Geological Survey, 2015. The National Map [WWW Document]. Natl. Map, 3D Elev. Progr. Web page.
Van Lear, D.H., Carroll, W.D., Kapeluck, P.R., Johnson, R., 2005. History and restoration of the longleaf pine-grassland ecosystem: implications for species at risk. Forest Ecol. Manage. 211 (1), 150–165. https://doi.org/10.1016/j.foreco.2005.02.014.

Walters, C.J., 1986. Adaptive management of renewable resources. MacMillan Publishers Ltd., Basingstoke, UK.
Walters, C.J., Holling, C.S., 1990. Large-scale management experiments and learning by doing. Ecology 71 (6), 2060–2068. https://doi.org/10.2307/1938620.
Walters, J.R., Daniels, S.J., Carter III, J.H., Doerr, P.D., 2002. Defining quality of red-cockaded woodpecker foraging habitat based on habitat use and fitness. J. Wildlife Manage. 66 (4), 1064–1082. https://doi.org/10.2307/3802938.
Wang, F., Xu, Y.J., 2009. Hurricane Katrina-induced forest damage in relation to ecological factors at landscape scale. Environ. Monit. Assess. 156, 491–507. https://doi.org/10.1007/s10661-008-0500-6.
Webb, S.L., 1989. Contrasting windstorm consequences in two forests, Itasca State Park, Minnesota. Ecology 70, 1167–1180.
Wilkie, M.L., Holmgren, P., Castaneda, F., 2003. Sustainable forest management and the ecosystem approach: two concepts, one goal. Forest Management Working Papers, Working Paper FM 25. Forest Resources Development Service, Forest Resources Division. FAO, Rome.
Xi, W., Peet, R.K., Urban, D.L., 2008. Changes in forest structure, species diversity and spatial pattern following hurricane disturbance in a Piedmont North Carolina forest, USA. J. Plant Ecol. 1, 43–57. https://doi.org/10.1093/jpe/rtm003.
Zeng, H., Talkkari, A., Peltola, H., Kellomäki, S., 2007. A GIS-based decision support system for risk assessment of wind damage in forest management. Environ. Model. Softw. 22, 1240–1249. https://doi.org/10.1016/j.envsoft.2006.07.002.
Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.a., Smith, G.M., Ebooks Corporation, 2009. Mixed effects models and extensions in ecology with R. Statistics Biol. Health. https://doi.org/10.1007/978-0-387-87458-6.
Zwicker, S., Walters, J.R., 1999. Selection of pines for foraging by red-cockaded woodpeckers. J. Wildlife Manage. 63, 843–852.