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ABSTRACT

Background: Ongoing climate change is anticipated to increase the frequency and intensity of drought events, thereby affecting forest recovery dynamics and elevating tree mortality. The drought of 2018, with its exceptional intensity and duration, had a significant adverse impact on tree species throughout Central Europe. However, our understanding of the resistance to and recovery of young trees from drought stress remains limited. Here, we examined the recovery patterns of native deciduous tree sapling species following the 2018 drought, and explored the impact of soil depth, understory vegetation, and litter cover on this recovery.
Methods: A total of 1,149 saplings of seven deciduous tree species were monitored in the understory of old-growth forests in Northern Bavaria, Central Germany. The vitality of the saplings was recorded from 2018 to 2021 on 170 plots.
Results: Fagus sylvatica was the most drought-resistant species, followed by *Betula pendula*, *Acer pseudoplatanus*, *Quercus* spp., *Corylus avellana*, *Carpinus betulus*, and *Sorbus aucuparia*. Although the drought conditions persisted one year later, all species recovered significantly from the 2018 drought, albeit with a slight decrease in vitality by 2021. In 2018, the drought exhibited a more pronounced adverse effect on saplings in deciduous forests compared to mixed and coniferous forests. Conversely, sapling recovery in coniferous and mixed forests exceeded that observed in deciduous forests in 2019. The pivotal factors influencing sapling resilience to drought were forest types, soil depth, and understory vegetation, whereas litter and forest canopy cover had a negative impact.
Conclusion: Long-term responses of tree species to drought can be best discerned through continuous health monitoring. These findings demonstrate the natural regeneration potential of deciduous species in the context of climate change. Selective tree species planting, soil management practices, and promoting understory diversity should be considered when implementing adaptive management strategies to enhance forest resilience to drought events.

1. Introduction

In the summer of 2018, Central Europe was affected by one of the most severe summer droughts since the beginning of the 21st century (Büntgen et al., 2021; Ionita et al., 2021). The frequency and intensity of extreme weather events, causing drought or heavy rain, are predicted to increase in the 21st century as a consequence of decreasing temperature gradients in the Northern Hemisphere and related stable Rossby Waves (Hoegh-Guldberg et al., 2018; IPCC, 2019). In the face of global warming,

vegetation is mostly affected by drought periods, particularly if these are combined with summer heat waves, as was the case in 2018. The increase in temperature and drought frequency, intensity, and duration are affecting the productivity, dynamics, regeneration, and mortality of forest ecosystems (Ciais et al., 2005; Hacket-Pain et al., 2016; Choat et al., 2018; Senf et al., 2018; Beloiu et al., 2022a). In 2018, and partially in 2019, temperate forests across Europe experienced prolonged droughts and heat waves that caused drought-related tree mortality (Brun et al., 2020; Schuldt et al., 2020; Hari et al., 2020; Beloiu et al.,

2022b). Consequently, there is growing concern that large parts of forested areas will be affected due to the increasing frequency and intensity of extreme events (Albrich et al., 2020; Hammond et al., 2022).

Temperate forests in Europe are characterized by a low diversity of tree species (Beierkuhnlein, 2007). Productivity is limited to a short vegetation period with moderate seasonal conditions in terms of temperature and moisture. It is therefore essential to understand the effects of repeated drought on the survival and distribution of the most important species. An increase in tree mortality is observed in Central Europe in recent years (Senf et al., 2021). The summer drought of 2018 severely affected temperate forests in Central Europe (Vitasse et al., 2019; Schuldt et al., 2020). In Germany, forest covers 32% of the land area with 54% being dominated by coniferous, 31% by broadleaved and 13% by mixed forests (BMEL, 2012; Holzwarth et al., 2020). Of the coniferous forests, *Picea abies* and *Pinus sylvestris* are the most dominant species in Germany. They have been planted outside their natural range (in the lowlands) since the 18th century, where they replaced temperate broadleaved species such as *Fagus sylvatica* and *Quercus* spp. (Seim et al., 2022; Leuschner et al., 2022). Nowadays, however, these coniferous forests are severely affected by drought and subsequent bark beetle outbreaks (Seidl et al., 2016; Buras et al., 2018; Hlásny et al., 2021). Temperate broadleaved deciduous forests with natural regeneration dynamics of native tree species are expected to be more resilient to climate change. Many studies on broadleaved species focus on *F. sylvatica*, a dominant tree species in Central Europe. The 2018 drought challenged *F. sylvatica*'s resilience under climate change (Frei et al., 2022; Langer and Buβkamp, 2023), however the drivers underlying its sensitivity to drought across scales are not well known (Leuschner, 2020). Moreover, knowledge of the in-situ dynamics of native deciduous tree species populations is scarce (Beloiu et al., 2022b).

The capacity of forests to withstand a disturbance, adapt, and recover their functional capacity is a key concept in ecology and is referred to as resilience (Holling, 1973; Turner, 2010). Forest recovery specifically refers to the process of returning the forest ecosystem to a functional state, where it can provide the ecological services and functions that it provided before the damage occurred (Ingrisch and Bahn, 2018; Gessler et al., 2020). Forest resistance, on the other hand, refers to the capacity of a forest ecosystem to withstand and maintain its state and functions in the face of disturbance (Ingrisch and Bahn, 2018). Knowing which tree species are more resistant, versus those which are most affected, and how each recover from extreme droughts will help us better understand the processes that enhance forest stability and resilience. Furthermore, this plays a key role in understanding how to develop nature-based solutions to mitigate risk and prevent damages (Beierkuhnlein, 2021).

As young trees represent the potential forest of the future, the response of saplings to drought stress is important for assessing the potential for and limits to forest ecosystem adaptation (Beloiu, 2022). It is not fully understood which tree species and species assemblages are most adaptable to increasing temperatures and summer drought (McDowell et al., 2008). Numerous research employs greenhouse experiments and model simulations to investigate the sensitivity of trees to climate extremes (Schall et al., 2012; Mette et al., 2013; Buhk et al., 2016). However, it is important to consider tree response to drought under natural conditions in the field including a variety of site conditions and demographic stages, as they have a major impact on growth and survival (Gimbel et al., 2015; Beloiu et al., 2020).

Enhanced growth of understory vegetation cover in forests is often related to forest type, light availability, forest disturbances, topography, soil moisture, and nutrients. In the absence of forest encroachment, the structure and density of understory vegetation remain relatively stable over time (Cole et al., 2017). Litter cover and thickness are influenced by forest type, tree health, age, climate, and soil conditions (Dölle et al., 2017; Petritan et al., 2020). Deciduous trees produce more litter than conifers due to their annual leaf shedding, but their decomposition tends to be faster than that of conifers (Prescott et al., 2000; Barba et al., 2016). Under drought stress, litter cover can play both positive and negative

roles in tree growth and survival. On the one hand, litter cover can act as a protective layer, reducing water loss from the soil and helping to maintain soil moisture levels (Knapp and Seastedt, 1986; Deutsch et al., 2010). This can be especially beneficial during dry periods when water is scarce. On the other hand, a thick litter layer of especially deciduous trees has the potential to retain rainwater, hence limiting the water that reaches the soil and the roots (Walsh and Voigt, 1977). Understory vegetation increases soil water infiltration and reduces soil evapotranspiration (Dubbert et al., 2014). Thus, these factors, along with soil depth and water-holding capacity, influence soil drought (Miller and Poole, 1983). Even though understory vegetation and litter cover influence water availability both near the forest floor and in the topsoil, the influence of these factors on tree recovery after a drought is not known.

Here we assess the response of tree sapling species to the 2018 drought and their subsequent recovery by 2021. We evaluate the influence of soil depth, understory vegetation, litter cover, and forest cover across different forest types on recovery patterns. Tree vitality was measured in 170 forest plots in central-eastern Germany during 2018–2022. We focus mainly on deciduous tree species, as these are naturally the dominant species in the temperate biome of Central Europe and are considered more suitable in the face of climate change. Specifically, we aim to address the following questions: (i) What are the differences between tree species in terms of their resistance to and recovery from the 2018 drought? (ii) What is the influence of soil depth, litter, understory vegetation, and forest cover across deciduous, mixed, and coniferous forests on tree resistance to drought and recovery from drought? Answering these questions will allow us to better understand the link between site conditions and tree species recovery which is critical for forest regeneration and climate change adaptation.

2. Materials and methods

2.1. Study area

The study area is located in the Central Germany, spanning across the northern part of Bavaria (Fig. 1). In this area, the greatest leaf loss and crown defoliation were observed in 2019 and 2020 (StMELF, 2020). The area is dominated by deciduous, mixed, and coniferous forests. The predominant tree species in the canopy are European beech (*Fagus sylvatica* L.), pedunculate oak (*Quercus robur* L.) and sessile oak (*Quercus petraea* (Matt.) Liebl.), Norway spruce (*Picea abies* (L.) Karst.) or Scots pine (*Pinus sylvestris* L.). The petrography of the bedrock is very diverse, including clay and siltstones, limestones, as well as sandstones (Doppler et al., 2004). The diverse geological conditions result in a broad spectrum of soil types in the study area.

The climate of the study area is characterized by an annual average precipitation of 957 mm, and an annual average temperature of 7.1 °C in the period 1970–2020 (DWD, 2021a, b; Beloiu et al., 2022b). Over the past 70 years, the study region experienced a temperature increase of about 1.2 °C and a shift in the precipitation regime, with significantly less precipitation in the spring (Fig. 2a and b). Between 2017 and 2021, substantial precipitation deficits occurred repeatedly (Fig. 2c). The deficit of groundwater recharge (in the period 2011 to 2020 compared to the reference period 1971 to 2000) amounts to decreases of between 17% and 22% (LfU Bayern, 2021). Historically, the most severe droughts were recorded in 1971–1974, 2003, and 2018. However, 2018 was an extremely dry year. In 2018, the study region experienced a combination of high temperatures and low precipitation in both spring and summer. Similarly, temperature and precipitation varied greatly in 2019. The precipitation and temperature data were extracted for the study sites from the raster dataset (1 km × 1 km) of the German Meteorological Service.

2.2. Data acquisition

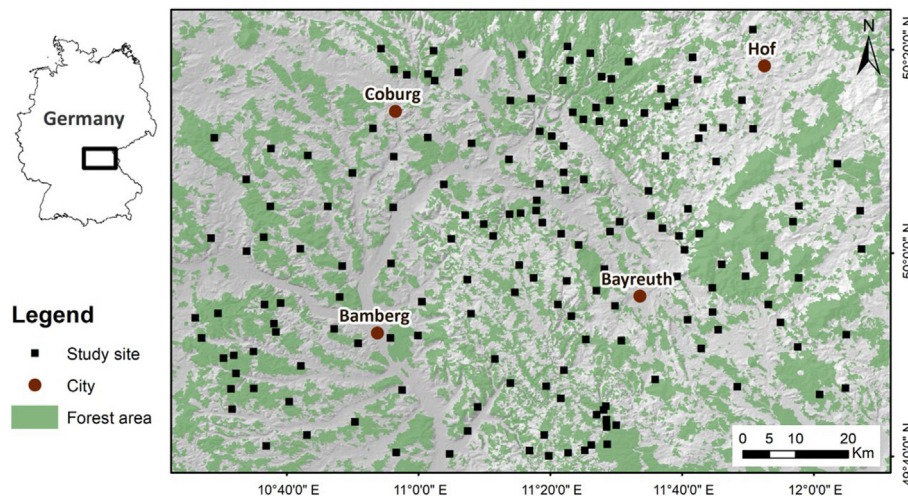Fieldwork was conducted in the years 2018, 2019, 2020, and 2021, in

Fig. 1. Overview of the study area in Upper and Lower Franconia with the 170 sample plots. Forest cover based on digital landscape model (DLM) 1:250,000 (BKG, 2019).
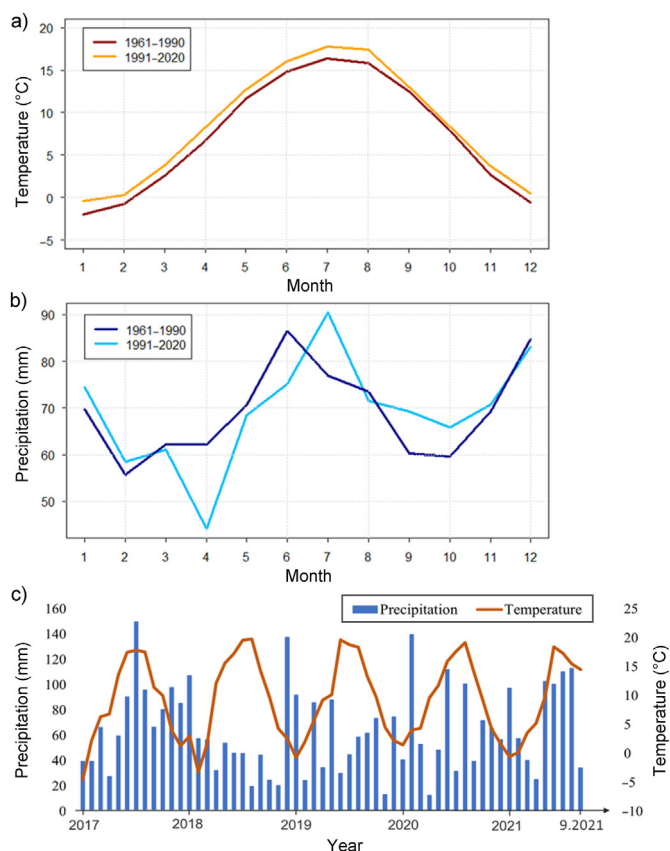

Fig. 2. Monthly precipitation and temperature patterns across the study region between the mean of the period 1961–1990 and 1991–2020 (a, b) and between January 2017 and September 2021 based on the climatic data from the German Meteorological Service (c).

late summer from August to September. During this time, 170 plots between 261 and 722 m a.s.l. were monitored. The 170 plots were distributed over an area of approximately 15,680 ha (Fig. 1). During the first data collection, at each plot, 10 young trees were marked (at least 1.3 m tall and DBH <10 cm) within a randomly selected area of 100 m^2 (Beloiu, 2022). In total, data were collected from 1,531 saplings. Tree vitality was recorded annually and assigned to a vitality class, and

thereby assessed in terms of crown defoliation, as this is a visible indicator of drought stress. A total of 40 tree species were tagged, and individual statistics were performed using only the seven species with the highest sample size ($n > 50$). Thus, after data cleaning, i.e., removing the damaged or not re-found saplings, a total of 1,483 saplings were considered for analysis. Table 1 lists the species studied, their abundance, and their vitality during the study years.

The species considered for the study represent widely distributed species in the study area and the species with the largest sample sizes. The species are sycamore maple (*Acer pseudoplatanus* L.), a widely distributed species, and *F. sylvatica*, the dominant species in Central Europe under natural conditions, which are both considered drought sensitive (Leuschner et al., 2001; San-Miguel-Ayanz et al., 2016). The others are mountain ash (*Sorbus aucuparia* L.) and silver birch (*Betula pendula* Roth.), as two pioneer tree species, common hornbeam (*Carpinus betulus* L.), whose distribution is limited by high summer temperatures, common hazel (*Corylus avellana* L.), which is adapted to warm climates (San-Miguel-Ayanz et al., 2016), and *Quercus* spp., which are considered to be drought tolerant (Härdtle et al., 2013). The two oak species *Q. petraea* and *Q. robur* were recorded separately but grouped under *Quercus* spp., as their characteristics show great plasticity and hybrid forms arise (Aas, 1991; Jensen et al., 2008).

The vitality classes are defined as follows: 1 = undamaged: no leaves are damaged by drought or show significant color changes; 2 = partially damaged: individual damaged leaves and branches of the young trees; but most of the leaves are undamaged; 3 = completely damaged: all leaves and branches of the plant show drought damage, this class includes specimens that died during or after the drought.

The cover of understory vegetation, litter, and bare soil was recorded as a percentage for the 10 m × 10 m plot area in the summer of 2020 (area fraction of litter, bare soil, and understory vegetation, respectively together summed to 100%). The percentage of these site-specific factors is an indicator of site microclimate and could influence species recovery in 2021. About 1–2 years following the drought, the die-off leaf mass decomposes and returns to normal levels (Prescott et al., 2000; Jacob et al., 2009). Hence, these measurements were done in the third year after the drought to avoid the potential impact of the 2018 drought on understory vegetation and litter cover. The understory vegetation is defined here by the herbaceous layer with forbs, ferns, non-grasses herbaceous species, and small shrubs from the family of *Rosa* spp. and *Rubus* spp., excluding tree saplings (Dölle et al., 2017). Besides mosses and ferns, a total of 41 plant families were represented within the plots. Forest canopy cover was recorded in percentage for each plot and the forest type (deciduous, coniferous and mixed) was determined.

Table 1
Number of saplings in each vitality class per year. No., the total number of tree saplings. Vitality classes: 1 = undamaged; 2 = partially damaged; 3 = completely damaged.

Tree species	No.	Vitality 2018			Vitality 2019			Vitality 2020			Vitality 2021		
		1	2	3	1	2	3	1	2	3	1	2	3
Fagus sylvatica	550	260	235	55	445	82	23	451	63	36	435	67	48
Sorbus aucuparia	161	13	86	62	112	31	18	59	72	30	54	68	39
Carpinus betulus	123	19	87	17	101	14	8	85	28	10	97	14	12
Betula pendula	84	34	47	3	65	17	2	68	12	4	60	20	4
Acer pseudoplatanus	81	31	41	9	70	6	5	64	13	4	55	19	7
Corylus avellana	81	28	46	7	65	13	3	63	16	2	68	9	4
Quercus spp.	69	24	43	2	47	20	2	54	13	2	36	30	3
Other species	334	114	178	42	222	89	23	228	75	31	192	101	41
Total	1483	523	763	197	1127	272	84	1072	292	119	997	328	158

Soil depth (horizon O, A and B in cm) defines the depth from the topsoil profile to the weathered bedrock and the depth of the loose material to which the roots can easily penetrate. The Pürckhauer gouge auger was used to determine the thickness of the soil.

2.3. Data analysis

The ability to recover after the severe 2018 drought of each tree species is expressed by the Recovery Index (RI) (Lloret et al., 2011). Recovery is estimated as the reverse ratio of vitality after and during the 2018 drought. The RI was calculated for the studied years, i.e. 2018 to 2019 and 2018 to 2021. This resulted in three recovery classes (RI classes) with values 0, 1, and 2, namely RI-0, RI-1, and RI-2. RI-0 implies an incomplete recovery in sapling performance and a decrease in vitality after the drought event; RI-1 implies a consistent vitality over the respective period; and RI-2 indicates that the performance of the respective tree species following drought is better in comparison to the drought period 2018 and thus that the species has improved its vitality. To statistically assess the drivers of recovery, ordinal logistic regression models from MASS package (Ripley, 2023) were used, where the response variable was sapling recovery from 2018 to 2019 and the explanatory variables were litter cover, understory vegetation cover, soil depth, forest type and forest canopy cover.

Changes in sapling vitality between the years and between vitality classes were assessed using Fischer's exact test for count data and pairwise comparison (Fisher, 1934; Herve, 2023). To test the normality of the data distribution, the Shapiro-Wilk test was used. The influence of the environmental factors considered on recovery was examined using the Kruskal-Wallis test. Dunn's test for multiple comparisons was performed as a post hoc test (p-values were adjusted with the Bonferroni method) to determine the significantly different groups. The considered parameters were litter, understory vegetation, and soil depth. For all statistical calculations, the software RStudio (version 4.1.0), with additional packages FSA, RVAideMemoire (Herve, 2023), rcompanion (Mangiafico, 2019), ggpubr, psych, ggplot2, and car, was used.

3. Results

3.1. Sapling's resistance and recovery patterns

The vitality of most tree species has significantly increased after the 2018 drought – showing a general recovery. Nevertheless, a significant but slow delayed decline in vitality was observed from 2019 to 2020, while vitality remained the same between 2020 and 2021 (Fig. 3). During the 2018 drought, out of a total of 1,483 saplings, only 35% showed strong resistance to drought, whereas 52% of all specimens were partially damaged and 13% were completely damaged (Fig. 3). One year later, in 2019, 34% of the partially damaged and 7% of the completely damaged saplings recovered. In the following years, 2020 and 2021, >70% of the saplings maintained their high vitality. However, from 2019 to 2021, the percentage of partially and completely damaged saplings increased by
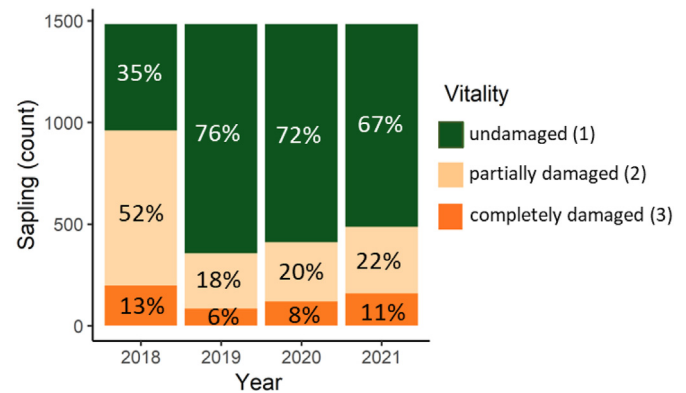

Fig. 3. Vitality of tree saplings from 2018 to 2021 and their percentage per class.

4% and 5%, respectively (Fig. 3). The change within the vitality classes between the study years was significant (Fig. 4a).

3.2. Species-specific patterns

Out of the seven species studied, *F. sylvatica* showed the highest resistance to the 2018 drought (47% of saplings undamaged), followed by *B. pendula* (40%), *A. pseudoplatanus* (38%), *Quercus* spp. (35%), *C. avellana* (35%), and *C. betulus* (15%) and *S. aucuparia* (8%) (Fig. 4b–h). *Fagus sylvatica* showed a significant recovery from summer 2018 to summer 2019 and maintenance of this condition in the following years (Fig. 4b). Similarly, the other species, *B. pendula*, *A. pseudoplatanus*, *Quercus* spp., and *C. avellana*, had a high recovery from 2018 to 2019 and rather stable maintenance of their vitality over the next years (Fig. 4c–f). However, during summer of 2021, *A. pseudoplatanus*, and *Quercus* spp. recorded decreasing vitality compared to 2020 ($p < 0.05$). *Carpinus betulus* showed low resistance in 2018, but 80% of saplings recovered in 2019 and maintained their vitality over the years (Fig. 4g). In contrast, the pioneer species *S. aucuparia* showed the lowest resistance in 2018, followed by a strong recovery in 2019 and a sharp decline in vitality in 2020 and 2021 (Fig. 4h).

3.3. Drivers of sapling recovery

Generally, saplings maintained their vitality when grew on deeper soils ($p < 0.05$; Fig. 5a). Coniferous forests had significantly deeper soils than deciduous or mixed forests (Appendix A, Fig. S1c). Saplings recovered well on shallow soils, but there were also saplings that did not recover on either soil depth, with the pattern tending towards shallow soils (Fig. 5b). The significance of the relationship between soil depth and sapling recovery was mainly determined by plots with *F. sylvatica* ($p < 0.001$), with some patterns present for the other species but not significant ($p < 0.05$).
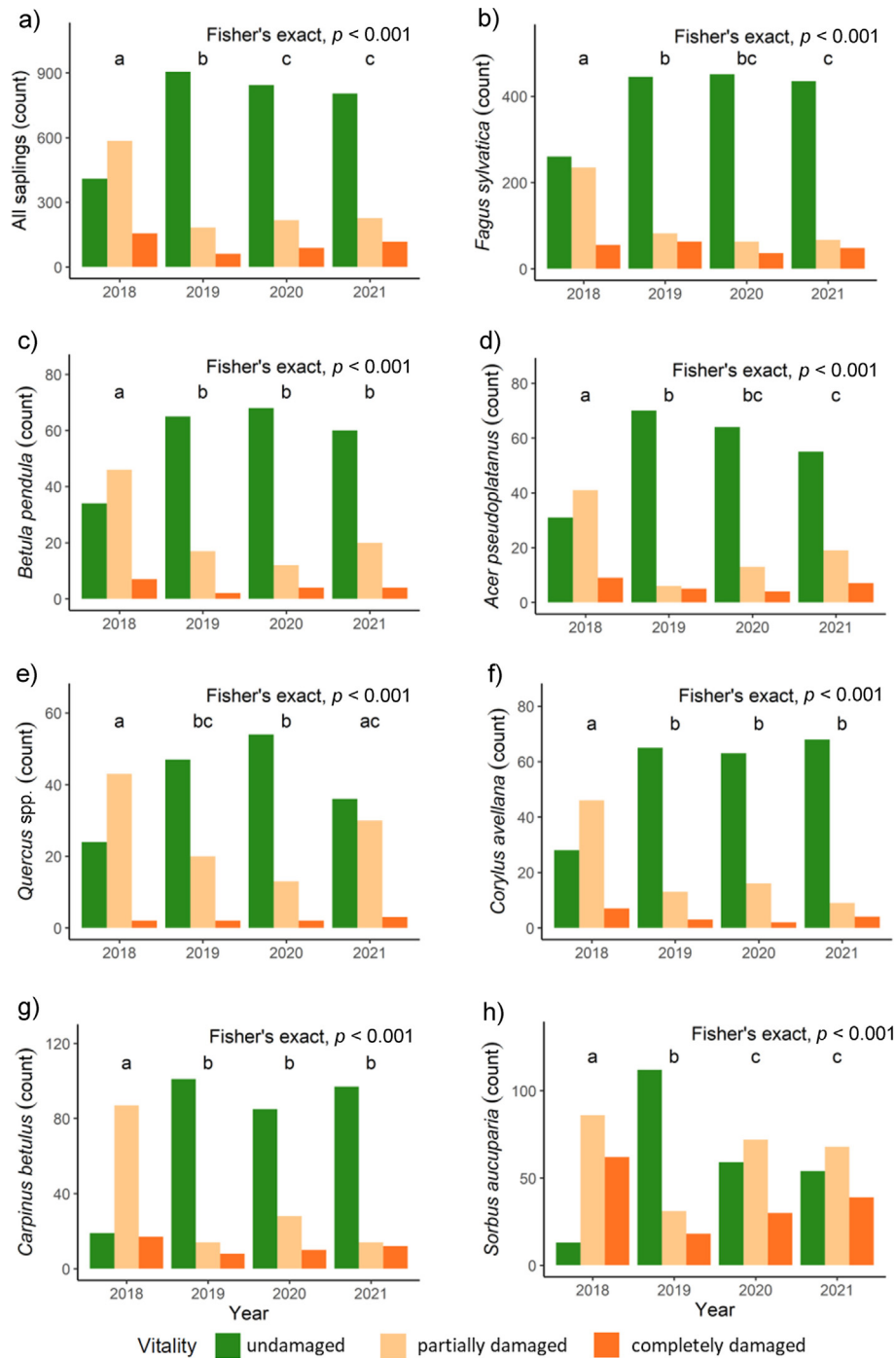
Fig. 4. Vitality status of the tree species' saplings during and after the 2018 drought in the years 2019, 2020, and 2021. Letters in the figures indicate significant differences between groups based on Fisher's exact test.

Tree saplings growing at sites with high litter and low understory vegetation cover were most affected by drought in 2018, and they recovered better in sites with understory vegetation cover that was higher than litter cover (Fig. 6a and b and Appendix B, Models 1 and 2). Specifically, the recovery of *F. sylvatica*, *C. betulus*, and *A. pseudoplatanus* after the drought was significantly influenced by understory vegetation (i.e. the herbaceous layer formed mainly by forbs and grasses, excluding tree saplings) and litter cover (Fig. 6a–c), but no influence was found for the other species, *B. pendula*, *Quercus* spp., *C. avellana* and *S. aucuparia* ($p >$ 0.05). We found no significant correlation between soil depth, precipitation, and understory vegetation, as well as between temperature and litter cover ($p > 0.05$). *Fagus sylvatica* saplings were more resilient and

recovered at sites with low litter but high vegetation cover ($p < 0.0001$) (Fig. 6d and e), but failed to recover at sites with high litter and low understory vegetation (Fig. 6f). *Acer pseudoplatanus* saplings preserved their vitality from 2018 to 2021 in sites with low litter cover and high vegetation cover (Fig. 6g–i). At sites with high litter and low vegetation cover, part of the *A. pseudoplatanus* saplings either did not recover at all or others recovered significantly. Hence, saplings at sites with high litter and low vegetation cover were most affected by drought in 2018. *Carpinus betulus* recovered better after the drought in sites with less litter cover and more vegetation cover (Fig. 6j and k). However, sites with low litter and low understory vegetation cover presented both saplings that maintained vitality and saplings that were damaged but did not recover (Fig. 6l).
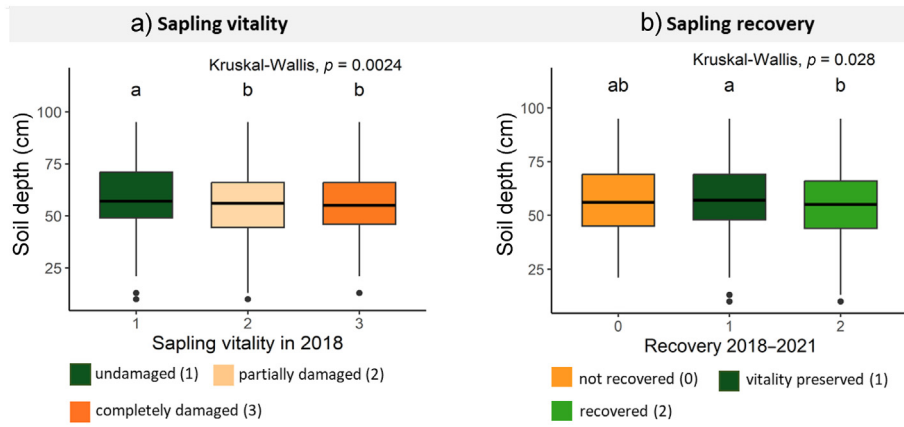
Fig. 5. (**a**) Vitality of tree saplings in 2018 and (**b**) recovery of tree saplings from 2018 to 2021 as a function of soil depth.
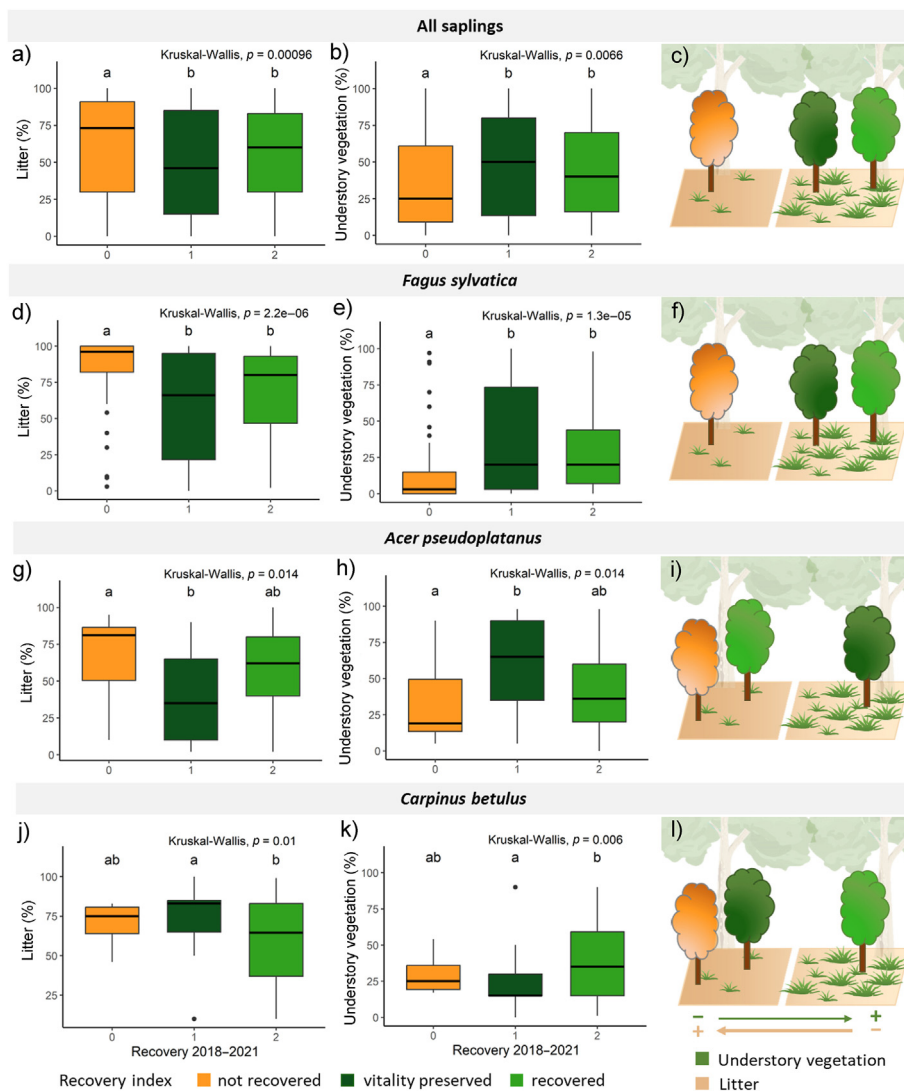

Fig. 6. Differences in recovery from 2018 to 2021 given the litter and understory vegetation (i.e. ground layer vegetation) for all species and for *Fagus sylvatica*, *Acer pseudoplatanus*, *Carpinus betulus*; illustration of tree sapling recovery on sites with low (−) vegetation and (+) high litter and sites with high (+) vegetation and (−) low litter cover according to the statistical analysis.

In addition, litter and understory vegetation cover showed clear patterns depending on the forest type. Litter cover, for example, increases from coniferous to mixed and deciduous forests, while understory vegetation cover and soil depth decrease (Appendix A, Fig. S1a, b, c). The 2018 summer drought had a greater impact on saplings in deciduous forests than on mixed and coniferous forests. Sapling recovery was higher

in mixed and coniferous forests than in deciduous forests. Further, saplings growing in sites with high forest canopy cover had also reduced recovery compared to saplings growing in sites with low forest canopy cover (Appendix B, Models 3 and 4).

4. Discussion

4.1. Sapling resistance and recovery from the 2018 drought

During the 2018 drought summer, considerable drought stress damage was observed across many forests in Central Europe (Schuldt et al., 2020). In this study, we assessed (1) the resistance and recovery of tree saplings growing in temperate forests during and after the 2018 summer drought and (2) the influence of soil depth, understory vegetation, and litter cover on sapling recovery. Our results show that 64% of all monitored tree saplings exhibited damage during 2018 summer. Nevertheless, by late summer 2019, the majority of saplings in each species had recovered (with only 21% still displaying damage).

From 2019 to 2020, sapling vitality did not change substantially, except for *S. aucuparia*, which rapidly deteriorated in its vitality within one year. This species has an especially shallow root system, which therefore might benefit earliest from percolating rainwater. However, no such benefit was evident after 2019. The rainy growing season of 2021 thus did not have a significant positive effect on tree recovery visible in late summer 2021. This could be explained by the fact that, during the dry period from 2018 to 2020, tree species mainly invested in their belowground root biomass to increase water availability, which is why they showed more drought stress-induced damage aboveground, such as biomass shedding (Pretzsch et al., 2013). Furthermore, another study on mature trees showed increasing growth 1–5 years after the precipitation year (Jiang et al., 2019), while another one showed delayed consequences of drought, such as reduced growth and incomplete recovery for 3–4 years after severe drought (Anderegg et al., 2015).

Further monitoring and the comparison of these results with results across different forest ecosystems could provide us a more general picture of the trends in saplings recovery subsequent drought stress under natural conditions. In this context, assessing forest responses to extreme climate events should be integrated into a forest monitoring network in order to allow continuous and comparable measurements between different forest ecosystems and across time (Zweifel et al., 2023). Moreover, more automatic approaches, should be considered for quantitative assessments of tree species health over larger areas (Kälin et al., 2019; Sandric et al., 2022; Beloiu et al., 2023).

The two species *C. betulus* and *C. avellana* seem to have benefited directly from the higher precipitation in 2021. Similarities exist concerning their root system, which is medium-deep rooted (Kutschera and Lichtenegger, 2002). Further, the recovery of tree species should not be considered in a generalizing manner, but rather as a function of the site and environmental conditions. Also, the performance over the years varies greatly between species, but also between individuals within a species. Although many studies attribute high drought sensitivity to *F. sylvatica* (Durrant et al., 2016; Martinez del Castillo et al., 2022), saplings in the study area have shown high resilience to drought.

4.2. Drivers of sapling recovery

Soil depth showed to be an important indicator of sapling resilience to drought, particularly for *F. sylvatica*, as it influences the availability of water and nutrients for plant roots (Miller and Poole, 1983). However, saplings growing in shallower soils recovered well after the 2018 drought stress. In general, deeper soils can store more water and nutrients, providing a buffer against drought stress. Further, coniferous forests with high understory vegetation are an indicator of more resilient forest sites compared to deciduous forests with high litter cover. In a previous study, Beloiu et al. (2020) showed that saplings with a larger diameter at breast height (dbh) and saplings growing in sites with a larger tree canopy cover

were less resistant to drought. The high percentage of sapling recovery after the 2018 drought can be also explained by the increasing precipitation in spring 2019 (Fig. 2c) (Beloiu et al., 2022b). High recovery was possible even on shallow soils as a result of the sapling's capacity to take up water from the uppermost soil layer (Gessler et al., 2022). Other studies on mature trees and seedlings have shown a strong tree growth increase after drought events particularly for trees severely impacted (Pretzsch et al., 2013; Kunz et al., 2016).

4.2.1. Fagus sylvatica and Carpinus betulus recovery

Fagus sylvatica and *C. betulus* recovered better from the 2018 drought when there was both less litter cover and more understory vegetation at their site. First, this shows a correlation between damaged trees and high litter on the forest floor, confirming that leaf litter is a serious sign of drought stress. *F. sylvatica*, in turn, contributes to a widespread litter accumulation by an above-average litter production (about 900 g•cm^{-2} litter per year) (Kutschera and Lichtenegger, 2002). The forest type and thus the origin of leaf biomass on the forest floor had a significant impact on the recovery of the saplings, as coniferous and deciduous trees have different decomposition rates and water retention.

Even in the same environment, tree species have diverse root adaptations to cope with the stress imposed by drought (Maseda and Fernandez, 2006; Lübbe et al., 2017). Although it has been demonstrated that *F. sylvatica* and *A. pseudoplatanus* expand their water intake deeper as the soil dries up, the primary water uptake zone is just the top 0–0.7 m (Brinkmann et al., 2019). Another study revealed that *F. sylvatica* saplings used more than 50% of their water from the uppermost 5 cm soil layer at the beginning of the 2018 drought (Gessler et al., 2022). The deep-rooted *Q. petraea* preferentially takes up water from deeper soil layers most of the time, but shifts its water uptake to the percolated topsoil in response to rain. Whereas *F. sylvatica* takes up water from both the upper and deeper parts of the soil before, during, and after the precipitation event (Volkmann et al., 2016), using more than half of the precipitation that fell during the current growing season (Brinkmann et al., 2018). To quickly absorb rainwater, *F. sylvatica* concentrates its water intake on the top soil, especially during drought conditions.

When the plot area has a high litter cover, it indicates that the humus forest soil is overlain by an additional layer through which rainwater must percolate before it reaches the topsoil, and thus the main root mass of *F. sylvatica*. On the one hand, this additional percolation duration represents time, especially under summer temperatures when much of the water is at risk of evaporating and is thus unable to reach the soil and roots. Walsh and Voight (1977), for example, showed that up to 25% of the rainwater from a low-intensity precipitation event can be completely retained by the soil through a thick layer of *F. sylvatica* leaves. As a result, a high litter cover, as is the case in deciduous forests, has negative effects due to water retention during precipitation events. In the situation of severe water shortage, as was the case from 2018 to 2020, the litter layer could determine the severity of tree damage and explain the significant differences among recovery classes. On the other hand, exposed soil (without litter cover) also means a higher risk of desiccation, allowing more direct evaporation from the upper substrate, but this was not the case in our study.

More understory vegetation can contribute to a wetter microclimate near the soil as this layer of vegetation can serve as an evaporation barrier or shade provider just above the soil. Experiments concluded that the understory vegetation layer inhibits soil evapotranspiration and does not reduce the water-use efficiency of deciduous forests, even when evapotranspiration is high (Dubbert et al., 2015). For this reason, *F. sylvatica* may have recovered significantly better in areas with more understory vegetation, consistent with its stable performance at the highest vegetation cover (Fig. 5). Thus, the species may be more dependent on the support of a moist-cool microclimate near the ground when water is scarce due to evaporation from the topsoil.

The differences between RI classes are less significant for *C. betulus* than for *F. sylvatica*. Compared to *F. sylvatica*, *C. betulus* vitality remained

the same in sites with high litter cover and low understory vegetation. Therefore, litter cover did not have a drastically negative effect on the performance of *C. betulus*. While litter cover can limit water percolation, it can also shade the soil, making the tree reliant on previous groundwater. *Carpinus betulus* does not differ from *F. sylvatica* in many characteristics on the surface, but there is a clear difference in terms of understory morphology: *C. betulus* roots deeper than *F. sylvatica* (Köstler et al., 1968; Warda, 1998). Especially at a young age (up to 15 years), the considerable depth development of its taproot is striking, so that with a little dense substrate, depths of 1.2–1.3 m can be reached early (Gulder, 1996). Thus, unlike *F. sylvatica*, it can generally draw water from deeper soil layers and rely less on percolating rainwater. This would be accompanied by the fact that a higher litter layer has a stabilizing effect on the vitality of *C. betulus*, whereas the vitality of *F. sylvatica* deteriorates with a higher one – *C. betulus* is not primarily dependent on percolating water in the topsoil and may instead benefit from the moisture-retaining effect of a litter layer.

4.2.2. Acer pseudoplatanus recovery

The isohydric species *A. pseudoplatanus* may benefit from additional nutrients from litter during drought (Pretzsch et al., 2012). However, the species showed more resistance with less litter cover. There are currently still some gaps in our knowledge about the exact nature of the root system of *A. pseudoplatanus*. A field study in the Franconian Forest, which is part of the study area, found the largest root proportion in the uppermost humic soil layers, but surprisingly high root depths were also observed (Nordmann, 2009). Kutschera and Lichtenegger (2002) also clearly attribute the largest proportion of its root mass to the upper soil layers. Furthermore, they state that it has the requirement of a balanced water supply, which is why very permeable soils should be saturated, at least in the deeper root zone. The problem is that groundwater levels have been falling constantly throughout Bavaria for several years, and lower soil layers thus tend to be less saturated with water. Because of this, it would make sense to focus root development on the upper soil. It is well known that *A. pseudoplatanus* responds to water deficiency by forming a very shallow and extraordinarily intensely branched root system (Dahmer, 1997; Jensen et al., 2008). Like *F. sylvatica*, when the soil dries out, the area largely used for water uptake is limited to the upper 0–0.7 m (Brinkmann et al., 2019). *A. pseudoplatanus* may therefore rely more on percolating rainwater instead of subsoil water.

Similar to *F. sylvatica*, the significant vitality deterioration of *A. pseudoplatanus* saplings on sites with less understory vegetation could be due to the degree of moisture and coolness removed from the topsoil by low litter cover being compensated by a higher cover of understory vegetation. In addition, understory vegetation can have a positive effect on the rootability of the soil (Chen et al., 2004). One of the few site criteria for *A. pseudoplatanus* to grow is that the soil be adequately rootable (Nordmann, 2009). While the extensive occurrence of certain grass species has often been associated with the poorer performance of tree species, the positive effects of a nitrate flora on its growth have been emphasized (Jensen et al., 2008). Our results showed that *A. pseudoplatanus* saplings that grew on sites with more understory vegetation were more damaged by the drought, possibly due to competition for resources, but also recovered better after the drought.

5. Conclusions

The 2018 drought was characterized by higher temperatures and significantly lower precipitation, which affected tree species across Central Europe. Our results showed that *F. sylvatica* had the highest resistance to drought, followed by *B. pendula*, *A. pseudoplatanus*, *Quercus* spp., *C. avellana*, *C. betulus*, and *S. aucuparia*. This information can be valuable for forest managers when selecting tree species for reforestation or afforestation projects in areas prone to drought. Generally, the deciduous tree species studied had high recovery capacity: despite being affected by the severe drought of 2018, they demonstrated the capacity

to recover in 2019. The microclimate favoured by the local synergies between forest types (coniferous and mixed), soil depth and understorey vegetation, was most favourable for the resistance of the saplings and their recovery from drought. This finding highlights the resilience of deciduous tree species in response to extreme weather events, which is important to consider in forest management and conservation planning. Tree saplings growing in sites with deeper soils and more understory vegetation were more resistant to drought than those growing in sites with more litter cover.

The slight decrease in vitality observed in several species by 2021, despite recovery from the 2018 drought, emphasizes the need for long-term monitoring of forest ecosystems. Continuously tracking the health of tree species can provide valuable insights into their long-term response to drought and other stressors. These findings can guide researchers and forest practitioners in implementing adaptive management strategies to enhance forest resilience to drought events. This may include selective tree species planting, soil management practices, and promoting understory vegetation to support tree health and survival during extreme climate events. Understanding how temperate deciduous tree species recover from drought stress is important for maintaining forest functions and adapting temperate forests to climate change.

Data availability

The data used are already published on the TRY database (www .try-db.org) and by Beloiu et al. (2022) in the supplementary materials.

Authors' contributions

Mirela Beloiu: Conceptualization, Data acquisition, Investigation, Methodology, Visualization, Writing – Original Draft; Valeska Schönlau: Conceptualization, Data acquisition, Methodology, Formal analysis, Writing – Original Draft; Carl Beierkuhnlein: Conceptualization, Data acquisition, Supervision, Writing – Review & Editing.

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.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://do i.org/10.1016/j.fecs.2023.100140.

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