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Changes in forest stand structure and tree species composition of protected forest habitats after 10 years: Analyzes from different Natura 2000 sites in Saxony-Anhalt, Germany

Veränderungen in der Bestandesstruktur und Baumartenzusammensetzung von geschützten Waldlebensraumtypen nach 10 Jahren: Analysen aus verschiedenen Natura 2000-Gebieten in Sachsen-Anhalt, Deutschland

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Abstract

In recent years, forests in Germany have experienced considerable disturbances, yet there is limited information on the extent to which forests within the Europe-wide Natura 2000 network of protected areas (Directive 92/43/ECC) have also been affected. However, calls for greater flexibility of the Habitats Directive to address potential climate change effects have already been made.

The objective of this study was to analyze changes in selected forest habitat types by comparing current recording results with those from approximately ten years ago. We analyzed a selection of forest stands ($n = 224$) encompassing the forest habitat types 9110, 9130, 9170, 9180*, and 91E0* within four Natura 2000 sites in the Harz Mountains and Harz Foothills in Saxony-Anhalt, Germany, and focused on stand structure and tree species composition. The following parameters were recorded and evaluated: (1) canopy layer cover, (2) large deadwood pieces per hectare, (3) tree species composition and (4) vitality of selected individual trees by recording crown defoliation.

The study revealed (1) a decline in the upper canopy layer cover, consisting of older and larger trees, as well as an increase in tree regeneration. In addition, (2) greater large deadwood density per hectare and (3) a change in tree species composition were observed. Our analysis indicates that (4) forest stand structure has a greater influence on crown defoliation than site characteristics.

Our study shows that forest habitat types studied in the Harz region have changed significantly over the course of a decade. However, we contend that there is currently no compelling rationale to challenge the protective status of the forests examined at the regional level or the delineations of forest habitat types at the European level. To effectively address climate change impacts, it is essential to expand the methodological approach in the future, e.g. by incorporating satellite data into regular monitoring activities.

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Erweiterte deutsche Zusammenfassung am Ende des Artikels

1. Introduction

German forests have faced increasing disturbances and changes in recent decades. Windthrow and bark beetle outbreaks have been the primary disturbance agents in European temperate forests (e.g., Seidl et al. 2011, Thom et al. 2013, Senf & Seidl 2021). However, other abiotic and biotic factors, such as drought, snow, hail, fungi or other animals damaging trees, are gaining importance (Patacca et al. 2022). Climate change is expected to increase the frequency, intensity, and severity of these disturbances (e.g., Seidl et al. 2017).

Significant changes in the forests in Germany have been documented (e.g., Buras et al. 2020, Schuldt et al. 2020) following consecutive droughts in 2018 and 2019 (Vogel et al. 2019, Hari et al. 2020). These changes included, in some cases, area-wide dieback of forest stands and canopy cover loss (e.g., Schuldt et al. 2020, Thonfeld et al. 2022, Kacic et al. 2023), increased mortality rates of trees (Obladen et al. 2021, Meyer et al. 2022), and declines in canopy height and above-ground biomass (Kacic et al. 2023). Furthermore, studies have revealed an increase in indications of drought stress in various tree species, including early wilting (Brun et al. 2020), pronounced leaf browning (Rohner et al. 2021), and early leaf drop (Schuldt et al. 2020), as well as increasing crown transparency (e.g., BMEL 2019, 2020, 2021). It was also shown that both natural and human induced changes were smaller in protected compared to unprotected forests (Sommerfeld et al. 2018).

Nevertheless, previous studies have not explicitly investigated changes in forests stands within protected areas of the European Natura 2000 network, which are designated for natural habitat types of community interest and aim to ensure their long-term conservation (Directive 92/43/EEC; Habitat Directive = HD). Some authors argue that protected areas and habitat types in the European Union will experience (considerable) alterations, including loss of protected status, due to climate change in the forthcoming decades (Nila et al. 2019, Steinacker et al. 2019, Maciejewski et al. 2020). However, there is a lack of field studies examining possible changes caused by different abiotic, biotic and anthropogenic disturbance factors in habitat types, also due to missing baseline data. Therefore, the available evidence that could serve as a basis for discussions on optimal protection and management strategies is limited.

With the establishment of Natura 2000 sites, initial data on stand structure and tree species composition of different habitat types have been collected including a qualitative evaluation of their conditions ranging from a = excellent habitat conditions, b = medium conditions, to c = inadequate conditions. These underutilized data provide a valuable basis for comparing the current situation of forests in Natura 2000 sites with past conditions. We used these data, collected approximately 10–15 years ago (baseline survey), to analyze the possible changes in tree species composition and stand structure of various forest habitat types in four Natura 2000 sites in Saxony-Anhalt, Germany. In selected stands, we recorded data on stand structure, deadwood, and tree species composition in 2021 and 2022 (resurvey) using the same methods applied in the baseline survey.

In light of the previously described dieback events in German forests, we expected (1) a decreasing coverage of the upper canopy layer and, as a result, (2) an increasing amount of deadwood. The increased light availability at the ground will stimulate

(3) richness and density of the tree regeneration. In contrast to these structural changes, we expected that (4) the tree species composition will remain largely stable when considering all layers of the stand. However, shifts in the proportions of certain species or in specific layers may still occur. These changes will affect the qualitative evaluation results of the habitat types.

2. Material and Methods

2.1 Study region and Natura 2000 sites

The study area, located in the eastern Harz Mountains and Harz Foothills in Saxony-Anhalt, Germany, has experienced significant forest dieback and tree mortality in recent decades (Thonfeld et al. 2022, Kacic et al. 2023). The research was conducted at selected forest stands within four Natura 2000 sites (Fig. 1, Supplement E1). The region's climate includes 540–700 mm of mean annual precipitation sum, mean temperatures from 6–9 °C, with elevations ranging from 140–540 m above sea level.

The investigated forest stands belong to the following habitat types (Table 1): *Luzulo-Fagetum* beech forests (9110), *Asperulo-Fagetum* beech forests (9130), *Galio-Carpinetum* oak-hornbeam forests (9170), slope and ravine forests *Tilio-Acerion* (9180*) and alluvial forests with *Alnus glutinosa* and *Fraxinus excelsior* (91E0*). Asterisks (*) indicate priority habitat types, which are considered of particular importance for conservation efforts in the European Union (European Commission 2013a). The stands are managed in accordance with the provisions outlined in the State Ordinance for the Protection of Natura 2000 Sites in Saxony-Anhalt (N2000-LVO LSA) by the Saxony-Anhalt State Forest Enterprise.

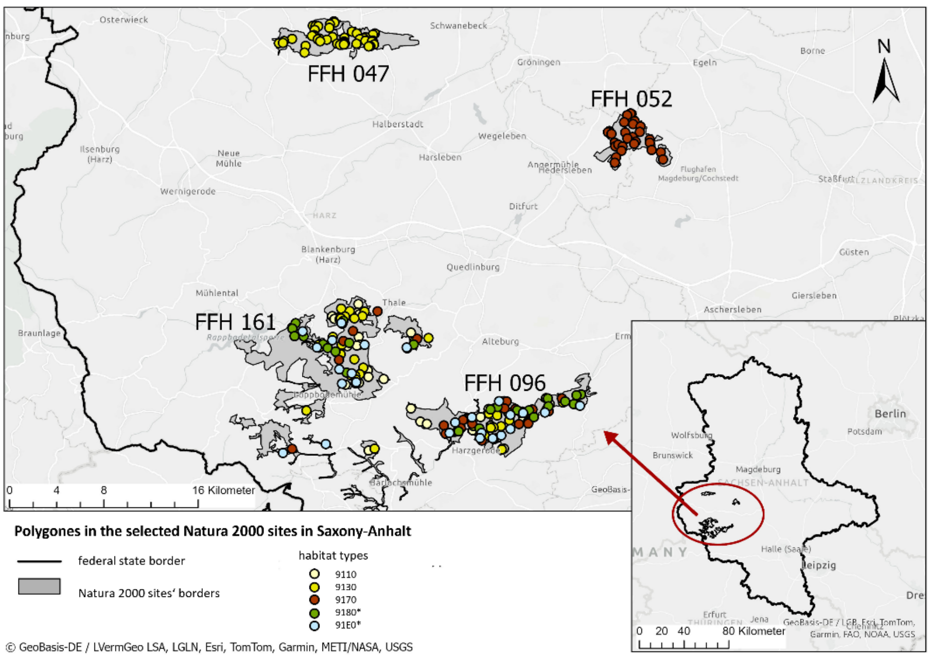


Fig. 1. Location of study sites (polygons) in the German federal State Saxony-Anhalt.

Abb. 1. Lage der Untersuchungsflächen (Polygone) im Bundesland Sachsen-Anhalt.

Table 1. Habitat types (European Commission 2013a, LAU 2014) and number of study polygons which have been included in the investigation.

Tabelle 1. Betrachtete Lebensraumtypen (European Commission 2013a, LAU 2014) sowie die Anzahl der untersuchten Polygone je Lebensraumtyp.

habitat type	name	main tree species	number of polygons
9110	*Luzulo-Fagetum* beech forests	*Fagus sylvatica*	35
9130	*Asperulo-Fagetum* beech forests	*Fagus sylvatica*	84
9170	*Galio-Carpinetum* oak-hornbeam forests	*Carpinus betulus* *Quercus petraea* *Quercus robur* *Tilia cordata*	55
9180*	*Tilio-Acerion* forest of slopes, screes and ravines	*Acer platanoides* *Acer pseudoplatanus* *Fraxinus excelsior* *Tilia cordata* *Tilia platyphyllos* *Ulmus glabra*	25
91E0*	Alluvial forests with *Alnus glutinosa* and *Fraxinus excelsior* (*Alno-Padion*, *Alnion incanae*, *Salicion albae*)	*Alnus glutinosa* *Fraxinus excelsior* *Prunus padus*	25

2.2 Sampling

We employed a stratified-randomized sampling approach, using data from a recording conducted approximately 10–15 years prior (2009–2015) as part of the obligations under the EU's Habitat Directive (HD recording, LAU 2014). The data were provided by the State Office for Environmental Protection Saxony-Anhalt and served as (1) the basis for the sampling design and (2) a baseline (baseline survey) for later comparisons with actual data (resurvey).

The baseline survey delineated habitat types into polygons based on qualitative characteristics (LAU 2014) including forest stand structure (e.g., layering and development stages, deadwood), species composition, and impairment factors (e.g., browsing or severe forest management impact, presence of non-native species) that were measured in the field. Each polygon aimed to be as homogeneous as possible regarding these characteristics (LAU 2014).

The pool of sites for sampling consisted of a total of 1353 polygons of the corresponding habitat types located in four Natura 2000 sites. Only polygons under the management of the Saxony-Anhalt State Forest Enterprise were included in the pool of areas.

To select polygons for each habitat type for a resurvey, we formed nine distinct sampling strata. We used two criteria for stratification: (1) conservation status, which reflects the overall condition of the forest stand (including structure, species composition, impairment), and (2) layering and development stages, which particularly highlights the age structure within the stand. Both criteria were assessed in the baseline survey using a predefined three-level rating scheme (a = excellent, b = medium, c = inadequate), thus combining both criteria resulted in the nine distinct sampling strata shown in Supplement E2. For most habitat types (9110, 9180*, 91E0*) we selected seven polygons per stratum, ranging from 1 to 5 hectares. When fewer than seven polygons per stratum were available, all polygons were selected. For the two most common habitat types (9130 and 9170), 15 polygons were selected per stratum. The varying number of polygons selected per stratum (7 vs. 15) was chosen to ensure that at least 10% of the area of the stratum of each habitat type was represented in the sample. Altogether, 224 polygons were selected, averaging 3.3 ± 1.2 ha in size and covering approximately 729 ha in total (Fig. 1, Table 1).

2.3 Recording methods

To assess the current state of habitat types in the Harz Mountains and Harz Foothills, structural and vitality parameters were collected in the selected polygons between July and September 2021 and 2022.

Recording of the structural and compositional parameters

In each polygon, we resurveyed three parameters across the entire area: "layering and development stages", "large deadwood", and "tree species composition" (resurvey). We used the same field survey methods as the baseline survey according to the mapping and assessment standards for habitat types in Saxony-Anhalt (HD-recording; LAU 2014), ensuring data consistency over time.

For the parameter "layering and development stages", we estimated visually the percentage cover of canopy layers (CL1, CL2, CL3) and of seven predefined development stages (see Table 2) within each polygon. For the parameter "large deadwood", we counted the number of large deadwood pieces (lying and standing) with a minimum diameter at breast height of 50 cm and length of 3 m. For "tree species composition", we estimated the percentage cover of different tree species in each canopy layer to

Table 2. Parameters for the recording of forest habitat type conditions, including definitions, measurement units and type of condition which they indicate (LAU 2014). All parameters were collected in the entire polygon. (DBH = diameter at breast height, h = tree height).

Tabelle 2. Zusammenstellung der Parameter für die Erfassung des Zustandes der Waldlebensraumtypen, einschließlich deren Definition, Maßeinheiten und Art des Zustandes, den sie anzeigen (LAU 2014). Alle Parameter werden im gesamten Polygon erhoben. (DBH = Brusthöhendurchmesser, h = Baumhöhe).

	definition	levels and meaning	units	indicator for
layering and development stages	cover of each canopy layer/ development stage estimated visually within the polygon	layering (canopy layers (CL)) CL1 – DBH ≥ 20 cm, h > 18 m CL2 – DBH ≥ 13 cm – < 20 cm, h > 7 m – ≤ 18 m CL3 – DBH < 13 cm, h ≤ 7 m development stage 1 – DBH < 13 cm, h ≤ 1,5 m 2 – DBH < 13 cm, h > 1,5 – ≤ 7 m 3 – DBH ≥ 13 – < 20 cm, h > 7 – ≤ 18 m 4 – DBH ≥ 20 – < 35 cm, h > 18 m 5 – DBH ≥ 35 – < 50 cm, h > 18 m 6 – DBH ≥ 50 – < 80 cm, h > 18 m 7 – DBH ≥ 80 cm, h > 18 m	percent	spatial and age structure
large deadwood	number of lying and standing deadwood pieces	deadwood objects with DBH ≥ 50 cm, length/height ≥ 3 m)	number per hectare	availability of microhabitats and detection of past mortality events
tree species composition	proportion of the total stand of regular occurring main and non-characteristic tree species	main tree species: listed for each habitat type in the HD recording manual (LAU 2014, see Table 1). non-characteristic tree species: any tree species not listed for the habitat type	proportion of the total stand in %	completeness of the habitat-typical tree species inventory

calculate their proportion in the total stand. Therefore, the percentage cover of the tree species was initially recorded in tenths for each canopy layer according to their occurrence in the stand. Species with less than one-tenth cover ("r" = single individual and "+" = more than one individual) are excluded from further consideration. The proportion of each tree species in the total stand was then calculated by weighting the layer proportions with the sum of the cover of all three canopy layers (see Table 2).

Finally, the recorded data were categorized into the three predefined value categories (a, b, c, see Supplement E3) for each parameter and each polygon.

Recording of the vitality parameter

In addition to the structural parameters, which were also recorded during the baseline survey, we collected vitality data on individual trees.

We used the degree of relative defoliation of the individual tree crown (= crown defoliation) as an indicator for tree vitality (Eichhorn et al. 2020). The degree of crown defoliation was recorded in 5% intervals in comparison to a fully leafed tree crown (complete foliage = 0% defoliation, completely defoliated crown = 100% defoliation), focusing on parts of the crown unaffected by shading or mechanical influences from neighboring trees (Meining et al. 2007).

Crown defoliation was assessed in a randomly selected subset of polygons ($n = 5$ per stratum, if available). Within each polygon, the six dominant trees (tree class 1 to 3; Kraft 1884) closest to the polygon center were evaluated. For each tree, the tree species and additional variables to describe the stand situation were recorded (Table 3): (1) relative crown distance (Eichhorn et al. 2020), (2) development stage (LAU 2014) and (3) tree class (Kraft 1884). In total 744 trees situated at 124 distinct polygons were evaluated.

To further describe the site parameters of the polygons, parameters such as soil moisture, slope, exposition und management were determined from forest management plans. Since the polygon boundaries do not coincide with forest management units, these parameters were categorized into broad categories (Table 3). Due to the long and narrow shape of habitat type 91E0* polygons, the required site parameters could not be determined. Consequently, these polygons were excluded from all analyses related to tree vitality.

2.4 Analysis

All analyses were performed with R Version 4.5.0. (R Core Team 2025).

Structural parameters

We assessed temporal changes in structural parameters by comparing data from the baseline survey and resurvey using Wilcoxon signed-rank tests. We conducted separate analyses for the three canopy layers and large deadwood to examine the effects of habitat type and data collection time (i.e., baseline survey and resurvey), utilizing a generalized linear mixed model (GLMM) with glmmTMB package (Brooks et al. 2017, McGillycuddy et al. 2025).

The model incorporated fixed effects for habitat type and data collection time, and included a random intercept for Natura 2000 sites to account for variability among them. Subsequently, an ANOVA was performed using the car package (Fox & Weisberg 2019) to determine the main effects of the predictors.

Tree species composition and diversity

We used a non-metric multidimensional scaling (NMDS) ordination to illustrate differences in tree species composition between habitat types and compositional changes from the baseline survey to the resurvey. NMDS based on the percentage cover of all tree species occurring in each of the three canopy

Table 3. Compilation of the stock parameters which were recorded in addition to the crown defoliation on each selected individual tree, as well as stand parameters that were determined from the forest management plans, including definitions, and measurement units.

Tabelle 3. Zusammenstellung der Bestandsparameter, die neben der Kronenverlichtung an jedem ausgewählten Einzelbaum aufgenommen wurden, sowie der Standortparameter, die aus den Forsteinrichtungsdaten ermittelt wurden, einschließlich deren Definition und Maßeinheiten.

Parameter	Definition	levels and meaning
stock parameters		
relative crown distance (Eichhorn et al. 2020)	as the distance to the surrounding trees in relation to the crown diameter	1 – canopies overlap 2 – crowns touch one another 3 – gap between crowns up to 1/3 of average crown diameter 4 – gap between crowns up to 2/3 of average crown diameter 5 – gap between crowns from 2/3 up to 1/1 of average crown diameter 6 – gap between crowns > than 1/1 of average crown diameter
development stage (LAU 2014)	combination of tree height and diameter at breast height (DBH)	each individual tree was assigned to the appropriate category (see layering and development stages (Table 2))
tree class of dominant trees (Kraft 1884)	characterization of individual trees according to their social position and growth dynamics	1 – predominant 2 – dominant 3 – co-dominant
tree species	The tree species was noted for each tree recorded.	-
site parameters		
soil moisture	-	1 – fresh 2 – medium-fresh 3 – dry
slope	-	1 – ≤ 9° inclination 2 – ≥ 10° - ≤ 39° inclination 3 – ≥ 40° - ≤ 90° inclination
exposure	-	n.e. – no exposure n – north e/w – east/west s – south
management	Only the management between 2012 and 2021 is taken into account.	m – polygon aligns with forest management units, confirming any management activities (e.g, selection cutting, thinning, care of woods) no – polygon aligns with forest management units, confirming no management activities uc – unclear management: polygon does not align with forest management units, indicating significant discrepancies

layers in both time periods (i.e., baseline survey and resurvey) using the Bray-Curtis distance. In addition, differences in tree species composition were tested with a permutative multivariate ANOVA (perMANOVA) using the Adonis permutation test based on the Bray-Curtis index. The analyses were performed in R using the metaMDS and adonis functions within the vegan package (Oksanen et al. 2022).

To assess changes in tree species diversity, we calculated the Shannon index as a measure of diversity based on the proportion of tree species in the total stand and their percentage cover in the three canopy layers across the baseline survey and resurvey. To account for the presence of rare species, a proportion of 0.1 was allocated to "r" and 0.5 was allocated to "+". We applied rarefaction to standardize our samples using an average sample size of approximately 45 and the rarefy function from the vegan package (Oksanen et al. 2022) to ensure robust comparisons across habitat types while maintaining statistical integrity.

We conducted a "winner-loser-analysis" to assess whether main tree species, most common accompanying and non-characteristic tree species increased or declined over time within each habitat type. Tree species were classified as "winner" if their proportion of the total stand or percentage cover increased significantly over time, and as "loser" if these metrics decreased significantly. We also identified "immigrants" (species that were previously absent) and "absentees" (species that are no longer present). Species with no significant changes in proportion were labeled as "stable". The Wilcoxon signed-rank test was used to detect significant changes between both data collection times.

Changes in the evaluation of the structural and compositional parameters

To determine changes in the evaluation of the structural and compositional parameters of the HD recording, we compared their value categories from the baseline survey and the resurvey. Each polygon was classified for each parameter into one of three categories: (1) improved (change from category b-a, c-a, c-b), (2) unchanged (remaining in category a, b, c) and (3) deteriorated (shift from a-b, a-c, b-c, loss of habitat type status).

We calculated the Stuart-Maxwell-test using the \`DescTools\` package (Signorell et al. 2014) to test whether there were significant changes in the distribution of value categories "a", "b", and "c" between the two data collection times. Since this test requires identical categories in both data collection times, polygons that could no longer be assigned to a habitat type ($n = 9$) were excluded, resulting in an analysis of 215 polygons.

Effects of the stand and site parameters on crown defoliation

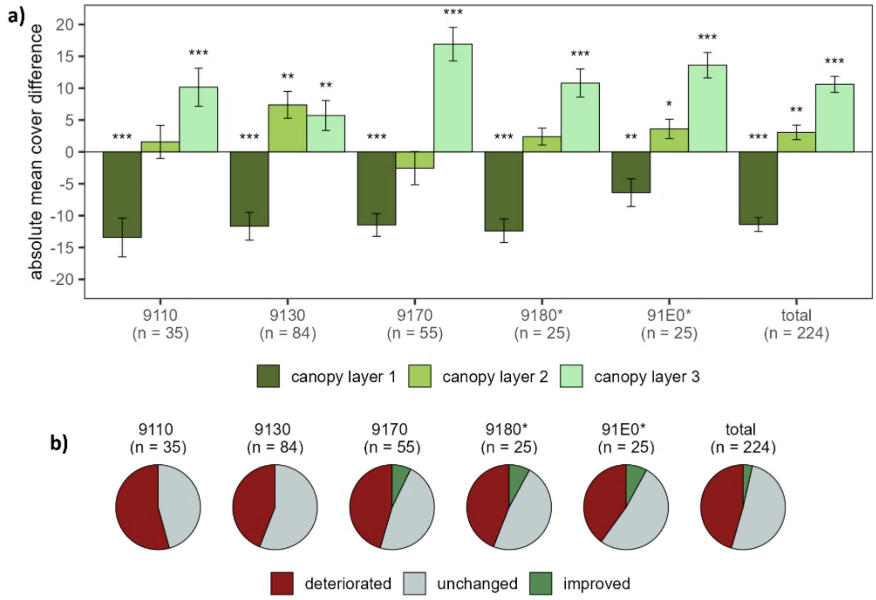
We employed a generalized linear mixed model (GLMM) using the glmmTMB package (Brooks et al. 2017, McGillycuddy et al. 2025) to assess the impact of site conditions and stand structure on crown defoliation. The model incorporated habitat type and all condition parameters as fixed effects and included a random intercept for polygons to account for variability among them. Subsequently, an ANOVA was carried out to assess the main predictor effects, using the car package (Fox & Weisberg 2019).

3. Results

3.1 Layering and development stages

The canopy structure of habitat types changed notably, with a decrease in upper canopy layer coverage and an increase in understory coverage (Fig. 2a).

The cover of canopy layer 1 decreased significantly between the baseline survey (mean: 61.7, SE: 1.3) and the resurvey (mean: 50.3, SE: 1.2). This decline was corroborated by a generalized linear mixed model (GLMM) analysis followed by an ANOVA (Supplement E4), revealing significant effects of habitat type ($p < 0.05$) and time ($p < 0.001$) on canopy layer 1 coverage.



c)

		resurvey			
		a	b	c	none
baseline survey	a	18	13	39	0
	b	6	13	49	0
	c	0	2	83	0

Fig. 2. Layering and development stages: **a)** difference in canopy layer cover between baseline survey and resurvey as well as results of the Wilcoxon sign-rank test ((*) = $p \leq 0.1$, * = $p \leq 0.05$, ** = $p \leq 0.01$, *** = $p \leq 0.001$), **b)** proportion of polygons with deteriorated, unchanged and improved condition between baseline survey and resurvey, **c)** changes in the number of polygons in the value categories (a = excellent, b = medium, c = inadequate, none = polygon no longer meets the minimum criteria for this parameter) across all habitat types (see Supplement E3).

Abb. 2. Bestandsstruktur: **a)** Differenz der Deckungen der Baumschichten (dunkelgrün = Baumschicht 1, mittelgrün = Baumschicht 2, hellgrün = Baumschicht 3) zwischen der Erstkartierung (baseline survey) und Nachkartierung (resurvey) sowie die Ergebnisse des Wilcoxon-Vorzeichen-Rang-Test ((*) = $p \leq 0{,}1$; * = $p \leq 0{,}05$; ** = $p \leq 0{,}01$; *** = $p \leq 0{,}001$), **b)** Anteil der Polygone mit verschlechtertem (rot), unverändertem (grau) und verbessertem Zustand (grün) zwischen Erst- und Nachkartierung, **c)** Veränderung der Anzahl der Polygone je Bewertungsstufe (a = ausgezeichnet, b = mittelmäßig, c = unzureichend, none = Polygon erfüllt nicht mehr die Mindestkriterien dieses Bewertungsparameters) über alle Lebensraumtypen hinweg (siehe Anhang E3).

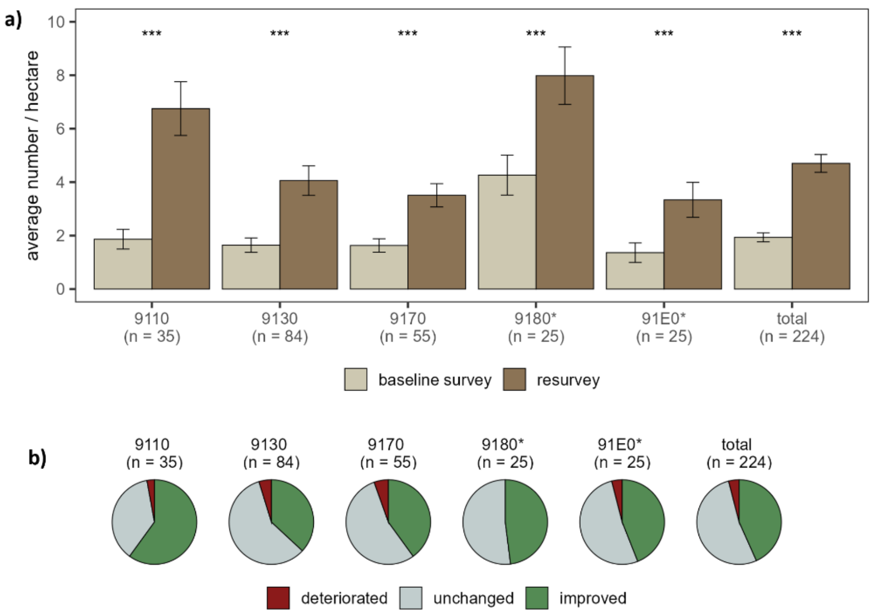
Canopy layer 2 increased slightly by approximately 3%, and a GLMM followed by an ANOVA (Supplement E4) indicated no significant effects. In contrast, canopy layer 3 showed a significant increase from 31.9% (SE: 1.8) to 42.5% (SE: 1.7), also marked by significant effects of habitat type ($p < 0.01$) and time ($p < 0.001$, Supplement E4).

These changes altered the assignment of the polygons to the value categories. An improvement was observed in 3.6%, while a deterioration was noted in 45.5%, and no differences were identified in 50.9% of the polygons (Fig. 2b, c). Across habitat types, significant differences were observed between the baseline survey and resurvey ($n = 215$, $\chi^2 = 84.4$, $df = 2$, $p < 0.001$).

3.2 Large Deadwood

A notable increase in large deadwood density was observed across all habitat types between both data collection times (Fig. 3a).

The mean number of large deadwood pieces per hectare increased from 1.9 pcs/ha (SE: 0.2) to 4.7 pcs/ha (SE: 0.3). This increase was further confirmed by a generalized linear mixed model (GLMM) analysis followed by an ANOVA (Supplement E4), which revealed high significant ($p < 0.001$) effects of habitat type and time on the number of large deadwood pieces per hectare.



c)

		resurvey			
		a	b	c	none
baseline survey	a	23	4	0	0
	b	46	46	5	0
	c	11	40	49	0

Fig. 3. Large deadwood: **a)** number of large deadwoods per hectare in baseline survey and resurvey as well as results of the Wilcoxon sign-rank test ((*) = $p \leq 0.1$, * = $p \leq 0.05$, ** = $p \leq 0.01$, *** = $p \leq 0.001$), **b)** proportion of polygons with deteriorated, unchanged and improved condition between baseline survey and resurvey, **c)** changes in the number of polygons in the value categories (a = excellent, b = medium, c = inadequate, none = polygon no longer meets the minimum criteria of this parameter) across all habitat types (see Supplement E3).

Abb. 3. Starkes Totholz: **a)** Anzahl des starken Totholzes pro Hektar in der Erst- (baseline survey, hellbraun) und Nachkartierung (= resurvey, dunkelbraun) sowie die Ergebnisse des Wilcoxon-Vorzeichen-Rang-Test ((*) = $p \leq 0{,}1$; * = $p \leq 0{,}05$; ** = $p \leq 0{,}01$; *** = $p \leq 0{,}001$), **b)** Anteil der Polygone mit verschlechtertem (rot), unverändertem (grau) und verbessertem Zustand (grün) zwischen Erst- und Nachkartierung, **c)** Veränderung der Anzahl der Polygone je Bewertungsstufe (a = ausgezeichnet, b = mittelmäßig, c = unzureichend, none = Polygon erfüllt nicht mehr die Mindestkriterien dieses Bewertungsparameters) über alle Lebensraumtypen hinweg (siehe Anhang E3).

Furthermore, these shifts prompted a reclassification of the polygons according to their respective value categories. 43.3% of the polygons showed an improvement in the evaluation, while a deterioration was observed in 4.0% and the rating remained constant in 52.7%. These changes were significant across habitat types ($n = 215$, $\chi^2 = 70.6$, $df = 2$, $p < 0.001$, Fig. 3b, c).

3.3 Tree species composition

Significant changes in tree species composition were identified across all habitat types between the baseline survey and the resurvey.

Significant differences among habitat types were identified by non-metric multidimensional scaling (NMDS) (F (4, 443) = 80.3, $p < 0.01$, $R^2 = 0.4$, Fig. 4) based on their main tree species. The ordination also revealed a small shift in tree species composition between the two data collection times (F (4, 446) = 4.9, $p < 0.01$, $R^2 = 0.01$). The centroids of almost all habitat types (9110, 9130, 9170, 91E0*) slightly shifted towards the center of the ordination indicating a beginning tree species homogenization among habitat types (Fig. 4). These compositional changes are also reflected in the increasing tree species diversity across canopy layers and for all habitat types (Table 4).

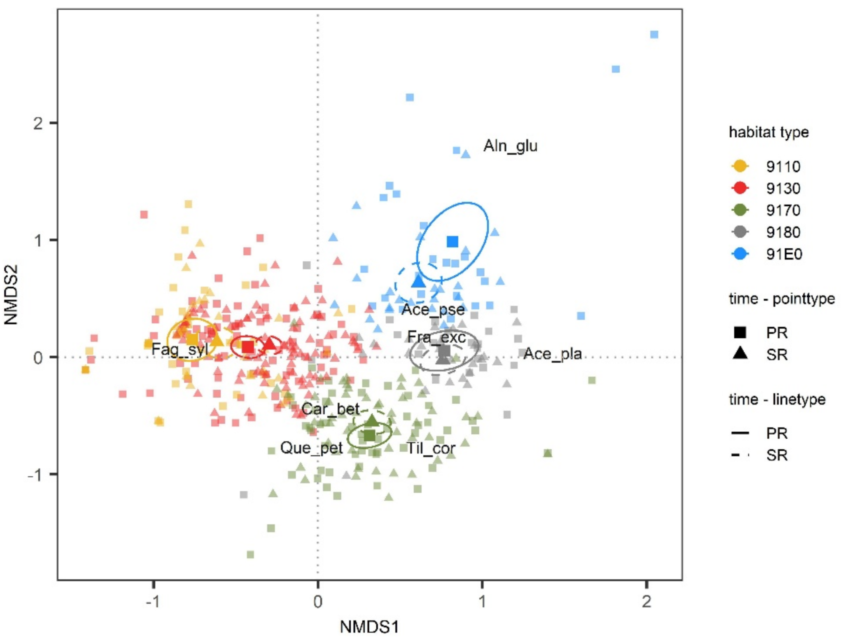


Fig. 4. NMDS (Stress: 0.2) based on percentage cover of tree species in each canopy layer and habitat type for baseline survey and resurvey. The diagram includes the confidence interval of the habitat types (ellipse) and the corresponding centroid. The displayed tree species are shown according to their proportion of the total stand.

Abb. 4. NMDS (Stress: 0,2) basierend auf dem Deckungsgrad der Baumarten in den jeweiligen Baumschichten und Lebensraumtypen in der Erstkartierung (baseline survey) und der Nachkartierung (resurvey). Dargestellt sind zudem die Vertrauensintervalle der Lebensraumtypen (Ellipse) und des entsprechenden Zentroids. Die angezeigten Baumarten werden entsprechend ihres Anteils am Gesamtbestand dargestellt.

Table 4. Mean Shannon index of habitat types' canopy layers (*n* = sample size) using rarefaction, for the baseline survey (B) and resurvey (R), as well as the results of the Wilcoxon sign-rank test (W, (*) = $p \leq 0.1$, * = $p \leq 0.05$, ** = $p \leq 0.01$, *** = $p \leq 0.001$).

Tabelle 4. Mittlerer Shannon-Index für die Baumschichten der Lebensraumtypen (*n* = Stichprobengröße) unter Verwendung von Rarefaction, für die Erstkartierung (B) und Nachkartierung (R), sowie die Ergebnisse des Wilcoxon-Vorzeichen-Rang-Test (W, (*) = $p \leq 0{,}1$; * = $p \leq 0{,}05$; ** = $p \leq 0{,}01$; *** = $p \leq 0{,}001$).

habitat type	*n*	time	total stand		canopy layer 1		canopy layer 2		canopy layer 3	
			mean	W	mean	W	mean	W	mean	W
9110	35	B	0.6 ± 0.1	**	0.4 ± 0.1	-	0.4 ± 0.1	**	0.4 ± 0.1	***
		R	0.7 ± 0.1		0.4 ± 0.1		0.6 ± 0.1		0.8 ± 0.1	
9130	84	B	0.9 ± 0.1	***	0.6 ± 0.0	***	0.8 ± 0.1	*	0.8 ± 0.1	-
		R	1.1 ± 0.0		0.7 ± 0.0		0.9 ± 0.0		0.9 ± 0.1	
9170	55	B	1.4 ± 0.0	***	0.8 ± 0.1	***	0.8 ± 0.1	*	1.2 ± 0.1	-
		R	1.5 ± 0.0		1.0 ± 0.1		1.0 ± 0.1		1.4 ± 0.1	
9180*	25	B	1.7 ± 0.0	***	1.3 ± 0.1	**	1.2 ± 0.1	*	1.4 ± 0.1	***
		R	1.9 ± 0.1		1.4 ± 0.1		1.4 ± 0.1		2.0 ± 0.0	
91E0*	25	B	1.2 ± 0.1	***	0.8 ± 0.1	-	0.9 ± 0.1	**	1.2 ± 0.1	***
		R	1.5 ± 0.1		0.9 ± 0.1		1.3 ± 0.1		1.8 ± 0.1	
total	224	B	1.1 ± 0.0	***	0.7 ± 0.0	***	0.8 ± 0.0	***	1.0 ± 0.0	***
		R	1.3 ± 0.0		0.8 ± 0.0		1.0 ± 0.0		1.2 ± 0.0	

Across all habitat types, there was a significant decline in the cover of the main tree species of canopy layer 1 (Fig. 5a, Table 5). We observed, a significant decrease of *Fagus sylvatica* in beech habitat types (9110, 9130), *Quercus petraea* in oak-hornbeam forests (9170), and *Fraxinus excelsior* in alluvial forests (91E0*) and in Tilio-Acerion forests (9180*).

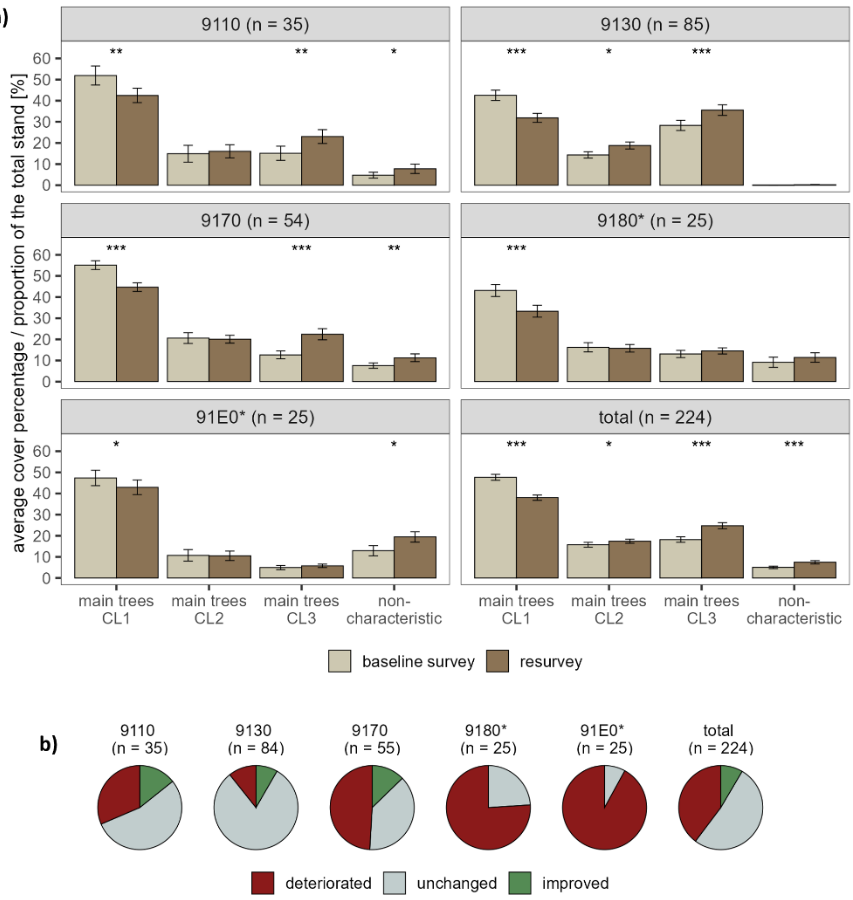
The main tree species within canopy layer 2 remained relatively stable across most habitat types (Fig. 5a, Table 5), except for 9130, where a significant increase in *Fagus sylvatica* was observed.

Concurrently, a significant increase of the main tree species in the tree regeneration (canopy layer 3) was documented across all habitat types (Fig. 5a), especially concerning *Fagus sylvatica* in beech forests (9110, 9130). In oak-hornbeam forests (9170), significant increases were only observed for *Carpinus betulus* and *Tilia cordata*, while *Quercus petraea* showed a low percentage of cover in this layer (Table 5).

Furthermore, non-characteristic tree species experienced a significant rise throughout the different habitat types across canopy layers (Fig. 5a). This was notably marked by a significant increase in *Fagus sylvatica*, particularly in habitat type 9170 and 91E0*, primarily due to robust regeneration of this species (Table 5).

The changes in tree species composition resulted in an improvement of the evaluation for 8.5% of the polygons, while the evaluation rating deteriorated for 39.7% and remained the same for 51.8% of the polygons (Fig. 5b, c). Significant differences were found in the conservation status assessments across all habitat types ($n = 215$, $\chi^2 = 34.0$, $df = 2$, $p < 0.001$, Fig. 5c).

a)



c)

		resurvey			
		a	b	c	none
baseline survey	a	82	37	27	6
	b	11	16	16	3
	c	6	2	18	0

Fig. 5. Tree species composition: **a)** Percentage cover of the main tree species in the three canopy layers (CL) and the proportion of non-characteristic species in the total stand between baseline survey and resurvey as well as results of the Wilcoxon sign-rank test ((*) = $p \leq 0.1$, * = $p \leq 0.05$, ** = $p \leq 0.01$, *** = $p \leq 0.001$), **b)** proportion of polygons with deteriorated, unchanged and improved condition between baseline survey and resurvey, **c)** changes in the number of polygons in the value categories (a = excellent, b = medium, c = inadequate, none = polygon no longer meets the minimum criteria of this parameter) across all habitat types (see Supplement E3).

Abb. 5. Gehölzarteninventar: **a)** Deckungsgrade der Hauptbaumarten in den drei Baumschichten (CL) und dem Anteil am Gesamtbestand der nicht-charakteristischen Baumarten zwischen Erst- (baseline survey, hellbraun) und Nachkartierung (resurvey, dunkelbraun) sowie die Ergebnisse des Wilcoxon-Vorzeichen-Rang-Test ((*) = $p \leq 0{,}1$; * = $p \leq 0{,}05$; ** = $p \leq 0{,}01$; *** = $p \leq 0{,}001$), **b)** Anteil der Polygone mit verschlechtertem (rot), unverändertem (grau) und verbessertem Zustand (grün) zwischen Erst- und Nachkartierung, **c)** Veränderung der Anzahl der Polygone je Bewertungsstufe (a = ausgezeichnet, b = mittelmäßig, c = unzureichend, none = Polygon erfüllt nicht mehr die Mindestkriterien dieses Bewertungsparameters) über alle Lebensraumtypen hinweg (siehe Anhang E3).

Table 5. Presentation of the mean proportions of the total stand and the mean percentage cover of the tree species (main tree species = underlined, non-characteristic = blue) in the three canopy layers for the baseline survey (BS) and resurvey (RS). The status of the tree species is given as a result of the winner-looser analysis (w = winner, l = looser, s = stable, i = immigrant, a = absentees). The results of the Wilcoxon signed-rank test are included ((*) = $p \leq 0.1$, * = $p \leq 0.05$, ** = $p \leq 0.01$, *** = $p \leq 0.001$).

Tabelle 5. Darstellung der mittleren Anteile am Gesamtbestand und der mittleren Deckungsgrade der Baumarten (Hauptbaumarten = unterstrichen, nicht-charakteristische Arten für den Lebensraumtyp = blau) in den drei Baumschichten für die Erstkartierung (BS) und Nachkartierung (RS); Status der Baumart als Ergebnisse der Gewinner-Verlierer-Analyse (w = Gewinner, l = Verlierer, s = stabil, i = Einwanderer, a = Abwesende); Ergebnissen des Wilcoxon-Vorzeichen-Rang-Test ((*) = $p \leq 0,1$; * = $p \leq 0,05$; ** = $p \leq 0,01$; *** = $p \leq 0,001$).

tree species	total stand			canopy layer 1			canopy layer 2			canopy layer 3		
	mean		status	mean		status	mean		status	mean		status
	BS	RS		BS	RS		BS	RS		BS	RS	
9110												
Fag syl	79.3	79.8	s	55.1	45.1	l **	19.7	20.1	s	14.5	23.2	w **
Ace pse	7.6	9.9	s	7.0	6.5	s	7.0	9.0	s	1.5	4.1	s
Ace pla	0.0	4.8	s	-	-	-	-	5.0	i	-	-	-
Car bet	11.9	18.2	s (*)	7.5	7.3	s	4.9	6.0	s	2.8	6.5	s
9130												
Fag syl	68.9	67.5	s	43.9	33.0	l ***	14.6	20.3	w **	29.1	36.3	w ***
Ace pla	1.3	3.6	s	-	-	-	2.7	0.3	s	-	7.0	i
Ace pse	7.9	9.6	s	5.5	10.5	w **	3.1	5.4	w *	9.2	9.0	s
Car bet	9.5	17.0	w ***	6.1	7.5	s	5.7	8.8	w ***	5.2	12.1	w ***
9170												
Car bet	29.9	33.9	w **	19.8	15.3	s (*)	18.7	18.4	s	8.3	17.0	w ***
Que pet	35.7	26.9	l ***	40.4	32.8	l ***	7.5	7.0	s	6.0	6.7	s
Til cor	16.9	18.8	s (*)	11.9	12.0	s	9.0	8.6	s	12.3	18.2	w **
Ace pla	1.3	5.3	w *	-	5.0	i	0.3	2.3	w *	1.9	5.8	w *
Ace pse	9.9	14.9	w **	5.9	10.1	s (*)	3.8	5.0	s	11.1	17.1	w **
Fag syl	9.3	14.1	w **	5.7	8.2	s	5.7	5.4	s	5.4	12.3	w **
9180*												
Ace pla	8.5	9.6	s	7.0	4.0	s	4.0	5.0	s	3.4	5.4	w *
Ace pse	17.9	18.9	s	11.6	10.9	s	5.3	5.9	s	3.5	5.0	w *
Fra exc	33.3	22.7	l ***	21.7	13.0	l ***	9.4	8.0	s	7.6	5.4	s
Til cor	18.1	19.3	s	14.2	15.3	s	5.4	5.9	s	3.6	5.1	s (*)
Til pla	16.9	12.7	s	17.8	11.8	s	4.8	4.3	s	-	5.0	i
Ulm gla	4.6	4.2	s	-	-	-	3.7	2.1	s (*)	3.0	3.3	s
Car bet	10.9	15.6	w ***	7.4	6.9	s	5.6	7.8	w **	2.3	6.3	w ***
Fag syl	10.5	12.1	s	7.4	6.6	s	5.5	4.8	s	3.0	7.6	w **
91E0*												
Aln glu	54.1	53.6	s	39.3	41.2	s	9.0	11.0	w **	3.9	5.8	s (*)
Fra exc	22.4	8.9	l **	18.6	8.5	l ***	6.3	1.2	l *	2.8	1.8	s
Pru pad	2.8	0.8	s	-	-	-	3.0	-	a	3.0	1.5	s
Ace pla	4.7	8.8	s	5.0	6.5	s	-	1.0	i	-	4.0	i
Ace pse	18.1	25.0	w **	10.5	13.1	w *	5.6	7.6	w **	3.7	8.4	w ***
Car bet	6.1	9.3	w *	6.8	4.0	s (*)	3.5	5.4	w **	2.1	5.2	w **
Fag syl	5.6	13.3	w ***	6.8	6.8	s	1.9	5.2	w **	2.1	9.1	w ***

Nine polygons were unassignable to any status category (a, b, c) as the trees species composition no longer met the minimum criteria for habitat type classification. These were mainly polygons of the habitat type 91E0* (seven polygons) and one polygon each of habitat types 9170 and 9180*. Two main reasons led to the loss of the habitat type status of 91E0*. Firstly, the proportion of the main tree species in the stand fell below 30%, primarily driven by a decrease in the portion of common ash (*Fraxinus excelsior*) in the first canopy layer. Secondly, non-characteristic species exceeded 30% of the stand, mainly due to the increases in *Fagus sylvatica* and *Carpinus betulus* in the third canopy layer. In habitat type 9170, the main tree species dropped below 30% of the stand, while in habitat type 9180*, non-characteristic species, predominantly *Fagus sylvatica*, accounted more than 30%.

3.4 Vitality parameters

Our analysis indicates that stand structure parameters exert a greater influence on crown defoliation compared to site parameters.

The site parameters (Fig. 6a) had a minimal effect on mean crown defoliation, although drier, steeper, and south-facing polygons showed a significantly higher crown defoliation.

In contrast, stand structure parameters (Fig. 6b) significantly impacted the mean crown defoliation, with increased defoliation in older development stages, with greater relative crown distance, for dominant trees, and in stands with *Fagus sylvatica* and *Quercus petraea* compared to the group of other tree species.

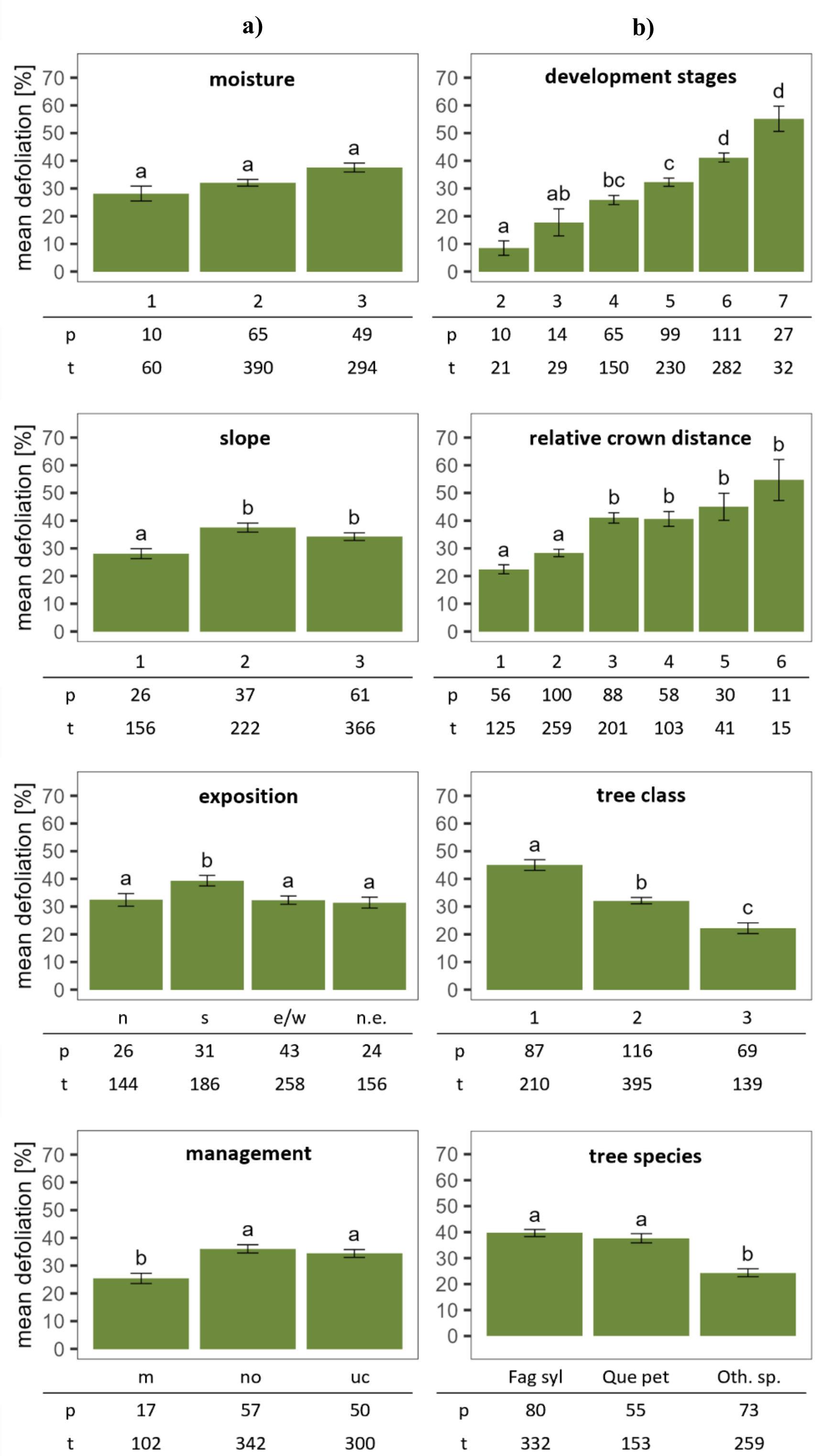
Generalized linear mixed model (GLMM) followed by an ANOVA (Supplement E5) analysis confirmed high significant effects ($p < 0.001$) of development stages, relative crown distance, and tree species. Tree class, moisture, and exposition showed marginal significance ($p < 0.1$), whereas slope and management had no significant effect.

4. Discussion

Global changes cause a transformation of forest ecosystems, species losses, geographical shifts and changes in communities (Keeley et al. 2018, Fischer et al. 2019), e.g., desynchronization in the interaction between species, changes in competitive conditions and changes in the abiotic conditions of habitats in Europe (European Commission 2013b). Furthermore, the aforementioned changes have also impacted Natura 2000 sites (Dempe et al. 2012).

Alteration in habitat types

Our results show notable alterations in the forest stand structure and tree species composition of the observed habitat types in the Harz Mountains and Harz Foothills. As postulated, the coverage of the first canopy layer, comprising large and mature trees, decreased. This is also reflected in increased crown defoliation and dieback events, which have resulted in an increase in deadwood. In general, larger trees are more susceptible to the effects of drought than smaller trees due to hydraulic limitation, which are attributed to the height of the trees, the larger transpiring crown, and increased radiation exposure (Ryan et al. 2006, McDowell et al. 2008, Bennett et al. 2015, McDowell & Allen 2015). The opening up of the upper canopy fostered the lower vegetation layers, including tree regeneration (Collet et al. 2002, Mihók et al. 2005, Collet & Chenost 2006, Bobiec 2007, Tinya et al. 2019, Thom et al. 2023).


a)
b)
mean defoliation [%]
moisture
a a a
1 2 3
p 10 65 49
t 60 390 294
development stages
a ab bc c d d
2 3 4 5 6 7
p 10 14 65 99 111 27
t 21 29 150 230 282 32
slope
a b b
1 2 3
p 26 37 61
t 156 222 366
relative crown distance
a a b b b b
1 2 3 4 5 6
p 56 100 88 58 30 11
t 125 259 201 103 41 15
exposition
a b a a
n s e/w n.e.
p 26 31 43 24
t 144 186 258 156
tree class
a b c
1 2 3
p 87 116 69
t 210 395 139
management
b a a
m no uc
p 17 57 50
t 102 342 300
tree species
a a b
Fag syl Que pet Oth. sp.
p 80 55 73
t 332 153 259
0 10 20 30 40 50 60 70

Contrary to our fourth hypothesis, the tree species composition underwent significant changes during the relatively short observation period of ten years. Buras & Menzel (2018) also posit that there will be a future shift in the composition of tree species. As evidenced by our research, the proportions of hornbeam (*Carpinus betulus*) and sycamore (*Acer pseudoplatanus*) increased in the observed habitat types. Additionally, the proportion of European beech (*Fagus sylvatica*) increased in both habitat types 91E0* (alluvial forests) and 9170 (oak-hornbeam forests) where it is not characteristic. The increase of beech in alluvial forests can be attributed to two factors: frequent beech regeneration and an indirect increase caused by ash dieback. It is also possible that the regeneration of *Fagus sylvatica* is the result of site-specific factors. Firstly, the habitat type 9170 has mainly developed on former beech sites due to anthropogenic use (Demant et al. 2024). Secondly, habitat type 91E0* occurs in narrow stream valleys, allowing beech to grow in higher-lying stream areas. As a result of the increased proportions of *Carpinus betulus* and *Fagus sylvatica*, there was a notable decline in the number of polygons classified as habitat type 91E0*.

The observed changes may be attributed to high temperatures and dry summers (Schuldt et al. 2020). In Europe, the 2003 heatwave was long considered as the most severe drought event over the last century (Fink et al. 2004, García-Herrera et al. 2010). Despite this, long-term forest stand surveys have shown no significant structural changes (Kudernatsch et al. 2019, Günther et al. 2021) or crown defoliation (Dammann et al. 2010) from that period. In contrast, the droughts in 2018 and 2019 (Vogel et al. 2019, Hari et al. 2020) have exerted an even more pronounced impact on forests across many regions in Europe (Buras et al. 2020). In Saxony-Anhalt, the mean annual temperature in both years was 2.4 °C above the long-term average (1961–1990), ranking them among the warmest years on records (Sutmöller 2018, 2019). Precipitation in 2018 was only 45% of the typical amount for the vegetation period (Sutmöller 2018), and insufficient groundwater regeneration during the winter of 2018/2019 led to another drought year in 2019 (Boergens et al. 2020). Such extreme conditions had not yet occurred in Saxony-Anhalt prior 2018 and 2019. Since the amount of precipitation and its distribution over the year, as well as temperature dynamics, are significant factors influencing the vitality of trees (Dulamsuren et al. 2017, Knutzen et al. 2017, Móricz et al. 2021), it seems plausible to attribute the observed changes primarily to the recent disturbance events caused by exceptional drought. However, there might be

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Fig. 6. Mean crown defoliation for **a)** site parameters (moisture, slope, exposition, management) and **b)** stand parameters (development stages, relative crown distance, the tree class according to Kraft, tree species (Fag syl = *Fagus sylvatica*, Que pet = *Quercus petraea*, Oth. sp. = other species)) (see Table 3). The sample size for both the number of polygons (p) and the number of trees (t) is given under the appropriate diagrams. Results of the Kruskal-Wallis-Test in letters (different letters = significant differences) above the bars.

Abb. 6. Mittlere Kronenverlichtung für **a)** Standortparameter (Feuchte, Hangneigung und Exposition, Bewirtschaftung) und **b)** Bestandesparameter (Wuchsklasse, Kronenschlussgrad und Kraft'sche Baumklasse und Baumart (Fag syl = *Fagus sylvatica*, Que pet = *Quercus petraea*, Oth. sp. = andere Baumarten)) (siehe Tabelle 3). Der Stichprobenumfang sowohl für die Anzahl der Polygone (p) als auch für die Anzahl der Bäume (t) wurde unter den entsprechenden Diagrammen angegeben. Ergebnisse des Kruskal-Wallis-Tests als Buchstaben (verschiedene Buchstaben = signifikante Unterschiede) über den Säulen.

the recent disturbance events caused by exceptional drought. However, there might be additional factors, such as natural successional process or forest management, that should also be taken into account. For instance, in later forest succession stages temporary openness can occur due to natural decay causing the death of canopy trees or accumulation of deadwood. Created gaps allow for increased light penetration to the understory layers (Bobiec et al. 2000, Franklin et al. 2002, Drößler & Meyer 2006).

Management practices may also have contributed to the observed alterations (Keren et al. 2018, Willim et al. 2022). Previous research indicates that management can negatively affect the variability of stand structure features such as tree size diversity (Dieler et al. 2017), and the quantity and quality of deadwood (Kapusta et al. 2020, Hansen et al. 2023). Other studies also found changes as a result of the abandonment of management, especially, in oak-hornbeam-forests (habitat type 9170, Vollmuth 2021). These changes include an increase in *Fagus sylvatica* within strict forest nature reserves (Schmidt 2000, Dölle et al. 2013, Heinrichs et al. 2021), and shifts in species composition in forests previously managed as coppice or coppice-with-standards, which continue to impact their current state (Vacek et al. 2019). As these stands are left to spontaneous development, alterations in the tree species composition and stand structure have been documented often leading to a reduction in the main tree species proportion and an increase in non-characteristic species (Müllerová et al. 2015, Kudernatsch et al. 2019, Vančura et al. 2022).

Unfortunately, many of the aforementioned aspects could not be investigated in greater depth in our study mainly because polygon boundaries do not coincide with forest management units which led to a lack in comprehensive data on stand history and only limited information on forest management practices. Given its importance, future research should explicitly take forestry interventions into account to reveal factors that foster resistance and resilience as well as predisposing factors regarding disturbance events and climate change (e.g., Seidl et al. 2011, Thom et al. 2013, Aszalós et al. 2022).

Diseases or pathogens affecting specific tree species have also contributed to the observed changes. For instance, the effects of ash dieback which can be seen also in Natura 2000 sites (Östbrant et al. 2017). This condition has caused shifts in tree species composition and canopy cover. Specifically, *Fraxinus excelsior* declined in the tree layer, while its regeneration has increased, leading to reduced overall tree layer cover (Schei et al. 2024).

In general, the discussed influencing factors also affect each other. Certain management practices may either impair or enhance the resilience of the stand with respect to climate change (Antonucci et al. 2021, Petritan et al. 2021, Meyer et al. 2022, Huth et al. 2025).

Future development of forest habitat types, conservation objectives & monitoring

Climate change is expected to increasingly affect Europe's protected areas (Badeck et al. 2007, Reichmuth et al. 2025) and habitat types (Petermann et al. 2007, Demant et al. 2024), however, impacts will probably vary in the different habitat types.

While several vegetation and tree distribution models projected that beech forests will more or less persist even under climate change (Hickler et al. 2012, Beierkuhnlein et al. 2014, Mauri et al. 2022), other models yielded contradictory results (Hanewinkel et al. 2014, Knutzen et al. 2017, Buras & Menzel 2018, Thurm et al. 2018, Del Martinez Castillo et al. 2022, Hinze et al. 2023). In the context of the current discussion, our study indicates that the proportion of *Fagus sylvatica* in the total stand appears to remain stable in beech forests. Although its proportion in the upper canopy layer is declining, its proportion in the understory is increasing.

Similarly, the impact of climate change on slope ravine forests (9180*) is challenging to ascertain. One reason for this is that the habitat type encompasses a range of environments including both cool, moist and warm, dry types (LAU 2014). It seems probable that climate change will have an intensified negative impact on the wetter types (Müller-Kroehling et al. 2007, Demant et al. 2024). Conversely, there is the possibility of an increase in the warm, dry characteristics (Ewald 2009). In our study, the proportion of the main tree species in the total stand, except *Fraxinus excelsior*, remained stable. However, there was an increase of *Fagus sylvatica* in the understory, which is a non-characteristic species for this habitat type in Saxony-Anhalt. This shift could potentially result in the loss of habitat type status in the future, highlighting the need for careful monitoring.

One habitat type likely benefitting from climate change is the oak-hornbeam forest (9170) (Müller-Kroehling et al. 2007). The majority of studies assume a low climate sensitivity for this habitat type (Petermann et al. 2007, Demant et al. 2024). Additionally, it may benefit indirectly from the reduced competitive power of beech (Demant et al. 2024) and dry periods in summer (Hölzel 2009). However, it is a maintenance-dependent habitat type (Demant et al. 2024) that only occurs in patches, which limits its capacity to adapt to climate change (Ewald 2009). Nevertheless, our results indicate stable proportions of the main tree species *Carpinus betulus* and *Tilia cordata* in the total stand, along with an increase of the non-characteristic species *Fagus sylvatica* in the understory. We also identified a lack of oak regeneration in the oak-hornbeam-forests (9170), which is a prevalent issue (Schmidt 2000, Dölle et al. 2013, Heinrichs et al. 2021). Regeneration is influenced by various site- and stand-specific variables and their interactions (Annighöfer et al. 2015), as well as by developmental stages (Petritan et al. 2025). Light availability is a primary factor, however, browsing pressure, competition in the understory, and ground vegetation cover also exert significant influence (e.g., Rumiantsev et al. 2018, Kohler et al. 2020). Current canopy mortality alone does not improve oak regeneration due to a dark understory and should be paired with a species-selective understory thinning (Lenk et al. 2025) and deer exclosures.

Alluvial forests may benefit from increased flooding frequency following heavy rainfall events and summer heat (Müller-Kroehling et al. 2007, Hölzel 2009). Conversely, there is a risk of desiccation (Ewald 2009, Demant et al. 2024). Additionally, the death of ash trees, one of the two main tree species, due to *Hymenoscyphus fraxineus* calamities represents another challenge (Langer et al. 2022) that also caused a loss of habitat type status of polygons in our study. Furthermore, the increase of the non-characteristic species *Fagus sylvatica* in the understory underscores the importance of ongoing monitoring and probably also the need of restoration activities.

There is currently no consensus on how to address the changes in habitat types in terms of their characteristics and distribution (Brunzel & Hill 2022, Ewald et al. 2022).

The Habitats Directive aims to maintain a favorable conservation status across biogeographic regions (Art. 2, para. 2, 91/43/ECC), but climate change is likely to alter habitat distribution (Fischer et al. 2019). Some authors argue for more flexibility in the Directive, particularly in terms of management (Koning et al. 2014) and phased conservation area designation, which could allow for the de-designation of areas that no longer meet conservation goals (Hendler et al. 2010, Alagador et al. 2014). Conversely, an increase in flexibility may result in a reduction in the level of protection currently afforded to these habitats (Winkel et al. 2015). In contrast, Koning et al. (2014) and Winkel et al. (2015)

emphasized the necessity for more rigorous conservation measures to adapt to climate change and enhance the resilience of protected area networks. Others argue that the Directive is already adequately flexible (e.g., Ewald et al. 2022).

Given the uncertainties, the monitoring of Natura 2000 sites and habitat types will become increasingly important in the future. In this study, we used existing data from the HD recording and assessed the status of the habitat types based on established guidelines. Despite limitations such as a restricted repertoire of methods, this approach successfully ensured the comparability of the newly collected data with field data from about a decade earlier by using a consistent methodology. These data, available on a large scale, are essential for rapid assessment of forest conditions in Natura 2000 sites, especially in the context of climate change. We therefore recommend more frequent use of existing monitoring data in current research to detect changes in habitat type characteristics and to inform evidence-based discussion on the potential flexibility of the Habitat Directive (Geyer et al. 2015).

Finally, to effectively address climate change impacts it is essential to expand the range of methods, e.g. by satellite data analysis or airborne images (Vanden Borre et al. 2011, Kissling et al. 2024), and to incorporate data sources like forest management plans (Alterio et al. 2023) into regular monitoring activities.

Erweiterte deutsche Zusammenfassung

Einleitung – In den Wäldern in Deutschland sind in den letzten Jahren deutliche Störungen und Veränderungen zu beobachten. Zu diesen zählen sowohl Absterbeereignisse und Strukturveränderungen (z. B. Buras et al. 2020, Schuldt et al. 2020, Kacic et al. 2023) als auch die Zunahme von Vitalitätseinschränkungen an Einzelbäumen (z. B. BMEL 2019, 2020, Brun et al. 2020, Rohner et al. 2021).

Jedoch untersuchten bisherige Studien nicht explizit die Veränderungen in europarechtlich geschützten Waldhabitaten des europäischen Schutzgebietsnetzes Natura 2000. Dies ist jedoch von besonderem Interesse, da Fauna-Flora-Habitat-Schutzgebiete (FFH-Gebiete) mit dem Ziel ausgewiesen worden sind, natürliche Lebensraumtypen von gemeinschaftlichem Interesse langfristig zu erhalten (Richtlinie 92/43/EWG). Darüber hinaus gibt es vor dem Hintergrund von Klimawandel und den Auswirkungen von Trockenheit und Dürre auf Waldbestände durchaus bereits Forderungen nach einer Flexibilisierung der FFH-Richtlinie in Bezug auf Management und Ausweisung von Schutzgebieten oder Lebensraumtypen (Hendler et al. 2010, Alagador et al. 2014, Schabel et al. 2024).

Vor ungefähr einem Jahrzehnt wurden in vielen Natura 2000-Gebieten Erhebungen zum Status Quo der Lebensraumtypen, einschließlich einer qualitativen Bewertung ihres Zustandes (a = hervorragende Ausprägung, b = mittlere Ausprägung, c = schlechte Ausprägung), durchgeführt (= Erstkartierung, 2009 bis 2015). Anhand dieser Daten wurden Veränderungen der Struktur und Baumartenzusammensetzung verschiedener Waldlebensraumtypen in Sachsen-Anhalt untersucht. Dafür wurden in ausgewählten Beständen in den Jahren 2021 und 2022 Daten zur Bestandsstruktur, zum Totholzvorkommen und zur Baumartenzusammensetzung mit der gleichen Aufnahmemethodik wie in der Erstkartierung gesammelt (= Nachkartierung). Es wurden folgende Veränderungen angenommen: (1) Abnahme der Deckung der oberen Baumschicht, (2) Zunahme der Anzahl von starkem Totholz pro Hektar, (3) Zunahme der Deckung der Verjüngung sowie (4) keine Veränderung der Baumartenzusammensetzung im Gesamtbestand, d. h. unter Einbeziehung aller Baumschichten. Diese Veränderungen wirken sich außerdem auf die Ergebnisse der qualitativen Bewertung der Lebensraumtypen aus.

Material und Methoden – Die Untersuchungen wurden im Harz und Harzvorland in Sachsen-Anhalt in vier Natura 2000-Gebieten (FFH-Gebiete, Abb. 1) und in den folgenden fünf ausgewählten Waldlebensraumtypen (LRT, siehe Tab. 1) durchführt: Hainsimsen-Buchenwälder (9110), Waldmeister-Buchenwälder (9130), Labkraut-Eichen-Hainbuchenwälder (9170), Schlucht- und Hangmischwälder (9180*) und Erlen- und Eschenwälder an Fließgewässern (91E0*).

Im Rahmen der Erstkartierung wurden entsprechend der Kartierungsanleitung des Landes Sachsen-Anhalt (LAU 2014) ähnliche Waldbestände anhand qualitativer Merkmale, wie Bestandesstruktur (z. B. Schichtung und Totholz), Artenzusammensetzung und Beeinträchtigungen (z. B. Wildverbiss, Vorkommen nicht-heimischer Arten) abgegrenzt (= Polygone) und den verschiedenen Waldlebensraumtypen zugeordnet. Je nach Ausprägung dieser Merkmale wurden die Polygone drei vordefinierten Wertekategorien (a, b, c) zugeordnet.

Die Daten der Erstkartierung (n = 1353 Polygone) bildeten die Grundlage für eine randomisiert-stratifizierte Stichprobenziehung. Dazu wurden je LRT die Bewertungskategorien des Gesamterhaltungszustands (Beschreibung für den allgemeinen Zustand des Waldbestandes) und des Parameters Bestandsstruktur (Beschreibung der Altersstruktur des Waldbestandes) kombiniert, sodass sich neun Straten (siehe Anhang E2) ergaben. Für jedes Stratum wurden i.d.R. sieben Polygone von einer Größe zwischen 1 und 5 Hektar ausgewählt, sodass insgesamt mindestens 10 % der Fläche des jeweiligen Stratums je LRT kartiert wurden. Insgesamt wurden 224 Polygone ausgewählt (Abb. 1).

In diesen Polygonen wurde eine erneute Datenaufnahme nach LAU (2014) durchgeführt. Erfasst und bewertet wurden: (1) Bestandsstruktur, Deckung der Baumschichten und vordefinierte Wuchsklassen, (2) Anzahl starken Totholzes pro Hektar, (3) Gehölzarteninventar (Tab. 2, Anhang E3). Zusätzlich erfolgte (4) die Erfassung der Vitalität ausgewählter Einzelindividuen durch die Einschätzung der Kronenverlichtung (Meining et al. 2007).

Für die Untersuchung der Baumartenzusammensetzung wurde zum einen eine NMDS (Nicht-Metrische Multidimensionale Skalierung) mit den Deckungsgraden der Baumarten in drei Baumschichten gerechnet. Zum anderen wurde eine Analyse der Gewinner- und Verlierer-Hauptbaumarten sowohl mit dem Anteil am Gesamtbestand als auch mit den Deckungsgraden der Baumarten in den einzelnen Baumschichten durchgeführt.

Außerdem wurden die möglichen Veränderungen in der Verteilung der Wertekategorien der Parameter mit einem Randhomogenitätstest untersucht.

Eine Analyse möglicher Einflussfaktoren (Tab. 3) auf die Kronenverlichtung erfolgte durch ein GLMM (generalisiertes lineares gemischtes Modell).

Ergebnisse – Es konnten deutliche Veränderungen in der Struktur und Artenzusammensetzung der untersuchten Lebensraumtypen zwischen den beiden Erfassungen festgestellt werden.

So wurde ein signifikanter Rückgang der Deckung der oberen Baumschicht beobachtet, während gleichzeitig die Deckung der Verjüngung signifikant zunahm (Abb. 2).

Außerdem konnte eine signifikante Zunahme in der Anzahl starken Totholzes je Hektar festgestellt werden (Abb. 3).

Die NMDS-Analyse verdeutlichte eine Trennung der Lebensraumtypen entsprechend ihrer Hauptbaumarten. Gleichzeitig zeigte sich auch eine leichte Annäherung der Lebensraumtypen hinsichtlich ihrer Baumartenzusammensetzung zwischen der Erstkartierung und der Nachkartierung (Abb. 4).

Des Weiteren konnte festgestellt werden, dass die Deckungsgrade der meisten Hauptbaumarten in der oberen Baumschicht signifikant zurückgingen, während gleichzeitig die Deckungsgrade der meisten Hauptbaumarten in der Verjüngung signifikant zunahmen (Abb. 5, Tab. 5). Außerdem nahm der Anteil nicht-lebensraumtypischer Arten signifikant zu. Hervorzuheben ist dabei die Zunahme von *Fagus sylvatica* am Gesamtbestand in den Eichen-Hainbuchen-Wäldern (LRT 9170) und den Auenwäldern (LRT 91E0*), die vor allem durch eine starke Verjüngung dieser Art bedingt ist (Tab. 5).

Der Randhomogenitätstest zeigte für alle untersuchten Parameter signifikante Veränderungen in der Verteilung der Wertekategorien zwischen den beiden Kartierungen. Insgesamt erfüllten neun Polygone in der Nachkartierung nicht mehr die Kriterien eines Lebensraumtyps. Mehrheitlich handelte es sich hierbei um den Lebensraumtyp 91E0*.

Die Analyse der Einflussfaktoren auf die Kronenverlichtung ergab, dass vor allem die Bestandesparameter (Wuchsklasse, Kronenschlussgrad) und die Baumart einen signifikanten Einfluss haben. Im Gegensatz dazu zeigten Standortparameter und Bewirtschaftung keinen signifikanten Einfluss (Abb. 6, Anhang E5).

Diskussion – Insgesamt konnten deutliche Veränderungen in der Struktur und Zusammensetzung der Wälder in den untersuchten Natura 2000-Gebieten festgestellt werden. Der Rückgang der oberen Baumschicht sowie die Zunahme von starkem Totholz sind auf Absterbeereignisse und Vitalitätseinbußen der älteren Bäume zurückzuführen (z. B. Ryan et al. 2006, Bennett et al. 2015). Durch das geöffnete Kronendach kommt es folglich zu mehr Lichteinstrahlung auf den Boden, wodurch die Verjüngung profitiert (z. B. Tinya et al. 2019, Thom et al. 2023). Die Veränderungen in der Baumartenzusammensetzung zeigen sich zum Teil in der deutlichen Zunahme von *Acer pseudoplatanus*, *Carpinus betulus* und *Fagus sylvatica*.

Als mögliche Erklärung für die festgestellten Veränderungen kommt die Trockenheit der Jahre 2018 und 2019 (Vogel et al. 2019, Hari et al. 2020) in Betracht, von der Sachsen-Anhalt besonders betroffen war (Sutmöller 2018, 2019). Da die Verteilung und Menge von Niederschlägen sowie die Temperatur die Vitalität von Bäumen beeinflusst (Dulamsuren et al. 2017, Knutzen et al. 2017), scheint es plausibel dies als ein Hauptfaktor anzunehmen. Aber auch weitere Faktoren, wie natürliche Sukzessionsprozesse oder die Waldbewirtschaftung sollten ebenfalls berücksichtigt werden. So kommt es im Laufe der natürlichen Sukzession in der Zerfallsphase ebenfalls zu Kronendachöffnungen, die in einer erhöhten Menge an Totholz und einer verstärkten Verjüngung resultieren (Bobiec et al. 2000, Drößler & Meyer 2006). Studien konnten außerdem zeigen, dass sowohl die Bewirtschaftung (Dieler et al. 2017, Kapusta et al. 2020, Willim et al. 2022) als auch deren Aufgabe (Müllerová et al. 2015, Schmidt 2000, Dölle et al. 2013) zu Veränderungen in der Bestandesstruktur und Artenzusammensetzung führen.

Der Klimawandel wird voraussichtlich erhebliche Auswirkungen auf die Schutzgebiete (u. a. Reichmuth et al. 2025) und Lebensraumtypen (u. a. Demant et al. 2024) in Europa haben. Es gibt jedoch keinen Konsens darüber, wie auf strukturelle und artbezogene Veränderungen in Lebensraumtypen reagiert werden soll (Koning et al. 2014, Ewald et al. 2022). Einige fordern Anpassungen der FFH-Richtlinie für mehr Flexibilität in der Bewirtschaftung und Ausweisung von Schutzgebieten (Hendler et al. 2010, Alagador et al. 2014), während andere befürchten, dass dies die Schutzbemühungen schwächen könnte (u. a. Winkel et al. 2015). Im Gegensatz dazu wird argumentiert, dass strengere Naturschutzmaßnahmen notwendig sind, um die Anpassungsfähigkeit und Widerstandsfähigkeit von Schutzgebietsnetzen zu erhöhen (Koning et al. 2014, Winkel et al. 2015). Trotz der festgestellten Veränderungen innerhalb der Lebensraumtypen, geben die Ergebnisse dieser Studie derzeit keinen Anlass, die Schutzgüter oder die Vorgaben der FFH-Richtlinie in Frage zu stellen.

Aufgrund der beobachteten Veränderungen der untersuchten Lebensraumtypen, der unvorhersehbaren Entwicklung der Lebensraumtypen mit fortschreitendem Klimawandel (Müller-Kroehling et al. 2007, Petermann et al. 2007, Hölzel 2009, Demant et al. 2014) und des langsamen Baumwachstums ist ein räumlich und zeitlich engmaschigeres Monitoring als bisher notwendig. Darüber hinaus ist es von entscheidender Bedeutung das Spektrum der Methoden zu erweitern, z. B. durch die Auswertungen von Satelliten- und Luftbildern (Vanden Borre et al. 2011, Kissling et al. 2024), und diese in regelmäßigen Monitoring-Aktivitäten einzubeziehen, um den Auswirkungen des Klimawandels besser Rechnung zu tragen.

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Authors contributions

The authors confirm contributions to the paper as follows: study conception: AB, DO, HW, TK; data and sample collection: DO, HW, TK, ML; analysis: HW, DO with inputs from AB; interpretation of the results: HW, AB, PM; draft manuscript preparation: HW, PM, AB; funding acquisition and project administration: AB, DO. All authors reviewed the results and approved the final version of the manuscript.

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Supplements

Additional supporting information may be found in the online version of this article.

Zusätzliche unterstützende Information ist in der Online-Version dieses Artikels zu finden.

Supplement E1. Site conditions of the selected Natura 2000 sites, including the years of the previous HD recording and the number of forest polygons recorded in these areas.
Anhang E1. Standortbedingungen der ausgewählten Natura 2000-Gebiete, inklusive der Jahre der ersten FFH-Kartierung und der Anzahl der in diesen Gebieten erfassten Polygone.

Supplement E2. Overview of the nine sampling strata: a combination of conservation status and parameter "layering and development stages" (Supplement E3).
Anhang E2. Übersicht der neun Stichprobenstraten: eine Kombination des Gesamterhaltungszustandes und dem Parameter Bestandsstruktur (Anhang E3).

Supplement E3. Simplified overview of the value categories ("a", "b", "c") used to evaluate the investigated parameters of the habitat types under consideration (LAU 2014).
Anhang E3. Vereinfachte Übersicht über die Wertestufen ("a", "b", "c", siehe Abschnitt 2.2.) für die Bewertung der untersuchten Parameter (LAU 2014).

Supplement E4. Results of the GLMM and subsequent ANOVA showing the main predictors on the structural parameters (cover of the three canopy layers and deadwood occurrence).
Anhang E4. Ergebnisse des GLMM und der anschließenden ANOVA, die die Haupteffekte der Prädiktoren auf die Strukturparameter (Deckung der drei Baumschichten und Totholzvorkommen) zeigen.

Supplement E5. Results of the GLMM and subsequent ANOVA showing the main predictors on the crown defoliation.
Anhang E5. Ergebnisse des GLMM und der anschließenden ANOVA, die die Haupteffekte der Prädiktoren auf die Kronenverlichtung zeigen.

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Supplement E1. Site conditions of the selected Natura 2000 sites (n/a = no measurement episode given), including the years of the previous HD recording and the number of forest polygons recorded in these areas.

Anhang E1. Standortbedingungen der ausgewählten Natura 2000-Gebiete (n/a = keine Messzeitraum angegeben), inklusive der Jahre der ersten FFH-Kartierung und der Anzahl der in diesen Gebieten erfassten Polygone.

Natura 2000 sites	Lat./Lon.	Area [km²]	Average annual		Altitude (a.s.l)	Year of baseline recording	Number of study polygons					
			precipitation [mm]	temperature			9110	9130	9170	9180*	91E0*	total
Huy (FFH047)	51.96 N / 10.98 E	20	543 [a] (1961–1990)	8 °C [a] (1961–1990)	⌀ 250 m [a]	2010−11	43	-	-	-	-	43
Hakel (FFH052)	51.88 N / 11.34 E	13	550 [b] (n/a)	8–9 °C [b] (n/a)	140−245 m [b]	2011−15	-	-	27	-	-	27
Selketal (FFH096)	51.67 N / 11.18 E	45	500−700 [c] (1951 – 1980)	6 −8,5 °C [c] (1951–1980)	190−540 m [c]	2009−10	16	16	23	13	15	83
Bodetal (FFH161)	51.71 N / 10.97 E	57	600−700 [d] (n/a)	7−8 °C [d] (n/a)	400−530 m [d]	2010−11	19	25	5	12	10	71

[a] LAU (2012): Managementplan für das FFH-Gebiet „Huy nördlich Halberstadt“. Landesamt für Umweltschutz Sachsen-Anhalt (Ed.), Halle (Saale).

[b] LAU (2015): Managementplan für das EU-Vogelschutzgebiet „Hakel“ einschließlich des FFH-Gebietes „Hakel südlich Kroppenstedt“. Landesamt für Umweltschutz Sachsen-Anhalt (Ed.), Halle (Saale).

[c] LAU (2010): Managementplan für das FFH-Gebiet „Selketal und Bergwiesen bei Stiege“ und den dazugehörigen Ausschnitt des EU-SPA „Nordöstlicher Unterharz“. Landesamt für Umweltschutz Sachsen-Anhalt (Ed.), Halle (Saale).

[d] LAU (2011): Managementplan für das FFH-Gebiet „Bodetal und Laubwälder des Harzrandes bei Thale“ und den dazugehörigen Ausschnitt des EU SPA „Nordöstlicher Unterharz“. Landesamt für Umweltschutz Sachsen-Anhalt (Ed.), Halle (Saale).

Supplement E2. Overview of the nine sampling strata: a combination of conservation status and parameter "layering and development stages" (Supplement E3).

Anhang E2. Übersicht der neun Stichprobenstraten: eine Kombination des Gesamterhaltungszustandes und dem Parameter Bestandsstruktur (Anhang E3).

State of the mapping parameter:		**Short description of stratum**
conservation status	layering and development stages	
A (good conservation status)	a (well-structured with age phase)	good conservation status with a natural structure and a high cover of old trees* > 50 %
	b (moderate structured / moderate age phase)	good conservation status with a natural structure and a moderate cover of old trees* > 30 %
	c (not well structured / without age phase)	good conservation status with low or no cover of old trees* < 30 %, but with > 30 % woody cover
B (moderate conservation status)	a (well-structured with age phase)	moderate conservation status with a natural structure and a high cover of old trees* > 50 %
	b (moderate structured / moderate age phase)	moderate conservation status with a natural structure and a moderate cover of old trees* > 30 %
	c (not well structured / without age phase)	moderate conservation status with low or no cover of old trees* < 30 %, but with > 30 % woody cover
C (bad conservation status)	a (well-structured with age phase)	bad conservation status with a natural structure and a high cover of old trees* > 50 %
	b (moderate structured / moderate age phase)	bad conservation status with a natural structure and a moderate cover of old trees* > 30 %
	c (not well structured / without age phase)	bad conservation status with low or no cover of old trees* < 30 %, but with minimum > 30 % woody cover

* DBH > 50 cm and height > 18m (9110, 9130, 9170, 9180*), DBH > 35 cm and height > 18m (91E0*)

Supplement E3. Simplified overview of the value categories (“a”, “b”, “c”) used to evaluate the investigated parameters of the habitat types under consideration (LAU 2014). Explanation: DBH = Diameter at breast height.

Anhang E3. Vereinfachte Übersicht über die Wertestufen (“a”, “b”, “c”, siehe Abschnitt 2.2.) für die Bewertung der untersuchten Parameter (LAU 2014). Erklärung: DBH = Brusthöhendurchmesser.

	Habitat type	**Value category**		
		a (excellent)	b (medium)	c (inadequate)
layering and development stages	9110	≥ 50 % canopy cover of trees with DBH > 50 cm and height > 18 m	< 50 % − ≥ 30 % cover of trees with DBH > 50 cm and height > 18 m	wood canopy cover ≥ 30 %
	9130			
	9170	≥ 30 % canopy cover of trees with DBH > 50 cm and height > 18 m		
	9180			
	91E0	≥ 50 % canopy cover of trees with DBH > 35 cm and height > 18 m	< 50 % − ≥ 30 % cover of trees with DBH > 35 cm and height > 18m	
deadwood	9110	≥ 5 pcs/ha	≥ 1 pcs/ha	< 1 pcs/ha
	9130			
	9170			
	9180			
	91E0			
tree species composition	9110	- proportion main tree species ≥ 50 % - proportion non-characteristic tree species for habitat type ≤ 10 %	- proportion main tree species ≥ 50 % - proportion non-characteristic tree species for habitat type ≤ 20 %	- proportion main tree species ≥ 30 % − < 50 % - proportion non-characteristic tree species for habitat type ≤ 30 %
	9130			
	9170	- proportion main tree species ≥ 50 %, - proportion non-characteristic tree species for habitat type ≤ 10 % - 3 main tree species - proportion *Q. petraea* /*Q. robur*: ≥ 25%	- proportion main tree species ≥ 50 % - proportion non-characteristic tree species for habitat type ≤ 20 % - 2 main tree species - proportion *Q. petraea* /*Q. robur*: ≥ 10 %	- proportion main tree species ≥ 30 % − < 50% - proportion non-characteristic tree species for habitat type ≤ 30 % - 1 main tree species
	9180	- proportion main tree species ≥ 50 %, - no non-characteristic tree species for habitat type - 3 main tree species	- proportion main tree species ≥ 50 % - proportion non-characteristic tree species for habitat type ≤ 10 % - 2 main tree species	- proportion main tree species ≥ 30 % − < 50 % - proportion non-characteristic tree species for habitat type ≤ 30 % - 1 main tree specie
	91E0	- proportion main tree species ≥ 70 %, - no non-characteristic tree species for habitat type - 2 main tree species	- proportion main tree species ≥ 50 % - proportion non-characteristic tree species for habitat type ≤ 10 % - 1 main tree specie	- proportion main tree species ≥ 30 % − < 50% - proportion non-characteristic tree species for habitat type ≤ 30 %

Supplement E4. Results of the GLMM and subsequent ANOVA showing the main predictors on the structural parameters (cover of the three canopy layers and deadwood occurrence) ((*) = $p \leq 0.1$, * = $p \leq 0.05$, ** = $p \leq 0.01$, *** = $p \leq 0.001$).

Anhang E4. Ergebnisse des GLMM und der anschließenden ANOVA, die die Haupteffekte der Prädiktoren auf die Strukturparameter (Deckung der drei Baumschichten und Totholzvorkommen) zeigen ((*) = $p \leq 0{,}1$, * = $p \leq 0{,}05$, ** = $p \leq 0{,}01$, *** = $p \leq 0{,}001$).

Predictor	**Habitat type**			**Data collection time**			**Habitat type * data collection time**		
	χ2	***df***	***p***	***χ2***	***df***	***p***	***χ2***	***df***	***p***
cover canopy layer 1	11.9	4	*	830.8	2	***	8.6	4	-
cover canopy layer 2	5.1	4	-	3.4	1	(*)	5.4	4	-
cover canopy layer 3	14.5	4	**	31.7	1	***	5.6	4	-
deadwood	44.4	4	***	31.6	1	***	9.1	4	(*)

Supplement E5. Results of the GLMM and subsequent ANOVA showing the main predictors on the crown defoliation ((*) = $p \leq 0.1$, * = $p \leq 0.05$, ** = $p \leq 0.01$, *** = $p \leq 0.001$).

Anhang E5. Ergebnisse des GLMM und der anschließenden ANOVA, die die Haupteffekte der Prädiktoren auf die Kronenverlichtung zeigen ((*) = $p \leq 0{,}1$, * = $p \leq 0{,}05$, ** = $p \leq 0{,}01$, *** = $p \leq 0{,}001$).

Predictor	***χ2***	***df***	***p***
Site parameter			
moisture	3.0	1	(*)
slope	2.6	2	-
exposition	6.5	3	(*)
management	1.1	2	-
Stand parameter			
development stages	30.5	5	***
relative crown distance	23.2	1	***
tree class	3.0	1	(*)
tree species	30.0	2	***