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**RESEARCH ARTICLE**

# Fire, insect and disease-caused tree mortalities increased in forests of greater structural diversity during drought

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## Abstract

1. Structural diversity is an emerging dimension of biodiversity that accounts for size variations in organs among individuals in a community. Previous studies show significant effects of structural diversity on forest growth, but its effects on forest mortality are not known, particularly at a large scale.

2. To address this knowledge gap, we quantified structural diversity using stem structural diversity (SSD) based on both tree diameter and height. We obtained U.S. Forest Service Forest Inventory and Analysis (FIA) data from over 2400 plots across southcentral U.S. forests that have suffered a recent drought. Using data from multiple sampling times, we calculated SSD and compared the relative importance of SSD, species diversity, functional diversity and other stand attributes in determining tree mortalities caused by fire, insects and diseases. We also used FIRETEC, a physics-based fire model, to test the effect of SSD on canopy consumption by fire.

3. Our results showed that (1) SSD was positively associated with tree mortalities caused by all three disturbances; (2) species richness was negatively associated with insect- and disease-caused mortalities; (3) functional diversity was negatively associated with fire- and disease-caused mortalities and (4) more phylogenetically related species had more similar mortality rates by insect and disease but not fire. Moreover, the FIRETEC model showed increasing canopy consumption by fire in stands with greater SSD.

4. Together, the different tree mortalities during drought associated with SSD more consistently than the other biodiversity metrics were evaluated.

5. *Synthesis.* Our results suggest that SSD could be considered in modelling forest dynamics and planning management to sustain forest health under disturbances.

**KEYWORDS**
forest health, plant population and community dynamics, plant–climate interactions, plant–herbivore interactions, plant–pathogen interactions, stand structure, tree mortality

# 1 | INTRODUCTION

Warm temperatures, superimposed on low precipitation, intensify drought magnitude and can cause severe tree mortality (Brodribb et al., 2020), which could be further exaggerated by fire, insect and disease disturbances. Drought can increase fire severity by decreasing fuel moisture (Holden et al., 2018; Littell et al., 2016; Ma et al., 2021) and contributing to greater fuel loads, that is, drought-induced leaf-off events (Ruthrof et al., 2016). This increased fire severity often leads to greater tree mortality (Stephens et al., 2018). Moreover, insect outbreaks following drought are widely observed (Anderegg et al., 2015; Canelles et al., 2021; Jactel et al., 2019), and several types of insects (especially bark beetles) preferentially attack stressed trees or trees of specific characteristics, for example, large size (Koontz et al., 2021; Stephenson et al., 2019; Tai et al., 2019). Drought–pathogen interactions may also amplify tree mortality (Field et al., 2020; Wood et al., 2018). Therefore, it is crucial to understand variations in these tree mortalities across different stand conditions to improve projection of forest dynamics and management of forest resources under drought. As a critical stand condition, forest biodiversity affects tree mortality during drought as diverse forest ecosystems may be more resilient and resistant to disturbances (Jactel et al., 2021).

Forest biodiversity can be quantified by a range of metrics, representing different perspectives (e.g. species, function), and to that end, structural diversity is an emerging metric from a structural perspective. It estimates niche partitioning from variation in size, shape and location of organs (in this case, the stem and canopy) among individuals (LaRue et al., 2019). For example, structural diversity can be quantified by stem structural diversity (SSD) that is defined in a two-dimensional space of diameter at breast height (DBH) and height (Figure 1), where the diversity is the mean distance of every individual in a sampling unit to the centroid of all individuals. Stands with low structural diversity (Figure 1a) had a shorter mean distance of each individual to the centroid than stands with high structural diversity (Figure 1b). In general, the more uniform the stand, the lower the structural diversity. Forest management based on structure diversity achieves increasing interests (Palik et al., 2021), and recent advances in vegetation models also focus on detailed representation of structural diversity when simulating forest dynamics (Fisher et al., 2018). The above attentions on structural diversity stem from its significant effects on forest productivity in tropical (Ali et al., 2019), sub-tropical (Ali & Yan, 2017), temperate (Gough et al., 2019; Liang et al., 2007; Ullah et al., 2021) and boreal forests (Lei et al., 2009). Thus, structural diversity is also proposed to be a better biodiversity metric to study forest dynamics than other commonly used metrics (Mensah et al., 2020). Notably, although Liang et al. (2007) showed significant structural diversity effects on forest mortality, potential variation in the effects on mortality by different causes remains poorly understood.

Greater biodiversity is generally believed to mitigate tree mortality given that it facilitates ecological niche partitioning among individuals to improve availability and sharing efficiency of resources
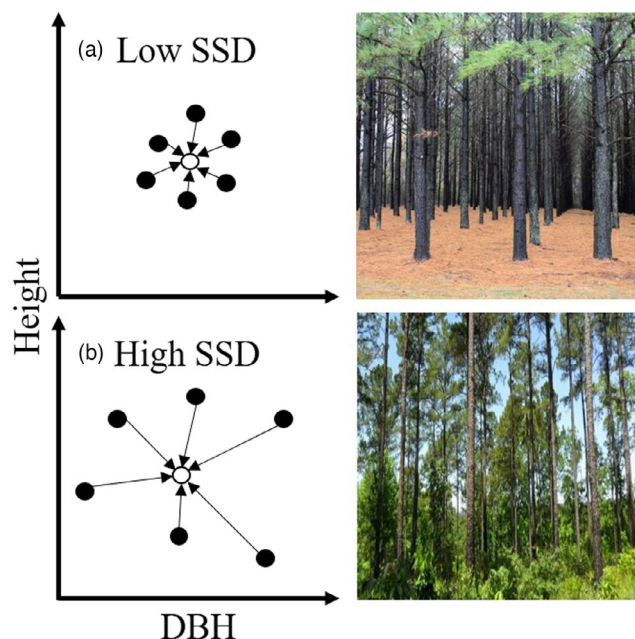


**FIGURE 1** Conceptual diagrams and related field photos of the comparison between loblolly pine stands of low (a) versus high (b) structural diversities. The conceptual diagram is based on a two-dimensional space defined by tree DBH and height. Each black point in the diagram represents DBH and height of an individual tree, and each empty point represents the centroid of all individuals in a sampling unit based on their average DBH and height. Each arrow represents the distance from the location of an individual to the centroid

among neighbours (Liang et al., 2015; Reich et al., 2012), particularly when resources become limited, for example, during drought. However, structural diversity effects on tree mortality might be mixed. On the one hand, greater structural diversity may alleviate tree mortality due to increased tree vigour facing insect and disease disturbances. The increased vigour results from enhanced niche partitioning for resource uptake in stands of greater structural diversity (Palik et al., 2021). For example, greater structural diversity facilitates multi-layered canopies (Gough et al., 2019), potentially enhancing light interception particularly for understorey individuals, such as saplings, though a reduced light interception is also proposed by Ali and Yan (2017). Meanwhile, greater structural diversity may interrupt fuel continuity, reducing fire spread and fire-induced mortality (Koontz et al., 2020). On the other hand, greater structural diversity may increase tree mortality because fuel continuity is potentially increased by more ladder fuels in stands of more diverse structure, leading to canopy fire (Hood et al., 2018). Greater structure diversity may also increase occurrences of insects and diseases caused by more colonization choices and concentration of insect pheromones in these stands (see more details in Section 4). Therefore, there is a critical need to examine the contrasting effects of structural diversity on tree mortality, particularly using large-scale forest survey data across extensive spatial areas and a broad variety of woody species.

Focusing on the increase in tree mortality under drought conditions, we quantified effects of structural diversity given the other factors related to forest biodiversity (e.g. species richness, functional diversity), stand attributes (basal area, stand origin, stand age), tree morphological characteristics (e.g. tree height) and drought magnitude. We also considered the phylogenetic relatedness of the wide variety of species used in our analysis. We hypothesized that structural diversity is a significant predictor of fire-, insect- and disease-caused mortalities. Moreover, we used a physics-based fire model to test whether canopy consumption by fire increased with greater structural diversity.

## 2 | MATERIALS AND METHODS

### 2.1 | Tree mortality data

We compiled data from the U.S. Forest Service Forest Inventory and Analysis (FIA) programme (https://www.fia.fs.fed.us/) for the state of Oklahoma, which experienced a severe drought from late 2010 through mid-2015 (Basara et al., 2019). We extracted the data from FIA plots that experienced fire, insect or disease disturbances given two reasons: (1) In the other plots, the potential low mortality could be caused by factors unrelated to stand conditions, such as geographical barrier for insect and disease spread. Note that our study focused on explaining factors in tree morality under the disturbances instead of occurrences of these disturbances; (2) including the other plots could make a complicated statistical analysis owing to zero-inflated datasets (Zuur et al., 2009). Individuals used

in our analysis were measured at least twice (i.e. before and during or after the drought) and alive in the first measurement to make sure mortality occurred in the study period. We used a method similar to Bradford and Bell (2017) to confirm that initial diameter and diameter change were reasonable (i.e. tree diameter changes less than −2.5 cm or greater than 12.5 cm were carefully inspected and excluded if other data, such as tree heights, species codes, etc., appeared suspect or inconsistent). Our analysis included 25,099 trees (including 2954 dead trees) from 2439 plots (called subplots in FIA; plot radius is ~7.5 m) (Figure 2). The mortality cause of each dead tree is available from the FIA database (Burrill et al., 2018). Of the dead trees used in this study, 37.7% were coded as disease-caused mortality, 14.7% were coded as fire-caused mortality and 4.1% were coded as insect-caused mortality. The remaining dead trees (43.4%) were coded as dying from competition or extreme weather (e.g. wind damage).

### 2.2 | Structural diversity

Multiple structural measures were used to calculate structural diversity. For example, structural diversity can be calculated by canopy measurements with ground-based Lidar (Gough et al., 2020; LaRue et al., 2020), but the limited availability of Lidar data impedes application to understanding large-scale forest dynamics. Commonly available measures, for example, diameter at breast height (DBH) and height, have also been used to calculate structural diversity, but these metrics only focus on variation in one dimension (Storch et al., 2018). Given different eco-physiological functions of DBH and
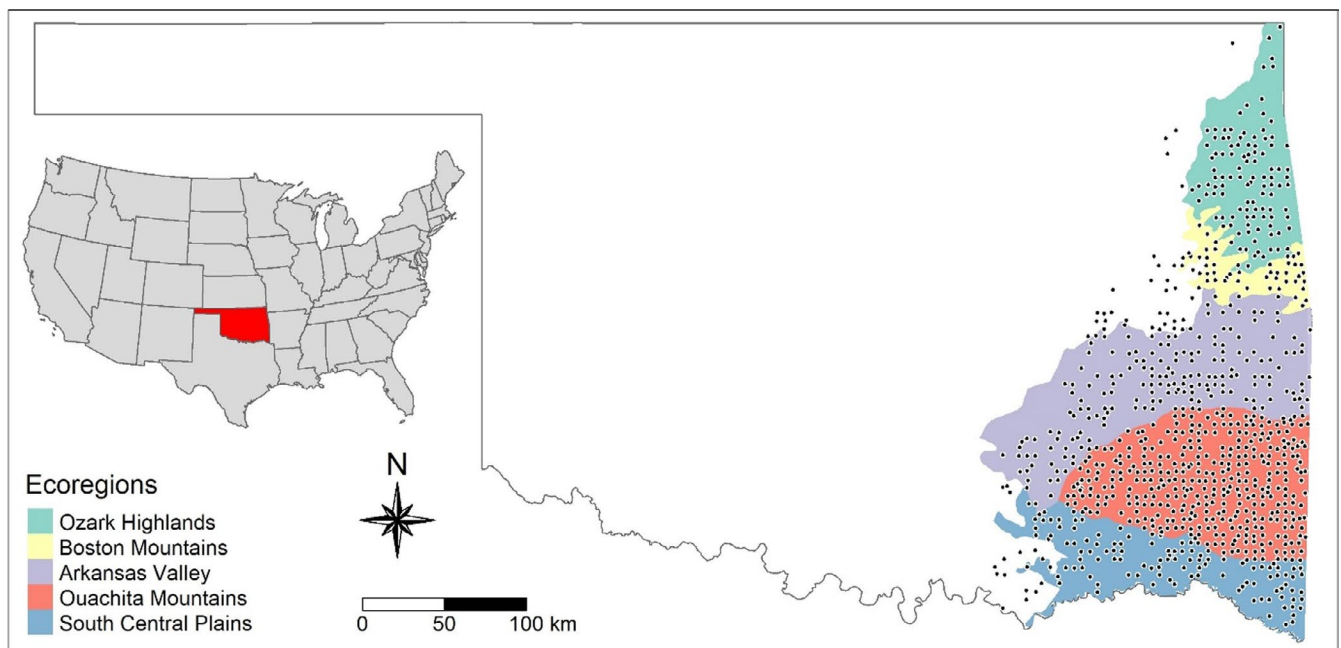


**FIGURE 2** Distribution of FIA plots in Oklahoma used in this study. Plots cover five ecoregions characterized by forest ecosystems with a broad range of species, drought magnitudes and stand conditions. Note that a few plots outside the above ecoregions were used because they are still forested plots measured in the FIA programme. The inset map denotes the location of Oklahoma (highlighted in red) in the contiguous U.S.

height, both measures should be considered in analysing structural diversity effects. However, potential collinearity between DBH and height makes it difficult to include both factors in a single model. Therefore, we introduce a metric, termed stem structural diversity (SSD), to estimate structural diversity simultaneously considering DBH and height. SSD is calculated similarly to functional dispersion, which estimates functional diversity with multiple functional traits (Laliberté & Legendre, 2010). SSD calculates the mean distance of every individual in a sampling plot to the centroid of all individuals in a two-dimensional space defined by DBH and height as explained above in Figure 1.

## 2.3 | Other predictors of tree mortality

Predictors of tree mortality consisted of variables at both individual tree and stand levels. At the individual tree level, we used tree height as a predictor of tree mortality. We calculated stand-level predictors per FIA subplot because trees in one subplot likely share the same conditions (e.g. disturbance history, soil characteristics, microclimate) (Burrill et al., 2018). The stand-level predictors include basal area, stand age, stand origin, species diversity, functional diversity, structural diversity and drought magnitude. Stand age was used as a predictor because physiological functions (e.g. photosynthesis rates) decline as trees age, resulting in increased susceptibility to insect and disease infestation which can contribute to eventual mortality. Meanwhile, because structural diversity may vary with age, it is important to test the correlation between age and structural diversity when understanding structural diversity effects on tree mortality. Note that tree age is not measured in most trees, so stand age (or age of dominant trees) was used in previous studies based on large-scale survey data (Luo et al., 2020). We also included stand origin (i.e. natural or planted stand) to consider management effects on forest dynamics. Species diversity was calculated as species richness, that is, number of species per unit area. Note that Shannon's Index was also considered, but it did not improve model fitting. Functional diversity was calculated as functional dispersion using the R package 'FD' (Laliberté et al., 2015) and based on six functional traits: specific leaf area, leaf carbon: nitrogen ratio, wood density, leaf phenology type (i.e. evergreen vs. deciduous), maximum height and nitrogen fixation ability. These traits are related to plant growth under drought (Peìrez-Harguindeguy et al., 2013; Zhang et al., 2021). Other drought-related traits were not considered in our study, such as water potential value inducing 50% loss of maximum hydraulic conductance (P50), given their limited availability for the wide variety of species studied. These functional trait data were extracted from the TRY database (Kattge et al., 2020). When extracting data, we first considered trait data from the study region. For species or traits with missing values, we expanded to data sources outside the above region. We calculated stem structural diversity using a similar approach to functional dispersion based on stem height and diameter (diameter at breast height). Basal area was calculated as the cross-sectional area of tree stems per area. We used mean monthly

climate water deficit (CWD) between dates of two repeated forest surveys to quantify drought magnitude. Higher values of CWD indicate increased drought stress on plants (Stephenson, 1998). CWD is suggested to be a better indicator of plant drought stress than other indices, such as SPEI and PSDI (Zang et al., 2020). CWD was extracted from the TerraClimate database (http://www.climatologylab.org/terraclimate.html) (Abatzoglou et al., 2018).

## 2.4 | Physics-based fire behaviour model simulations

We employed FIRETEC, a physics-based computation fluid dynamics model of fire behaviour and fire–atmosphere interactions, to test the effect of SSD on canopy consumption by fire. FIRETEC incorporates the macroscale effects (~1–10 m) of combustion, radiation, convective heat transfer and aerodynamic drag. A detailed description of the physical and chemical formulations of FIRETEC can be found in Linn and Harlow (1998) and Linn et al. (2002). We chose FIRETEC to perform this analysis because it has been used to model canopy-fire spread (Hoffman et al., 2016), as well as evaluate sensitivities of fire spread to perturbation in atmospheric conditions (Jonko et al., 2021) and vegetation structure (Atchley et al., 2021). We used the model to simulate fire spread through 10 forest stands. Each stand has 1894 loblolly pine trees spread across a 400 m × 400 m area. The DBH of trees in a stand were simulated using normal distributions with a same mean (40 cm) but different standard deviation (from 1 to 10) among different stands. Thus, the 10 stands had the same mean tree size but different structural diversity. Tree height, height to canopy and crown radius of each tree were then calculated using allometric equations and parameter values for loblolly pine in southern forests of the United States (Keyser, 2020). Allometric equations are widely used to quantify relationship between different tree organs for a wide variety of species, thus stand structure can be well represented in our simulation. Details of these input data can be found in Figure S1. All other model inputs, including surface fuel characteristics, surface and canopy fuel moisture, and initial wind conditions, were consistent among the stands.

## 2.5 | Statistical analyses

We used generalized linear mixed models to analyse tree mortality (dead tree = 1, alive tree = 0) caused by fire, insect and disease. We first standardized the predictors (average = 0 and SD = 1) to make slopes of these predictors comparable in the models. To remove multicollinear predictors, we used the variance inflation factor (VIF) >10 as a standard to identify predictors with strong multicollinearity (Table S1; James et al., 2013), and the VIF values were calculated using R package 'CAR' (Fox & Weisberg, 2019). We also tested quadratic terms of the quantitative factors studied, but all the terms were not significant. The model formulation of fire-, insect- and disease-caused mortalities of the $i$th tree of

the $j$th species in the $k$th plot are shown in Equations 1–3, respectively. Because multiple species were included in our models, we accounted for dependence (e.g. phylogenetic relatedness) among species by adding species (both phylogenetic and non-phylogenetic components) as random factors. There are 26 species in total covered by our study: 24 were already in Smith and Brown (2018), and the other two were added to the Smith and Brown phylogeny at the basal node of co-genera species. The derived phylogeny is ultrametric.

$$M_{fire,i,j,k} = HT_{i,j,k} + BA_k + SO_k + SD_k + FD_k + SSD_k + Dry_k + \varepsilon_j, \quad (1)$$

$$M_{insect,i,j,k} = BA_k + SO_k + SD_k + FD_k + SSD_k + \varepsilon_j, \quad (2)$$

$$M_{disease,i,j,k} = HT_{i,j,k} + BA_k + SA_k + SO_k + SD_k + FD_k + SSD_k + Dry_k + \varepsilon_j$$
$$(3)$$

where $M_{fire,i,j,k}$, $M_{insect,i,j,k}$ and $M_{disease,i,j,k}$ were mortality probability of the $i$th tree of the $j$th species in the $k$th plot caused by fire, insect and disease, respectively. $HT_{i,j,k}$ was the tree height of the $i$th tree of the $j$th species in the $k$th plot. $BA_j$ was the basal area of the $j$th plot. $SA_j$ was the stand age of the $j$th plot. $SO_j$ was the stand origin of the $j$th plot. $SD_j$ was the stand diversity of the $j$th plot. $FD_j$ was the functional diversity of the $j$th plot. $SSD_j$ was the stem structural diversity of the $j$th plot. $Dry_j$ was the drought magnitude of the $j$th plot. $\varepsilon_j$ was the residual for the $j$th species and included both phylogenetic and non-phylogenetic relatedness.

Assumptions of linearity, equal variance and normality were examined by the residual plots along the predictors, fitted values and the normal quantile plot, respectively. We built the multiple logistic regression models with the random effects using R package 'PHYR' (Li et al., 2020), and all analyses were considered significant at $\alpha = 0.05$. We used a general additive model to analyse the relation between stem structural diversity and percent of canopy consumptions. The model was built by R package 'MGCV' (Wood, 2021).

## 3 | RESULTS

### 3.1 | Significant factors contributing to fire-, insect- and disease-caused mortalities

Our fire model had explanatory power (or $R^2$) of 24.8% and prediction power (or AUC, area under curve) of 84.7%. SSD, basal area and CWD were positively associated with fire-caused mortality, but plots with greater tree height and functional diversity had significantly less mortality (Figure 3a). The $R^2$ and AUC of the insect model were 44.9% and 94.9%, respectively. Higher SSD increased the tree mortality, but greater species richness and basal area decreased the tree mortality (Figure 3b). The $R^2$ and AUC of the disease model were 19.5% and 79.8%, respectively. Higher SSD, basal area and stand age increased the tree mortality, but greater species richness and functional diversity decreased the mortality (Figure 3c).

### 3.2 | Phylogenetic and non-phylogenetic components of random effects

Tree mortality caused by fire did not show any evidence for the phylogenetic component of random intercepts of species (estimated variance ≈ 0, $p = 1$, Figure 4a), suggesting that the variation in fire-caused mortality was largely independent with their evolutionary history. The non-significant phylogenetic component is shown in Figure 4b where the variation in the fire-caused mortality was relatively similar among species, instead of being clustered in specific species group. On the other hand, both insect- and disease-caused mortalities had a strong phylogenetic component of random intercepts of species (estimated variances = 1.9 and 0.3, respectively, both $p < 0.001$, Figure 4a) suggesting that closely related species had similar mortality. The significant phylogenetic component of insect- and disease-caused mortalities is shown in Figure 4b where both *Pinus* species exhibited higher mortality by insects, and *Quercus* species were subject to higher mortality by disease than other species.

### 3.3 | Effect of stem structural diversity on canopy consumption by fire

FIRETEC simulation yielded a nonlinear relationship between stem structural diversity and canopy consumption by fire. The consumption decreased slightly at lower SSD values and then increased at higher SSD (Figure 5a). The smoother for structural diversity used in the general additive model was significant ($p = 0.0002$, Figure 5a), and the model explained 89.6% variation in consumption. Figure 5b shows the visualizations of fires simulated by FIRETEC for two of the 10 simulated stands. Stand 1 had the lowest SSD value, while stand 10 had the highest SSD. Compared to stand 1, stand 10 had more intense canopy fire and larger burning area at the same time during the simulation.

## 4 | DISCUSSION

### 4.1 | SSD was positively associated with tree mortality caused by all three disturbances

During the recent drought in Oklahoma, our study showed that fire-caused tree mortality increased in forest stands with higher SSD. Higher SSD indicates greater variation in stem size across individuals in a forest stand, and the high variation may lead to an increase in ladder fuels (or fire ladders) facilitating canopy fire (or torching) that directly causes tree mortality (Hood et al., 2018). In contrast, higher structural diversity, derived from Normalized Difference Vegetation Index (NDVI), was associated with reduced fire-induced tree mortality possibly by interrupting fuel continuity in Koontz et al. (2020). Note that we quantified structural diversity using different measures than Koontz et al. (2020). Stem height and diameter used in our study may be a more appropriate measure of structural diversity
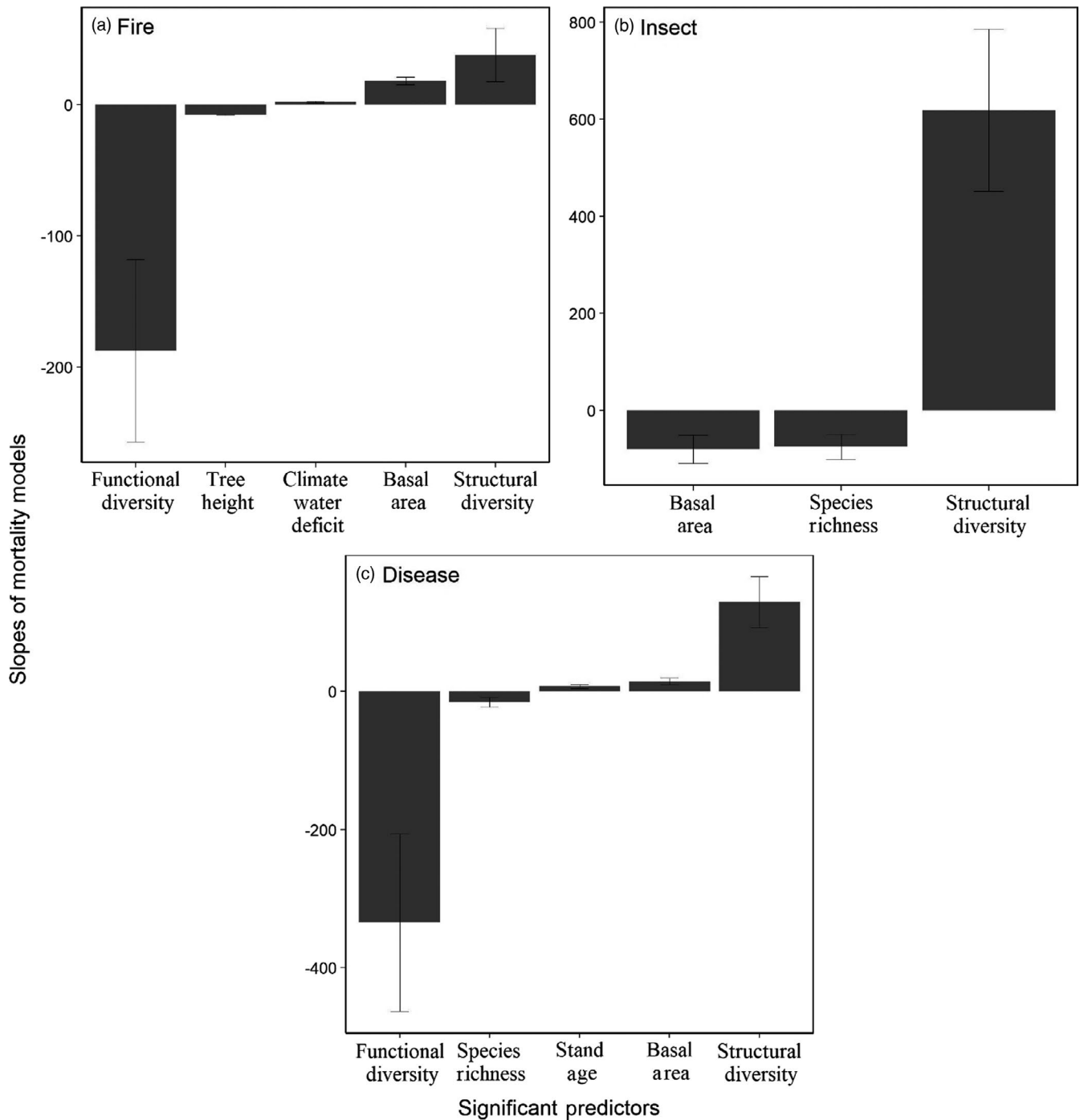
**FIGURE 3** The slopes of significant predictors ($p < 0.05$) in the models of fire- (a), insect- (b) and disease (c)-caused mortalities. Error bars denote standard errors of the predictor slopes

than NDVI because NDVI is more sensitive to biochemical changes (e.g. chlorophyll content, foliar nitrogen content) than structural ones (e.g. leaf area index). For instance, Gamon et al. (1995) showed that NDVI was insensitive to structural changes particularly in stands of high leaf area indices. Furthermore, instead of detecting structural changes, some remote sensing-based vegetation indices were confounded by structure (Knyazikhin et al., 2013). Moreover, the above different SSD effects between our and previous studies may result from the nonlinear relation between SSD and canopy consumption.

When SSD is low, consumption decreased with increasing SSD that may lead to the observations in Koontz et al. (2020). However, with high SSD, there is a positive effect of SSD on the canopy consumption, leading to our observations of more fire mortality in stands with increasing SSD. Given these significant effects, SSD can be used to inform forest management to facilitate tree survival from fire. For example, thinning is widely used to mitigate fire impacts on forest growth by reducing stand density, partially due to its effect on fuel continuity (Stephens et al., 2018). In addition to stand density,
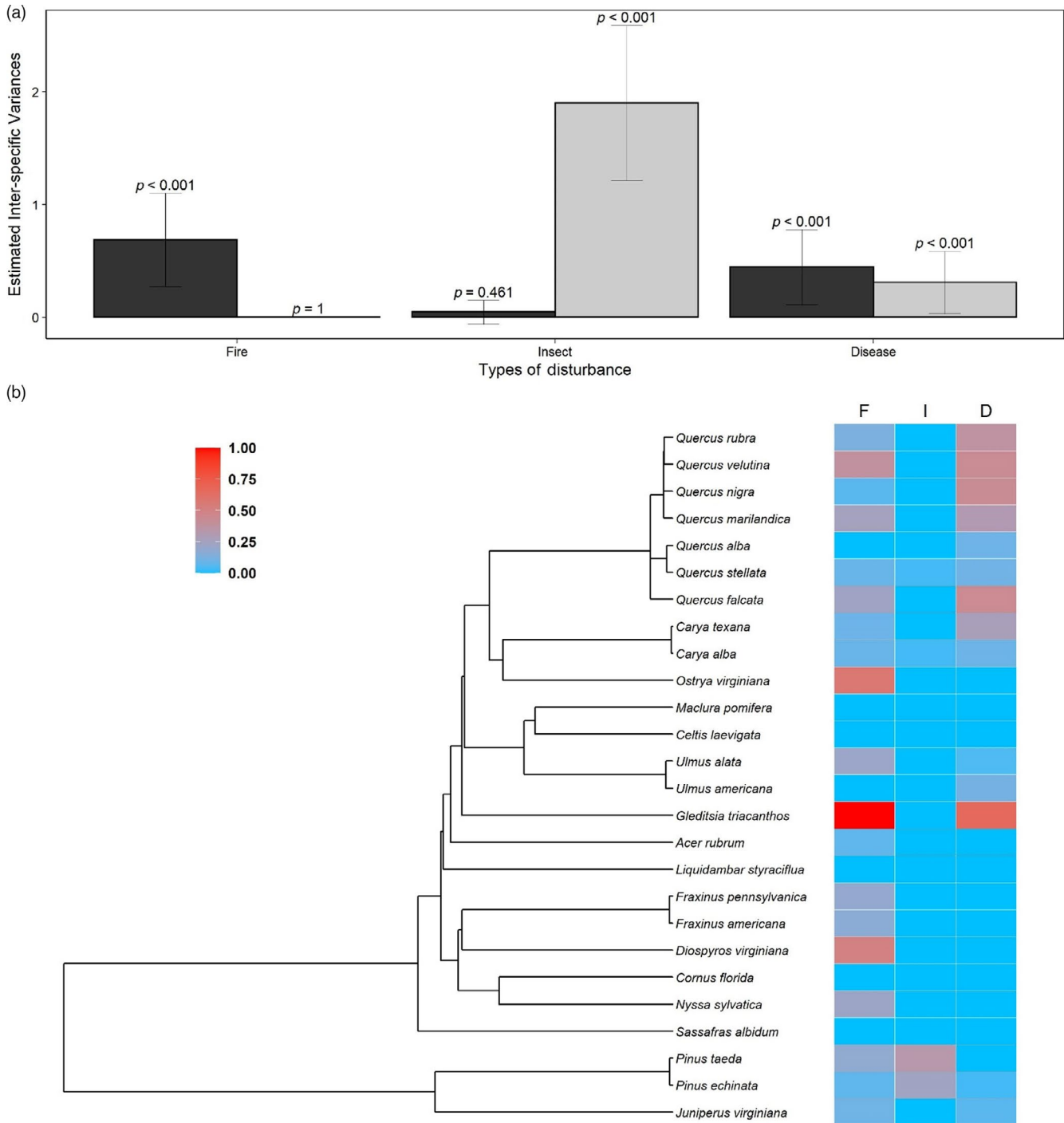
**FIGURE 4** (a) Estimated interspecific variances of mortality caused by the three disturbances. The black bars represent non-phylogenetic variance, while the grey bars represent phylogenetic variance. *p* values denote significance of the random effects based on likelihood ratio tests. (b) A phylogenetic tree of 26 species studied and their probabilities of mortality caused by F (fire), I (insect) and D (disease)

SSD could be another factor considered in thinning practices given the potential effect of SSD on the vertical spread of fire via ladder fuels. Neglecting the effect of ladder fuels potentially reduces the efficiency of forest management to facilitate forest adaptation to fire disturbance.

Our study also showed increased insect- and disease-caused mortalities in forests with higher SSD, and their reasons are likely

complex. First, the insect damage widely occurred on *Pinus* species in our study and this insect guild is dominated by bark beetles both numerically and in terms of impact. Notably, a parabolic relationship exists between age and tree susceptibility to bark beetles because young trees do not have thick enough phloem where beetles can establish, while old trees may have bark that is too thick to be colonized by beetles (Ylioja et al., 2005). Thus, both very young and very
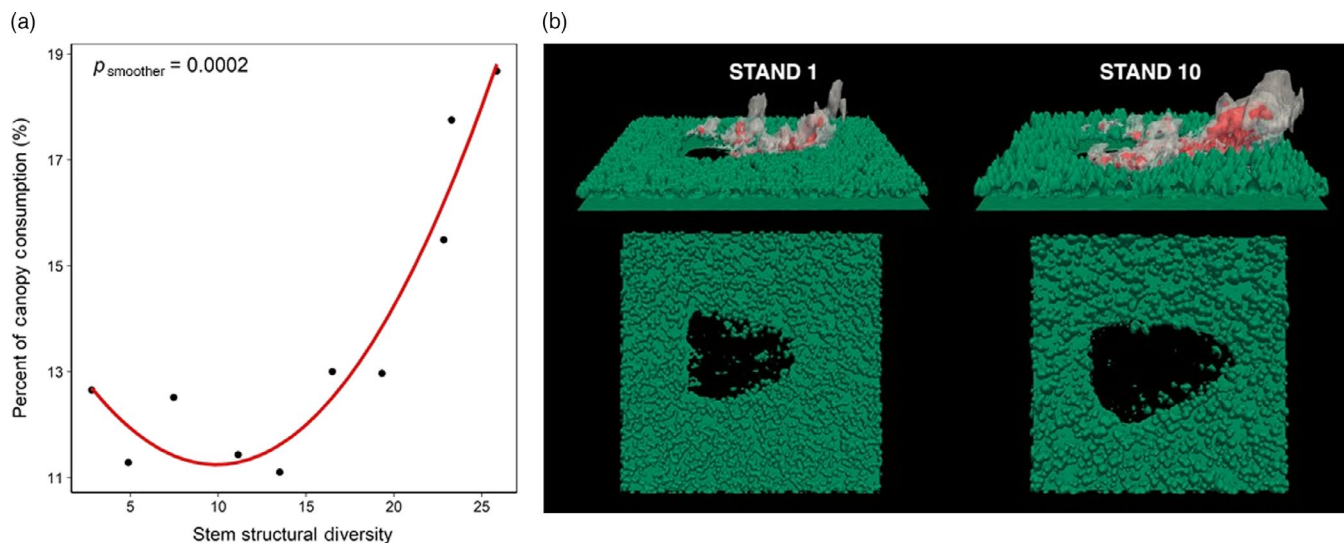
(a)



(b)



**FIGURE 5** (a) The nonlinear relation between stem structural diversity and percent of canopy consumed by fire. The regression line was fitted by a general additive model with span = 2.535, which was determined by the general additive model. (b) Visualizations of canopy fire and area burned in stands of the lowest (Stand 1) and highest (Stand 10) SSD

old stands may not be suitable for beetle establishment. Meanwhile, these stands were more uniform, that is, stands of low SSD were characterized by small (<10 cm) or large (>30 cm) mean diameter (Figure S2.A) and young (<40 year) or old (>100 year) stand age (Figure S2.B). In other words, low SSD stands may be less suitable to beetle establishment. Second, a higher SSD could reduce light transmittance to trees growing in the lower canopy (Ali & Yan, 2017), leading to light stress (Bourdier et al., 2016). Stressed trees tend be more susceptible to insects and pathogens than healthy ones (Coyle et al., 2015; Roberts et al., 2020); this pattern is well documented for tree mortality caused by both insects (e.g. *D. ponderosae* and *D. frontalis*) (Hood et al., 2016; Negrón et al., 2017) and diseases (Bendixsen et al., 2015; Costanza et al., 2020; McIntire et al., 2018). Third, there may also be a greater concentration of insect pheromones in forests with higher SSD where the different sized trees are barriers to wind. The limited wind likely reduces pheromone dissipation which can help facilitate insect outbreaks. For example, overstocked pine stands are more susceptible to *D. frontalis* attacks (Nowak et al., 2015) partially because pheromones emitted by adult beetles are not dissipated by prevailing winds (Thistle et al., 2004, 2011), thus lingering in the air and serving as attractants to other *D. frontalis*. The increased pheromone densities potentially lead to more insect attacks because some insects (e.g. secondary bark beetles) employ kairomone communication from host trees or other beetle species (Borden, 1989; Miller et al., 2011; Vité et al., 1972).

## 4.2 | Species and functional diversity were negatively associated with tree mortality

We found fire-caused tree mortality was negatively correlated with functional diversity but not species diversity quantified by species richness. Functional diversity was calculated by plant functional

traits that likely affect fuel flammability, such as specific leaf area, leaf carbon:nitrogen ratio and wood density (Alam et al., 2020; Grootemaat et al., 2015; Murray et al., 2013). A greater functional diversity of a stand increases the variation in fuel flammability, potentially leading to interruption of fuel continuity. This interruption could reduce fire-caused mortality due to the impacts of fuel quality on fire severity (Walker et al., 2020). Notably, given the strong correlation between remote sensing-based vegetation index (e.g. NDVI) and these functional traits (Asner et al., 2017), the aforementioned positive effects of NDVI-based diversity in Koontz et al. (2020) may result more from functional diversity than structural diversity.

The notion of increased mortality from insects (Jactel & Brockerhoff, 2007; Jactel et al., 2021) and disease (McCracken & Dawson, 1998) in forest stands with lower species and functional diversity is not new (Coyle et al., 2002). However, these effects are not straightforward, as many factors contribute to tree mortality, especially in a changing climate. For instance, the negative relationship between species richness and insect damage became less pronounced with increasing mean annual temperature (Poeydebat et al., 2021). However, we observed a significant negative effect of tree species diversity on insect-caused mortality using forest survey data measured during a drought period. Moreover, these effects may vary by species, for example, in contrast to preferred conifer species, the risk of bark beetle infestation for less preferred hosts is increased by higher species richness increases (Berthelot et al., 2021). The effects are also contingent on diet breadth of specific insects, for example, damage from specialist insects could be reduced in diverse stands owing to low host occurrence (Guo et al., 2019). Unfortunately, information on the specific insects causing damage is not available from the FIA dataset. Future studies could combine regular forest survey datasets with insect datasets to understand the effects of herbivore diet breadth (e.g. Guo et al., 2019) on tree mortality.

## 4.3 | Tree phylogeny influenced mortality caused by insects and diseases

Fire, insect and disease differentially impacted phylogenetic-related groups of trees. The fire impact was largely non-phylogenetic, and different trees' mortality rates were largely independent suggesting that closely related species did not suffer similar mortality rates. This result makes ecological sense because fire acts like a general 'herbivore' (Bond & Keeley, 2005) and affects all trees almost equally, particularly when there is high fire severity caused by drought exceeding fire tolerances of most species. Conversely, insect-caused mortality showed a strong phylogenetic influence, indicating that closely related trees had very similar insect-caused mortality rates. For example, we found the high insect-caused mortality in *Pinus* species (Figure 3a) which likely contributed to the model results where the majority of variance was the phylogenetic component. *Pinus* species are susceptible to bark beetles, and rates of bark beetle-caused mortality often increase when trees are stressed by drought (Huang et al., 2020; Negrón et al., 2009; Netherer et al., 2019). Unlike fire, insects tend to preferentially attack specific groups of plant species that likely have coevolved similar defensive responses over time (Jactel et al., 2021). Thus, it is not surprising that the phylogenetic component contributed to the majority of interspecific variation in insect-caused mortality.

While fire acts like a general 'herbivore' and insects are more host specific, disease seems to be in the middle of the gradient, with almost equal phylogenetic and non-phylogenetic components of interspecific variation in the disease-caused mortality. Both components were significantly different from zero, suggesting that some groups of trees responded independently regardless of their phylogenetic distances, while others' responses to disease showed a phylogenetic signal. Disease-caused mortality occurred mostly in *Quercus* species and *Gleditsia triacanthos* in our study (Figure 3a). Stressed and dying *Quercus* trees have been found to be attacked by *Biscogniauxia* fungi (Bendixsen et al., 2015; Freeman et al., 2019; Nugent et al., 2005), while *G. triacanthos* is known to be impacted by several fungal diseases (Bedker & Wingfield, 1983; Crowe et al., 1982).

## 5 | CONCLUSIONS

Manipulation of structural diversity has long been a consideration in forest management using variable retention and patch cutting as an alternative to clear-cutting (Franklin et al., 1997; Seymour et al., 2002). However, there can be lags in incorporating concepts into management practice (Fahey et al., 2018) caused by knowledge gaps in understanding effects of structural diversity on forest dynamics. These knowledge gaps are partially addressed by our study showing the SSD effects on different tree mortalities during drought. Our study suggests reducing SSD could contribute to multiple benefits to alleviate tree mortality, such

as constraining the formation of ladder fuels or facilitating wind spread to dissipate aerial pheromones. Notably, given the impact of aerial pheromones on secondary insects, SSD-based management may be effective to mitigate outbreaks of secondary insect under drought, particularly when intensifying drought leads to more pest damage (Jactel et al., 2012). Benefits realized by reducing SSD could be further examined to improve the understanding of structural diversity. Future studies could focus on variations in forest ingrowth and growth with SSD to achieve a more holistic understanding of structural diversity effects on forest productivity. Our results showed that drought was significantly related to the fire-caused mortality, but not to the other mortalities. It agrees with preliminary results from another study of our team suggesting non-significant direct effect of drought on forest growth, but significant indirect one through its effects on stand attributes, for example, structural diversity and basal area. The indirect drought effects are also found in Ouyang et al. (2021). Thus, there are still knowledge gaps for future studies related to mechanisms driving drought impacts on forest dynamics. There are other causes of mortality related to drought, for example, storm damage (Csilléry et al., 2017), that we did not evaluate. Storm damage could be also affected by structural diversity given its effects on wind speed, but this mortality cause has not been explicitly recorded in the FIA database. Thus, future studies could evaluate additional mortality causes to develop a better understanding of structural diversity effects on tree mortality. Finally, with advancing technology and increasing data availability, future studies could consider additional factors not included in our study to improve the understanding of tree mortality in a changing climate, such as structural diversity quantified by canopy measures using Lidar sensors (Gough et al., 2020; LaRue et al., 2020).

### CONFLICT OF INTEREST
None of the authors have a conflict of interest.

### AUTHORS' CONTRIBUTIONS
L.Z. designed the study and analysed the data; L.Z., D.R.C., D.L., and A.J. interpreted the results and wrote the first draft of this manuscript; A.J. conducted the modelling analysis with FIRETEC.

## PEER REVIEW

## DATA AVAILABILITY STATEMENT

Our study used forest survey data from the Forest Inventory and Analysis (FIA) programme of U.S. Forest Service. The forest survey data are publicly available from the FIA website: https://www.fia.fs.fed.us/.

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