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Damage prediction for planted longleaf pine in extreme winds

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ABSTRACT

Severe wind disturbances are forecast to increase in frequency and intensity with climate change putting forest trees at greater risk of wind damage. Of particular concern are mature and old-growth forests of wind-prone regions which host considerable biodiversity. Landscape configuration, stand structure, and tree characteristics affect susceptibility to wind damage. In managed forests and restoration contexts, these factors could be manipulated to enhance resistance to severe wind events. We measured landscape, stand, and tree characteristics, and damage in longleaf pine (*Pinus palustris* Mill.) forests in southwest Georgia and Northwest Florida affected by Hurricane Michael (2018) and used these data to model wind damage. We hypothesized that wind damage would increase with wind exposure and decrease with diameter-to-height ratio (taper). We found that lower wind exposure and higher taper resulted in substantially lower wind damage. We conclude that maintaining lower stand density during stand development could reduce wind damage by increasing individual tree resistance to wind. Management and restoration activities that increase resilience to threats from extreme weather can help maintain persistence and landscape restoration of global biodiversity hotspots in wind-prone regions.

1. Introduction

Tropical cyclones, tornados, and other severe wind disturbances affect forests globally (Altman et al., 2013; Keim et al., 2007; Lee et al., 2008; Zhang Xu et al., 2021), and severe winds may impede conservation of ecologically important mature and old-growth forests in tropical cyclone-prone regions (Lin et al., 2020; Mo et al., 2023; Zampieri et al., 2020). Moreover, the frequency and intensity of wind disturbances are likely to increase with climate change (Diffenbaugh et al., 2013; Elsner et al., 2015; Elsner, 2006), potentially increasing impacts on forests. Some evidence suggests that the increasing intensity of Atlantic tropical cyclones can be attributed to increasing heat storage and dissipation in the Atlantic Ocean (Bhatia et al., 2019; Elsner et al., 2008; Knutson et al., 2019). Other research suggests that storm frequency is increasing without an accompanying increase in storm intensity (Fisher et al., 2020; Robbins et al., 2011). In either case, forest damage from severe winds is likely to increase.

Anticipated changes in storm meteorology are expected to put old-growth forests at risk—particularly those of Japan, Southeast Asia, and the southeastern US (Balaguru et al., 2023; Lin et al., 2020; Rau et al., 2022). Continued increases in tropical storm activity in the Atlantic Ocean and Caribbean Sea can disrupt timber markets (Henderson et al., 2022) and alter the structure, function, and composition of coastal forests (Sharma et al., 2021), including natural forests and managed timberlands. In 2005, a single hurricane (Hurricane Katrina) caused enough tree mortality to offset 50–140% of the annual US carbon sink in forest trees (Chambers et al., 2007). In 2018, winds from Hurricane Michael struck Florida, US affecting at least 28% of longleaf pine (*Pinus palustris* Mill.) ecosystems, which are endangered (Noss et al., 1995; St. Peter et al., 2020; Zampieri et al., 2020). Predicting mortality from tropical storms is crucial to predicting their ecological and economic impacts now and in future climates (Cannon et al., 2023; Henderson et al., 2022; Schrum et al., 2020).

In some forest types, large-scale efforts are underway to restore and conserve ecosystems through reforestation (Bollinger et al., 2023; McIntyre et al., 2018). Understanding how to mitigate wind risk during restoration can guide management and landscape-scale planning in imperiled forests. For example, longleaf pine forests and woodlands

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were historically prevalent across much of the southeastern US, host many endangered species, and have been reduced to only 3% of their historic range (Noss et al., 1995). They also regularly experience tropical cyclone winds (Cannon et al., 2023; Zampieri et al., 2020). Longleaf pine planting is supported by several programs that provide incentives for its establishment and stewardship (USDA, NFWF, NRCS). America's Longleaf Restoration Initiative, for example, has a goal to increase longleaf pine forests by 1.4 million ha by 2024 (Bollinger et al., 2023). Planted longleaf pine stands can generate economic returns similar to loblolly pine especially on lower-quality sites (Mills and Stiff, 2013; Susaeta and Gong, 2019). Thus, early commercial success of longleaf pine managed for timber may be an important pathway to bolster landscape-scale restoration of the ecosystem.

Most studies addressing wind resistance in longleaf pine ecosystems have focused on natural stands, with only a few addressing planted stands. Because species composition and stand structure in natural stands (e.g., low stand density, multicohort) are unlike those in planted stands, studies in natural longleaf stands are not readily applicable to planted stands. For example, a study in mixed stands 50 km east of the Hurricane Hugo eyewall reported that only 17% of longleaf pine trees were damaged compared to 52% of loblolly pine, but this report included only two sites (Hook et al., 1991). Rutledge et al. (2021) found that mortality of longleaf pine was less than half that of slash pine during Hurricane Michael (2018) but did not differentiate between planted and naturally regenerated stands. Johnsen et al. (2009) did include planted longleaf stands when comparing differences in tree mortality from Hurricane Katrina (2005) and found that among several planted southern pine stands, longleaf pine was less susceptible to damage than loblolly and slash pine; however, the study focused on a single site, single age class (45 years old), and a narrow range of sizes. Thus, there is a lack of adequate information available to understand potential tree and stand factors contributing to damage in planted longleaf pine stands across a variety of ages.

Landscape, site, and individual tree-scale factors interact in complex ways to affect wind damage in forests (Gardiner, 2021). Landscape and site factors such as soil drainage and configuration of surrounding forest land cover affect wind damage; however, the effect of soil drainage on wind damage is inconsistent. Higher damage was associated with wetter soils in coniferous forests in Europe and in loblolly and slash pine forests in the southeastern US (Fortuin et al., 2023; Lohmander and Helles, 1987; Ray and Nicoll, 1998), but the opposite was true for oak species in mixed pine and hardwood forests in the southeastern US (Rutledge et al., 2021). Further, wetter but not saturated soils in pine forests in Europe and wetter soils within root plates of hinoki cypress in Japan increased resistance to overturning (Defossez et al., 2021; Kamimura et al., 2012). Larger stand area and higher proportion of forest cover in nearby stands may offer protection from wind damage (Lohmander and Helles, 1987; Seidl et al., 2013; Zeng et al., 2004). Scott and Mitchell (2005), for example, found that the proportion of trees damaged in high wind events increased as the proportion and size of openings in a nearby forest increased, suggesting that landscape configuration is an important predictor of wind damage.

At smaller spatial scales, forest structure and individual tree characteristics interactively affect wind damage by affecting the wind environment. In dense, closed-canopy stands, wider tree spacing increases canopy roughness and exposes trees to greater wind stress, but in lower density stands, wider tree spacing can reduce canopy roughness and wind stress (Albini and Baughman, 1979; Raupach, 1994). In contrast, shelter from neighboring trees and smooth canopy surfaces in dense stands expose trees to lower wind stress (Scott and Mitchell, 2005). Stand height also affects susceptibility to wind damage; canopy-top wind speeds increase with stand height which increases wind stress on trees (Raupach, 1992). On the individual tree scale, both tree height and stem diameter are correlated with wind damage. Taller trees are generally more susceptible to wind because they have increased moment arms and turning moments, leading to higher stress on tree stems (Hale et al., 2012). In addition, taller, canopy emergent, trees are less sheltered by shorter, neighboring trees and have larger crown areas exposed to wind. However, the increased susceptibility of taller trees can be, in part, mitigated by larger stem diameter. Larger diameter trees (for a given height) are generally less susceptible to wind damage (Dunham and Cameron, 2000; Gardiner et al., 2000).

The ratio of stem diameter to tree height (taper) has a strong effect on wind resistance (Cremer et al., 1982). Coniferous trees adapt to higher wind exposure by increasing taper and developing larger stems that are more resistant to breakage (Bonnesoeur et al., 2016; Meng et al., 2008; Nicoll et al., 2019; Telewski, 1995). Trees in dense stands develop low taper and are more susceptible to wind but may suffer low damage because of shelter from neighboring trees. Reduction in stand density, either through management or natural disturbance, exposes trees to greater wind stress and can increase susceptibility to wind damage for up to 10 years while trees acclimate to new wind conditions (Albrecht et al., 2012). However, active management of planted pine stands often requires thinning. Careful consideration of taper along with stand density may help to minimize risk of wind damage during stand development.

Increasing wind resistance of planted stands of longleaf pine can contribute to critical landscape-scale restoration efforts for the ecosystem. Thus, the objective of this study is to further restoration efforts for the species by determining what factors drive wind resistance in managed longleaf pine stands. We investigated the relative role of wind speed (i.e., maximum sustained wind speed during a tropical cyclone), shelter from nearby forests, depth to root restrictive layer, stand density, mean stand height, height relative to mean stand height (relative height), and tree taper in determining longleaf pine tree wind damage. Further, because taper is especially important to wind resistance in forest restoration where stands may be thinned more heavily, we also investigated how stand density, stand height, and relative tree height affect longleaf pine tree taper. We hypothesized that higher wind speed, taller stands, lower stand density, taller relative tree height, lower taper, shallower depth to a root restrictive layer, and lower surrounding forest shelter would be associated with higher probabilities of damage. We also hypothesized that increased exposure to wind stress in lower density stands, taller stands, and in trees with higher relative heights would result in higher tree taper.

2. Methods

2.1. Data collection and processing

On October 10, 2018, Hurricane Michael made landfall on the US coast in the Florida panhandle as a Category 5 hurricane with sustained winds of 257 km h^{-1}. It maintained pressures consistent with Category 2 storms as it moved inland into southwest Georgia, 100 km north-northeast, before continuing farther northeast (Fig. 2; Rutledge et al., 2021). The storm affected a large swath of land in northwestern Florida and southwestern Georgia, which have a high concentration of naturally regenerated and planted longleaf pine forests and woodlands (LPEGDB, 2018; Zampieri et al., 2020).

We surveyed mortality from wind damage in stands of planted longleaf pine in the path of Hurricane Michael between September 2019 and March 2020 (Fig. 1). We located 87 plots of planted longleaf pine on 11 publicly and privately owned properties covering 15,033 km^2 from northwest Florida to southwest Georgia. This area represented a wind intensity gradient and a range of longleaf pine stand conditions (Fig. 2, Tables 1 and 2). Sample plots were circular, 0.04 ha in area (11.3 m radius), and located > 50 m from stand boundaries (e.g., roads or agricultural fields). We recorded plot centers using a GPS with a horizontal accuracy of 0.6 m (A101 Smart Antenna, Hemisphere GPS, Scottsdale, AZ, US). Within each plot, we assessed the damage status of each tree (intact, leaning, tipped, or snapped) and measured attributes indicative of tree stability and resistance to wind damage. We measured

Fig. 1. Examples of wind damage severity progressing from low damage (A) to high damage (D) caused by Hurricane Michael at sampling plots in southwest Georgia and northwest Florida, US Photo credits: Aubrey Plymale (A, B, D) and Tyler Macmillan (C).

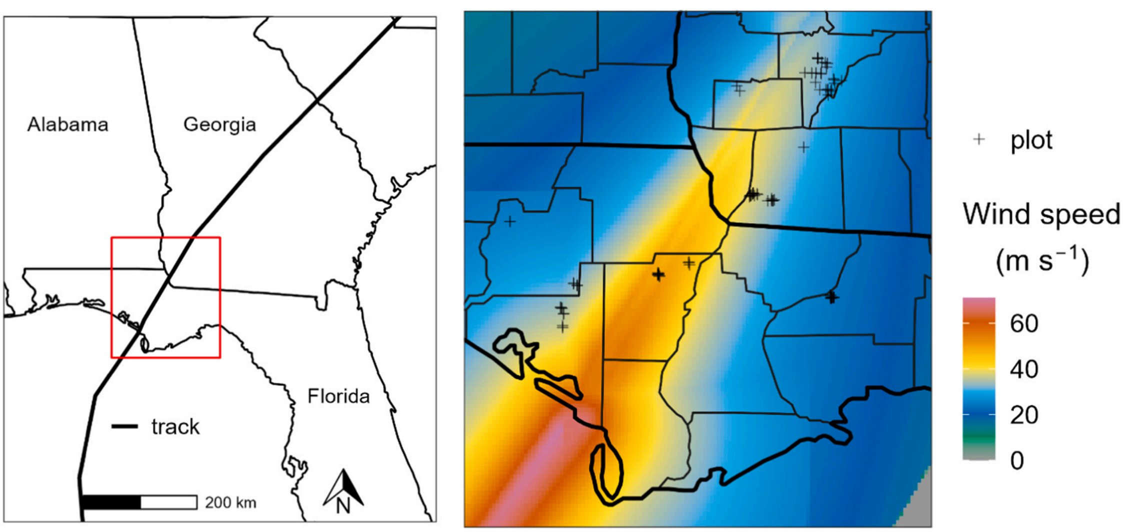

Fig. 2. Maximum predicted wind speed (gust) during Hurricane Michael and post-hurricane damage sample plot locations in southwest Georgia and northwest Florida USA. The red box in the left panel indicates the area of detail shown in the right panel.

Table 1
Descriptive statistics of potential predictor variables for models of damage in planted longleaf pine stands in Southwest Georgia and Northwest Florida, USA.

Variable	Mean (SD)	Range
Dbh (cm)	14.9 (5.9)	1.6–55
Taper (cm m^{-1})	1.3 (0.4)	0.4–5
Relative height (m m^{-1})	1 (0.2)	0.2–2.4
Mean stand height (m)	11.9 (3.7)	3.8–23.4
Wind speed (m s^{-1})	34.1 (6.9)	23.7–49.6
Density (trees ha^{-1})	818.9 (358.3)	150–1725
Cover (m^2 m^{-2})	0.8 (0.1)	0.3–1

tree height, snap height for trees that had snapped, and lean angle for trees that were leaning using a laser rangefinder (TruPulse 360 °R, Laser Tech, Centennial, CO, US). We measured diameter at breast height (dbh) using a standard dbh tape. Heights were measured to the nearest 0.1 m, diameters were measured to the nearest 0.1 cm, and angles were measured to the nearest 0.1 degree. Stand density was the count of trees > 1 cm dbh in a plot reported in trees ha^{-1}, and mean stand height was the mean height of trees in a plot. We calculated relative height as the ratio of individual tree height to mean plot tree height, and stem taper as the ratio of dbh to height. To assess the potential effect of a root-restrictive soil layer, if present, we used an auger to remove soil to a depth of 1.1 m and used texture and color cues to identify depth of transitions from coarse-textured surface horizons to fine texture or spodic subsurface horizons (recorded to $\pm$ 0.05 m).

To estimate maximum sustained wind speed and direction of peak winds, we used the *Hurrecon* model (Boose et al., 2001) implemented using the *Hurrecon* package in R (Cannon, 2022; Cannon et al., 2023). The *Hurrecon* model generates estimates of hurricane wind fields by fitting a lognormal function to observations of hurricane wind speed and

Table 2
Descriptive statistics of planted longleaf pine stands in Southwest Georgia and Northwest Florida sampled for wind damage following Hurricane Michael. Values are means with standard deviation in parentheses.

Site	Stands	Lat/Long	Wind speed	Density	BA	QMD	Height	Taper
Chipola	4	(30.53, −85.17)	49 (0.3)	406 (133)	40 (10)	17.9 (0.8)	16 (0.8)	1.13 (0.08)
Choctawhatchee	2	(30.73, −85.80)	25 (0)	325 (71)	59 (15)	24 (0.5)	17.4 (0.5)	1.36 (0.01)
Econfina	12	(30.42, −85.56)	34 (1.4)	623 (360)	30 (17)	13.2 (6.8)	10.1 (5.4)	1.33 (0.14)
Elmodel	3	(31.33, −84.49)	33 (0.1)	692 (189)	62 (14)	17 (0.8)	12.2 (0.5)	1.39 (0.11)
Ichauway	21	(31.25, −84.46)	31 (1.3)	792 (346)	55 (20)	15.5 (4.1)	10 (2.8)	1.56 (0.31)
Lake Talquin	14	(30.45, −84.43)	24 (0.1)	559 (276)	39 (21)	15 (5.1)	11 (4.1)	1.34 (0.25)
Mayhaw	2	(31.21, −84.83)	32 (0.9)	850 (283)	55 (33)	13.9 (2)	12.1 (1.6)	1.12 (0.04)
Private1	3	(30.57, −85.04)	46 (0.1)	650 (109)	83 (13)	20.2 (0.6)	15.5 (1.5)	1.31 (0.13)
Private2	6	(30.53, −85.17)	49 (0.2)	600 (115)	53 (10)	16.9 (1.4)	13.8 (1.7)	1.21 (0.11)
Private3	1	(31.00, −84.55)	32 (NA)	725 (NA)	94 (NA)	20.3 (NA)	14.7 (NA)	1.35 (NA)
Silver Lake	19	(30.82, −84.74)	36 (2.1)	670 (414)	69 (21)	20.8 (8.4)	16.5 (4.3)	1.22 (0.22)

Wind speed = maximum sustained winds (m s-1), Density = stand density (trees ha-1), BA = basal area (m-2 ha-1), QMD = quadratic mean dbh (cm), height = tree height (m), taper = ratio of dbh to height

size from the National Hurricane Center (Landsea and Franklin 2013). Because wind speed observations are available at 6-hour intervals, the *Hurrecon* package uses bilinear interpolation of individual readings to generate raster data representing the maximum sustained (1-min) wind speed and direction. We extracted the maximum sustained wind speed and direction for each plot at a resolution of 500 m using the R Project for Statistical Computing and the packages *Hurrecon* and *Terra* (Cannon, 2022; Hijmans, 2024; R Core Team, n.d.).

We assessed the effects of landscape configuration on wind resistance by quantifying forest fragmentation around the plots. We measured the proportion of forest cover within 300 m downwind of each plot with aerial imagery, classifying into forested and non-forested vegetation using supervised classification. We retrieved 4-band (red, green, blue, infrared) images for the study area between September and November 2017 (I.e., pre-hurricane) from the National Agricultural Imagery Program (NAIP), United States Geological Survey (USGS 2022; Fig. 3). Within a 300 m radius area surrounding each plot, we classified pixels (Hogland et al. (2018) using modules from the Python programming language; *Spectral* was used for supervised classification (Boggs, 2014) and *Scikit-learn* to classify imagery using a random forest classifier (Pedregosa et al., 2011). We trained pre-hurricane images into the following classes: mature longleaf canopy, mature hardwood canopy, grassy field, dry agricultural field, bare ground, shadow, green agricultural field, open water, and mature planted pine. We then reclassified pixels into forested (i.e., mature longleaf pine, hardwood canopy or planted pine), and non-forested classes (overall model accuracy of reclassified imagery: 0.9998; Supplementary Table S1). To assess potential wind buffering effects, we quantified forest cover in the direction of maximum sustained wind speed. The wind speed profile is not expected to vary beyond a horizontal distance equivalent to 10 tree heights (Gardiner et al., 1997; Scott and Mitchell, 2005). Our maximum tree heights were ca. 30 m, therefore, we divided classified images within 300 m of plots into 8 wedge-shaped polygons corresponding to cardinal and ordinal directions and extracted the proportion of forested pixels in the wedge in the direction of maximum sustained wind speed, as predicted by the *Hurrecon* model.

2.2. Statistical analyses

We used generalized linear mixed models to estimate the effects of maximum wind speed, stand density, tree traits, and landscape factors on wind damage. We used the forestry concept of unacceptable growing stock (i.e., main stem break, uprooted, or leaning > 30°) as the criteria for classifying a tree as damaged, and modeled damage using a binomial distribution with a logit link via the R function *glmer* (Bates et al., 2015). We used a general linear mixed model to estimate the effects of stand density, stand height, and relative height on tree taper via the R function *lme* (Pinheiro et al., 2023). We included plot as a random effect (n=87) in all models to account for correlations among trees measured in the same plot. Some stands contained two (n=15) or three (n=2) plots. To assess spatial autocorrelation, we used the R packages DHARMa and nlme to examine residuals (Hartig, 2022; Pinheiro et al., 2023). We found residuals to be randomly distributed around the mean, and a semivariogram indicated constant variance with respect to distance

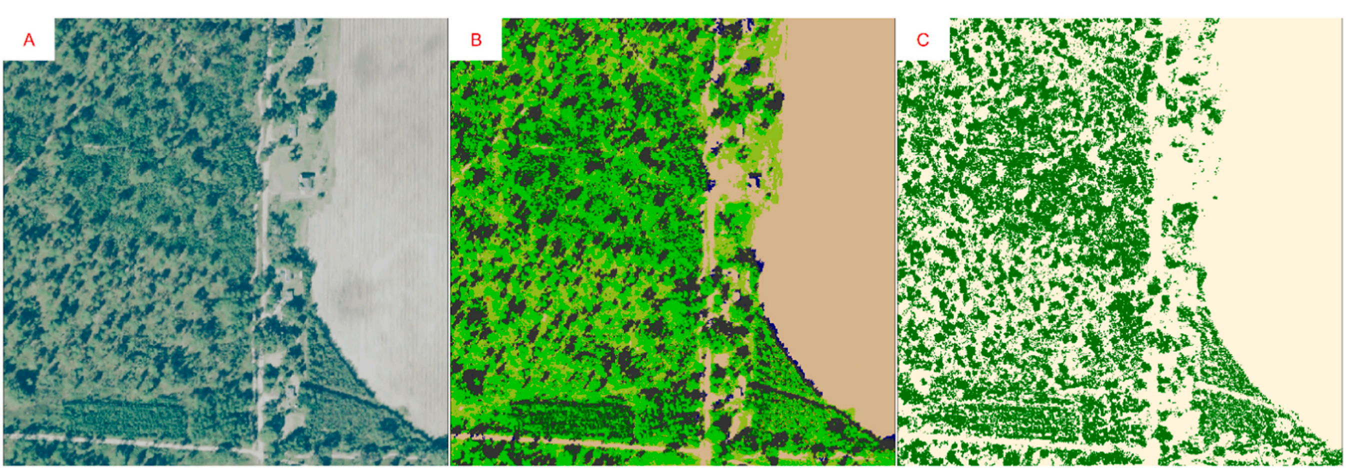

Fig. 3. Estim *f*eation of forest cover within 300 m of sample plots using NAIP imagery. In the first step, 600-by-600 m square images centered on sample plots (A) were classified into 10 landcover classes (B). In the second step, the classified images were reclassified into two classes representing tall vegetation that would shelter sample plot trees from wind damage and short vegetation that would not (C).

among plots. We therefore treated plot as independent in all models. To assess multicollinearity in explanatory variables, we calculated variance inflation factors (VIF; Fox and Monette, 1992) for each predictor variable and computed Spearman correlation between each pair of variables. We removed dbh from further analysis due to its high VIF (VIF > 5; James et al., 2013) and high correlation with tree height.

The initial model for wind damage included stand height, relative tree height, tree taper, stand density, maximum sustained wind speed, and upwind forest cover. Depth to a root restrictive layer was not included in models because we infrequently encountered finer textured spodic soils (< 9%) and found those data were insufficient for statistical testing. Because we were interested in how tree size and spacing affect tree damage over a range of wind speeds, we also included all two-way interactive effects between tree height, relative height, taper, stand density, and wind speed.

The initial model for tree taper included stand height, relative tree height, tree taper, stand density, maximum sustained wind speed, and upwind forest cover as predictors. Because we were interested in how stand density might influence wind resistive characteristics of trees, we also included all two-factor interactive effects of stand density, stand height, and tree relative height.

We used a modified stepwise procedure informed by a combination of *p*-values for each factor's effect and Akaike's information Criterion (AIC) values to eliminate uninformative predictor variables from models. Starting with the initial model, we iteratively removed the effect with the highest non-significant p-value ($\alpha = 0.05$), provided that it was not included in a higher-level interaction and its removal did not result in an increase in AIC. We considered models with the lowest AIC score and models within 2 AIC units of that model to have substantial support as the best model (Burnham and Anderson, 2002). For the stem taper model, we verified assumptions by examining deviance residuals and QQ-plots. For the damage model, we quantified goodness of fit using the area under the receiver operating characteristic (ROC) curve via the R package *pROC* (Robin et al., 2011). The proportion of variance explained in the model was computed via marginal and conditional R-squared values, which include fixed effects only and both fixed and random effects, respectively (Nakagawa et al., 2017). To illustrate how model effects affected probabilities of wind damage and value of taper over their ranges of variation, we estimated marginal means via the R function *emmeans* (Lenth, 2016).

3. Results

3.1. Wind damage

Wind damage in planted longleaf pine was best predicted by models that included maximum sustained wind, upwind forest cover, mean stand height, stand density, relative tree height, taper, and interactions among these factors. Two models were separated by < 2 AIC units, indicating substantial support for both (Table 3). In the lowest AIC model, wind damage was significantly affected by stand density, but its effect depended on mean stand height, tree taper and relative tree height (Tables 3 and 4). It was also significantly related to tree taper, which depended on relative tree height. In addition, the model within 2 AIC units of the best model indicated that damage was related to maximum sustained wind, but its effect depended on mean stand height. The best model accounted for 50% of the variation in wind damage (marginal $R^2 = 0.50$) and the random effect of stand accounted for an additional 11% (conditional $R^2 = 0.61$; Table 3). The area under the ROC curve for the best model was 0.903.

Wind damage decreased as upwind forest cover increased ($p = 0.005$; Fig. 4). With all other effects in the model at their averages, the probability of wind damage decreased from 0.23 with 50% upwind forested cover to 0.10 with 90% upwind forested cover.

Wind damage increased with maximum sustained wind speed, and although one of our lowest-AIC models included the interactive effect of maximum sustained wind speed and stand height, variation in wind damage with stand height was not significant ($p = 0.378$; Fig. 5A). We had no data for short trees in wind speeds > 35 m s^{-1}. The effect of stand density on wind damage varied by stand height (Fig. 5B). Higher stand density had little effect on wind damage in 4 m tall stands ($p = 1.000$) but decreased wind damage in 12 and 20 m tall stands ($p < 0.001$). In stands with a density of 500 trees ha^{-1}, damage probability was ca. 0.20 regardless of stand height. However, in stands with 1100 trees ha^{-1}, wind damage decreased with stand height ($p = 0.204$) and was 0.20 in 4 m tall stands, 0.08 in 12 m tall stands, and 0.03 in 20 m tall stands.

The effects of stand density on the probability of wind damage also varied by tree taper and relative tree height (Fig. 5 and 6B). Higher stand density decreased wind damage for trees with average (1.25 cm m^{-1}) and high (2 cm m^{-1}) taper ($p < 0.001$), but increased wind damage for trees with low (0.5 cm m^{-1}) taper ($p = 0.327$). Higher taper strongly decreased wind damage regardless of stand density ($p < 0.001$; Fig. 6). Increasing stand density decreased wind damage for trees with average relative height (1.0 $\mathrm{ht}:\overline{\mathrm{ht}}_{\mathrm{st}}$) from 0.20 in stands with 500 trees ha^{-1} to 0.08 in stands with 1100 trees ha^{-1} ($p < 0.001$) and for trees with high relative height (1.5 $\mathrm{ht}:\overline{\mathrm{ht}}_{\mathrm{st}}$) from 0.63 in stands with 500 trees ha^{-1} to 0.10 in stands with 1100 trees ha^{-1} ($p < 0.001$). Stand density had little

Table 3
Comparison of models of wind damage in planted longleaf pine stands in southwest Georgia and northwest Florida, US. Bold font indicates models with significant support as the best model (AIC < 2, Burnham and Anderson, 2002). The "all effects" model included all main and two-way interactive effects. Italicized font and leading minus signs indicate effects that were not significant at a 95% confidence level and were removed from the "all effects" model sequentially.

	Model	AIC	Deviance	df	R^2_m	R^2_c	Δ_{iRc}
0	intercept-only (null)	2021.0	2017.0	2278	0.51	0.00	380.5
1	all effects	1659.5	1623.5	2278	0.62	0.51	19.1
2	*-rht*ws*	1655.3	1621.3	2278	0.62	0.51	14.8
3	*-ht_{st}*taper*	1651.0	1619.0	2278	0.62	0.51	10.5
4	*-ws*taper*	1646.8	1616.8	2278	0.62	0.51	6.3
5	*-rht*ht_{st}*	1642.7	1614.7	2278	0.62	0.51	2.2
6	***-ws*density***	**1642.2**	**1616.2**	**2278**	**0.61**	**0.50**	**1.7**
7	***-ws*ht_{st}***	**1640.5**	**1616.5**	**2278**	**0.61**	**0.50**	**0.0**

R^2_m and R^2_c = Nakagawa's marginal and conditional R2, df = residual degrees of freedom, AIC = Akaike's information Criterion, ΔI is the difference in AIC from the lowest AIC model, rht = relative tree height, htst = mean stand height, and ws = maximum sustained wind speed.

Table 4
Type III tests of fixed effects with Satterthwaite's adjustment to degrees of freedom for the best model of probability of wind damage in planted longleaf pines stands in southwest Georgia and northwest Florida, USA.

Effect	Num. DF	Den. DF	X^2 value	Pr>X^2
(Intercept)	1	2278	159.18	<0.001
Relative height	1	2278	43.43	<0.001
Taper	1	2278	84.71	<0.001
Density	1	2278	16.00	<0.001
Stand height	1	2278	1.77	0.183
Forested cover	1	2278	7.80	0.005
Wind speed	1	2278	103.44	<0.001
Taper:Relative height	1	2278	45.44	<0.001
Density:Relative height	1	2278	41.04	<0.001
Density:Taper	1	2278	21.01	<0.001
Density:Stand height	1	2278	4.25	0.039
†Wind Speed:Stand height	1	2278	1.81	0.178

Table includes the numerator degrees of freedom (Num. DF), denominator degrees of freedom (Den. DF), the value of the X2 (X2 value) statistic and its corresponding P-value (Pr>X2).
† Effect statistics from model 6 (Table 3).

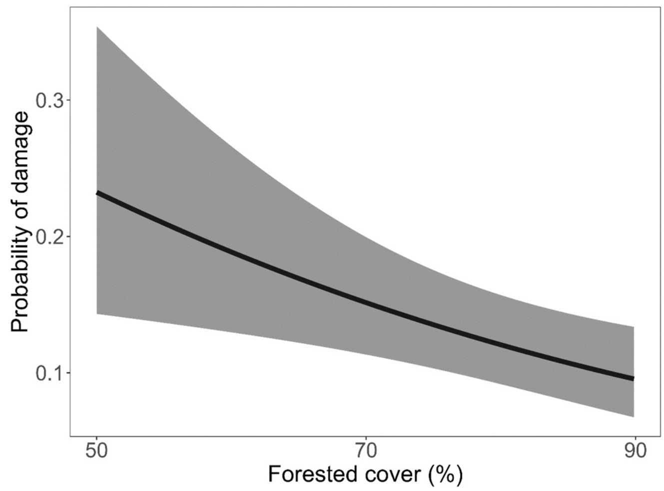

Fig. 4. Modeled probability of wind damage in planted longleaf pine stands showing a decrease in wind damage as upwind forested cover increases. Probabilities are estimated marginal means of wind damage as a function of upwind forested cover. Shaded area shows 95% confidence interval. All other effects in the model were at their average values.

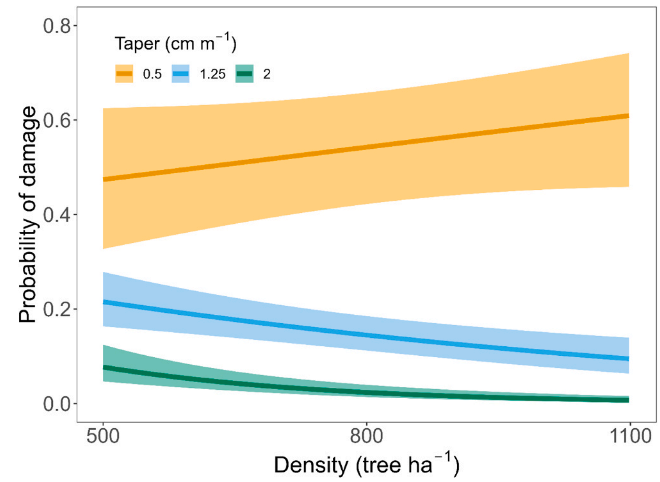

Fig. 6. Modeled probability of stem taper on wind damage of planted longleaf pine showing the increase in probability of damage for low taper trees when growing in dense stands. Probabilities are estimated marginal means of wind damage in planted longleaf pine stands as a function of stand density at three values of tree taper. All other effects in the model were at their average values.

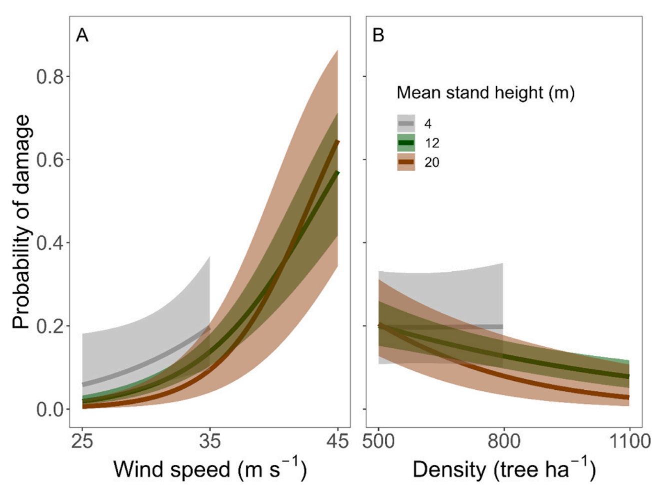

Fig. 5. Modeled probability of wind damage in planted longleaf pine stands showing (A) an exponential increase in damage in taller stands as wind speed increases and (B) decrease in damage in taller stands as stand density increases. Probabilities are estimated marginal means of wind damage as a function of (A) maximum sustained wind speed and (B) stand density at three values of mean stand height. Shaded areas show 95% confidence interval. All other effects in the model were at their average values. We lacked data for short stands at wind speeds > 35 m s^{-1} and density > 800 trees ha^{-1} so omitted predictions for those conditions.

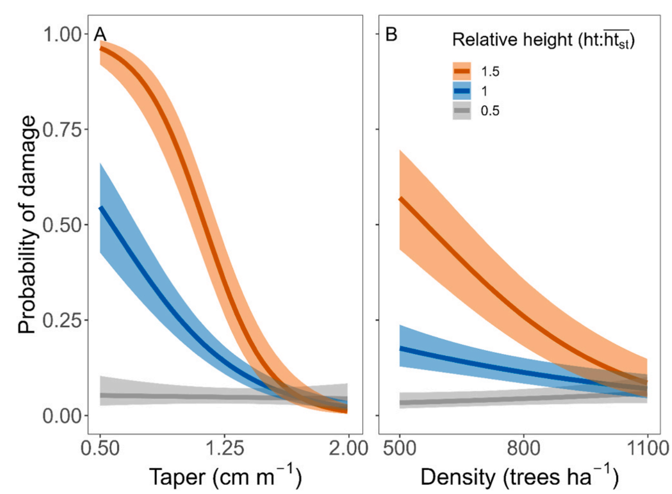

Fig. 7. Modeled ratio of tree height to mean stand height on probability of wind damage showing (A) trees that are taller than average are highly vulnerable if they have low taper, and (B) trees that are taller than average are more vulnerable when they are in sparse stands. Probabilities are estimated marginal means of wind damage in planted longleaf pine stands as a function of (A) tree taper and (B) stand density at three values of relative tree height. All other effects in the model were at their average values.

effect on wind damage for trees with low relative height (0.5 $\mathrm{ht} : \overline{\mathrm{ht}}_{\mathrm{st}}$; $p = 0.271$).

Tree taper also influenced wind damage, but it strongly depended on relative tree height (Fig. 7A). Taper had little effect in reducing the probability of wind damage to trees with low relative height (0.5 $\mathrm{ht} : \overline{\mathrm{ht}}_{\mathrm{st}}$; $p = 0.945$), but wind susceptibility decreased with increasing taper from 0.55 to 0.02 for trees with average relative height ($p < 0.001$) and sharply decreased from 0.96 to 0.01 for trees with high relative height ($p < 0.001$).

3.2. Tree taper

Tree taper was best predicted by models that included the interactive effects of stand density with relative height and stand density with mean stand height (Tables 5 and 6). Tree taper generally decreased with increasing stand density (Fig. 8A, B), but its effect depended on both stand height (Fig. 8A) and relative tree height (Fig. 8B). In 20 m tall stands, taper decreased with increasing stand density from 1.13 to 0.62 cm m^{-1} ($p < 0.001$), and in 12 m tall stands, taper decreased with increasing stand density from 1.40 to 1.13 cm m^{-1} ($p < 0.001$). Increasing stand density had little effect on taper in 4 m tall stands ($p = 0.790$). Taper in trees with low relative height decreased from 1.60 cm m^{-1} in low density stands to 1.29 cm m^{-1} in high density stands ($p < 0.001$). For trees with high relative height, taper decreased more gradually from 1.21 cm m^{-1} in low density stands to 1.08 cm m^{-1} in high density stands ($p < 0.001$).

4. Discussion

Characteristics that increased wind exposure resulted in greater wind

Table 5
Comparison of models of taper in planted longleaf pine stands in southwest Georgia and Northwest Florida, US. Bold font indicates models with significant support as the best model (AIC < 2, Burnham and Anderson, 2002). The "all effects" model included all main and two-way interactive effects. Italicized font and leading minus signs indicate effects that were not significant at a 95% confidence level and were removed from the "all effects" model sequentially.

	Model	AIC	Deviance	df	R^2_m	R^2_c	Δ_i
1	intercept-only (null)	5485.0	5479.0	2277	0.00	0.41	155.5
2	all effects	5337.9	5319.9	2277	0.27	0.47	8.4
3	**-rht*ht$_{st}$**	**5329.5**	**5313.5**	**2277**	**0.27**	**0.47**	**0.0**

R^2_m and R^2_c = Nakagawa's marginal and conditional R2 (Nakagawa et al., 2017), df = residual degrees of freedom, AIC = Akaike's information Criterion, ΔI is the difference in AIC from the lowest AIC model, rht = relative tree height, htst = mean stand height.

Table 6
Type III tests of fixed effects with Satterthwaite's adjustment to degrees of freedom for models of taper in planted longleaf pines stands in southwest Georgia and northwest Florida, USA.

Effect	Num. DF	Den. DF	F value	Pr>F
Stand height	1	76.41	49.08	<0.001
Density	1	80.07	31.12	<0.001
Relative Height	1	2190.04	132.47	<0.001
Stand height:Density	1	84.95	12.35	0.001
Relative height:Density	1	2190.04	16.61	<0.001

Table includes the numerator degrees of freedom (Num. DF), denominator degrees of freedom (Den. DF), the value of the F statistic (F value) and its corresponding P-value (Pr>F).

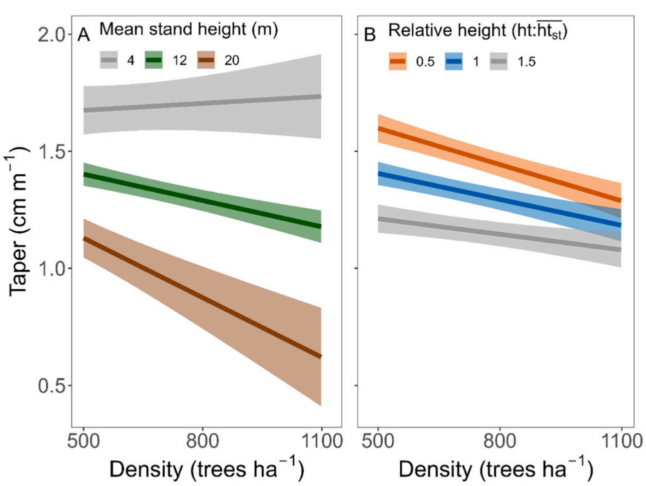

Fig. 8. Estimated marginal mean tree taper in planted longleaf pine stands affected by Hurricane Michael as a function of stand density at (A) three values of stand height and (B) three values of relative tree height. Shaded areas show 95% confidence interval. All other effects in the model were at their average values.

damage during Hurricane Michael, but one of those characteristics, low stand density, also resulted in high taper which was strongly associated with lower wind susceptibility. The connection between stand density and taper is well documented and related to exposure to more common, less-damaging winds; trees in lower density stands sway more which stimulates secondary growth thereby increasing taper (Albrecht et al., 2012; Meng et al., 2008, 2006). This suggests different wind mitigation strategies depending on forest management goals. Management of high density and uniform tree stands may increase wind resistance but is incompatible with the open and variable desired stand structure for fire-maintained pine woodlands. In the context of restoration of open-canopy woodlands with a rich, biodiverse understory, emphasis should be on creating high taper of individual trees through lower stocking and frequent thinning, whereas in the context of short-rotation timber production, the emphasis should be on thinning sufficiently to ensure tree vigor while still maintaining an unbroken, smooth canopy surface. Because we are concerned with restoration of an imperiled forest ecosystem, we focus discussion on severe wind mitigation in open-canopy woodlands.

Forest thinning is of clear importance to assessment and prediction of wind damage in forested stands and would likely have informed our models, yet records of forest thinning are difficult to obtain for larger landscape or regional predictions of wind damage. High wind damage in relatively tall trees in lower density stands (Fig. 7B) could be indicative of recent thinning. However, because thinning dates and prescriptions were unavailable for many of our sample stands, we were unable to account for this effect. Soil texture can also interact with tree size to influence wind stability (Rutledge et al., 2021). Although we aimed to assess how shallow clay layers affect susceptibility to wind damage, we encountered a clay layer in < 9% of our sample plots, thus excluded those data from our models. Longleaf pine toppling appeared higher on the fringes of small wetlands where clay layers occur within 1 m of the soil surface following Hurricane Michael (Andrew Whelan, personal observation), but this soil condition was rare in our study.

Damaging winds are likely to become more common with warming climate, underscoring the importance of minimizing risk of loss to high winds in forested stands. Overall, our results point to several management strategies that can enhance wind resistance and thereby bolster landscape restoration of imperiled ecosystems in hurricane-prone regions. We identified tree and stand characteristics that resulted in lower susceptibility to wind damage and suggest that wind risk can be reduced in managed stands by promoting (1) unfragmented landscapes, (2) age mosaics, and (3) increased tree taper. Our results on the effects of site, stand, and tree characteristics on wind damage in planted longleaf pine stands are largely consistent with previous research in diverse forest types (Gardiner, 2021).

First, longleaf pine stands are more wind resistant in unfragmented landscapes. We found that wind damage decreased with higher upwind forest cover consistent with previous studies (e.g., Scott and Mitchell, 2005). Unfragmented forest landscapes create more drag in high winds resulting in lower canopy-top wind speeds (Poëtte et al., 2017). Wind damage often occurs when trees are exposed to wind loading to which they are not yet acclimated such as along edges of recently thinned stands (Zeng et al., 2007). Predicting the direction of severe winds may be difficult in cyclonic storms, but severe wind gusts throughout the US Gulf Coastal plain are predominantly westerly or bidirectional (i.e., southwesterly and northeasterly; Martin and Konrad, 2006). Thus, focusing longleaf pine reforestation efforts in areas adjacent to existing forest cover or in a way that reduces forest fragmentation may reduce susceptibility to wind damage and contribute to landscape-scale restoration.

Second, consistent with previous research, damage severity increased with wind speed (H. Valta et al., 2019), and we found that increased damage in taller stands was counteracted by a decrease in damage with stand density. The slightly higher damage in tall stands at higher wind speeds (e.g., > 40 m/s) is likely due to increasing canopy-top wind speed with stand height (Quine et al., 2021), and the reduction in damage with stand density may be a result of canopy closure. As stands grow taller and tree crowns larger, tree canopies intersect causing roughness density and aerodynamic roughness to decrease, lowering wind stress on individual trees (Gardiner, 2021; Poëtte et al., 2017; Raupach, 1992). These effects would likely increase with planting density. Increased clashing of branches in intersecting tree crowns may also disperse wind energy and reduce wind damage (Kamimura et al., 2022; Milne, 1991; Rudnicki et al., 2008; Schindler et al., 2012). Lower susceptibility to wind damage with increasing stand density arises from shelter and support of neighboring trees but comes with a cost to tree taper. We found lower tree taper with increasing stand height, especially in taller stands (Fig. 8A). This likely decreased strain in the wood fibers due to wind, which has been found to increase diameter growth (Meng et al., 2006). Although high stand density may lower susceptibility to wind damage, it may result in low average taper and high susceptibility following reduction in stand density. Because trees in dense stands are reliant on each other for support, loss of only a few trees can eventually propagate to widespread damage throughout the stand (Kamimura et al., 2019). Similarly, thinning dense stands may be problematic for restoration of open canopy longleaf pine woodlands.

Third, damage was lowest among trees with high taper. As tree dbh increases relative to height, resistance to stem breakage increases by dbh^3 and resistance to overturning increases by dbh^2 (Gardiner et al., 1997). However, Gardiner et al. (1997) found that crown weight increased more quickly than dbh^2 resulting in a decrease in resistance to overturning. Although we did not distinguish between stem breakage and overturning, the dramatic decrease in wind damage with higher taper suggests that for longleaf pine, increased susceptibility to wind damage due to increased crown weight is small in comparison to the decrease in susceptibility conferred by a stem more resistant to breakage. Indeed, Dunham and Cameron (2000) found that Sitka spruce trees with larger crowns were more resistant to wind damage. Trees with high taper were infrequently damaged even if they were subject to high wind exposure (i.e., relatively tall trees in low density stands). Because trees acclimate to windy environments by increasing taper (Telewski, 1995), high damage in tall trees with average and low taper, and in lower density stands suggests that these trees had yet to acclimate to higher wind exposure, as would be the case shortly after a reduction in stand density (Fig. 7A, B).

Fourth, wind damage was low among trees with low relative height, suggesting that management strategies that increase multi-layered canopies may increase wind resistance in planted longleaf pine stands. Trees that rise above mean canopy height are subject to substantially greater wind stress, because they are likely to have larger crowns with higher drag and wind speed increases logarithmically above vegetation canopies (Oke, 1987). Gardiner et al. (2005) found trees 1.5 times the mean height of the stand had 15 times higher extreme-wind loading than trees of mean stand height. On the other hand, short trees are less susceptible to wind damage because they are more sheltered from the wind by taller neighbors and wind speeds rapidly decrease with canopy depth (Hale et al., 2012; Moore et al., 2018). Trees that are 2/3 mean canopy height, as we modeled here, are below the theoretical height within the canopy of a wide range of crops and trees where mean wind speed reduces to zero (Oke, 1987). Although the bulk of wind energy is absorbed higher in the canopy, winds at this height may still cause damage as strong winds intermittently reach lower canopy depths (Gardiner, 1994). Several studies of longleaf pine point to the importance of age structure in increasing wind resistance. Gardiner et al. (2005) showed that smaller trees in a shelterwood/group selection system enhanced wind resistance in larger trees either by absorbing wind energy or providing support and damping. Polinko et al. (2022) suggested that uneven-aged management of longleaf pine forests can enhance recovery of longleaf pine stands. Arko et al. (2024) suggested that typical hurricane-created gaps in naturally regenerated longleaf pine woodlands were small (0.15–0.20 ha) potentially due to survival of midstory trees which provided canopy continuity when dominant trees were removed.

4.1. Management implications

Landowner goals for longleaf pine management can vary widely but ecological management of planted longleaf pine savannas requires thinning to promote open structure and herbaceous biodiversity. Thinning exposes residual trees to increased wind loading, and residual trees acclimate accordingly over time. Generally, removal of neighbors with thinning promotes increased taper over time, which results in increased wind resistance (Gonzalez-Benecke et al., 2012; Meng et al., 2008), but wind damage may be higher for 5–10 years following thinning (Albrecht et al., 2012; Dhôte, 2005; Hanewinkel et al., 2014; Lohmander and Helles, 1987). Management strategies that promote high taper could reduce wind damage during stand development and in mature stands. Lower stocking, frequent low intensity thinning, and thinning strategies that focus on retention of dominant and codominant trees that are acclimated to higher wind exposure can mitigate increases in susceptibility to wind damage. Cremer et al. (1982) concluded that lower stocking density, and frequent, selective thinning from below reduced susceptibility to wind damage in planted stands of *Pinus radiata*. Valinger and Fridman (2011) suggested that early thinning reduced wind damage in mixed pine and spruce forests in southern Sweden, and Hanewinkel et al. (2014) suggested that long-term, single-tree selection thinning in uneven aged forests led to low wind damage in fir, spruce, and beech forests in Switzerland. Because thinning operations can be costly, we scrutinized our results for support for the benefits of thinning. Although we found that higher stand density decreased wind damage, wind resistance conferred by high stand density may rely on a uniform, closed canopy that may be incompatible with ecological approaches to managing longleaf pine ecosystems that emphasize canopy openness. Careful consideration regarding timing and intensity of thinning can promote ecological restoration of longleaf pine systems while maintaining resistance to severe wind.

5. Conclusions

Longleaf pine is among the most wind-resistant southern trees but can break in strong winds such as those generated by Hurricane Michael. Our research in the aftermath of this tropical cyclone created a predictive model of probability of individual tree damage at specified wind speed based on stand and tree characteristics. The interplay between tree taper and shelter from neighboring trees presents an unavoidable tradeoff; silvicultural actions which increase taper inevitably decrease shelter from neighbors, increasing vulnerability to wind damage at least temporarily while trees acclimate to increased resources with increased diameter growth. Depending on their goals, silviculturists may follow several paths to improve windstorm resistance, e.g., dense stands composed of trees with even height but low taper versus sparse stands composed of high-taper, wind resistant individuals.

Large-scale restoration and management efforts aim to accelerate the recovery of ecosystems such as longleaf pine. Our study shows that restoration efforts that promote unfragmented landscapes, stand age mosaics, and high taper may produce stands that are less susceptible to wind damage. Parameters for our model were obtained across wind speeds ranging from mild to extreme and have predictive capability for a wide range of conditions up to Category 4 tropical cyclones. Our predictive model can be linked to regional wind models and thus forms a basis for developing actuarial approaches to investments in tree planting and forest management. As anthropogenic climate change accelerates and windstorms become more frequent and powerful, predictive models for resistance of natural systems become ever more important.

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CRediT authorship contribution statement

Andrew Whelan: Writing – Original draft preparation, Formal analysis, Visualization, Investigation. **Seth W. Bigelow**: Funding acquisition, Formal analysis, Conceptualization, Methodology, Writing – Review & Editing. **Christina L. Staudhammer**: Funding acquisition, Conceptualization, Writing – Review & Editing. **Gregory Starr**: Funding acquisition, Conceptualization, Writing – Review & Editing. **Jeffery Cannon**: Methodology, Supervision, Writing – Review & Editing.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Seth W. Bigelow, Christina L. Staudhammer, Gregory Starr report financial support was provided by National Science Foundation. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2024.121828.

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