



Artificial gaps but not thinning persistently enhance forest structural heterogeneity

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Abstract

The strong focus on wood production has led to structural homogenization of managed forests worldwide, reducing habitat heterogeneity and thereby β -diversity of forest dwelling taxa. The Enhanced Structural Beta Complexity (ESBC) approach aims to counteract this by actively creating a heterogeneous structural mosaic in production forests. This is achieved by applying combinations of different deadwood retention treatments and spatial timber removal patterns (thinning vs. gaps) in neighboring forest patches. In a field experiment, heterogeneous ESBC-treated forest districts (10–20 ha) were implemented in temperate broad-leaf forests and paired with homogeneous control districts. Heterogeneity in the ESBC districts was created by applying 15 treatments in forest patches of 50 m \times 50 m. The treatments combined cutting 30% of the stand basal area, either regularly distributed throughout the whole patch (thinning) or aggregated in the patch center (gap), with deadwood retention. We quantified the changes of forest structure in 90 forest patches using a 7-year time series of repeated terrestrial laser scanning and calculated three indices: stand structural complexity index, understory complexity index, and canopy openness. While thinning had only minor effects, the removal of equal amounts of timber through gap felling greatly affected all structural indices. In canopy gaps, structural development was highly dynamic between years and impacted by deadwood retention treatments. Mostly driven by the pronounced structural changes in canopy gaps, ESBC treatments effectively lead to structurally heterogeneous forests throughout the post-intervention period. Therefore, the ESBC approach is a promising tool for integrating biodiversity conservation in multifunctional forests.

Keywords Canopy gaps · Multi-temporal LiDAR · SSCI · Structural complexity · Terrestrial laser scanning

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Introduction

With increasing pressures on forest biodiversity and ecosystem functioning in times of global change, innovative forest management approaches that reconcile wood production with conservation goals need to be put under trial (Martin et al. 2015; Thom et al. 2017; Ammer et al. 2018; Forzieri et al. 2022; Li et al. 2023). Among the desired features of future multipurpose forests are old-growth structures usually absent in common production forests (Bauhus et al. 2009). Key examples of such structures are deadwood and canopy gaps, both of which are crucial for many forest-dwelling species and profoundly affect ecosystem functions (Lassauce et al. 2011; Kern et al. 2014; Muscolo et al. 2014; Sandström et al. 2019). A further desired feature is the structural complexity of forest stands (McElhinny et al. 2005; Seidel et al. 2019). Although several definitions and indices are in use, here we apply the definition of Ehbrecht et al. (2021), i.e., structural complexity is the “degree of heterogeneity in biomass distribution in three-dimensional space” on the local forest stand scale, driven by the interaction of vegetation density and layering. Evidence suggests that stand structural complexity is often positively correlated with forest biodiversity and ecosystem functioning, driven by increased habitat availability and optimized resource use (Lindenmayer et al. 2000; Ishii et al. 2004; LaRue et al. 2019; Seidel and Ammer 2024). However, light-demanding or thermophilic species can also be less abundant in highly complex forests, as this is associated with dense structures and hence reduced light availability and a more buffered microclimate at the forest floor (Pierick et al. 2025).

However, these features—gaps, deadwood, and structural complexity—do not necessarily develop most quickly with a hands-off approach when management is abandoned for conservation purposes in production forests (Keeton 2006; Bauhus et al. 2009; Schall et al. 2021). Therefore, an approach suggested for future forest management is to actively promote them by retaining standing and lying deadwood and creating canopy gaps in managed forests (Enhanced Structural Complexity, ESC). Having been first implemented in North America (Keeton 2006) and recently also in the Black Forest in Germany (Asbeck et al. 2023), the ESC approach has shown positive effects on biodiversity at the stand level in both experiments (McKenny et al. 2006; Dove and Keeton 2015; Eckert et al. 2021).

So far, ESC trials have been applied only at the stand (α) level, e.g. in research plots of 0.25 ha (Asbeck et al. 2023) or 2 ha (Keeton 2006). However, biodiversity decline processes often operate on larger spatial scales, that is, the β - and γ -diversity scale of landscapes, i.e., at least several hectares (Mori et al. 2018; Seibold et al. 2019; Mitesser et al. 2025). In temperate European forests, production-oriented

silvicultural practices have increased landscape homogenization and consequently contributed to forest biodiversity loss (Müller et al. 2023; Decker et al. 2026). Inversely, structurally heterogeneous forests at the landscape level promote biodiversity and ecosystem multifunctionality (van der Plas et al. 2016; Hilmers et al. 2018; Schall et al. 2020; Heidrich et al. 2023; Uhl et al. 2024). This can be attributed to heterogeneity-biodiversity relationships (Heidrich et al. 2020; Eisenhauer et al. 2023). Therefore, we extended the ESC concept to the β level (Enhanced Structural Beta Complexity, ESBC, Müller et al. 2023). In this framework, a spatial mosaic of many different modifications of forest structure and deadwood retention is applied in forest districts of 10 – 20 ha in order to increase landscape-level structural heterogeneity. Based on the notion that increased structural heterogeneity at this scale will offer more habitats for species with different niches, the ultimate goal of ESBC interventions is to increase β -, and thereby γ -diversity (Müller et al. 2023).

After implementing experimental modifications of the forest structure, it is important to validate that they efficiently altered the forest structure not only directly after the interventions, but also in the long term. LiDAR-based technologies, i.e. airborne (ALS), terrestrial (TLS), or mobile (MLS) laser scanning, offer novel opportunities for measuring aspects of forest structure potentially relevant to biodiversity (Davies and Asner 2014; Hilmers et al. 2018; Wildermuth et al. 2023) and are a promising tool for evaluating the success of such treatments (Kikuchi et al. 2024). Specifically, structural complexity derived from TLS has been shown to be related to biodiversity (Grevé et al. 2018; Juchheim et al. 2020; Perles-Garcia et al. 2021). Tracking structural changes of forests using multitemporal LiDAR data is an effective, increasingly used approach (Vepakomma et al. 2010; Yrttima et al., 2020; Willim et al. 2022; Höwler et al. 2024; Trotto et al. 2024). However, in the past, the focus of multitemporal LiDAR applications was often on canopy gap dynamics (Li et al. 2018; Hagemann et al. 2022), carbon dynamics (Cao et al. 2016; Dalponte et al. 2019), biomass (Huang et al. 2013; Pflugmacher et al. 2014; Knapp et al. 2018) or changes in tree height (Noordermeer et al. 2019) rather than changes in stand structural heterogeneity or complexity (Cimdins et al. 2024). Furthermore, studies applying repeated TLS or MLS measurements rarely included multiyear comparisons (Calders et al. 2015; Griebel et al. 2015; Olivier and Robert 2017; Neudam et al. 2022, but see Willim et al. 2022 and Trotto et al. 2024). Particularly rare are studies with a focus on controlled artificial disturbances that used repeated measurements.

Here, we present a 7-year time series of repeated TLS measurements from a forest biodiversity and ecosystem functioning experiment in which ESBC interventions have

been applied in temperate forest districts (Müller et al. 2023). The ESBC interventions comprise 15 different treatments combining gap felling or thinning with deadwood retention, and are designed to create structurally heterogeneous forest districts. By tracking the development of forest structure in 90 forest patches before and after the experimental interventions, our objective was to assess the potential of ESBC as a future practice for reaching structural targets in multipurpose forest management. We analyze temporal trends in forest structure at two spatial scales, i.e., (1) on the scale of forest patches (analogous to the α level in biodiversity theory), with a focus on mean values of structural indices, and (2) on the scale of forest districts comprising several patches (analogous to the β level in biodiversity theory), with a focus on variation around the mean. In other words, we investigate both local structural complexity at the patch level, and the larger-scale heterogeneity of structural complexity at the district level. More specifically, we address the following research questions.

Q1 (α level): How did the 15 treatments of the ESBC measures affect the forest structure at the patch level?

Q2 (β level): Did the heterogeneity in forest structure increase in districts managed according to the ESBC approach, compared to the state before the interventions, and compared to homogeneously managed districts?

Methods

Study area

The study was carried out in the University Forest of the University of Würzburg near Sailershausen, in the Haßberge region in Bavaria, Germany (Fig. S1). The study area is located at an altitude of approximately 330–380 m above sea level and received 704.6 mm of mean annual precipitation between 1991 and 2020 (DWD, 2024). The forest stands in which the experiment was set up are species-rich temperate broad-leaved forests dominated by *Fagus sylvatica* L., *Acer* L. spp., *Fraxinus excelsior* L., *Carpinus betulus* L. and *Quercus* L. spp. with stand ages ranging from 72 to 97 years (in 2024). They are managed according to the continuous cover forestry concept (Mason et al. 2022, Pommerening, 2023).

Experimental interventions

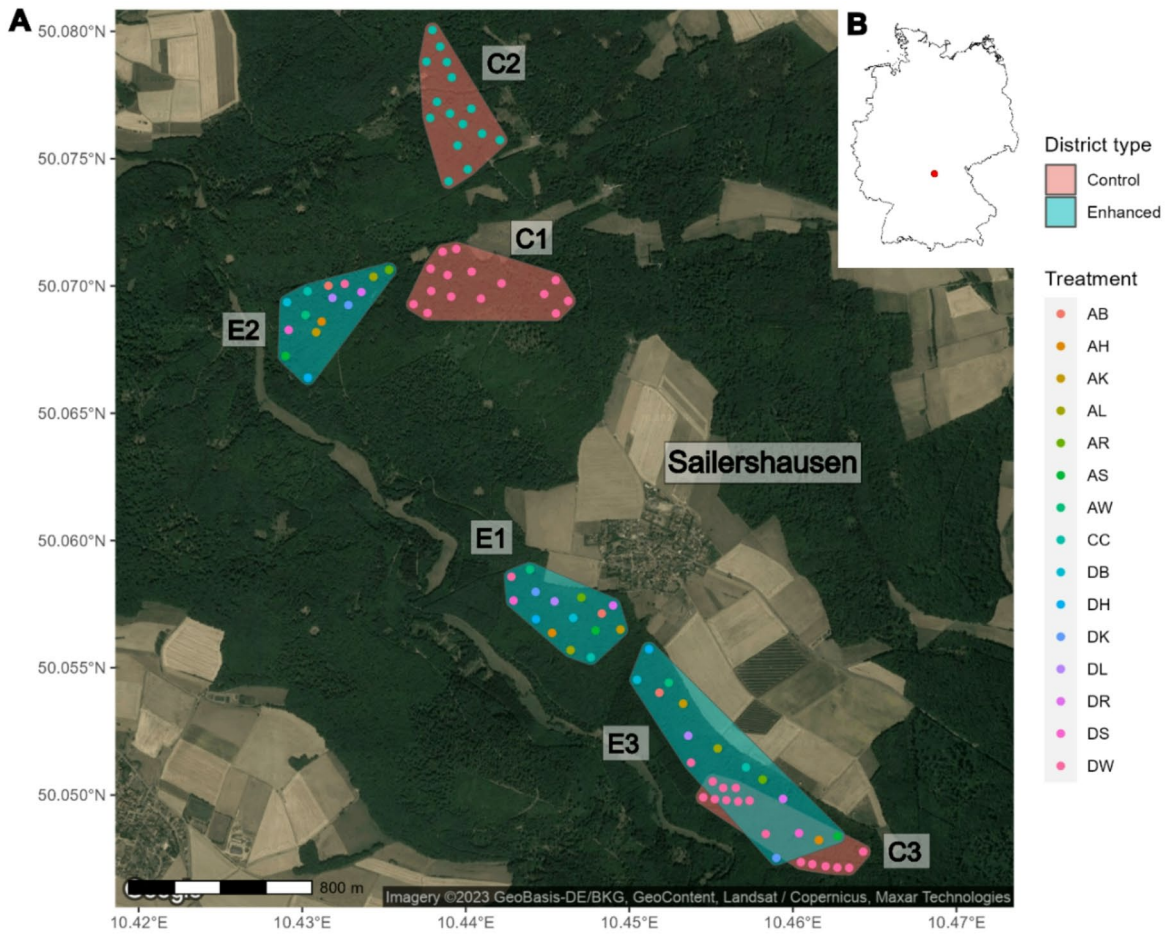
The experiment was established in six forest districts (forest areas of 12–20 ha in size). Within each district, our sampling units were 15 forest patches (squares of 50 m \times 50 m), which sums up to a total of 90 patches (Table S1). In winter 2018/2019, experimental forest management measures

(Enhanced Structural Beta Complexity interventions, ESBC) were carried out in the patches. These treatments have a dimension of deadwood availability, and a dimension of spatial arrangement of the intervention that leads to different levels of light availability (Fig. 1, Table S2).

In the deadwood dimension, there are seven types of treatments (Fig. 1). In all cases, the treatment was applied to approximately 30% of the standing basal area. For Total removal, Stumps, Crowns and Logs, the trees were felled with a harvester. For Total removal, all stumps from the felled trees were removed from the soil with an excavator. For Crowns and Logs, the crowns or logs of all felled trees were left on the ground in the patch. In the Snags treatment, the trees were topped at around 5 m height. For Logs+snags, half of the target trees were topped and the other half was felled, with the logs being left behind on the soil. In the Habitat trees treatment, several kinds of measures were taken to artificially create dying and half-dead trees: Approximately a third of the trees were abraded with a harvester to injure the bark, in another third, artificial tree hollows were created with a chain saw, and the last third were cut through half of the stem at mid height and then tipped with a harvester.

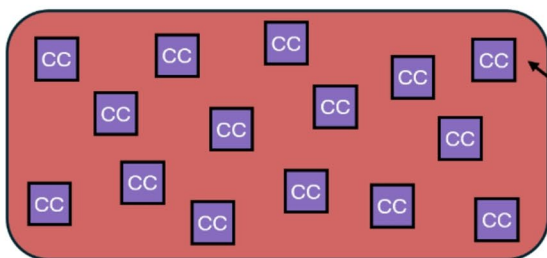
Each of the deadwood treatment types was executed both in an Aggregated and in a Distributed version (i.e., the light availability dimension of the treatments). For the Distributed treatments, the interventions were established evenly throughout the patch (equivalent to silvicultural thinning operations). For the Aggregated treatments, the respective measure was applied to all trees in a radius of 15 m around the center of the patch, creating a gap (around 750 to 900 m² in size and around 30 m in diameter) in the middle of the patch. The 14 treatments (seven deadwood types \times two light availability types) were complemented by a Control treatment where no intervention took place (Fig. 1, Müller et al. 2023).

Of the six districts, three were assigned Control districts (C1–3). In these districts, no active, standardized intervention was conducted in the course of the experiment. However, two of the districts, C1 and C3, had been thinned from above by the local forestry office just before the launch of the experiment with a very similar intervention intensity and spatial configuration as the experimental Distributed treatments. In the district C2, no thinning operation had been conducted for several years. This was confirmed both by communication with the responsible forest manager and expert assessment in the field. Therefore, we classified all 15 patches in districts C1 and C3 as Distributed Stumps treatment, and in C2 as Control treatment. Both versions of Control districts represent homogeneous production forests, just in different phases of the thinning cycle. The other 3 districts were assigned Enhanced districts (E1–3). There, a



Aggregated	AR	AW	AL	AS	AB	AK	AH	CC
	DR	DW	DL	DS	DB	DK	DH	
Distributed	DR	DW	DL	DS	DB	DK	DH	Control
	Total tree removal	Stumps	Logs	Snags	Logs + snags	Crowns	Habitat trees	

Control district: 15x the same treatment



Enhanced district: all 15 treatments

Forest patch (50 m x 50 m)

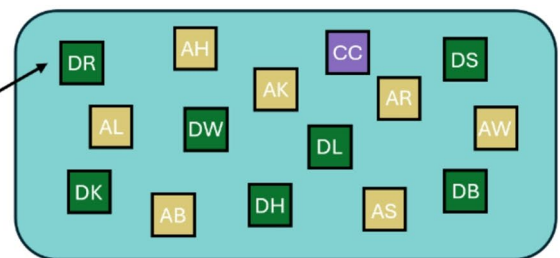


Fig. 1 Study area and experimental design. **A** Maps of the study area. The 6 forest districts with respectively 15 forest patches located around the village Sailerhausen. **B** Location of the study area in Germany. **C** Schematic visualization of the 15 treatments and how they are implemented in Control and Enhanced districts in the ESBC approach

different ESBC intervention was applied to each of the 15 patches (Table S1, cf. Müller et al. 2023). It is important to note the difference in terminology between the Control treatment, which means that no intervention was conducted in a forest patch, and Control districts, which describes several patches with identical treatments.

In 39 of the patches, 6 m × 6 m fenced enclosures were installed around the patch center to prevent roe deer browsing (Lettenmaier et al. 2025, Tables S1, S2).

Terrestrial laser scanning and data processing

We measured the forest structure in all patches once a year during summer via terrestrial laser scanning (TLS). The first scans were performed in summer 2018 before the interventions took place. At that point, two of the Control districts (C2 and C3) had not yet been assigned, which is why they were not scanned in 2018. From 2020 on, all patches were scanned once every summer until 2024 at a permanently marked central position with 44.4 million measurements per scan by a Faro Focus 3D 120 (Faro Technologies Inc., Lake Mary, USA) laser scanner mounted on a tripod at breast height (1.3 m), using a field of view of 305 degrees in vertical direction and 360 degrees in horizontal direction. The angular step width was set at 0.035°, and was subsampled at 1/16 of the original resolution during processing as introduced by earlier studies (e.g. Ehbrecht et al. 2021).

Naturally, scanning at a single position provides a rather local perspective on forest structure that does not capture the entire variability within a patch. Caution is advised when extrapolating from a single scan to a larger scale. However, scanning from single-scan positions has been conducted before and was shown to provide meaningful data (Palace et al. 2016), particularly for time series comparing scans from the exact same position (Portillo-Quintero et al. 2014).

After scanning, all scans were processed using Faro Scene (Faro Technologies Inc., Lake Mary, USA) by applying the standard filters and exporting the data as XYZfiles for quality check visualization and further processing. We had to retroactively remove 19 of the originally 510 observations, because we became aware of technical problems with these scans only when processing the point clouds after the field campaigns (e.g. the scanner had moved during the scanning process). Using Mathematica 12 (Wolfram Research, Champaign, USA), we calculated the stand structural complexity index (SSCI, Ehbrecht et al. (2017)), understory complexity index (UCI, Willim et al. (2019)) and canopy

openness according to Zheng et al. (2013) for a 60° zenithal opening angle from the XYZ files.

The SSCI describes the structural complexity of a forest stand based on the fractal dimension of the scanned structures (Ehbrecht et al. 2017). Typically, forest stands with a high SSCI are multilayered, dense, and feature a high degree of space filling (Ehbrecht et al. 2017, 2021; Stiers et al. 2018).

Just like the SSCI, the UCI uses fractal geometry to describe the complexity of vegetation structures, however, it is focused on the understory between 0.8 m and 1.8 m above the forest floor. High values indicate the presence of dense understory vegetation (Willim et al. 2019; Seidel et al. 2021). SSCI and UCI were shown to correlate to some degree (e.g. Kikuchi et al. 2024), since the understory is also considered in parts in the SSCI index, however the indices are also frequently used in conjunction (Seidel et al. 2021).

Canopy openness, defined as the fraction of unit area covered by vertical projection of the tree crowns (Gonsamo et al. 2013), was used long before the advent of laser scanners (e.g., Gerhard, 1996) and is, when measured with TLS, a direct measure for light availability at the position of the scanner. The computation of canopy openness from TLS data relies on a projection of all scanned laser points detected in a 60° vertically oriented, upside-down search cone on a virtual image plane, as originally introduced by Zheng et al. (2013) and further described by Ehbrecht et al. (2019).

Data analysis

Development of forest structure in treatments (α level)

For answering research question Q1 (treatment effects on the development of forest structure on the stand level), we fitted one Bayesian (generalized) linear mixed model (LMM or GLMM) for each forest structure index. We modeled SSCI and UCI with LMM after log-transforming the highly right-skewed UCI and standardizing both indices to facilitate prior selection. Canopy openness is limited to the interval between 0 and 1 with observations at the bounds, and was furthermore bimodally distributed within some groups. To handle the bounded response variable with observations being exactly 0 or 1, we modeled canopy openness with a Bayesian ordered beta regression model in the parameterization of Kubinec (2023). In all models, we included treatment, year (as a categorical variable), and their interaction as fixed effects. To control for potential effects of the enclosures, we also included the scaled time since fencing (set to 0 for patches without central enclosure) and its interaction with the light component of the treatments (Aggregated, Distributed, Control) as fixed effects. As random effects, we

included random intercepts for patch nested within district. Data analysis was performed in R v. 4.3.0. (R Core Team 2023). The models for SSCI and UCI were fitted in the R package brms v. 2.19.0 (Bürkner 2017), the ordered beta regression for canopy openness with the package ordbetareg v. 0.7.2 (Kubinec 2023). We used weakly informative priors on all parameters. Detailed descriptions of the model equations, priors, model fitting, and diagnostics are given in Method S1 and Method S2.

We were primarily interested whether (1) within each treatment, the forest structure indices in the years 2020–2024 differed from the pre-intervention forest structure in 2018, and (2) within each year, the forest structure indices from the 14 non-control treatments differed from the Control treatment. We also tested whether time since fencing had an effect on forest structure indices within the Aggregated, Distributed, and Control treatments, respectively. We tested these contrasts two-sidedly using the `brms::hypothesis()` function, which performs evidence ratio tests on the posterior. We used the `r2_bayes()` function from the R package performance v. 0.9.2 (Lüdtke et al. 2021) to obtain conditional and marginal R^2 values for the models.

Development of structural heterogeneity in Enhanced vs. Control districts (β level)

In a second approach, we wanted to know whether the district-level heterogeneity in forest structure increased in (heterogeneously managed) Enhanced districts, compared to the state before the intervention, and compared to the (homogeneously managed) Control districts (Q2). To tackle this question, we applied models where not, as in most approaches, the predicted means of the response variables depended on the predictors of interest, but instead the estimated residual (unexplained) variation of the data (Zuur et al., 2009, Chapter 4.1). We postulate that a broad spread of the data within districts at one point in time is equivalent to high heterogeneity (for that district type and time). By comparing model parameters that describe this residual variation for Control versus Enhanced districts or pre-intervention versus post-intervention years, we could test whether heterogeneity differed credibly between district types and years.

Therefore, we fitted Bayesian (G) LMM with the time since fencing and its interaction with the light component of the treatment as the only fixed effects, to control for browsing effects. Apart from that, this model type only accounts for the random differences between districts and years via random intercepts (year nested within district), therefore leaving all variation within each district and year unexplained to be able to estimate the total unexplained within-district variation. We fitted different dispersion or precision

parameters that describe the spread of the residuals for Enhanced and Control districts, and for each year, separately. In testing whether the dispersion/precision parameters for Enhanced districts after the intervention differed from those for Control districts, and for Enhanced districts before the intervention, we could infer credible effects of the type of district management (Enhanced or Control) on within-district forest structural heterogeneity.

We standardized SSCI, log-transformed and standardized UCI, and fitted both with LMM. The residual spread was described with σ (standard deviation) parameters of a normal distribution. Canopy openness was again modelled as an ordered beta regression. The residual spread was described with the ϕ (precision) parameters of a beta distribution in the mean/precision parametrization. Again, we used the packages brms v. 2.19.0 (Bürkner 2017) and ordbetareg v. 0.7.2 (Kubinec 2023) to fit the models and applied weakly informative priors. The model formulas and further information are given in Method S3 and Method S4.

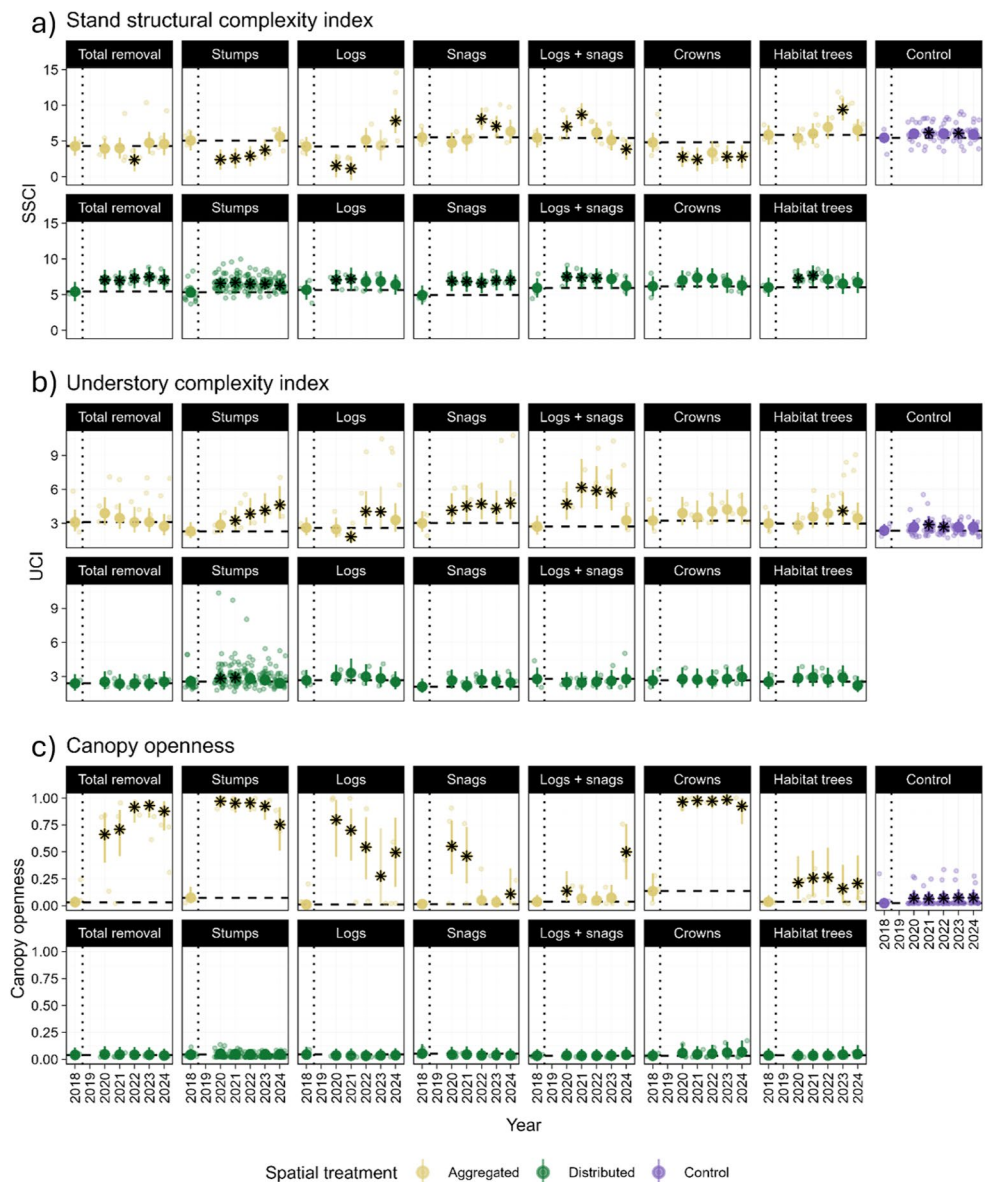
To test whether the σ and ϕ parameters for Enhanced districts after the intervention differed from the respective parameters in the Control districts and before the intervention, we performed two-sided evidence ratio tests using the `hypothesis()` function of brms. It is important to note that, due to us working in a Bayesian instead of a frequentist statistical framework, statistical results are evaluated in terms of credibility, not significance. Effects or differences are considered credible when the 95% credible interval of the respective parameter or predicted mean (quantiles of its posterior probability distribution) does not include the value against which the contrast is tested.

Results

Development of forest structure in treatments (a level)

In the Control treatment, stand structural complexity index (SSCI) was slightly increased in 2021 and 2023 compared to the pre-intervention state (Fig. 2). In the Distributed treatments, initial credible post-intervention increases were observed for most treatments, except for Crowns. However, the SSCI decreased again and was statistically non-distinguishable from the pre-intervention state after three to four years in the Habitat trees, Logs, and Logs + snags treatments. In the Aggregated treatments, the responses of SSCI varied strongly depending on the deadwood treatment: There are examples of an increase for at least some years (Habitat trees, Snags), a decrease (Crowns, Stumps, Total removal), an initial increase, followed by a later decrease (Logs + snags), and the reverse pattern (Logs). None of the

Fig. 2 Forest structure indices in dependency of year for each treatment (α level). The smaller, light points display the data. The solid, larger points show the marginal predictions from a Bayesian linear mixed model (“Treatment effects” model type, see Method S1 and S2 for model description), with the bars indicating the 95% credible interval. The asterisks mark whether a predicted value for a group was credibly different from the prediction for 2018 within the same treatment. This was tested using evidence ratio tests with 95% credible intervals (Table S4). The dotted vertical lines mark the time of the intervention. The dashed horizontal lines show the predicted value for 2018 as a reference of comparison



patterns was stable over the whole post-intervention period (Fig. 2a), Tables S3, S4). When tested whether non-control treatments differed from Control within each year, no credible effects were found in 2018 (Fig. S1). In all subsequent years, at least three of the Aggregated treatments, but none of the Distributed, differed from the Control. These differences in the Aggregated treatments were, depending on the treatment and year, either positive or negative (Fig. S1, Tables S3, S4). The fixed effects explained 54.5% of variance in the LMM for SSCI; the total explained variance (fixed+random effects) was 75.4% (Table S5).

The understory complexity index (UCI) in the Control treatments in 2021 and 2022 was credibly higher than in 2018 (Fig. 2b). In the Distributed treatments, UCI differed from pre-intervention levels in the Stumps treatment in 2020 and 2021 only. For the Aggregated treatments, responses of

UCI to interventions varied. There was a mostly consistent increase after the interventions in Logs+snags, Snags, and Stumps, but in Logs+snags, UCI decreased to pre-intervention levels again in 2024. In Logs, an initial decrease preceded a subsequent increase. In Habitat trees, UCI was only slightly increased in 2023. In Crowns and Total removal, no credible differences from the pre-intervention state were found in any of the years (Fig. 2b), Tables S6, S7). Comparing UCI of non-control and Control treatments within each year, only Aggregated Crowns differed credibly from Control in 2018 (Fig. S2). In the post-intervention years, none of the Distributed treatments differed from Control, but in each year, several Aggregated treatments had credibly higher UCI values than Control, with inconsistent patterns in respect to which of the treatments were affected. The only credible negative deviation from the Control treatment was

Aggregated Logs in 2021 (Fig. S2, Tables S6, S7). The fixed effects explained 55.3% of variance in the LMM for UCI; the total explained variance was 80.9% (Table S5).

Canopy openness was credibly increased compared to 2018 in all years in the Control treatment (Fig. 2c)). In the Distributed treatments, no credible deviations from the pre-intervention state were found. In the Aggregated treatments, canopy openness was consistently larger after the interventions, with the exception of the Logs+snags and Snags treatments, where a credible positive effect was only present in some of the years (Fig. 2c), Tables S8, S9). When comparing canopy openness of Control and other treatments within years, only Crowns was credibly higher than Control in 2018 (Fig. S3). In the post-intervention years, Distributed treatments did not differ in any case from Control treatments, but Aggregated treatments had credibly higher levels of canopy openness in almost all cases, with inconsistent patterns between the years. Crowns, Stumps, and Total removal were different from Control in all post-intervention years (Fig. S3, Tables S8, S9). The fixed effects explained 81.1% of variance in the GLMM for Canopy openness; the total explained variance was 94.4% (Table S5). The time since the establishment of enclosures had a credible positive effect on SSCI in the Aggregated treatments, and on UCI in the Aggregated and Distributed treatments, with the effect in the Aggregated treatments being much more pronounced. On Canopy openness, it had a negative effect in the Aggregated treatments only (Fig. S4, Tables S4, S7, S9).

Development of structural heterogeneity in Enhanced vs. Control districts (β level)

SSCI was credibly more heterogeneous in Enhanced districts than in Control districts in all post-intervention years, but did not differ between Enhanced and Control districts in 2018. In Control districts, the heterogeneity in the years 2020–2023 did not differ from 2018, but in 2024 it was credibly lower than 2018. In the Enhanced districts, the heterogeneity in all post-intervention years was higher than in 2018 (Fig. 3a), Fig. S5, Tables S10, S11).

UCI in the Enhanced districts was credibly more heterogeneous than in the Control districts in 2023 only. The Control districts were credibly less heterogeneous in 2023 than in 2018. Apart from that, the post-intervention heterogeneity levels did not differ from pre-intervention levels neither for Control nor Enhanced districts (Fig. 3b), Fig. S5, Tables S12, S13).

Canopy openness was already more heterogeneous in the Enhanced districts than in the Control districts before the interventions. After the interventions, heterogeneity remained constant in the Control districts and increased markedly in the Enhanced districts, leading to credibly

higher heterogeneity in the Enhanced than in the Control districts for all years (Fig. 3c), Fig. S5, Tables S14, S15).

Discussion

Development of forest structure after interventions (α level)

In our large-scale field experiment, Distributed interventions similar to traditional silvicultural thinning actions had little or no effect on any of the three forest structure indices. Although the post-intervention stand structural complexity index (SSCI) was slightly increased compared to the pre-intervention state in most of the Distributed treatments, within-year contrasts between Control and Distributed treatments were never credibly different from 0. The finding of only barely measurable structural changes in the Distributed treatments is consistent with spaceborne remote sensing data from the same forest patches, where metrics derived from Sentinel-1 and Sentinel-2 products were highly sensitive to Aggregated, but not to Distributed interventions (Kacic et al. 2024, 2025). Other studies from a wide range of different forests report clear and long-lasting effects of thinning on different aspects of forest structure (Horner et al. 2010; Dodson et al. 2012; Waters et al. 2018; Wang et al. 2022), including structural heterogeneity and structural diversity (Gauthier et al. 2015; Pretzsch and Hilmers 2024). However, in these examples, inventory-based forest structure indices that are derived from the distribution of stem diameters were used, while the indices used in this study are more influenced by the distributions of leaves and branches in space than by stems. Despite expectations of increased understory growth following canopy openings (Bailey and Tappeiner 1998; Dodson et al. 2012), the stagnating understory complexity is consistent with theory. According to Beer Lambert's law of light attenuation, light transmitted to the forest floor increases far less than proportionally with the reduction of the initial stocking (cf. Hale 2003), although approximately 30% of basal area was removed. Furthermore, light availability is just one potential limiting resource for vegetation development on the forest floor (Wagner et al. 2009, 2011). Moreover, closure of small, thinning-induced gaps following crown expansion of the remaining mature trees only left a short window of opportunity for understory growth (Hawthorne et al., 2013; Kuehne et al. 2015), as shown by the lack of effects in canopy openness after Distributed interventions.

When removing equal amounts of timber in an aggregated rather than a distributed spatial arrangement (i.e., creating a central canopy gap), the results were completely different. All three structural indices changed markedly in

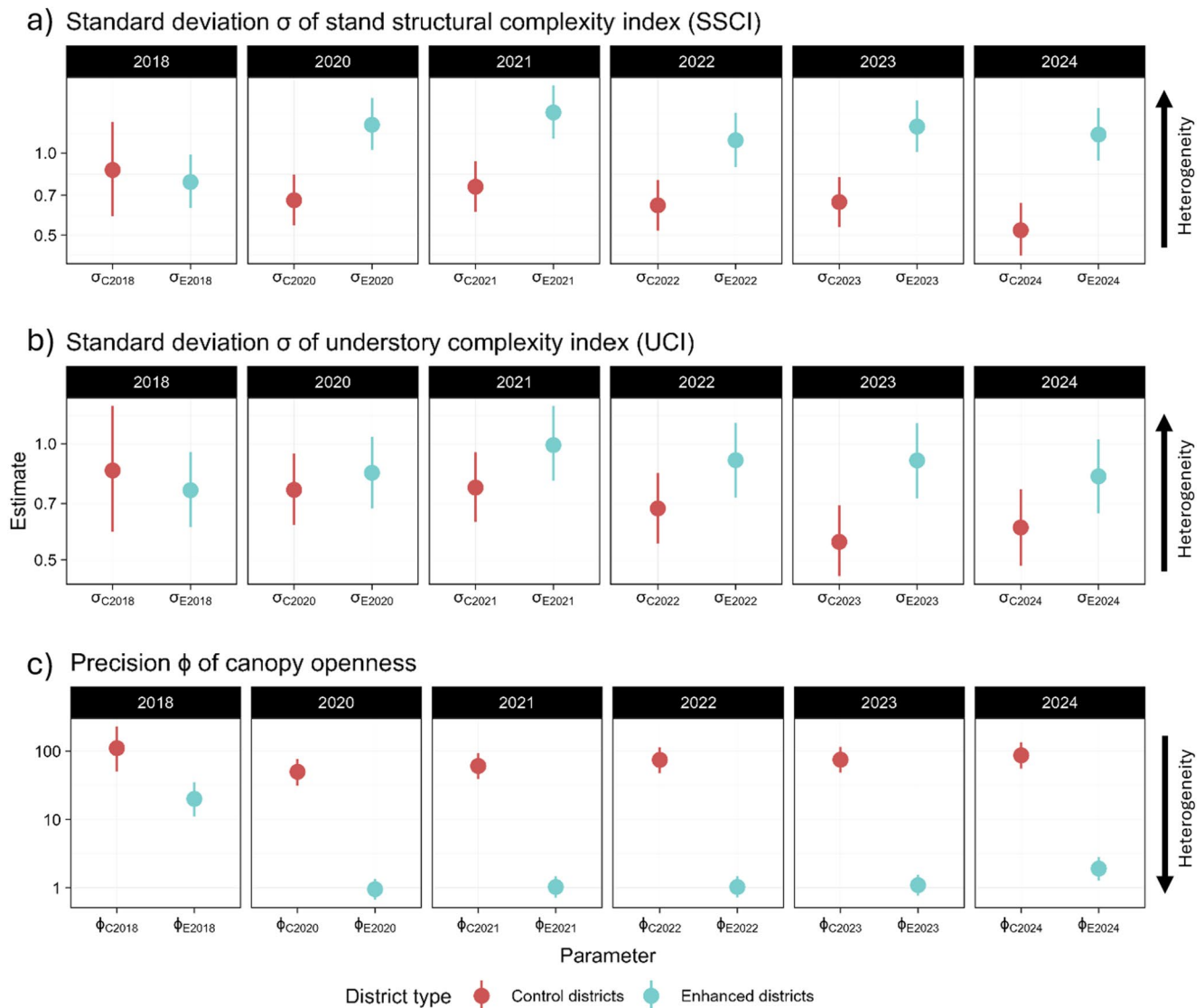


Fig. 3 Heterogeneity parameters of forest structure indices in Control versus Enhanced forest districts (β level). Shown are estimated σ (standard deviation in a normal distribution) or ϕ (precision in a beta distribution) parameters for each district type and year (see “District heterogeneity” model type, Methods S3 and S4). For **a** and **b**, higher parameter values signify higher within-district heterogeneity for the respective district type and year, for **c** vice versa. Displayed are the posterior means of the parameters with 95% highest density intervals.

Higher district-level structural heterogeneity is indicated by higher values of σ or lower values of ϕ (compare also with respective data and model predictions in Fig. S6). Within each row (i.e., between district types and years), parameters with non-overlapping 95% highest density intervals can be considered credibly different from each other. For inference from hypothesis tests on differences between the parameters, see Tables S11, S13 and S15

most of the Aggregated treatments after the interventions. The creation of these artificial canopy gaps with a diameter of 30 m led to an immediate increase in canopy openness. The effect sizes were drastic, canopy openness changed from values close to 0 to almost 1 in several of the treatments, spanning almost the whole possible range of canopy openness. As expected, increased resource availability (primarily light, but potentially also soil water due to reduced root competition by overstorey trees (cf. Müller and Wagner 2003; Ammer and Wagner 2002) caused intensive growth

of herbs, shrubs, and tree regeneration in the gaps, reflected by increasing understory complexity index (UCI) in most Aggregated treatments (Whitmore 1989; Zhu et al. 2014; Vilhar et al. 2015; Kern et al. 2017; Stiers et al. 2019; Thom et al. 2022; Lettenmaier et al. 2025). The most pronounced changes of UCI were observed in the Logs+Snags treatment, where average UCI increased from around 3, a typical value for mature managed beech forests, to around 6, which is an exceptionally high UCI, indicating a dense, highly complex understory (Willim et al. 2019). The development

of SSCI in Aggregated treatments is less straightforward than that of UCI and canopy openness. While we expected an initial decrease in SSCI caused by the removal of structures, followed by an increase due to the growth of structurally complex understory layer vegetation in all treatments, this could only be confirmed for Logs and Stumps. In the other Aggregated treatments, all kinds of different patterns, often highly dynamic, were found. Generally, high dynamics of SSCI are typical for early successional stages (Willim et al. 2022). With a baseline SSCI of around 5 for most treatments, the dynamic changes to SSCI values from around 3 to around 8 spanned almost the entire range typically observed in temperate forests (Ehbrecht et al. 2021).

Why certain deadwood treatments responded in specific ways is only explicable in some of the cases. In Total removal and Crowns, SSCI was always lower than or equal to the pre-intervention state. These were also the only Aggregated treatments where UCI did not increase, while canopy openness remained high in both treatments. This indicates that the heavy disturbance caused by excavating the stumps in Total removal, and the remaining crown deadwood in Crowns, may have damaged already established plants and inhibited the emergence of additional understory vegetation, with the effects persisting even six years after the interventions.

Since the scans were conducted within fenced enclosures in a subset of our patches, we corrected for the effects of time since enclosure installation in our models. As expected, browsing exclusion caused a marked increase in SSCI and UCI and a slightly decreased canopy openness over time in Aggregated treatments. These structural changes indicate that before interventions and enclosure installations, tree regeneration was suppressed by both canopy trees casting shade and severe ungulate browsing (Lettenmaier et al. 2025). The interaction of light availability and browsing pressure is crucial for recruitment processes, and many tree species can only regenerate successfully when both light availability is increased and ungulate browsing is prevented (Kupferschmid et al. 2014; Annighöfer et al. 2015; Tamura and Nakajima 2017; Schäfer et al. 2019; Barrere et al. 2021; Royo and Carson 2022). Hence, intensive ungulate browsing can affect aspects of forest structure, including forest structural complexity, for decades (Ammer 1996; Didion et al. 2009; Ramirez et al. 2019; Reed et al. 2022). Therefore, ungulate densities will likely be of crucial importance for the long-term structural trajectories of forest stands after ESBC interventions.

For a more profound understanding of the development of forest structure in specific treatments, the experimental interventions of interest should be repeated in future experiments with more replicates, as the design of this experiment was customized primarily for the comparison

of homogeneously versus heterogeneously managed forest districts (Müller et al. 2023). Nevertheless, our results clearly demonstrate that by harvesting equal amounts of timber in different spatial patterns, and varying which types of deadwood are retained, practitioners can effectively regulate post-harvest structural complexity of forest stands. While thinning interventions comparable to our Distributed treatments will affect stand structure only slightly, gap cuttings comparable to our Aggregated treatments can either increase or decrease local structural complexity during the following years, depending on the development of the emerging tree regeneration.

Structurally heterogeneous forests through ESBC measures (β level)

Immediately after the interventions, Enhanced districts showed greater heterogeneity of SSCI and canopy openness than before. These differences persisted throughout the observation period, meeting our expectations and confirming that the goal of the ESBC measures, to create structurally heterogeneous forest districts, was met. For UCI, no such pattern could be statistically validated yet (except for 2023, but the difference did not remain credible in 2024). As the treatment-specific results show, forest structure indices remained stable in the Distributed treatments, but varied dynamically in the Aggregated treatments, with different temporal patterns depending on the retained deadwood type. We therefore conclude that the enhanced structural heterogeneity of SSCI and canopy openness was almost exclusively driven by the Aggregated treatments and diverse structural responses to different deadwood retention types in them. Consequently, our results underline that gap-based silviculture approaches have a promising potential of creating structurally heterogeneous forest landscapes (Seidel et al. 2016; Thom and Keeton 2020; Aszalós et al. 2022).

Implications for biodiversity

The manipulations of forest structure, especially the Aggregated treatments, will certainly have direct drastic effects on the microclimate in the forest patches (Ehbrecht et al. 2017, 2019; Thom et al. 2020). Whether directly or indirectly through the modified microclimate, structural changes will likely impact biodiversity in the patches. For multiple taxa, forest structural complexity and related structural variables have been shown to be potent predictors of biodiversity (Jung et al. 2012; Gao et al. 2014; Rappa et al. 2022; Wildermuth et al. 2024). Although Distributed treatments did not have lasting effects on our forest structure indices, the enrichment of closed canopy stands with deadwood will probably promote biodiversity (McKenny et al. 2006; Dove

and Keeton 2015; Seibold et al. 2015; Eckert et al. 2021; Rothacher et al. 2023; Dyson et al. 2024). Resulting from such patch-level effects (α scale), the district-level structural heterogeneity in the Enhanced forest districts will presumably lead to increased district-level β -diversity, and ultimately γ -diversity and ecosystem multifunctionality, which is investigated in the ongoing field experiment (Müller et al. 2023).

Conclusions

The TLS-derived forest structure indices validate that by implementing ESBC measures, forests can be successfully enhanced in structural heterogeneity at the landscape level. The increased heterogeneity of stand structural complexity was almost exclusively achieved by spatially aggregated interventions, highlighting the potential of gap-based silviculture to create structurally heterogeneous forest landscapes. In gaps, structural development remained highly dynamic during the 6-year post-intervention period. This demonstrates that in early successional stages after disturbances, measurements of forest structure at only one or two points in time can yield misleading results. Future research will reveal whether the ESBC measures increase β - and γ -level biodiversity and ecosystem multifunctionality. If so, they are a promising approach to strengthen biodiversity conservation in multifunctional forests.

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Data availability The data are available at <https://doi.org/10.5281/zenodo.15075106>.

Code availability The code is available at <https://github.com/KerstinPierick/Artificial-gaps-but-not-thinning-persistently-enhance-forest-structural-heterogeneity>.

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