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Influences of Structural and Species Diversity on Forest Resistance to Drought

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ABSTRACT

Biodiversity can enhance forest resistance to drought, but the forms of diversity involved and conditions under which diversity confers resistance remain unclear. We used Forest Inventory and Analysis (FIA) plot data to examine whether four variables—structural richness (variation in tree heights, stand density, canopy cover and/or spatial heterogeneity), species richness (number of tree species), structural evenness and species evenness—are associated with the resistance of net primary productivity to drought and whether these relationships change with drought severity and by ecoregion. Structural richness was positively associated and species evenness was negatively associated with resistance, but the strength of these relationships varied by ecoregion. Relationships between structural richness and resistance and between species evenness and resistance became stronger under more severe droughts, supporting the stress gradient hypothesis. Forest managers cannot readily change abiotic conditions but could increase structural richness and select certain species to enhance forest resistance to drought.

1 | Introduction

Biodiversity can enhance the resistance of forests to climate variability (Liu et al. 2022), yet whether such resistance arises due to species diversity or structural diversity remains unclear, as do the relative roles of richness versus evenness (Hordijk et al. 2023). One aspect of climate variability, drought, can be particularly problematic in forest ecosystems since drought can increase tree mortality and reduce tree growth, productivity and carbon sequestration (Castro et al. 2018; Clark et al. 2016). Droughts are becoming more severe and more frequent throughout many areas of the world, including the United States (IPCC 2021). Although abiotic conditions such as soil and climate can influence forest responses to drought (Itoh et al. 2012), forest managers cannot readily change these abiotic factors. However, forest managers can influence species and structural diversity (i.e., the variation in tree heights, diameters and arrangements; LaRue, Fahey, et al. 2023; Staudhammer and LeMay 2001), which are key actions proposed to enhance forest resistance to drought in a dynamic and uncertain future (Messier et al. 2022).

Diversity-stability theory suggests that higher species diversity can reduce the temporal variation in community productivity (McCann 2000; Liang et al. 2022). Community stability may arise due to species asynchrony or due to species stability (Thibaut and Connolly 2013; Wang et al. 2024). Species asynchrony occurs when species with different niches respond differently to changes in environmental conditions, creating compensatory dynamics where increases in productivity of one species are offset by decreases in productivity of another species, thus stabilising community-level productivity (Loreau et al. 2021). Species stability occurs when individual species exhibit only small fluctuations around their long-term mean productivity (Wang et al. 2024). Focusing on one metric of stability, resistance (i.e., the ability of an ecosystem to maintain productivity during a disturbance; Lloret et al. 2011), experimental studies in grasslands provide strong evidence that herbaceous species diversity enhances resistance to climate extremes (Isbell et al. 2015). However, studies examining resistance in forest ecosystems show mixed results, with ambiguous attribution of mechanisms in cases where productivity is sustained (Hordijk et al. 2023; Liu et al. 2022; Schnabel et al. 2021; Wagg et al. 2017).

Evidence suggests that forest structural diversity could confer resistance to drought (Atkins et al. 2023) given strong connections between measures of structural diversity and productivity, biomass and resource-use efficiencies. For example, stand size distributions influence competition for resources such as moisture and light (Ishii et al. 2004; Forrester and Bauhus 2016) while stand density can influence tree mortality (Flake and Weisberg 2019; Restaino et al. 2019), and tree height can influence susceptibility to drought (Bennett et al. 2015; Stovall et al. 2019). Structurally and biologically diverse forests may use resources more efficiently, respond asynchronously to changing conditions and thus better resist disturbances. Greater structural diversity is often associated with a wider variety of tree species (Gough et al. 2019), sizes, functional types, rooting characteristics and ages (Parker and Russ 2004) and is an indicator of mature and old-growth forest status (Woodall et al. 2023). Although structural diversity and species diversity are often positively correlated (Crockett et al. 2023; Hakkenberg et al. 2016), more information is needed to better understand the specific roles of structural diversity in conveying drought resistance at the community (e.g., stand) level.

We anticipate that relationships between species diversity, structural diversity and resistance to drought will vary with drought severity. The stress gradient hypothesis (SGH) suggests that the nature of species interactions varies, and facilitation can become important, as environmental conditions become more stressful (Bertness and Callaway 1994). For drought events, facilitation could occur through mechanisms such as (i) microsite shading, where taller trees provide shade to shorter trees, thereby reducing soil surface temperatures and creating more humid microsites that help alleviate drought stress; and (ii) hydraulic redistribution, where trees with deep roots enable water movement from deeper to shallower soils through differences in water potential (Neumann and Cardon 2012; O'Brien et al. 2017). Although the SGH was initially suggested for ecosystems which developed under higher physical stress conditions (either frequency or magnitude), changing species interactions may also occur over time (Pretzsch et al. 2013; Zhang et al. 2012). In addition, as resources (e.g., water availability) become increasingly scarce, competition among individuals is expected to intensify; however, species-rich communities often experience less competition than species-poor communities, thereby helping to sustain productivity during drought (Tilman 1982). The mechanisms of facilitation and competition reduction both influence the complementarity effect of biodiversity (Loreau and Hector 2001), but are extremely difficult to distinguish in practice (Forrester and Bauhus 2016). We predict that as moisture availability declines under more severe droughts, the relationships between diversity and forest resistance will become stronger. Furthermore, this response may vary with soil bulk density and nitrogen availability, potentially explaining differences in productivity and drought resistance across forests. Soils with lower bulk density usually retain moisture longer, helping forests maintain productivity during dry conditions thus increasing resistance to drought (Assouline 2006). Soil nitrogen influences root-shoot allocation in plants and can indicate soil fertility, thus influencing diversity directly and resistance indirectly (Agren and Franklin 2003).

Here, we assess whether tree species diversity and structural diversity enhance drought resistance in forests across the USA by examining forest inventory plots that experienced drought conditions. We specifically test two hypotheses: (i) structural richness, species richness, structural evenness and species evenness are each positively associated with resistance to drought (Table 1); and (ii) according to the stress gradient hypothesis, each of these variables shows stronger associations with resistance during more severe droughts.

2 | Material and Methods

2.1 | FIA Data: Structural and Species Diversity

We used the USDA Forest Service Forest Inventory and Analysis (FIA) data from across the USA (Burrill et al. 2021) to calculate metrics of species richness, forest structure and stand age. The FIA forest plots come from a stratified random sample; the FIA program created a tessellation of hexagons across the country (each approximately 2428 ha) and randomly selected a sampling point within each hexagon. We applied selection criteria (described in each section below) that provided a sample of 1096 plots (Figure S1). We obtained exact FIA plot coordinates, rather than publicly available perturbed coordinates, with special permission from the USDA Forest Service after executing a material transfer agreement.

For comparability among plots, we included FIA data where plots consisted of four subplots of 7.3 m in radius (0.0672 ha per plot), all four subplots contained trees, and at least 90% of the plot was covered by forest. We excluded trees in the FIA 'macroplots' (for plots in the western USA where macroplots existed)—regions surrounding the area of the 'subplots'. Forest technicians recorded the species identity, diameter at breast height (DBH) and estimated heights of trees greater than 12.7 cm (5 in) DBH. Tree data from subplots were pooled to provide plot-level data.

We calculated multiple metrics of structure and diversity from the forest plot data. To calculate structural richness and structural diversity, we allocated trees into height bins of 1.52 m (5 ft) and DBH bins of 5.08 cm (2 in). We calculated height and DBH

TABLE 1 | Predicted relationships between key variables and forest resistance to drought.

Explanatory variable	Hypothesised relationship	Rationale
Species richness	Positive	Communities with a greater number of species are more likely to have: (i) species that respond differently to drought, thus lowering variability and stabilising community-level productivity; (ii) a greater number of niches, thereby reducing competition for resources such as water and maintaining high mean productivity; and (iii) at least one species that is very drought tolerant, helping to maintain high mean productivity
Structural richness	Positive	Greater diversity of tree heights and diameters (i.e., structural richness) provides a greater likelihood that trees will respond different to drought and allows the forest stand to use available resources more completely and efficiently
Species evenness	Positive Negative	Species evenness may have both positive and negative influences: (+) High evenness of species' abundances promotes balanced use of available resources and a reduction in competition for resources such as water, as well as a greater likelihood of species stability, leading to greater resilience against drought. (−) In communities where one (or a few) species is exceptionally drought tolerant, communities with low evenness may show greater resistance than communities with high evenness
Structural evenness	Positive	When trees are evenly distributed across heights and diameter classes, each component of the vertical stratum has a balanced opportunity in resource use and resources can be used more efficiently
Biomass	Positive Negative	Biomass may have both positive and negative influences: (+) Forest stands with greater biomass are more well established, and therefore likely to have developed wider and deeper root networks. (−) Forest stands with greater biomass may have larger resource demands (e.g., water) and thus be more sensitive to drought
Stand age	Positive Negative	Stand age may have both positive and negative influences: (+) Older stands may have deeper and more established root networks, enabling trees to continue water uptake for longer under dry conditions. (−) Older stands may include larger trees with greater water demands, and thus are more susceptible to drought
Soil bulk density	Negative	Lower bulk density is associated with higher water holding capacity (more pores for water storage and greater organic content), and thus may help retain soil moisture for longer during drought, helping trees to maintain productivity

richness as the number of categories found within each FIA plot (Crockett et al. 2023; Dănescu et al. 2016; LaRue, Knott, et al. 2023), which ranged from 2 to 19 and 1–14 for height and DBH richness, respectively. Since height and DBH are related, we conducted a principal component analysis (PCA) using height richness and DBH richness and extracted the first principal component as the metric of structural richness. For alternate metrics of forest structure, we repeated the steps above to calculate height and DBH diversity using the Shannon index (rather than richness) as our metric of structural diversity, where the relative numbers of trees within each height or DBH bin were used as weights in the structural diversity metric. We calculated height evenness and DBH evenness using Pielou's metric (to be comparable to species calculations described below), conducted a PCA, and extracted the first principal component as a metric of structural evenness. We also calculated the mean tree height, basal area, number of stems, biomass and Reineke's stand density index for each forest plot (Chivhenge et al. 2024). We calculated species richness as the number of different tree species within each forest plot (which ranged from 1 to 17), calculated Shannon diversity based on the relative abundances of the tree species, and calculated Pielou's evenness. Forest plots may contain multiple 'forest conditions'—subsections of the plot that technicians delineated as having disparate characteristics such as reserved status, landowner group, forest type, stand size class, regeneration status, or tree density. Technicians measured tree age for a few trees within each forested condition, and we calculated stand age for each plot using a weighted average where age was weighted based on the area covered by each forested condition.

2.2 | Forest Productivity

We obtained maps of annual net primary productivity (NPP) from 1990 to 2020 at a 30×30 m pixel resolution from Google Earth Engine. These NPP maps were derived from Landsat

data, the MOD17 algorithm and meteorological data (Robinson et al. 2018). For each FIA plot, we calculated the average NPP for each year across a 3×3 pixel grid around the plot centre. We removed any plots with more than two missing values (e.g., areas that were not forested) in the 3×3 grid. On average, productivity of the plots was approximately 7.16 Mg C·ha^{-1}·year^{-1}. We included forest plots where the average NPP was at least 0.5 Mg C·ha^{-1}·year^{-1} during the pre-drought years and at least 0.1 Mg C·ha^{-1}·year^{-1} during the drought, since changes in NPP at very low levels of NPP can greatly influence estimates of resistance, and applying these thresholds help the model residuals meet assumptions of normality. These thresholds affected < 2% of plots, and we repeated the core analyses without these thresholds and found very similar results (Figure S2). We included plots with at least 10% forest cover during the 2011 year (roughly the midpoint of observations and a year for which the forest cover map was readily available).

2.3 | Ancillary Variables

To compare the influence of richness variables versus biophysical variables on resistance, and because biophysical variables also influence richness itself, we included pre-drought climate values, ecoregion and soil factors as explanatory variables in statistical analyses. Using monthly Daymet climate data (Thornton et al. 2020), we calculated long-term mean values for maximum temperature, minimum temperature and annual precipitation for each plot for 20 years preceding the drought. Since maximum and minimum temperature are highly correlated, we used the average of these for the long-term pre-drought temperature. We used the EPA Ecoregions of North America (US EPA 2018) to identify the 'level one' ecoregion associated with each FIA plot. We extracted data from the SoilGrids 2.0 database at a 1 km^2 resolution and calculated an average value across the soil layers for bulk density and total nitrogen concentration (ISRIC (International Soil Reference and Information Center) 2022; Poggio et al. 2021).

2.4 | Identifying Drought Events

We identified suitable drought events for each forest plot based on the standardised precipitation-evapotranspiration index (SPEI) (Vicente-Serrano et al. 2010) with the Thornthwaite equation (Thornthwaite 1948) using the R package 'SPEI' (v1.8.1; Beguería and Vicente-Serrano 2023). SPEI measures the cumulative difference between precipitation and potential evapotranspiration over a user-specified time horizon prior to the target month.

Although numerous drought indices are available (e.g., Palmer drought severity index, North American drought monitor), SPEI is useful for two reasons. First, SPEI enables comparison across locations since the index is standardised to the average climate conditions and variability of a given location (Vicente-Serrano et al. 2010). SPEI is similar to a *z*-score; values are roughly normally distributed and values of ±1 are one standard deviation from zero. Negative SPEI values indicate dry conditions; positive values indicate wet conditions. Second, SPEI can be applied at multiple timescales. We calculated SPEI values for target months from May to October using timescales from 3 months to 24 months in 3-month increments (i.e., 3, 6, ..., 24). Timescales indicate the number of months included in the calculations. For example, a 3-month SPEI for May includes climate information from March, April and May; a 12-month SPEI for October includes climate information from November of the previous year through October.

We assessed the relationship between NPP and SPEI values across all these months and timescales and selected the SPEI month and timescale that showed the strongest relationship with NPP for subsequent analyses. To do this, we selected FIA plots with 15+ years of NPP data. For each plot, we detrended the NPP time series using a linear regression since NPP generally changes as young forests age (Amiro et al. 2010; He et al. 2012). If there was no significant temporal trend, we used the initial (non-detrended) values. We calculated the R^2 value between the detrended NPP and SPEI for each plot. Finally, we extracted the median R^2 values across all plots and selected the SPEI month and timescale with the highest R^2 value for subsequent analyses, which was August using a 9-month timescale (Figure S3).

We examined SPEI values over time at each FIA plot to identify suitable drought years for statistical analyses. We selected plots that showed "normal" SPEI values (i.e., between −1 and +1) for each of the three years prior to the drought so that previous years with considerable drought or wetness would not substantially affect the drought year of interest. We included plots where FIA data were collected in the three years prior to the drought. If an individual plot had multiple years that met these criteria, we included the year of the most extreme drought. Finally, we extracted drought events as years with an SPEI value of less than −2 for our main statistical modelling, as this value represents two standard deviations beyond normal conditions and beyond this threshold productivity starts to decline sharply. This yielded a sample size of 1096 forest plots, with different drought years for different forest plots across the USA (Figure S1). To test the SGH (whether relationships vary with drought severity), we also extracted drought years (again allowing for different years in different plots) using SPEI thresholds of −1, −1.25, −1.5 and −1.75 (Figure S4).

We calculated resistance for each plot as the natural log ratio of productivity during the drought ($NPP_{drought}$) to the average productivity in the three years before the drought (NPP_{before}) (Lloret et al. 2011).

$$\text{Resistance} = \ln\left(NPP_{drought} / NPP_{before}\right)$$

2.5 | Statistical Analyses

We conducted path analysis to determine whether our hypotheses were consistent with the data using the 'lavaan' R package (v0.6-15; Rosseel 2012). Path analysis is well suited to large-scale observational datasets such as in this study because this approach allows scientists to propose and then test causal models of the relationships among variables (Shipley 2016; Grace et al. 2016). Statistical techniques such as general linear models typically only model the direct effects of each explanatory variable on the outcome variable (e.g., drought resistance). In contrast, path analysis

specifies relationships among explanatory variables, enabling explicit modelling of intermediate variables and their indirect effects. An indirect effect occurs when one explanatory variable ($x1$) influences another explanatory variable ($x2$), which then influences the outcome variable (y); here, $x1$ indirectly affects y through the path: $x1 \rightarrow x2 \rightarrow y$, while $x2$ directly affects y. Since path analysis allows scientists to propose and test causal model, this approach enables more nuanced evaluations of causal relationships than traditional approaches such as linear models.

After formulating our hypotheses (Table 1), we constructed six path diagrams outlining our proposed causal links. In addition to the variables of temperature, precipitation, soil bulk density, soil nitrogen and stand age, these six path diagrams included: (a) structural richness and species richness, (b) structural richness, species richness and biomass, (c) structural richness and structural evenness, (d) species richness and species evenness, (e) structural evenness and species evenness and (f) structural richness, species richness, structural evenness and species evenness. We report results from model (f) in the main text (Figure 1) and from models (a–e) in the Supporting Information (Figures S5–S9) since model (f) explained the greatest fraction of the variation in drought resistance and included all four variables central to our hypothesis. We applied a weight-of-evidence approach to evaluate each model fit (Grace 2020) by iteratively (i) checking for omitted important links, (ii) adding the most important missing link (indicated by the expected chi-squared change from the modification indices) or removing a non-significant relationship outside our central richness and evenness hypotheses and (iii) re-evaluating the model.

For this modelling, we log-transformed species richness, stand age, biomass, stand density index, basal area, number of stems and soil nitrogen concentration to meet assumptions of normality. We scaled all variables to a mean of zero with unit variance so that relationships between each variable and resistance are compared on a common scale. We applied the lavaan spatial correction approach (Byrnes 2023) to account for spatial autocorrelation when calculating the standard error of coefficients and p-values.

We conducted our main modelling with an SPEI threshold of −2. We assessed the sensitivity of our results to different metrics of forest structure by replacing the richness-based index for structural diversity with the following metrics: Shannon index for structural diversity, biomass, basal area, stand density index, number of stems and mean tree height. Since plausible explanations for links between richness and evenness could invoke either direction of causality, we specified a shared covariance between species richness and species evenness, and also between structural diversity and structural evenness. We ran a multigroup model with EPA level one ecoregions containing at least 20 forest plots to assess whether path coefficients varied across the USA. A multigroup model retains a consistent model structure across different groups (i.e., ecoregions), but allows the path coefficients in the causal diagram to vary for each individual group. We interpret the path coefficients in some ecoregions with caution due to low sample sizes in those areas (e.g., forests in the marine west coast and Great Plains; see Figure 2 for sample sizes). We also ran a multigroup model to evaluate whether path coefficients varied between conifer, broadleaf and mixed forests. Based on the best path diagram from earlier steps, we tested the SGH with a multigroup model using drought thresholds of −1, −1.25, −1.5, −1.75 and −2 to determine whether the relationships between richness, evenness and resistance differed under more severe droughts. We repeated this test of the SGH using only those plots which experienced droughts in

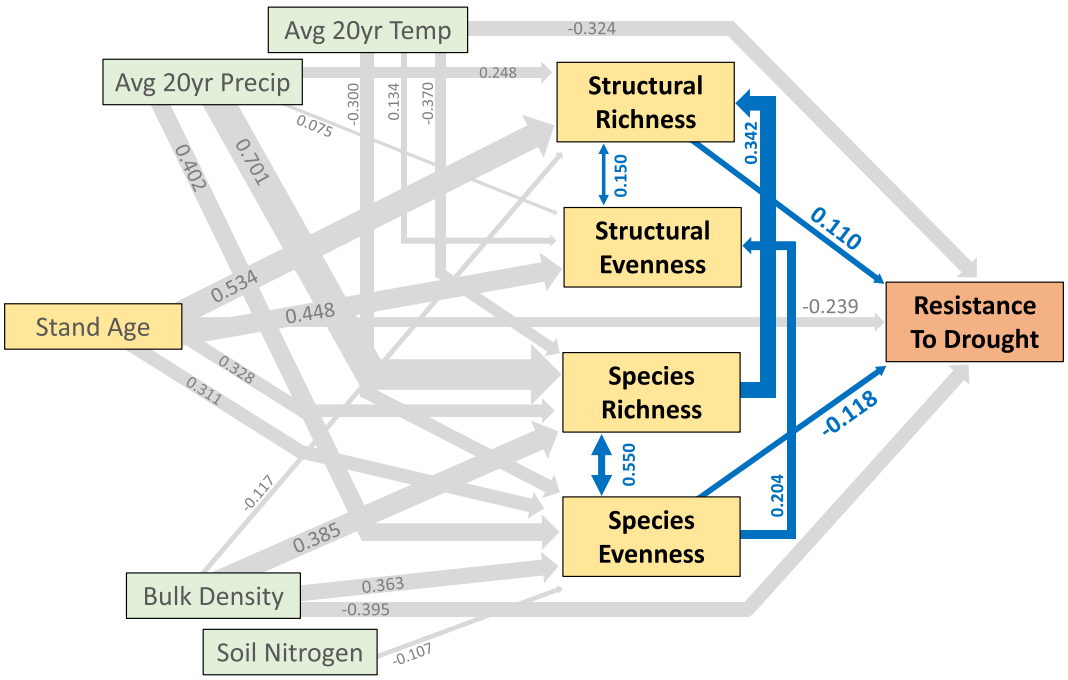

FIGURE 1 | Path diagram with standardised model coefficients showing the relationships among explanatory variables and resistance to drought. Structural richness enhanced resistance to drought, while the direct relationship between species evenness and resistance was negative. Blue arrows indicate the main hypotheses of interest. Arrow widths are proportional to the magnitudes of the path coefficients; these are not linear correlation indices but rather standardised path coefficients with larger values (and thicker lines) indicating stronger relationships. The double headed arrows indicate a shared covariance. The p value of the overall model was 0.988, indicating that the model was not inconsistent with the data.

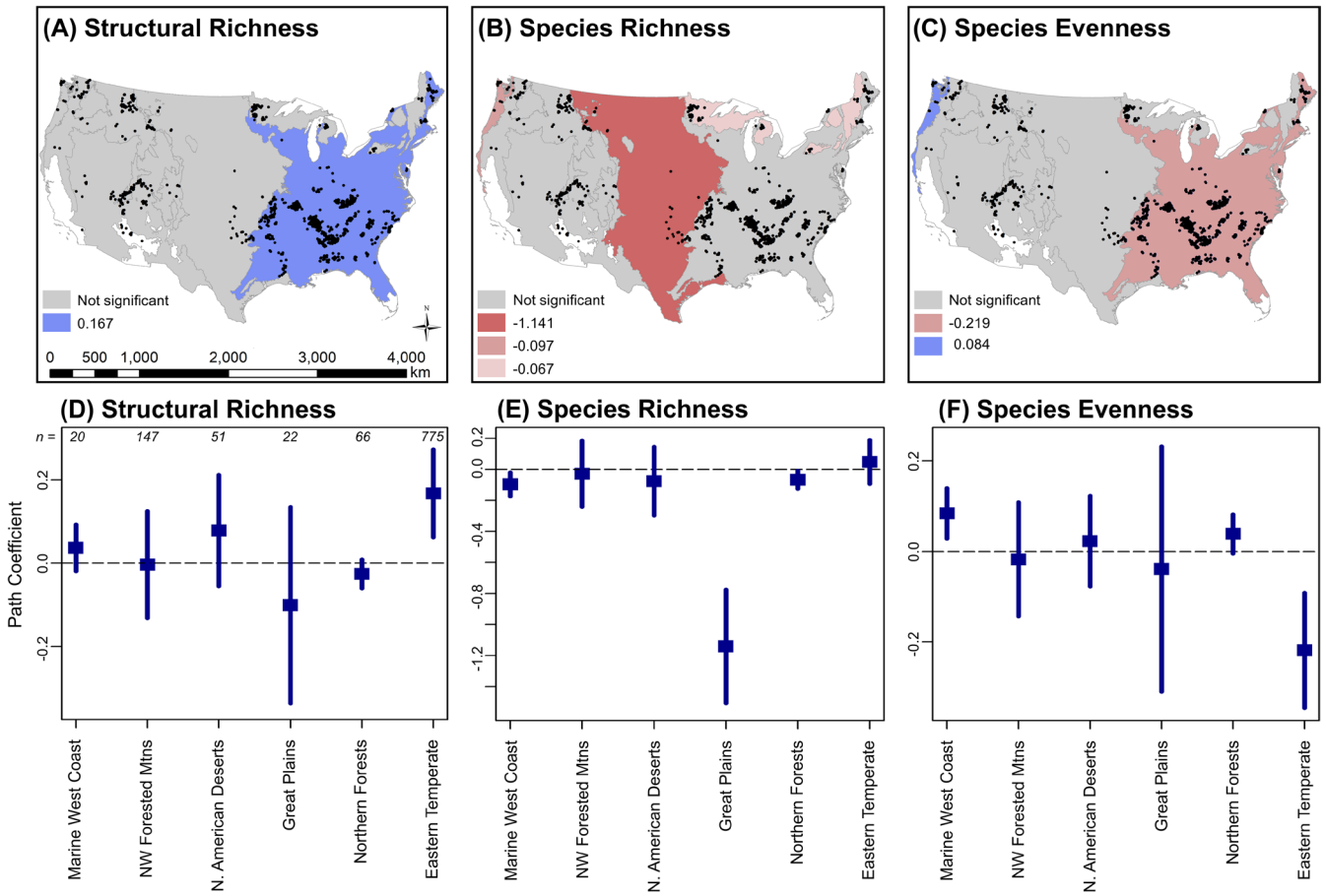

FIGURE 2 | The standardised path coefficients between resistance and (A, D) structural richness, (B, E) species richness and (C, F) species evenness vary across EPA ecoregions of the USA. In panels A, B and C blue areas indicate positive relationships with resistance, red areas indicate negative relationships, grey areas indicate non-significant relationships and white areas indicate no FIA plots to derive relationships. In panels A, B and C, points indicate forest plots ($n = 1096$) that were exposed to drought conditions (i.e., an SPEI value of less than −2). For privacy reasons, forest plots are displayed using the publicly available coordinates rather than the exact coordinates used in analyses. In panels D, E and F, lines indicate 95% confidence intervals. The sample size (n) in each ecoregion is shown above the graph in panel D.

at least two SPEI categories and found qualitatively similar results (Figure S10). Although examining plots which experienced all five categories of drought severity would be helpful, unfortunately with long repeat cycles between forest inventories and the 20-year timeseries of NPP, only seven plots experienced three categories of drought severity and no plots experienced four or five categories.

Lastly, we compared the outcomes from our path analysis model (f) with those derived from a multiple regression using a backwards selection procedure. We modelled drought resistance as a function of structural richness, species richness, structural evenness, species evenness, average temperature, precipitation, stand age, soil nitrogen and soil bulk density. We focus on the path analysis results in subsequent sections because the multiple regression produced nearly identical findings (Figure S11). We conducted analyses using R version 4.3.1 and generated maps using ArcGIS.

3 | Results

Path analysis demonstrated that structural richness had a positive relationship (0.110) with drought resistance (Figures 1 and S5). Path models using structural richness (i.e., an aggregate measure of tree height and diameter size classes) and structural Shannon diversity showed a better fit (i.e., a lower AIC score) than path models that replaced structural richness with another metric of forest structure (i.e., biomass, basal area, stand density index, average height, or number of stems; Figure S12). Since we found similar results between two metrics of biodiversity—richness and Shannon diversity (see Methods section)—we report results from richness in the main text (Figure 1) and from Shannon diversity in the supplemental information (Figure S13). The relationship between structural evenness and drought resistance was non-significant.

Species evenness showed a negative relationship with resistance (−0.118; Figure 1). Species richness showed a non-significant relationship in the path analysis when species evenness was included (Figure 1), and a negative relationship (−0.149) with resistance in the path model that did not include species evenness (Figure S5). These path coefficients indicate standardised effect sizes, describing the magnitude and direction of relationships.

We found relationships between the four primary explanatory variables of interest (structural and species richness and evenness). We observed a strong relationship between species evenness and species richness (0.550) and a modest relationship between

structural evenness and structural richness (0.150) (Figure 1; both relationships were specified in the model as a shared covariance without a causal direction). There was a positive relationship between species evenness and structural evenness (0.204) and between species richness and structural richness (0.342).

Despite these effects in the global model (i.e., using all data), the relationship between structural richness and resistance varied across ecoregions (Figure 2) and forest types (Figure 3). Structural richness was positively associated with resistance in eastern temperate forests (0.167) but showed nonsignificant relationships in other ecoregions. Species richness was negatively associated with resistance in the Great Plains (−1.15), marine west coast (−0.0967) and northern forests (−0.067) ecoregions. Species evenness was positively associated with resistance in the marine west coast ecoregion (0.084) and negatively associated with resistance in the eastern temperate forests (−0.219). In broadleaf forests, structural richness had a positive influence on resistance (0.218). There were no significant differences in species richness or evenness across forest types.

We found evidence supporting the stress gradient hypothesis for structural richness and for species evenness. For structural richness, the path coefficient between structural richness and resistance was greater under more severe droughts (i.e., SPEI thresholds of −1.75 and −2) than more moderate droughts (i.e., −1 to −1.5) (Figure 4). The coefficients for the structural richness-resistance relationship under SPEI values of < -1.75 and < -2 were similar, suggesting that the influence of structural richness does not continue to increase beyond SPEI values of −1.75. For species evenness, the relationship with resistance also became stronger (i.e., more negative) under more severe droughts. For species richness, evidence for the stress gradient hypothesis was mixed; although the relationship with resistance became stronger when increasing SPEI thresholds from −1 to −1.75, however, at an SPEI threshold of −2, there were wide confidence intervals, and the path coefficient was not significant.

Overall, we found that the associations between resistance and structural richness and species evenness were modest in comparison to the stronger associations between resistance and stand age, average temperature and soil bulk density (Figure 1). Stand age was negatively associated with resistance. Stand age also indirectly influenced resistance through the influence of both structural richness (indirect positive effect) and species evenness (indirect negative effect). Structural and species richness and evenness increased in older forest stands compared to younger forest stands. The average 20-year temperature was negatively associated with resistance, as well as negatively associated with structural evenness, species richness and species evenness. Out of all explanatory variables, soil bulk density

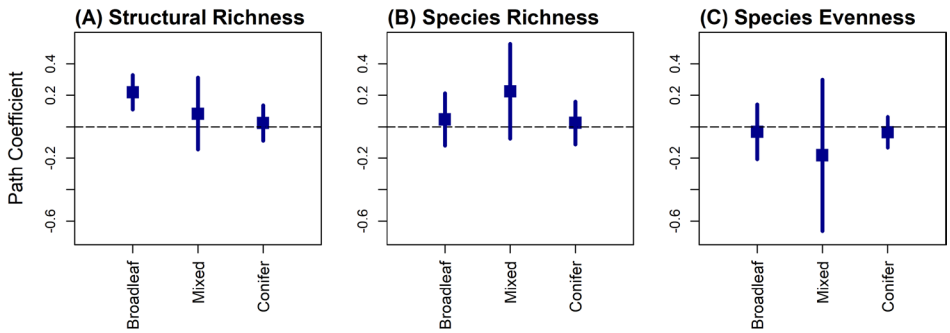

FIGURE 3 | The standardised path coefficients between resistance and (A) structural richness, (B) species richness and (C) species evenness across different forest types—broadleaf, mixed and conifer forests. Lines indicate 95% confidence intervals.

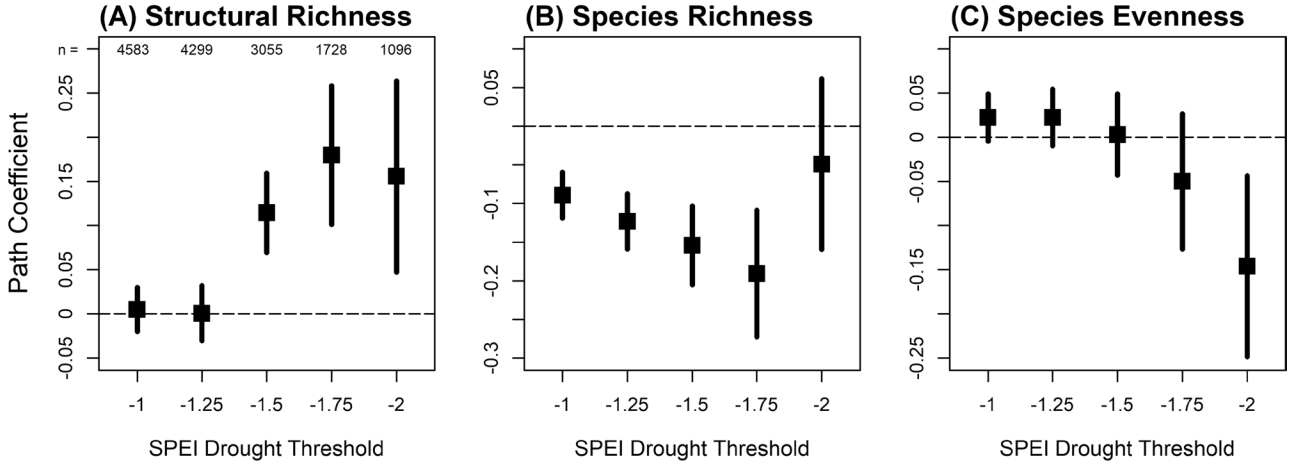

FIGURE 4 | Standardised path coefficients between resistance and (A) structural richness, (B) species richness and (C) species evenness under different SPEI drought thresholds. Lines indicate 95% confidence intervals. The sample size (*n*) for each SPEI category is shown in the top of panel (A).

showed the strongest association with drought resistance; low bulk density and thus greater water holding capacity were associated with enhanced resistance.

4 | Discussion

4.1 | Roles of Structural & Species Diversity Versus Composition

Although structural richness was positively associated with resistance, relationships of species richness and evenness with resistance partially ran counter to our predictions based on biodiversity-ecosystem function theory (Tilman et al. 2014; Wang et al. 2024). While diverse species assemblages should stabilise community-level productivity (Loreau et al. 2021), positive diversity-resistance relationships in forests are not ubiquitous (de Sauvage et al. 2023; Grossiord et al. 2014). Two factors may explain our findings about species richness and evenness. First, although the *direct* effect of species richness on resistance was non-significant, species richness had an *indirect* positive effect on resistance through structural richness (Figure 1). Our results are consistent with the hypothesis that structural diversity provides a more direct measure than species richness of the niche space occupied within a community (LaRue, Fahey, et al. 2023); suggesting that structural diversity may provide a stronger indicator of physical traits important for drought resistance (discussed below). Second, species composition could have greater effects on resistance than species richness (Archaux and Wolters 2006). Tree species have evolved different strategies for dealing with drought (Anderegg and HilleRisLambers 2016; McDowell 2011), with some species better able to maintain productivity during dry conditions (McNulty et al. 2014; Pardos et al. 2021). Species on either end of the isohydric-anisohydric spectrum (Tardieu and Simonneau 1998) often maintain leaf water potential (isohydric) or downregulate (anisohydric) during drought, leading to greater vulnerability from carbon starvation or hydraulic failure, respectively (McDowell et al. 2008). Potential influences of composition versus diversity may vary with regional adaptations to drought. For example, drought-tolerant species should be more abundant in environments where droughts are more common or severe. The Great Plains ecoregion showed a negative relationship between species richness and resistance (−1.15; Figure 2); this region contained a higher proportion of drought-tolerant species (e.g., *Juniperus ashei*) than other ecoregions, and across the FIA plots higher abundances of *Juniperus* spp. were associated with lower species diversity (Figure S14). However, since our study includes more than 280 tree species, with many found in few locations, identifying roles of all species in mitigating drought would be challenging, but in some cases, the specific identities of species may outweigh the benefits of diversity.

Structural richness may have shown a positive relationship with resistance in broadleaf forests, but not in conifer or mixed forests (Figure 3) for two reasons. First, with needle-shaped leaves and lower evapotranspiration, conifer forests are often better adapted to withstand drought (Moran et al. 2017). Second, broadleaf forests have more overlapping tree crowns than coniferous forests, influencing shading to trees in lower canopy layers (Atkins et al. 2022; Béland and Baldocchi 2021). This microsite shading reduces soil surface temperatures, creating more humid microsites that help reduce stress and maintain NPP during drought (Von Arx et al. 2013). Therefore, structural diversity in broadleaf forests is more likely to influence productivity among neighbouring trees, and be more important for drought resistance. These mechanisms between forest types may lead to the observed differences in structural diversity-resistance relationships across ecoregions (Figure 2); eastern temperate forests (which showed a positive relationship) have more deciduous trees than northern forests or northwest forested mountains (both non-significant relationships).

A debate persists about which structural attributes make forests resistant to drought (McDowell et al. 2018; Stovall et al. 2019). Instead of focusing on individual-level properties (i.e., short versus tall trees) within a site, we focused on stand-level properties (i.e., diversity and evenness of tree heights) across different sites. Although several metrics of forest structure (e.g., biomass, basal area, Reineke's stand density) explained similar amounts of the variation in resistance, structural diversity provided the most parsimonious model (Figure S12). As height diversity (a component of structural diversity) provides a key indicator of mature and old-growth forests (Woodall et al. 2023), future conservation efforts that identify and manage such resources may indirectly confer drought resistance, and adaptative management efforts (i.e., assisted migration plantings that increase structural diversity) may confer long-term drought resilience.

4.2 | Stress Gradient Hypothesis

We predicted that relationships between diversity and resistance become stronger under more severe droughts, since diverse communities can reduce competition or provide facilitation effects, especially with limited water resources (O'Brien et al. 2017; Warren et al. 2009). Our findings were largely consistent with this prediction for structural richness and species evenness, but not for species richness potentially due to influences of species composition.

Belowground tree structure likely mediates impacts of drought, since a variety of rooting depths may reduce competition for water and also enable hydraulic lift, where deep roots facilitate water movement from deeper to shallower soils, thereby helping trees maintain productivity during drought (Neumann and Cardon 2012; O'Brien et al. 2017). We relied on aboveground structural diversity since belowground information was not available. However, future studies could elucidate potential synergies or trade-offs between aboveground and belowground structural diversity and the mechanisms involved (e.g., root/shoot ratios, light versus water capture efficiency).

4.3 | Relative Influence of Different Variables

Biophysical variables showed stronger associations with resistance than did structural or species diversity (Figure 1) perhaps due to the country-wide study extent. Different ecoregions experience different climate regimes, and only some areas may be water limited (e.g., Great Plains, North American deserts), as NPP does not vary substantially with SPEI in some ecoregions

(e.g., marine west coast; Figure S15). Soil bulk density exhibited a direct negative association with resistance (−0.395) likely because lower bulk density increases water infiltration into the soil and greater pore volume increases soil water holding capacity, thereby helping trees access water and maintain productivity during drought (Assouline 2006). Although soil nitrogen did not directly influence resistance, nitrogen affects species evenness (Figure 1), which in turn may promote/inhibit recruitment of species better/less able to withstand drought conditions.

4.4 | Considerations and Caveats

Inherent noise in remote sensing data could influence estimates of NPP prior to and during drought (Zhao and Running 2010), propagating error into estimates of resistance. This uncertainty may particularly impact results in areas of low productivity—where small changes in absolute productivity cause large changes in resistance—often arid areas commonly affected by drought. In addition, satellite-based estimates of NPP may not adequately reflect understory and belowground productivity (Newman et al. 2006)—which remain important research questions for future studies.

Although we proposed mechanisms for why diversity might increase forest resistance to drought (Table 1), repeated droughts over time can shape forest structure and diversity. Regions repeatedly experiencing drought may become home to species better able to withstand fluctuations in temperature, precipitation and drought conditions (Anderegg et al. 2013; Martínez-Vilalta and Lloret 2016). In particular, water availability in forests greatly influences canopy height (Koch et al. 2004), which raises the potential for additional factors not included in our models to influence relationships between diversity and function (Chisholm and Dutta Gupta 2023). In addition, with ongoing changes in climate, many species are moving to regions with conditions to which they are better suited, thus leading to novel species assemblages (Fei et al. 2017; Thom et al. 2017; Vissault et al. 2020). Forests that have experienced drought may be more vulnerable to pests and fire (and vice versa), and multiple stressors may cause cumulative impacts on forest productivity (McNulty et al. 2024).

4.5 | Summary

Overall, our results demonstrated a positive relationship between structural diversity and resistance. We found modest support for the stress-gradient hypothesis; path coefficients showed stronger relationships between structural diversity and resistance and between species evenness and resistance under more severe droughts than under modest droughts. Our results imply that increasing structural diversity and selecting drought tolerant species could foster forest resistance to moderately severe and severe droughts. Although biophysical conditions (e.g., soil bulk density) are difficult to alter, forest managers and policymakers have agency to shape species composition and structural diversity (e.g., prescribed burning, selective thinning; Dieler et al. 2017). Forest managers could capitalise on new technologies, such as spaceborne lidar and radar (Dubayah et al. 2020) to assess forest structure and diversity globally (Crockett et al. 2023) and identify opportunities for restoration and management. Small increases in resistance within individual forest stands could have substantial implications for aggregate forest productivity and carbon storage at country-wide scales as changes in climate continue to cause more frequent and severe droughts.

Author Contributions

Conceptualisation: Erin T.H. Crockett, Jingfeng Xiao, Qinfeng Guo, Jeff W. Atkins, Ge Sun. Data acquisition: Jingfeng Xiao, Erin T.H. Crockett, Kevin M. Potter, Scott V. Ollinger, Christopher W. Woodall, Justin Holgerson. Performed analyses: Erin T.H. Crockett. Interpretation of results: Erin T.H. Crockett, Qinfeng Guo, Jeff W. Atkins, Jingfeng Xiao, Ge Sun, Kevin M. Potter, Jennifer K. Costanza, Scott V. Ollinger, Christopher W. Woodall, Steven McNulty, Carl Trettin, Justin Holgerson. Supervision: Jingfeng Xiao, Qinfeng Guo, Jeff W. Atkins, Ge Sun. Writing – original draft: Erin T.H. Crockett. Writing – review and editing: Qinfeng Guo, Jeff W. Atkins, Jingfeng Xiao, Ge Sun, Kevin M. Potter, Jennifer K. Costanza, Scott V. Ollinger, Christopher W. Woodall, Steven McNulty, Carl Trettin, Justin Holgerson.

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Data Availability Statement

We used publicly available data (i) for Landsat-based maps of net primary productivity from Google Earth Engine (Robinson et al. 2018, doi: 10.1002/rse2.74), (ii) for climate variables from the Daymet database (https://doi.org/10.3334/ORNLDAAC/1852), (iii) from the SoilGrids database 1000 m^2 product (https://files.isric.org/soilgrids/latest/data_aggregated/), (iv) for EPA Ecoregions (https://www.epa.gov/eco-research/ecoregions-north-america) and (v) forest canopy cover (https://data.fs.usda.gov/geodata/rastergateway/treecanopycover). Although much data about each FIA plot is publicly available, the locations of plots listed in public datasets are perturbed to protect plot integrity and landowner confidentiality. We acquired actual plot coordinates for this project from the US Forest Service after requesting special permissions and executing a material transfer agreement. For privacy reasons, the maps shown in the paper use the perturbed publicly available coordinates. The R code used in analysis can be obtained from the Zenodo repository https://zenodo.org/records/18614289.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Data S1:** ele70351-sup-0001-Figures.pdf.