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Structural reorganization in beech forests in central Germany as response to drought-induced mortality in the overstory

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ABSTRACT

Prolonged periods of extreme heat and drought are changing forest health and forest structure. Loss of vitality, signs of dieback, and mortality of trees are reported in many regions of the world. There is a need for information on the quantification of drought effects on forest structure in order to detect drought stress at an early stage. Furthermore, forest structure is linked to growth processes that result from single tree and stand dynamics. In this study, we used mobile laser scanning to objectively assess forest structure in European beech (*Fagus sylvatica* L.) stands differently affected by drought. We used the box-dimension as a holistic measure of structural complexity that jointly describes both distribution and amount of plant material in a forest, and canopy cover as a measure for overall defoliation. We observed large canopy gaps in heavily damaged stands, but the overall structural complexity of the forest stands remained unchanged. However, when dividing the 3D forest stand model from mobile laser scanning into 5 m height layers, we noticed a "structural flip" with reduced structural complexity in the upper parts of the forests and increased structural complexity in the lower strata. This indicates that the forests are responding to drought with increased mortality of mature trees, resulting in increased light availability in the understory and consequently increased growth of the understory trees. The rather indifferent overall structural complexity of the investigated forests was due to the reorganization of structures by shifting the major foliage layer from top-to-bottom and is interpreted as a successful ecosystem-scale response to the drought events. However, it is unclear how these forests will respond to repeated droughts. The "structural flip" should therefore be regarded as an early warning signal pointing to increased ecosystem stress, though the stress level has not yet exceeded the adaptive capacity in the investigated forest.

Introduction

The extreme drought, heat, and precipitation deficits of the last few years had a serious impact on forests and have led to increasing tree mortality and forest dieback in many regions around the world (Allen et al., 2010; Schuldt et al., 2020; Hartmann et al., 2022). In this context, native tree species are affected to varying degrees. In Germany, for example, the mortality rate of all tree species combined increased from 0.20 % in 2018 to 1.73 % in 2020, and for Norway spruce (*Picea abies* (L.) H.Karst) even from 0.15 % to 4.28 % (2018–2020) (BMEL, 2023). However, not only Norway spruce, which was cultivated outside its natural range, is suffering and dying as a result of drought and subsequent bark beetle infestation (Netherer et al., 2021). Also, European beech (*Fagus sylvatica* L.), which would naturally dominate large parts of the forests of Central Europe (Ellenberg and Leuschner, 2010), is suffering greatly from the series of very dry and hot years (Walthert et al., 2021). In many places, it shows significant losses in vitality and even signs of dieback (Langer and Bußkamp 2023). The damage can mainly be attributed to beech vitality loss, a complex disease of European beech that can occur as a result of precipitation deficits combined with high temperatures and high solar radiation intensities (Tropf et al., 2022). Beech vitality loss can be characterized by a significant reduction in vitality, sparse and small-leafed foliage, loss of fine branches, crown defoliation, as well as infestation with fungi and beetles (Brück-Dyckhoff et al., 2019; Langer, 2019). Looking at the degree of crown defoliation, the vitality loss of European beech becomes evident: the proportion of significant crown defoliation (across all age classes) of European beech in Germany increased from 39 % (2018) to 47 % (2019) and then to 55 % (2020) (BMEL, 2023). This shows that the ongoing climatic changes affect tree vitality and are thus directly affecting tree

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growth, mortality rates (Allen et al., 2010), and forest structure.

Following Gadow et al. (2012), the structure of forests describes the distribution of tree attributes within a forest ecosystem. McElhinny et al. (2005) further defined forest stand structure including two components: stand structural attributes (abundance, relative abundance, richness, size variation, spatial variation) and stand structural complexity. Stand structural complexity in turn can be defined as all dimensional, architectural, and distributional patterns of plant individuals and their organs in a given space at a given point in time (McElhinny, 2002; Seidel et al., 2020; Seidel and Ammer, 2023). In the past, tree attributes were mostly assessed manually, which required a considerable amount of time and personnel resources. At present, an assessment of tree attributes and a quantification of forest structural complexity is possible in a very detailed, objective, and efficient manner based on light detection and ranging (LiDAR) technology (e.g., Atkins et al., 2018). As a result, indices summarizing the overall structural complexity of forests were developed, such as the stand structural complexity index (Ehbrecht et al., 2021), canopy rugosity (e.g., Atkins et al., 2018), or the box-dimension (e.g., Seidel, 2018; Seidel et al., 2019; Heidenreich and Seidel, 2022). Compared to previous approaches, these aforementioned, more holistic, indices differ fundamentally. They are not based on assessing individual tree attributes but instead quantify structural complexity based on the actual distribution of all plant elements in a forest.

In this study, we assessed and evaluated forest structural complexity based on fractal analysis using the box-dimension (D_b) derived from mobile laser scanning. This solely mathematical approach can be used to objectively monitor a forest's status quo and development with respect to structural complexity (Heidenreich and Seidel, 2022; Neudam et al., 2022; Seidel and Ammer, 2023). Hereby, growth processes and tree vitality which are influenced by resource availability and competition, but also by abiotic and biotic disturbances, can be captured. In addition, we used canopy cover to quantify potential defoliation, which is a common indicator for stand-level health (BMEL, 2023). Since beech continues to be of high importance in current and future silvicultural measures in Germany (Ammer et al., 2005), we addressed the question whether beech forests in central Germany are undergoing structural changes in response to the recently observed drought-induced decline in vitality.

Material and methods

Study sites and study objects

The study sites for this investigation were located in Germany and distributed over the three federal states of Hesse, Lower Saxony, and Thuringia (see Table 1). In each state, eight study sites with a size of 0.25 ha and with varying degrees of drought damage were selected, resulting in a total of 24 study sites. The selection of the study sites was based on the following criteria: no extreme site conditions for European beech (e.g., alternating moisture, waterlogging, block overstory, steep slopes), minimum proportion of admixed tree species, at least 20 mature trees per study site, site elevation $<$ 500 m above sea level, and possibility to classify the stands at each site into one of four drought damage categories: healthy, slightly damaged, damaged, and heavily damaged. This classification was based on expert opinions in cooperation with the Northwest German Forest Research Institute (NW-FVA) according to the assessment procedure for the Forest Status Report (BMEL, 2023) as well as the ICP-Forest visual assessment of crown condition (Eichhorn et al. 2016). Each category was replicated twice in each federal state. We consider the different drought damage levels selected here as a space-for-time substitution approach.

Using the hand-held ZEB Horizon (GeoSLAM Ltd., Nottingham, United Kingdom) mobile laser scanner with simultaneous localization and mapping (SLAM), all study sites were scanned in summer 2022 during the months of June to September. Each scan was started at one corner point of a study site, followed by successive walks around the remaining corner points. Thereby, the walking pattern overlapped the edge of the study site so that the boundaries of the site coincided with the trajectory of the scan. After that, the study site was walked in serpentine lines and crossed diagonally to capture as much forest structure as possible. Finally, a scan was terminated at the starting point (see Fig. 1) to create a closed loop.

Point cloud processing MLS

The acquired three-dimensional point clouds from the mobile laser scanning were automatically processed and exported (LAZ files) using GeoSLAM Hub 6.2.1 (GeoSLAM Ltd., Nottingham, United Kingdom). The point clouds were subsampled, noise filtered, and cut to a size of 50 m x 50 m using Cloud Compare (version 2.11.3, www.danielgm.net).

Table 1
Basic description of the investigated study sites (plot).

Plot	State	GPS-coordinates	Drought damage	Age	Altitude [a.s.l.] [m]	Mean height dominant trees [m]	Mean basal area [m^2/ha]
1	Hesse	N51° 31.957′ E9° 34.871′	slightly damaged	131	297	34.72	8.95
2	Hesse	N51° 04.764′ E8° 43.732′	heavily damaged	135	430	29.64	5.33
3	Hesse	N50° 26.368′ E9° 06.160′	heavily damaged	167	296	38.39	12.51
4	Hesse	N51° 18.102′ E9° 52.550′	damaged	142	359	42.25	10.20
5	Hesse	N50° 58.166′ E9° 01.431′	damaged	137	387	42.01	9.56
6	Hesse	N50° 56.967′ E9° 07.339′	undamaged	112	394	36.61	13.67
7	Hesse	N51° 11.703′ E9° 33.909′	undamaged	89	365	36.28	11.85
8	Hesse	N50° 56.627′ E9° 19.228′	slightly damaged	139	360	38.13	11.59
9	Lower Saxony	N51° 24.894′ E9° 46.752′	heavily damaged	111	421	30.03	8.25
10	Lower Saxony	N51° 24.493′ E9° 47.054′	heavily damaged	103	352	34.85	7.74
11	Lower Saxony	N51° 29.166′ E9° 42.222′	damaged	122	255	35.96	6.35
12	Lower Saxony	N52° 10.834′ E9° 20.604′	slightly damaged	130	212	38.76	9.02
13	Lower Saxony	N52° 14.203′ E9° 19.038′	damaged	154	232	37.08	13.81
14	Lower Saxony	N52° 14.537′ E9° 19.626′	slightly damaged	67	181	38.96	14.11
15	Lower Saxony	N52° 47.695′ E8° 59.234′	undamaged	114	61	34.10	9.74
16	Lower Saxony	N52° 14.499′ E9° 7.682′	undamaged	79	202	27.21	11.33
17	Thuringia	N51° 20.164′ E10° 21.256′	slightly damaged	123	412	38.93	10.54
18	Thuringia	N51° 22.058′ E10° 14.835′	undamaged	92	496	34.59	13.49
19	Thuringia	N50° 55.731′ E10° 19.130′	damaged	100	467	29.38	12.10
20	Thuringia	N50° 31.696′ E11° 18.113′	damaged	199	543	36.21	13.86
21	Thuringia	N50° 52.743′ E12° 3.471′	slightly damaged	156	273	38.06	10.43
22	Thuringia	N50° 59.867′ E11° 44.080′	heavily damaged	101	303	37.65	14.28
23	Thuringia	N51° 1.309′ E11° 17.061′	undamaged	138	378	37.37	17.40
24	Thuringia	N51° 21.908′ E10°35.589′	heavily damaged	184	424	36.00	7.83

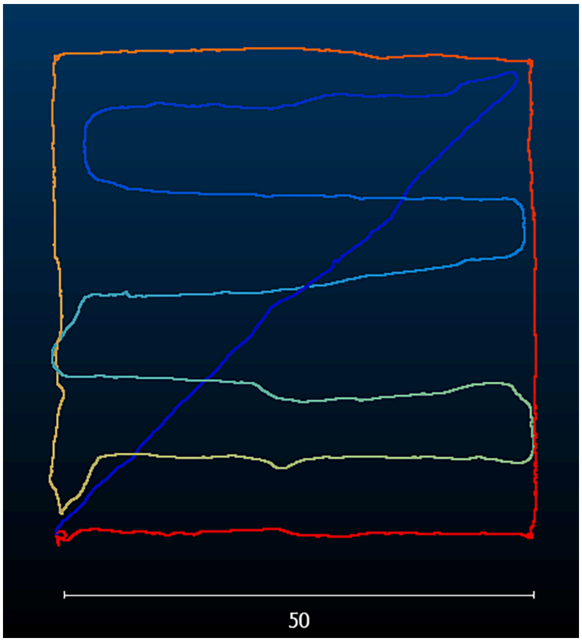

Fig. 1. Exemplary walking pattern of a study site (top view).

Terrain normalization with ground points was conducted using LIDAR 360′s (version 4.1, GreenValley International Ltd., California, USA) function "normalize by ground points". The measures canopy cover and box-dimension (D_b) were calculated using Mathematica (Version 12, Wolfram Research, Champaign, Illinois, USA). Canopy cover was determined after applying a 20 cm- voxelization to the point clouds (20×20×20 cm voxel model) and was defined as the percentage of 20×20 cm ground cells with one or more voxels above (same x-y- cell). The box-dimension, as a proxy for the stand structural complexity of the stands, was determined as outlined in Seidel (2018). In short, the forest point cloud was converted into voxel models of varying resolution, from 20 cm (lower cut-off) to a single voxel enclosing the entire forest patch (upper cut-off). Then, the logarithm of the voxel sizes (expressed in relation to the largest box) and the logarithm of the number of voxels needed to enclose all forest elements were opposed in a x-y-plot. Finally, a linear least-square regression was fit to the data and the x-axis (voxel size) was inverted. The slope of the regression line then equals the box-dimension (cf. Mandelbrot, 1977). The box-dimension was calculated for the entire plot as well as for vertical layers of 5 m thickness cf. Willim et al. (2020), in order to allow the analysis of potential vertical pattern within a plot.

Regeneration assessment

In order to assess the density of the regeneration on all study sites, a total of 16 sampling points per study site were taken. Due to the small size of the study sites (0.25 ha), four sampling points were located in the study plot. Another four sampling points were located at the edge and eight right outside of the study site. The sample points were 4 m^2 in size each. Tree regeneration was assessed > 100 cm height. Only regeneration below 7 cm diameter at breast height (DBH) was examined. All tree species found were summarized in groups:

- **European beech** (*Fagus sylvatica* L.),
- **oak** (*Quercus rubra* L., *Quercus robur* L., *Quercus petraea* (Matt.) Liebl.),
- **European ash** (*Fraxinus excelsior* L.),
- **maple** (*Acer pseudoplatanus* L., *Acer campestre* L., *Acer platanoides* L.), and
- **other species** (*Abies alba* Mill., *Betula pendula* Roth, *Carpinus betulus* L., *Castanea sativa* Mill., *Larix decidua* Mill., *Picea abies* (L.) H. Karst., *Pinus sylvestris* L., *Populus tremula* L., *Prunus padus* L., *Salix caprea* L., *Sorbus aucuparia* L., *Sorbus torminalis* (L.) Crantz, *Taxus baccata* L., *Tilia* spec., *Ulmus glabra* Huds.).

Statistical analysis

Statistical analyses were performed using the open source software R (version 4.3.1, R Core Team, 2023) with a significance level of $p < 0.05$. The Kolmogorov-Smirnov test for sample sizes with $n > 50$ as well as the Shapiro-Wilk test for sample sizes with $n < 50$ were applied to test for normal distribution of the data. Levene's test was used to test for variance homogeneity. Kruskal-Wallis and subsequent post-hoc Kruskal-Dunn test (with Bonferroni correction) as well as one-way ANOVA were performed to test for significant differences in the variables box-dimension (D_b) and canopy cover between the four drought damage classes.

Results

The range of canopy cover was not significantly different among the four drought damage classes (Fig. 2). Nevertheless, it can be seen that canopy cover continuously decreased from the drought damage class "undamaged" (mean ± standard deviation: 96.7 ± 6.4 % canopy cover) to the drought damage class "heavily damaged" (71.7 ± 15.8 % canopy cover).

Fig. 3 shows the overall structural complexity of the study sites expressed through the box-dimension (D_b) for the four different drought damage classes. There was no significant difference in D_b between the four drought damage classes.

While there was no significant difference in stand structural complexity on the plot level, we found a significant difference in D_b within the drought damage class "undamaged" between the height layers 5–10 m and 20–25 m (Fig. 4). Structural complexity was significantly lower in the height layer 5–10 m (mean ± standard deviation:

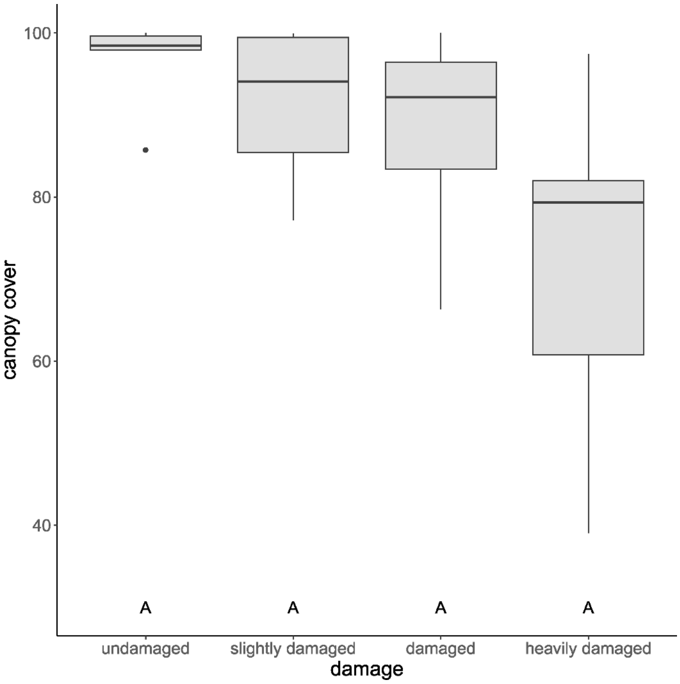

Fig. 2. Range of canopy cover [%] between the four drought damage classes. Capital letters indicate significant differences between the drought damage classes at $p < 0.05$ (non-parametric, Kruskal-Wallis test with Bonferroni correction).

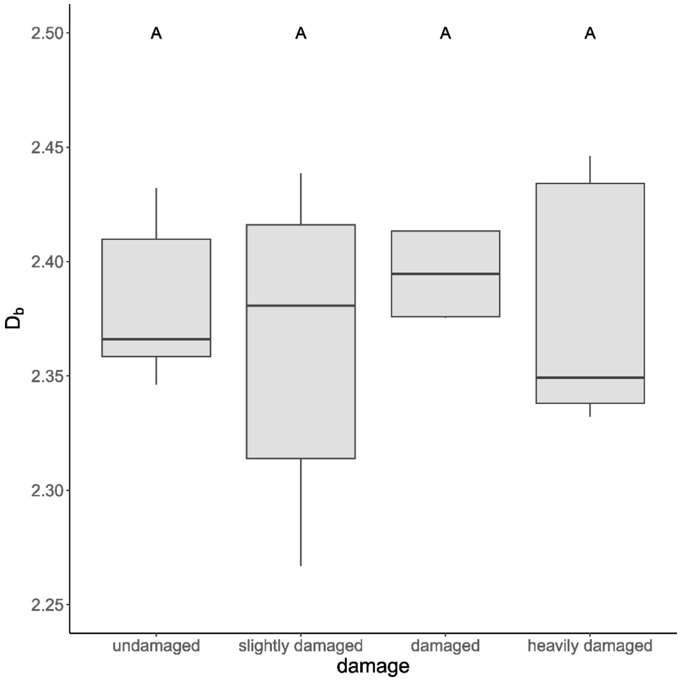

Fig. 3. Range of box-dimension (D_b) between the four drought damage classes. Different capital letters indicate significant differences between the drought damage classes at $p < 0.05$ (non-parametric, Kruskal-Wallis test with Bonferroni correction).

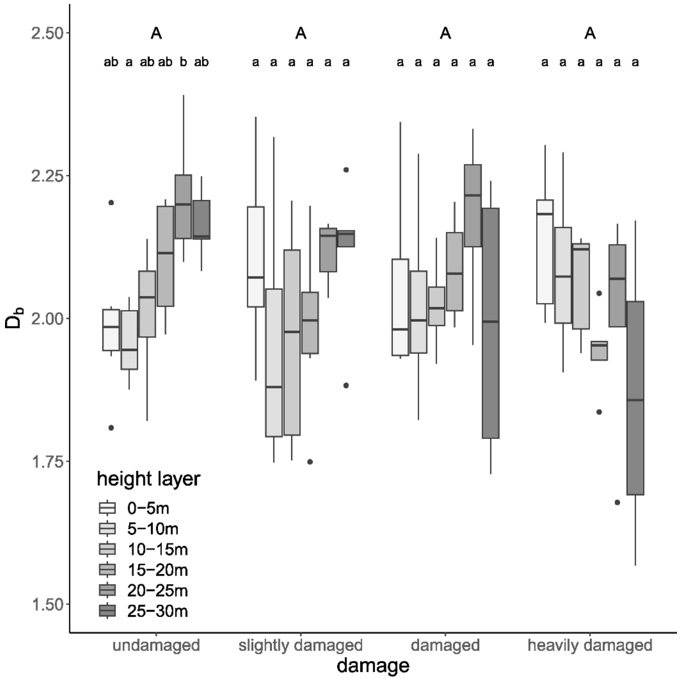

Fig. 4. Range of box-dimension (D_b) between the four drought damage classes and between height layers of 5 m. Different lower-case letters indicate significant differences between height layers, different capital letters indicate significant differences between the drought damage classes at $p < 0.05$ (non-parametric, Kruskal-Wallis test with Bonferroni correction).

1.96 ± 0.21) compared to the height layer 20–25 m (2.21 ± 0.21). For the other drought damage classes, there was no significant difference – neither between the drought damage classes nor between the height layers. Nevertheless, it can be observed that D_b increased with increasing height layer in the undamaged stands and decreased with increasing height layer in the heavily damaged stands.

There was a difference between the drought damage classes undamaged and heavily damaged in the mean voxel percentage per height layer for the four drought damage classes (Fig. 5). Below 13 m height (see red horizontal line in Fig. 5), heavily damaged stands showed the highest mean voxel percentage while undamaged stands showed the lowest mean voxel percentage. At 13 m height, the two lines crossed and above 13 m height and up to approximately 30 m height, heavily damaged stands showed the lowest and undamaged stands the highest mean voxel percentage.

Fig. 6 provides a graphical visualization of 3D point clouds obtained from undamaged and damaged European beech stands as used in our analysis.

Regeneration assessment

The number of seedlings and saplings per hectare (n/ha) was not significantly different among the investigated four drought damage classes (Fig. 7a). However, significant differences were found between the tree species groups: In all drought damage classes, the number of European beech trees was significantly higher compared to oak, ash, and other tree species. When comparing the number of beech to the number of maple seedlings and saplings, a significant difference in damaged stands was found(an outlier with 6563 maple trees/ha in the heavily damaged stands is very likely the reason for the non-significance between maple and beech). For the undamaged and slightly damaged stands, no significant difference was found between the number of beech and maple trees per hectare.

In Fig. 7b, the count of species in the overstory was compared to the count of species in the understory. Beech was predominant in the understory across all damage levels. With a few exceptions (maple, ash), beech was also predominant below the 1:1 line.

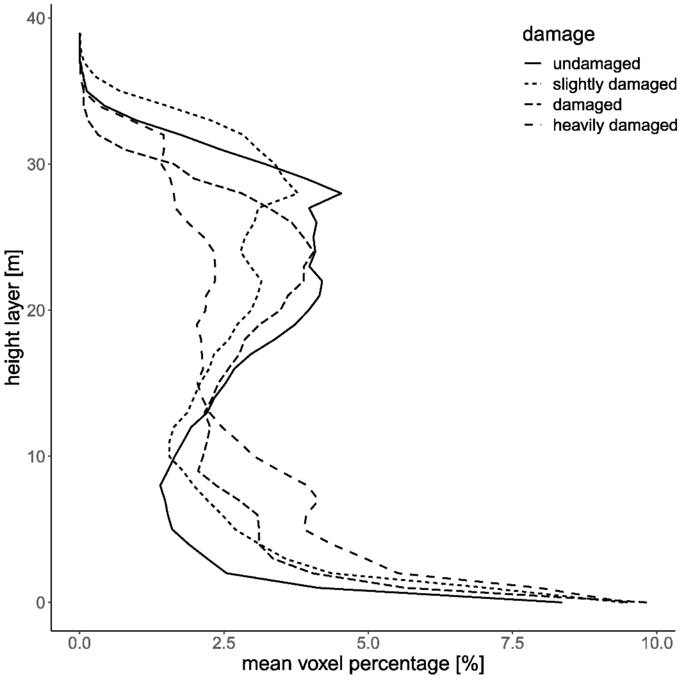

Fig. 5. Mean voxel percentage [%] per height layer for each drought damage class. Solid line for undamaged stands, dotted line for slightly damaged stands, dashed line for damaged stands, and double dashed line for heavily damaged stands.

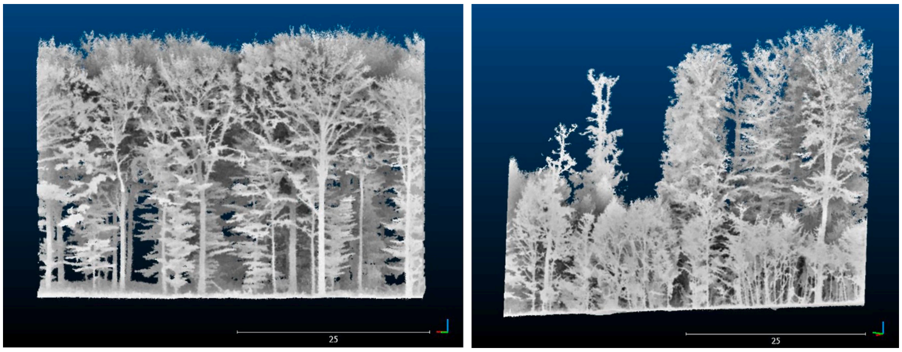

Fig. 6. Exemplary point cloud visualizations of an undamaged (a) and a heavily damaged (b) European beech stand.

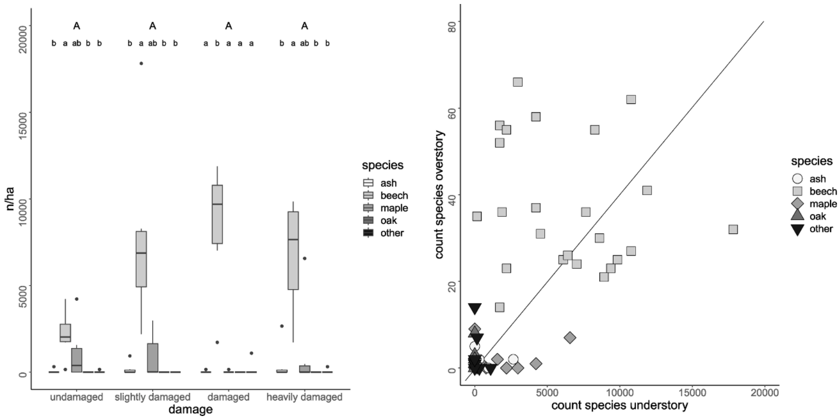

Fig. 7. (a) Range of number of trees per hectare (n/ha) with a height greater than 100 cm among the four drought damage classes and among investigated tree species. (b) count of species in the overstory compared to count of species in the understory with 1:1 line. The investigated tree species for (a) and (b) were summarized to: beech (*Fagus sylvatica* L.), oak (*Quercus rubra* L., *Quercus robur* L., *Quercus petraea* (Matt.) Liebl.), ash (*Fraxinus excelsior* L.), maple (*Acer pseudoplatanus* L., *Acer campestre* L., *Acer platanoides* L.), and other species (*Abies alba* Mill., *Betula pendula* Roth, *Carpinus betulus* L., *Castanea sativa* Mill., *Larix decidua* Mill., *Picea abies* (L.) H.Karst., *Pinus sylvestris* L., *Populus tremula* L., *Prunus padus* L., *Salix caprea* L., *Sorbus aucuparia* L., *Sorbus torminalis* (L.) Crantz, *Taxus baccata* L., *Tilia* spec., *Ulmus glabra* Huds.). Different lower case letters indicate significant differences between tree species, different capital letters indicate significant differences between the drought damage classes at $p < 0.05$ (non-parametric, Kruskal-Wallis test with Bonferroni correction).

Discussion

The health of European forests declined after several very hot and very dry years (e.g., Hartmann et al., 2022). In this study, we found no significant differences between the different classes of drought damage (Fig. 3) when comparing the overall structural complexity using the box-dimension, a measure that is usually rather sensitive to structural differences in forest plots (Seidel et al., 2020; Stiers et al., 2020; Heidenreich and Seidel, 2022; Neudam et al., 2022; Willim et al., 2022). This was surprising, as the stands showed obvious signs of reduced health in the overstory, including severe defoliation and partial crown dieback, resulting in their classification into the four drought damage classes based on visual assessment as commonly done in the German forest health monitoring. However, despite missing statistical significance, likely due to the rather small sample size, canopy cover as an indicator of crown defoliation reflected the field observation. A clear trend towards decreasing canopy cover with increasing degree of damage was observed (Fig. 2), with a median canopy cover dropping from about 98 % in the undamaged stands to around 80 % in the heavily damaged stands.

Only, the more detailed analysis of the spatial pattern of structural complexity in different vertical layers finally allowed discovering a “structural flip”, for which significance was not always given (Fig. 4), but trends were clearly visible (Figs. 4 and 5). We argue that the flip of the location of the strata that host the major part of the complexity of the stand from top (Fig. 4, group undamaged, 15–25 m) to bottom (Fig. 4, group heavily damaged, 0–15 m) is a logical response to drought induced mortality of the overstory trees. Overstory beech trees were reported to suffer from drought as they are subjected to greater solar radiation, heat, and hydraulic stress or failure compared to smaller trees (Pretzsch et al., 2018). Meyer et al. (2022) also reported that larger canopy trees showed higher mortality rates in managed forests, although it remained unclear if this was due to hydraulic failure. However, if drought conditions are harsh enough, understory or subordinate trees were found to also show reduced vitality (e.g., Mathes et al., 2023; for unmanaged stands see also Meyer et al., 2022). On the study sites investigated here, overall precipitation was obviously sufficient in the past to enable a quantifiable ecosystem response, i.e., the development of an understory layer that was remarkably complex in structure, even compensating the respective losses in the overstory. Earlier studies showed that for beech, the critical line at which constant decline in health can be expected is somewhere around <350 mm (Leuschner et al., 2023). The sites in our study all experienced at least 646 ± 59 mm of annual rainfall on average in 2022.

Once the growth of the mature trees is restricted by water shortage, their access to light is no longer an advantage. More light becomes available in lower strata and benefits the smaller trees leading to the observed structural flip. As a result, the overall structural complexity remains fairly the same as the structural loss in the upper stand layer was compensated for by the smaller trees in the lower stand layers (see Fig. 7). This is in accordance with Bennett et al. (2015) and Meyer et al. (2022) (for managed stands) who also observed higher mortality rates for mature trees compared to smaller (suppressed) trees in recent drought years. Additionally, Pretzsch et al. (2023) and Schmied et al. (2023) found changed growth pattern with smaller trees benefitting from the weakening of their mature neighbors and the smaller trees additionally partly compensating growth losses and mortality of larger trees at the stand-level. This study showed that beech has successfully regenerated and that the condition of the forests in the observed areas is still in an acceptable state. However, it also showed that mixing had not yet taken place and that active planting will be required to promote the proportion of mixed forests in the face of climate change. From our data it appears that beech will again be dominating the investigated forests in the next cohort of canopy trees.

Conclusion

The results of our study clearly indicate that beech forests in central Germany show signs of a structural reorganization as a consequence of recent drought. Using space-for-time substitution we observed a "structural flip" through the loss of structural complexity in the upper stand layers compensated by additional structural complexity in the lower stand layers. Therefore, when comparing beech forests in different stages of vitality loss, we could not observe overall losses in structural complexity, an important ecosystem characteristic related to many ecosystem functions and services. We argue that this indicates a successful ecosystem-scale response to the drought events. The effects of intensified or repeated droughts and thus of legacy effects of previous droughts are however unknown. We regard the observed structural differences as an early warning signal pointing to great ecosystem stress. However, in the investigated beech forests in central Germany we see no clear signs yet for an immediate threat to the future of beech. We argue however, that potential changes in the dominant canopy species might result in significant changes to the ecosystems, e.g. those species that dwell from beech seeds during mast, to name only one example.

CRediT authorship contribution statement

Kirsten Höwler: Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Niccolò Vallebuona:** Writing – review & editing, Data curation. **Tadeus Wern:** Writing – review & editing, Data curation. **Christian Ammer:** Writing – review & editing, Resources, Methodology. **Dominik Seidel:** Writing – review & editing, Validation, Supervision, Software, Resources, Project administration, Methodology, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

Dominik Seidel reports financial support was provided by Federal Ministry of Food and Agriculture (BMEL). Dominik Seidel reports financial support was provided by Federal Ministry for the Environment, Nature Conservation, Nuclear Safety and Consumer Protection (BMUV). Dominik Seidel reports financil support was provided by Fachagentur Nachwachsende Rohstoffe e. V. (FNR). Other 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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