

Stand-level structural characteristics dictate hurricane resistance and resilience more than silvicultural regime in longleaf pine woodlands

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ABSTRACT

Hurricanes frequently impact coastal forests throughout the southeastern United States and are expected to increase in frequency and intensity in the future. Given this projection, interest has grown in adopting forest management practices that can reduce the risk of hurricane damage by increasing stand resistance and resilience. Empirical evidence suggests that uneven-aged stands are more resistant and resilient to hurricanes than even-aged stands, due to their heterogeneous stand structure and multiple age classes. Nevertheless, opportunities to compare the impact of hurricanes on stands managed under different silvicultural regimes at the same location are uncommon. Moreover, no research has detailed how different stocking regulation methods influence hurricane risk in uneven-aged stands. An opportunity to conduct a natural experiment presented itself in 2004 when Hurricane Ivan passed 24 km west of the Escambia Experimental Forest in southern Alabama, USA. At the time of the storm, the experimental forest contained long-term experiments examining the performance of longleaf pine (*Pinus palustris*) managed under different silvicultural systems. Here, we report on the resistance and resilience of three even-aged stands compared to six uneven-aged stands that were managed under BDq (two stands), Volume Control Guiding Diameter Limit (VC-GDL) (two stands), and Diameter Limit Cutting (DLC) (two stands) stocking control methods.

Average stand resistance (proportion of basal area remaining in 2005) was not statistically different among even-aged (0.866) and uneven-aged stands (all variants pooled) (0.858) $p > 0.05$. Among uneven-aged variants, resistance was highest in the VC-GDL stands (0.876) and lowest in the DLC stands (0.840). Across all stands, resistance was positively related to stand density ($p = 0.03$) and negatively associated with increases in quadratic mean diameter ($p = 0.03$) and size class diversity ($p = 0.01$). Post-hurricane (2005) departure indices found left shifts (shift in density towards smaller size classes) in the diameter distribution of 33 % of even-aged stands and 83 % of pooled uneven-aged stands. Among uneven-aged variants, significant left shifts in diameter distribution were greatest in stands managed with VC-GDL and lowest with BDq. Average post-hurricane resilience (post hurricane basal area recovery) was statistically similar in the pooled uneven-aged stands (0.42) and even-aged stands (0.37). Yet, stands with greater tree size class diversity demonstrated increased resilience. Regardless of management regime, stands carrying a high density of smaller diameter trees are more resistant to hurricane damage than stands managed at a lower density with a higher proportion of larger diameter trees. Moreover, while not statistically significant, our findings suggest that uneven-aged stands possess a greater potential for rapid hurricane recovery than even-aged stands. Therefore, land managers seeking to foster hurricane resistance and resilience should consider modifying stand prescriptions to carry a higher proportion of stocking in smaller size classes.

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1. Introduction

Mitigating the effects of disturbance is a critical management objective in disturbance prone environments. In the southeastern United States, hurricanes have historically affected forests every 13 years and are expected to increase in frequency and intensity with climate change (Keim et al. 2007; Kim et al. 2017; Ting et al. 2019). Wind is the primary threat posed to inland forests by hurricanes, as trees are often uprooted, bent, snapped, or incur varying degrees of crown damage. Thus, interest in developing silvicultural strategies to increase resistance and resilience to wind damage has recently increased in longleaf pine ecosystems (Bigelow et al. 2021).

Silvicultural treatments are known to influence wind damage through their effects on stand structure (Everham and Brokaw 1996; Mitchell, 2013). Because of their structural diversity in tree height and diameter, and perhaps because of individual tree differences in the ratio of height to diameter in irregular versus regular forests, uneven-aged silviculture is thought to enhance wind resistance (Bodin and Wiman 2007; Stanturf et al. 2007; Schelhaas 2008; Jactel et al. 2009; Bauhaus et al. 2017). The first element at play is the relationship between the diameter and height of a given tree. For example, stands of Norway spruce (*Picea abies*), trees of a given diameter in even-aged stands were taller (thus, with a higher slenderness ratio) than those from uneven-aged stands (Assmann 1970). Several authors have reported that a lower slenderness ratio of trees in uneven-aged stands was a favorable pre-condition for resistance to wind damage (Kenk and Guehne 2001, Mason 2002). These data suggest that trees from uneven-aged stands might have a lower form class and greater taper, and by inference a greater force is required to break their stems, conferring resistance to the effects of wind compared to trees from even-aged stands. It is, however, important to note that tree slenderness is a function of competition with neighboring trees and even-aged stands grown at low densities may exhibit even greater taper to those in uneven-aged stands. Another factor might be the degree to which the differences in stem density and stocking of midstory and understory trees in uneven-aged irregular stands compared to even-aged stands affects the propagation of wind. For example, the presence of understory is hypothesized to reduce the loading of taller trees in wind tunnel studies (Gardiner et al. 2005). In discussing the effects of climate change on forests, Brang et al. (2014) propose that because a given disturbance agent often affects trees of similar size, having a diversity of tree sizes in a stand confers some degree of resistance to that agent, further suggesting that uneven-aged management may improve wind resistance.

While uneven-aged stands broadly represent a stable forest condition featuring a reverse-J-shaped diameter distribution that is maintained in perpetuity with some fluctuations in stocking and structure between any two successive harvests, stand attributes of even-aged stands are always changing (Nyland 2016). Young even-aged stands are usually characterized by high tree density, low basal area, and minimal structural complexity within a left-skewed normal diameter distribution. Over time, prolonged differentiation results in a decrease in stand density and increase in basal area and structural complexity which is reflected by a left-skewed normal diameter distribution with increasingly lower kurtosis. When even-aged stands grow past the stem exclusion phase (Oliver and Larson, 1996), they may add an additional age-class resulting in a bimodal diameter distribution. Structural comparisons between even-aged and uneven-aged stands therefore vary with the developmental stage of even-aged stands and are context dependent. For example, it is possible that uneven-aged stands are continuously susceptible to windthrow due the presence of taller trees and higher harvest frequency, while even-aged stands tend to be little affected by windthrow in their early developmental stages (Nolet and Béland, 2017, Potter et al. 2022).

Uneven-aged management may also increase wind resilience. Irregular, multi-aged stands are themselves the result of multiple disturbance events that establish or release new age cohorts, and thus are likely capable of absorbing future disturbances (Lafond et al., 2014; Oliver and

Larson, 1996). Due to the presence of a single cohort, even-aged stands may not possess the capacity to rapidly recover from disturbance via recruitment as rapidly as uneven-aged stands. This potential advantage would be particularly important in conifer dominated systems where sprouting is uncommon (Del Tredici 2001). While such processes are consistent with the respective recruitment dynamics of uneven-aged and even-aged stands (Ashton and Kelty 2018), to our knowledge, no study has directly compared the hurricane resistance and post-storm resilience of different stand types growing under similar edaphic conditions.

Another factor that could impact wind resistance is the method of stocking regulation used in uneven-aged management. Regulation methods such as the Basal area-Diameter limit-Q-factor (BDq) method of structural regulation and the Diameter Limit Cutting (DLC) method rigidly regulate the maximum size diameter class retained compared to methods such as Volume Control-Guiding Diameter Limit (VCGDL), which is somewhat more flexible in its retention of trees exceeding the maximum size class retained in the residual stand (Reynolds et al. 1984; Guldin 2011). Depending on the maximum diameter class retained under BDq and DLC, this subtle distinction between stocking regulation methods may have strong implications on wind resistance in the southeastern United States, as recent studies suggest wind damage increases with tree size creating the potential for differing degrees of wind damage (Kleinman and Hart 2017; Zampieri et al. 2020; Bigelow et al. 2021 Sharma et al. 2021). Yet, due to the stochastic nature of hurricanes and the dispersed geographic locations of silvicultural field trials, no studies have examined this possibility.

An opportunity to conduct such a study presented itself on the morning of September 16, 2004, when Hurricane Ivan struck the east Gulf Coastal Plain near Gulf Shores Alabama. The track of the hurricane crossed Escambia County, Alabama with winds of 193 km/h, and 20.32 cm of rainfall. The eye wall of the hurricane passed 24 km west of the Escambia Experimental Forest, operated by the Southern Research Station of the United States Department of Agriculture's Forest Service in cooperation with the T.R. Miller Mill Company in Brewton, Alabama. Several replicated long-term silvicultural experiments existed in the forest at the time of the hurricane allowing us to compare the resistance (basal area percent loss, departure from pre-storm diameter distribution) and post-storm resilience (basal area recovery) of six mature longleaf pine stands maintained in an uneven-aged structure with BDq, DLC, and VCGDL stocking regulation and three even-aged stands. Specifically, we examined the following hypotheses: 1) uneven-aged stands are more resistant and resilient to storm damage than even aged-stands; 2) uneven-aged stocking regulation methods differ in their resistance and resilience; and 3) damage to trees in different size classes vary with management regime. The findings of this natural experiment provide a direct comparison of how Hurricane Ivan affected the development of longleaf pine (*Pinus palustris*) stands on a common site managed under different silvicultural regimes; and provides insight into how different harvesting regimes influence resistance and resilience to wind damage.

2. Methods

2.1. Site description

Our study was conducted at the Escambia Experimental Forest (EEF) near Brewton, Alabama, United States (31°01'N, 87°04'W). The climate at EEF is considered humid-subtropical. Average temperatures at EEF are highest in August (22.7–32.8°C) and lowest in January (4.4–16.7°C). Precipitation at EEF is abundant (1,680 mm) and occurs relatively evenly throughout the year in the form of rain. EEF is located on rolling hills topography and is 75 m above sea level. The soils at EEF developed from unconsolidated marine sediments and are classified as belonging to the Troup Series (loamy, kaolinitic, and thermic Grossarenic Kandiudults), which contain well-drained sandy and loamy sediments. Longleaf pine is the dominant tree species at EEF occupying approximately 95 % of the canopy with minor components of water oak

Table 1

Stand size, study initiation year, and management regime, stocking regulation method (Volume Control Guiding Diameter Limit (VC-GDL), Diameter Limit Cutting (DLC), and BDq), and harvesting history for each stand included in this study.

Stocking Regulation		Management	Stand	Stand Size (ha)	Site	Approximate	Approximate Canopy Height (m)	Stocking Regulation
Type	Regime	Number		Index	Stand Age	*	Initiation	
N/A	Even-aged	1	9	70	57	21.3	2004	
N/A	Even-aged	2	9	70	57	21.3	2004	
N/A	Even-aged	3	9	70	57	21.3	2004	
BDq	Uneven-aged	65	12.1	70	100	24.4	1982	
BDq	Uneven-aged	115	16.2	70	100	24.4	1996	
DLC	Uneven-aged	125	15.4	70	100	24.4	1992	
DLC	Uneven-aged	83	14.1	70	100	24.4	1996	
VC-GDL	Uneven-aged	147/148	14.6	70	100	24.4	1978	
VC-GDL	Uneven-aged	102	13.8	70	100	24.4	1996	

*Canopy height was estimated from [Farrar \(1981\)](#).

Table 2

Inventory statistics for periods pre, during and post Hurricane Ivan.

Method	Stand	Year	Trees per hectare	Basal area ($m^2\text{ha}^{-1}$)	Quadratic mean diameter (cm)
even-aged	Stand 1	2003	228	18.63	32.30
		2005	173	14.32	32.47
		2010	169	14.77	33.45
even-aged	Stand 2	2003	312	13.98	23.91
		2005	312	14.4	24.26
		2010	312	15.87	25.47
even-aged	Stand 3	2003	228	20.57	33.94
		2005	203	17.52	33.18
		2010	196	17.84	34.11
BDq	Stand 65	2002	399	14.76	21.73
		2007	385	13.78	21.35
		2012	424	15.27	21.44
BDq	Stand 115	2000	262	13.42	25.54
		2005	238	11.9	25.28
		2010	261	13.25	25.44
DLC	Stand 125	2000	380	15.68	22.93
		2006	347	15.56	23.9
		2011	341	15.99	24.45
DLC	Stand 83	2000	187	13.99	30.86
		2006	161	11.45	30.14
		2011	165	11.27	29.52
VC-GDL	Stand 147/148	2003	272	14.42	25.99
		2008	255	12.36	24.85
		2013	281	13.59	24.84
VC-GDL	Stand 102	2004	322	14.89	24.29
		2009	285	12.91	24.03

(*Quercus nigra*), sweetgum (*Liquidambar styraciflua*), and southern red oak (*Q. falcata*). The understory is comprised of a mix of shrubs and herbaceous species including gallberry (*Ilex spp.*), bracken fern (*Pteridium aquilinum*), shiny blueberry (*Vaccinium myrsinites*) and greenbriers (*Smilax spp.*) On average, stands at the EEF were prescribed burned with a low intensity ground fire on a three-year fire return interval before and after Hurricane Ivan (2 – 4-year return interval).

2.2. Harvesting treatments

Nine stands were included in this study ([Table 1](#)). Six stands were managed with an uneven-aged regime. The stocking regulation method used in the uneven-aged stands was a modified group selection in the BDq and VC-GDL methods and a modified diameter-limit in the DLC ([Farrar and Boyer, 1991](#)). Three stands were managed under an even-aged regime prior to Hurricane Ivan.

2.2.1. Uneven-aged stands

2.2.1.1. VC-GDL. Two uneven-aged stands were managed with the VC-GDL stocking regulation method ([Table 1](#)). The VC-GDL method is an adaptation of Bolley's approach such that the allowable cut essentially equals average annual growth, as described by [Knuchel \(1946\)](#). Application of this idea in southern pines was pioneered by Reynolds at the Crossett Experimental Forest ([Reynolds 1969, Baker et al. 1996, Farrar 1996, Guldin et al. 2017](#)). Among the attributes uneven-aged methods is a continuous cover of trees on the site given continued management and the absence of catastrophic disturbance. VC-GDL is a simple regulation method to apply in the field; the guiding diameter limit for the proposed cutting cycle harvest is based on the sawtimber volume growth observed since the last cutting cycle harvest. The method has been sustained for more than seven decades in the two stands at the Crossett Experimental Forest ([Guldin 2011, Bragg and Guldin 2015](#)). In both VC-GDL stands (Stands 147 and 102) ([Table 1](#)), the guiding diameter limit (VC-GDL) was generally 18" (45.72 cm), but marking flexibility resulted in retention above and thinning below the GDL across a broader range of sawtimber-sized diameter classes than would have been considered under a strict diameter limit harvest. The harvests had a removal target of 1.5 Mbf/acre Doyle leaving a post-cut residual sawtimber volume of 4.5 to 5 Mbf/acre Doyle, which is equivalent to an average removal target of $2.2 \text{ m}^2\text{ha}^{-1}$ and an average of $15.0 \text{ m}^2\text{ha}^{-1}$ of residual basal area on these sites. Stand 147 had the most entries out of all uneven-aged stands and was cut in 1978, 1988, and 1998. Stand 102 was cut in 1996. Inventories of all trees 9.1 cm dbh and larger in Stand 147 were conducted in 1977, 1987, 1992, 1997, 2003, 2008, and 2013. Inventories in Stand 102 were conducted in 1995, 1999, 2004, and 2009 ([Table 2](#)).

2.2.1.2. BDq. Two uneven-aged stands were managed with the BDq stocking regulation method ([Baker et al. 1996; Farrar 1996](#)) ([Table 1](#)). Three stand variables (B,D,q) uniquely define the reverse j-shaped curve thought to characterize balanced uneven-aged stands—the residual basal area B, maximum retained diameter class D, and the quotient q which represents the mean ratio between the density of a diameter class and the next largest diameter class. The goal of the BDq approach is to establish a hypothetical target stand structure using the BDq parameters, match the existing stand to the BDq target, and harvest in diameter

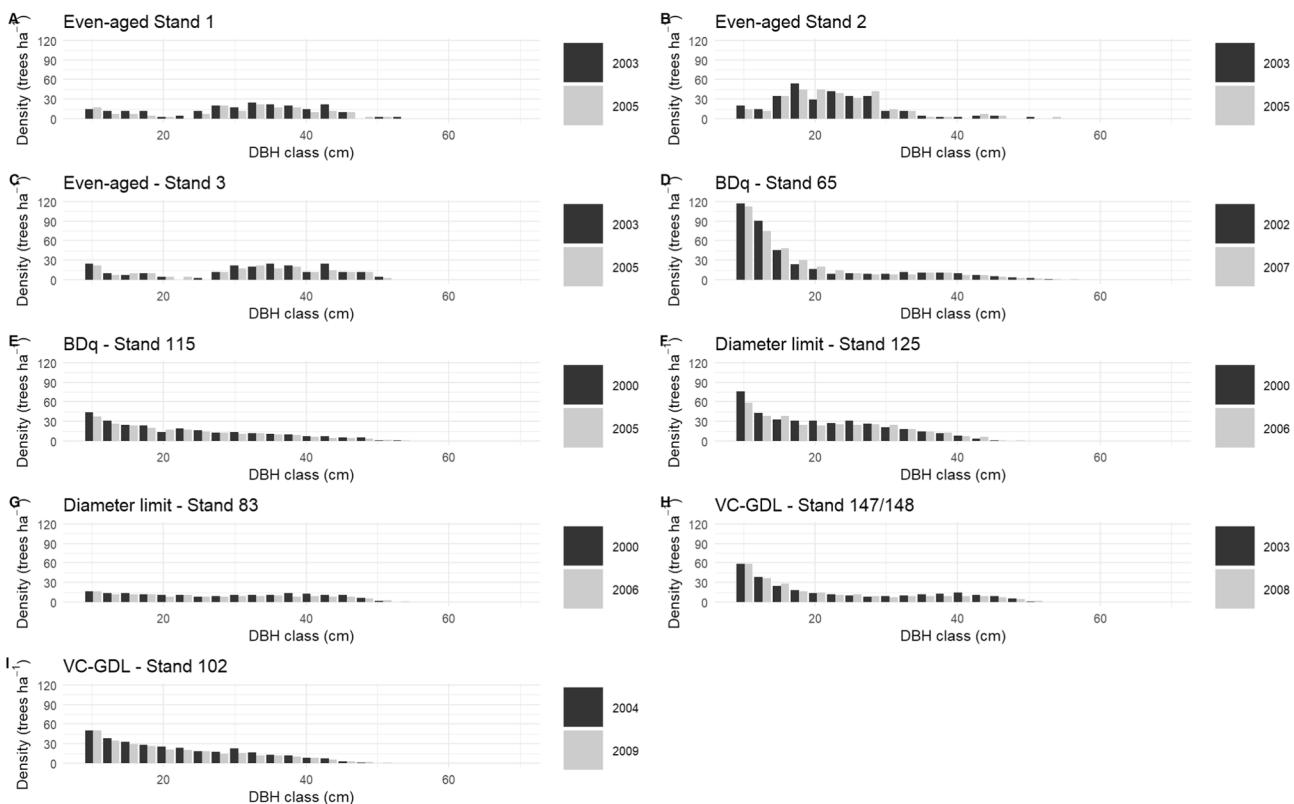


Fig. 1. Diameter distributions immediately pre and post Hurricane Ivan (2004).

classes surplus to the target in a way that meets the target residual basal area B. In Stand 65, the target B, D, and q parameters were set to $11.5 \text{ m}^2 \text{ha}^{-1}$, 50.8 cm, and a q (2.54 cm dbh classes) of 1.2. For Stand 115, the target B, D, and q parameters were set to $13.8 \text{ m}^2 \text{ha}^{-1}$, 50.8 cm and a q (2.54 cm dbh classes) of 1.2. Stand 65 was cut in 1982 and 1992 while stand 115 was cut in 1996. Inventories (living status and diameter measurement) of all trees 9.1 cm dbh and larger were conducted in Stand 65 in 1982, 1987, 1991, 2002, 2007, and 2012. Inventories of Stand 115 were conducted in 1995, 2000, 2005, and 2010 (Table 2).

2.2.1.3. DLC. Two uneven-aged stands were managed with the DLC stocking regulation method (Table 1). This basic selection system utilizes a rudimentary form of volume regulation by removing all volume in and above a strict diameter limit with a residual basal area target of $13.8 \text{ m}^2 \text{ha}^{-1}$. As implemented in both DLC stands (Stands 125 & 83) (Table 1), all trees above the target 40.6 cm diameter limit, regardless of quality and condition, are marked to cut, and all trees regardless of quality below the diameter limit are retained. Stand 125 was cut in 1992 and stand 83 was cut in 1996. Inventories of all trees 9.1 cm dbh and larger were conducted in 1991, 1996, 2000, 2006 and 8/2011 in Stand 125. Inventories in Stand 83 were completed in 1995, 2000, 2006, and 2011 (Table 2).

2.2.2. Even-aged stands

Three even-aged stands, each approximately 9 ha in size, were used to represent even-aged management (Table 1). These stands naturally originated following a bumper seed crop event in 1947 (Croker, 1956) and developed without further silvicultural intervention. All even-aged stands were first measured in 2003 when stand density and basal area averaged 256 trees per hectare (range 228–312 trees per hectare) and $17.73 \text{ m}^2 \text{ha}^{-1}$ (range $13.98\text{--}20.57 \text{ m}^2 \text{ha}^{-1}$), respectively. Quadratic mean diameter ranged between 23.91 cm and 33.94 cm in 2003 (Table 1). Following Hurricane Ivan in 2004, stand inventories were conducted in 2005 and 2010 (Table 2). Natural stand development over

more than five decades led to some recruitment of small-sized trees and canopy stratification. This pattern was most apparent in Stand 3 which, in 2003, featured relatively lower basal area ($13.98 \text{ m}^2 \text{ha}^{-1}$), higher stocking (312 trees per hectare), and smaller average diameter (23.91 cm) compared to the other even-aged stands (Table 1, Fig. 1).

2.3. Stand structure, resistance and resilience calculations

Relative stand density was calculated using additive stand density index (SDI; Stage 1968):

$$SDI = \sum N_i \left(\frac{D_i}{25} \right)^{1.605} \quad (1)$$

where D_i is the center of the i^{th} diameter class (cm) and N_i is trees per hectare of the i^{th} diameter class. Stand structural complexity was evaluated as the ratio of additive SDI to Reineke's stand density index $SDI = TPH \left(\frac{D_q}{25} \right)^{1.605}$ (Reineke, 1933), where TPH is trees per hectare and D_q is quadratic mean diameter (cm) (Ducey 2009). Size class diversity between stands was compared using the Shannon index (H), calculated as:

$$H = \sum p_i \ln p_i \quad (2)$$

where p_i is the proportional abundance of the i^{th} diameter class. Proportional abundance was evaluated as tree density (trees per hectare of the i^{th} diameter class) and basal area ($\text{m}^2 \text{ha}^{-1}$ of the i^{th} diameter class). Shannon index was calculated using the diversity function of the R package Vegan (Oksanen et al. 2020).

Comparisons between diameter distributions pre- and post-Hurricane Ivan were made using Menning's departure index, which estimates the magnitude as well as direction of a change in post-Hurricane Ivan distribution relative to the pre-Hurricane Ivan distribution (Menning et al. 2007):

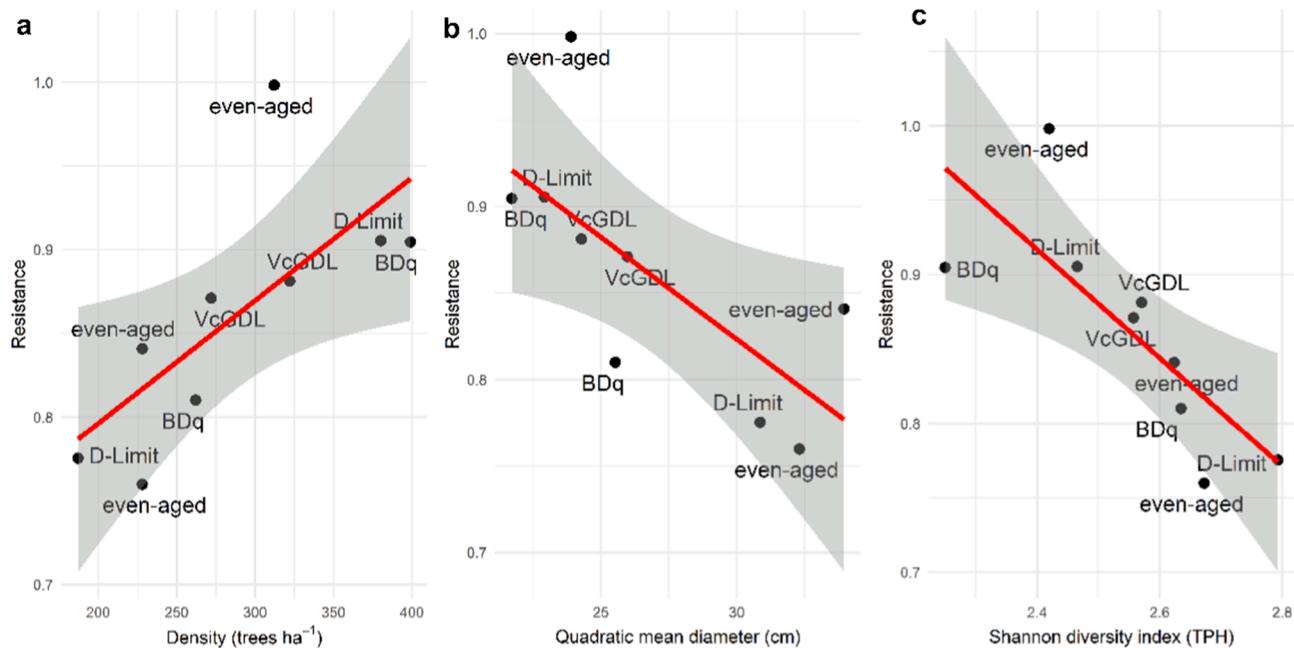


Fig. 2. Net loss (stand resistance) from Hurricane Ivan (2004) regressed against pre-Hurricane Ivan inventory stand density, quadratic mean diameter, and Shannon's diversity index (calculated using TPH).

Table A1
Regression analysis with Net Loss (stand resistance) as a dependent variable.

	Estimate	Standard Error	Statistic	P value
Resistance ~ Trees per hectare				
(Intercept)	0.35	0.08	4.30	0.00
tph	0.00	0.00	-2.66	0.03
Resistance ~ Quadratic mean diameter				
Estimate	Standard Error	Statistic	P value	
(Intercept)	-0.18	0.12	-1.44	0.19
qmd (cm)	0.01	0.00	2.61	0.03
Resistance ~ Shannon diversity index (TPH)				
Estimate	Standard Error	Statistic	P value	
(Intercept)	0.79	0.28	2.80	0.03
Shannon Diversity Index	-0.36	0.11	-3.30	0.01

$$M = \left(\frac{2}{k-1} \right) \sum_{i=1}^k \left[\left(p_i - \frac{f_i}{n_f} \right) (k+1-i) \right] \quad (3)$$

where k is the number of bins in the histogram, f_i is the count of trees in the i^{th} bin of the test distribution, n_f is the cumulative number of trees in all bins of the test distribution, and p_i is the cumulative number of trees in the i^{th} bin of the reference.

To estimate stand conditions in the absence of the disturbance caused by Hurricane Ivan and account for differences between measurement periods, stands were modelled using the Southern Variant of the Forest Vegetation Simulator (FVS Staff, 2008; Dixon 2022). Each stand was initiated using the closest inventory prior to Hurricane Ivan (2004) and projected until the most recent inventory (Table 1). Growth response to Hurricane Ivan was evaluated using calculations of resistance and resilience (*sensu* D'Amato et al., 2013). Stand resistance to Hurricane Ivan (basal area loss) was calculated as:

$$1 - \frac{(BA_m - BA_e) - (BAI_{pre} \times n_{year})}{BA_m} \quad (4)$$

where BA_m is the predicted basal area in square meters per hectare

for each stand in the measurement immediately following Hurricane Ivan, BA_e is the measured basal area for each stand in the measurement immediately following Ivan, BAI_{pre} is the modelled BAI prior to the hurricane (2003 – 2004), and n_{year} is the number of years between the measurement periods pre- and post-Hurricane Ivan. This method allowed for comparison between stands with different inventory periods by assuming the rate of basal area growth following the disturbance was maintained and was linear. For inventories conducted outside the summer months, a full growing season was included in the appropriate growth period, however, inventories that were conducted in the middle of the growing season (June) were truncated to half a year.

Hurricane Ivan resilience was defined as:

$$\frac{BAI_{post}}{BAI_{pre}} \quad (5)$$

where BAI_{post} is the mean basal area increment (BAI) in the period following the hurricane and BAI_{pre} is the modelled BAI prior to the hurricane (2003 – 2004). Hurricane resilience was not calculated for VC-GDL stand 2 as there were insufficient measurements to calculate BAI_{post} . Stands that had high resistance to Hurricane Ivan (resistance > 0.998) or experienced disturbance other than Hurricane Ivan, resulting in a negative resilience score, were omitted from the analysis.

2.4. Statistical analysis

All analyses were completed in R version 4.1.1 (R Core Team 2021). Group level comparisons between even-aged and pooled uneven-aged stands were evaluated using analysis of variance. Relationships between stand structure (stand density, basal area, quadratic mean diameter, SDI summation, Shannon index), and resistance or resilience were evaluated using a linear model. We also evaluated the statistical significance of the departure index (M) using a 95 % confidence interval of 999 iterations of departure indices calculated from a test distribution where a proportion of trees (corresponding to the number of trees lost in each treatment) were randomly removed independent of diameter class (Menning et al. 2007).

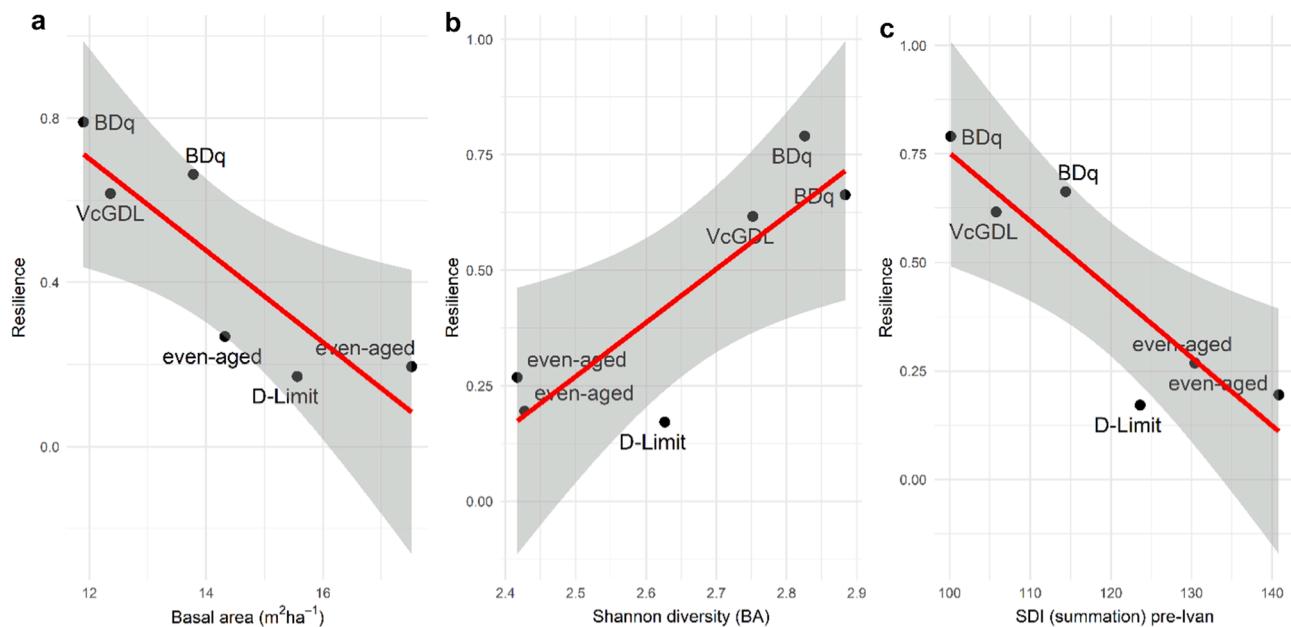


Fig. 3. Stand resilience (basal area recovery) from Hurricane Ivan (2004) regressed against post-Ivan basal area (m^2ha^{-1}), Shannon's diversity index (calculated using BA), and pre-Ivan stand density index. Stands where resilience could not be calculated (VC-GDL stand 2), stands that experienced disturbance following Hurricane Ivan (DCL stand 2), and stands that experienced minimal damage (even-aged stand 3) are not shown.

Table A2

Regression tables for stand resilience (basal area recovery) as a dependent variable.

	Estimate	Standard Error	Statistic	P value
Resilience ~ Basal area (m^2ha^{-1})				
(Intercept)	2.04	0.47	4.32	0.01
Basal area	-0.11	0.03	-3.40	0.03
Resilience ~ Shannon diversity index (BA)				
	Estimate	Standard Error	Statistic	P value
(Intercept)	-2.63	0.92	-2.86	0.05
Shannon Diversity Index	1.16	0.35	3.36	0.03
Resilience ~ Pre-Ivan SDI (summation)				
	Estimate	Standard Error	Statistic	P value
(Intercept)	2.33	0.47	4.90	0.01
Pre Ivan SDI (summation)	-0.02	0.00	-3.98	0.02

3. Results

Pre-Ivan stand density averaged 748 trees per hectare (range 461–983 trees per hectare) and 14.53 m² per hectare of basal area (range 13.42 – 15.68 m²ha⁻¹) in the uneven-aged stands. Quadratic mean diameter averaged 25.2 cm (range 21.7 – 30.9 cm) across uneven-aged stands. The even-aged stands contained an average of 629 trees per hectare (range 560 – 768 trees-per-hectare) and 17.73 m² per hectare of basal area (range 13.98 – 20.57 m²/ha; Fig. 1; Table 1). Quadratic mean diameter was 30.0 cm (range 23.9 – 33.9 cm) pre-Ivan. Uneven-aged stands showed significantly more structural complexity as indicated by the pre-Ivan SDI ratio ($p < 0.05$; not shown).

Stand resistance (basal area retained) was positively associated with stand density and negatively associated with quadratic mean diameter and Shannon's Diversity index ($p < 0.05$: Fig. 2; Table A.1). Response to hurricane damage was variable across even- and uneven-aged systems. Stand resistance to Hurricane Ivan was statistically similar between even- and uneven-aged methods ($p > 0.05$). Across all uneven-aged stands, stand resistance to Hurricane Ivan averaged 0.858. Among the uneven-aged stocking regulation methods, resistance was highest in the

VC-GDL method averaging 0.876 and lowest in the DLC method (mean 0.840; Table 3). The DLC produced the most variable response to Hurricane Ivan, as resistance ranged from 0.775 to 0.905). Resistance across the even-aged stands averaged 0.866, ranging from 0.760 to 0.998.

Departure indices suggested left shifts in 33 % of even-aged stands and 83 % of uneven-aged stands. Significant left shifts among uneven-aged stands were most severe in the VC-GDL method (Stand 147/148; $M = -0.04$, range -0.53 to 1.47 and least severe with the BDq method (Stand 115; $M = -0.01$, range -0.50 – 1.50). The only significant left shift among even-aged stands occurred in Stand 3 ($M = -0.04$, range -1.1 to 0.90 respectively). Even-aged stands 1 and 2 indicated significant right shifts ($M = 0.01$, range -0.94 – 1.06 $M = 0.02$, range -0.61 – 1.39). Similar to stand resistance, the DLC method was the most variable with stands experiencing both significant left (negative) and right (positive) shifts. The DLC stands also represented the only significant right shift in the modelled stands, reflecting the long duration, and subsequent change in distribution, between measurements.

Smaller, pulp / chip-n-saw merchantable size classes (12.7 – 27.9 cm d.b.h) were less susceptible to hurricane damage than sawtimber sized trees (>27.9 cm dbh). Only one stand managed under DLC (Stand 125) showed a significant left shift (decrease in size) in product class distributions following Hurricane Ivan ($M = -0.02$, range -0.91 – 1.09). The BDq method was the only uneven-aged method to show a significant left shift in both stands ($M = -0.02$, range -0.49 – 1.51 and $M = -0.002$, range -0.51 – 1.49). The VC-GDL method had the largest right shift (Stand 102; $M = 0.05$, range -0.36 – 1.64) among uneven-aged stands. Even-aged Stand 3 had the largest significant left shift ($M = -0.02$, range -0.82 – 1.18) and no even-aged stands demonstrated right (positive) shifts.

4.1. Resilience

Stand resilience (basal area recovery) to Hurricane Ivan was statistically similar between uneven-aged stands (mean 0.42) and even-aged stands (0.37). Stand resilience following Hurricane Ivan was positively associated with Shannon diversity index and negatively associated with post-Ivan basal area and pre-Ivan SDI ($p < 0.05$: Fig. 3; Table A.2). Basal area in the first inventory following Ivan was lower than the predicted basal area for all stands (Fig. 4). Among uneven-aged stands, the BDq

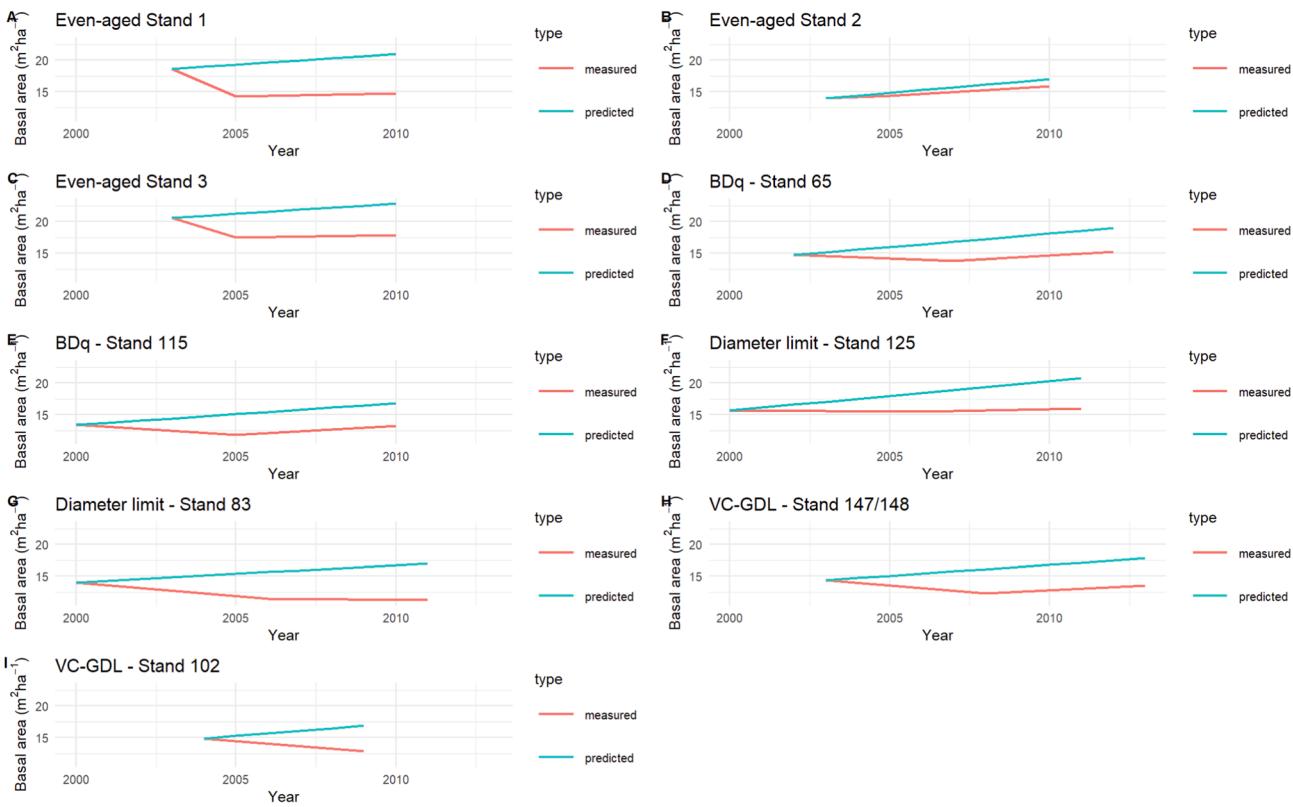


Fig. 4. Predicted and empirical basal area (m^2 per ha) through time for four stands. Note: VC-GDL stand 2 was inventoried only once post hurricane.

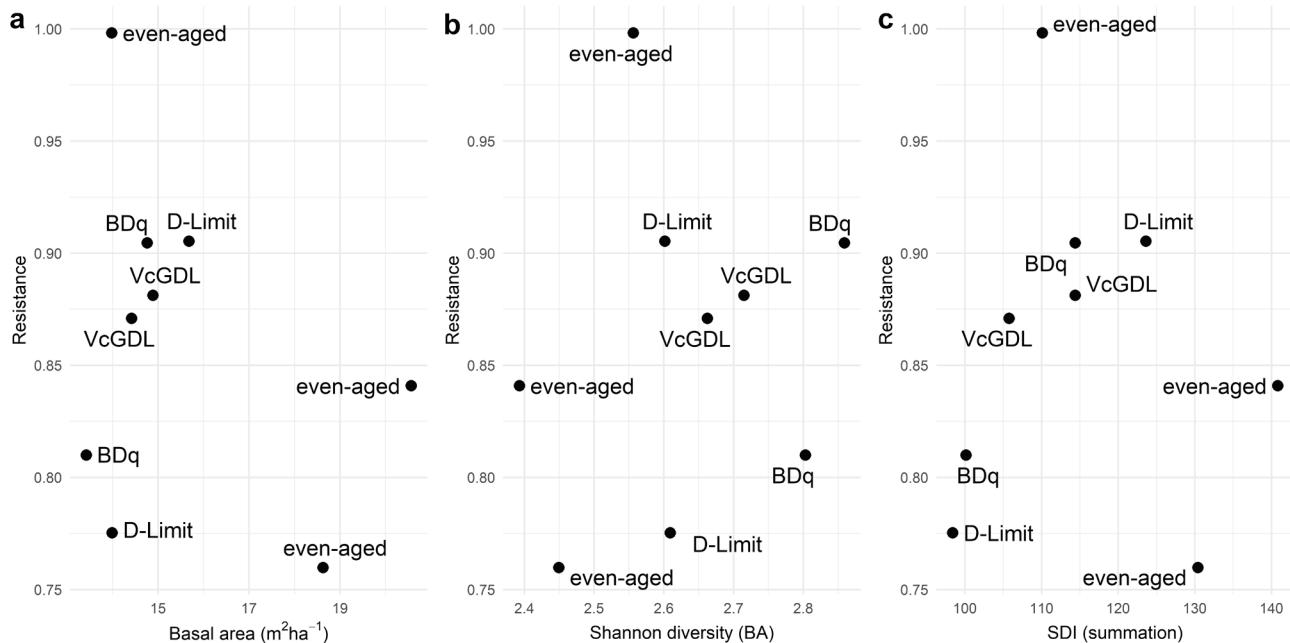


Fig. A1. Net loss (stand resistance) from Hurricane Ivan (2004) regressed against pre-Hurricane Ivan inventory basal area ($\text{m}^2 \text{ha}^{-1}$), quadratic mean diameter, Shannon's diversity index (calculated using BA), and stand density index.

method (Stand 115) was the most resilient (resilience = 0.79) and the DLC method was least resilient (Fig. 3). Curiously, DLC Stand 83 decreased in basal area between the two measurement periods following disturbance, resulting in a negative value of resilience (-0.13). The second DLC replicate (Stand 125) was the least resilient stand of the uneven-aged stands (resilience = 0.19). Of the even-aged stands, resilience was highest in even-aged Stand 3 (0.66) and lowest in even-aged

stand 1 (0.19 respectively).

4. Discussion

Overall, we did not find any significant difference between resistance and resilience capacities of even-aged and uneven-aged stands. There was considerable variability among the three even-aged stands as well as

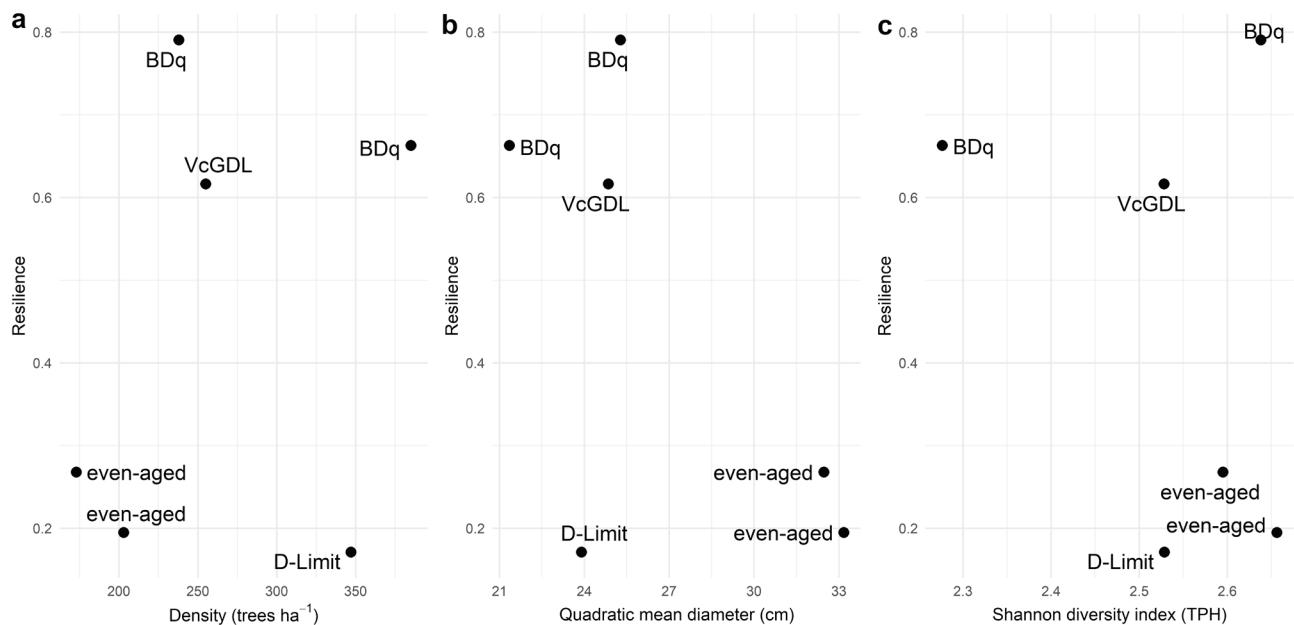


Fig. A2. Stand resilience (basal area recovery) from Hurricane Ivan (2004) regressed against post-Ivan stand density, quadratic mean diameter, and Shannon's diversity index (calculated using TPH). Stands where resilience could not be calculated (VC-GDL stand 2), stands that experienced disturbance following Hurricane Ivan (DCL stand 2), and stands that experienced minimal damage (even-aged stand 3) are not shown.

the three methods used to regulate stocking in uneven-aged stands. In addition, there were several stand-level structural relationships that corresponded with resistance and resilience across management regimes. Irrespective of management regime, we found that stand density increased stand resistance while tree size diversity (Shannon diversity index based on density of size classes) and QMD had the opposite effect. Stand resilience, however, was negatively related to post-hurricane basal area and pre-hurricane SDI (summation) and positively related to post-hurricane size class diversity (Shannon diversity index based on basal area of size classes).

Tree size, stand density, and diameter distribution are commonly reported to affect stand resistance to wind (Kupfer et al. 2008, Mitchell 2013, Taylor et al. 2019, Zampieri et al. 2020). At the individual tree level, the interaction between stem diameter and tree height play an important role in predicting the probability of stem breakage and uprooting. Increases in diameter are directly related to the force required to break stems (Mitchell 2013, Gardiner 2021). The stands at Escambia Experimental Forest all survived the impact of Hurricane Ivan enduring high winds and heavy rainfall with resistance appearing to be related to the density of large trees at the upper tail of stand diameter distributions. All stands were naturally regenerated and likely developed at high densities which resulted in increased tree slenderness, an important predictor of tree resistance to wind (Peltola 2006; Garms and Dean, 2019). The uneven-aged stands had similar numbers of trees 30 cm dbh and larger immediately before the storm. But the number of trees 40 cm dbh and larger varied among stands and was consistent with (and inversely related to) basal area lost in each stand. Similarly, nearby stands recently harvested to a shelterwood density, with a residual average diameter approximately 40 cm dbh, were largely devastated. Although speculative, this observation supports the relationship between tree size and susceptibility to wind as well as enhanced risk to wind damage following harvesting activities (Hale et al., 2012; Hanewinkel et al., 2014; Rutledge et al., 2021; Gardiner 2021). The differing time periods between inventories in our data prevented a more robust investigation into In addition to diameter, wind loading in trees is directly related to tree height. Approximate canopy height was estimated to be lower in even-aged stands which, given the similarity in site productivity, is likely related to differences in stand age. As a result, even-aged stands were likely more resistant than their uneven-aged

counterparts. Nevertheless, this effect is confounded by the influence of structural heterogeneity that existed in uneven-aged stands as a result of management.

The response of individual trees to wind is also affected by stand structure and management (Hale et al., 2012). After a major storm in Switzerland, Hanewinkel et al. (2014) observed less damage in uneven-aged stands compared to even-aged stands and that the damage caused by the storm decreased as stand structure more closely approximated the reverse J-shaped diameter distribution. These patterns seem to hold true in our study stands as well. Though reverse-J diameter distributions are purely an idealized stand structure in managed stands, the presence of this distribution reflects stand structural heterogeneity. Regardless of management regime, stands more closely adhering to an inverse J structure endured the storm better than stands featuring a homogenous stand structure. Considering that an inverse-J structure represents a larger proportion of trees in smaller diameter classes, the relationship between stand structural heterogeneity and stand resistance remains a function of the proportion of large trees in a stand. Of the uneven-aged stands examined, three stands have only received a single harvesting treatment and, thus, haven't developed multiple cohorts. Two-cohort stands often develop more similarly to single-cohort stands than multi-cohort stands due to the dominance of the older cohort (Oliver and Larson, 1996). While stand structure was more heterogeneous in uneven-aged stands compared to even-aged stands, all stands had a relatively high level of structural diversity (Shannon's $H > 2$) which may have influenced the comparison of stand resistance to wind between even- and uneven-aged management. In addition, structural diversity (Shannon's H) appears to be directly correlated to stand density or basal area depending on the method of calculation in our study. Though Shannon's diversity index should be independent of stand density (Lexerød and Eid, 2006), the similarity in stand origins and relatively limited duration under active uneven-aged regulation may have contributed to this relationship. As such, stand density, and its associated influence on tree diameter, likely played a considerable role in the resistance of stands to Hurricane Ivan.

Ecological resilience is intimately linked to stand resistance. Simply put, the survival (resistance) of stand features existing prior to the disturbance directly relate to the ability of a stand to return to pre-disturbance conditions. For example, Brang (2001) observed that the

survival of midstory and understory trees promoted recovery of forests in the European Alps affected by wind. We found that stand resilience, as indicated by basal area increment recovery, was lower in stands that contained a high amount of basal area compared to stands with lower basal area post-hurricane. One possible explanation is that the cumulative basal area increment of smaller diameter trees, and by inference younger trees or trees in a subordinate canopy position, have not yet reached the basal area increment of the larger diameter trees that were removed by the storm. This is also supported by the relationship between stand density index pre-hurricane and resilience where increased competition prior to Hurricane Ivan resulted in a slower recovery of basal area increment in the following period. Increased stand resilience to disturbance in uneven-aged stands is hypothesized to be a function of the presence of vigorous younger age classes following disturbance that will quickly reoccupy growing space. In our study, Shannon's diversity index was positively related with stand resilience following disturbance, supporting this hypothesis. However, the relationship between Shannon's diversity index was only important when calculated using basal area, suggesting that competition between individuals also influences stand resilience. Longleaf pine can remain in the grass stage, allocating photosynthate primarily to root production for as long as ten years. This, combined with characteristic sporadic cone production may have muted the resilience response in uneven-aged stands, particularly in stands that had only received one entry (Brockway et al. 2006). In addition, residual crown damage from the storm or falling neighboring trees may have slowed the growth of residual trees.

The chance occurrence of a major storm event affecting a set of long-term studies presents a unique and rare opportunity to evaluate resistance and resilience in stands managed under different silvicultural regimes. However, our natural experiment is based on minimal replications of stand type and is therefore limited in statistical power. In addition, variation in inventory periods in stands following Hurricane Ivan prevented a more robust analysis regarding dimensional diversity and storm resistance or resilience (*sensu* Bauhaus et al. 2017). Thus, the results of this study should be interpreted with a degree of caution. Though it is useful to evaluate differences in silviculture regimes and regulation methods on a similar site, the effect of site and other landscape factors cannot be overlooked (Mitchell 2013; Peterson and Cannon, 2021; Rutledge et al. 2021).

Estimates from the volume salvaged and the timber damage assessment following the hurricane indicate the storm removed approximately-five-to-fifteen years of growth in these stands. In other words, about one regularly scheduled cutting cycle harvest in uneven-aged stands was lost as a result of the storm. In essence, the damage created by the storm and the subsequent salvage activity removed sawtimber volume more or less equivalent to that which the foregone cutting cycle harvest would have removed. Evidence suggests that the storm removed trees more in the sawtimber size classes, again which is what would be expected in any of the three uneven-aged stand regulation methods.

5. Conclusions

Management regime had little impact on resistance or resilience. However, much of this could be attributed to the pre-hurricane structural variability of our stands. Stand resistance was largely dictated by the interplay between stand density and tree size. Stands featuring a high pre-storm density of smaller (pulpwood and chip-n-saw size) trees were generally more resistant to damage than low-density stands with greater numbers of larger (sawtimber size) representation. Collectively, this suggests that truncating even-aged rotations, reducing maximum tree size class in selection systems, or increasing the proportion of stocking in smaller size classes, would improve hurricane resistance. Despite the lack of statistical significance, our findings of improved hurricane resilience with size class diversity indicate that uneven-aged stands have the potential to recover faster from hurricane damage

than even-aged stands. Thus, uneven-aged management may present a better option for land managers seeking to enhance forest resilience in hurricane prone areas. Unfortunately, promoting hurricane resistance and resilience may come to the detriment of other important management objectives in the longleaf pine ecosystem including timber production, habitat for the red-cockaded woodpecker (*Picoides borealis*), or fire resistance. Consequently, the value of widely adopting a hurricane centric management strategy at the stand level is questionable. At the landscape level, a strategic combination of even- and uneven-aged silvicultural regimes may contribute to high economic and ecological gains by reducing the amount of wind-exposed timber while providing ecosystem services associated with the longleaf pine woodlands.

CRediT authorship contribution statement

A.D. Polinko: Methodology, Formal analysis, Writing – original draft, Writing – review & editing. **J.L. Willis:** Data curation, Writing – original draft, Writing – review & editing. **A. Sharma:** Writing – original draft, Writing – review & editing. **J.M. Guldin:** Conceptualization, Formal analysis, Writing – original draft, Writing – review & editing.

Declaration of Competing Interest

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

Data availability

Data will be made available on request.

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Appendix A

[Fig. A1](#).[Fig. A2](#).

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