RESEARCH ARTICLE

Management alters drought-induced mortality patterns in European beech (*Fagus sylvatica* L.) forests

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ABSTRACT

- The high tree mortality during the dry and hot years of 2018–2019 in Europe has triggered concerns on the future of European beech (*Fagus sylvatica* L.) forests under climate change and raised questions as to whether forest management may increase tree mortality. We compared long-term mortality rates of beech between managed and unmanaged stands including the years 2018-2019 at 11 sites in Hesse, Germany.
- We hypothesized that mortality would increase with climate water deficits during the growing season, initial stand density, decreasing dominance of trees, and decreasing intensity of tree removals. Initial stand density, tree removals, the climate water balance and the competitive status of trees were used as predictor variables.
- Mean annual natural mortality rates ranged between 0.5% and 2.1%. Even in the drought years, we observed no signs of striking canopy disintegration. The significantly higher mortality (1.6–2.1%) in unmanaged stands during the drought years 2018 and 2019 was largely confined to suppressed trees. There was no significant increase of mortality in managed stands during the drought years, but a shift in mortality towards larger canopy trees.
- Our study did not confirm a general influence of management, in the form of tree removals, on mortality rates. Yet, we found that during drought years, management changed the distribution of mortality within the tree community. To analyse the effects of management on mortality rates more comprehensively, a wider gradient in site moisture conditions, including sites drier than in this study, and longer post-drought periods should be employed.

INTRODUCTION

Climate change and associated increasing frequency and intensity of droughts and heatwaves have increased tree mortality rates worldwide (Allen *et al.* 2010; Choat *et al.* 2012; Breshears *et al.* 2013). Droughts also trigger other types of forest disturbances, in particular herbivorous insect attacks and fires (Anderegg *et al.* 2015; Seidl *et al.* 2017). Increased tree mortality has manifold and diverging impacts on forest ecosystems and the services they provide to society (*e.g.* Anderegg *et al.* 2013; Hanewinkel *et al.* 2013; Ruiz-Benito *et al.* 2017; Senf *et al.* 2021). While disturbances in forests often have positive effects on biodiversity (Swanson *et al.* 2011; Lehnert *et al.* 2013), tree mortality exceeding a certain threshold in frequency and intensity will probably act negatively on the long-term supply of many ecosystem services (Anderegg *et al.* 2013). For example, elevated tree mortality exposes forestry enterprises to higher economic risks and reduces the predictability, quality and amount of merchantable wood (Neuner & Knoke 2017).

Furthermore, in Central Europe projected decreasing summer precipitation, higher temperatures and thus hotter and longer droughts (IPCC 2012) are expected to significantly change the growth, reproduction and survival of many plants, including tree species (Chaves *et al.* 2003). The recent droughts

of 2018 and 2019 have already triggered a wave of mortality in many tree species of temperate European forests (Schuldt *et al.* 2020). High levels of mortality occurred not only in drought-sensitive and disturbance-prone species, such as Norway spruce (*Picea abies* (L.) H. Karst.), where this may have been expected (Christiansen & Bakke 1988; Grodzki *et al.* 2004; Schuldt *et al.* 2020), but also the extent of crown dieback and mortality of European beech (*Fagus sylvatica* L.) in different parts of Central Europe surprised many forest managers and scientists (*e.g.* Schuldt *et al.* 2020; Obladen *et al.* 2021).

European beech is the most abundant native broadleaf tree species in Central Europe and thus the foundation species of most natural forest ecosystems (Leuschner & Ellenberg 2017). Many forest-dwelling organisms are associated with *F. sylvatica*, especially with old individuals of this species (Brunet *et al.* 2010; Walentowski *et al.* 2014). Increased future mortality rates of beech would critically affect ecological, economic and social benefits of Central European forests (Bonan 2008; Anderegg *et al.* 2013). Moreover, in recent decades *F. sylvatica* has been widely planted for the conversion and restoration of secondary conifer forests, towards establishment of more natural and mixed stands (*e.g.* Spiecker 2003; Heine *et al.* 2019; Ammer *et al.* 2008). Hence, both the adaptation to climate change and the future management of beech-dominated forests

are major issues for their sustainable use and biodiversity conservation (Krumm *et al.* 2020; Antonucci *et al.* 2021).

Despite long-term experience in managing European beech forests, judging the sensitivity of beech to extremes of environmental conditions, in particular increasing drought events, is currently controversial. In a recent comprehensive review, Leuschner (2020) classified beech as moderately drought sensitive. Other studies suggest a higher drought sensitivity of this tree species (Köcher *et al.* 2009; Scharnweber *et al.* 2011; Obladen *et al.* 2021). Nevertheless, in the early 2000s, a critical review that questioned the future suitability of beech under climate change (Rennenberg *et al.* 2004) was challenged by many forest scientists (Ammer *et al.* 2005), pointing to evidence from pollen records (Huntley *et al.* 1989), studies on tree growth (Felbermeier 1994; Ammer 2000; Pretzsch & Ďurský 2002) or on the dynamics in strict forest reserves (Meyer *et al.* 2000). In his worldwide account of the ecology of beech forests, Peters (1997) showed that European beech forests occur even at average annual temperatures of 14°C. Climate envelope models indicate that beech forests would persist as the dominant natural vegetation even under climate change (Kölling *et al.* 2007), and Bolte *et al.* (2007) suggested that the adaptability of beech was still underestimated. It was observed that beech had spread on waterlogged and dry sites which had previously been assigned by vegetation scientists to other more tolerant tree species communities (Leuschner 1998). Monitoring of strict forest reserves revealed consistent positive trends in the distribution and proportion of beech over the decades (Rohner *et al.* 2012; Meyer *et al.* 2016, 2017).

An opposite trend from strict forest reserve monitoring data was first reported for the observation period 2014–2017 (UBA 2019). Moreover, significant growth depressions of beech on sites with <350 mm rainfall during the vegetation season were observed (Müller-Haubold *et al.* 2013; Knutzen *et al.* 2017). Walthert *et al.* (2021) emphasized the vulnerability of beech to drought because of high rates of embolism. In several studies, however, adaptations of the hydraulic system of beech to drought could be demonstrated (Wortemann *et al.* 2011; Aranda *et al.* 2015; Schuldt *et al.* 2016). The resilience of radial stem growth of beech after drought was shown to be high (Walentowski *et al.* 2017; Vitasse *et al.* 2019; Leuschner 2020), and even comparable to more drought-tolerant companion species in natural mixed forests on xeric sites (Kunz *et al.* 2018). The allocational capacity of beech to shift biomass from aboveground to belowground organs to capture more water, as sites become drier, was proposed as an important adaptation mechanism (Hertel *et al.* 2013). This shift in allocation pattern was observed in greenhouse experiments with seedlings (Schall *et al.* 2012). The overall results of the rainfall gradient studies of Knutzen *et al.* (2015, 2017) underlined the ambiguity of results concerning the adaptability of beech to climate-induced warming and drought. While, on the one hand, a high adaptation potential was demonstrated, on the other hand, it was concluded that beech may fail to withstand the predicted increasing aridity, even in the centre of its distribution range (Knutzen 2016). In addition to empirical studies, vegetation and species distribution models also provide equivocal projections. Whereas the studies of Hickler *et al.* (2012), Beierkuhnlein *et al.* (2014) and Mellert *et al.* (2016)

indicated that beech forests will constitute large parts of the natural vegetation even under projected climate change, Hanewinkel *et al.* (2014), Thurm *et al.* (2018) and Kölling & Mette (2021) projected major range losses of beech in Central Europe. These divergent results show that vegetation models poorly represent forest dieback (Jump *et al.* 2017). The above-mentioned shortcomings call for more experimental and observational studies on tree mortality to improve the baseline data.

Besides the issue of natural drought sensitivity, another crucial point of public debates and scientific discussions is whether the canopy of beech forests should be kept as closed as possible to maintain a cool microclimate (*e.g.* de Frenne *et al.* 2021) or whether stands should be thinned intensively to increase the vitality of individual trees (*e.g.* Bréda *et al.* 1995; Sohn *et al.* 2016). It is remarkable that comparable discussions on the effect of tree removals on the vitality of remaining European beech trees were held already 200 years ago (Schultze 1835). Because of the currently observed mortality in old managed and unmanaged beech forest stands, there has been a call to cease active forest management and maintain closed canopies that presumably reduce heat and transpirational stress. For example, a moratorium on tree harvesting in beech forests over 100 years old has been placed on the state forests of the German state Rhineland-Palatinate since 2020 (Landesforsten Rheinland-Pfalz 2020).

Understanding the complex ecological process of tree death (Franklin *et al.* 1987) is a prerequisite to assess the effects of management interventions on forest stands during and after drought events. Drought-related mortality in large trees may increase with exposure of their crowns because of a comparatively low hydraulic conductance (McDowell & Allen 2015) and a higher risk of cavitation. Hence, management-induced exposure of large crowns of *F. sylvatica* could substantially increase evaporative demand and thus water loss through transpiration and increase water stress in individual trees (Niinemets 2010; Bennett *et al.* 2015). In contrast, many studies have demonstrated the benefits of thinning for the resistance and resilience of radial tree growth in retained – and thus surviving – trees in relation to drought (Ammer 2016). The capacity to increase stem increment after thinning and partial harvesting in remaining European beech trees is known to be exceptionally high (Seebach 1845; Freist 1962; Pretzsch 2005; Barna *et al.* 2010), hence demonstrating the large potential of this tree species to exploit additional growing space through its high crown plasticity (Dieler & Pretzsch 2013). In contrast, another study found that climate sensitivity of radial growth in beech trees increases at lower stand density (Mausolf *et al.* 2018). However, higher growth variability, as in this case, should not be mistaken as a stress signal but seen as an indication that trees with more growing space, in contrast to those growing under high competition, actually have the capacity to respond to favourable climate conditions with increases in radial increment (*e.g.* Skiadaresis *et al.* 2021). There are, however, few studies on the effect of thinning and partial harvesting on drought-related tree mortality (*e.g.* Giuggiola *et al.* 2013). We are not aware of such a study in European beech stands. Also, no quantitative assessment of mortality in managed *versus* unmanaged early-mature to mature beech forests has been carried out so far.

Combining studies in unmanaged strict forest reserves (SFR) with a comparable managed reference area (MRA) may contribute to bridge this knowledge gap. Through persistent monitoring activity, a pool of long-term data on tree demography has been acquired in SFR over several decades, allowing a comparison of tree mortality between managed and unmanaged forests (Meyer 2020). Complemented with recent inventories and additional data, ex-post natural experiments (Diamond 1983) can readily be designed. In our study we hypothesized that natural mortality of beech trees would:

(i) increase in periods with a high deficiency in the climate water balance during the growing season, in particular during the drought years 2018 and 2019;
(ii) be lower at sites with a favourable water balance than at drier sites;
(iii) increase with decreasing dominance (canopy status) of an individual tree;
(iv) increase with initial stand density; and
(v) decrease with increasing tree removals.

MATERIAL AND METHODS

Study sites

For this study, we used a subset of strict forest reserves (SFR) in the German federal state of Hesse to conduct a study on the natural mortality of beech trees in mature managed and unmanaged stands. We considered the SFR in Hesse was particularly well suited because: (a) most comprise a managed reference area (MRA), (b) long-term data on tree demography are available to compare natural mortality in the 2018 and 2019 drought years to mortality in preceding periods, and (c) large parts of Hesse are in the centre of the natural range of European beech forests.

Beech forest reserves were included in this study if they met two criteria. First, the unmanaged SFR needed to have an adjacent, regularly managed reference area. Second, two forest inventories had been conducted before 2018. According to these selection criteria, 11 study sites were selected (Fig. 1, Table 1).

Whereas in the SFR no trees had been felled, forest management in the reference stands followed a close-to-nature approach of selective tree removal (Fig. 2). Depending on age and tree dimensions, tree removal was done either in the form of crown thinning, i.e. removing the strongest competitors of crop trees, or at later stages in the form of target diameter harvesting, i.e. removing mostly commercially mature trees (ca. 55–70 cm DBH, depending on quality). In this form of silviculture, small trees in intermediate and overtopped crown classes are deliberately retained to shade the ground and the stems of crop trees.

Development of basal area

At the beginning of the first observation period, the mean basal area of the initial living stand (≥7 cm DBH) was nearly identical in both SFR and MRA (Fig. 4a). The harvesting from the MRAs and the no-intervention management in the SFRs led to distinct basal area differences between stands in subsequent periods (overall mean in 2020: 17.5 m^2 ha^{-1} in MRA and 33.3 m^2 ha^{-1} in SFR; Fig. 4a).

Climate water balance

The water availability during the growing season from 1 May to 30 September was quantified as the mean climate water balance per sample plot (Fig. 3). For this purpose, precipitation and evaporation data from nearby weather stations were interpolated by weighting the values from individual stations with their distance from the sample plot. Height above sea level and exposure were additionally considered in the interpolation algorithm.

Selection of sample plots

This study was based on data collected under the protocol for monitoring forest structure and vegetation in the forest reserves of Hesse (Meyer et al. 2018). Between 1988 and 2017, tree species, status (living/dead) and DBH of all trees >7 cm were recorded in 0.1-ha circular plots, distributed in a 100 × 100 m grid over the SFR and MRA areas (Table 1). The observation periods varied in length in relation to the individual inventory year. The available data on tree species composition (own inventory), tree age and site conditions (forest management and site mapping data retrieved from the state forest enterprise HessenForst) were used to design the tree mortality study. The basic idea was to reassess the tree communities already inventoried in past surveys to: (1) derive mortality rates for the drought period 2018/2019, and (2) compare them with mortality rates from the previous observation periods.

In this study we focused on mature beech forests. To ensure a high degree of comparability between sample plots and study sites, we restricted the reassessments to sample plots (1) with a stem number of beech ≥50% in the living stand (≥7 cm DBH), and (2) where the age of the dominant tree species was ≥100 years in 2020.

We aimed to assess at least five sample plots within each stand previously inventoried (Table 2). To assess the influence of site conditions on tree mortality, we generated plot-wise data for the terrain water balance and nutrient supply status. The fine-scaled terrain water balance status was aggregated to two levels: 'favourable to very favourable' (hereafter: favourable) and 'moderately favourable to moderately dry' (hereafter: drier). The nutrient supply status was classified as eutrophic, mesotrophic plus, mesotrophic or oligotrophic.

In the first step of the analysis, we calculated the number of sample plots meeting the above defined criteria per study site, SFR and MRA, and the levels of terrain water balance and nutrient supply status. Only those levels were retained which were represented by at least five sample plots per SFR and MRA. To ensure a balanced design, we selected the same number of plots in SFR and MRA per study site. For instance, if six suitable plots could be found in the SFR and eight in the MRA, only six plots were selected to cover the MRA. In the inventory during the vegetation period 2020, a maximum of ten plots per study site were sampled. The final selection of sample plots was random; in total, we selected 276 sample plots (Table 2).
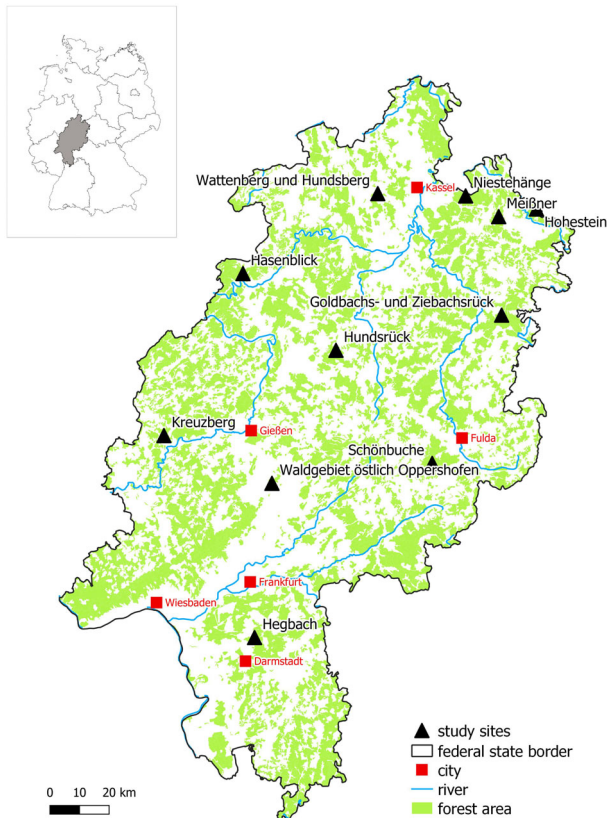
Fig. 1. Location of study sites in the German federal state Hesse. Geodata: Hessian Administration for Land Management and Geoinformation, © 2021.

Assessment of tree communities on selected sample plots

The fieldwork started after leaf development was completed in May 2020 and ended in June 2020. During this observation period, dead trees could be easily identified, tree vitality status could be assessed, and time of death could be attributed to the years 2018/ 2019 or earlier. The re-assessment was restricted to those trees that were alive in the first inventory (Table 1; 1988–1994).

The following attributes were assessed:

- individual tree number (re-identification of individual trees based on polar coordinates from the previous inventory)
- tree species
- tree diameter (DBH at 1.3 m)
- vitality status or time of death, divided into the following categories:
  o living
  o dying (trees in very poor health (<10% of original foliage) and expected to die within the next growing season
  o dead for more than 2 years (year of death before 2018)
  o died recently in 2018/2019
- cause of mortality: natural or harvesting removal
- additional remarks regarding tree health (*e.g.* sun scald, crown damage/breakage, insect infestation, bark necrosis, stem exudates, etc.)

Data were entered in a field computer using the software FieldMap (IFER – Monitoring and Mapping Solutions, Prague,

Czech Republic). Data of the previous inventories were available in the field for control purposes.

Data analysis

Annual mortality rates were calculated for the three observation periods (equation 1). The first period covered the time between the first and second inventory, the second period spanned from the second inventory to 2017, and the third period comprised the drought years 2018 and 2019. All analyses were restricted to the initial stand of living trees ≥7 cm DBH at the first inventory. The individual fate of each tree from this initial population was tracked across these three periods. We calculated overall and natural mortality rates based on the three criteria for cause of mortality (see above; equation 1; Sheil & May 1996).

$$m\,(\%) = \left(1 - \sqrt[a]{\frac{N_2}{N_1}}\right) \cdot 100 \qquad (1)$$

where:

$m\,(\%)$ = mortality rate per year [%]

N_1, N_2 = stand density (stem number or basal area) at the beginning of the period (N_1), remaining stand density at the end of the period (N_2)

a = period length [years]

Basal area of the living stand (m^2 ha^{-1}) was taken as a proxy for initial stand density. The basal area of removed trees per year (m^2 ha^{-1} year^{-1}) indicated the degree to which density was actively reduced by forestry measures.

Data preparation, statistical testing and graphical representation were carried out using SAS version 9.4. The Scheefé *post-hoc* multi-comparison tests were applied to reveal significant differences ($P < 0.05$) between observation periods and between treatments (unmanaged *versus* managed). To ensure equal weighting of the forest reserves, we weighted observations by the inverse of the plot number of each forest reserve to calculate means and for testing. To assess possible demographic drivers of natural mortality, we analysed whether dominant or suppressed trees were primarily affected. For that purpose, we calculated the ratio between mortality rate in terms of stem number and in terms of basal area (dominance index; equation 2). If mainly dominant trees (indicated by a basal area larger than the median basal area of the plot) die, the dominance index is <1, while values of the dominance index >1 indicate that mortality affects mainly suppressed trees with a relatively low basal area.

$$dominance\ index\ of\ mortality\ rate = \frac{m\,(\%)_N}{m\,(\%)_{BA}} \qquad (2)$$

where:

$m\,(\%)_N$ = proportion of trees that died per year [%]

$m\,(\%)_{BA}$ = proportion of basal area that died per year [%]

To implement the dominance index in a probabilistic model of tree mortality, on the basis of tree individuals (logistic

Table 1. Basic information on the study sites (for additional information see https://www.nw-fva.de/NwInfo/tablemap.jsp).

name	size of reserves and reference areas SFR/MRA [ha]	altitudinal range [m a.s.l.]	designation [year]	parent material	annual precip. [mm]	average annual temp. [°C]	Inventory years
Niestehänge	69/60	410–530	1988	sandstone	950	7.0	1988, 2003
Goldbachs- und Ziebachsrück	31/37	300–370	1988	sandstone, loess	770	8.0	1988, 2009
Schönbuche	28/27	390–460	1988	sandstone	880	7.4	1988, 2010
Wattenberg und Hundsberg	42/34	380–510	1988	basalt	800	7.5	1988, 2017
Meißner	43/43	570–740	1988	basalt, loess	1000	6.5	1988, 2010
Hohestein	27/24	490–560	1989	limestone	900	7.0	1988, 2007
Hasenblick	46/42	370–490	1988	clay slate	950	7.2	1988, 2012
Waldgebiet östl. Oppersh.	21/20	210–240	1988	clay, loess	700	8.6	1988, 2015
Hegbach	28/14	140–160	1988	sandstone	720	9.5	1988, 2002
Kreuzberg	48/34	290–400	1989	diabas, basalt	915	8.0	1990, 2010
Hundsrück	21/24	280–320	1993	basalt, loess	720	7.9	1994, 2010

Designation refers to the year in which reserves were established and when active forest management ceased.
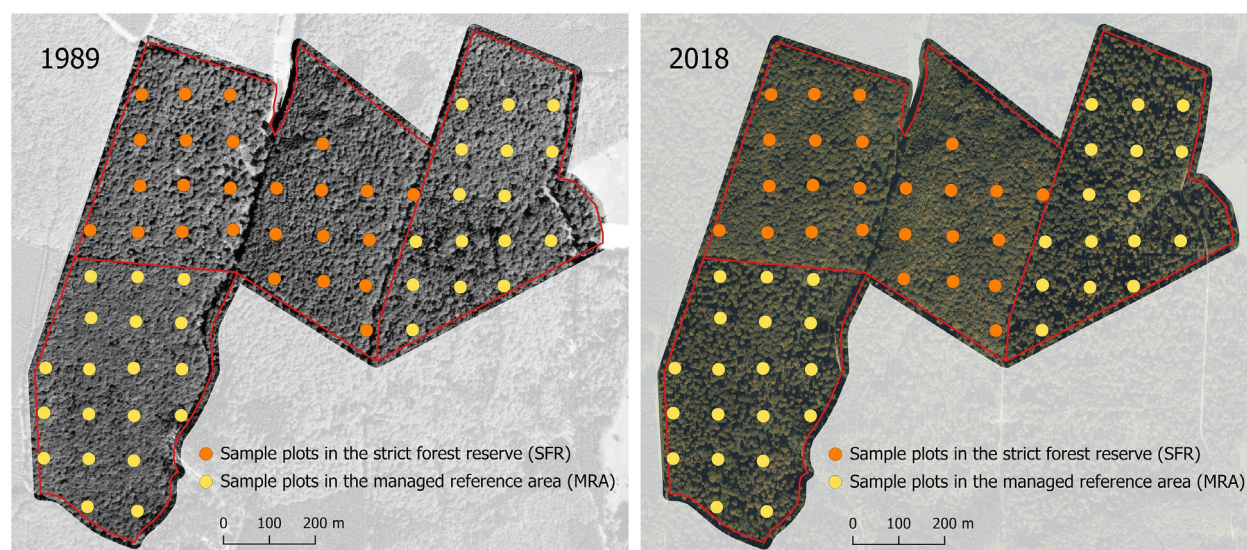

Fig. 2. Forest stand conditions in 1989 (left) and in 2018 (right) and locations of sample plots within the study site "Goldbachs- und Ziebachsrück". In 2018, the canopy in the strict forest reserve is dense and closed, whereas in managed reference areas the canopy is relatively open and individual tree crowns of dominant trees are more exposed. Aerial photograph: Hessian Administration for Land Management and Geoinformation, © 2021.

model), we used the dominance index of a single tree (equation 3).

$$dominance\ index\ single\ tree = \frac{p_N}{p_{BA}} \quad (3)$$

where:

p_N = contribution of the single tree to the total number of trees per plot [%]

p_{BA} = contribution of the single tree to the total basal area per plot [%]

To address our hypotheses, the mortality rates and the dominance indices of mortality rates were modelled in relation to site conditions and stand attributes. In all models, the reserve identity was included as a categorical variable to estimate any reserve-specific modification of the intercept.

To describe site conditions, we applied the following attributes: terrain water balance, nutrient availability class, topography, exposure and height a.s.l. Stand attributes included initial basal area [m² ha⁻¹], basal area harvested per year [m² ha⁻¹ year⁻¹], proportion of admixed tree species [% living basal area at first inventory] and stand age at first inventory.

Model building started with selection of an optimum general linear model (proc glmselect, in SAS version 6.4) as indicated by the AIC (Akaike information criterion). Hereafter, a general additive model was built with the selected variables to test
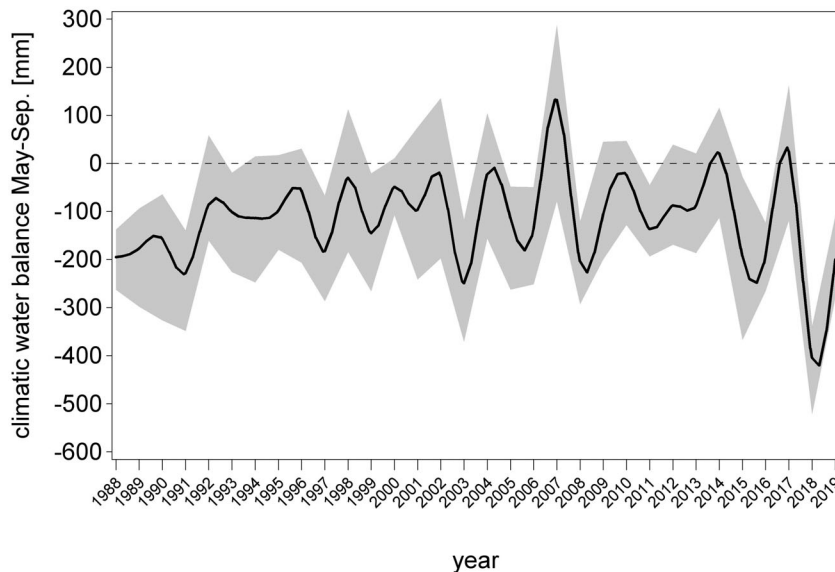
Fig. 3. Mean climate water balance of the growing season per year during the observation period. Arithmetic mean of the values for all 276 sample plots, grey shading: 5th–95th percentile.

for linearity (proc gam in SAS version 6.4, degrees of freedom = 5). If no significant smoothing effect was detected, model building ended at this step. Otherwise, the smoothing plot was inspected and the variables having significant non-linear effects were transformed using an adequate log- or exponential-formulation. With these transformed variables, the next optimum model was selected according to the AIC and tested for non-linearity. This procedure was repeated until a final model without significant non-linear effects was obtained.

For mortality rates and dominance indices, we built models only for the whole observation period because the variability of predicted variables was too high for satisfactory period-wise modelling.

Furthermore, we analysed the effect of the climate water balance in the observation periods to see whether the drought years 2018 and 2019 influenced mortality. For that purpose, we employed logistic models for the probability of single beech trees dying naturally, including the following independent variables:

- length of the observation period [years]
- forest reserve
- dominance index of single trees
- initial basal area [m^2 ha^{-1}]
- basal area removed [m^2 ha^{-1} year^{-1}]
- mean climate water balance of the observation period [mm in the growing season]

We started with a model that contained both reserve identity and length of the observation period. Further variables were added and retained only if they increased the AUC (area under the ROC curve) and were significant.

RESULTS

Stem number development and frequency of mortality events

Overall, 6,583 trees (all species) were recorded on the 276 plots at the first inventory (Table 3). Of these, 63% (4,166) of these trees were still alive in 2020, resulting in 2,417 trees that had

died naturally or were removed between the first and the third inventory in 2020.

The relevance of natural beech mortality per period and treatment is indicated as the percentage of plots affected by mortality (Table 4). These figures, however, strongly depend on stem density and length of the observation period. While beech was affected by mortality on more than half of the sample plots in both treatments in the first period, the frequency of plots with beech mortality fell sharply in the second period. In the years 2018 and 2019, beech mortality occurred only in 14% of the sample plots in managed stands, whereas this figure was more than twice as high in the strict forest reserves.

Mortality rates and dominance indices

Periods and treatments

On drier sites, mean annual natural mortality rates of beech ranged from 0.5–2.1% in the SFRs and 0.5–0.7% in the MRAs (Fig. 4b). On more favourable sites, mortality rates ranged from 0.6–1.6% in SFRs and 0.7–1.0% in MRAs. In the managed stands, mortality rates showed a steady, yet statistically non-significant, increase. A statistically significant increase in natural mortality in the years 2018 and 2019 could be confirmed in the SFRs (1.6% on favourable sites; 2.1% on drier sites). However, differences between the treatments were not statistically significant in the drought years.

Mortality rates in SFRs appeared to be characterized by higher dominance indices (equation 2) than those in MRAs (Fig. 4c). This was possibly a result of higher stand density driving mortality of smaller trees (Fig. 4a). However, this difference between the two stand types was significant only on favourable sites and in the third observation period. In the MRA stands on favourable sites, the degree to which dominant trees were affected by mortality was significantly higher in the third period, as indicated by a lower dominance index (Fig. 4c). This pattern was also found at drier sites but was not significant.

In each case, dominance indices were still >1, suggesting that suppression by neighbouring trees increased the probability of death in all periods and treatments, although to different degrees.
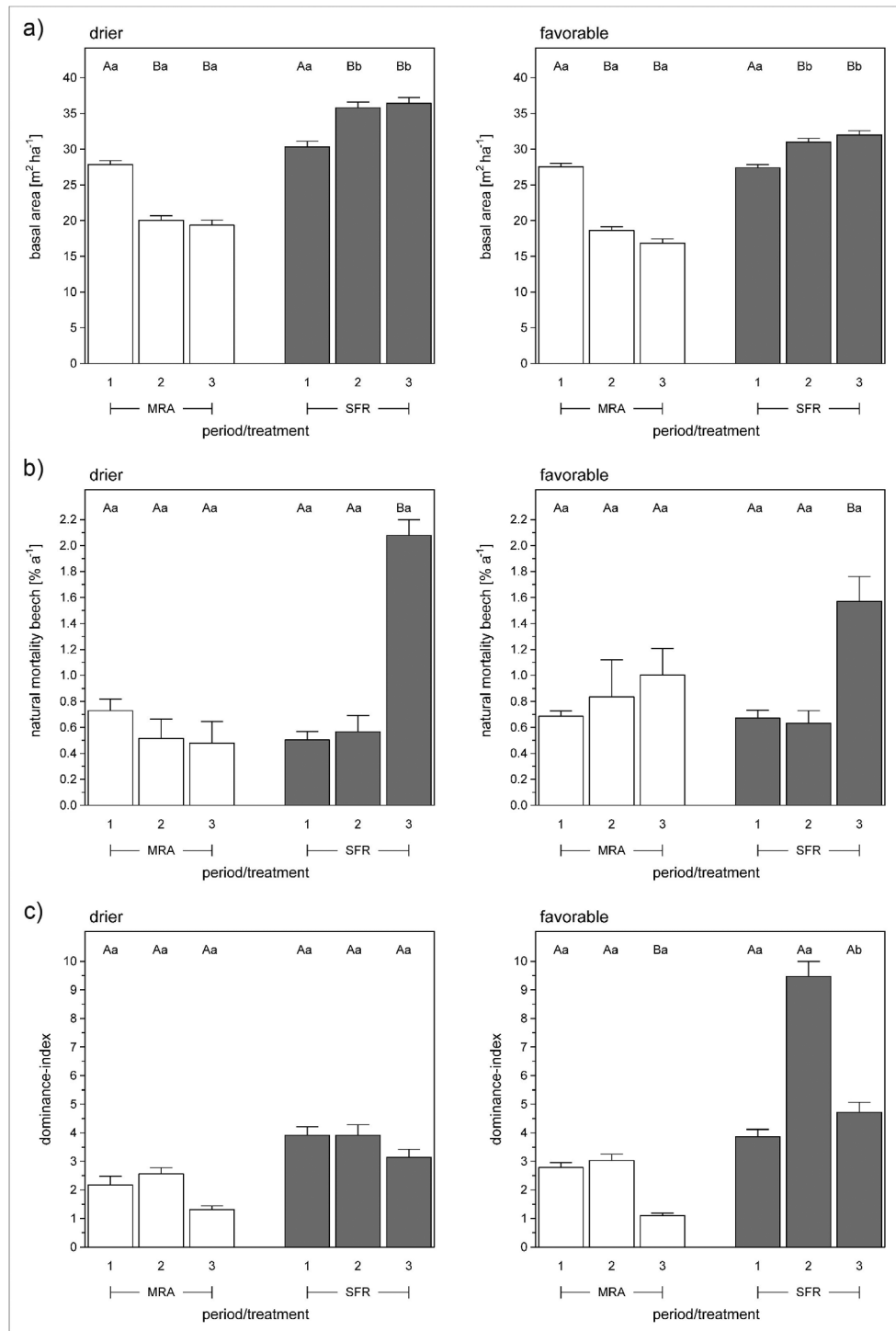
Table 2. Number of selected sample plots per forest reserve (study site), treatment (SFR = strict forest reserve, MRA = regular forest management) and terrain water balance/nutrient supply status combination.

name	treatment	terrain water balance	nutrient supply	No. of plots	sum
Niestehänge (801)	SFR	favourable to v. favourable	mesotrophic	10	20
	MRA	favourable to v. favourable	mesotrophic	10	
Goldbachs- und Ziebachsrück (802)	SFR	favourable to v. favourable	mesotrophic	10	40
	SFR	mod. favourable to mod. dry	mesotrophic	10	
	MRA	favourable to v. favourable	mesotrophic	10	
	MRA	mod. favourable to mod. dry	mesotrophic	10	
Schönbuche (803)	SFR	favourable to v. favourable	mesotrophic	10	20
	MRA	favourable to v. favourable	mesotrophic	10	
Wattenberg und Hundsberg (804)	SFR	favourable to v. favourable	eutrophic	7	26
	SFR	mod. favourable to mod. dry	eutrophic	6	
	MRA	favourable to v. favourable	eutrophic	7	
	MRA	mod. favourable to mod. dry	eutrophic	6	
Meißner (805)	SFR	favourable to v. favourable	eutrophic	10	20
	MRA	favourable to v. favourable	eutrophic	10	
Hohestein (808)	SFR	favourable to v. favourable	eutrophic	9	18
	MRA	favourable to v. favourable	eutrophic	9	
Hasenblick (809)	SFR	favourable to v. favourable	mesotrophic	10	36
	SFR	mod. favourable to mod. dry	mesotrophic	8	
	MRA	favourable to v. favourable	mesotrophic	10	
	MRA	mod. favourable to mod. dry	mesotrophic	8	
Waldgebiet östl. Oppershofen (810)	SFR	favourable to v. favourable	eutrophic	5	26
	SFR	favourable to v. favourable	mesotrophic plus	8	
	MRA	favourable to v. favourable	eutrophic	5	
	MRA	favourable to v. favourable	mesotrophic plus	8	
Hegbach (811)	SFR	favourable to v. favourable	mesotrophic	9	18
	MRA	favourable to v. favourable	mesotrophic	9	
Kreuzberg (813)	SFR	favourable to v. favourable	eutrophic	8	32
	SFR	mod. favourable to mod. dry	eutrophic	8	
	MRA	favourable to v. favourable	eutrophic	8	
	MRA	mod. favourable to mod. dry	eutrophic	8	
Hundsrück (826)	SFR	favourable to v. favourable	mesotrophic	10	20
	MRA	favourable to v. favourable	eutrophic	10	
overall					276

Table 3. Overall number of trees sampled at the beginning of each period in the managed reference areas (MRA) and the strict forest reserves (SFR).

	period		
treatment	1.	2.	3.
MRA [plot number = 138]	3,330	1,758	1,499
SFR [plot number = 138]	3,253	2,777	2,667
sum	6,583	4,535	4,166

The periods corresponded to (1) the time between the first and second inventory, (2) the time from the second inventory to 2017, and (3) the drought years 2018 and 2019.

Table 4. Percentage of sample plots with natural mortality of beech trees per observation period and treatment on very favourable – favourable sites.

	period		
treatment	1.	2.	3.
MRA [plots = 106]	75	27	14
SFR [plots = 106]	55	32	30
overall	63	29	22

The periods corresponded to (1) the time between the first and second inventory, (2) the time from the second inventory to 2017, and (3) the drought years 2018 and 2019.

index were not significant (results not shown). Hence, no site attributes were retained as explanatory variables in the final model. As site conditions were not significant, the models for the effects of stand attributes were built for the whole sample of 276 plots.

The final model for the effects of stand attributes on natural beech mortality rates explained 28% of the total variation and only 16% were assigned to reserve identity (Table 5). Smoothing effects were not significant, so model building resulted in a linear model. Initial stand density was excluded in the variable selection procedure. Stand age had a strong effect in decreasing mortality rates. As hypothesized, tree removal decreased mortality, but at a very low rate, hardly contributing to the coefficient of determination (adjusted R^2) and only suggesting a trend ($P = 0.0848$).

In the process of model building, we could not identify stand attributes that explained a significant proportion of the variation in the dominance index of natural mortality.

Logistic model of mortality

The final logistic model of natural beech mortality contained the following significant predictors: period length, reserve identity, dominance index of a single tree, basal area removed and climate water balance (Table 6). The AUC of 0.790 indicates good to excellent model performance (Hurst *et al.* 2011). The re-scaled coefficient of determination was 0.1851.

We also tested other additional site variables and interaction effects. These only yielded minor increases in AUC (fourth digit at maximum) and rescaled R^2. Hence, for simplicity and to maintain the focus on our hypothesis, we chose the simple model of pre-defined variables.

To illustrate effect of the variables, we calculated a combination of model outcomes for the 5th and 95th percentile and the mean of true distributions of the variable dominance index, removals per year and climate water balance (indicated as low, moderate or high in Fig. 5). We estimated annual probabilities for the mean of all 11 SFRs, resulting in 27 combinations covering most of the true variation in the dataset (Fig. 5).

Tree removal intensity had only a minor (but increasing) effect on the probability of mortality. In periods with a highly negative climate water balance, mortality rates were approximately twice as high as in wet periods. The probability of mortality also increased with increasing competition experienced by tree individuals (high dominance index).

DISCUSSION

The variation in site conditions regarding terrain water balance and nutrient supply captured in our study design represents 95.8% of the whole forest area in the state of Hesse. Thus, our results are highly representative for beech forests in this region, but they did not capture the very dry end of site conditions.

Table 5. Final models for the effects of site and stand attributes on the natural mortality rate of beech [% year^{-1}] in the whole observation period.

model	attribute	cumulative adj. R^2	parameter estimate	P > ItI
site attributes	intercept		0.353	0.0548
	forest reserve	0.1520	−0.411 to 0.642	<0.0001*
	favourable / drier	0.1570	0.209 / 0	0.1090
stand attributes	intercept		3.137	<0.0001
	forest reserve	0.1633	−1.144 to 0.032	<0.0001*
	age [years]	0.2747	−0.264	<0.0001
	removals [m² ha^{-1} year^{-1}]	0.2801	−0.014	0.0848

*Significance P > F.

Table 6. Final logistic model of natural beech mortality.

parameter	parameter estimate	P > ChiSq
intercept	−4.899	<0.0001
forest reserve	−1.919 to 0.862	<0.0001
period length [years]	0.101	<0.0001
dominance index	0.097	<0.0001
removals [m² ha^{-1} year^{-1}]	0.016	0.0078
climate water balance	−0.002	0.0016

Although our study covered 11 different forests, we could not detect a dramatic mortality signal or signs of widespread canopy disintegration throughout the drought years 2018 and 2019. The mortality rates of European beech trees in managed and unmanaged stands during the drought period 2018–2019 were relatively low (0.5–2.1%) when compared to European beech forests in other, drier parts of Germany during this period (Schuldt *et al.* 2020). For example, Obladen *et al.* (2021) reported a much higher mortality rate of 7% in 2018 for a beech forest in northern Bavaria. The difference to our results may be attributable to the lack of sites with low precipitation or very shallow and rocky soils in our design. The results, however, correspond to the mortality rate of the latest forest health monitoring of the state Hesse, with 0.3% reported for the years 2019–2020 (Paar *et al.* 2020). Compared to the long-term average mortality rate of 0.06%, this was the highest value recorded since 1984.

In our study, the removal of trees in managed forest stands had only a small influence on natural tree mortality. Its explanatory power was less than that of the climate water balance of the site and the intensity of competition, which promoted mortality of trees of lower canopy status.

Confirmed and rejected hypotheses

The logistic model confirmed the hypothesis that natural mortality of beech trees increased in periods with a high climate water deficit during the growing season, which characterized the drought years 2018 and 2019. However, when mortality rates, instead of probabilities, were analysed, this result could not be reproduced independently of the treatments. The increase of mortality rates during the recent drought years was significant only in the unmanaged stands, whereas in the managed stands there was no consistent temporal trend.

Further, we had to reject the hypothesis that mortality rates would decrease on the investigated sites with a favourable water balance. On the contrary, the general linear model indicated a slight increase in mortality at more favourable sites. This finding confirms the observation that drought-related mortality is a wide-spread phenomenon that occurs from very dry to moist forest types that are normally not water-limited (Allen *et al.* 2010).

Based on the logistic model we could confirm the hypothesis that with decreasing tree dominance status, and hence increasing competition, the probability for a tree to die increases. In contrast to managed stands, the high dominance index, in unmanaged stands throughout all observation periods indicated that the acceleration of mortality during drought years was largely restricted to suppressed trees. In managed stands, the shift of mortality from suppressed to more dominant trees during the drought years indicated a higher degree of canopy disintegration than in the unmanaged stands. However, as the mortality rates are still low, there was no indication of a true drought-induced break-up of the canopy.

Both initial stand density and tree removals had only minor or inconsistent effects on natural beech mortality. Initial stand density was therefore excluded as a predictor variable in both modelling approaches. Tree removals acted slightly in decreasing on mortality rates in the general linear model but had an increasing effect on mortality rates in the logistic model.
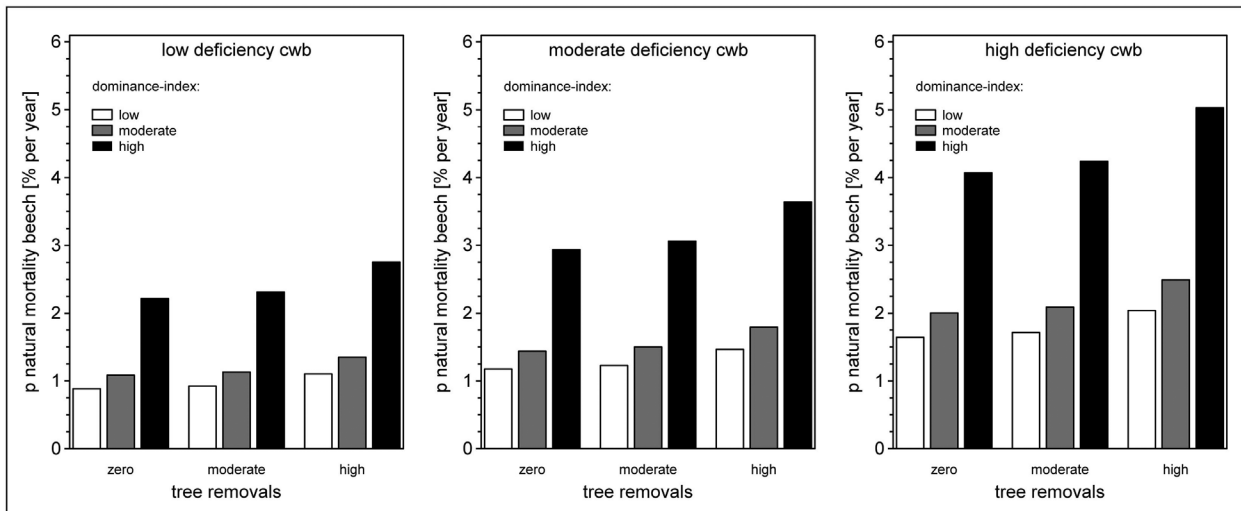
Fig. 5. Effects of the different predictors on the probability of annual natural mortality in European beech as estimated with a logistic model. The 5th percentile, arithmetic mean and 95th percentile of the true distribution of the predictor values were used to illustrate the effect of low, moderate and high values of the predictors.

Hence, these two hypotheses related to stand density could not be supported. The treatments, and thus the stand density, modified tree mortality only during the drought years 2018 and 2019 through accelerating density-dependent mortality rates in dense and unmanaged stands and shifting mortality to less suppressed trees in the more open managed stands. Thus, effects of stand density became apparent only in the form of interaction with drought, but not as an independent factor as such.

Impacts of stand density on mortality

The influence of forest management in the context of this study is largely characterized by changes in stand density, which can influence tree vitality and hence mortality in several ways. A reduction in basal area through tree removals increases the growing space and access to resources (light, soil water, nutrients) and hence reduces competitive stress. The positive impact of thinnings on the growth performance of trees during or after drought has been demonstrated for several genera and regions (Sohn et al. 2016). Intensive thinning has therefore been proposed to improve resilience and resistance of retained trees to drought stress (van der Maaten 2013; Sohn et al. 2016; Diaconu et al. 2017). Stands with less dense canopies and consequent reductions in stand transpiration and interception following thinning (Bréda et al. 1995) are often characterized by higher soil water availability for residual trees (e.g. Aussenac & Granier 1988; Brooks & Mitchell 2011). In addition, trees promoted through thinning may develop more extensive individual root systems that increase their capacity to extract water from the soil during and after drought periods (Whitehead et al. 1984; Aussenac & Granier 1988; Misson et al. 2003). The intraspecific competition among F. sylvatica trees has been shown to be an important driver of tree drought sensitivity, where trees under high competitive stress are less tolerant to high temperatures and low water supply (Cescatti & Piutti 1998; Mölder & Leuschner 2014). It is thus not surprising that this approach has also been shown to be effective in reducing drought impacts in early mature to commercially mature (90–140 years old) beech stands (e.g. Gerhardt et al. 2016; Diaconu et al. 2017). Here, dominant and co-dominant trees have a higher growth recovery and resilience after drought events (Diaconu et al. 2017). In addition, thinning led to decreasing vessel sizes and, thus, presumably to safer water transport through reduced risk of embolism and hence hydraulic failure in beech trees (Diaconu et al. 2016). In addition, it has been shown that the higher resource acquisition capacity per tree with increasing growing space can reduce drought-induced mortality (McDowell et al. 2008; Allen et al. 2010) and predisposition to insects and diseases (e.g. Chmura et al. 2011). Beech trees with low relative growth rates, as is typically the result of intense competition, therefore show a higher risk of mortality (Gillner et al. 2013). In our study, the reductions in stand density in managed stands were likely responsible for the lower mortality rates, in particular of smaller trees (high dominance indices), when compared to SFRs.

At the same time, stand density and its regulation through thinning and harvesting influence the microclimate. For example, thinning exposes individual tree crowns more to direct solar radiation and increases wind movement in the canopy. As a consequence, transpiration and evaporative water loss may increase as compared to unthinned stands, in particular shortly after felling measures before the canopy closes again through crown expansion (e.g. Brooks & Mitchell 2011). This adverse effect of thinning and canopy openings may particularly affect older trees with large crowns and hence large potential transpirational demand. The hydraulic system in these trees will be balanced between the transpirational demand of the crown and the capacity of the root system to take up soil water. Such a hydraulic system may not cope with a substantial increase in transpiration through a sudden exposure of the crown, leading to shedding of leaves and partial or total crown dieback. The sudden exposure of the shaded part of the canopy, which has a lower resistance to drought-

induced hydraulic failure (Herbette *et al.* 2010), may enhance this process. In our study, these underlying mechanisms may explain the shift of tree mortality to trees of larger dimensions (lower dominance index) in the recent drought period in managed forests with more exposed individual crowns (see Fig. 2). However, we can only speculate here since the retrospective approach used in our study is not suited to reveal the underlying microclimatological and physiological effects of management on the drought response of trees. It has been observed that in many instances, natural tree mortality is not a sudden event but represents the end of a long process of growth decline that may span several decades (Cailleret *et al.* 2017). This is likely the case for the suppressed and overtopped trees, where mortality is driven by competition. Whether this is also the case for dominant trees or whether death is more abrupt and the result of hydraulic failure, could be revealed through comparison of radial growth patterns before death through coring of dead and live trees (Cailleret *et al.* 2017). Comparable to our study also Taccoen *et al.* (2021) have found over-mortality of suppressed trees as a consequence of drought.

The results of our study indicate that management in the form of tree removals influences drought-related mortality differently for trees of different canopy status. Whether and under what conditions the positive influence of management on tree mortality (mostly of smaller trees) may turn into a negative effect on large trees should be investigated through more detailed analyses of microclimate, physiological and growth responses and possible attacks of secondary pests and pathogens.

Beech dieback and diseases

Research on beech dieback in the past can provide important insights to better understand the observed recent wave of mortality during the drought years 2018 and 2019. At least since the middle of the 19th century, waves of beech dieback have been reported for Western, Central and Southeast Europe. The main identified causes were beech bark disease, but also drought events and subsequent attacks of pest species, such as splendour beetles (*Agrilus viridis* L.) or bark beetles (*Taphrorychus bicolor* (Herbst)) (Lauprecht 1868; Ehrlich 1934; Bonnemann 1982; Lakatos & Molnár 2009; Köhler *et al.* 2015). It was recognized early that the intensity of beech dieback events was related to regional site characteristics, such as presence of shallow limestone soils (Lauprecht 1868). Most particularly in the 1950s and 1960s, extensive waves of beech dieback in Germany triggered several studies (Borchers 1961; Schwerdtfeger 1961; Dimitri 1967). Elevated beech mortality was attributed not only to drought but also to deep frost, biotic agents and environmental pollution (Ruge 1950; Schwerdtfeger 1961; Eckstein *et al.* 1984). It is now understood that the beech bark disease is mainly caused by the woolly beech scale (*Cryptococcus fagisuga* Lind.) and subsequent *Neonectria* infections (Lunderstädt 1992, 2002; Köhler *et al.* 2015). In a recent study across three regions in Germany, Köhler *et al.* (2015) found that the infestation rates of the woolly beech scale do not depend on management intensity as such but on tree age and canopy openness. In our study, the mechanisms of drought-related mortality could not be determined. In future studies that investigate the influence of management intensity on drought-related mortality it would be highly desirable to consider the additional and

interactive effects of biotic agents, also for several years following drought events. The presence of biotic agents could reverse mortality predictions (Trugman *et al.* 2021). Future work is needed to explore the interactions between drought, heat, site, management intensity as well as pests and pathogens to improve our understanding of the prevailing mechanisms of mortality (Jactel *et al.* 2012).

CONCLUSIONS

We analysed the influence of forest management in the form of tree removals on drought-related mortality of European beech trees through comparison of mortality rates in 11 strict forest reserves and their adjacent managed reference areas in the state of Hesse, Germany. Our results showed that overall mortality rates, even during the extreme drought years 2018–2019, were relatively low when compared to beech forests in other parts of Central Europe. There was no general influence of forest management on tree mortality. The significantly higher mortality during the recent drought years in unmanaged stands, when compared to managed stands, occurred largely in overtopped trees and is likely a result of the combination of competition and drought-related stress. Whether the observed shift of mortality from overtopped towards larger canopy trees in managed stands during the recent drought event is attributed to hydraulic failure of more exposed trees requires further investigation. While the forests selected for this study represent average site conditions for European beech forests in the Central European mountain ranges, further studies of forest management influences on drought-related mortality should expand the gradient in soil water availability, cover a wider range of tree ages and be conducted for several years after drought events to develop a more comprehensive picture than was possible here. This should be accompanied by analyses of the underlying mechanisms of mortality.

CONFLICT OF INTEREST

The authors confirm that they do not have any conflicts of interest to declare.

AUTHOR CONTRIBUTIONS

PM conceptualized (lead), curated data (lead), methods (lead), visualization (lead) and writing of the original draft (equal), as well as reviewing and editing (supporting). AS and AM helped with writing and editing (supporting). JB was involved in

conceptualization, methodology, co-writing the original draft, writing, reviewing and editing (supporting).

DATA AVAILABILITY STATEMENT

The data are made publicly accessible in the Dryad repository under https://doi.org/10.5061/dryad.v41ns1rz2.

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