Nutrient regime modulates drought response patterns of three temperate tree species

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HIGHLIGHTS

- Drought response analyses of fir, beech, and spruce along an ecological gradient
- Balanced nutrient regime was beneficial under extreme droughts.
- Beneficial post-drought climatic conditions facilitated recovery potential of beech.
- Recurrent droughts were not associated with reduced resilience.
- Beech and spruce showed a long-term decline in drought resilience.

GRAPHICAL ABSTRACT
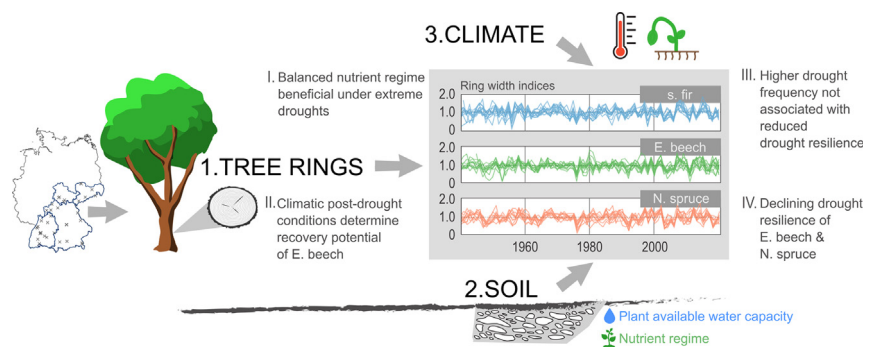
ARTICLE INFO

ABSTRACT

Against the backdrop of global change, the intensity, duration, and frequency of droughts are projected to increase and threaten forest ecosystems worldwide. Tree responses to drought are complex and likely to vary among species, drought characteristics, and site conditions. Here, we examined the drought response patterns of three major temperate tree species, s. fir (*Abies alba*), E. beech (*Fagus sylvatica*), and N. spruce (*Picea abies*), along an ecological gradient in the South – Central – East part of Germany that included a total of 37 sites with varying climatic and soil conditions. We relied on annual tree-ring data to assess the influence of different drought characteristics and (micro-) site conditions on components of tree resilience and to detect associated temporal changes. Our study revealed that nutrient regime, drought frequency, and hydraulic conditions in the previous and subsequent years were the main determinants of drought responses, with pronounced differences among species. Specifically, we found that (a) higher drought frequency was associated with higher resistance and resilience for N. spruce and E. beech; (b) more favorable climatic conditions in the two preceding and following years increased drought resilience and determined recovery potential of E. beech after extreme drought; (c) a site's nutrient regime, rather than micro-site differences in water availability, determined drought responses, with trees growing on sites with a balanced nutrient regime having a higher capacity to withstand extreme drought stress; (d) E. beech and N. spruce experienced a long-term decline in resilience. Our results indicate that trees under extreme drought stress benefit from a balanced nutrient supply and highlight the relevance of water availability immediately after droughts. Observed long-term trends confirm that N. spruce is suffering from persistent climatic changes, while s. fir is coping better. These findings might be especially relevant for monitoring, scenario analyses, and forest ecosystem management.

1. Introduction

Forests play a key role in carbon and water cycles, provide other indispensable ecosystem services, and have high ecological, recreational, and socioeconomic value (Bonan, 2008; Pan et al., 2011). However, these services are under threat since forest ecosystems are considered particularly vulnerable to the unprecedented changes in the global climate (European Environment Agency, 2017; Lindner et al., 2010). As the intensity, duration, and frequency of heat waves and droughts are projected to continue to increase (Intergovernmental Panel on Climate Change, 2021; Samaniego et al., 2018; Szejner et al., 2020), droughts are expected to become the most critical limiting factor for tree growth on a global scale (Babst et al., 2019). Drought can significantly affect tree productivity (Ciais et al., 2005), allometry (Dai et al., 2020; Pretzsch et al., 2012), and regeneration (Comita and Engelbrecht, 2014) and alter the spatial distribution of species in the long-term (Allen and Breshears, 1998; Clark et al., 2016; Rigling et al., 2013). In addition, increasing and prolonged drought stress may promote the risk of tree mortality (Allen et al., 2010; Hartmann et al., 2018), especially in drought-prone areas (Charney et al., 2016), and has already been observed for boreal (Michaelian et al., 2011; Peng et al., 2011), temperate (van Mantgem et al., 2009), and tropical forests (McDowell et al., 2018) at large scales. The temperate forests of Europe, for instance, have experienced several drought spells in recent years that have resulted in excessive forest mortality (Orth et al., 2016; Schuldt et al., 2020; Senf et al., 2020).

The two predominant coniferous and deciduous tree species of Central European forests, Norway spruce (*Picea abies* H. Karst., hereafter 'N. spruce') and European beech (*Fagus sylvatica* L., 'E. beech'), are of crucial importance for forestry from an economic and ecological perspective. Silver fir (*Abies alba* Mill., 's. fir') frequently co-occurs with N. spruce and E. beech and can play an important role as a stabilizing element, e.g. for water retention or windthrow resistance (Dobrowolska et al., 2017; San-Miguel-Ayanz et al., 2016). Therefore, the quantification of these species' drought sensitivity has been the focus of dendroecological studies (Gillerot et al., 2021; Vitasse et al., 2019a; Zang et al., 2014). Several studies have shown that E. beech can be considered a drought-sensitive species (Leuschner, 2020; Scharnweber et al., 2011; Zimmermann et al., 2015), especially at the core of its distribution range (Cavin and Jump, 2016). But, given projected climate scenarios, the most severe impacts are expected at the southernmost distribution limit due to a further increase in drought intensity (Del Martinez Castillo et al., 2022). N. spruce is considered to be highly sensitive to dry conditions as several dendroecological studies have shown (Vitasse et al., 2019a; Zang et al., 2014). This was also confirmed by studies with saplings (Oberhuber, 2017), simulation studies (Thiele et al., 2017), and throughfall exclusion experiments (Grams et al., 2021; Pretzsch et al., 2020). In Germany, the highest susceptibility to drought was found outside its natural range where N. spruce was commonly cultivated in the past (Zang et al., 2011). While E. beech and N. spruce are classified as drought-sensitive species, s. fir has proven to be more resistant to drought stress in the center of its natural range (Bouriaud and Popa, 2009; Vitasse et al., 2019a). However, Cailleret et al. (2014) and Gazol et al. (2015) have shown that this is different towards the dry distribution margin in the Mediterranean region, where a long-term growth decline due to increasing aridity has been observed since the 1980s. Differences among tree species are related to different ecological and physiological traits (Hartmann, 2011; McDowell et al., 2008), such as the capability of stem rehydration overnight (Salomón et al., 2022) or the adaptability of fine-root systems (Nikolova et al., 2020).

Previous studies on growth responses to drought have mainly focused on differences among tree species (Song et al., 2021; Vitasse et al., 2019a), tree sizes (Zang et al., 2012), social positions (Grote et al., 2016), competition (Bottero et al., 2017), mixtures (Pretzsch et al., 2013), as well as drought onset and severity (Gao et al., 2018). However, in the face of global change, research accounting for changes in drought frequency or the immediate climatic conditions before and after a drought is becoming increasingly important (Bose et al., 2020a; Gao et al., 2018;

Jiang et al., 2019; Jiao et al., 2021). Such factors are crucial to consider since prolonged or repeated droughts can deplete the soil water storage (Goulden and Bales, 2019; Samaniego et al., 2018), leading to nutrient imbalances within trees (Gessler et al., 2016; Hevia et al., 2019) or damaging key structural components (Gessler et al., 2020; Serra-Maluquer et al., 2018). This can lead to root (Brunner et al., 2015) or branch dieback (Jacobs et al., 2021) also in subsequent years due to a lack of hydraulic recovery (Arend et al., 2022). Thus, cumulative effects of recurrent drought stress may cause extended legacy effects on tree growth and vitality (Peltier and Ogle, 2019; Szejner et al., 2020), e.g. due to hampered tree leaf area recovery (Bose et al., 2020a) or the need of rebuilding the fine-root system (Mainiero and Kazda, 2006). This can weaken the ability of trees to cope with subsequent droughts (L. D. L. Anderegg et al., 2013) and thus enhance the risk of tree mortality in the long-term (Bigler et al., 2006; McDowell et al., 2010). Trees growing under frequent drought stress may have developed an ecological memory for these antecedent conditions (Ogle et al., 2015), which may lead to increased sensitivity to drought (Peltier et al., 2022) or have positive effects through phenotypic acclimations, such as adjustments of root biomass (Brunner et al., 2015) or smaller xylem conduits (Gessler et al., 2020) that improve drought tolerance.

Differences in site conditions are known to affect tree growth and drought responses significantly (Bose et al., 2020a; Rehschuh et al., 2017), but studies focusing on nutrient and water availability have been scarce and were primarily conducted at the stand level (DeSoto et al., 2020; Gazol et al., 2017; Lebourgeois et al., 2013; Lévesque et al., 2016). However, regeneration studies have already shown the importance of micro-site conditions (Diaci et al., 2020), which may also co-determine drought reaction patterns of mature trees (Buras et al., 2018), e.g. due to differences in available water holding capacity (Chakraborty et al., 2021) and may affect mortality risk (Hajek et al., 2022). This effect could vary among tree species due to the differences in water uptake depth (Brinkmann et al., 2019), while the overall plant water availability is highly dependent on physical soil properties (Jury et al., 1991) and thus influences drought susceptibility of trees (Rehschuh et al., 2017). Soil chemical properties can also affect drought response patterns. For instance, generally high nutrient availability may prove unfavorable to tree survival when droughts occur as biomass was primarily invested above ground (Gessler et al., 2016), potentially predisposing trees to suffer from carbon starvation (Mitchell et al., 2013) or hydraulic failure (McDowell et al., 2008). On the other hand, a sufficient nutrient supply can increase the water-use efficiency during droughts and enable a faster recovery afterwards (Gessler et al., 2016).

Here, we investigated the drought responses of s. fir, E. beech, and N. spruce along a unique ecological gradient that covered different nutrient regime levels and climatic conditions. The gradient was derived from an ecological niche modelling approach and ranged from southern to central and eastern Germany, encompassing 37 sites. In combination with dendrochronological data, we scrutinized how different (micro-) site conditions and drought characteristics modulate different components of tree resilience to drought and examined potential temporal trends. The four objectives of our study were the following:

(a) To assess growth responses of s. fir, E. beech, and N. spruce trees to recurrent droughts of varying severity; H_I: we hypothesized that more severe and frequent droughts would lead to a decrease in drought resilience.

(b) To quantify the influence of climatic conditions in the years before and after a drought on the response patterns of trees; H_{II}: we hypothesized that more favorable conditions in the preceding and subsequent years could compensate for dry conditions in the drought year itself and affect the recovery potential of trees. We further expected differences among species.

(c) To evaluate whether tree response to drought gets modulated by the site's nutrient regime, micro-site differences in plant-available water capacity, and long-term climatic conditions; H_{III}: we hypothesized

that the nutrient regime of a site would be a major determinant of drought response with trees on sites with balanced nutrient supply being less susceptible to droughts; that trees with access to higher available water capacity would benefit from these conditions relative to other trees in the same stand; and that trees growing at drier environments would respond less strong to droughts.

(d) To examine possible temporal changes in drought response patterns; H$_{IV}$: we hypothesized that long-term trends would differ among tree species.

2. Materials and methods

2.1. Site selection along an ecological gradient

An appropriate research design was required that covered spatial and temporal dimensions in order to address the research objectives. Hence, we investigated the retrospective growth responses of s. fir, E. beech, and N. spruce to droughts (temporal) along an ecological gradient in southern, central, and eastern Germany with different climatic and soil conditions (spatial). Pre-selection of the sites was based on an ecological gradient consisting of two factors: an ecological niche modelling approach formed the basis for the first factor, which resulted in four different classifications of fundamental macroclimatic niche zones (optimal, intermediate, marginal, rear edge) for each tree species (Dorado-Liñán et al., 2018; Mellert et al., 2016), while the second factor accounted for the nutrient regime at three different levels (base-poor, medium, base-rich). The three levels of the nutrient regime were based on the German site classification system (Standortskartierung, 2016). This classification from acidic (base-poor) to carbonate soils (base-rich) characterized the availability of base cations throughout the soil profile and summarized the nutrient status along the soil pH-gradient (Härdtle et al., 2004; Mellert et al., 2018; Walentowski et al., 2006). A more detailed explanation of the niche modelling approach can be found in Supplement S1 and is accompanied by Fig. S1.

The different niche and nutrient classes resulted in twelve combinations (four fundamental macroclimatic niche zones × three nutrient regime levels = twelve strata). The four fundamental macroclimatic niche zones were only used for site selection to obtain a broad precipitation and temperature gradient. They weren't used for further analysis. For each species and combination, we established a representative site in a forest stand, where the respective target species had a share of at least 75 % of the total stand basal area. Forest stands with a history of frequent or heavy thinning were avoided to minimize potential management effects. We focused on mature stands with a minimum mean age of 70 years, all of which were larger than 4.5 ha. In total, we sampled 37 sites (see Table S1), as two sites were selected for E. beech in the stratum of optimal climate and medium nutrient regime. This special case was due to the fact that two sites with significantly different annual average temperature (6 °C and 8 °C) were available for that stratum. The detailed site locations in Germany are shown in Fig. 1b. The climate along the resulting gradient varied from warm-dry to wet-cool. This can be seen in Fig. 1a, which visualizes the climatic position of the study sites within the entire climate-space of the species' occurrences. The annual mean temperature ranged from 5.4 to 9.9 °C (9.5 to 14.1 °C in the growing season from March to September), while the mean total annual precipitation was between 594 and 1916 mm (373 to 1225 mm in the growing season) for the period considered in our study (1940–2020). Over this investigation period, all sites experienced several droughts, while recent years were characterized by progressively drier conditions (Fig. 1c). The sites were located at elevations between 105 and 925 m a.s.l. Predominant soil types were Luvisols (base-rich sites), Podzols (base-poor), and Cambisols (all three nutrient classes) with varying nutrient supply and plant-available water capacity. Table S2 provides an overview of site characteristics.

2.2. Field data collection

Fieldwork at the 37 selected sites took place from October 2020 to October 2021. At each of these sites, we selected 15–20 dominant trees in closed stands for measurements and sampling. None of the trees showed obvious signs of felling damage or pest infestations. All trees were at least 30 m apart. To obtain annual growth increments, we sampled each selected tree with a 5 mm borer (Haglöf, Sweden) at breast height (dbh$_{1.3m}$) and the current diameter at the same height was recorded. Two cores were taken from the eastern and northern cardinal direction to minimize the influence of reaction wood (Pretzsch et al., 2013), resulting in a total of 30–40 extracted cores per site. Overall, 1126 cores were collected from 563 trees (195 × beech, 180 × spruce, 188 × fir).

We examined basic physical soil properties in the immediate vicinity to quantify plant-available water capacity for each sampled tree. For this purpose, the soil was sampled with an auger down to 1 m depth or to the parent material, whichever was reached first. A small soil profile was also dug to assess the humus layers and the topsoil horizons. Evaluated field parameters were the thickness of organic layer and mineral soil horizons, soil texture, bulk density, and fine earth content. Further, we classified humus form and soil type. All parameters were assessed according to Ad-hoc-Arbeitsgruppe Boden (2005). For the validation of the nutrient regime, soil pH was measured with a field pH measurement kit ('Hellige Pehameter'), and the presence of calcium carbonate was tested with a 10 % HCl solution.

2.3. Tree ring data processing

The air-dried cores were sanded with progressively finer sandpaper (120–400 grit) to highlight annual ring boundaries. Subsequently, the cores were measured to the nearest of 1/100 mm using the digital positioning table LINTAB 5 and the software TSAPWIN (both Rinntech, Heidelberg). We then performed visual crossdating (Stokes and Smiley, 1996) by examining all cores for distinct growth patterns. Here, we were guided by exceptionally narrow or wide tree rings that were common to the vast majority of tree-ring series at each site and within each species (Schweingruber et al., 1990). In addition, crossdating accuracy was verified statistically using cross-correlation functions implemented in the library *dplR* of the statistical environment R (Bunn, 2008, 2010; R Core Team, 2021). For further analysis, we chose the period 1940–2020, as this was covered by most of our tree-ring series at all sites. To remove age- and size-related growth trends and associated low frequency variation, we transformed the measured raw ring-width series into dimensionless ring-width indices (RWI) by fitting a 30-year cubic spline with a 50 % frequency response cut-off to our series (Cook et al., 1992; Fritts, 1976). In the next step, the two RWI series per tree were averaged, resulting in a total of 563 RWI series. Subsequently, a chronology for each site was built by averaging all respective RWI using Tukey's biweight robust mean.

2.4. Climate data and drought identification

For all our study sites, we obtained climate data from the 1 km × 1 km grid of the German Meteorological Service (DWD Climate Data Center (CDC), 2021). Monthly data of precipitation (mm) and mean, maximum, and minimum temperature (°C) were available for the entire period we considered for our study (1940–2020). We relied on the Standardized Precipitation Evapotranspiration Index (SPEI) (Vicente-Serrano et al., 2010) to define drought events, as it uses a multiscalar approach that allows consideration of different drought durations, has relatively low data requirements, and is sensitive to global warming (Vicente-Serrano et al., 2010). However, it should be noted that ecologically relevant patterns of soil moisture may not always be fully represented by the index. We applied the Hargreaves equation (Beguería and Vicente-Serrano, 2017; Hargreaves, 1994) to derive potential evapotranspiration (PET) and subsequently monthly climatic water balance (CWB = precipitation − PET). We performed correlation analyses between residual tree-ring chronologies and
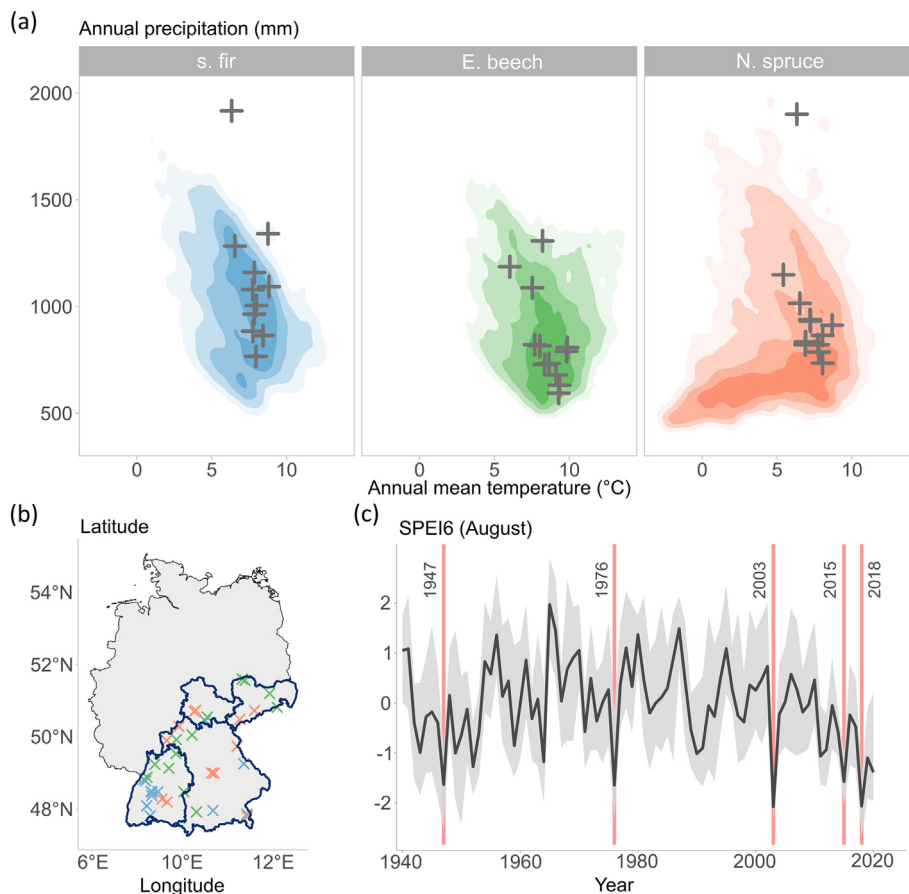
Fig. 1. Climate-space diagrams (a) for s. fir (blue), E. beech (green), and N. spruce (red). Colored areas refer to forest field observations of the respective species in Europe (99 % of all observations are inside the colored areas). Darker colored areas indicate a higher density of observed occurrences of a species. Grey crosses display the climatic position of the 37 study sites. Geographical data on tree species occurrences were obtained from Mauri et al. (2017), while climate data were extracted from WorldClim 2 (Fick and Hijmans, 2017). The geographic location of the study sites in Germany is shown in (b), while the annual development of a selected drought index, SPEI6 (Aug), for the period 1940–2020 is given in (c). Details are given in Section 2.4. The black line shows the overall average, while the grey ribbon indicates the variation between sites. Red vertical lines represent the five years with the driest vegetation periods on average. Climate data for (c) were obtained from the 1 km × 1 km grid of the DWD Climate Data Center (CDC) (2021). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

the SPEI within the period of 1940–2020 at different time scales (3, 6, and 12 months) to determine the time frame in which SPEI is most relevant to growth (see Fig. S2). The highest correlations for SPEI were observed for different time scales in the months of June, July, and August. We chose the August SPEI integrated over 6 months (SPEI6, March to August), as this period was shown to encompass the duration of cambial activity of N. spruce (Rossi et al., 2008) and E. beech (Čufar et al., 2008) in Central Europe. The correlations between SPEI6 in August and species-specific tree growth by site are mapped in Fig. S3. Following Slette et al. (2019), we considered all years within the period 1940–2020 with a SPEI6 < −1 as potential droughts.

2.5. Quantification of drought responses

We relied on the indices resistance (Rt), recovery (Rc), and resilience (Rs) to fathom the capacity of E. beech, N. spruce, and s. fir to cope with increasing droughts. These complementary indices were first proposed by Lloret et al. (2011) and were defined as follows:

$$Resistance_i = Dr_i / PreDr_i \qquad (1)$$

$$Recovery_i = PostDr_i / Dr_i \qquad (2)$$

$$Resilience_i = PostDr_i / PreDr_i \qquad (3)$$

where Dr_i represents the growth within the drought year i itself, $PreDr_i$ the average growth in a preceding two-year period, and $PostDr_i$ the average growth in the two subsequent years after each drought. In this context, *resistance* describes a tree's capacity to withstand a drought's negative impact, while the index *recovery* reflects the ability to recover immediately. Last, the index *resilience* captures the short-term capacity of a tree to regain its pre-drought growth level. Detrended RWI data were used to calculate the indices described. Instead of two years, we also considered other reference period lengths (see Fig. S4). Following an approach by Bottero et al. (2021), we finally selected a two-year reference period because we detected an autocorrelation of >0.5 for one and two years lags in our tree-ring series (see Fig. S5).

2.6. Consideration of drought frequency and pre- and post-drought conditions

We followed two other approaches to account for repeated or longer-lasting droughts and different climatic conditions in the pre- and post-drought periods. First, as suggested by Bose et al. (2020a), we determined the drought frequency by counting the droughts ten years prior to each identified drought event. Second, we relied on an approach by DeSoto et al. (2020) to determine the relative intensity of each drought event by considering the climatic conditions in the two years before and

after. In accordance with the resilience index formulas of Lloret et al. (2011), we calculated:

$$SPEI_{resist,i} = SPEI_i / PreSPEI_i \qquad (4)$$

$$SPEI_{recov,i} = PostSPEI_i / SPEI_i \qquad (5)$$

$$SPEI_{resil,i} = PostSPEI_i / PreSPEI_i \qquad (6)$$

where $SPEI_i$ is the SPEI6 (Aug) in the drought year i itself, $PreSPEI_i$ the average SPEI6 (Aug) in the two-year long pre-drought period, and $PostSPEI_i$ the average SPEI6 (Aug) in the two-year period after the drought. Since SPEI values can be both positive and negative (they usually range from -3 to $+3$), we added an arbitrary number of $+10$ to all SPEI values before division to avoid division by negative values. Before modelling (see Section 2.8), the calculated indices were scaled and centered so that the arbitrary addition of $+10$ did not affect the model output and the effect sizes were still comparable. Fig. S6 provides an overview of the calculated relative SPEI indices.

2.7. Estimation of individual plant-available water capacity

For each mineral soil horizon at each sampled tree, the available water capacity was estimated separately using the pedotransfer-function based on soil texture and bulk density measured in the field (Ad-hoc-Arbeitsgruppe Boden, 2005). We set the available water capacity for organic surface layers to 30 % (Hammel and Kennel, 2001). Then, the individual available water capacities of the mineral soil horizons and organic surface layers were summed up for the entire soil profile for each sampled tree to estimate the total plant-available water capacity (awc). The variation of awc within each site is visualized in Fig. S7.

2.8. Modelling approach

We followed an information-theoretic approach to address our research objectives (a), (b), and (c). Before defining any statistical model, we checked for (multi-) collinearity between the potential predictor variables by calculating correlation coefficients and determining variance inflation (VIF). Only predictors with $VIF < 3$ were kept. The response variables (resistance, recovery, resilience) were log-transformed to homogenize variances and normalize residuals. For each response variable, we developed three models that accounted for different levels of drought intensity (mild $= -1.5 < SPEI \leq -1$; severe $= -2 < SPEI \leq -1.5$; extreme $= SPEI \leq -2$) as suggested by Slette et al. (2019), resulting in overall nine models. Predictor variables were scaled and centered to facilitate the models' interpretability and allow for direct comparison between regression coefficients (Schielzeth, 2010). Linear mixed effect models (LMM) were applied, accounting for nesting in our data (for details see below) and thus avoiding overly progressive significances due to pseudo-replication (Burnham and Anderson, 2002). We created full LMMs (global models) including fixed effects accounting for (1) drought intensity (SPEI6 August) and (2) frequency, (3) available water capacity (awc), (4) pre- and post-drought conditions ($SPEI_{resist,recov,resil}$), (5) tree size ($dbh_{1.3m}$), (6) nutrient regime (base-poor, medium, base-rich), (7) tree species, (8) site aridity (average ratio between annual precipitation and PET for the period 1940–2020), and (9) biologically meaningful interactions selected based on predefined hypotheses (see Table S3). The optimal random effect structure was determined based on the Akaike Information Criterion (AIC) and likelihood ratio tests. An initially assumed nesting of trees within sites did not improve model fit. Thus, we only incorporated a random effect on the site level (random intercept) in the global models (Schielzeth and Nakagawa, 2013). Potential final models, nested in the global models, were selected based on the ranking of the second-order AIC (AICc) (Burnham and Anderson, 2002), supported by an automated model selection procedure (Barton, 2020). To further add multi-model inference and to help with model selection uncertainty, Akaike weights were computed

(Burnham and Anderson, 2002). The final model selection was based on the lowest AICc values and highest Akaike weights. We calculated the coefficient of determination and marginal and conditional R^2 for the assessment of variance explained by the model and the included predictors (Nakagawa and Schielzeth, 2013). Model assumptions were tested by plotting residuals versus fitted values and each explanatory variable. In addition, we validated the model fits through posterior predictive checking, i.e., by simulating replicated data sets given the fitted model (Gelman et al., 2021). To conduct pairwise comparisons between groups, we evaluated differences in drought response among species (s. fir, E. beech, N. spruce), drought severity (mild, severe, extreme), and nutrient regime (base-poor, medium, base-rich) using nonparametric Kruskal-Wallis tests, followed by a Wilcoxon rank sum test with a Bonferroni correction.

To identify potential temporal trends in drought response, i.e. objective (d), we also created three additional models (separately for Rt, Rc, and Rs) that included only data from severe and extreme droughts, as the previous analysis yielded poor model fits for mild drought (see Section 3.3). Consistent with the previously described approach, we created a global model that included predictors that accounted for (1) tree species, (2) drought frequency, (3) nutrient regime, and (4) site aridity interacting with the different (5) drought years that were defined as severe or extreme. Model selection, structure, assumptions, and testing were identical to the previous models and differed only in the predictors and interactions included.

We used the statistical environment R, version 4.1.2 (R Core Team, 2021), for all analyses and calculations. In more detail, we used the R-packages *dplR* (Bunn, 2008), *treeclim* (Zang and Biondi, 2015), and *pointRes* (van der Maaten-Theunissen et al., 2021) for tree-ring analyses and calculation of drought tolerance indices. The *SPEI package* (Beguería and Vicente-Serrano, 2017) was utilized for determining SPEI values integrated over different periods. To create the maps, we relied on the packages *rnaturalearth* (South, 2017), *raster* (Hijmans et al., 2022), and *sf* (Pebesma et al., 2022). The packages *lme4* (Bates et al., 2015), *lmerTest* (Kuznetsova et al., 2017), *MuMln* (Barton, 2020), *performance* (Lüdecke, 2021), *effects* (Fox et al., 2020), and *rstatix* (Kassambara, 2021) were used for statistical analyses. Further, the meta-package *tidyverse* (Wickham et al., 2019) was used for analyses, data handling, and visualizations.

3. Results

3.1. Tree growth and chronology statistics

We observed similar growth patterns between trees and sites of the same species. Fig. 2 represents the course of the site chronologies and highlights drought years which were common to at least 80 % of all sites per species, while Fig. S8 provides a detailed overview of the growth trajectories in dependence on the sites' nutrient regime. The expressed population signal (EPS) was consistently above the commonly used threshold of 0.85 for all sites (Wigley et al., 1984), indicating a strong common signal and a good representation of the dominant and survivor trees of the population by the sample chronologies (Briffa and Jones, 1992; Speer, 2010). This complies with the high congruence between the RWI within each site, reflected in high values of Gleichläufigkeit (glk), ranging from 0.62 to 0.73 (Eckstein and Bauch, 1969). A detailed overview of the chronology statistics is given in Table S4.

3.2. Growth responses to drought

Across all 37 sites, we identified 9 to 18 individual years that represented potential site-specific droughts ($SPEI \leq -1$) during the study period (1940–2020). Each site experienced at least one extreme, one severe, and one mild drought (Table S5). Overall, 2003 and 2018 were the most pronounced drought years, followed by 1947, 1976, and 2015 (Fig. 2). Drought responses varied widely depending on species, drought severity, and nutrient regime (Table S6). In general, lowest resistance and resilience were observed under extremely dry conditions, with N. spruce being the most affected tree species (Fig. 3). E. beech and N. spruce did not differ in
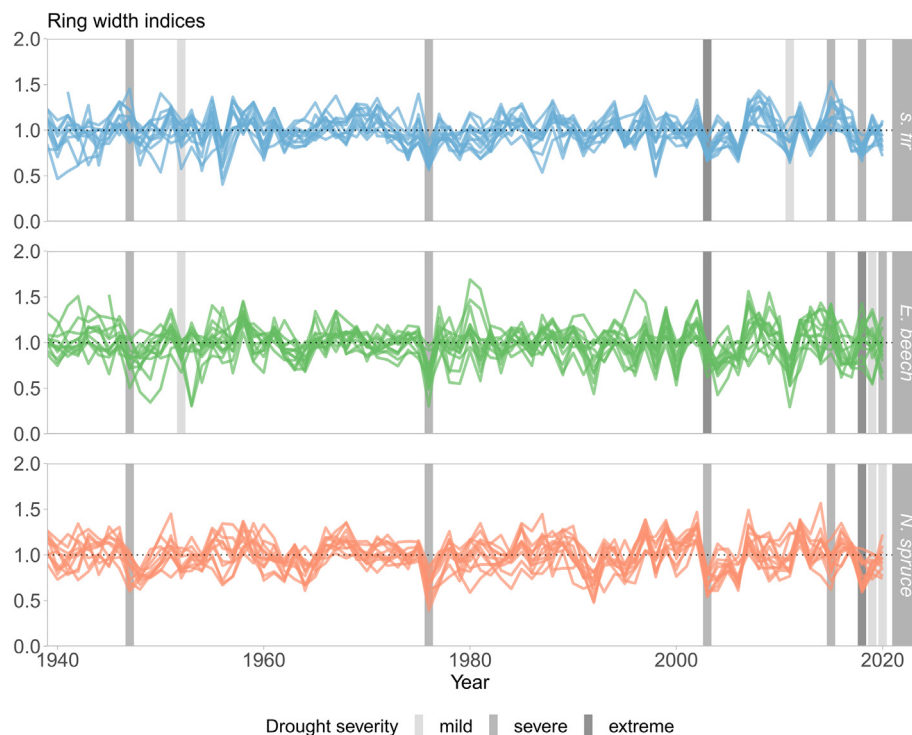
Fig. 2. Growth patterns of s. fir (blue), E. beech (green), and N. spruce (red) from 1940 to 2020. Each line represents a site chronology ($n = 37$). The grey bars indicate drought years (SPEI6 < -1), which were common to at least 80 % of all sites per species. Colour intensity represents different classifications of drought severity (mild = $-1.5 < SPEI6 \leq -1$; severe = $-2 < SPEI6 \leq -1.5$; extreme = SPEI6 ≤ -2), whereas the SPEI6 values were averaged across sites per species and drought year. The darker the colour the more intense the drought was on average. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

their response patterns to severe drought, while s. fir showed significantly higher resistance and resilience. Mild droughts had little or no impact, but tree responses varied considerably, with s. fir being less resistant than the other two species.

Nutrient regime affected drought response patterns (Table S6, Fig. 4), with trees growing at sites with a medium nutrient regime being most resistant to extreme drought, while resilience of trees at base-rich and medium sites was similar. E. beech showed the greatest variation in its response to severe and extreme droughts, particularly during extreme droughts with a medium nutrient regime (Rt = 1.17 ± 0.68). S. fir showed high resistance and resilience to severe droughts (Fig. 3). However, low resistance in response to extreme drought events was observed (0.76 ± 0.21), followed by rapid recovery (1.26 ± 0.28), resulting in high resilience (0.93 ± 0.26). N. spruce trees were most sensitive to severe and extreme droughts, especially to the latter (Fig. 3), where they showed little variation in their resistance (0.62 ± 0.19, i.e. 38 % growth reduction on average). During the subsequent two-year period after extreme droughts, most N. spruce trees failed to reach pre-drought growth levels (Rs = 0.79 ± 0.22).

3.3. Drivers of drought responses

For models accounting for mild droughts, predictors described only between 1.1 and 2.3 % of the underlying variance in the response variables (Table S7), and inappropriate model fits were observed. Therefore, we focus only on the models, including data on severe and extreme droughts. Tree species identity, drought frequency, nutrient regime, and associated interactions were the most important predictors of tree responses (Table 1). N. spruce exhibited significantly lower resistance than s. fir, which was also true for resilience under extremely dry conditions. E. beech showed higher resistance to extreme drought than s. fir, but its resilience was consistently lower. Regardless of tree species, a high frequency of droughts within the ten years prior was associated with a positive response to extreme drought. Large effect sizes highlighted the importance of this

predictor (Table 1). In addition, significant interactions between drought frequency, species, and nutrient regime were present for both drought classes. In general, N. spruce and E. beech benefited from higher drought frequency in terms of resilience, while s. fir was negatively affected under severely dry conditions (Fig. 5, Table 1).

Differences in recovery after extreme droughts were found between species, with N. spruce recovering significantly less than s. fir when repeated droughts characterized the past decade. The indices introduced to represent climatic conditions before and after severe droughts showed that trees benefited significantly from better water availability during the reference periods. Under extremely dry conditions, we found differences among species. While post-drought climatic conditions did not significantly impact s. fir and N. spruce behavior, E. beech benefited from high water supply in the post-drought period (high values of SPEI$_{recov}$ and SPEI$_{resil}$; Fig. 6). Large effect sizes further underscored the importance of the post-drought conditions for E. beech (Table 1). The nutrient regime of the sites modulated the drought response patterns. Trees growing on base-rich sites were more susceptible than those on base-poor sites but recovered more quickly (Table 1). We found that significantly lower resistance to severe drought was associated with higher drought frequency at sites with medium nutrient regime in comparison to base-poor sites. In contrast, higher resistance was linked to higher drought frequency at all nutrient levels (Fig. S9). Significant interactions were found between drought severity and nutrient regime. While more intense droughts generally led to lower resistance, the opposite was true during extreme droughts for trees growing under a medium nutrient regime. Tree size was only included in the models for severe droughts. Resistance in N. spruce increased significantly with tree size. Lower resilience was associated with larger trees for both E. beech and N. spruce, while the opposite was true for s. fir. The available water capacity for each tree was omitted from all models, indicating that the variation in drought responses within a site could not explain the variance between trees. In addition, the long-term climatic differences among sites (site aridity) were also not one of the main factors driving drought
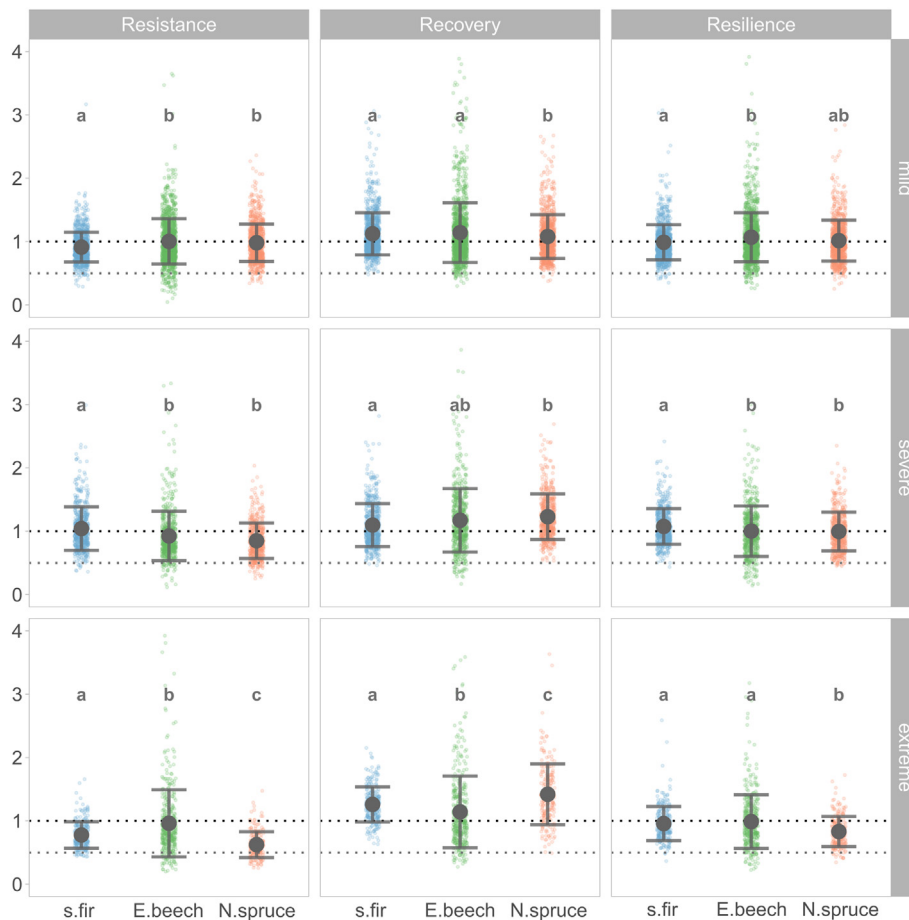
Fig. 3. Differences in drought resilience components (columns) among tree species (blue = s. fir, green = E. beech, red = N. spruce) to varying drought intensity (rows). The grey circles indicate the group mean and the branches the standard deviation. The black dotted lines represent no response of the trees (Rt, Rc, Rs = 1), while the grey dotted line indicates a very pronounced, negative response to drought (Rt, Rc, Rs = 0.5). Different letters refer to pairwise comparisons among groups assessed with non-parametric Wilcoxon rank sum tests with Bonferroni correction. Two groups sharing one or more letters were not significantly different ($p > 0.01$). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

response. Overall, predictors that accounted for drought characteristics, tree size, and nutrient regime explained between 0.13 and 0.5 of the total variances, as indicated by the marginal R^2 values (Table 1). When fixed and random effects were accounted for, the total explained variance (conditional R^2) ranged from 0.41 to 0.69.

3.4. Temporal trends

We observed varying patterns of drought responses over time (Table 2). While the resistance of E. beech and s. fir increased over time, it decreased for N. spruce. Large effect sizes highlighted the importance of differences among tree species when accounting for temporal trends. Contrary, this pattern changed for resilience with E. beech and N. spruce showing a pronounced decrease over time, while the resilience of s. fir slightly increased (Fig. S10). The variance explained by the predictors was between 0.11 and 0.25, while the total explained variance ranged from 0.16 to 0.34 (Table 2).

4. Discussion

We investigated components of tree resilience to drought stress in relation to (micro-) site conditions and drought characteristics of three major temperate tree species along a broad ecological gradient in Germany that included 37 sites with different climatic and soil conditions. We further examined changes in drought responses over time.

4.1. Growth responses of fir, beech, and spruce depending on drought severity

Our results support that growth responses to drought vary among tree species (Gazol et al., 2018; Song et al., 2021; Vitasse et al., 2019a), but strongly depend on drought characteristics (Gao et al., 2018), such as severity (Greenwood et al., 2017), frequency (Bose et al., 2020a), and climatic conditions in previous and subsequent years (Jiang et al., 2019; Jiao et al., 2021). Overall, N. spruce trees responded strongly to drought. This was especially evident during extreme drought, where we noticed a prolonged decline in growth. A pattern that has frequently been observed in N. spruce throughout Central Europe, particularly outside its natural distribution range, and that confirms the general assumption of the high susceptibility of this species to drought (Lévesque et al., 2013; Vitasse et al., 2019a; Zang et al., 2011). In contrast, we observed a significantly higher resistance and resilience of s. fir to severe and extreme drought conditions, consistent with studies in similar geographical regions (Bottero et al., 2021; Vitali et al., 2017). Therefore, s. fir is often considered to be better adapted to future climatic changes in the center of its natural range (Bouriaud and Popa, 2009; Vitasse et al., 2019a). However, we observed a higher recovery for N. spruce to severe and extreme droughts due to the inherent negative relationship between the indices resistance and recovery (Lloret et al., 2011), as trees with lower resistance also have higher recovery potential. Thus, this doesn't reflect an actual higher recovery capacity of N. spruce (Bottero et al., 2021; Schwarz et al., 2020). While E. beech was previously found to be a drought susceptible species (Leuschner, 2020; Muffler et al.,
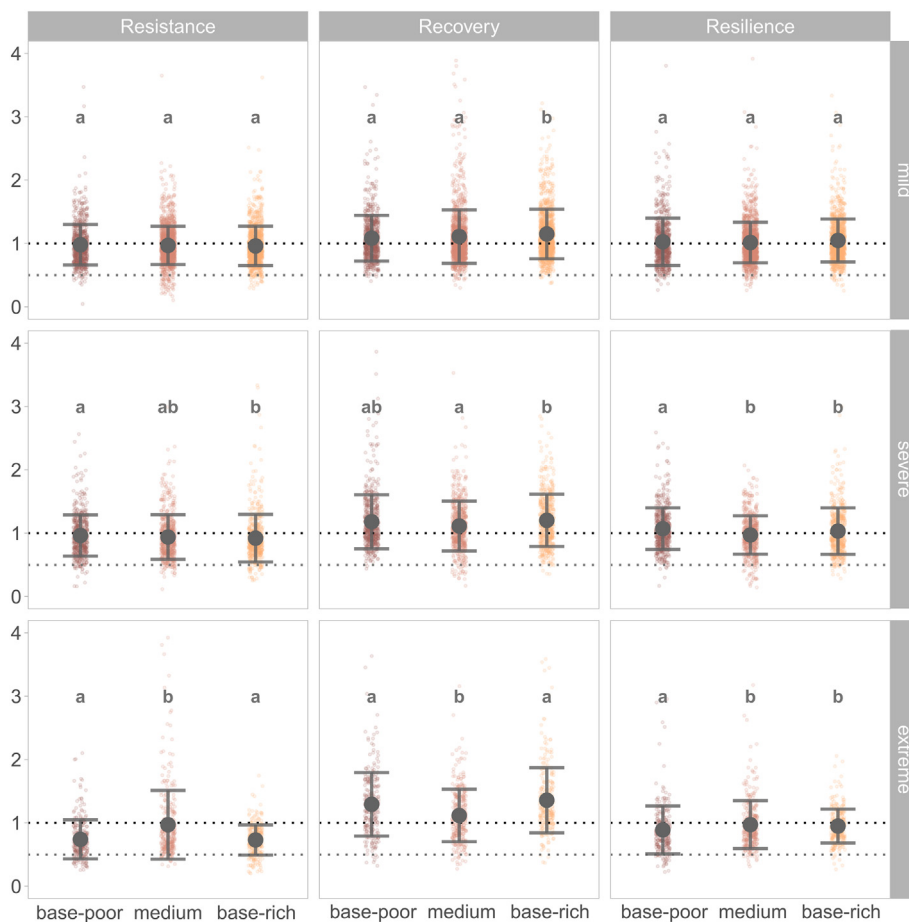
Fig. 4. Differences between resistance, recovery, and resilience (columns), separated by nutrient regime and drought severity classifications (rows). The grey circles indicate the group mean and the branches the standard deviation. The black dotted lines represent no response of the trees (Rt, Rc, Rs = 1), while the grey dotted line indicates a very pronounced, negative response to drought (Rt, Rc, Rs = 0.5). Different letters refer to pairwise comparisons among groups assessed with non-parametric Wilcoxon rank sum tests with Bonferroni correction. Two groups sharing one or more letters were not significantly different (*p* > 0.01).

Table 1
Parameter estimates and standard errors (se) of the final models for severe (left) and extreme (right) droughts resulting from the multi-model comparison.

Severe drought	Estimate (se)			Extreme drought	Estimate (se)		
Fixed effect variables	Resistance	Recovery	Resilience	Fixed effect variables	Resistance	Recovery	Resilience
Intercept	0.04 (0.07)	0.13 (0.06)°	0.06 (0.07)	*Intercept*	−0.20 (0.08)*	0.08 (0.11)	−0.04 (0.05)
E. beech	−0.15 (0.8)°	−0.09 (0.07)	−0.21 (0.1)*	*E. beech*	0.09 (0.08)	−0.22(0.14)	−0.09 (0.07)
N. spruce	−0.24 (0.08)**	0.13 (0.07)	−0.11 (0.1)	*N. spruce*	−0.34 (0.09)**	0.20 (0.12)	−0.19(0.07)*
spei6	0.01 (0.02)	−0.05 (0.02)**		*spei6*	0.20 (0.05)***	−0.30 (0.03)***	< −0.001 (0.04)
spei$_{resist,recov,resil}$	0.06 (0.01) ***	0.06 (0.01)***	0.06 (0.01)***	*spei*$_{resist,recov,resil}$		< 0.001 (0.03)	−0.02 (0.02)
size	0.03 (0.01) *	0.02 (0.01)	0.06 (0.01)***	*frequency*	0.22 (0.05)***	0.30 (0.1)*	0.14 (0.01)***
frequency	−0.002 (0.02)	−0.07 (0.02)***	−0.02 (0.02)	*base-rich*	−0.23 (0.09)*	0.30 (0.12)*	
base-rich	−0.08 (0.08)	−0.07 (0.07)		*medium*	0.08 (0.09)	0.10 (0.12)	
medium	0.03 (0.07)	−0.16 (0.07)*		*E. beech × spei6*	−0.26 (0.05)***		−0.20 (0.04)***
E. beech × size	0.14 (0.02) ***	−0.21 (0.02)***	−0.07 (0.02)**	*N. spruce × spei6*	0.03 (0.06)		0.05 (0.05)
N. spruce × size	−0.11 (0.02)***	0.02 (0.02)	−0.11 (0.02)***	*E. beech × frequency*	0.15 (0.04)***	0.11 (0.06)°	
E. beech × frequency	0.20 (0.02)***		0.13 (0.02)***	*N. spruce × frequency*	0.01 (0.05)	−0.18 (0.07)**	
N. spruce × frequency	0.16 (0.03)***		0.15 (0.02)***	*E. beech × spei*$_{resist,recov,resil}$		0.30 (0.06)***	0.12 (0.04)***
base-rich × spei6	0.03 (0.02)	< −0.001 (0.02)		*N. spruce × spei*$_{resist,recov,resil}$		−0.1 (0.05)	0.03 (0.04)
medium × spei6	0.13 (0.02)***	−0.10 (0.02)***		*base-rich × spei6*	0.11 (0.06)°	−0.07 (0.06)	
base-rich × frequency	−0.05 (0.02)*	0.07 (0.02)**		*medium × spei6*	−0.22 (0.04) ***	0.41 (0.04)***	
medium × frequency	−0.18 (0.02)***	0.20 (0.03)***		*base-rich × frequency*	0.01 (0.05)	−0.09 (0.06)	
				medium × frequency	−0.13 (0.04)**	0.09 (0.05)°	
R^2_m	0.333	0.227	0.127	R^2_m	0.504	0.389	0.250
R^2_c	0.527	0.416	0.459	R^2_c	0.697	0.661	0.409
Observations	1599	1599	1599	Observations	848	848	848
Akaike weight	1	1	1	Akaike weight	0.22	0.44	0.36

Note: S. fir on base-poor sites functions as a reference. Parameter estimates are directly comparable due to prior scaling and centering. Medium and base-rich = nutrient regime classifications; frequency = drought frequency; size = dbh$_{1.3m}$; spei6 = spei6 August; spei$_{resist,recov,resil}$ = relative drought intensity; $R^2_{c,m}$ = conditional & marginal R-squared; Akaike weight = probability of selected model being the best model. Significance levels: *** ≤0.001, ** ≤0.01, * ≤0.05, ° ≤0.1.
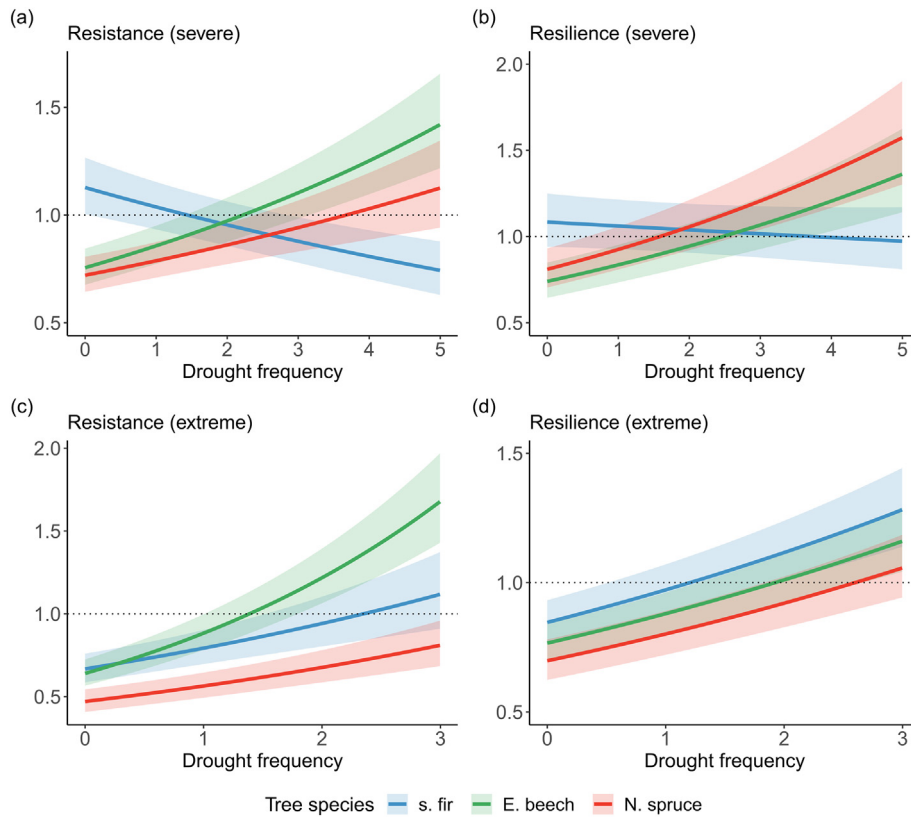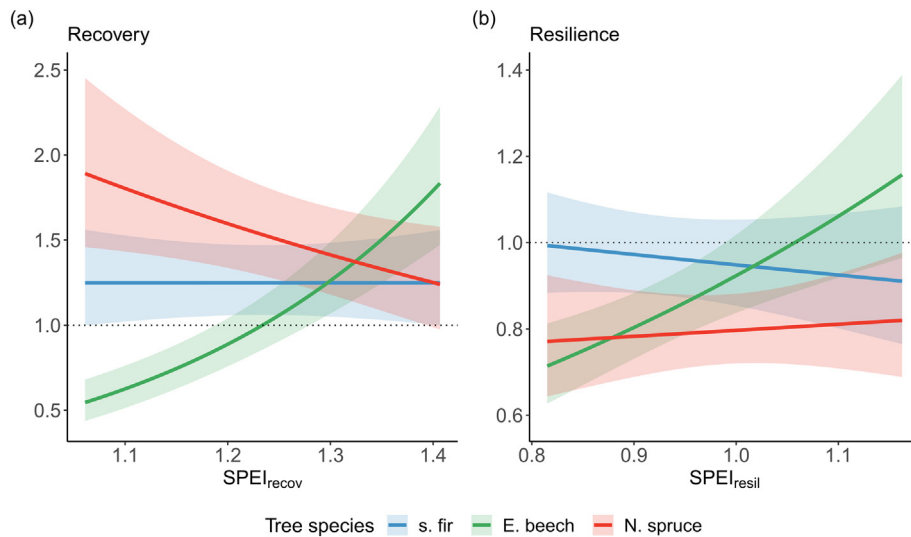
Fig. 5. Linear mixed effects model predictions for resistance (a,c) and resilience (b,d) in response to severe (upper panels) and extreme droughts (lower panels) depending on the drought frequency within the ten years prior. The coloured ribbons refer to the 95 % confidence intervals. Note the different scales on the x- and y-axes. Other variables were set to mean. Details are given in Table 1.

2020), our results could only partially confirm this at the core of its distribution range, where E. beech is considered to be particularly prone to drought stress (Cavin and Jump, 2016). Further, we observed considerable plasticity in the drought responses of E. beech (Fig. 3), which was previously observed by Dorado-Liñán et al. (2018) at its southernmost distribution limit. As expected, more severe drought events generally resulted in

greater growth losses (Gao et al., 2018). Still, response patterns to mild droughts were highly variable, and our models could not explain the underlying variance. This may be because what was defined as a mild drought may not have been an ecological drought in the true sense at some sites, an issue previously raised by Zang et al. (2019). In addition, mild drought stress might be fully managed by stomatal closure or osmotic regulation,

Fig. 6. Linear mixed effects model predictions for recovery (a) and resilience (b) in response to extreme droughts depending on climatic conditions in the post-drought period (SPEIrecov and SPEIresil). The coloured ribbons refer to the 95 % confidence intervals. Note the different scales on the x- and y-axis. Other variables were set to mean. Details are given in Table 1.

Table 2
Parameter estimates and standard errors (se) of the final models aimed at describing temporal trends in responses to severe and extreme droughts.

Trend severe & extreme drought	Estimate (se)		
Fixed effect variables	Resistance	Recovery	Resilience
Intercept	− 0.09 (0.03)*	0.11 (0.04)**	0.02 (0.03)
year	0.03 (0.01)**	− 0.01 (0.01)	0.03 (0.01)*
E. beech	− 0.08 (0.05)	− 0.05 (0.06)	− 0.13 (0.03)***
N. spruce	− 0.21 (0.05)***	0.09 (0.06)	− 0.12 (0.04)**
frequency	0.14 (0.01)***	− 0.06 (0.01)***	0.09 (0.01)***
*year * E. beech*	0.10 (0.02)***	− 0.15 (0.02)***	− 0.05 (0.02)**
*year * N. spruce*	− 0.11 (0.02)***	0.05 (0.02)*	− 0.07 (0.02)***
*year * frequency*	0.02 (0.01)***	0.05 (0.01)***	0.07 (0.01)***
R^2_m	0.246	0.120	0.112
R^2_c	0.339	0.239	0.159
Observations	2447	2447	2447
Akaike weight	0.68	0.42	0.34

Note: S. fir serves as a reference. Parameter estimates are directly comparable due to prior scaling and centering. Frequency = drought frequency; $R^2_{c,m}$ = conditional & marginal R-squared; Akaike weight = probability of selected model being the best model. Significance levels: *** ≤ 0.001, ** ≤ 0.01, * ≤ 0.05, ° ≤ 0.1.

allowing immediate recovery and thus not significantly affecting growth (Gessler et al., 2020). Contrary, extreme drought stress may lead to a substantial growth decline, damage tree tissues and cause persistent physiological damage making trees susceptible to subsequent droughts (W. R. L. Anderegg et al., 2020; Gessler et al., 2020).

4.2. Pre- & post-drought conditions crucial for drought responses

Our results highlight the role of climatic conditions in the preceding and following years, which is crucial given the expected increase in duration and frequency of extreme drought events (Intergovernmental Panel on Climate Change, 2021; Spinoni et al., 2018). We observed that high resistance, recovery, and resilience to severe droughts was associated with beneficial climatic conditions during reference periods and vice versa, supporting our initial hypothesis (H_II). Such effects were also noticed for managed Scots pine (*Pinus sylvestris*) stands in Germany (Sohn et al., 2016) and E. beech and oak (*Quercus pubescens*) forests in northern Spain (González de Andrés et al., 2021). In addition, we found differences among species during extreme droughts, with E. beech's recovery potential increasing substantially with improved water conditions in post-drought years. Findings by Jiang et al. (2019) support the importance of post-drought conditions by showing that exceptionally wet years following drought can compensate for growth deficits that occurred meanwhile. An experiment by Cermák et al. (1993) showed that rewatering after a drought resulted in quick response of declining E. beech trees, indicating a high capacity for recovery (Leuschner, 2020). Jiao et al. (2021) noted that drought duration and post-drought hydrological conditions were among the main drivers of vegetation recovery, with long-term droughts being particularly important to forest ecosystems. Prolonged droughts can deplete the soil water storage (Goulden and Bales, 2019), leading to cumulative effects that exacerbate tree impacts by damaging key structural components (Gao et al., 2018; Gessler et al., 2020; Serra-Maluquer et al., 2018). A slower recovery was linked to more extended droughts due to the need to rebuild fine-root systems (Mainiero and Kazda, 2006; Sohn et al., 2016), which is essential for a successful recovery (Hagedorn et al., 2016; Leuschner, 2020). This could be particularly important for conifers, as slow recovery was associated with higher mortality risk (DeSoto et al., 2020). Severe droughts can lead to defoliation in subsequent years due to a lack of hydraulic recovery (Arend et al., 2022), which is deteriorated by prolonged droughts as short-term leaf recovery is hindered (Bose et al., 2020a) and canopy transparency continues to increase (Jacobs et al., 2021). This may impair a tree's resilience to recurrent droughts (Camarero et al., 2018).

4.3. Recurrent drought stress

Severe, prolonged, and frequent droughts may cause damage to key structural and physiological parts, which can have long-term effects on tree growth and vitality (Kannenberg et al., 2020; Peltier and Ogle, 2019). Repeated droughts can cause nutrient imbalances (Gessler et al., 2016), reduce the amount of stored carbohydrates (Peltier and Ogle, 2019; Sergent et al., 2014), and consequently increase recovery time (Mitchell et al., 2016) and the risk of tree mortality (Sánchez-Pinillos et al., 2022). Bose et al. (2020a) found that lower drought resistance of Scots pine trees was related to higher drought frequency along a broad gradient in Europe. Using the same approach, we found unexpected contrasting patterns for E. beech, N. spruce, and to some extent for s. fir, in the core of their distribution range. Higher drought frequencies were associated with higher resistance and resilience for E. beech and N. spruce, while different responses were observed for s. fir depending on drought severity. However, it must be mentioned here that this could also be attributed to the nature of the calculation, as mild droughts were considered for calculating drought frequency even though these might not have had a considerably impact on tree growth as discussed before. Hence, a high frequency of more intense droughts may have different, more severe effects that hinder a potential acclimation to dry conditions (Brodribb et al., 2020). Considering this, our results suggested that trees that had experienced multiple droughts in previous years were less responsive to recurrent droughts, refuting our hypothesis (H_I). Gessler et al. (2020) stated that an organism's phenotype might be adapted to an improved stress response due to its ecological memory of antecedent stress conditions (Ogle et al., 2015; Walter et al., 2011) and past growth development (Pretzsch, 2021a, 2021b), as well as its genetic capacity. This is supported by Peltier and Ogle (2019), who found regional differences in response to recurrent droughts and argue that beneficial acclimations can be a possible explanation for why some trees are more plastic in their response. For instance, roots' anatomical and physiological alterations and biomass adjustments have already been identified as possible acclimation processes (Brunner et al., 2015). After a drought, trees were found to invest more assimilates below ground, increasing rooting depth and root-to-shoot ratios (Brunner et al., 2015; Hagedorn et al., 2016). These acclimations may also prevail across generations (Bose et al., 2020b). However, different findings from Encinas-Valero et al. (2022) also suggest a potential for maladaptation to environmental stress, as increased phenotypic plasticity of the fine-root system was associated with a decline in vitality of stressed holm oaks (*Quercus ilex*). Trees at arid sites have been shown to store more non-structural carbohydrates (NSC) in response to limited photosynthesis (Piper et al., 2017). Thus, under drier conditions, more NSC could be available if another drought occurs (Peltier and Ogle, 2019). Further, smaller xylem conduits might be formed in response to frequent droughts, which were associated with lower susceptibility to hydraulic failure (Brunner et al., 2015; Eilmann et al., 2009; Guet et al., 2015). Smaller conduits are linked to lower growth rates, which could therefore also be interpreted as a sign of acclimation (Gessler et al., 2020). This would support findings that low growth prior to a drought promotes resilience (Bose et al., 2020a; Zang et al., 2014).

4.4. Drought responses modulated by nutrient regime

Our results proved that nutrient regime was a significant factor in drought response. In general, nutrient availability is known to be one of the major limitations of global tree growth and productivity (Fisher et al., 2012). Nitrogen (N), in particular is considered a limiting nutrient in many terrestrial ecosystems, but high atmospheric N deposition has led to a reversal where other elements, such as phosphorus (P), become more limiting (Binkley and Fisher, 2019; Peñuelas et al., 2013). Along our established gradient, the availability of P and most trace elements can be considered optimal at medium levels (Blume et al., 2009; Mellert et al., 2018). Soils with medium nutrient regime often combine low base saturation in the topsoil with high base saturation in the subsoil (e.g., most

Luvisols), which usually provides a balanced nutrient supply for optimal tree growth (Mellert and Göttlein, 2013). Nutrients are known to directly affect the uptake and use of water and carbon (C) (Gessler et al., 2016), which is crucial during dry periods (McDowell et al., 2008). This is supported by previous studies that highlighted the role of soil fertility on drought response patterns (DeSoto et al., 2020; Sergent et al., 2014). We found a high drought susceptibility of trees growing on base-rich sites, which was underlined by a strong relationship between their growth and SPEI6, especially in N. spruce and E. beech (Fig. S3). Trees on base-poor sites showed high resistance and resilience to severe drought conditions, while responding strongly to extreme drought stress (Fig. 4). In comparison, trees with a medium, more balanced nutrient regime showed significantly higher resistance and resilience to extreme droughts, partially confirming our initial hypothesis (H$_{III}$). These patterns largely align with observations that better soil fertility increased resistance (DeSoto et al., 2020). Thurm et al. (2016) found that high resistance of E. beech and Douglas-fir (*Pseudotsuga menziesii*) was associated with base-poor soils, while Lévesque et al. (2016) reported that the C/N-ratio was a better growth predictor. The latter revealed that the effect of nutrient supply was more pronounced under dry conditions, with lower C/N-ratios promoting the growth of s. fir, E. beech, and N. spruce. Although, high N deposition was linked to increased temperature sensitivity and lower drought tolerance (Hess et al., 2018; Villar-Salvador et al., 2013) due to a reduced root biomass (Dziedek et al., 2016). Gessler et al. (2016) laid out the framework of how nutrient supply can shape drought response patterns of trees. For instance, generally high nutrient availability leads to preferential aboveground biomass allocation, larger vessel diameters, or increased stomatal conductance, which likely predisposes trees to hydraulic constraints and thus hydraulic failure due to increased risk of cavitation. In addition, higher C costs may be detrimental during periods of C deficiency. On the other hand, high nutrient supply could be beneficial for recovery due to enhanced water-use efficiency and the fact that nutrients are required to rebuild tissue damaged during drought. Our results were partially consistent with these assumptions, as base-rich sites responded strongly to extreme drought (low resistance) but recovered rapidly in the two subsequent years, whereas trees on base-poor sites recovered less well. This could be also attributed to the fact that base-poor soils are often deficient in nutrients, such as potassium (K), which has been shown to be essential for mitigating drought stress (Sardans and Peñuelas, 2015). In contrast, trees growing on sites with medium nutrient regime, i.e., under optimal conditions, showed high plasticity in their responses. Gessler et al. (2016) further clarified that prolonged and more intense droughts negatively affect the uptake and assimilation of nutrients and C, as well as water transport. Increasing frequency of droughts may lead to nutrient imbalance within trees in the long-term (Gessler et al., 2016; Hevia et al., 2019), which could be exacerbated by the observed deterioration of mineral nutrition of trees in Europe (Jonard et al., 2015).

4.5. Negligible influence of differences in micro-site and long-term water availability

We hypothesized that micro-site differences (awc) and spatial variability in long-term water supply (site aridity) would be essential factors in drought responses (H$_{III}$). However, our results didn't indicate that. D'Orangeville et al. (2018) had previously observed that drought characteristics played a primary role over physical soil properties. This is consistent with results from France, where awc was not an essential tree growth predictor (Lévesque et al., 2016). But we were unable to account for differences in competition (Castagneri et al., 2021) or management history (Hilmers et al., 2022; Schmied et al., 2022), which could have affected drought responses and may have distorted micro-site differences in awc. Further, a recent drought study on E. beech showed that reduced water uptake from the drying topsoil did not result in compensating water uptake from deeper soil layers (Gessler et al., 2021). Thus, trees may not have benefited from a higher water table in deeper soil layers at sites with higher awc. Contrary, Rehschuh et al. (2017) observed a higher drought sensitivity

of trees growing on shallow and sandy soils. Chakraborty et al. (2021) found micro-site influences of awc supporting the assumption that plant-available water across the root zone affects post-drought growth (Kannenberg et al., 2020). The absence of long-term water availability effects could be attributed to the fact that we relied on the mean annual P/PET-ratio, which does not account for seasonal differences, as already mentioned by Serra-Maluquer et al. (2018). However, other studies reported more pronounced drought impacts at drier sites (W. R. L. Anderegg et al., 2015; Jiao et al., 2021) and the opposite (Martínez-Vilalta et al., 2012).

4.6. Temporal changes in response patterns

We identified temporal changes in drought responses that differed among tree species, confirming hypothesis H$_{IV}$. Resistance and resilience of s. fir was found to increase over time, affirming the assumption of a comparatively drought-resistant species with a high potential to cope with the upcoming changes (Vitasse et al., 2019b; Zang et al., 2014). However, this might differ towards the dry distribution margin, where increasing aridity led to an overall decline in s. fir growth in the past decades (Gazol et al., 2015). In contrast, our study confirms that N. spruce appears inferior to the predicted changes, as we observed a significant decline in resistance and resilience over time. Treml et al. (2021) also found that an increasing proportion of N. spruce trees at low elevations are experiencing extreme growth reductions, consistent with findings of their growth decline over the past two decades throughout central-eastern Europe (Bosela et al., 2021). We observed that the drought resistance of E. beech increased over time, while its resilience decreased. Thus, we found a lagged response, i.e. legacy effects, in E. beech to past drought events and a progressive loss in resilience considering the first two years following drought. González de Andrés et al. (2021) described similar patterns for the same species in northeastern Spain, closer to its rear edge. In this region, such long-term declining trends in resilience have been observed in the past (Serra-Maluquer et al., 2019). Across much of its range, E. beech growth is projected to decline, including in its center, where our study was conducted (Del Martinez Castillo et al., 2022). In general, declining trends in drought tolerance could indicate an enhanced mortality risk to recurrent droughts (DeSoto et al., 2020), which is crucial in the face of the predicted climatic changes.

5. Conclusions

We revealed different drought response patterns of s. fir, E. beech, and N. spruce along an ecological gradient in the South – Central – East part of Germany. We found that nutrient regime, drought frequency, and the hydraulic conditions in the previous and subsequent years were significant determinants of drought response. Higher drought frequency was associated with higher resistance and resilience for N. spruce and E. beech, suggesting that there might be a potential for acclimation. In general, more humid conditions in the two preceding and following years increased drought resistance, recovery, and resilience to severe droughts and were particularly important for the recovery of E. beech after extreme droughts. In addition, we found that trees growing under balanced nutrient regime conditions were better able to withstand extreme droughts. N. spruce showed the most substantial growth reductions under severe and extreme droughts, while s. fir exhibited comparatively high drought resilience, which increased over time. In contrast, the resilience of E. beech and N. spruce progressively decreased, indicating a higher vulnerability to the predicted climatic changes, especially for N. spruce.

CRediT authorship contribution statement

Gerhard Schmied: Conceptualization, Methodology, Formal analysis, Visualization, Investigation, Writing – original draft. **Torben Hilmers:** Methodology, Formal analysis, Writing – review & editing. **Karl-Heinz Mellert:** Conceptualization, Writing – review & editing. **Enno Uhl:**

Conceptualization, Methodology, Writing – review & editing. **Vincent Buness:** Investigation, Writing – review & editing. **Dominik Ambs:** Investigation, Writing – review & editing. **Mathias Steckel:** Conceptualization, Investigation, Writing – review & editing. **Peter Biber:** Methodology, Writing – review & editing. **Muhidin Šeho:** Conceptualization, Writing – review & editing. **Yves-Daniel Hoffmann:** Investigation, Writing – review & editing. **Hans Pretzsch:** Supervision, Project administration, Conceptualization, Methodology, Writing – review & editing.

Data availability

Data will be made available on request.

Declaration of competing interest

None declared.

Acknowledgments

Appendix A. Supplementary information

Supplementary information to this article can be found online at https://doi.org/10.1016/j.scitotenv.2023.161601.

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