

## Rapid beech decline under recurrent drought stress: Individual neighborhood structure and soil properties matter

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### ABSTRACT

During the summer of 2022, an acute drought once more afflicted central and southern Europe. This marked the third episode (after 2015 and 2018) of severe aridity in large parts of Germany within the last decade, leading to increased soil water depletion. Consequently, from July 2022 onward, European beech trees (*Fagus sylvatica* L.) exhibited early withering and pronounced premature defoliation. Nevertheless, crown defoliation exhibited substantial variation among trees within the same forest stands, prompting questions regarding the causal factors. In our study, we scrutinized twelve mature drought-impacted, beech-dominated forest stands in northern Bavaria, arranged along a gradient of different nutrient regime levels (base-rich, intermediate, base-poor), with co-occurring vital ( $\leq 40\%$  crown defoliation) and declining ( $\geq 60\%$  crown defoliation) trees. Within each stand, we selected an equal number of vital and declining trees, culminating in a total of 332 target trees. Dendrochronological patterns were analyzed to identify a potential timing of growth separation between vitality classes. Moreover, we used a Bayesian modelling framework to discern whether disparities in tree vitality hinged on competition, structure, small-scale differences in plant-available water capacity, and spatial clustering of declining competitors. We further explored the factors influencing the magnitude of growth decline post-2018 and how these were modulated by the site's nutrient regime. Our study unveiled that (i) low competition with increased size diversity bolstered tree vitality; (ii) declining trees were spatially aggregated; (iii) vital and declining trees exhibited strikingly similar growth trajectories in the past, which underwent a drastic shift following 2018, indicating a potential for a rapid vitality decline under recurrent severe drought stress; (iv) plant-available water capacity emerged as a crucial determinant of vitality and growth subsequent to 2018; (v) growth decline was most pronounced at base-poor and intermediate sites. Our findings underscore the importance of accommodating small-scale differences in soil and stand characteristics and advocate for silvicultural guidance towards reduced stand densities in combination with a more heterogeneous structure to mitigate beech dieback in drought-prone forest stands.

### 1. Introduction

In summer 2022, central-western Europe and the Mediterranean were hit by a prolonged drought, which was exacerbated by a persistent anticyclonic anomaly over Western Europe that caused enhanced soil water depletion through increased evapotranspiration (Faranda et al.,

2023). In large parts of Germany, this again led to severely dry conditions (Copernicus Climate Change Service (C3S), 2023), after recent years had already been characterized by unprecedented multi-year drought events (Hari et al., 2020; Rakovec et al., 2022). Climate change projections predict that such exceptional successive droughts will increase in their frequency and duration (Hari et al., 2020;

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Intergovernmental Panel on Climate Change (IPCC), 2021), with critical implications for boreal (Sánchez-Pinillos et al., 2022), tropical (McDowell et al., 2018), and temperate forest ecosystems (Bréda et al., 2006; Millar and Stephenson, 2015). Droughts are becoming the greatest constraint on tree growth at a global scale (Babst et al., 2019), and have been identified as one of the main causes for widespread (Allen et al., 2010; Allen et al., 2015) and excessive tree mortality (Senf et al., 2020).

During the dry summer of 2022, early leaf discoloration, wilting, and premature senescence of broadleaved forest trees were observed in some parts of Germany, as for example in Lower Franconia (Fäth and Kneisel, 2023). This behaviour is common under extreme droughts (Bréda et al., 2006; Schultdt et al., 2020) and is particularly related to the climatic conditions in spring and summer for European deciduous trees (Bigler and Vitasse, 2021). While moderately warm springs and summers can delay leaf discoloration (Liu et al., 2016; Xie et al., 2018), severe heat and drought stress (Bigler and Vitasse, 2021; Xie et al., 2018) and associated low soil water potential lead to earlier onset of defoliation (Walther et al., 2021). Even though it was argued that early leaf fall could be a strategy to reduce the transpiring leaf area and thus prevent hydraulic failure (Bréda et al., 2006), recent studies provide evidence that this is more likely a direct consequence of it (Arend et al., 2022; Walther et al., 2021). Moreover, premature leaf fall can be considered as an indicator of vitality decline (Wohlgemuth et al., 2020), as it is linked to a higher proportion of crown dieback and increased susceptibility to secondary damage in subsequent years (Frei et al., 2022).

European beech (*Fagus sylvatica* L., hereafter beech) is one of the most widespread tree species in Europe and showed severe defoliation symptoms during recent drought periods (Frei et al., 2022; Rohner et al., 2021; Schultdt et al., 2020), especially in Central Europe (Michel et al., 2022). Despite its broad ecological niche, beech is a drought-sensitive species (Leuschner, 2020) with a high capacity to recover even from persistent drought stress (Pretzsch et al., 2020), particularly when mixed with other species (Pretzsch et al., 2013). However, future growth decline is expected throughout much of its distribution range (Martinez del Castillo et al., 2022), with the centre of its range having been proven to be particularly vulnerable in the past (Cavin and Jump, 2016). The high vulnerability to prolonged drought stress can be attributed to its high transpirational water loss, which persists even with substantial levels of embolism and defoliation (Walther et al., 2021).

While an abrupt decline in beech crown vitality was observed in response to extreme droughts (Rohner et al., 2021), it was found to be preceded by a long-term growth decline (Gillner et al., 2013; Neycken et al., 2022). Sustained growth reduction with an inability to recover may hence be considered as an early-warning signal of mortality susceptibility (Cailleret et al., 2017; DeSoto et al., 2020). Nevertheless, drought reactions of temperate tree species are partially contingent upon local nutrient availability (Schmied et al., 2023; Sergent et al., 2014). For instance, beech reaches its drought limit more rapidly on base-poor soils compared to base-rich soils (Mellert et al., 2018a), implying heightened drought tolerance under base-rich conditions where it exhibits exceptional competitiveness (Ellenberg & Leuschner, 2010). Consequently, growth decline patterns antecedent to crown deterioration may also exhibit variations amid different nutrient regime levels. An ample nutrient supply can enhance water-use efficiency during dry periods and facilitate subsequent recovery (González de Andrés et al., 2022); conversely, high nutrient levels may predispose trees by investing primarily in aboveground biomass over the long term (Gessler et al., 2016).

Forests afflicted by drought frequently exhibit a high variability of crown vitality within a singular stand (Frei et al., 2022; Klesse et al., 2022; Neycken et al., 2022). Trees showing pronounced signs of canopy degradation coexist with vital trees, raising questions about underlying causes. Possible explanations include relations to genotype (Pfenninger et al., 2021), individual growth variability (Camarero et al., 2015), disparities in wood density and nutrient imbalances (González de Andrés et al., 2022; Hevia et al., 2019), light availability and tree species

diversity (Chakraborty et al., 2017), as well as tree dimensions and competition (Klesse et al., 2022). Nevertheless, the impact of small-scale differences in water availability, stand structure, and spatial clustering of dying trees is frequently overlooked and remains inadequately comprehended.

Although previous studies highlighted the small-scale heterogeneity of soil properties and associated soil moisture within single temperate forest stands (Carrière et al., 2020; Fäth et al., 2022; Ma et al., 2014; Rieder and Kneisel, 2023), plant-available water capacity was not identified as one of the main drivers of drought responses of beech across a broad precipitation gradient in Germany (Schmied et al., 2023). However, that could be different at sites where water availability is the main growth constraint (Chakraborty et al., 2021). In general, unfavourable soil conditions such as shallow soils or high gravel/sand and clay content were found to be detrimental to beech height growth (Mellert et al., 2023) and vitality (Obladen et al., 2021) after extreme droughts, resulting in substantial crown dieback compared to deep soils with higher water holding capacity (Frei et al., 2022; Walther et al., 2021). Thus, small-scale soil differences could influence water stress during dry periods and play an important role in tree survival (Carrière et al., 2020), potentially causing spatially clustered dieback patterns within a forest stand (Frei et al., 2022).

Beech forest dieback is a significant forestry concern, necessitating improved resilience strategies (Schultdt et al., 2020). While long-term solutions involve integrating more drought-tolerant species and fostering diversification (Hlásny et al., 2014; Pardos et al., 2021), short-term responses can include modulating competition (relating to aboveground space occupation) and structure (relating to tree size diversity) through thinning (Bradford et al., 2022; Elkin et al., 2015). Despite conflicting evidence on the benefits of reduced competition (Giuggiola et al., 2013; Klesse et al., 2022; Mausolf et al., 2018), it seems to improve water availability at drought-stricken sites (Bradford et al., 2022). Certain silvicultural approaches may further enhance structural diversity, offering improved temperature buffering and resilience (Brang et al., 2014; De Frenne et al., 2021; O'Hara and Ramage, 2013). However, loss of foliage or tree death can decrease temperature buffering, thereby intensifying drought stress and promoting spatial tree decline (De Frenne et al., 2021; Zellweger et al., 2020). We hypothesize that small-scale differences in competition and size diversity significantly impact the spatial variability of crown dieback and growth decline.

Here, we studied spatial and temporal patterns of beech decline in twelve mature, beech dominated, and drought-afflicted forest stands in northern Bavaria. Sites were selected along a gradient of different nutrient regime levels (base-rich, intermediate, base-poor) with co-occurring vital and declining beech trees. We assessed premature crown defoliation during the exceptionally dry summer 2022 of overall 332 trees and analyzed their annual growth patterns over the past 80 years. Our objective was to identify possible causes of variability in crown vitality and growth decline within the same forest stands by considering small-scale differences in plant-available water, size diversity, competition, and clustering of declining trees, while incorporating the site's nutrient regime. Antecedent studies frequently adopted a moncausal methodology, for instance, concentrating solely on stand characteristics or considering merely stand-level differences, disregarding the small-scale heterogeneity of forest soils, the role of nutrient supply, and stand structure composition. To tackle this gap in knowledge, we pursued the following research objectives:

- To examine differences in growth patterns among vital and declining trees, depending on the nutrient regime of the sites. We hypothesized that declining trees, unlike vital trees, experience a long-term growth decline that precedes crown dieback and varies with nutrient availability.
- To examine whether differences in stand structure and small-scale differences in plant-available water capacity influence

beech dieback. We hypothesized that high size diversity and low competition are beneficial for tree vitality and that small-scale differences in plant-available water capacity and spatial clustering of declining trees contribute to tree vitality differences within stands.

- (c) To analyse whether the growth response to the recurrent drought stress within recent years is influenced by stand structure and small-scale differences in plant-available water, and whether it is modulated by the site's nutrient regime. We hypothesized that growth decline would be most severe at base-poor sites with increased plant-available water capacity having a positive effect on individual growth.

## 2. Material and methods

### 2.1. Study site selection

From August to mid-September 2022, we selected twelve drought-damaged beech sites in Lower Franconia, Germany. The pre-selection of beech sites was based on forest damage reports from Bavarian foresters in a reporting portal of the Bavarian Forest Institute (LWF) after severe drought damage occurred in large parts of central and lower Franconia in the summer of 2022. Suitable forest stands were dominated by mature beech (>75 % of the total stand basal area) with a minimum age of 70 years, an overall canopy closure of at least 0.4, and a minimum size of 4.5 ha. All selected stands originated from natural regeneration and were frequently thinned in the past, resulting in structural differences within the same forest stand. However, no management activities were conducted in the past ten years. Only forest stands where strong signs of crown dieback were observed by local foresters in recent years (after 2018) were considered as sample sites. Based on their soil nutrient regime they were classified in three levels: base-rich, intermediate, and base-poor (Schmied et al., 2023). This classification from acidic (base-poor) to carbonate soils (base-rich) was considered as a proxy for the availability of base cations throughout the soil profile and thus, summarized the nutrient status along the soil pH-gradient (Härdtle et al., 2004; Mellert et al., 2018b; Walentowski et al., 2006). We validated the nutrient regime grading by measuring the soil pH with a field pH

measurement kit ('Hellige Pehameter') and checking for the presence of carbonate with a 10 % HCl solution. Overall, we sampled four sites for each nutrient regime level (see Table 1 for an overview). The site locations are mapped in Fig. 1a. All sites were located at an elevation between 235 m and 445 m a.s.l. in the warmest and driest region of Bavaria. The sites are characterized by similar climatic conditions, with an annual mean temperature between 7.9 °C and 9.6 °C and annual mean precipitation sum between 672 and 807 mm. Under these conditions, all study sites were located in the centre of the species' range, as indicated by their location in the species' climate-space (Fig. 1b). The prevalent soil types were cambisols/luvisols at base-rich sites, cambisols/planosols/podzols at intermediate sites, and cambisols/vertisols at base-poor sites (Table 1).

### 2.2. Tree selection and field sampling

At each of the twelve sites, we selected 12 to 15 vital beech trees ("vital") and an equal number of trees with declining vitality due to drought damage ("declining"), resulting in overall 332 target trees. The vitality classification into vital and declining trees was based on visual estimation of recent defoliation and crown dieback with binoculars, following suggestions by Dobbertin (2005). Crown defoliation was assessed in 5 % steps by comparing each target tree to a reference tree, which was considered to have the maximum amount of foliage at that site. We considered trees with a crown transparency of at least  $\geq 60\%$  to be declining, while vital trees had crown transparency of  $\leq 40\%$ . Thus, a clear distinction between the vitality classes was provided. Dead trees or completely defoliated trees (100 % defoliation) were not considered. The crown defoliation was assessed by the same person for all trees to avoid estimation differences due to potential observer bias. Only (co-)dominant trees with similar diameter at breast height (DBH<sub>1.3m</sub>) and a minimum distance of 30 m between each other were chosen. Target trees with signs of pronounced fructification were not selected.

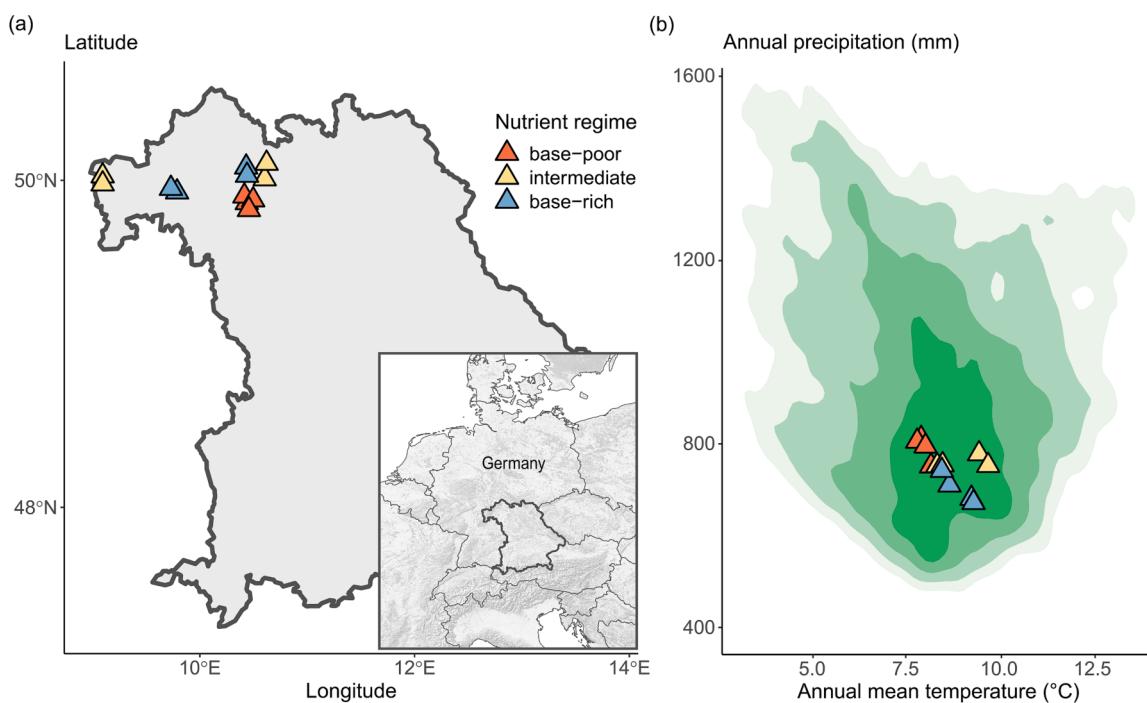
For all target trees, tree height and crown base height were measured with a Vertex ultrasonic hypsometer (Haglöf Inc., Madison). DBH was measured with a girth tape and the respective X and Y coordinates were mapped with a multiband GPS device with an accuracy of 1–4 m (Garmin Ltd., Schaffhausen). In addition, after the end of the growing season

**Table 1**

General information on the 12 study sites located in northern Bavaria. The category "beech share" describes the basal area share of beech compared to other tree species at the site and is based on the evaluation within 10 m circles around each target tree. For elevation and beech share, the site means and the standard deviations between target trees are presented. Temperature and precipitation refer to the annual average over the past 30 years.

Site ID	Site name	Longitude E	Latitude N	Nutrient regime	Elevation (m)	beech share (%)	Temperature (°C)	Precipitation (mm yr <sup>-1</sup> )	Parent material	Prevalent soil type
2214	Oberschwarzach	10°26,3'	49°51,4'	base-poor	445 ± 6.5	88 ± 14	7.9	807	sand- & claystone	cambisols
2215	Sudrach	10°25,3'	49°53,4'	base-poor	416 ± 15.9	87 ± 14	8.2	747	sand- & claystone	cambisols; vertisols
2216	Geusfeld	10°29,1'	49°52,8'	base-poor	424 ± 14.4	95 ± 9	7.9	803	sand- & claystone	cambisols; vertisols
2217	Schoenaich	10°27,1'	49°49,9'	base-poor	427 ± 5.2	85 ± 16	8.0	789	sand- & claystone	cambisols
2218	Zeil am Main	10°36,6'	50°1,7'	intermediate	356 ± 11.7	80 ± 20	8.3	734	sand- & claystone	cambisols
2219	Koenigsberg	10°37,0'	50°4,2'	intermediate	390 ± 20.5	80 ± 14	8.4	740	sand- & claystone	cambisols; planosols
2220	Sailershausen I	10°26,5'	50°3,6'	base-rich	298 ± 6.6	83 ± 15	8.6	700	limestone <sup>1</sup>	cambisols; luvisols
2221	Sailershausen II	10°26,1'	50°3,7'	base-rich	332 ± 13.1	75 ± 16	8.4	729	limestone <sup>1</sup>	cambisols; luvisols
2222	Himmelstadt I	9°45,9'	49°55,8'	base-rich	287 ± 15.6	89 ± 14	9.1	672	limestone <sup>1</sup>	cambisols; luvisols
2223	Himmelstadt II	9°45,8'	49°55,8'	base-rich	235 ± 23.8	87 ± 14	9.1	672	limestone <sup>1</sup>	cambisols; luvisols
2224	Aschaffenburg	9°5,8'	50°0,7'	intermediate	237 ± 11.6	94 ± 11	9.3	771	mica schist <sup>1</sup>	cambisols; podzols
2225	Kleinostheim	9°5,6'	50°2,0'	intermediate	294 ± 20.8	89 ± 14	9.6	744	mica schist <sup>1</sup>	cambisols

<sup>1</sup> with occasional loess pockets.



**Fig. 1.** Map of Bavaria showing the locations of the sample sites (a) and their position within the climate-space of beech (b). Coloured areas in (b) refer to forest field observations of beech in Europe (99% of all observations are within the coloured areas). Darker shaded areas indicate higher density of observed occurrences. Geographic data on field observations of beech were obtained from Mauri et al. (2017), while climate data were extracted from WorldClim 2 (Fick and Hijmans, 2017). The symbol colour refers to the different nutrient regime levels of the sites: base-poor, intermediate, base-rich.

(mid-October to mid-November 2022), two cores were taken in the opposite direction and perpendicular to the slope using a 5 mm Pressler increment borer. Thus, a total of 664 cores were taken in the field, which were stored and air-dried in wooden frames.

For the quantification of small-scale differences (at the tree-level) in plant-available water, basic physical soil properties were determined for each target tree using the methodology of Schmied et al. (2023). In the immediate vicinity of each target tree, the soil was sampled with a Pürckhauer auger to a depth of 1 m or to the parent material if this was reached first. In addition, a small soil profile was dug at each target tree to examine the humus layers and topsoil horizons. Soil texture, bulk density, fine earth content, and thickness of the organic layer and mineral soil horizons were recorded according to the Ad-hoc-Arbeitsgruppe Boden (2005), and the humus form and soil type were classified.

### 2.3. Tree-ring data processing

All tree cores were glued on wooden mounts and sanded with progressively finer sandpaper (120–800 grit) to facilitate the determination of annual ring boundaries. We measured the cores to the nearest of 1/100 mm using the digital positioning table LINTAB 5 and the software TsapWin (both Rinnotech, Heidelberg). We visually crossdated all tree-ring series under consideration of pointer years with extraordinary narrow rings, common to most series (Schweingruber et al., 1990; Stokes and Smiley, 1996). Missing tree-rings were added manually by choosing a very small value of 1/1000 mm for easy identification. Further, statistical crossdating was conducted with the help of skeleton plots. We converted annual ring-widths into basal area increments (bai) using the formula  $bai_t = \pi^*(r_t^2 - r_{t-1}^2)$ , where  $r$  is the radius of the tree at breast height and  $t$  the respective growth year. As we were also sampling the bark when we took the cores, we were able to measure the individual thickness of the bark for each tree. Therefore, we subtracted bark thickness from each tree's DBH before reconstructing past DBH-values used to calculate bai. Finally, the outside-in (bark to pith) function

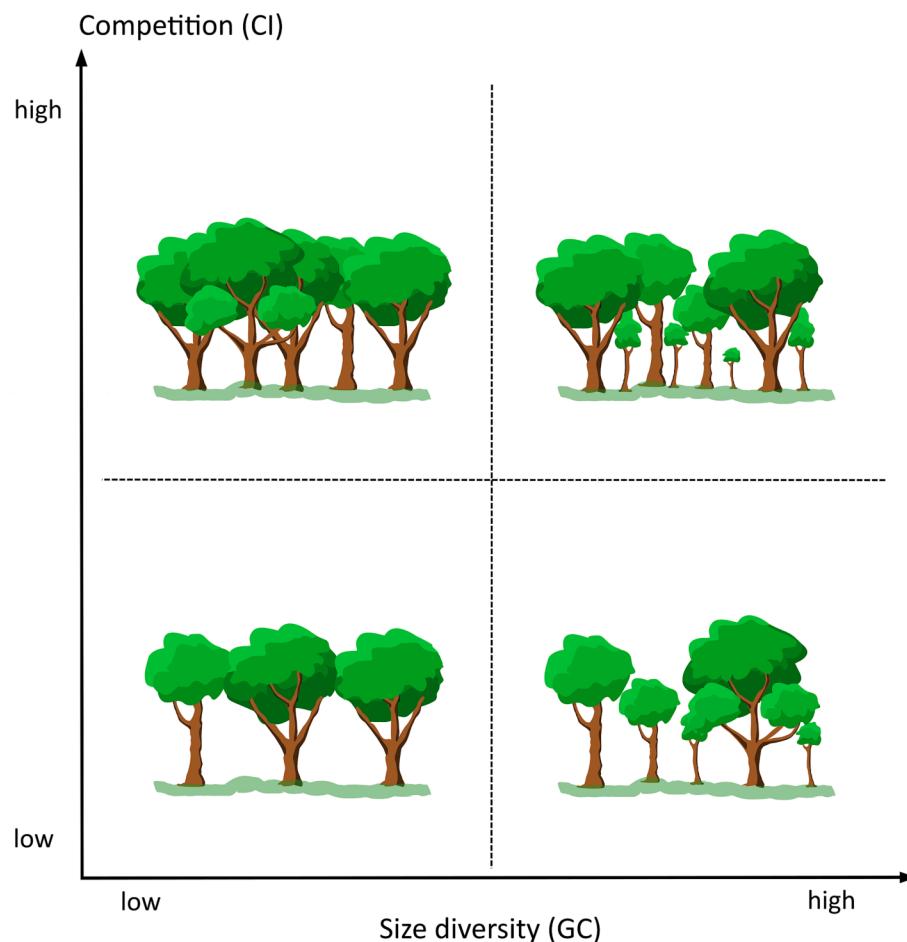
from the dplR package was used to obtain bai values. We relied on bai instead of raw ring-width data because it better reflects the biomass increment of trees and is less dependent on tree size and cambial age (Biondi, 1999; Biondi and Qeadan, 2008; Bouriaud et al., 2005). Subsequently, the two resulting bai-series per tree were averaged to obtain an individual series for each single target tree.

### 2.4. Climate data

Time series of monthly precipitation (mm) and mean, maximum, and minimum temperature (°C) covering the period 1940–2022 were extracted from the 1 km × 1 km grid of the German Meteorological Service (DWD Climate Data Center (CDC), 2023) for all twelve study sites. We calculated the multi-scalar Standardized Precipitation Evapotranspiration Index (SPEI) as an indicator of water availability in specific years (Vicente-Serrano et al., 2010). We derived potential evapotranspiration (PET) using the Hargreaves equation (Beguería and Vicente-Serrano, 2017; Hargreaves, 1994) and subsequently calculated monthly climatic water balance (CWB = precipitation – PET). We integrated SPEI values over six months (SPEI6, March to August) because a previous study in the same study region revealed high correlations between growth of beech and SPEI for this period (Schmied et al., 2023), encompassing the duration of its cambial activity in Central Europe (Čufar et al., 2008).

### 2.5. Estimation of growth decline

Preliminary tree-ring analyses revealed that 2018 was a tipping point after which significant growth differences between vital and declining trees occurred (see chapter 3.1 Growth patterns). To assess individual growth differences in response to the recurrent drought stress after 2018, we followed an approach similar to Lloret et al. (2011) by calculating the relative growth after 2018 of each target tree  $i$  as an indicator for individual growth decline ( $GD$ ):



**Fig. 2.** Conceptual framework for the interaction of competition (CI) and size diversity (GC) used in the study to describe small-scale differences in stand structure. The CI (y-axis) accounts for overall competition, while GC (x-axis) determines whether competing trees were similar (low GC) or unequal in size (high GC).

$$GD_i = \frac{bai_{[2019-2022]}}{bai_{[2014-2017]}}$$

Where  $bai_{[2019-2022]}$  is the average growth over the past four years, including the exceptionally dry years of 2019 and 2022, as well as the relatively wet year 2021.  $bai_{[2014-2017]}$ , on the other hand, represents the average growth of the four years prior to 2018 when, except for 2015, which was considered as a drought year, normal hydrologic conditions prevailed. Climatic conditions were very similar at all sites (for details see Fig. 3a). Therefore, growth decline (GD) captures the individual tree responses to recurrent drought stress and, due to inclusion of 2021, their interim recovery potential under more favourable conditions.

#### 2.6. Competition, tree size diversity, and defoliation of competitors

Within a 10 m radius of each target tree  $i$ , we recorded the diameter of all competing trees  $j$  with a DBH  $\geq 7$  cm and measured the distance  $dist$  to target tree  $i$  with a vertex ultrasonic hypsometer (Haglöf, Sweden). Based on this information, we calculated the distant-dependent competition index (CI) after Hegyi (1974), which is defined as follows:

$$CI_i = \sum_{j=1}^n \frac{DBH_j}{DBH_i} \times \frac{1}{dist_{ij}}$$

Higher CI values indicate stronger competition for target tree  $i$  at the time of the survey. The minimum distance of 30 m between the target trees guaranteed that there were no overlaps of competing trees.

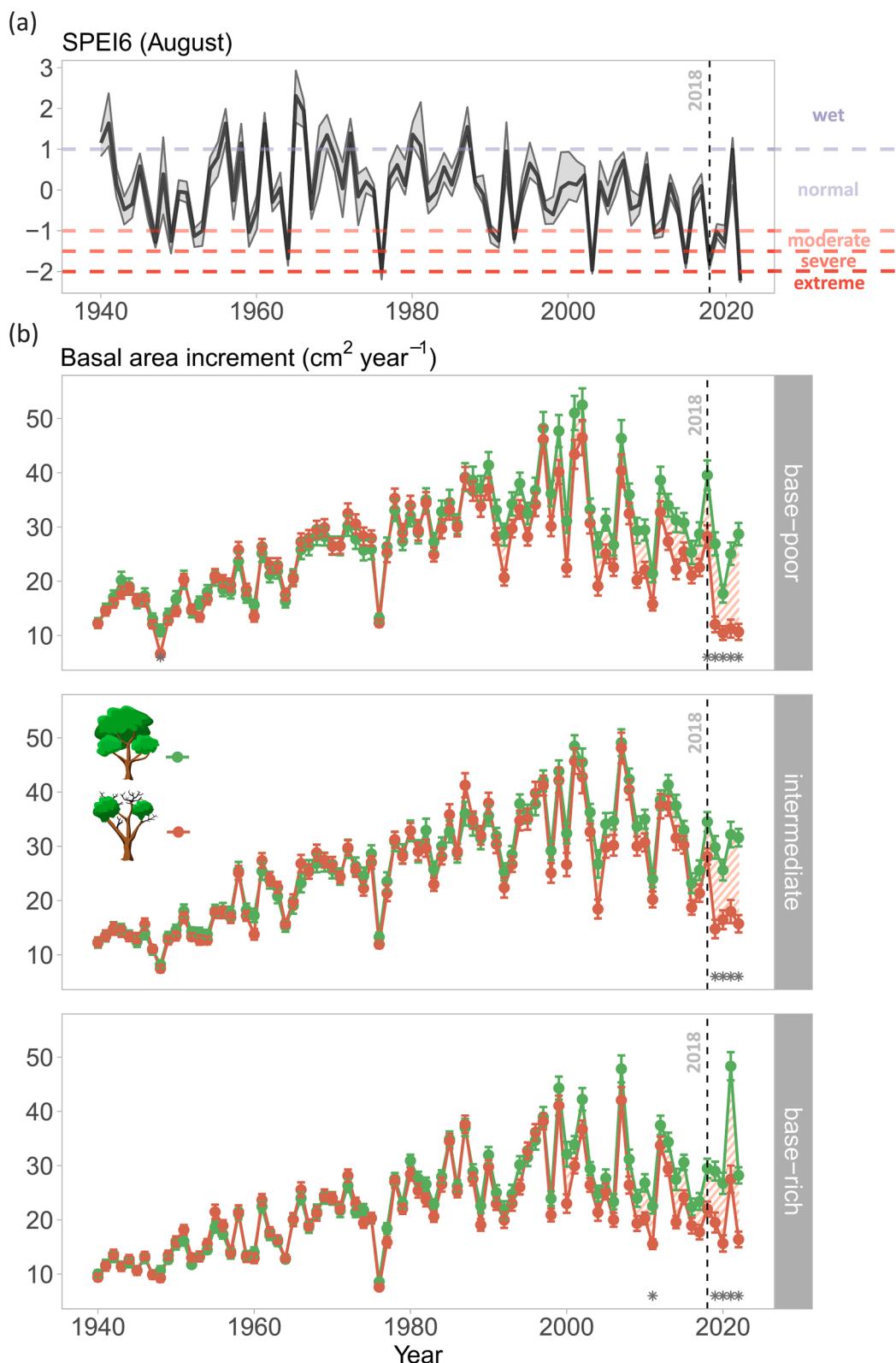
In addition, we calculated the Gini coefficient (GC) of the diameters of all trees within the 314 m<sup>2</sup> circles around each target tree. GC

indicates the diversity of tree sizes within the respective circles (Forrester, 2019). We calculated the GC as follows:

$$GC_i = \frac{\sum_{j=1}^n \sum_{k=1}^n |x_j - x_k|}{2n(n-1) \times \bar{x}}$$

where  $x_j$  and  $x_k$  denote size for the  $j$ 'th and the  $k$ 'th tree within each circle  $i$  with  $j = 1 \dots n$  trees. The GC is a measure of equitability and is based on dispersion estimates of tree size. GC values range from 0 to 1, with values near zero referring to a uniform distribution of tree sizes and higher GC values indicating greater heterogeneity (Pretzsch, 2019; Valbuena et al., 2012). We considered the interaction between CI and GC as relevant for describing small-scale structural differences between target trees. The conceptual framework behind this interaction is illustrated in Fig. 2.

Further, we determined the defoliation of all competitors to detect influences of spatially clustered dieback patterns. Consistent with the estimations of the target trees, we assessed the crown transparency of all competing trees (DBH  $\geq 7$  cm) within the 314 m<sup>2</sup> circles. We averaged competitor defoliation for each tree by considering individual tree size. Larger trees were thereby accorded greater weight, as we anticipated that they would play a more important role in the microsite conditions around each target tree. Moreover, evaluating defoliation of understory trees posed a heightened challenge and therefore a higher susceptibility to errors, which we endeavoured to accommodate by attributing lesser weight to them.



**Fig. 3.** (a) Development of the annual SPEI index integrated over six months from March to August. The black line refers to the overall average, while the grey band shows the variation between sites. The dashed horizontal lines represent drought classification thresholds as proposed by Slette et al. (2019). (b) Growth trajectory of studied declining (red) and vital (green) beech trees over the period from 1940 to 2022, separated by nutrient regime (base-poor = upper panel; intermediate = centre; base-rich = lower panel). Shaded area highlights growth differences between vitality classes. Gray stars indicate years with highly significant differences between vital and declining trees (Wilcoxon rank sum tests;  $p \leq 0.001$ ). Data points are means  $\pm$  standard error with  $47 \leq n \leq 57$ . (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

## 2.7. Estimation of small-scale differences in water availability

Based on the field estimates of bulk density, soil texture, and soil depth at each target tree, we used pedotransfer-functions (PTF) to evaluate the available water capacity of the soil for each mineral soil horizon separately. The available water capacity for organic surface layers was set at 30 % (Hammel and Kennel, 2001). Subsequently, all available water capacity values for the entire soil profile (mineral horizons and humus) were summed up for each target tree to estimate the plant-available water capacity in the effective root zone (AWC). Differences in AWC also accounted for variations in topography within some sites. For example, target trees growing at ridge positions within the stand typically had a smaller AWC due to a shallower soil and higher share of coarse fragments. Variations in AWC between and within all study sites are shown in Figure S1.

## 2.8. Statistical analyses

For each year, growth differences between vital and declining trees were analyzed using Wilcoxon rank sum tests that accounted for a non-normal distribution under consideration of the site's nutrient regime (research objective (a)). For research questions (b) and (c), we used generalized linear mixed-effect models (GLMM) within a Bayesian framework. Prior to modelling, all potential predictor variables were checked for (multi-) collinearity by calculating correlation coefficients and determining variance inflation (VIF). The VIF of all continuous predictors was  $< 2$ , suggesting that the information reflected by the predictors was highly independent (Dormann et al., 2013). We standardized all variables to allow for direct comparison between regression coefficients (Schielzeth, 2010), to get reliable approximations of the posterior, and to help with building reasonable priors (McElreath, 2020). We used a GLMM with a binomial distribution and a logit link to examine whether differences in stand structure, plant-available water capacity, and spatial clustering affect beech dieback in northern Bavaria (research objective (b)). The corresponding GLMM included the vitality status of each tree (vital = 0; declining = 1) as our response variable, while the predictors accounted for (1) competition (CI), (2) size diversity (GC), (3) plant-available water capacity (AWC), (4) competitor defoliation (CD), and interactions among (5) CI and GC. We further hypothesized that the effect of competitor defoliation on target tree vitality might be partially driven by plant-available water capacity of the target tree. We tested this potential causal relationship by incorporating a second regression term to our existing model, which additionally modelled competitor defoliation as a function of plant-available water. To address research objective (c), we used a GLMM with a lognormal distribution and a log link. The relative growth after 2018 (GD) was set as our response variable, while (1) competition (CI), (2) size diversity (GC), (3) plant-available water capacity (AWC), (4) nutrient regime (NR = base-poor, intermediate, base-rich), and interactions among (5) CI and GC were incorporated as predictors. For both models, sample sites were included as varying effects to account for potential spatial autocorrelation and site-specific differences. For objective (c), we allowed the different nutrient regime levels to have varying intercepts and slopes. The detailed model structures can be found in Tables S1 and S2. We relied on a Bayesian framework to allow for consideration of prior information and to account for parameter uncertainty (Gelman et al., 2021; McElreath, 2020). Weakly informative priors were used for all priors to constrain parameters to a plausible range. Prior plausibility was evaluated using prior predictive simulation (McElreath, 2020). We used Markov Chain Monte Carlo (MCMC), more specifically the Hamiltonian Monte Carlo (HMC) sampler and its extension, the No-U-Turn Sampler (NUTS), implemented in the software Stan (Carpenter et al., 2017) for Bayesian inference. We ran four chains, each with 4000 samples (first 2000 removed due to warm-up) to achieve robust convergence of joint posteriors. Model fits were evaluated by Bayesian R<sup>2</sup> and through posterior predictive checking, i.e., by simulating replicated data sets given

the fitted model (Gelman et al., 2021). We used Pareto-smoothed importance sampling cross-validation (PSIS) (Vehtari et al., 2017) for detection of potential influential observations (McElreath, 2020). MCMC convergence was verified with trace plots and the Gelman-Rubin statistic ( $\hat{R}$ ).

We used statistical environment R, version 4.2.2, for all analyses and visualizations (R Core Team, 2022). In particular, we relied on the library brms (Bürkner, 2017) for statistical analyses and Bayesian inference; bayesplot (Gabry et al., 2019; Gabry and Mahr, 2017) and ggplot2 (Wickham et al., 2019) for visualizations; tidybayes (Kay, 2020) and tidyverse (Wickham et al., 2019) for data wrangling; raster (Hijmans et al., 2022) and sf (Pebesma et al., 2022) for handling of spatial data; SPEI for determination of SPEI values (Beguería and Vicente-Serrano, 2017); and dplR for processing tree ring data (Bunn, 2008).

## 3. Results

### 3.1. Growth patterns

We observed very similar growth patterns in vital and declining trees (Fig. 3b). This was indicated by the strong coherence of interannual growth variability among the trees, with an inter-series correlation (rbar) ranging from 0.55 to 0.82 (Table 2). For most trees, narrow rings were measured in 1948, 1976, 2003/2004, 2011, and after 2018, whereas very wide rings were consistently measured in 2002 and 2007. Narrow rings were often associated with major drought years, which were particularly frequent at the study sites over the past decade (see Fig. 3a). First slight growth differences were observed at base-poor and base-rich sites in the early 2000s, which changed drastically during (at base-poor sites) and after (at intermediate & base-rich sites) the major drought in 2018. Regardless of the sites' nutrient regime, we observed a distinctive growth separation between declining and vital trees after 2018 (Wilcoxon rank sum tests;  $p \leq 0.001$ ). Declining trees growing at base-poor and intermediate sites maintained very low growth compared to vital trees over the last four years (see mean ring width between 2019 and 2022 in Table 2), while trees at base-rich sites exhibited remarkably high growth during the relatively wet year 2021 (Fig. 3a + b). In general, vital trees continued to grow at a higher level and appeared to recover better in response to the beneficial conditions in 2021 (Fig. 3b).

### 3.2. Drivers of beech dieback

Our binomial GLMM revealed that the crown condition of beech was strongly related to the defoliation status of its competing trees, as highlighted by the large effect sizes (Fig. 4a). Greater defoliation of adjacent trees resulted in a considerably higher likelihood of declining vitality of target trees, indicating a spatial clustering of declining trees within the affected forests. Figure S2 shows the spatial locations of all sampled target trees and gives information about the individual competition and the average defoliation of all respective competitors. The small-scale differences in plant-available water capacity were a strong determinant of tree vitality (Fig. 4a). Trees with higher plant-available water capacity were less likely to decline in vitality. Moreover, predictions under the fitted model revealed that the strong negative effect of competitor defoliation was only weakly modulated by the plant-available water of the target trees (Figure S3). An increase in plant-available water slightly reduced the probability of competitor defoliation. In general, competition had a slightly negative effect on the vitality status of target trees, while greater size diversity had a slightly positive effect (Fig. 4a). The interaction between these two predictor variables showed that at low GC levels (GC = -1; standardized), the probability of vitality decline tended to decrease with increasing competition, with considerable uncertainty (Fig. 4b). However, at high size diversity (GC = 1), increased competition had a detrimental effect on tree vitality. Overall, low competition with increased size diversity

**Table 2**

Characteristics of sampled target trees (mean  $\pm$  standard deviation) at all twelve forest sites. Defoliation refers to the estimated defoliation of the target trees. The inter-series correlations ( $r_{\text{bar}}$ ) were calculated using raw ring width data. Ring widths and  $r_{\text{bar}}$  refer to the period with a sample size more than four (Period  $n \geq 5$ ) for each site and vitality class.

Site ID	Nutrient regime	Vitality classification	Defoliation (%)	Number of trees	DBH (cm)	Period ( $n \geq 5$ )	Mean ring width (mm $\text{yr}^{-1}$ )	Mean ring width (mm $\text{yr}^{-1}$ ) 2019–2022	$r_{\text{bar}}$
2214	base-poor	Vital	24 $\pm$ 7	15	53.3 $\pm$ 16.1	1926–2022	2.45 $\pm$ 1.1	1.45 $\pm$ 0.7	0.62
		Declining	75 $\pm$ 11	15	53 $\pm$ 8.7	1932–2022	2.46 $\pm$ 1.2	0.46 $\pm$ 0.4	0.72
2215	base-poor	Vital	26 $\pm$ 7	15	56.8 $\pm$ 10.3	1904–2022	2.20 $\pm$ 0.9	1.19 $\pm$ 0.5	0.62
		Declining	74 $\pm$ 10	15	50.1 $\pm$ 7.1	1907–2022	1.96 $\pm$ 0.8	0.46 $\pm$ 0.4	0.73
2216	base-poor	Vital	26 $\pm$ 10	15	66.3 $\pm$ 9.5	1881–2022	1.97 $\pm$ 0.8	1.69 $\pm$ 0.7	0.58
		Declining	73 $\pm$ 7	15	64.8 $\pm$ 8	1861–2022	1.83 $\pm$ 0.8	0.95 $\pm$ 0.6	0.59
2217	base-poor	Vital	33 $\pm$ 6	12	54 $\pm$ 7.7	1915–2022	2.16 $\pm$ 1	1.01 $\pm$ 0.5	0.69
		Declining	73 $\pm$ 8	12	55.1 $\pm$ 9	1904–2022	2.06 $\pm$ 0.9	0.57 $\pm$ 0.5	0.72
2218	intermediate	Vital	25 $\pm$ 8	15	60.4 $\pm$ 9.7	1904–2022	2.18 $\pm$ 0.8	1.78 $\pm$ 0.9	0.70
		Declining	70 $\pm$ 6	15	56.7 $\pm$ 8.3	1900–2022	2.07 $\pm$ 0.9	1.23 $\pm$ 0.7	0.73
2219	intermediate	Vital	27 $\pm$ 7	15	56.6 $\pm$ 9.7	1918–2022	2.32 $\pm$ 1	1.63 $\pm$ 0.5	0.59
		Declining	77 $\pm$ 9	15	56.8 $\pm$ 7.2	1902–2022	2.17 $\pm$ 1.1	0.72 $\pm$ 0.5	0.71
2220	base-rich	Vital	28 $\pm$ 9	12	51.1 $\pm$ 6.3	1918–2022	2.24 $\pm$ 0.9	1.91 $\pm$ 1.0	0.70
		Declining	72 $\pm$ 10	12	46.1 $\pm$ 5.4	1917–2022	1.9 $\pm$ 0.8	1.4 $\pm$ 1.0	0.79
2221	base-rich	Vital	26 $\pm$ 7	15	50.1 $\pm$ 5	1916–2022	2.08 $\pm$ 0.8	1.7 $\pm$ 0.6	0.78
2222	base-rich	Declining	73 $\pm$ 9	15	49 $\pm$ 7.1	1908–2022	1.99 $\pm$ 0.9	1.02 $\pm$ 0.6	0.82
		Vital	26 $\pm$ 6	15	52.9 $\pm$ 5.7	1893–2022	1.96 $\pm$ 0.8	1.87 $\pm$ 0.8	0.75
2223	base-rich	Declining	71 $\pm$ 9	15	51.7 $\pm$ 4.6	1896–2022	2.00 $\pm$ 0.8	1.01 $\pm$ 0.6	0.76
		Vital	25 $\pm$ 8	12	58.6 $\pm$ 8.5	1906–2022	2.20 $\pm$ 0.8	2.76 $\pm$ 0.8	0.70
2224	intermediate	Declining	71 $\pm$ 8	12	56.4 $\pm$ 6.5	1897–2022	2.11 $\pm$ 0.8	1.7 $\pm$ 1.0	0.65
		Vital	16 $\pm$ 6	13	54.2 $\pm$ 6.4	1919–2022	2.37 $\pm$ 0.8	1.71 $\pm$ 0.6	0.61
2225	intermediate	Declining	76 $\pm$ 11	13	52.5 $\pm$ 4.6	1911–2022	2.16 $\pm$ 0.9	0.92 $\pm$ 0.6	0.67
		Vital	12 $\pm$ 9	12	55.2 $\pm$ 6.9	1912–2022	2.04 $\pm$ 0.9	1.71 $\pm$ 0.8	0.55
		Declining	74 $\pm$ 12	12	53.9 $\pm$ 7.9	1911–2022	1.97 $\pm$ 0.9	0.89 $\pm$ 0.8	0.64

considerably reduced the probability of vitality decline.

Our binomial GLMM showed satisfactory performance. Simulations of replicated data sets under the fitted model were consistent with observed data distributions (Figure S4), while MCMC convergence was reasonable, as indicated by trace plots (Figure S5) and constant  $\hat{R}$  values of 1.00. The Bayesian  $R^2$  revealed that the model explained 18.4 % of the total variance.

### 3.3. Determinants of growth decline after 2018

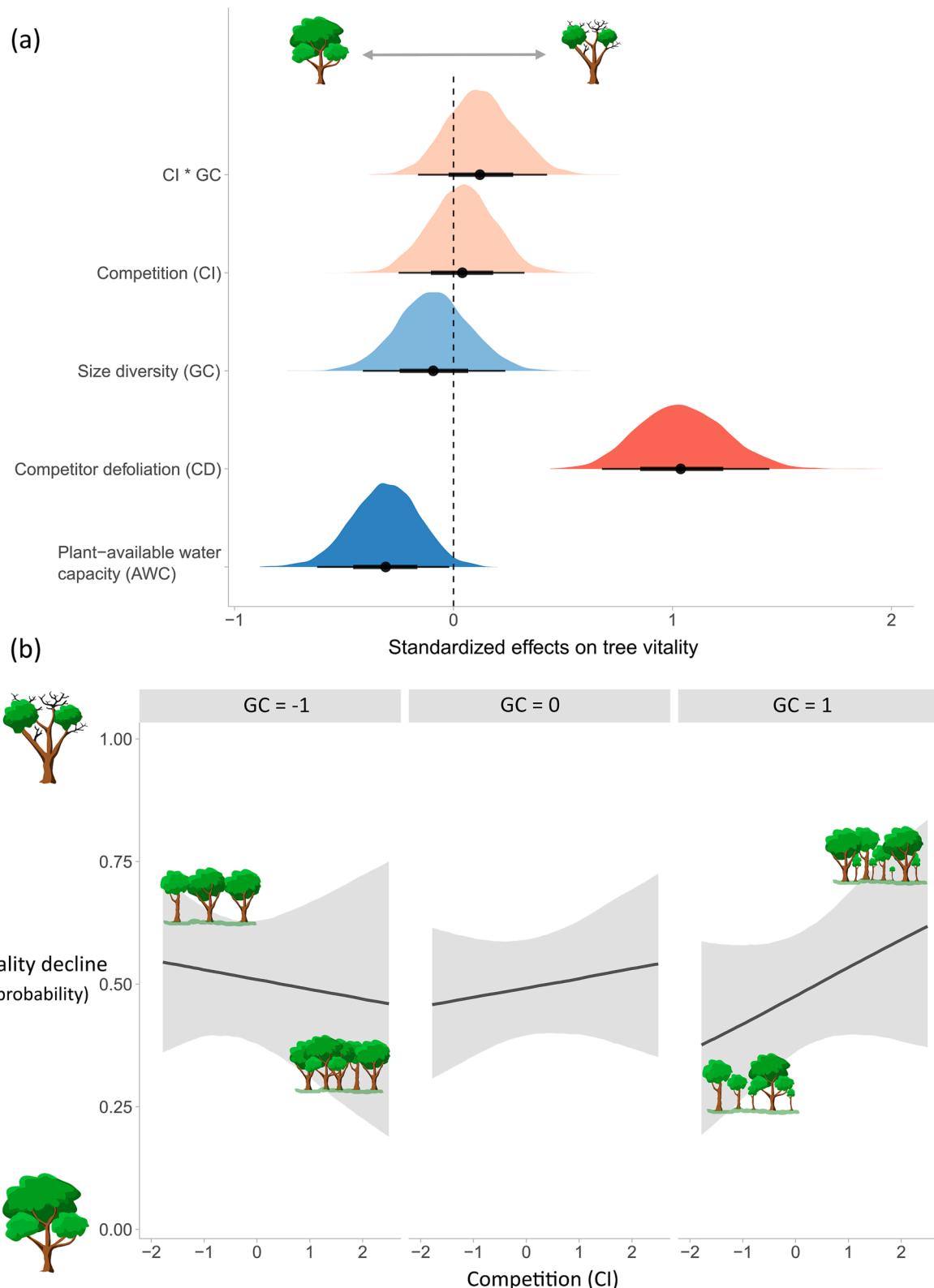
Our lognormal GLMM showed that the relative growth after 2018 was strongly affected by the different nutrient regime levels, as highlighted by the large effect sizes (Fig. 5a). While base-rich site conditions had a positive effect on relative growth after 2018, the intermediate and especially the base-poor nutrient regime levels exhibited a strong negative effect. Direct comparisons (contrasts) of nutrient regime effects underscored the strong growth differences between base-rich and base-poor/ intermediate sites (Fig. 5b). Small-scale differences in plant-available water capacity had a positive effect on relative growth after 2018 (Fig. 5a). Lower water availability led to a greater decline in growth. In contrast, competition and size diversity had only small effects on individual growth decline (Fig. 5a). While we observed no effect of

competition on relative growth after 2018 for uniformly structured stands ( $GC = -1$ ), we found a negative effect of competition for increased size diversity ( $GC = 1$ ). Here, low competition was beneficial (Fig. 5c).

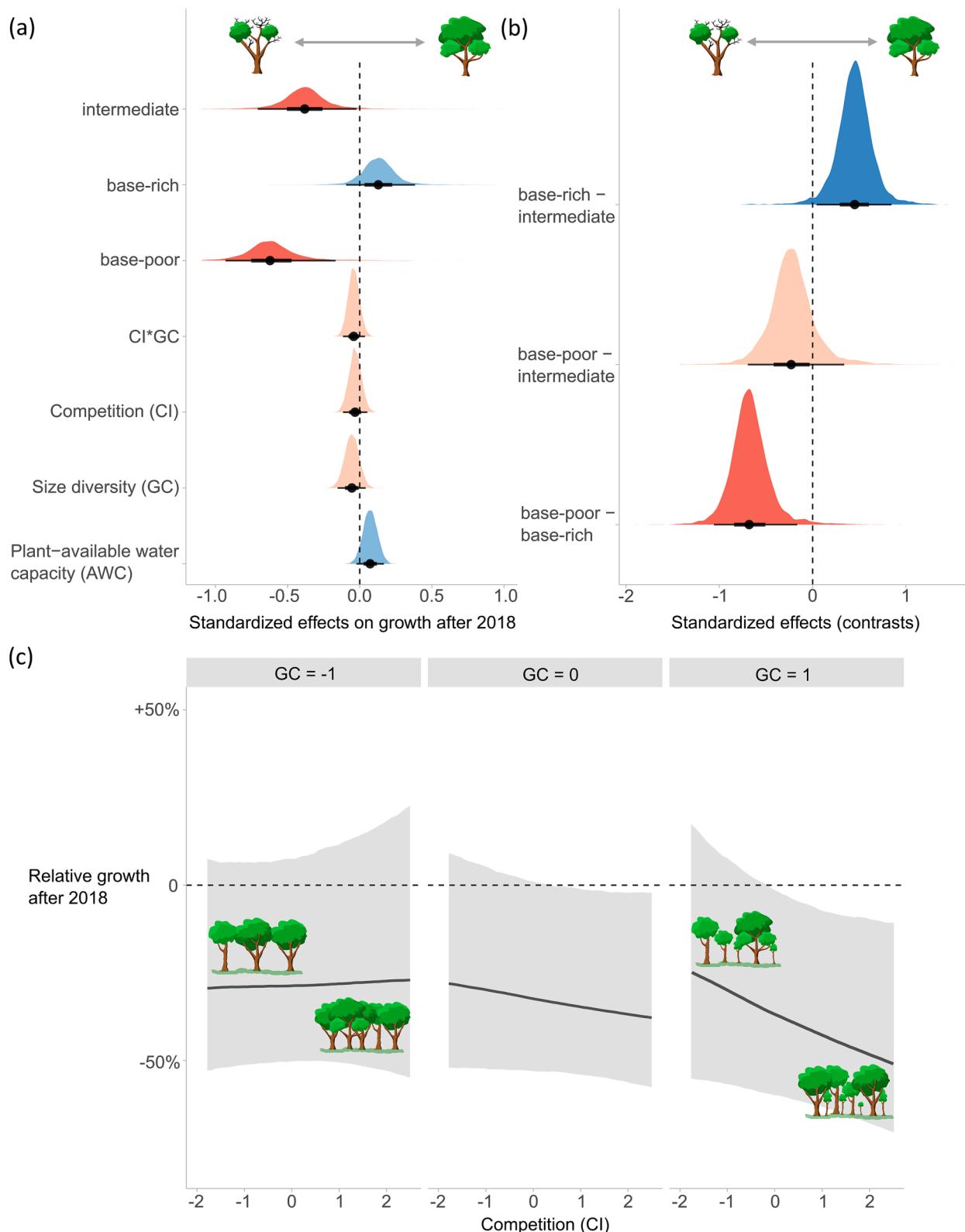
The performance of our lognormal Bayesian GLMM was reasonable. Predicted and observed data distributions were very similar (Figure S6), indicating that the selected predictors within the chosen model structure were able to reproduce the different patterns of growth decline. MCMC convergence was appropriate (Figure S7), and  $\hat{R}$  values were constant at 1.00, whereas the model accounted for 29.2 % of the total variance.

## 4. Discussion

We investigated the patterns and causes of variability in crown vitality and growth decline in drought-damaged beech stands along a gradient of different nutrient regime levels. Strongly defoliated trees in summer 2022 showed a rapid growth decline in response to recurrent drought stress since 2018, especially at base-poor sites. Strongest drivers of tree vitality were small-scale differences in plant-available water and vitality of neighbouring trees. In addition, low competition with unequal tree size distribution was beneficial for tree vitality and relative growth.



**Fig. 4.** (a) Standardized effects of small-scale differences in stand structure (GC, CI), plant-available water capacity (AWC), and competitor defoliation (CD) on target tree vitality based on the Bayesian GLMM with binomial distribution. Standardized effects indicate how much the response variable changes when the respective predictor variable is changed by one standard deviation. Visualized are the posterior mean (black points), the 50 % and 95 % probability range (black lines), as well as the corresponding distributions. Stronger effects are highlighted by darker colours (blue = positive effect; red = negative). Note that negative values indicate here a lower probability of dieback and vice versa. (b) Triptych plots of posterior predicted probability of vitality decline for different levels of competition (CI) and size diversity (GC). Size diversity (GC) was set to low (-1, left), mean (0, middle), and high (1, right), while competition ranged across the entire range to highlight the effects of their interaction. Visualized are the posterior predicted mean and the corresponding 95 % compatibility interval. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)



**Fig. 5.** (a) Standardized effects of stand structure (GC, CI), plant-available water capacity (AWC), and nutrient regime (base-poor, intermediate, base-rich) on relative growth after 2018 based on the lognormal Bayesian GLMM. (b) Posterior distributions of differences in slope between different nutrient regime levels (=contrasts). The posterior mean (black points), the 50 % and 95 % probability range (black lines), as well as the corresponding distributions are presented for figures (a) and (b). Stronger effects are highlighted by darker colours (blue = positive; red = negative). (c) Triptych plots of posterior predicted relative growth after 2018 for different levels of competition (CI) and size diversity (GC). Size diversity (GC) was set to low (-1, left), mean (0, middle), and high (1, right), while competition ranged across the entire range to highlight the effects of their interaction. Visualized are the posterior predicted mean and the corresponding 95 % compatibility interval. The dashed reference line indicates no growth change after 2018. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

#### 4.1. Rapid growth decline of defoliated trees

Our study revealed that there was a clear growth superiority of vital compared to declining trees since 2018, highlighting a rapid growth decline of now defoliated trees in response to recurrent severe drought stress. This coincided well with the decline in crown vitality reported by local foresters during this period (Thierfelder, 2020). These findings are in contrast with observations of Neycken et al. (2022) and Gillner et al. (2013), who found a long-term growth decline prior to crown dieback of beech in northern Switzerland, respectively east Germany. However, the sampled trees in these studies already exhibited more severe crown defoliation (Neycken et al., 2022) or heavier damages (Gillner et al., 2013), which could indicate a longer-lasting growth decline prior to dieback. Camarero et al. (2021), on the other hand, found shorter periods of five to ten years of significant growth divergence between declining and non-declining beech trees in northern Spain, which is more similar to the patterns we found. In general, previous growth patterns can be considered as early-warning signals for tree mortality (Cailleret et al., 2017). Higher variability in annual growth (Cailleret et al., 2019), increased autocorrelation of previous growth (Camarero et al., 2015), lower recovery after droughts (DeSoto et al., 2020), and lower growth rates (Cailleret et al., 2017; Klesse et al., 2022) have been associated with a higher probability of severe crown damage, respectively mortality. However, growth reductions prior to mortality can be abrupt or gradual (Berdanier and Clark, 2016; Cailleret et al., 2017; Herguido et al., 2016), suggesting whether dieback is due to hydraulic failure (abrupt) or carbon depletion and degraded hydraulic performance (gradual) (Cailleret et al., 2017). In our study, declining trees showed an abrupt and critical slowdown in annual growth with a poor capacity to regain previous growth levels at base-poor and intermediate sites. Therefore, we consider this sharp growth decline as a potential tipping point for the onset of their mortality (Scheffer et al., 2012). This would further suggest that intense premature leaf fall is an indicator of vitality decline (Wohlgemuth et al., 2020) due to loss of hydraulic conductance (Arend et al., 2022), rather than a strategy to cope with extremely unfavourable conditions (Bréda et al., 2006). However, the strong growth reduction we observed in defoliated trees might be biased in terms of stand-level observations because we only considered (co-)dominant trees in our study. For instance, Pretzsch et al. (accepted) recently observed a growth partitioning in favour of smaller trees during persistent dry conditions, which is in line with findings from Switzerland (Bose et al., 2021). In addition, we still observed high growth levels for vital trees. Thus, smaller and surviving trees might partially compensate for growth losses and mortality of larger trees at the stand-level.

#### 4.2. Plant-available water capacity as essential determinant of beech vitality

Small-scale differences in plant-available water were an important predictor of beech vitality and relative growth under recurrent severe drought stress. Higher plant-available water capacity resulted in a lower probability of vitality decline and higher relative growth rates after 2018. Although plant-available soil water capacity has not been identified as a key driver of drought responses in temperate tree species across a broad precipitation gradient in Germany (Schmied et al., 2023) and a large water availability gradient in Switzerland (Lévesque et al., 2016), it appears to become increasingly important during repeated droughts (Chakraborty et al., 2021). This is supported by findings from George et al. (2022) that increasing trends in tree mortality were linked to a persistent decrease in soil moisture. Moreover, Mellert et al. (2023) found that height growth differences within mature forest stands were co-determined by small-scale differences in plant-available water capacity at sites with low water regime. Our results confirm the importance of soil water for crown vitality (Frei et al., 2022; Walthert et al., 2021) and underscore the relevance of small-scale heterogeneity in soil properties within single forest stands under unfavourable conditions

(Carrière et al., 2020; Chakraborty et al., 2021). Several studies showed that trees on shallow soils exhibit higher drought sensitivity (Rehschuh et al., 2017), stronger growth decline (Chakraborty et al., 2021), and substantial crown dieback (Klesse et al., 2022; Walthert et al., 2021) compared to deep and silty soils due to lower plant-available soil water. This is in line with large-scale observations from Central Texas, USA, where increased crown dieback after drought occurred in areas with soil depth below 50 cm (Schwantes et al., 2018). While trees primarily use water from the topsoil under normal conditions, particularly deciduous trees switch their water uptake to deeper soil layers during drought (Brinkmann et al., 2019; Meusburger et al., 2022). However, beech has a comparatively shallow root water uptake depth, which was found to be crucial for how quick hydraulic vulnerability thresholds were reached (Kahmen et al., 2022). Further, beech trees growing on shallow soils have in general only a limited possibility to reach water from deeper soil layers, predisposing them to dry conditions and causing early defoliation and crown damage (Walthert et al., 2021). Frei et al. (2022) and Obalden et al. (2021) found elevated dieback patterns for beech on soils with increased gravel or clay content. Latter concluded that a desiccated soil due to repeated drought stress can cause clay shrinkage and thus, damage the fine-root system. This is particularly important for beech since its fine-roots are considered to be relatively sensitive to soil water deficits (Leuschner, 2020). In our study, we observed increased clay contents mainly at cambisols/luvisols on base-rich sites. Higher gravel and sand contents, which imply a faster water infiltration and seepage, were mostly found at base-poor and intermediate sites.

Moreover, it has been assumed that the small-scale heterogeneity in soil properties is an important driver of patchy or scattered distributions of drought-damaged trees within forests (Frei et al., 2022). Our study showed strong evidence that declining trees appeared spatially clustered, which is in line with previous observations for beech from Spain (Camarero et al., 2021) and Switzerland (Frei et al., 2022). However, we found only a small effect of each target tree's plant-available water capacity on the vitality of its neighbouring trees (Figure S3). We consider three possible explanations for this observation: (1) the soil within the forest might be highly diverse, such that the plant-available water capacity varies even within the 314 m<sup>2</sup> circles around each target tree; (2) other factors, such as genetic differences (Pfenninger et al., 2021) or tree size (Klesse et al., 2022) of the competitors, which we have not considered, could affect the vitality of the competitors; (3) competitor defoliation could have an additional and direct impact on the vitality of the target tree. For instance, defoliation leads to a decrease of temperature buffering within the forest, potentially exacerbating drought stress under extremely dry conditions (De Frenne et al., 2021). Further, less canopy foliage enhances the radiation within the forest, promoting forest floor vegetation (Hedwall et al., 2013) and subsequently increasing the competition for water. In contrast, vitality decline or mortality of neighbouring trees could also affect the remaining trees positively due to increased water availability (Chin et al., 2023).

#### 4.3. Low competition with increased size diversity beneficial for tree vitality

We found that low competition with unequal tree size distribution had a positive effect on target tree vitality and relative growth. In contrast, a higher competition was slightly better when competing trees had a similar size. This suggests that silvicultural approaches, such as single-tree and group selection, which promote higher structure (Brang et al., 2014) while moderately reducing competition, were beneficial to tree vitality in drought-prone beech stands. This is in line with findings by Gebhardt et al. (2014) who recommended moderate and repeated thinnings to increase water availability for remaining trees. Heavy thinnings, on the other hand, might elevate radiation (Lagergren et al., 2008), boost wind speed (Aussenac, 2000), increase transpiration of ground vegetation (Gebhardt et al., 2014) and forest canopy (Chen et al., 2020), and enhance tree sensitivity to vapour pressure deficits

(Bachofen et al., 2023), leading to a predisposition to drought damage under extremely dry conditions. However, Bradford et al. (2022) found that large reductions (circa 50 %) in forest basal area reduced drought-related mortality of ponderosa pines (*Pinus ponderosa*) by up to 80 %, particularly in areas that experienced recurrent severe drought stress. Positive effects of a greatly reduced basal area and thus less dense forest stands were also observed for other coniferous (Giuggiola et al., 2013; Sohn et al., 2016) and deciduous (Diaconu et al., 2017; Klesse et al., 2022) tree species in Europe. We further observed a detrimental effect of increased size diversity on target tree vitality and relative growth when competition was high. This effect can most likely be attributed to enhanced intraspecific competition for water. Experimental removals of understory vegetation and trees have shown an improved soil water availability and better performance of overstory Scots pine trees (*Pinus sylvestris*) at xeric sites (Giuggiola et al., 2018), as the understory can contribute considerably to stand-level water loss (Gebhardt et al., 2014). However, at lower stand densities, greater tree size diversity and related structural diversity could be beneficial due to attenuated short-wave radiation, reduced wind speed, lower soil temperatures, and improved buffering against macroclimatic temperature extremes (De Frenne et al., 2021; Zellweger et al., 2020). This is supported by the results of Kovács et al. (2017), who found that a more stable forest microclimate was associated with greater variation in tree size. Therefore, maintaining beech stands with lower density and increased structure might be a reasonable trade-off for forest management to address future risks of growth decline and dieback. This finding is particularly important considering that beech standing stocks have increased in recent decades (Pretzsch et al., 2014). Coming from these relatively high densities, a reduction in stand density due to mortality could further be a natural acclimation process to drier conditions at the stand-level (Pretzsch et al., accepted).

However, it must be noted that our results only apply for forest stands with a relatively closed canopy (canopy closure  $\geq 0.4$ ). Hence, large gaps or open field conditions, which might have severe consequences for the remaining trees in the long-term (Dulamsuren et al., 2022), were not considered.

#### 4.4. Nutrient regime affects individual growth decline

Our results highlight the relevance of the site's nutrient regime when considering for growth responses of individual trees to recurrent drought stress. This is supported by its large effect sizes in our models (Fig. 5) and is consistent with previous studies, which revealed that drought responses of temperate tree species are modulated by their nutrient supply (Lévesque et al., 2016; Schmied et al., 2023; Sargent et al., 2014), as nutrients play an essential role in water and carbon uptake and its utilization (Gessler et al., 2016). In our established gradient, we assume that soils at intermediate sites offer more favourable conditions for tree growth because they often combine low base saturation in the topsoil with high base saturation in the subsoil, implying a balanced nutrient regime (Mellert and Göttsche, 2013). In addition, the availability of phosphorus and several trace elements is usually optimal for trees on soils at sites with an intermediate nutrient regime (Blume et al., 2009; Mellert et al., 2018b). Base-poor soils, on the other hand, often have deficient nutrient supplies and lack important elements, such as potassium (K), which is critical for water-use efficiency and mitigating drought stress in plants (Sardans and Peñuelas, 2015). Mellert et al. (2018a) showed that the species-specific climatic drought limit of trees depends on the nutrient regime of the soil, with beech reaching its drought limit faster on base-poor soils than on base-rich soils, indicating higher drought tolerance under base-rich conditions. This corresponds well with its strong competitiveness at base-rich sites (Ellenberg and Leuschner, 2010) and is consistent with our results. While trees at base-poor and intermediate sites experienced an abrupt growth decline after 2018, their counterparts on base-rich sites showed a higher capacity to benefit from more favourable conditions in 2021,

resulting in overall higher relative growth rates. Similarly, Schmied et al. (2023) observed that trees at base-rich sites were susceptible to extreme drought stress but showed a high capacity to recover, whereas trees at base-poor sites exhibited a considerably lower recovery. However, trees with a balanced nutrient regime were observed to have a higher capacity to withstand extreme drought stress (Schmied et al., 2023). In contrast, we found that on intermediate sites the growth decline was more pronounced than on base-rich sites, but less than on base-poor sites. In general, improved nutrient supply can have advantages and disadvantages for tree vitality and growth. On the one hand, high nutrient availability might be detrimental for tree survival as biomass is primarily accumulated aboveground, larger vessel diameters are formed, and stomatal conductance might be increased. This could predispose trees to hydraulic failure or carbon starvation during severe droughts due to increased risk of cavitation, respectively increased carbon costs. On the other hand, enhanced nutrient availability could be beneficial for tree survival and recovery because water-use efficiency increases and nutrients are essential for rebuilding drought-damaged tissue (Gessler et al., 2016).

Although we found that trees at base-rich sites exhibited a less strong growth decline, we want to emphasize that this does not mean that base-rich sites are not susceptible to dieback. We observed severe crown dieback at all sites. However, trees at base-rich sites seem to benefit better from interim favourable conditions in terms of growth than trees at base-poor or intermediate sites.

#### 4.5. Conclusions

Our study provides novel insights into the causes of co-occurring vital and declining beech trees following recurrent severe drought stress. We investigated the growth patterns of beech trees with varying crown vitality and found a rapid growth decline of now defoliated trees in response to the unfavourably dry conditions after 2018, which may be exacerbated in the future given projected climate change scenarios. We observed a particularly abrupt and severe growth decline of trees on base-poor sites, indicating an increased risk of future dieback. We examined potential drivers of variability in crown vitality and growth decline of individual beech trees and revealed that small-scale differences in plant-available water capacity and vitality of neighbouring trees were important determinants. Further, we found that low competition with increased size diversity was beneficial for tree vitality and relative growth.

Overall, our findings emphasize a critical growth decline of beech trees that showed strong and early defoliation and highlight the importance of small-scale differences in soil and stand characteristics for tree survival. We therefore recommend a more differentiated stress monitoring that takes into account the heterogeneity of site conditions and incorporates information on soil nutrient regime. In addition, forest modelling should not only focus on tree size and competition, but also consider the structure of the neighbourhood. Our results are of particular importance to forest practitioners, as forest management strategies that promote greater size diversity while regulating competition were found to reduce the probability of crown dieback. This can be achieved with uneven-aged silvicultural systems that work with long regeneration periods, such as single-tree and group selection approaches.

#### CRediT authorship contribution statement

**Gerhard Schmied:** Conceptualization, Methodology, Investigation, Formal analysis, Writing – original draft, Visualization, Data curation. **Hans Pretzsch:** Conceptualization, Methodology, Writing – review & editing, Supervision, Project administration. **Dominik Ambs:** Methodology, Investigation, Writing – review & editing. **Enno Uhl:** Conceptualization, Methodology, Writing – review & editing. **Julia Schmucker:** Investigation, Writing – review & editing. **Julian Fäth:** Investigation, Writing – review & editing. **Peter Biber:** Formal analysis, Writing –

review & editing. **Yves-Daniel Hoffmann:** Investigation, Writing – review & editing. **Muhidin Šeho:** Conceptualization, Writing – review & editing. **Karl Heinz Mellert:** Writing – review & editing. **Torben Hilmers:** Conceptualization, Methodology, Writing – review & editing, Supervision.

## Declaration of Competing Interest

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

## Data availability

Data will be made available on request.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2023.121305>.

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