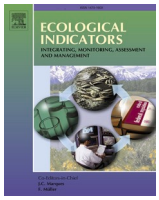
Ecological Indicators 171 (2025) 113117

Contents lists available at ScienceDirect

Ecological Indicators

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



Original Articles

Forest demographic changes across Texas associated with hot drought

Shakirudeen Lawal [a,*], Frank H. Koch [b], Robert M. Scheller [a], Jennifer Costanza [b]

[a] Department of Forestry and Environmental Resources, North Carolina State University, NC 27695-8001, USA
[b] USDA Forest Service, Southern Research Station, Research Triangle Park, NC 27709, USA

ARTICLE INFO

Keywords:
Disturbance
Drought
Demographic shifts
Signalling pathway
Resilience
Forests

ABSTRACT

Recent changes of tree species demography in Texas likely can be attributed to climatic disturbances, particularly hot drought (i.e., drought exacerbated by extreme heat). In this study, we examined demographic change over East, Central and West Texas over a 16-year period (2004–2019), including a widely documented 2011 hot drought event. We used Forest Inventory and Analysis (FIA) data to evaluate changes in tree count for the nine most abundant tree genera in Texas. Furthermore, we examined the associations between tree demography and the distribution of climate variables including the 12-month Standardized Precipitation Evapotranspiration Index (SPEI12), potential evapotranspiration (PET), precipitation, vapour pressure deficit (VPD), maximum temperature and the Heat Wave Magnitude Index daily (HWMId). Using Pearson Correlation Coefficient, we examined the influence of hot drought on forest demography by examining four size classes (seedlings, saplings, small trees and large trees). We found that there were declining trends for most genera between 2004 and 2019, particularly in the seedling and sapling size classes. In East Texas, there were significant decreasing trends of *Quercus* spp. seedling counts and sapling counts. We also observed significantly declining seedling and sapling counts of *Liquidambar* and the sapling count of *Ulmus*. Decreasing counts were most prominent in Central Texas and West Texas, though the patterns and trends were variable among genera. In West Texas, there were declines through time in all but the largest size class for *Juniperus* and *Prosopis*. Furthermore, we found that hot drought was correlated with declines in seedling and sapling counts. We demonstrate opportunities for monitoring demographic change, which can be a baseline for improved ecosystem management.

1. Introduction

Disturbances are critical drivers of forest ecosystem dynamics (Turner, 2010). Disturbances alter species demography, seed and species dispersal, modify ecosystem functioning, aid in biogeochemical and nutrient cycling, impact carbon storage capacity, contribute to biomass loss and limit biodiversity (Solomon and Kirilenko, 1997; Schimel et al., 2000; Iverson et al., 2005; Lindenmayer and Noss, 2006; Mouillot et al., 2013; Mayer et al., 2017., Seidl et al., 2017). However, there have been widespread alterations of forests' characteristic disturbance regimes (i.e., patterns of disturbance frequency, severity, timing and causal agents) in recent decades (Costanza et al. 2023, Patacca et al., 2023), at least in part associated with climate change (Seidl et al., 2016; Seidl et al., 2017; Sommerfeld et al., 2018; Turner and Seidl, 2023). For instance, in the United States, it was reported that a 2011 hot drought (co-occurrence of drought and extreme heat) in Texas led to the loss of millions of trees (Schwantes et al., 2018; Klockow et al., 2018; Lawal et al., 2024). In Europe, high rates of tree mortality have also been attributed to intensification in disturbance regimes (Thom and Seidl, 2016; Hlasny et al., 2021; Senf and Seidl, 2021a; Senf and Seidl, 2021b). Given that the stability and functionality of forest ecosystems rely on their resilience to disturbances (Führer, 2000; Gunderson, 2000; Messier et al., 2019; Van Meerbeek et al., 2021; Holling, 1973; Seidl and Turner, 2022), there is a need to study the pattern of key forest characteristics, such as species composition, that can indicate potential for ecosystem change (Dakos et al., 2015; Scheffer et al., 2009; Scheffer et al., 2015).

Previous studies (e.g. McDowell *et al.*, 2020) showed that alterations in forest demography at a global scale could be traced to interactions of changing environmental drivers of forest dynamics such as atmospheric CO_2, vapor pressure deficit (VPD) and temperature with transient/sporadic disturbances such as drought, wildfire and insect outbreaks. Thus, examining how compositional shifts after disturbance diverge from historical patterns may signal compromises in ecosystem stability and resilience that could push forest ecosystems past the point of recovery (Turner and Seidl, 2023).

Drought is a disturbance that, alone or in combination with other

* Corresponding author.
E-mail address: lasd_dr@yahoo.com (S. Lawal).

https://doi.org/10.1016/j.ecolind.2025.113117
Received 23 October 2024; Received in revised form 13 January 2025; Accepted 14 January 2025
Available online 3 February 2025

forest disturbances, can have wide-ranging impacts on forests, and lead to changes in forest composition (Seidl et al., 2017). As climate warms, drought is increasing in intensity, duration, frequency, and/or extent in many places (Lawal et al., 2019a,b), and is compounded by extreme heat (Lawal et al., 2024). Although forests can tolerate drought conditions, current circumstances are straining the physiological limits of many forest ecosystems, and can increase mortality rapidly while suppressing growth and recruitment (Clark et al., 2016; McDowell *et al.*, 2020). Numerous studies (e.g. Kaiser *et al.*, 2013; Hawthorne and Miniat, 2017; Anderegg et al., 2020; Schuldt et al., 2020; Gazol and Camarero, 2022; Hartmann et al., 2022) have shown the association of compositional change in forest ecosystems with drought and temperature extremes. Gitlin *et al.* (2006) reported that soil moisture variability led to changes in the large-scale distribution of trees, while Bennett et al. (2023) showed that a temperature increase caused widespread tree mortality across several ecological regions. McCune and Keon (2002) and Schwantes et al. (2018) showed that greater vapor pressure deficit (VPD) and potential evapotranspiration (PET) caused by higher temperatures led to reduction in transpiration and stomata closure. Other studies (McDowell et al., 2008; Park Williams et al., 2013) found that drought – as manifested by these physiological responses – is a major driver of forest composition, and its occurrence is often attributed to various landscape shifts of tree distributions (Russell and Fowler, 2002). This may be especially true of hotter droughts (like the 2011 Texas drought) under climate change (Clark et al., 2016; Peters et al., 2015; Suarez et al., 2004; Batllori et al., 2020; McDowell *et al.*, 2020).

Other studies have examined how droughts affect trees and forests at larger spatial scales. For example, a climate change assessment study found that Scots pine (*Pinus sylvestris*), the most prominent tree species in much of Europe, has increased in annual biomass growth in the northern part but declined in southwest Europe (Pretzsch *et al.*, 2023), attributed partly to drought, which has become more frequent and intense in recent decades. In the United States particularly in conifer-dominated forests of the West and Southwest, there has been increasing frequency and magnitude of climate-exacerbated drought and accumulated evidence of compositional shifts (Adams *et al.*, 2009; Cayan et al., 2010; Strzepek et al., 2010; McDowell et al., 2016; Hansen and Turner, 2019; Overpeck and Udall, 2020; Zhang et al., 2021). Studies in eastern parts of the US (Peters et al., 2015; Hember *et al.*, 2017; Zhang et al., 2021) have similarly shown a strong positive correlation between forests compositional change and drought exacerbated by climate change. Alig and Butler (2004) and Knott et al. (2019) showed that forest types in the eastern US have undergone compositional changes in the last half century, with increases in oak-hickory in the north while lowlands hardwoods have declined in southern parts of the region, perhaps attributed to drought impacts. Moreover, the evolving characteristics of drought – due to interactions with other environmental drivers under climate change – may lead to unanticipated impacts on forest species assemblages, making studies that target specific at-risk ecosystems critically necessary.

Investigating forest demographic changes can reveal whether drought, especially hot drought, is already beginning to shift composition. In Texas, an extreme drought, coupled with heat, in 2011 had profound impacts on those forests (Lawal et al., 2024). Other studies have examined tree mortality that resulted from the hot drought (e.g., Moore et al., 2016; Crouchet et al., 2019; Edgar et al., 2019; Subedi et al., 2021; Lawal et al., 2024), but we still lack a nuanced understanding of forest demographic changes across Texas resulting from that event. In this regard, Texas provides a useful case study, both because of the exceptional nature of the 2011 drought and the state's diverse forest types. The Texas region experiences varied and large-scale disturbances such as wildfire and insect outbreaks, among others. We focused on hot drought because it is likely to be become an increasingly frequent phenomenon in Texas (Klockow *et al.*, 2020; King et al., 2024; Lawal et al., 2024), and the impacts can manifest over many decades, with associated risks including recruitment failure as well as species- and size-specific patterns of tree mortality. For example, Polley et al. (2018) reported that more frequent extreme drought is projected to eliminate a large fraction (as much as 85 %) of intermediate- to large-sized Ashe juniper (*Juniperus ashei*) in Central Texas, a region where historically it has been one of the dominant species (Schwantes et al., 2018). Examples like this argue for detailed assessments of ongoing and projected tree demographic changes in response to drought and extreme heat.

Therefore, our goal was to investigate trends in forest tree species demography in Texas associated with these conditions. To do this, we used field-based inventory data from USDA Forest Service Forest Inventory and Analysis (FIA). To represent forest dynamics over a 16-year period (2004–2019) – with the 2011 hot drought falling roughly in the middle – we computed demographic measures from the FIA data across four size classes (seedlings, saplings, small trees and large trees) for the nine most abundant tree genera in Texas. We characterized climate conditions over the 2004–2019 period with a suite of meteorological variables – precipitation, maximum temperature, VPD, soil moisture, and PET – as well as indices of drought (Spatiotemporal Evapotranspiration Index, SPEI) and extreme heat (Heat Wave Magnitude Index daily, HWMId). Our specific questions were: a) has extreme (or exceptional) hot drought conditions, even if they are not prolonged, caused forest demographic change? b) Do drought-tolerant genera make up a larger share of the remaining forest trees? c) Do declines or increases in species signal a potentially problematic lack of recruitment? d) Does drought susceptibility of species vary among size classes? In this regard, the aim of our study was to provide information on the resilience and stability of forest ecosystems in Texas as signalled by trends of forest demography and structure.

2. Data and methodology

2.1. Study area

Texas is ecologically diverse and is comprised of more than 200 plant communities (Subedi et al., 2021), For this study, we divided the state into three regions: East Texas, Central Texas, and West Texas (Fig. 1). East Texas is comprised of the Pineywoods ecoregion and the west edge of the Gulf Coastal Plain, and the region extends south to the Gulf of Mexico and consists of highly productive and diverse forests that are primarily dominated by pines (*Pinus*) (Burns and Honkala, 1990; Klockow et al., 2018, Klockow et al., 2023a; Klockow et al., 2023b). East Texas experiences humid summers and short, mild winters (Klockow et al., 2018). Central Texas consists of a mix of closed-canopy forests and open-canopy woodlands featuring junipers (*Juniperus*) as well as oaks (*Quercus*), mesquite (*Prosopis*) and other deciduous species (Yang and Crews, 2019; Lawal et al., 2024). West Texas is arid and dominated by desert vegetation; the region's limited forests mostly consist of mesquite and junipers.

We examined the composition of nine major tree genera that are most abundant across the state: *Juniperus, Quercus, Ulmus, Celtis, Triadica, Liquidambar, Diospyros, Prosopis* and *Pinus*. Table 1 shows the relative average abundance of those genera in Texas over the study period. Each is dominant in at least one region of the state. In addition, the genera's relative abundance in each region are shown in Table 2.

2.2. Forest regeneration and aboveground biomass datasets

Our primary data source for forest demographic measures was the Forest Inventory and Analysis Database (FIADB; US Forest Service database (https://www.fs.usda.gov/research/programs/fia). The FIA program gathers information from a network of inventory plots distributed across the country (Bechtold and Patterson, 2005; Patterson and Reams, 2005). A subset of these plots, called a panel, is used to obtain a statistically independent sample of a state or other region of interest (Klockow et al., 2023a; Patterson and Reams, 2005). The FIA program uses an annualized system whereby a fraction of the target

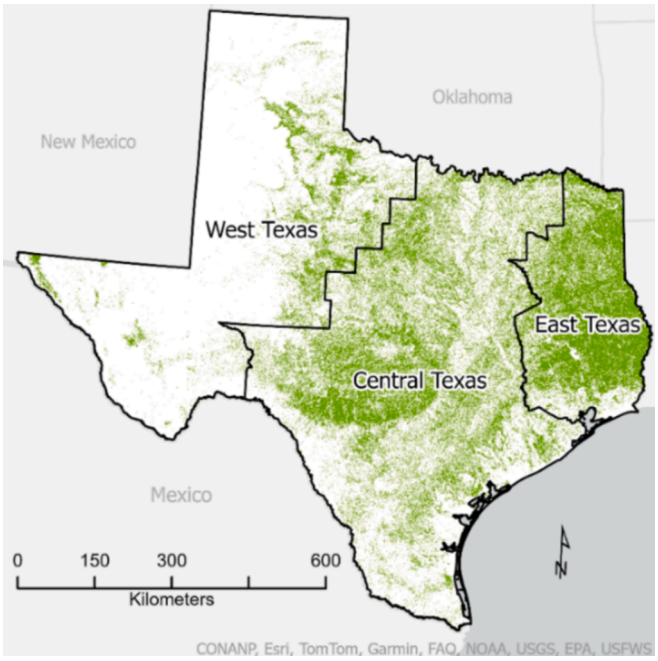


Fig. 1. Map of Texas showing the three sub-regions: East Texas, Central Texas and West Texas. The green pixels have >0 % tree canopy cover (i.e., a simple forest mask that also captures woodlands). This map of forest cover (30-m resolution) is adapted from a 2016 tree canopy cover product developed by the US Forest Service for the 2016 National Land Cover Dataset (NLCD). The sub-regions were developed from a county map available from the Forest Service's Geodata Clearinghouse. Each county was assigned to a sub-region according to its associated FIA survey unit (see Burrill et al., 2024, Appendix B): East Texas includes counties in units 1 and 2; Central Texas includes counties in units 3, 4 and 5; and West Texas includes counties in units 6 and 7. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1
Average count (in billions) of live seedlings, saplings, small trees, and large trees in Texas for the period 2004 – 2019. The genera are arranged in order of abundance. The size classes are defined based on diameter-at-breast-height (dbh): seedlings ($\leq$ 2.54 cm dbh), saplings (2.54 cm < dbh $\leq$ 12.7 cm), small trees (12.7 cm < dbh $\leq$ 25.4 cm) and large trees ($\geq$ 25.4 cm dbh). Data rounded up to nearest values.

Genera	Seedlings	Saplings	Small live trees	Large Live trees
Quercus	9.13	2.0	0.66	0.26
Juniperus	5.25	2.21	0.78	0.274
Prosopis	5.13	2	0.48	0.15
Ulmus	4.19	1.17	0.16	0.043
Pinus	3.43	1.23	0.6	0.24
Celtis	0.763	0.585	0.073	0.014
Diospyros	2.32	1.36	0.005	0.0002
Liquidambar	1.88	0.913	0.1144	0.0034
Triadica	0.84	0.33	0.0126	0.002

region's FIA plots (i.e., one panel) is inventoried every year, with the measurements of all plots (i.e., an inventory cycle) completed over a period of 5 years in East Texas and 10 years in Central and West Texas (Bechtold and Patterson, 2005). For our study, we labelled plots by their measurement year, which is the year a plot was visited in the field. We used 16 years of plot measurements (2004 – 2019).

Seed production, seedling survival, and sapling survival are indicators of the ability of forests to regenerate (Haq *et al.*, 2019). Following Scott *et al.* (2005) and Edgar et al. (2019), we computed annual estimates of counts per genus for four size classes: seedlings ($\leq$ 2.54 cm dbh), saplings (2.54 cm < dbh $\leq$ 12.7 cm), small trees (12.7 cm < dbh $\leq$ 25.4 cm) and large trees ($\geq$ 25.4 cm dbh). Essentially, the seedling and sapling count estimates served as measures of regeneration, while the small and large tree estimates served as proxies for forest health and aboveground biomass. In short, while individual FIA plots are visited every 5 or 10 years, it is possible to get annual estimates of these variables using "single panel" estimation.

There are a few key considerations when using "single panel" estimation. Because each individual panel provides a nearly systematic sample of the population (or in this case, subpopulation) of interest, (sub)population-level estimates are possible, but due to smaller sample sizes, they have greater uncertainty than estimates computed from all panels in an inventory cycle. In either case, it is regular procedure to stratify the plots in the sample in order to reduce variance (Edgar et al., 2019). We performed this stratification (variable strata per year) using classified maps obtained from a USFS tree canopy cover product developed for the 2016 National Land Cover Data (NLCD). We summed the strata-weighted estimates and their variances to derive (sub)population-level estimates and their variances. From these, we computed 95 % confidence intervals for the estimates (equivalent to $\pm$1.96 * standard error (SE) of the estimates.), in keeping with FIA practice with respect to population estimation (Scott *et al.*, 2005; Edgar et al., 2019). We followed this methodology to estimate the size class counts per genera for each subregion. For further details about sampling and forest attribute estimation from FIA data, see Westfall et al. (2022).

2.3. Climate drivers

The climate datasets we assessed include observed precipitation, summer and growing season maximum temperature (T_{max}), summer and growing season potential evapotranspiration (PET), reference evapotranspiration (ET_0) and vapour-pressure deficit (VPD), all obtained from gridMET climate data (see https://www.climatologylab.org/gridmet.html). We chose these climate variables because they are important drivers of drought that can be used to compute drought indices. The gridMET data have a spatial resolution of ~ 4km and daily temporal resolution which we regridded (using bilinear spline) to a monthly time step (Abatzoglou, 2013). We plotted the spatiotemporal distributions (average values within the three regions) of summer / growing season PET, summer / growing season T_{max}, precipitation and VPD (Fig. 2), as well as two derived indices (SPEI12 and HWMId, described below), across East Texas, Central Texas and West Texas. The purpose of this was to see whether any shifts in forest composition coincided with observable trends or patterns of variation in these variables.

2.3.1. Standardized precipitation evapotranspiration index (SPEI)

We computed 12-month SPEI (Spatiotemporal Evapotranspiration Index) from gridMET variables (Fig. 3). The SPEI (see Vicente-Serrano et al., 2010) can be computed at multiple timescales, which are retrospective; for instance, a 12-month timescale includes the current month plus the previous 11 months (Begueria *et al.*, 2014; Lawal et al., 2019a; Lawal et al., 2019b; Lawal et al. 2024). We used SPEI12 because we found previously that it served as a suitable descriptor for a climatological event (2011 hot drought; see Lawal et al., 2024) that caused widespread tree mortality in Texas. Some studies (e.g., Berdanier and Clark, 2016) have observed that long timescales are necessary when analysing drought impacts because forests do not readily exhibit post-disturbance effects unless the drought is of substantial duration and severity. However, our use of SPEI12 follows previous studies (e.g., Subedi et al., 2021) who found the timescale to be appropriate for studying the 2011 drought impact on forests.

We considered the meteorological definition of drought, a drought type that can lead to ecological and/or hydrological drought. Meteorological drought examines precipitation deficits beyond a threshold and baseline and how this impacts the forest ecosystem (Guo et al., 2023; Lawal et al., 2021, 2022; Ganguli and Ganguly, 2016). In calculating the SPEI, we used the FAO Penman-Monteith (PM) method to calculate

Table 2
As in Table 1 but for regions. S-T and L-T denote small live trees and large live trees respectively.

Genera	East				Central				West			
	Seedlings	Saplings	S-T	L-T	Seedlings	Saplings	S-T	L-T	Seedlings	Saplings	S-T	L-T
Juniperus	0.44	0.13	0.02	0.004	4.13	1.75	0.58	0.21	0.68	0.33	0.18	0.06
Quercus	3.25	1.06	0.18	0.11	5.75	0.94	0.47	0.14	0.13	0.013	0.013	0.007
Prosopis	0.006	0.001	0.001	0.001	2.13	0.94	0.22	0.08	3	1.06	0.26	0.07
Ulmus	1.75	0.55	0.06	0.013	2.43	0.62	0.1	0.03	0.012	0.002	0.001	6E-4
Pinus	3.38	1.19	0.59	0.24	0.04	0.03	0.006	0.003	0.013	0.009	0.006	6E-4
Celtis	0.313	0.075	0.016	0.004	0.2	0.41	0.05	0.009	0.25	0.1	0.007	0.001
Diospyros	0.26	0.04	0.002	2E-4	2	1.19	0.003	0.0001	0.06	0.13	0.0	0.0
Liquidambar	1.88	0.91	0.114	0.04	0.003	0.003	1E-4	4E-4	0.0	0.0	0.0	0.0
Triadica	0.75	0.29	0.026	0.002	0.09	0.04	0.01	3E-5	0.0	0.0	0.0	0.0

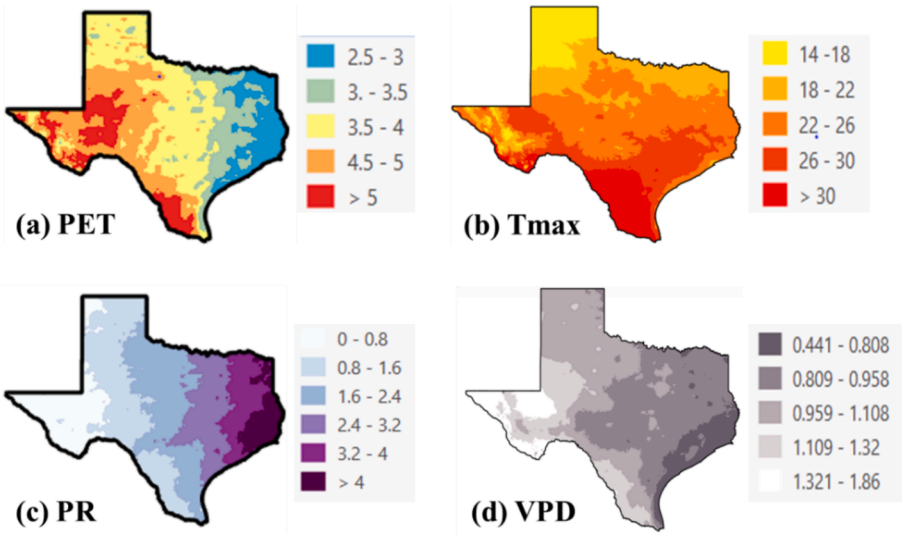


Fig. 2. Spatial distribution of (a) summer (JJA) potential evapotranspiration (PET; mm), (b) summer (JJA) maximum temperature (Tmax; ^{o} C), (c) precipitation (PR; mm) and (d) vapour-pressure deficit (VPD; kPa) for the period 2004 – 2019. The values represent average values per pixel.

potential evapotranspiration (PET), a key input which accounts for climate events such as El-Nino (that increases temperatures and vapour pressure deficits) along the tropical regions (Grossiord et al., 2020; Hollunder et al., 2022). The SPEI incorporates various drought characteristics like duration, spatiotemporal extent and severity (Mukherjee et al., 2018; Hollunder et al., 2022). As a meteorological drought index computed from climatic variables, SPEI is not intended to account for ecosystem resilience, which is evaluated in terms of both recovery and resistance (Oliver et al., 2015). Quantification of tree mortality and growth is crucial when evaluating the inimical impacts of drought on forests (Redmond et al., 2018). Nevertheless, drought timescale and severity remain essential considerations when assessing ecosystem resilience, As noted, we believe that a 12-month timescale for SPEI and associated climate drivers is sufficient for this purpose as well as ecologically justified.

2.3.2. Heat Wave magnitude Index daily (HWMId)

HWMId was used to characterize extreme heat, derived based on Russo *et al.* (2014) and calculated in Lawal et al. (2024) (Fig. 4). HWMId, calculated from the Heat Wave Magnitude Index (HWMI) is the number of heat waves with durations greater than or equal to three consecutive days above a daily temperature threshold, with 1981–2010 as the reference period as was applied in previous studies (Russo et al., 2017). Following Russo et al. (2014), the threshold is the 90th percentile of the daily maximum temperature distribution over a 31-day window. HWMId has an ordinal scale.

To analyse the time series evolution of the climate variables for the 16-year period, we computed and plotted the temporal distributions of SPEI12, HWMId, precipitation, vapour pressure deficit, summer PET and temperature. The hot drought indices (Figs. SPEI12 and HWMId; Lawal et al., 2024) also quantified the local magnitude of the hot drought in Texas as it accounts for the spatiotemporal variability across the regions.

2.4. Trend analysis of genera size class distribution

For each region, we computed annual (2004–2019) count estimates in each size class for the nine target tree genera. Next, we used the RANdom SAmple Consensus (RANSAC; Fischler and Bolles, 1981) regression model to calculate statistical values – p-value, skewness, trend, kurtosis, and error estimates – for the tree genera across the different size classes over the different regions. The RANSAC model is an iterative algorithm for robust estimation of parameters from random subsets of inliers from the complete data set. More information can be found in (https://scikit-learn.org/stable/modules/generated/sklearn.linear_model.RANSACRegressor.html; Fischler and Bolles, 1981). While we acknowledge that our data are less dense than remotely sensed data, the RANSAC model is robust to extrapolate feature changes. Although RANSAC is commonly used with remotely sensed data (imagery, lidar, etc.), in this study, we used it to analyze trends on size class distributions because it can produce robust results even in data sparse situations as in the case of FIA data.

Our trend analyses assessed whether a smaller size class (e.g. seedlings) declined for a genus while large trees continued to rise, thus signalling a lack of recruitment or a regeneration deficit. Furthermore, we evaluated potential compositional changes and made inference on the

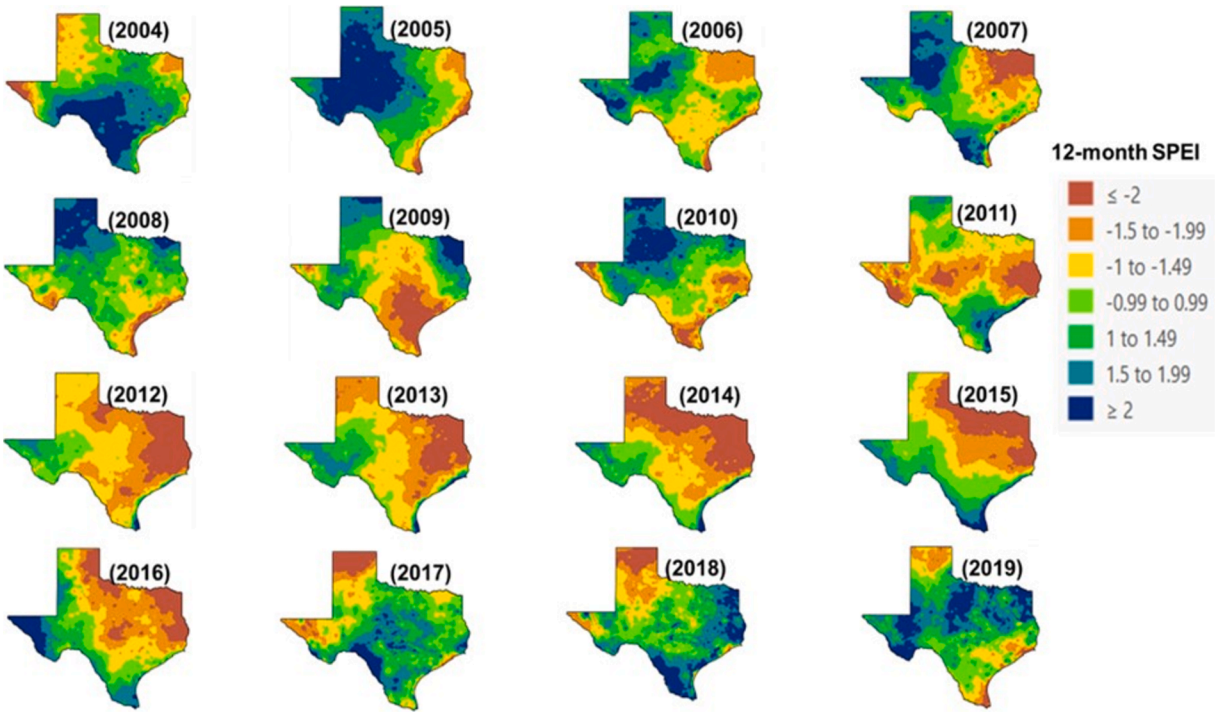


Fig. 3. Spatial distribution of average SPEI12 for the period 2004 – 2019. "Average" means the average of the 12 months in the depicted calendar year, and which is a lagged timescale. For example, the map for 2012 is, in large part, portraying moisture conditions from the previous calendar year, 2011.

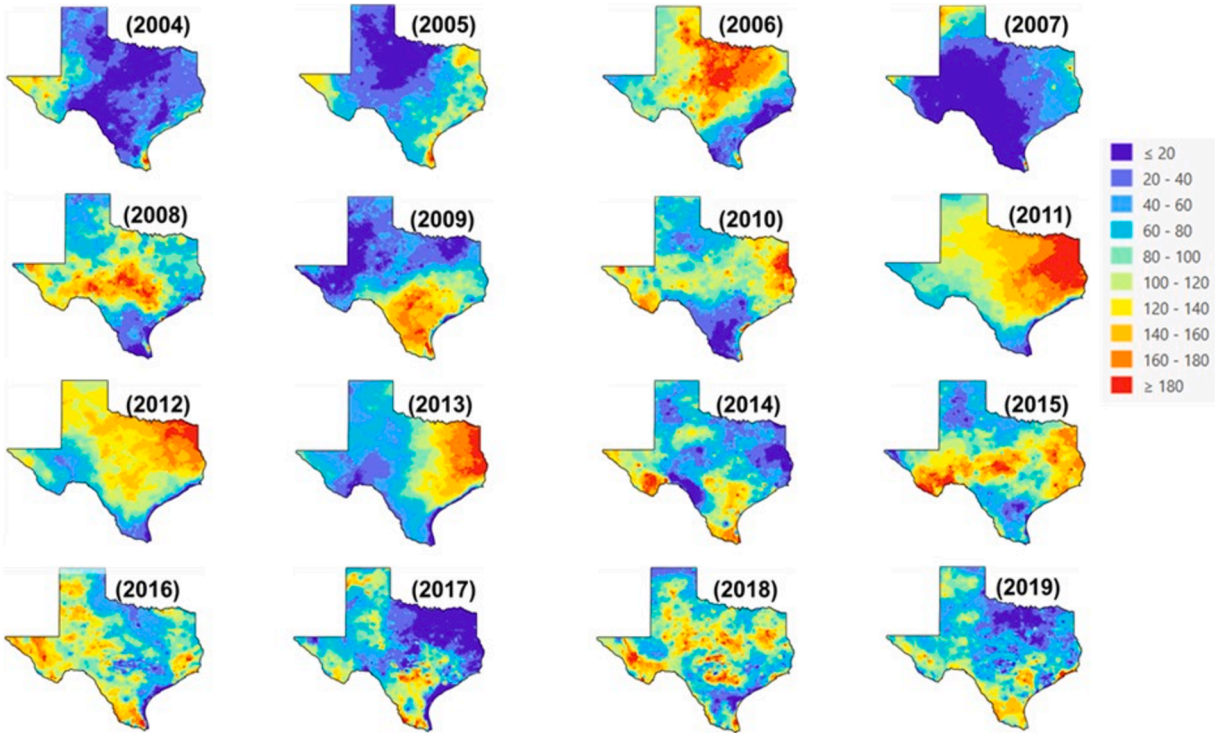


Fig. 4. As in Fig. 3 but for HWMId.

relative importance of switching genera (i.e. reshuffling) by assessing trends and other statistics with RANSAC. We framed resilience and stability based on Seidl and Turner (2022), who described post-disturbance signalling pathways as resilience (no change in structure and composition), restructuring (change in structure but not in composition), reassembly (change in composition but not structure) and replacement (change in composition and structure).

In addition, we calculated and plotted anomalies by subtracting the long-term mean of forest data from the mean data for 2011 (Eqn 1). Long-term mean connotes annual count estimates per genus and size class for the period, 2004–2019. Note, again, that the anomalies were calculated individually for the tree genera relative to 2011, and applied

to SPEI12, HWMId, and the size class count estimates. We selected 2011 as the baseline year because it was the period of an unprecedented hot drought in Texas.

Anomaly = mean (2011) – long-term mean (2004 – 2019) (1)

Furthermore, we examined the impacts of hot drought on Texas forest demographics using anomalies of SPEI12 and HWMId as measures of disturbance. We did this by correlating the anomalies of SPEI12 and HWMId with those of forest across different size classes (see Supplemental Figures for details of the anomalies). We recorded correlation coefficients (r-values) between the anomalies for the genera across different size classes in East Texas, Central and West Texas, for the period 2004 – 2019.

3. Results

3.1. Changes in genera count

Across the regions, there were declining trends in the counts of most of the genera (more evident in seedlings and saplings) between 2004 and 2019 (Fig. 5). The decreasing trends were most prominent in Central and West Texas (Fig. 5). The patterns and trends were variable among genera.

In terms of relative abundance (i.e., importance), each genus varied regionally. For example, the flat trends in *Prosopis* and *Celtis* in East Texas are not especially relevant given that neither genus is abundant in

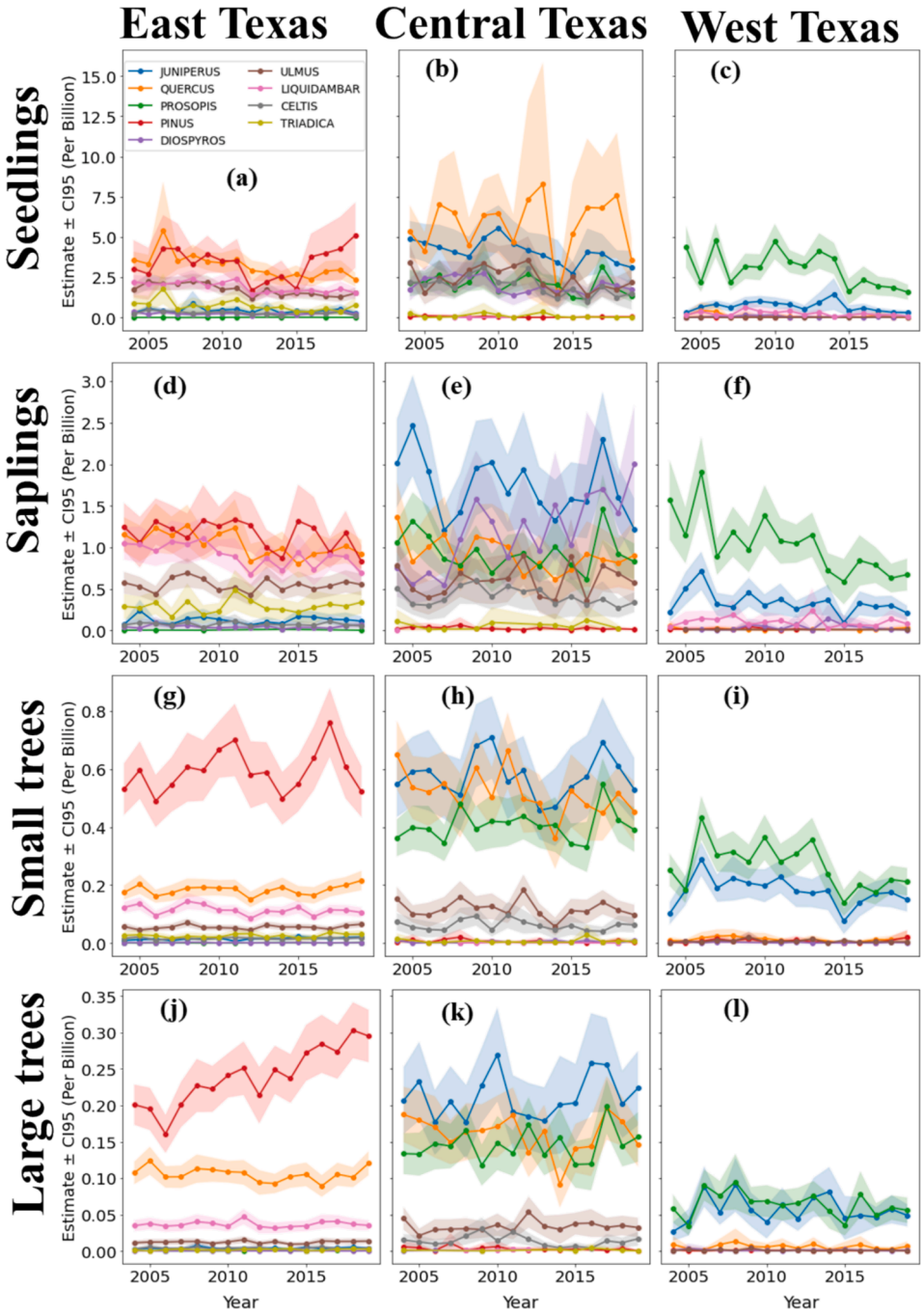


Fig. 5. Temporal distribution of estimates (in billions) of seedlings, saplings, small trees and large trees across East Texas, Central Texas, and West Texas, for the period 2004 – 2019. The distribution is depicted with 95 % confidence intervals, equivalent to ± 1.96 * standard error (SE) of the estimates. The trend lines (incl. variance of trend) are shown in Supplemental Figs. S1 and S2.

the region. However, the trends for *Pinus*, *Quercus* and *Liquidambar* do matter; there are signs of some reshuffling among these three in the post-drought (2011) period. These genera, along with *Ulmus*, showed declines in their count estimates after 2011, but gradual increases after 2015, particularly for *Pinus* and *Quercus*. The sharpest drops in count estimates in the region were in *Pinus*, although the genus modestly rebounded near the end of the analytical period. There is some evidence of demographic reshuffling as we observe an uptick in *Pinus* for small trees and a substantial increase for large trees, suggesting that the genus maintained positive growth through the hot drought. Moreover, there were increases through time for pines of every size class except saplings, which remained mostly flat or possibly showed a slight decrease over time. In any case, it does not appear that there are notable regeneration problems in the pines in East Texas, despite the evident impact of the 2011 drought on pine seedlings. The pines appeared to bounce back quickly. We attribute this to the fact that pines generated a high number of seedlings which may not necessarily be viable, and at population level weathered the hot drought conditions but not necessarily thrived. This suggests that pines may become more resilient to extreme climate conditions as they age.

In Central Texas, the genera of primary interest are *Juniperus*, *Quercus*, and *Prosopis*, although *Ulmus*, *Diospyros* and *Celtis* were also relatively abundant, particularly in the smaller size classes (i.e., seedlings and saplings). Three genera (*Pinus*, *Liquidambar* and *Triadica*) did not show observable trends in the region during the 16-year study period (Fig. 5 b,e,h,k). The other six genera either showed weak declines across the size classes or, in the case of *Juniperus*, *Quercus* and *Prosopis*, declines after 2011 followed by increasing counts after 2015. In addition, small and large tree estimates for *Quercus* and *Prosopis* converged through time. This signals some shuffling in importance between oaks and mesquite in Central Texas, which is perhaps only obvious with the small and large trees. Notably, *Quercus* was the only genus in Central Texas with a pronounced decline across size classes in 2013 (Fig. 5b,e,h,k), which we assume was caused by the hot drought. For example, oaks begin in 2004 as abundant or nearly abundant as junipers, but by the end of the period, they are similar to mesquite in abundance, with the exception of the seedling size class, where oaks are still most abundant. This suggests that oaks dropped in importance as a result of the hot drought, while junipers and mesquite rebounded after the event (Fig. 5 b,e,h,k).

In West Texas, *Juniperus* and *Prosopis* are essentially the only genera of interest (Fig. 5c,f,i,l). Over the region, there were declines through time in all but the largest size class for these two genera. This may suggest eventual loss of forest in West Texas due to an apparent regeneration deficit in its dominant genera. The largest trees seem to have tolerated conditions that smaller size classes did not, perhaps due to their developed structure. For instance, junipers can have up to a 15-m tap root that allows them to access soil water. Generally, *Prosopis* showed a stronger declining trend than *Juniperus*, particularly after the 2011 period (Fig. 5 c,f,i,l). Nonetheless, the disparity in the trends for the two genera is more prominent for seedlings and saplings, than in small and large trees (Fig. 5 c,f,i,l). Indeed, the large tree trends for both *Prosopis* and *Juniperus* were essentially flat or, at most, showed a slight decrease. This may suggest that, across genera, seedlings and saplings are more susceptible to exceptional disturbance like hot drought than larger trees (see further analyses below). However, it is important to consider that seedling viability can vary widely between genera.

3.2. Trends analyses of size classes

With respect to genera, RANSAC regression results showed significant decreasing trends of *Quercus* seedlings (trend = -1.1) and saplings (trend = -0.192) over East Texas, with small and large trees showing effectively flat trends (Table 3). This may point to potential regeneration problems for oaks in the region. We further examined individual oak species because the *Quercus* genus was strongly affected across Texas.

Table 3
Trends and p-values for the period 2004 – 2019 in East Texas. The values in bold indicate where the trend was significant. Absence of trend or data is shown as zero. P-values are for the slope of the RANSAC regression model over the 16-year period.

Genus	Seedlings	Saplings	Small trees	Large trees
Juniperus	−0.03 (0.94)	0.007 (0.4)	0.006 (0.000)	0.00009 (0.06)
Quercus	**−1.1 (0.001)**	**−0.192 (0.007)**	−0.004 (0.29)	0.009 (0.37)
Prosopis	0.003 (0.6)	**0.0003 (0.007)**	0.0002 (0.89)	−0.01 (0.892)
Ulmus	**−0.504 (0.00)**	0.005 (0.9)	−0.0006 (0.2)	0.005 (0.24)
Pinus	0.36 (0.54)	**−0.17 (0.06)**	**0.007 (0.00)**	0.3 (0.64)
Celtis	−0.1 (0.092)	−0.004 (0.21)	−0.0001 (0.84)	0.0008 (0.72)
Diospyros	−0.0071 (0.78)	−0.004 (0.87)	−5.4 (0.62)	−0.0002 (0.59)
Liquidambar	**−0.5 (0.001)**	**−0.19 (0.00)**	0.0007 (0.68)	−0.01 (0.13)
Triadica	**−0.44 (0.002)**	0.005 (0.94)	0.0007 (0.11)	0.002 (0.55)
Other	**−1.5 (0.00)**	**−0.28 (0.00)**	−0.002 (0.58)	−0.005 (0.78)
Total trees	− 0.4 (0.11)	−0.08 (0.4)	0.001 (0.9)	0.004 (0.9)
Q. stellata	−72.4 (0.15)	**−27 (0.032)**	**−13.1 (0.003)**	**−3.9 (0.09)**
Q. nigra	**−637 (0.00)**	**−56 (0.07)**	**20.5 (0.00)**	**2.3 (0.09)**
Q. virginiana	1.1 (0.68)	0.96 (0.162)	0.2 (0.19)	0.32 (0.32)
Q. phellos	−30.1 (0.66)	−30 (0.06)	4.180 (0.24)	0.28 (0.96)
Q. falcata	**–233.2 (0.00)**	**−75 (0.00)**	**−6.04 (0.02)**	**−3.3 (0.013)**
Q. alba	**−85.02 (0.00)**	−8.7 (0.30)	0.65 (0.59)	2.4 (0.03)
Other white oaks	−7.35 (0.58)	−3.72 (0.18)	−0.62 (0.23)	0.3 (0.45)
Other red oaks	−69.62 (0.47)	−1.74 (0.74)	2.9 (0.2)	−1.5 (0.3)

******* Trend (p-value).

With respect to the most abundant species in East Texas and statewide, *Q. nigra*, *Q. stellata* and *Q. falcata* seem the most concerning. Among these species, *Q. stellata* exhibited significant decreasing trends for saplings (−27), small trees (−13.1) and large trees (−3.9), *Q. nigra* showed declining trends for seedlings and saplings but increases for small and large trees, and *Q. falcata* exhibited declining trends for all size classes. By comparison, *Q. alba* had a declining trend only for seedlings. Our findings agree with those of Au *et al.* (2020). For *Pinus*, only saplings had a significant declining (−0.17) trend (Table 3) perhaps indicating reassembly in the region after hot drought. Moreover, *Pinus* had a significant and increasing trend (0.007) for small trees as well as increasing (but not significant) trends for seedlings and large trees, therefore suggesting post-disturbance stability and resilience of the genus. For seedlings of *Ulmus, Liquidambar* and *Triadica*, the trends were significant and declining. This was also true for saplings of *Liquidambar* (trend = -0.19). Note that the *Triadica* genus is represented by a single species, *T. sebifera*, which is non-native and highly invasive, so the genus is qualitatively different from the other genera mentioned here. It is also less abundant in East Texas than pines, oaks, sweetgum, and elms.

Over Central Texas, *Juniperus* declined across all size classes. As these are the two most important genera in the region, the fact that both showed significant declines across size classes is potentially meaningful (Table 4). In West Texas, *Prosopis* showed a significant increasing trend for seedlings but decreasing trends for saplings and small trees (Table 5). Combined with the relatively small (but statistically significant) decreases across size classes for *Juniperus*, the region's other dominant genus, we can infer that West Texas showed more resilience than the other two regions with respect to the smaller size classes.

Table 4
As in Table 3 but for Central Texas.

Genus	Seedlings	Saplings	Small trees	Large trees
Juniperus	**−0.96 (0.005)**	**−0.3 (0.009)**	**−0.3 (0.000)**	**−0.3 (0.1)**
Quercus	0 (−)	**−0.212 (0.03)**	**−0.21 (0.04)**	**−0.21 (0.1)**
Prosopis	−0.57 (0.074)	**−0.212 (0.03)**	0.017 (0.73)	0.007 (0.78)
Ulmus	−0.45 (0.17)	0.05 (0.54)	0.71 (0.5)	0.05 (0.5)
Pinus	−0.023 (0.24)	**−0.15 (0.06)**	−0.004 (0.252)	**−0.003 (0.012)**
Celtis	−0.7 (0.01)	−0.06 (0.24)	−0.06 (0.24)	0.06 (0.24)
Diospyros	**−0.512 (0.03)**	−0.14 (0.08)	0.002 (0.1)	**−0.0003 (0.04)**
Liquidambar	−0.004 (0.174)	0 (−)	0 (−)	0 (−)
Triadica	−0.07 (0.25)	−0.004 (0.9)	−0.004 (0.89)	0.87 (0.8)
Other	−1.35 (0.005)	−0.01 (0.84)	−0.01 (0.84)	−0.01 (0.84)
Total trees	**−0.5 (0.09)**	0.008 (0.8)	−0.003 (0.7)	3e-05 (0.6)
Q. stellata	−653 (0.02)	−30 (0.49)	−36 (0.030)	−11.9 (0.16)
Q. nigra	−113.4 (0.0)	−17 (0.28)	−3.75 (0.19)	−1.1 (0.1)
Q. virginiana	1227 (0.123)	−98.5 (0.27)	−13.5 (0.23)	0.93 (0.61)
Q. phellos	−45 (0.21)	0.57 (0.91)	−0.48 (0.92)	0.28 (0.96)
Q. falcata	−36.1 (0.0)	−0.4 (0.54)	−0.32 (0.11)	0.19 (1.0)
Q. alba	−6 (0.016)	0 (−)	0.21 (0.16)	0 (−)
Other white oaks	−143 (5)	−37.1 (0.018)	−4.7 (0.21)	−0.4 (0.95)
Other red oaks	−136 (0.26)	−35 (0.46)	−26 (0.006)	−2.9 (0.12)

******* Trend (p-value).

Table 5
As in Table 3 but for West Texas.

Genus	Seedlings	Saplings	Small trees	Large trees
Juniperus	−0.15 (0.121)	**−0.14 (0.06)**	**−0.04 (0.021)**	−0.001 (0.96)
Quercus	**−0.16 (0.007)**	−0.01 (0.38)	−0.005 (0.24)	−0.005 (0.47)
Prosopis	**1.28 (0.01)**	**−0.5 (0.00)**	**−0.08 (0.05)**	−0.008 (0.34)
Ulmus	−0.005 (0.31)	−0.001 (0.4)	−0.0008 (0.78)	−0.0004 (0.74)
Pinus	**−0.015 (0.006)**	**−0.01 (0.03)**	−0.002 (0.57)	−0.0008 (0.18)
Celtis	0.11 (0.22)	−0.017 (0.55)	−0.001 (0.71)	−0.0005 (0.5)
Diospyrous	−0.024 (0.373)	0.013 (0.7)	0 (−)	0 (−)
Liquidambar	0 (−)	0 (−)	0 (−)	0 (−)
Triadica	0 (−)	0 (−)	0 (−)	0 (−)
Other	−0.11 (0.01)	−0.03 (0.17)	−0.002 (0.29)	−0.0013 (0.57)
Total trees	**−0.212 (0.09)**	−0.8 (0.4)	−0.0007 (0.4)	−0.0008 (0.62)
Q. stellata	1.3 (0.1)	0.74 (0.017)	0.18 (0.17)	0.07 (0.36)
Q. nigra	0 (−)	0 (−)	0 (−)	0 (−)
Q. virginiana	−5.7 (0.93)	2.1 (0.674)	−1.61 (0.54)	−0.68 (0.31)
Q. phellos	0 (−)	0 (−)	0 (−)	0 (−)
Q. falcata	4.76 (0.75)	0 (−)	−0.36 (0.71)	0.02 (0.71)
Q. alba	0 (−)	0 (−)	0 (−)	0 (−)
Other white oaks	−74 (0.013)	−2.52 (0.57)	−0.66 (0.6)	−1.4 (0.48)
Other red oaks	−86 (0.0)	−8.44 (0.00)	−2 (0.08)	−0.09 (0.8)

******* Trend (p-value).

3.3. Climate drivers of forest dynamics

The magnitude of SPEI12 was lowest between 2011 and 2013 (Fig. 6a,g,m). Although there was extreme drought in 2011 over the regions (Fig. 6a,g,m), we also observed severe drought occurrence in 2014. The highest magnitude of increase in summer PET was observed in 2011, although West Texas showed consistently high magnitudes across the years (Fig. 6 b,h,n). We also observed a similar pattern for summer T_{max} (Fig. 6 c,i,o). Within the 16-year period, the magnitude of precipitation was noticeably higher in 2017 over East Texas and, to a lesser extent, over Central Texas, perhaps due to a hurricane (Fig. 6d). The magnitude of HWMId was higher in 2011 compared to other years, though comparably lower over West Texas (Fig. 6 e,k,q), while VPD was higher in a pattern similar to that observed for summer PET. In general, we can infer that the interaction of these climate drivers – and by extension, the 2011 hot drought event – may have been responsible for the observed declines in tree genera. This inference is based on Lawal et al. (2024), who found that the 2011 hot drought was largely responsible for tree mortality in Texas. In addition, the genera tended not to recover after SPEI12 turned positive (wet). One exception was that *Pinus* seedling counts in East Texas did seem to recover after 2011, i.e., they loosely followed the SPEI12 curve for East Texas (see above Fig. 5). Combined with the results for small and large trees in East Texas, perhaps there is some evidence of a modest shift towards pines and away from oaks in that region. With respect to Central and West Texas, we observe a second drought event documented in 2018 that could have impeded recovery. In summary, during the 2011 hot drought there were evident jumps in HWMId, PET and VPD (and Tmax to a lesser degree); SPEI12 was low but the extreme heat appears to have been more anomalous.

With respect to trends and warning signals of forest disturbance impacts in Texas, we examined the temporal distributions of anomalies for the nine tree genera.

Generally, there were declines in the counts for most of the genera although the magnitude varied. For *Quercus*, there were declines of seedlings and saplings in East Texas, but flat trends in West Texas, and intermittent change in the trend direction over Central Texas (Supplemental Fig. 3). Similarly, *Triadica* and *Liquidambar* showed prominent declining trends over East Texas (Supplemental Figs. S3e,f). For *Celtis*, there was no clear trend (Supplemental Fig. S3d) while *Pinus* spp. showed the largest variability compared to other tree genera (Supplemental Fig. S3h).

For small and large trees, *Ulmus, Celtis, Triadica, Liquidambar, Prosopis* and *Diospyros* did not show any clear trends of species composition (Supplemental Fig. S4 a,d,e,f,g,i). Over East Texas, *Pinus* showed a declining trend between 2011 and 2014 and increased afterwards (Supplemental Fig. S4h). For *Quercus*, there was variability in the estimates of anomalies in East and West Texas (Supplemental Fig. S4c).

The residuals (from time series decomposition) shown in Figs. S5 and S6 are the derived estimates after the removal of seasonality and trend during time series decomposition. For seedlings and saplings, there was lower variability of residuals of most of the genera over East Texas but across Central Texas, the variability was high. Similar patterns can be observed for the residuals of small and large trees. The figures show these patterns most obviously for *Juniperus*, *Quercus* and *Pinus*, and to a lesser extent for *Prosopis*, which makes sense since these are the genera that are important across more than one region.

3.4. Impacts of drought on forest disturbance

Hot drought contributed significantly to forest disturbance in Texas, with more size classes affected in East Texas than other regions (Tables 6–8). We should note that anomalies here were modelled as forest demographic disturbance, i.e., correlations between anomalies for SPEI12 and HWMId and anomalies for the size classes of the genera. In general, seedlings and saplings were more negatively affected by hot drought than small or large trees across all three regions. For East Texas, *Quercus, Prosopis* and *Liquidambar* (r = -0.2) had significant negative correlations in the sapling size class, while *Prosopis* also had a significant negative correlation in the small tree size class (r = -0.3), as did *Pinus*. With respect to large trees, *Diospyros* and *Ulmus* (r = -0.3 and −0.2

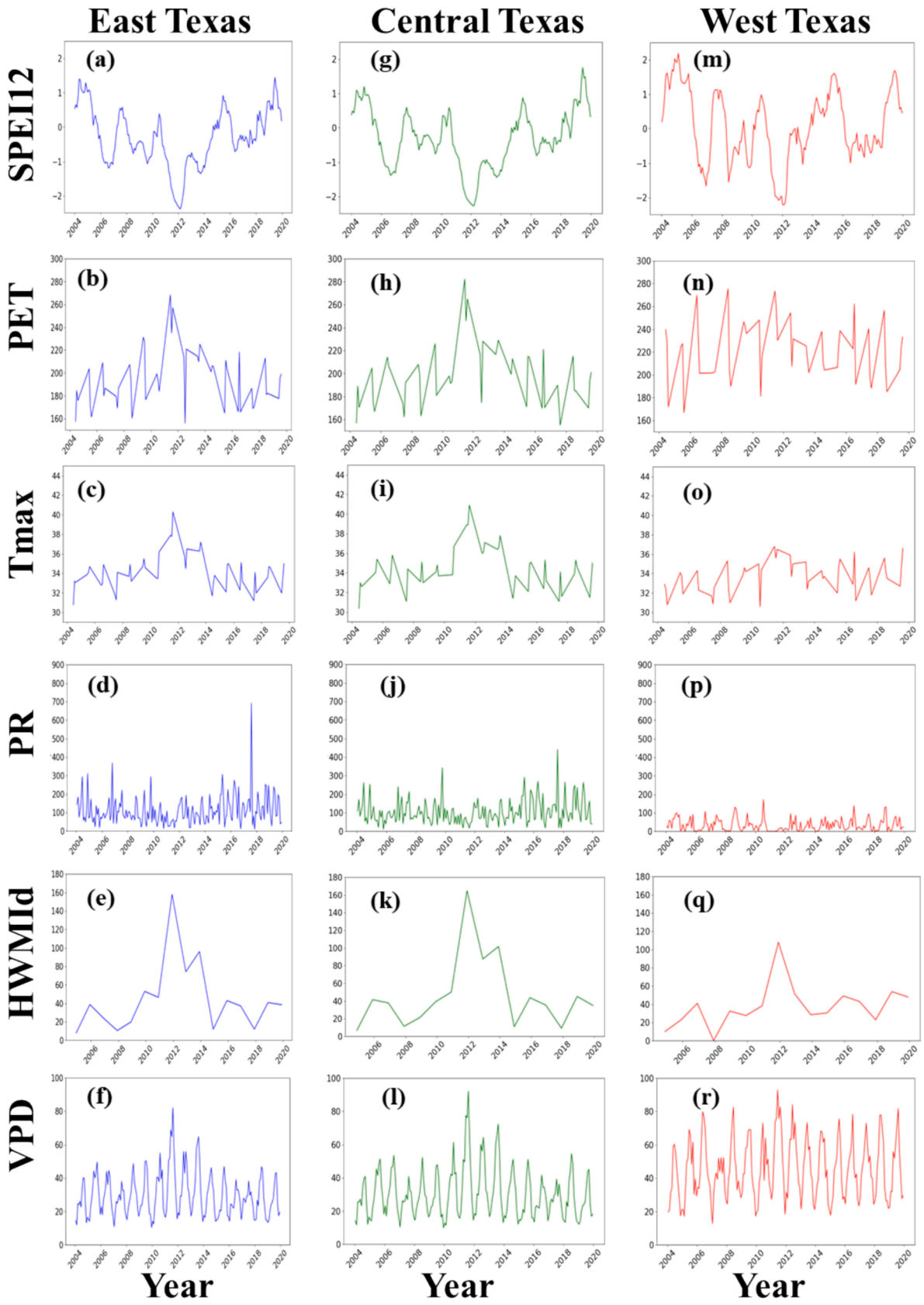


Fig. 6. Temporal distribution of drought and climate variables. (a) – (r) shows temporal distribution of 12-month SPEI (SPEI12), summer (JJA) potential evapotranspiration (PET, mm), summer (JJA) maximum temperature (Tmax, ^{o} C), precipitation (PR, mm), HWMId and vapour-pressure deficit (VPD, kPa) for the period 2004 – 2019. The values represent average values across all pixels in the region. East Texas is shown in (a) – (f), Central Texas is shown in (g) – (l) while West Texas is shown in (m) to (r).

Table 6
Correlation coefficient (r-values) between hot drought (SPEI12 and HWMId) and anomaly for the period 2004 – 2019 for genera in East Texas, indicate the random chance of occurrence between the variables. The values in bold indicate where $|r| > 0.2$.

Genus	Seedlings	Saplings	Small trees	Large trees
Juniperus	−0.12	−0.1	−0.07	0.13
Quercus	**0.21**	**−0.21**	**0.23**	**0.3**
Prosopis	0.1	**−0.2**	**−0.3**	**0.4**
Pinus	−0.14	−0.04	**−0.3**	−0.1
Diospyros	**0.45**	−0.05	0.18	**−0.3**
Ulmus	**−0.41**	0.1	**0.5**	**−0.2**
Liquidambar	**0.4**	**−0.2**	**0.5**	**0.6**
Celtis	**−0.2**	**0.3**	**0.5**	**0.3**
Triadica	**−0.3**	**−0.1**	**0.5**	**0.2**
Other	0.14	**0.6**	**0.2**	−0.07

Table 7
As in Table 6 but for Central Texas.

Genus	Seedlings	Saplings	Small trees	Large trees
Juniperus	**−0.4**	−0.03	**−0.2**	0.04
Quercus	**−0.5**	**0.4**	**0.5**	0.1
Prosopis	−0.1	0.1	**−0.2**	0.01
Pinus	**−0.4**	**−0.3**	**0.23**	**−0.2**
Diospyros	−0.01	**0.3**	0.07	0
Ulmus	**−0.2**	0.11	−0.12	**−0.3**
Liquidambar	0	0	**0.2**	**0.8**
Celtis	−0.1	**0.3**	**0.22**	**0.32**
Triadica	0.01	**0.44**	0.12	0
Other	0.07	**0.5**	−0.03	**−0.4**

Table 8
As in Table 6 but for West Texas.

Genus	Seedlings	Saplings	Small trees	Large trees
Juniperus	0.12	0.07	−0.1	**−0.3**
Quercus	0.13	**0.45**	0.12	**0.43**
Prosopis	**0.6**	**0.34**	**0.2**	**0.23**
Pinus	**−0.22**	0.03	−0.07	**0.8**
Diospyros	0.001	−0.14	0	0
Ulmus	−0.1	**0.91**	**0.45**	**0.7**
Liquidambar	0	0	0	0
Celtis	0.1	**0.31**	**0.4**	0.02
Triadica	0	0	0	0
Other	−0.17	**−0.8**	−0.04	**−0.4**

respectively) were more negatively affected than the other genera. In Central Texas, *Quercus* in the seedling size class was much more negatively affected by hot drought (r = -0.5) than the other genera, with *Juniperus* and *Prosopis* most affected in the small tree size class (r = -0.2) and *Ulmus* in the large tree size class (r = -0.3). *Pinus* and *Juniperus* in seedlings and large trees, respectively, were most affected over West Texas. The individual influence of drought and extreme heat in each region are shown in Supplemental Tables 1 – 6.

4. Discussion

4.1. Ecological compositional changes due to hot drought, resilience

Our analysis has revealed potentially long-term demographic changes over 16 years (2004 – 2019) in Texas. Although these effects largely occurred in seedlings and saplings, we expect that these changes will eventually alter the composition of small and large tree size classes. The recognition that seedling and sapling demographics determine canopy dynamics has long been recognized (Ponge et al., 1998, Vickers et al., 2019) even if the necessary long-term data have not always been adequate (Clark et al. 1999; Harris et al., 2022).

Our previous research (Lawal et al., 2024) demonstrated a substantial pulse of large tree (dbh > 12.7 cm) mortality associated with the hot drought conditions of 2011–2013. We can infer that a similar mortality pulse occurred for the smaller size classes (see McDowell et al., 2008, Adams et al., 2017), although FIA does not record the mortality of seedlings, and only recently began documenting sapling mortality in a manner similar to larger trees (e.g., recording of standing dead saplings became standard practice as of 2015). We can expect that mortality would vary widely by species and their traits (Harrison and LaForgia, 2019). The mortality of small trees is particularly difficult to capture (the dead stems are inherently fragile) and their species assignment is typically not possible.

Despite the expected, but unseen, pulse of small tree mortality associated with severe drought, the decline of these small size classes often spanned the entire period of record, suggesting that either, a) excess mortality occurred throughout the period of record, and/or b) natural regeneration was declining for the period of record (Clark et al., 1999). The distinction between seedling mortality and low regeneration (seed germination and establishment) (e.g., Milbau et al., 2017) is challenging to estimate for intermittent measurements such as FIA (Burrill et al., 2024). The larger question is: Why did small size classes decline when and where they declined? Here we offer a few hypotheses: 1) Basal area was increasing, and therefore creating a higher leaf area index (LAI), which reduced light levels at the forest floor and therefore limited regeneration, particularly for shade-intolerant tree species (Harcombe et al., 2002); 2) Ongoing climate changes – including a long decline in SPEI over the period of record – reduced regeneration and/or induced small size class mortality over a longer period than the severe drought of 2011–2013 (e.g., McDowell et al., 2008); and 3) other biotic or abiotic agents caused mortality. Furthermore, we should note that our study agrees with Subedi et al. (2021), who found high mortality of small trees in East Texas.

To examine the first hypothesis, we plotted basal area over time (Supplemental figs. 7 & 8). We summarized across all species, assuming that any increase in basal area would be correlated with higher LAI and lower light at the forest floor. We did not see any consistent trend in basal area that would support this hypothesis. To examine the second hypothesis – climate-induced regeneration decline or mortality (e.g., Shriver et al., 2022) – we generated exploratory models (linear and non-linear) of the number of seedlings and saplings against the climate data (by species and by region), and found some significant relationships (contrary to Shriver et al., 2022). Nevertheless, we do not believe we can rule out long-term climate shifts. The patterns of SPEI12 (Fig. 6a, g, m) were highly variable and even intermittent pulses of mortality could create long-term decline. Intermittent pulses of regeneration can sustain a population of trees (e.g., Savage et al., 1996, Kolb et al., 2020) and similarly, increased frequency of mortality pulses can cause long-term decline (Kolb et al., 2020, Pozner et al., 2022). This recruitment risk is not limited to climatic triggers but can also result from disturbances (e.g., fire, Tepley et al., 2017) and from browsing (Nardone et al., 2010). For example, Serra-Diaz et al. (2015) demonstrated the effect of disturbance mortality pulses in forest of California. Which brings us to our third hypothesis: Other biotic or abiotic agents (e.g., Barrette et al., 2017). Although we do not have the data necessary to disprove this hypothesis, there is limited anecdotal or empirical evidence that would suggest any sustained increases in human pressure, browsing pressure, prescribed fire, wildfire, or any other cause that would produce a sustained decline in some small size classes over this time period (but see Russell and Fowler 2002). Therefore, in response to our question regarding whether extreme (or exceptional) hot drought conditions, even if they are not prolonged, can cause forest demographic change, including in the short-term, we conclude that that this is the most likely explanation.

4.2. Hot drought as a driver of ecological transformation in Texas forest ecosystem

Hot drought is likely to cause ecological transformation across different landscapes (Moss et al., 2024). In our study, we observed nuanced species assemblages that signal potential transformation of forested landscapes in Texas. For example, in Central Texas, we observed that oaks became less important and abundant after the 2011 drought event. In addition, in agreement with Esquivel-Muelbert et al. (2019), we observed a differential recruitment rate in the region. Our study has demonstrated and agrees with the postulations of previous studies (e.g., Crausbay et al., 2022) about the risks of drought causing regime shifts and compositional changes in landscapes. Furthermore, our study (see Supplemental Tables S1 – S6) showed that not only can compounding stress and additional disturbances (extreme heat in this case) interact with drought but can also enable ecosystem transformation. This agrees with studies of Boulton et al. (2022) and Moss et al. (2024). As regards to whether declines or increases in species signal a potentially problematic lack of recruitment / regeneration deficit, our findings support this argument.

With respect to regional resilience to drought disturbance, Chaudhary *et al.* (2022) reported that East Texas shows a strong resilience, as there was marked recovery in post-drought growth rate and basal area, though they noted that neither was at the same level as during the pre-drought period. We also observed an inhibited post-drought growth of some genera and *Quercus* species (see Fig. 5). Nevertheless, we note that alterations in compositions of genera may have also been caused by stochastic changes in demography and/or competition (Young et al., 2015; Batllori et al., 2019).

Our findings suggest that pines may become more resilient to extreme climate conditions as they age. In addition, we can infer that the species demographics in West Texas are characteristic of long-term and perhaps mega-drought (as has been labelled in the Southwestern US). We also can infer that West Texas shows more resilience than the other two regions with respect to seedlings and small trees. In general, we can infer that the interaction of the climate drivers we analysed —specifically those associated with extreme moisture deficit and extreme heat – may have been responsible for decline in tree genera. This inference is based on Lawal et al. (2024), who found that the 2011 hot drought was largely responsible for tree mortality in Texas. Moreover, our study suggests that drought-tolerant genera will eventually make up a larger share of forest trees and that drought susceptibility of species varies among size classes.

Considering increasing global warming, we further postulate that the Texas region is likely to experience more frequent hot droughts – thus leading to a positive feedback loop whereby there is a larger ecological transformation due to high evaporative demand and less precipitation. Consequently, to address the risks of hot drought, there is a need to understand the sensitivities of different ecosystems, which vary geographically and compositionally, to increase resilience (Coble et al., 2017; Vilonen *et al.*, 2022). Thus, we suggest incorporating suitable species (water stress) traits into modelling ecosystem response to drought.

4.3. Variability in regional forest demography trends

Our study shows variable trends in forest demography across Texas regions. We observed more variable demographic trends in Central Texas, where there is higher diversity, than East and West Texas. Diversity in ecology, climate, soil and forest types are likely factors for the variability in composition (for seedlings and saplings) across different Texas regions.

Furthermore, these regions also experience climatological variability. For instance, over most of East Texas, the seasonal temperature is moderated (ranging between 11 °C and 19.4°F) by the Gulf Coast which is the primary source of precipitation (Larkin and Bomar, 1983). However, over West Texas, where average temperatures range between 13 °C and 20 °C along with annual precipitation of about 10 in., fewer than in East Texas, the major source of precipitation is the eastern Pacific Ocean and recycled moisture from land (Slade and Patton, 2003). In Central Texas, there is even more precipitation and temperature variability, with projections showing that the area will be warmer by mid-21st century, with annual temperatures expected to increase in temperature in case of extreme heat events (i.e., frequent temperatures of 38 °C and more) and decrease in soil moisture (IPCC, 2007).

Variable soil composition in Texas is an important factor in variable demography shifts. In West Texas, most of the soils have slow to rapid drainage, unlike Central Texas where the soils range from alkali sandy to loamy (websoilsurvey.nrcs.usda.gov; www.tx.nrcs.usda.gov). In addition to variable soil matter across the regions, natural variability and anthropogenic change (e.g. hot drought) also impact soil. Siebert et al. (2019) showed that extreme drought alters soil activity and functional composition. Consequently, essential ecosystem processes like nutrient recycling, decomposition and microbial activity are impacted by drought. We postulate that the co-occurrence of drought and extreme heat will have more significant impacts on forest demography as a result.

4.4. Utility of the FIA inventory data for analyzing species compositional shifts

We employed single-panel estimation of the FIA data to minimize effects of the temporal lag bias that occurs when using full inventory cycles (i.e., full sets of panels) for comparative estimation (Klockow et al., 2023a). This lag bias is particularly relevant for Central and West Texas due to their longer inventory cycle (10 years) than East Texas (5 years). Furthermore, single-panel estimation makes it more straightforward to evaluate any changing trends in estimates after a specific event such as the 2011 hot drought (Edgar et al., 2019; Klockow et al., 2023a). The annualized inventory design of FIA, while perhaps still best suited to full-cycle estimation, provides yearly, spatially balanced samples that enable such analyses (Westfall et al., 2022). However, single-panel estimation comes with some trade-offs: smaller sample sizes translate to greater uncertainty in the estimates, and rates of change are only approximate since they are not based on remeasurements of the same trees across inventory cycles (Klockow et al., 2023a).

Because each FIA plot is intended to represent a larger forest area (~2428 ha for full-cycle estimation), finer-scale forest characteristics and dynamics are difficult to capture, which is why there is growing interest in methods such as small area estimation (Frescino et al., 2022; Stanke et al., 2022). We also acknowledge that FIA data availability restricted the time window (2004–2019) of our analyses. Consequently, we cannot be sure that the demographic trends we observed will continue similarly in the future. Nevertheless, it seems clear that a significant disturbance like the 2011 hot drought can be expected to cause some forest demographic changes even in the short term.

5. Summary, conclusions, and recommendations

The recent alteration of forest demography in Texas likely can be attributed to climate disturbance, i.e., hot drought. In this study, we examined demographic changes in genera over East, Central and West Texas for the period 2004 – 2019, including a widely documented 2011 hot drought event. We used FIA data to evaluate changes in trend composition. We examined the changes in forest demography in association with observable trends of SPEI12 – our chosen drought metric – and several other climate drivers: potential evapotranspiration (PET), precipitation, vapour pressure deficit, maximum temperature and the Heat Wave Magnitude Index daily (HWMId). Also, we investigated the contribution of hot drought to forest disturbance across Texas region using Pearson correlation coefficients. To examine influence of drought as forest demography disturbance, we correlated the anomalies of

SPEI12 and HWMId with those of forest across different size classes (i.e. seedlings, saplings, small trees and large trees). Across the regions, we observed declining trends in the count estimates of most of the genera (more evident in seedlings and saplings), particularly in the seedling and sapling size classes, in response to hot drought.

While our analyses are comprehensive, we note that the modelled relationship between hot drought and compositional change may show higher predictability were a different data and model used. Nevertheless, our study has shown that the gap and opportunities for monitoring demographic change particularly in a climate hot bed like Texas, which can be a baseline for which a framework of improved management of the ecosystem may be facilitated.

CRediT authorship contribution statement

Shakirudeen Lawal: Writing – review & editing, Visualization, Validation, Supervision, Software, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Frank H. Koch:** Writing – review & editing, Visualization, Validation, Supervision, Investigation, Data curation, Conceptualization. **Robert M. Scheller:** Writing – review & editing, Visualization, Validation, Supervision, Project administration, Methodology, Conceptualization. **Jennifer Costanza:** Writing – review & editing, Visualization, Supervision, Formal analysis, Data curation, Conceptualization.

Funding

This research was funded by the US Department of Agriculture, Forest Service, including through agreement 21-JV-11330180-038 between the Forest Service and the North Carolina State University. The contents of the study are solely the responsibility and the creation of the authors and do not reflect the official views of the U.S. Forest Service.

Declaration of competing interest

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

Acknowledgements

The authors thank the US Department of Agriculture, Forest Service, Southern Research Station.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2025.113117.

Data availability

Data will be made available on request.

References

Abatzoglou, J.T., 2013. Development of gridded surface meteorological data for ecological applications and modelling. Int. J. Climatol. 33, 121–131.

Adams, HD, Guardiola-Claramonte, M., Barron-Gafford, G.A.., et al., 2009. Temperature sensitivity of drought-induced tree mortality portends increased regional die-off under global-change-type drought. Proceedings of the National Academy of Sciences of the United States of America 106, 7063–7066.

Adams, H.D., Barron-Gafford, G.A., Minor, R.L., Gardea, A.A., Bentley, L.P., Law, D.J., Breshears, D.D., McDowell, N.G., Huxman, T.E., 2017. Temperature response surfaces for mortality risk of tree species with future drought. *Environ. Res. Lett.* 12 (11), 115014.

Alig, R.; Butler, B. 2004. Area changes for forest cover types in the United States, 1952 to 1997, with projections to 2050. Gen. Tech. Rep. PNW-GTR-613. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 106 p.

Anderegg, W.R., Trugman, A.T., Badgley, G., Konings, A.G., Shaw, J., 2020. Divergent forest sensitivity to repeated extreme droughts. *Nat. Clim. Chang.* 10 (12), 1091–1095.

Au, TF, Maxwell, JT, Novick, KA, Robeson, SM, Warner, SM, Lockwood, BR, Phillips, RP, Harley, GL, Telewski, FW, Therrell, MD, Pederson, N, 2020. Demographic shifts in eastern US forests increase the impact of late-season drought on forest growth. Ecography 43, 1475–1486.

Barrette, M., Bélanger, L., De Grandpré, L., Royo, A.A., 2017. Demographic disequilibrium caused by canopy gap expansion and recruitment failure triggers forest cover loss. *For. Ecol. Manage.* 401, 117–124.

Batllori, E., et al., 2019. Compound fire-drought regimes promote ecosystem transitions in Mediterranean ecosystems. *J. Ecol.* 107 (3), 1187–1198.

Batllori E, Lloret F, Aakala T, Anderegg WRL, Aynekulu E, Bendixsen DP, Bentouati A, Bigler C, Burk CJ, Camarero JJ, Colangelo M, Coop JD, Fensham R, Floyd ML, Galiano L, Ganey JL, Gonzalez P, Jacobsen AL, Kane JM, Kitzberger T, Linares JC, Marchetti SB, Matusick G, Michaelian M, Navarro-Cerrillo RM, Pratt RB, Redmond MD, Rigling A, Ripullone F, Sangüesa-Barreda G, Sasal Y, Saura-Mas S, Suarez ML, Veblen TT, Vilà-Cabrera A, Vincke C, Zeeman B. Forest and woodland replacement patterns following drought-related mortality. Proc Natl Acad Sci U S A. 2020 Nov 24; 117(47):29720-29729. doi: 10.1073/pnas.2002314117. Epub 2020 Nov 2. PMID: 33139533; PMCID: PMC7703631.

Bechtold, W. A., Patterson, P. L., 2005. *The Enhanced Forest Inventory and Analysis Program—National Sampling Design and Estimation Procedures. General Technical Report SRS-80.* Asheville, NC: US Department of Agriculture Forest Service, Southern Research Station.

Beguería, S., Vicente-Serrano, S.M., Reig, F., Latorre, B., 2014. Standardized precipitation evapotranspiration index (SPEI) revisited: Parameter fitting, evapotranspiration models, tools, datasets and drought monitoring. Int. J. Climatol. 34, 3001–3023. https://doi.org/10.1002/joc.3887.

Bennett, et al., 2023. Sensitivity of South American tropical forests to an extreme climate anomaly. Nat. Clim. Chang. 13, 967–974, 10.1038/s41558-023-01776-4 ForestPlots.NET DOI: 10.5521/forestplots.net/2023_2.

Berdanier, A.B., Clark, J.S., 2016. Multiyear drought-induced morbidity preceding tree death in southeastern U.S. forests. *Ecol. Appl.* 26, 17–23. https://doi.org/10.1890/15-0274.

Boulton, C.A., Lenton, T.M., Boers, N., 2022. Pronounced loss of Amazon rainforest resilience since the early 2000s. *Nat. Clim. Chang.* 12 (3), 271–278.

Burns, Russell M., and Barbara H. Honkala, tech. coords. 1990. Silvics of North America: 1. Conifers; 2. Hardwoods. Agriculture Handbook 654. U.S. Department of Agriculture, Forest Service, Washington, DC. 877 p.

Burrill, Elizabeth A.; DiTommaso, Andrea M.; Turner, Jeffery A.; Pugh, Scott A.; Christensen, Glenn; Perry, Carol J.; Lepine, Lucie C.; Walker, David M.; Conkling, Barbara L. 2024. The Forest Inventory and Analysis Database, FIADB user guides, volume database description (version 9.2), nationwide forest inventory (NFI). U.S. Department of Agriculture, Forest Service. 1042 p. [Online]. Available at web address: https://www.fs.usda.gov/research/products/dataandtools/datasets/fia-datamart.

Cayan, D.R., Das, T., Pierce, D.W., Barnett, T.P., Tyree, M., Gershunov, A., 2010. Future dryness in the southwest US and the hydrology of the early 21st century drought. *Proc. Natl. Acad. Sci.* 107 (50), 21271–21276.

Chaudhary, Tilak & Xi, Weimin & Subedi, Mukti & Rideout-Hanzak, Sandra & Su, Haibin & Dewez, Nicholas & Clarke, Stephen. (2022). East Texas forests show strong resilience to exceptional drought. Forestry: An International Journal of Forest Research. 96. 10.1093/forestry/cpac050.

Clark, J.S., Beckage, B., Camill, P., Cleveland, B., HilleRisLambers, J., Lichter, J., McLachlan, J., Mohan, J., Wyckoff, P., 1999. Interpreting recruitment limitation in forests. *Am. J. Bot.* 86 (1), 1–16.

Clark, J.S., Iverson, L., Woodall, C.W., Allen, C.D., Bell, D.M., Bragg, D.C., Zimmermann, N.E., 2016. The impacts of increasing drought on forest dynamics, structure, and biodiversity in the United States. *Glob. Chang. Biol.* 22 (7), 2329–2352.

Coble, A.P., et al., 2017. Are Northeastern US forests vulnerable to extreme drought? *Ecol. Process.* 6, 1–13.

Costanza, J.K., Koch, F.H., Reeves, M.C., 2023. Future exposure of forest ecosystems to multi-year drought in the United States. Ecosphere 14 (5), e4525.

Crausbay, S.D., et al., 2022. A science agenda to inform natural resource management decisions in an era of ecological transformation. *Bioscience* 72 (1), 71–90.

Crouchet, S.E., Jensen, J., Schwartz, B.F., Schwinning, S., 2019. Tree mortality after a hot drought: distinguishing density-dependent and -independent drivers and why it matters. Front. for. Glob. Change 2, 21. https://doi.org/10.3389/ffgc.2019.00021.

Dakos, V., Carpenter, S.R., van Nes, E.H., Scheffer, M., 2015. Resilience indicators: prospects and limitations for early warnings of regime shifts. Philos. Trans. R. Soc. Lond. B Biol. Sci. 370 (1659), 20130263. https://doi.org/10.1098/rstb.2013.0263. PMCID: PMC4247400.

Edgar, C.B., Westfall, J.A., Klockow, P.A., Vogel, J.G., Moore, G.W., 2019. Interpreting effects of multiple, large-scale disturbances using national forest inventory data: A case study of standing dead trees in east Texas, USA. *For. Ecol. Manage.* 437, 27–40.

Esquivel-Muelbert, A., et al., 2019. Compositional response of Amazon forests to climate change. *Glob. Chang. Biol.* 25 (1), 39–56.

Fischler, M.A.; Bolles, R.C. Random Sample Consensus: A Paradigm for Model Fitting with Applications to Image Analysis and Automated Cartography. *Commun. ACM* **1981**, *24*, 381–395. https://doi.org/10.1145/358669.358692.

Frescino, T.S., McConville, K.S., White, G.W., Toney, J.C., Moisen, G.G., 2022. Small area estimates for national applications: a database to dashboard strategy for FIA using FIESTA. Front For. Global Change 5.

Führer, E., 2000. Forest functions, ecosystem stability and management. Forest Ecol. Manage. 132 (1). https://doi.org/10.1016/S0378-1127(00)00377-7. ISSN 0378-1127.

Ganguli, P., Ganguly, A.R. (2016). Space-time trends in U.S. meteorological droughts, J. Hydrol.: Regional Studies, Volume 8, 2016, Pages 235-259, ISSN 2214-5818, https://doi.org/10.1016/j.ejrh.2016.09.004.

Gazol, A., Camarero, J.J., 2022. Compound climate events increase tree drought mortality across European forests. *Sci. Total Environ.* 816, 151604.

Gitlin, A.R., Sthultz, C.M., Bowker, M.A., Stumpf, S., Paxton, K.L., Kennedy, K., Muñoz, A., Bailey, J.K., Whitham, T.G., 2006. Mortality gradients within and among dominant plant populations as barometers of ecosystem change during extreme drought. Conservation Biology 20, 1477–1486.

Grossiord, C., Buckley, T.N., Cernusak, L.A., Novick, K.A., Poulter, B., Siegwolf, R.T.W., Sperry, J.S., McDowell, N.G., 2020. Plant responses to rising vapor pressure deficit. *New Phytologist* 226 (6), 1550–1566. https://doi.org/10.1111/nph.16485.

Gunderson, L.H., 2000. Ecological resilience–in theory and application. *Annu. Rev. Ecol. Syst.* 31, 425–439. http://www.jstor.org/stable/221739.

Guo, W., Huang, S., Huang, Q., Leng, G., Mu, Z., Han, Z., Wei, X., She, D., Wang, H., Wang, Z., Peng, J., 2023. Drought trigger thresholds for different levels of vegetation loss in China and their dynamics. Agric. Forest Meteorol. 331, 109349. https://doi.org/10.1016/j.agrformet.2023.109349. ISSN 0168-1923.

Hansen, W.D., Turner, M.G., 2019. Origins of abrupt change? Postfire subalpine conifer regeneration declines nonlinearly with warming and drying. Ecological Monographs 89, e01340. https://doi.org/10.1002/ecm.1340.

Haq, S.M., Rashid, I., Khuroo, A.A., Malik, Z.A., Malik, A.H., 2019. Anthropogenic disturbances alter community structure in the forests of Kashmir Himalaya Tropical. Ecology 60 (1), 6–15. https://doi.org/10.1007/s42965-019-00001-8.

Harcombe, P.A., Bill, C.J., Fulton, M., Glitzenstein, J.S., Marks, P.L., Elsik, I.S., 2002. Stand dynamics over 18 years in a southern mixed hardwood forest, Texas, USA. *J. Ecol.* 90 (6), 947–957.

Harris, L.B., Woodall, C.W., D'Amato, A.W., 2022. Increasing the utility of tree regeneration inventories: Linking seedling abundance to sapling recruitment. *Ecol. Ind.* 145, 109654.

Harrison, S., LaForgia, M., 2019. Seedling traits predict drought-induced mortality linked to diversity loss. *Proc. Natl. Acad. Sci.* 116 (12), 5576–5581.

Hartmann, H., Bastos, A., Das, A.J., Esquivel-Muelbert, A., Hammond, W.M., Martínez-Vilalta, J., Allen, C.D., 2022. Climate change risks to global forest health: emergence of unexpected events of elevated tree mortality worldwide. *Annu. Rev. Plant Biol.* 73, 673–702.

Hawthorne, S., Miniat, C.F., 2017. Topography may mitigate drought effects on vegetation along a hillslope gradient. Ecohydrology 11, e1825.

Hember RA, Kurz WA, Coops NC. Relationships between individual-tree mortality and water-balance variables indicate positive trends in water stress-induced tree mortality across North America. Glob Chang Biol. 2017 Apr;23(4):1691-1710. doi: 10.1111/gcb.13428. Epub 2016 Sep 14. PMID: 27624980.

Hlásny, T., Zimová, S., Merganičová, K., Štěpánek, P., Modlinger, R., Turčáni, M., 2021. Devastating outbreak of bark beetles in The Czech Republic: Drivers, impacts, and management implications. Forest Ecology and Management 490, 119075. https://doi.org/10.1016/j.foreco.2021.119075.

Holling, C.S. Resilience and stability of ecological systems. *Ann. Rev. Ecol. System.*, vol. 4, 1973, pp. 1–23. *JSTOR*, http://www.jstor.org/stable/2096802.

Hollunder, K.R., Garbin, M.L., Rubio Scarano, F., Mariotte, P., 2022. Regional and local determinants of drought resilience in tropical forests. Ecol. Evol. 12 (5), e8943 PMID: 35646321; PMCID: PMC9130645 doi:10.1002/ece3.8943.

IPCC (International Panel on Climate Change), 2007, Climate Change 2007: Synthesis Report: Cambridge University Press, http://www.ipcc.ch/publications_and_data/publications_ipcc_fourth_assessment_report_synthesis_report.htm.

Iverson, L., Prasad, R., Anantha, M., Schwartz, Mark W., 2005. Predicting potential changes in suitable habitat and distribution by 2100 for Tree Species of the Eastern United States. J. Agric. Meteorol. 61 (1), 29–37.

Kaiser, K.E., McGlynn, B.L., Emanuel, R.E., 2013. Ecohydrology of an outbreak: mountain pine beetle impacts trees in drier landscape positions first. Ecohydrology 6, 444–454.

King, K.E., Cook, E.R., Anchukaitis, K.J., Cook, B.I., Smerdon, J.E., Seager, R., Harley, G. L., Spei, B., 2024. Increasing prevalence of hot drought across western North America since the 16th century. *Sci. Adv.* 10 (4) p.eadj4289.

Klockow, P., Vogel, J.G., Edgar, C., Moore, G.W., 2018. Differences in lagged mortality among tree species four years after an exceptional drought in east Texas. *Ecosphere* 9, 1–14.

Klockow, P.A., Edgar, C.B., Moore, G.W., Vogel, J.G., 2020. Southern pines are resistant to mortality from an exceptional drought in East Texas. Front. For. Glob. Change 3, 23. https://doi.org/10.3389/ffgc.2020.00023.

Klockow, P.A., Edgar, C.B., Domke, G.M., et al., 2023a. Tracking 20 years of forest demographics in east Texas, USA, using national forest inventory data. *Environ. Monit. Assess.* 195, 1478.

Klockow, Paul A, Christopher B Edgar, Marcella A Windmuller-Campione, Fred A Baker, Stand inventories as an early detection system for forest health threats, *Forest Sci.*, 69 (1), 2023, 1–9, https://doi.org/10.1093/forsci/fxac046.

Knott, J.A., Desprez, J.M., Oswalt, C.M., Fei, S., 2019. Shifts in forest composition in the eastern United States. *For. Ecol. Manage.* 433, 176–183.

Kolb, T.E., Flathers, K., Bradford, J.B., Andrews, C., Asherin, L.A., Moser, W.K., 2020. Stand density, drought, and herbivory constrain ponderosa pine regeneration pulse. *Can. J. For. Res.* 50 (9), 862–871.

Larkin, T.J., Bomar, G.W., 1983, Climatic Atlas of Texas: Texas Water Development Board Limited Publication 192, http://www.twdb.state.tx.us/ publications/reports/limited_printing/doc/LP192.pdf.

Lawal, S., Lennard, C., Jack, C., Wolski, P., Hewitsin, B., Abiodun, B., 2019a. The observed and model-simulated response of southern African vegetation to drought. *Agric. for Meteorol.* 279, 107698. https://doi.org/10.1016/j.agrformet.2019.107698.

Lawal, S., Lennard, C., Hewitson, B., 2019b. Response of southern African vegetation to climate change at 1.5 and 2.0 degrees global warming above the pre-industrial level. *Clim. Serv.* 16, 100134. https://doi.org/10.1016/j.cliser.2019.100134.

Lawal, S., Hewitson, B., Egbebiyi, T., Adesuyi, A., 2021. On the suitability of using vegetation indices to monitor the response of Africa's terrestrial ecoregions to drought. *Sci. Total Environ.* 792, 148282. https://doi.org/10.1016/j.scitotenv.2021.148282.

Lawal, S., Sitch, S., Lombardozzi, D., Nabel, J.E.M.S., Wey, H.-W., Friedlingstein, P., et al., 2022. Investigating the response of leaf area index to droughts in southern African vegetation using observations and model simulations. *Hydrol. Earth Syst. Sci.* 26, 2045–2071. https://doi.org/10.5194/hess-26-2045-2022.

Lawal, S., Costanza, J.K., Koch, F.H., Scheller, R.M., 2024. Modeling the impacts of hot drought on forests in Texas. Front. For. Global Change 7, 1280254. https://doi.org/10.3389/ffgc.2024.1280254.

Lindenmayer DB, Noss RF. Salvage logging, ecosystem processes, and biodiversity conservation. Conserv Biol. 2006 Aug;20(4):949-58. doi: 10.1111/j.1523-1739.2006.00497.x. PMID: 16922212.

Mayer, M., Sandén, H., Rewald, B., Godbold, D.L., Katzensteiner, K., 2017. Increase in heterotrophic soil respiration by temperature drives decline in soil organic carbon stocks after forest windthrow in a mountainous ecosystem. *Funct. Ecol.* 31 (5), 1163–1172. https://doi.org/10.1111/1365-2435.12805.

McCune, B., Keon, D., 2002. Equations for potential annual direct incident radiation and heat load. J. Veg. Sci. 13, 603–606.

McDowell, N., Pockman, W.T., Allen, C.D., Breshears, D.D., Cobb, N., Kolb, T., Plaut, J., Sperry, J., West, A., Williams, D.G., Yepez, E.A., 2008. Mechanisms of plant survival and mortality during drought: why do some plants survive while others succumb to drought? *New Phytologist* 178 (4), 719–739.

McDowell, G., et al., 2016. *Environ. Res. Lett.* 11, 033001.

McDowell NG, Allen CD, Anderson-Teixeira K, Aukema BH, Bond-Lamberty B, Chini L, Clark JS, Dietze M, Grossiord C, Hanbury-Brown A, Hurtt GC, Jackson RB, Johnson DJ, Kueppers L, Lichstein JW, Ogle K, Poulter B, Pugh TAM, Seidl R, Turner MG, Uriarte M, Walker AP, Xu C. Pervasive shifts in forest dynamics in a changing world. Science. 2020 May 29;368(6494):eaaz9463. doi: 10.1126/science.aaz9463. PMID: 32467364.

Messier, C., Bauhus, J., Doyon, F., et al., 2019. The functional complex network approach to foster forest resilience to global changes. *For. Ecosyst.* 6, 21. https://doi.org/10.1186/s40663-019-0166-2.

Milbau, A., Vandeplas, N., Kockelbergh, F., Nijs, I., 2017. Both seed germination and seedling mortality increase with experimental warming and fertilization in a subarctic tundra. *AoB Plants* 9 (5), p.plx040.

Moore, G.W., Edgar, C.B., Vogel, J.G., Washington-Allen, R.A., March, O.G., Zehnder, R., 2016. Tree mortality from an exceptional drought spanning mesic to semiarid ecoregions. Ecol. Appl. 26, 602–611. https://doi.org/10.1890/15-0330.

Wynne E Moss, Shelley D Crausbay, Imtiaz Rangwala, Jay W Wason, Clay Trauernicht, Camille S Stevens-Rumann, Anna Sala, Caitlin M Rottler, Gregory T Pederson, Brian W Miller, Dawn R Magness, Jeremy S Littell, Lee E Frelich, Abby G Frazier, Kimberley T Davis, Jonathan D Coop, Jennifer M Cartwright, Robert K Booth, Drought as an emergent driver of ecological transformation in the twenty-first century, *BioScience*, Volume 74, Issue 8, August 2024, Pages 524–538, https://doi.org/10.1093/biosci/biae050.

Mouillot, D., Graham, N.A., Villéger, S., Mason, N.W., Bellwood, D.R., 2013. A functional approach reveals community responses to disturbances. Trends Ecol. Evol. 28 (3), 167–177. https://doi.org/10.1016/j.tree.2012.10.004. Epub 2012 Nov 8 PMID: 23141923.

Mukherjee, S., Mishra, A., Trenberth, K.E., 2018. Climate change and drought: a perspective on drought indices. *Curr. Climate Change Rep.* 4, 145–163. https://doi.org/10.1007/s40641-018-0098-x.

Nardone, A., Ronchi, B., Lacetera, N., Ranieri, M.S., Bernabucci, U., effects of climate changes on animal production and sustainability of livestock systems, Livestock Sci., 130 (1–3), 2010, 57–69, ISSN 1871-1413, https://doi.org/10.1016/j.livsci.2010.02.011.

Oliver, T.H., Heard, M.S., Isaac, N.J.B., Roy, D.B., Procter, D., Eigenbrod, F., Freckleton, R., Hector, A., Orme, C.D.L., Petchey, O.L., Proença, V., Raffaelli, D., Suttle, K.B., Mace, G.M., Martín-López, B., Woodcock, B.A., Bullock, J.M., 2015. Biodiversity and resilience of ecosystem functions. *Trends Ecol. Evol.* 30 (11), 673–684. https://doi.org/10.1016/j.tree.2015.08.009.

Overpeck, J.T., Udall, B., 2020. Climate change and the aridification of North America. *Proc. Natl. Acad. Sci.* 117 (22), 11856–11858.

Park Williams, A., Allen, C., Macalady, A., et al., 2013. Temperature as a potent driver of regional forest drought stress and tree mortality. *Nat. Clim. Change* 3, 292–297. https://doi.org/10.1038/nclimate1693.

Patacca, M.M., Lindner, M.E., Lucasorja, T., Cordonnier, G., Fidej, B., Gardiner, Y., Hauf, G.J., Sinevičius, Labonne, S., Linkevičius, E., et al., 2023. Significant increase in natural disturbance impacts on European forests since 1950. Glob. Change Biol. 29 (2023), 1359–1376. https://doi.org/10.1111/gcb.16531.

Patterson, Paul L.; Reams, Gregory A. 2005. Combining panels for forest inventory and analysis estimation. Gen. Tech. Rep. SRS-80. Asheville, NC: U.S. Department of Agriculture, Forest Service, 79-84.

Peters, M.P., Iverson, L.R., Matthews, S.N., 2015. Long-term droughtiness and drought tolerance of eastern US forests over five decades. *For. Ecol. Manage.* 345, 56–64.

Polley, H.W., Johnson, D.M., Jackson, R.B., 2018. Projected drought effects on the demography of Ashe juniper populations inferred from remote measurements of tree canopies. *Plant Ecol* 219, 1259–1267. https://doi.org/10.1007/s11258-018-0876-5.

Ponge, J.F., André, J., Zackrisson, O., Bernier, N., Nilsson, M.C., Gallet, C., 1998. The forest regeneration puzzle. *Bioscience* 48 (7), 523–530.
Pozner, E., Bar-On, P., Livne-Luzon, S., Moran, U., Tsamir-Rimon, M., Dener, E., Schwartz, E., Rotenberg, E., Tatarinov, F., Preisler, Y., Zecharia, N., 2022. A hidden mechanism of forest loss under climate change: the role of drought in eliminating forest regeneration at the edge of its distribution. *For. Ecol. Manage.* 506, 119966.
Pretzsch, H., Heym, M., Hilmers, T., Bravo-Oviedo, A., Ahmed, S., Ammer, C., Avdagić, A., Bielak, K., Bravo, F., Brazaitis, G., Fabrika, M,, Hurt, V., Kurylyak, V., Löf, M., Pach, M., Ponette, Q., Ruiz-Peinado, R., Stojanovic, D., Svoboda, M., Wolff, B., Zlatanov, T., del Río, M. (2023). Mortality reduces overyielding in mixed Scots pine and European beech stands along a precipitation gradient in Europe, Forest Ecology and Management, Volume 539, 2023, 121008, ISSN 0378-1127, https://doi.org/10.1016/j.foreco.2023.121008.
Redmond, M.D., Weisberg, P.J., Cobb, N.S., Clifford, M.J., 2018. Woodland resilience to regional drought: dominant controls on tree regeneration following overstorey mortality. *J. Ecol.* 106 (2), 625–639. https://doi.org/10.1111/1365-2745.12880.
Russell, F.L., Fowler, N.L., 2002. Failure of adult recruitment in Quercus buckleyi populations on the eastern Edwards Plateau, Texas. *Am. Midland Natural.* 148 (2), 201–217.
Russo, S., Dosio, A., Graversen, R., Sillmann, J., Carrao, H., Dunbar, M., et al., 2014. Magnitude of extreme heat waves in present climate and their projection in a warming world. J. Geophys. Res. Atmos. 119, 12500–12512. https://doi.org/10.1002/2014JD022098.
Russo, S., Sillmann, J., Sterl, A., 2017. Humid heat waves at different warming levels. *Sci. Rep.* 7, 7477. https://doi.org/10.1038/s41598-017-07536-7.
Savage, M., Brown, P.M., Feddema, J., 1996. The role of climate in a pine forest regeneration pulse in the southwestern United States. *Ecosci.* 3 (3), 310–318.
Scheffer, M., et al., 2009. Early-warning signals for critical transitions. *Nature* 461, 53–59. https://doi.org/10.1038/nature08227.
Scheffer, M., Barrett, S., Carpenter, S., Folke, C., Green, A.J., Holmgren, M., Van Nes, E. H., 2015. Creating a safe operating space for iconic ecosystems. *Science* 347, 1317–1319. https://doi.org/10.1126/science.aaa3769.
Schimel, D., Melillo, J., Tian, H., McGuire, A.D., Kicklighter, D., Kittel, T., Rosenbloom, N., Running, S., Thornton, P., Ojima, D., Parton, W., Kelly, R., Sykes, M., Neilson, R., Rizzo, B., 2000. Contribution of increasing CO_2 and climate to carbon storage by ecosystems of the United States. *Science* 287, 2004–2006.
Schuldt, B., Buras, A., Arend, M., Vitasse, Y., Beierkuhnlein, C., Damm, A., Kahmen, A., 2020. A first assessment of the impact of the extreme 2018 summer drought on Central European forests. *Basic Appl. Ecol.* 45, 86–103.
Schwantes, A.M., Parolari, A.J., Swenson, J.J., Johnson, D.M., Domec, J.C., Jackson, R. B., Pelak, N., Porporato, A., 2018. Accounting for landscape heterogeneity improves spatial predictions of tree vulnerability to drought. New Phytol. 220, 132–146. https://doi.org/10.1111/nph.15274.
Scott, Charles T.; Bechtold, William A.; Reams, Gregory A.; Smith, William D.; Westfall, James A.; Hansen, Mark H.; Moisen, Gretchen G. 2005. Sample-based estimators used by the forest inventory and analysis national information management system. Gen. Tech. Rep. SRS-80. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southern Research Station, p. 53-77.
Seidl R, Turner MG. 2022. Post-disturbance reorganization of forest ecosystems in a changing world. *Proc. Natl. Acad. Sci., USA* **119**: e2202190119.
Seidl, R., Spies, T.A., Peterson, D.L., Stephens, S.L., Hicke, J.A., 2016. Searching for resilience: addressing the impacts of changing disturbance regimes on forest ecosystem services. *J. Appl. Ecol.* 53, 120–129.
Seidl, R., Thom, D., Kautz, M., Martin-Benito, D., Peltoniemi, M., Vacchiano, G., Wild, J., Ascoli, D., Petr, M., Honkaniemi, J., et al., 2017. Forest disturbances under climate change. *Nat. Clim. Chang.* 7, 395–402.
Senf, C., Seidl, R., 2021a. Mapping the forest disturbance regimes of Europe. *Nat. Sustain.* 4, 63–70.
Senf, C., Seidl, R., 2021b. Persistent impacts of the 2018 drought on forest disturbance regimes in Europe. *Biogeosciences* 18, 5223–5230.
Serra-Diaz, J.M., Scheller, R.M., Syphard, A.D., Franklin, J., 2015. Disturbance and climate microrefugia mediate tree range shifts during climate change. *Landsc. Ecol.* 30, 1039–1053.
Shriver, R.K., Yackulic, C.B., Bell, D.M., Bradford, J.B., 2022. Dry forest decline is driven by both declining recruitment and increasing mortality in response to warm, dry conditions. *Glob. Ecol. Biogeogr.* 31 (11), 2259–2269.
Siebert, J., Sünnemann, M., Auge, H., et al., 2019. The effects of drought and nutrient addition on soil organisms vary across taxonomic groups, but are constant across seasons. *Sci. Rep.* 9, 639. https://doi.org/10.1038/s41598-018-36777-3.
Slade, R.M., Jr. and Patton, J., 2003, Major and catastrophic storms and floods in Texas –215 major and 41 catastrophic events from 1853 to September 1, 2002: U.S. Geological Survey Water Resources Division Open-File Report 03-193.
Solomon, A.M., Kirilenko, A.P., 1997. *Global Ecol. Biogeogr. Lett.* 6, 139–148.
Sommerfeld, A., Senf, C., Buma, B., et al., 2018. Patterns and drivers of recent disturbances across the temperate forest biome. Nat Commun 9, 4355. https://doi.org/10.1038/s41467-018-06788-9.
Stanke, H., Finley, A.O., Domke, G.M., 2022. Simplifying small area estimation with rFIA: a demonstration of tools and techniques. *Front. for. Glob. Change* 5, 745874. https://doi.org/10.3389/ffgc.2022.745874.
Strzepek, K., Yohe, G., Neumann, J., Boehlert, B., 2010. Characterizing changes in drought risk for the United States from climate change. *Environ. Res. Lett.* 5 (4), 044012.
Suarez, M.L., Ghermandi, L., Kitzberger, T., 2004. Factors predisposing episodic drought-induced tree mortality in *Nothofagus*– site, climatic sensitivity and growth trends. *J. Ecol.* 92, 954–966.
Subedi, M.R., Xi, W., Edgar, C.B., Rideout-Hanzak, S., Yan, M., 2021. Tree mortality and biomass loss in drought-affected forests in east Texas, USA. J. For. Res. 32 (1), 67–80.
Tepley, A.J., Thompson, J.R., Epstein, H.E., Anderson-Teixeira, K.J., 2017. Vulnerability to forest loss through altered postfire recovery dynamics in a warming climate in the Klamath Mountains. *Glob. Chang. Biol.* 23 (10), 4117–4132.
Thom, D., Seidl, R., 2016. Natural disturbance impacts on ecosystem services and biodiversity in temperate and boreal forests. *Biol. Rev.* 91 (3), 760–781. https://doi.org/10.1111/brv.12193.
Turner, M.G., 2010. Disturbance and landscape dynamics in a changing world. *Ecology* 91, 2833–2849.
Turner, M.G., Seidl, R., 2023. Novel disturbance regimes and ecological responses. *Annu. Rev. Ecol. Evol. Syst.* 54, 63–83.
Van Meerbeek, K., Jucker, T., Svenning, J.C., 2021. Unifying the concepts of stability and resilience in ecology. *J. Ecol.* 109 (9), 3114–3132. https://doi.org/10.1111/1365-2745.13651.
Vicente-Serrano, S.M., Beguería, S., López-Moreno, J.I., 2010. A multiscalar drought index sensitive to global warming: the standardized precipitation evapotranspiration index. J. Climate 23, 1696–1718. https://doi.org/10.1175/2009JCLI2909.1.
Vickers, L.A., McWilliams, W.H., Knapp, B.O., D'Amato, A.W., Dey, D.C., Dickinson, Y.L., Kabrick, J.M., Kenefic, L.S., Kern, C.C., Larsen, D.R., Royo, A.A., 2019. Are current seedling demographics poised to regenerate northern US forests? *J. For.* 117 (6), 592–612.
Vilonen L, Ross M, Smith MD. What happens after drought ends: synthesizing terms and definitions. New Phytol. 2022 Jul;235(2):420-431. doi: 10.1111/nph.18137. Epub 2022 Apr 30. PMID: 35377474; PMCID: PMC9322664.
Westfall, J.A.; Coulston, J.W.; Moisen, G.G.; Andersen, H.-E., comps. 2022. Sampling and estimation documentation for the Enhanced Forest Inventory and Analysis Program: 2022. Gen. Tech. Rep. NRS-GTR-207. Madison, WI: U.S. Department of Agriculture, Forest Service, Northern Research Station. 129 p. https://doi.org/10.2737/NRS-GTR-207.
Yang, X, Crews, KA, 2019. Fractional Woody Cover Mapping of Texas Savanna at Landsat Scale. Land 8 (1), 9. https://doi.org/10.3390/land8010009.
Young, Truman P., et al. Initial success of native grasses is contingent on multiple interactions among exotic grass competition, temporal priority, rainfall and site effects. *AoB Plants* 7 (2015): plu081.
Zhang, F., Biederman, J.A., Dannenberg, M.P., Yan, D., Reed, S.C., Smith, W.K., 2021. Five decades of observed daily precipitation reveal longer and more variable drought events across much of the western United States. *Geophys. Res. Lett.* 48 (7) e2020GL092293.