Trees, Forests and People 8 (2022) 100231

Contents lists available at ScienceDirect

Trees, Forests and People

journal homepage: www.sciencedirect.com/journal/trees-forests-and-people

Short - term dynamics of structural complexity in differently managed and unmanaged European beech forests

Katharina Willim [a,*,1], Christian Ammer [b], Dominik Seidel [a], Peter Annighöfer [c], Julia Schmucker [c], Peter Schall [b], Martin Ehbrecht [b]

[a] Faculty of Forest Sciences, Department of Spatial Structures and Digitization of Forests, University of Göttingen, Büsgenweg 1, 37077 Göttingen, Germany
[b] Faculty of Forest Sciences, Silviculture and Forest Ecology of the Temperate Zones, University of Göttingen, Büsgenweg 1, 37077 Göttingen, Germany
[c] Chair of Forest Growth and Yield Science, TUM School of Life Sciences Weihenstephan, Technical University of Munich, Hans - Carl - von - Carlowitz - Platz 2, 85354 Freising, Germany

ARTICLE INFO

Keywords:
Fagus sylvatica L.
TLS
Stand structure complexity index (SSCI)
Disturbance
Forest structure
Forest management

ABSTRACT

The dynamics of forest structure influence forest ecosystem functions and are modified by forest management and natural disturbances. Here, we quantified the dynamics of stand structural complexity of differently managed and unmanaged European beech (*Fagus sylvatica* L.) forests. We determined changes of different aspects of stand structural complexity between 2014 and 2019 using terrestrial laser scanning data from 42, one hectare-sized forest plots, representing even - aged forest management, uneven - aged forest management and unmanaged stands. Unmanaged forests showed no significant changes in stand structural complexity within the time frame investigated, due to the absence of major disturbances. On the contrary, managed uneven - aged and even - aged forest stands showed more pronounced dynamics in stand structural complexity than the unmanaged forests. In this context, uneven - aged stands with higher initial canopy openness showed a higher increase in structural complexity than stands with lower canopy openness, which could be attributed to growth responses of understory vegetation in lower strata due to improved light availability at the beginning of the observed time period. Dynamics of structural complexity under even - aged forest management strongly differed between different developmental stages, with young thickets and mature timber stands showing highest increases in stand structural complexity. Overall, we did not observe significant decreases in stand structural complexity within the observed time frame. Our findings need to be viewed in the context of long-term dynamics of forest structure and contribute to the understanding of how forest management can affect short - term structural dynamics in beech forests.

1. Introduction

Managing for structural complexity is a currently debated option to promote the resilience of forest ecosystems towards natural disturbances (Ehbrecht et al., 2019; Fahey et al., 2015; Knoke and Seifert 2008; Messier and Puettmann 2011; Parker et al., 2004). Stand structural complexity is not only an important driver for ecosystem stability and resilience, but also for other ecosystem functions and services, including the regulation of microclimate (Ehbrecht et al., 2019; Kovács et al., 2017; Messier and Puettmann 2011; Seidel et al., 2020), forest productivity (Glatthorn et al., 2018; Gough et al., 2019; Pretzsch et al., 2015) and species richness of some taxa (Felipe-Lucia et al., 2018; Knuff et al., 2020). Better understanding how management affects the dynamics of stand structural complexity of forests is crucial to better predict forest ecosystem responses to intensifying disturbance regimes with ongoing climate change (Bauhus et al., 2009; Coumou and Rahmstorf 2012; Fenton et al., 2009). However, while effects of forest management on stand structural complexity in general are well understood, impacts of silvicultural interventions on the dynamics of stand structural complexity in Central Europe remain largely unexplored.

Focusing on the three - dimensional nature of forest structure, structural complexity describes the spatial arrangement of plant

* Corresponding author.
E-mail addresses: kwillim1@forst.uni-goettingen.de (K. Willim), Christian.Ammer@forst.uni-goettingen.de (C. Ammer), dseidel@gwdg.de (D. Seidel), peter.annighoefer@tum.de (P. Annighöfer), julia.schmucker@tum.de (J. Schmucker), peter.schall@forst.uni-goettingen.de (P. Schall), mehbrec1@gwdg.de (M. Ehbrecht).
[1] ORCID https://orcid.org/0000–0002–0129–3381

https://doi.org/10.1016/j.tfp.2022.100231
Received 2 January 2022; Received in revised form 22 February 2022; Accepted 22 February 2022
Available online 26 February 2022

material in three - dimensional (3D) space (Pretzsch et al. 2009). Higher structural complexity at the stand - level reflects itself in a homogenous three - dimensional distribution of plant material, due to the interaction of different structural attributes that result in a high space occupation within the stand (Ehbrecht et al., 2021; Seidel et al., 2019). For example, recent studies have shown that a high diversity in tree sizes, tree ages and crown morphologies reflect in a high space occupation within a stand, resulting in a high structural complexity (Ehbrecht et al., 2017; McElhinny et al., 2005; Stiers et al., 2020; Willim et al., 2020). Thus, dynamics of structural complexity can be attributed to changes of the spatial arrangement of tree plant material within the three - dimensional space, due to changes of tree sizes and crown morphologies, such as growth responses after harvesting interventions or disturbance induced tree mortality .

Forest stand structure is an important component of the interrelation of stand growth and resource availability (Fig. 1). With a disturbance event, e.g. a windthrow or the removal of trees, growth of seedlings, saplings and remaining trees may be increased due to increased availability of space and resources. In turn, the growth of tree individuals changes stand structure due to changes in the three - dimensional arrangement of plant material within the stand.

In many European forests *Fagus sylvatica* L. (hereafter beech) is one of the main native and dominant tree species (Bréda et al., 2006; Ellenberg and Leuschner 2010; Leuschner et al., 2006). Beech is characterized by a high crown plasticity and flexibility in growth response and therefore able to efficiently re-occupy canopy niche space that becomes available following disturbances (Feldmann et al., 2018; Pretzsch 2009; Pretzsch and Schütze 2009). In even - aged stands, the remaining stand̓s capacity to re-occupy canopy space after a disturbance declines with increasing age, as growth response in older stands is lower than in young stands (Assmann 1961; Pretzsch 2009). However, canopy space may also be (re-) occupied by the establishment and growth of naturally occurring seedlings and saplings as well as other understory vegetation in lower strata. Beech is especially known for its shade tolerance compared to other, more light demanding tree species and as such, seedlings, saplings or younger trees are able to expand their crowns even under low light level conditions (Emborg 1998; Madsen and Larsen 1997).

Light availability is one of the most important abiotic factors that determines tree growth, especially the growth of understory vegetation (Muscolo et al., 2014; Pretzsch 2009). The light availability on the forest floor is determined by canopy openness (Collet et al., 2001). In unmanaged beech forest reserves in Europe, canopy openness is mainly determined by small - scale natural disturbances, which create canopy gaps that control the light transmission to the understory (Feldmann et al., 2018). In different types of silvicultural management, understory dynamics are regulated by canopy release due to the removal of overstory trees (Agestam et al., 2003; Gayer 1886; Messier and Puettmann 2011; Schall et al., 2018).

The positive effect of improved light availability due to tree harvesting or natural disturbances on the growth response of trees in European forests is well understood Führer (2000), including the spatial relationship between gaps and regeneration development (Stiers et al., 2019). In this context, many studies have focused on the effect of the reduction of stand density on growth response (Ciancio et al., 2006; Pretzsch et al., 2015; Primicia et al., 2016) and dynamics of tree species composition (Canullo et al., 2017; Hédl et al., 2017; Pykälä 2004). So far, there is much less information about how forest management or disturbance induced changes of light availability affect the dynamics of structural complexity (Ammer et al., 2018).

Here, we investigate the short - term dynamics of structural complexity in differently managed and unmanaged beech - dominated forests in Central Germany. In order to cover the most common management systems in Central Europe, we selected forest management types representing even - aged and uneven - aged silvicultural management as well as unmanaged forest reserves typical for Germany (referred to as “unmanaged” hereafter) as reference systems. Recent studies have focused on quantifying stand structural complexity based on three - dimensional forest scenes derived from terrestrial laser scanning (TLS), because TLS has shown to be an efficient and reliable tool to assess three - dimensional forest structure precisely (Atkins et al., 2018; Camarretta et al., 2020; Hardiman et al., 2013; Willim et al., 2019). Therefore, we used TLS to assess structural complexity at two points in time, namely in the years 2014 and 2019. Based on the 3D forest scenes from both years, we calculated the changes of different aspects of structural complexity.

First, we investigated how dynamics of structural complexity differ between even - aged, uneven - aged and unmanaged stands. Second, we investigated whether different developmental stages under even - aged forest management show different short - term dynamics in structural complexity. Ultimately, we studied how canopy openness differed between the different forest management types and whether differences in canopy openness can explain the observed patterns of stand structural complexity dynamics. As any silvicultural intervention modifies canopy openness, we assumed that canopy openness is the main driver of short - term changes in stand structural complexity.

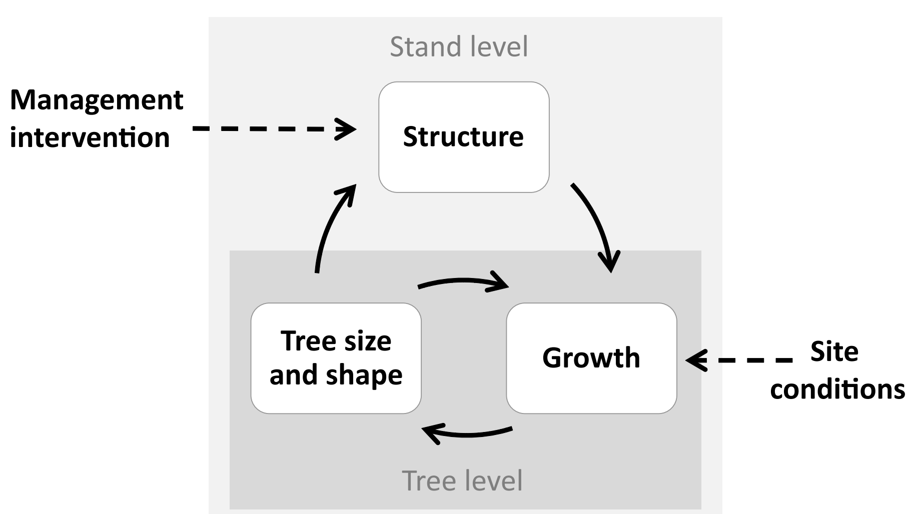

Fig. 1. Feedback loop modified after Pretzsch (2009), showing the relationship between stand structure, growth conditions, tree size and shape, with management intervention and site conditions as external factors.

2. Methods

2.1. Description of study sites and forest management types

As study site, we chose the Hainich - Dün region, which is part of the Biodiversity - Exploratories (www.biodiversity-exploratories.de). The Biodiversity Exploratories are a long - term research project that aims at investigating the impacts of land use on biodiversity and ecosystem processes (Fischer et al., 2010). The studied forest stands are located in Central Germany, 285 - 550 m above sea level (a.s.l). They are characterized by nutrient - rich soils, developed over loess or lacustrine limestone. The climate is characterized by a mean annual temperature of 6.5 - 8 C° and a mean annual precipitation of 500 - 800 mm (Fischer et al., 2010).

We selected a subset of 42 plots of 100 × 100 m (1 ha), with beech as main tree species. The selected plots represent different developmental stages of even - aged forest management, uneven - aged forest management and unmanaged stands. Even - aged stands, managed as shelterwood systems, are characterized by tree harvests in mature stands starting after a mast year in order to enable the natural regeneration. After successful establishment of regeneration, the remaining shelter trees are cut in several cutting interventions which are applied over a period of 20 - 40 years (Schall et al., 2018). On the landscape scale, shelterwood systems result in a patchwork of stands that belong to different developmental stages, ranging from thickets, to pole woods, immature and mature timber stands (see Table 1). Reaching the older pole wood stage, thinning from above takes place, in order to promote the growth of vigorous high quality target trees. In the last decades, the even - aged system has been more and more transformed by fine grained selective cutting regeneration systems. Here, the harvest of single trees, groups of trees and the creation of small canopy openings ($\leq$ 1000 m^2) is applied (Schall et al., 2018). As a result, mature stands may show a rather multi - layered vertical structure, with a high variability of different understory conditions (Ehbrecht et al., 2017). For example, single tree selection systems are characterized by tree removals of high frequency, but low intensity (Bartsch and Röhrig 2016). Interventions take place around every five years, mainly focusing on overstory trees that have reached a given target diameter (Schall et al., 2018). Forest stands of the single tree selection system are characterized by a multi - layered forest structure with a high spatial heterogeneity at stand - level, resulting in an uneven - aged structure with a high structural complexity (Ehbrecht et al., 2017; Pommerening 2002; Stiers et al., 2020; Willim et al., 2020).

We exclude from our study other concepts to define developmental stages or phases to study natural beech forest dynamics under quasi - equilibrium conditions, as e.g. Korpel (1995), Tabaku (2000); Bottero et al., (2011), or as Emborg (1998) and Drossler et al. (2016) in managed or formerly managed stands.

In the study area, most stands that are unmanaged today had been managed under coppice with standards and were then transformed to high forests in the past 150 years. Management was abandoned 23 - 50 years ago (Schall et al., 2018). Compared to the uneven - aged stands, these forests are characterized by a lower horizontal and vertical variability in structure.

2.2. Data collection and 3D point cloud processing

To capture the 3D distribution of foliage and woody material of the forest stands, in each 1 ha forest plot, a sample grid of nine systematically distributed scans was used. A distance of 30 m was kept between the adjacent scanning positions (Fig. 2). The first data collection was conducted in 2014, the second one was conducted in 2019. The same sample grid, including the same scan locations, was used for both data collections. Both times, we scanned during the growing season (May - September), when vegetation was foliated. Scans were conducted during dry weather conditions, with wind speed below 5 km*h^{-1}. We used a Faro Focus 3D 120 (Faro Technologies Inc., Lake Mary, USA) laser scanner for our measurements. This scanner model operates based on the phase - shift technology and covers a field of view of 300° in vertical and 360° in horizontal direction. It was set to scan with an angular resolution of 0.035°, resulting in around 44.4 million measurements per scan. The scanner was mounted on a tripod, operating at 1.3 m above ground. During all scans, the scanner's standard filters (Clear Contour- and Clear Sky - filter) were applied.

Using the Faro Scene® Software (Faro Technologies Inc., Lake Mary, USA), for each point cloud generated by one scan, standard filters (Dark Scan Points, Outliers) were applied. After this procedure, we processed the point clouds (xyz - format) in Mathematica, Version 12.0.0 (Wolfram Research, Champaign, USA). In order to consider different aspects of structural complexity, we computed different 3D measures from each generated 3D point cloud. First, the stand structural complexity index (SSCI) was computed, which was introduced by Ehbrecht et al., (2017) and is an effective measure to quantify the structural complexity of a forest stand (Ehbrecht et al., 2021; Stiers et al., 2018; Zemp et al., 2019). It is based on the mean fractal dimension of cross - sectional polygons, which were derived from the 3D point cloud (Ehbrecht et al., 2017). Because the fractal dimension is a scale - independent measure, the mean fractal dimension values are scaled by using the effective number

Table 1
Forest management types, developmental phases and stand characteristics for all plots in the exploratory Hainich - Dün. EA = Even - aged, UEA = Uneven - aged, UM = Unmanaged.

Plot number	Plot ID	Forest management type	Developmental phase	Canopy openness (2014) in (%)
1	HEW04	EA	Thicket	3.89
2	HEW15	EA	Thicket	10.21
3	HEW43	EA	Thicket	2.49
4	HEW44	EA	Thicket	10.86
5	HEW16	EA	Pole wood	2.35
6	HEW17	EA	Pole wood	2.7
7	HEW18	EA	Pole wood	2.84
8	HEW45	EA	Pole wood	2.54
9	HEW05	EA	Immature	3.94
10	HEW19	EA	Immature	4.76
11	HEW20	EA	Immature	3.44
12	HEW46	EA	Immature	3.42
13	HEW06	EA	Mature	3.6
14	HEW21	EA	Mature	6.61
15	HEW22	EA	Mature	18.14
16	HEW47	EA	Mature	3.48
17	HEW07	UEA	Mature	5.75
18	HEW08	UEA	Mature	2.53
19	HEW09	UEA	Mature	8.55
20	HEW26	UEA	Mature	6.10
21	HEW27	UEA	Mature	11.15
22	HEW28	UEA	Mature	9.49
23	HEW29	UEA	Mature	5.00
24	HEW30	UEA	Mature	6.23
25	HEW31	UEA	Mature	6.46
26	HEW32	UEA	Mature	6.09
27	HEW33	UEA	Mature	13.10
28	HEW48	UEA	Mature	3.28
29	HEW49	UEA	Mature	5.70
30	HEW10	UM	Mature	2.63
31	HEW11	UM	Mature	2.54
32	HEW12	UM	Mature	3.15
33	HEW34	UM	Mature	2.58
34	HEW35	UM	Mature	2.48
35	HEW36	UM	Mature	2.74
36	HEW37	UM	Mature	3.35
37	HEW38	UM	Mature	2.59
38	HEW39	UM	Mature	2.63
39	HEW40	UM	Mature	2.45
40	HEW41	UM	Mature	2.68
41	HEW42	UM	Mature	2.72
42	HEW50	UM	Mature	2.66

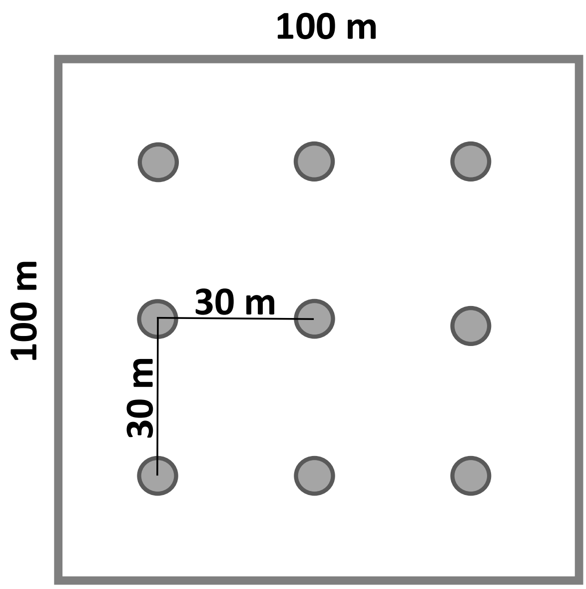

Fig. 2. Sample design for each 100 × 100 m (1 ha) plot. Grey circles represent the scan positions within the plot.

of layers (ENL), in order to consider the size and the vertical structure of the forest stand (Ehbrecht et al., 2017). Second, ENL, introduced by Ehbrecht et al., (2016), is based on a voxel - model, with cubic voxels of 20 cm side length, the number of 1 m - thick layers that are effectively occupied by foliage or woody components is quantified. Then, by applying the inverse Simpson - Index to the vertical distribution of foliage and woody components, ENL quantifies the number of vertical layers that are effectively occupied by foliage and woody components. Generally, ENL increases with increasing stand height and a more even distribution of plant material along the vertical axis. Third, as the forests understory complexity is an integral element of the overall stand structural complexity, we computed the understory complexity index (UCI), which was introduced by Willim et al., (2019). As for the calculation of the SSCI, the UCI uses fractal analysis to describe the shape complexity of a polygon. But in contrast to the SSCI, the UCI is based on the fractal dimension of a horizontal polygon, which was created from the understory of a voxelized (1 × 1 cm) 3D forest scene (Seidel et al., 2021). At the end of the computations, we had nine SSCI, ENL and UCI values for each plot. We then aggregated the nine SSCI, ENL and UCI values for each plot to mean values, to get a robust estimate of different aspects of stand structural complexity for each plot that was used for further statistical analyses.

Canopy openness was calculated in two steps. First, an opening angle of 60° from the laser scanner' s perspective was used to compute the percentage of canopy openness. Then the raw 3D point cloud was projected onto a plane by using a stereographic projection, following the procedure by Zheng et al., (2013). In order to investigate the effects of canopy openness on the dynamics of structural complexity, we used the canopy openness values from 2014 as initial state for the time frame being observed.

2.3. Statistical analyses

Statistical analyses were conducted in the software environment R, version 3.6.3 (R Development Core Team, 2020, Vienna, Austria). In order to quantify the dynamics of structural complexity for the investigated forest stands from 2014 to 2019, we used two approaches. First, we subtracted the structural complexity measures of 2014 from the values of 2019. Consequently, an increase in structural complexity resulted in positive Δ - values, whereas a decrease in structural complexity during the five years resulted in negative Δ - values. Forest stands with no changes in structural complexity had Δ - values around 0. We used the Δ - values in order to calculate differences in structural complexity dynamics between the different forest management types and to test the relationship between canopy openness and dynamics of structural complexity. In order to describe the variability of dynamics within the forest management types, as well as the structural changes on a stand - level, we additionally calculated the relative changes of the structural complexity measures during the 5 years.

In order to determine differences between the three forest management types, we tested for normal distribution using the Shapiro - Wilk test and the Levene test for homogeneity of variance. Because the data did not meet the conditions for parametric tests, we used the Kruskal - Wallis test to look for differences between even - aged, uneven - aged stands and unmanaged forest stands. For post - hoc analyses, we used the Wilcoxon rank sum test. The significance level was $p < 0.01$ for all tests. To test the relationship between canopy openness and the dynamics of structural complexity, we used linear regression models. A significant relationship was assumed, if $p < 0.01$.

3. Results

3.1. Dynamics of structural complexity between different forest management types and developmental stages

We found significantly lower Δ SSCI in the unmanaged stands compared to both managed forest management types (see Fig. 3a). The unmanaged forests had on average nearly no change (mean Δ SSCI of + 0.58%; see Table 2) in SSCI. Moreover, all unmanaged forest stands showed a low variability of dynamics in SSCI (standard deviation of SSCI ± 6.61%; see Table 2). Interestingly, negative Δ SSCI, i.e. reduced stand complexity, were observed in the unmanaged forests more often than in the managed stands.

The majority of the even - aged and uneven - aged managed forests showed Δ SSCI values above 0 (see Fig. 3a), which indicates an increase in SSCI from 2014 to 2019 (mean Δ SSCI of + 19.94%; see Table 2). For the uneven - aged forests, SSCI increased on average by 17.79% (see Table 2) from 2014 to 2019. In contrast to the unmanaged forests, we observed a quite high variability in dynamics of SSCI (± 24.52; see Table 2) between the forest stands within the uneven - aged management system. Some uneven - aged stands showed a strong increase in SSCI (see Fig. 3b, plot number 21,22 and 27), whereas other uneven - aged forest stands showed a lower increase in SSCI (see Fig. 3b, plot number 23,26,28,29) or nearly no change in SSCI (see Fig. 3b, plot number 17,18,20,24,25).

Comparable to the uneven - aged forest stands, the even - aged forests showed a considerable variability in dynamics of SSCI (see Fig. 3a). In contrast to the uneven - aged stands, the even - aged stands comprise forest stands of different developmental stages. We observed different dynamics in SSCI for the different developmental stages (see Table 2). Even - aged thickets and mature stands showed the highest increase in SSCI (+ 33.42% and + 26.29%), whereas SSCI in the immature timber stage increased by 15.7% and pole wood only by 4.35% (see Table 2).

We observed different dynamics of UCI and ENL for the different forest management types and developmental stages (see Table 2). The mature unmanaged stands showed on average a slight decrease in UCI (- 1.43%), whereas ENL increased by 12.11%. In contrast to the mature unmanaged forests, the even - aged and uneven - aged mature stands showed on average an increase in UCI (+ 22.27% and + 18.37%) and a slight decrease in ENL (see Table 2). Immature timber showed also on average an increase in UCI (+ 30.99%). The younger developmental stages thickets and pole wood both showed a decrease in UCI, with a stronger decrease in UCI in thickets (- 24.94%) than in pole wood (- 9.19%, see Table 2). ENL, in contrast, increased in the younger stages during the 5 years (see Table 2). In thickets ENL increased on average by 75.58%, whereas in pole wood ENL increased by 29.06%.

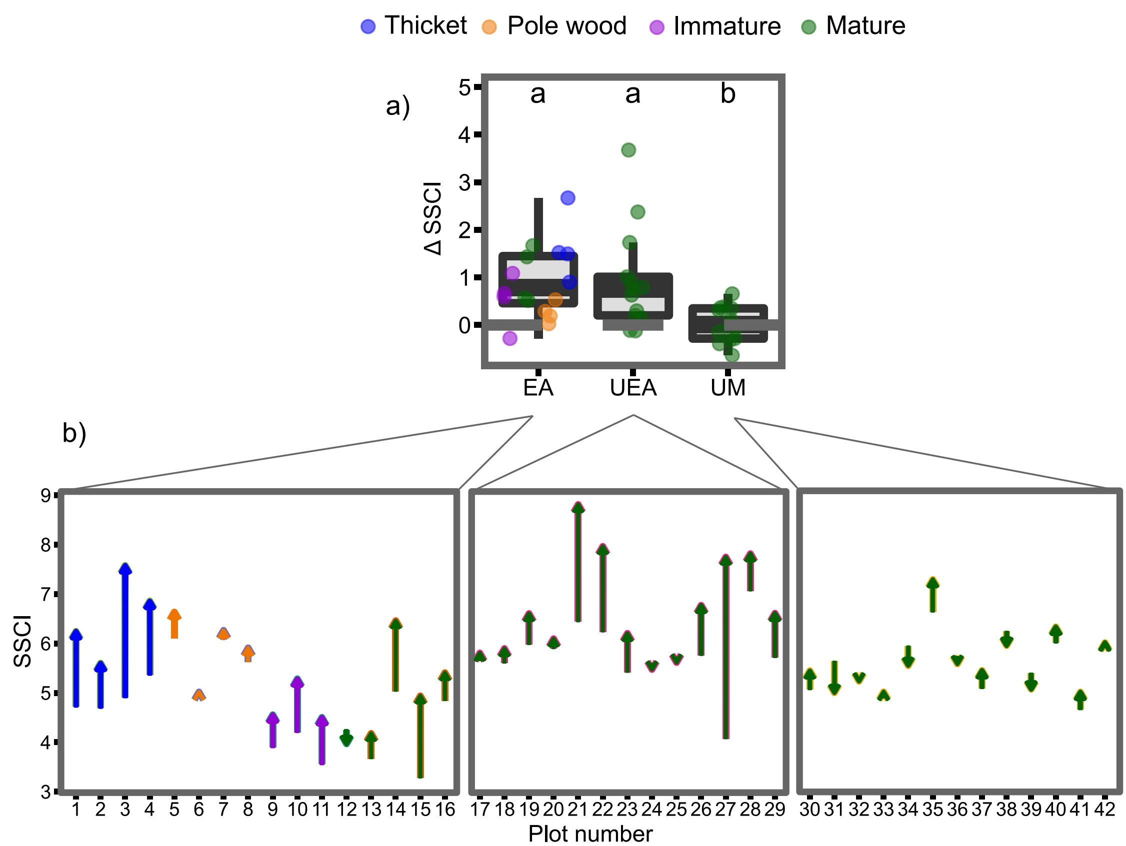

Fig. 3. Dynamics of stand structural complexity (SSCI) in different forest management types: EA = Even - aged (n = 16), UEA = Uneven - aged (n = 13) and UM = Unmanaged (n = 13). Different colors represent different developmental stages. a) Box - and - whisker plots showing Δ SSCI for the different forest management types. Letters indicate significant differences (p < 0.01) between the forest management types. Dashed line indicates no change of SSCI. (b) Arrows showing the change of SSCI for the single forest plots within the three different forest management types. Arrows pointing upwards indicate an increase in SSCI, whereas arrows showing downwards represent a decrease in SSCI.

Table 2
SSCI, ENL and UCI mean values and standard deviation (±) for the years 2014 and 2019 and the relative changes (%) of the three measures from 2014 to 2019. EA = Even - aged (n = 16): thicket (n = 4), pole wood (n = 4), immature timber (n = 4), mature timber (n = 4), UEA = Uneven - aged (n = 13) and UM = Unmanaged (n = 13).

	SSCI 2014	SSCI 2019	Rel. change SSCI (%)	ENL 2014	ENL 2019	Rel. change ENL (%)	UCI 2014	UCI 2019	Rel. change UCI (%)
EA	4.7	5.59	+ 19.94	15.13	16.7	+ 25.88	3.81	3.67	+ 4.78
	± 0.85	± 1.04	± 17.01	± 8.11	± 6.71	± 35.2	± 1.93	± 1.37	± 34.15
Thicket	4.92	6.57	+ 33.42	4.84	8.37	+ 75.58	6.71	4.88	- 24.94
	± 0.31	± 0.85	± 15.01	± 0.85	± 0.58	± 24.03	± 1.43	± 0.33	± 15.48
Pole wood	5.7	5.96	+ 4.35	10.44	13.45	+ 29.06	2.97	2.68	- 9.19
	± 0.52	± 0.69	± 3.42	± 1.59	± 1.84	± 3.01	± 0.39	± 0.25	± 7.42
Immature timber	3.98	4.58	+ 15.7	21.83	22.98	+ 5.56	2.21	2.92	+ 30.99
	± 0.32	± 0.54	± 15.52	± 1.54	± 0.50	± 5.50	± 0.17	± 0.94	± 36.87
Mature timber	4.2	5.25	+ 26.29	23.83	22	- 6.65	3.33	4.21	+ 22.27
	± 0.87	± 0.95	± 18.01	± 1.38	± 4.97	± 17.58	± 0.68	± 1.98	± 37.61
UEA	5.78	6.72	+ 17.79	17.71	17.17	- 1.20	2.97	3.5	+ 18.37
	± 0.68	± 1.05	± 24.52	± 2.72	± 2.69	± 19.55	± 0.73	± 1.17	± 26.58
UM	5.59	5.61	+ 0.58	19.56	21.87	+ 12.11	2.27	2.22	- 1.43
	± 0.58	± 0.66	± 6.61	± 2.39	± 2.33	± 5.10	± 0.41	± 0.32	± 8.91

3.2. Canopy openness in the different forest management types and its effect on the dynamics of structural complexity

In 2014, we observed differences in canopy openness between the three forest management types. The unmanaged forests had a significantly lower canopy openness than the managed even - aged and uneven - aged forest stands (see Fig. 4a). Additionally, the unmanaged forests showed a lower variability in canopy openness between the forest plots than both managed forest management types (see Fig. 4a). For the unmanaged forests, we could not find a significant relationship between canopy openness and dynamics of SSCI (see Fig. 4b). For the managed forests, we observed only for the uneven - aged stands a positive relationship between canopy openness and dynamics of SSCI ($r^2 = 0.64$, see Fig. 4b).

4. Discussion

Here, we present results from a study investigating the short - term dynamics of stand structural complexity in managed even - aged and uneven - aged stands as well as unmanaged forests. We observed

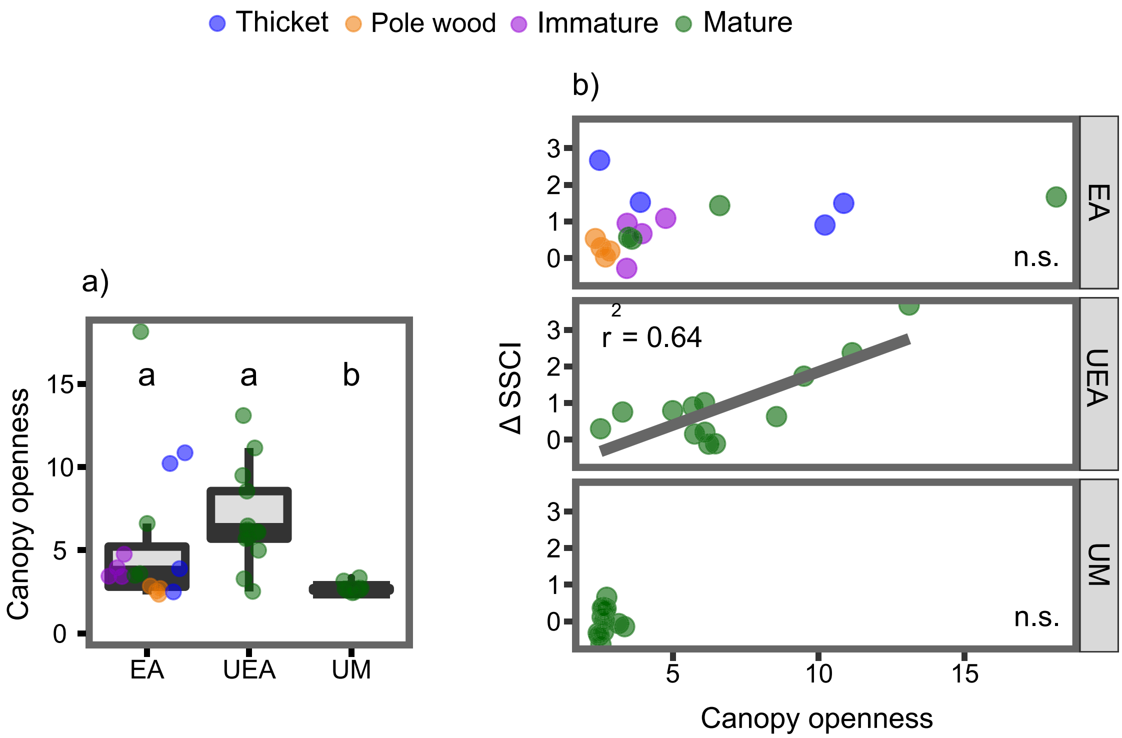

Fig. 4. Canopy openness for different forest management types and its relationship with dynamics of stand structural complexity (Δ SSCI). The different forest management types are: EA = Even - aged (n = 16), UEA = Uneven - aged (n = 13) and UM = Unmanaged (n = 13). Different colors represent different developmental stages. a) Box - and - whisker plots showing canopy openness for the different forest management types in 2014. Letters indicate significant differences ($p < 0.01$) between the forest management types. b) Relationship between canopy openness measured in 2014 and Δ SSCI for different forest management types. Non - significant relationships are marked by the abbreviation "n.s.".

different dynamics of structural complexity in differently managed and unmanaged beech - dominated forests, with unmanaged forests showing lower dynamics of stand structural complexity than managed forests.

The low initial canopy openness of the investigated unmanaged forest stands could be the main reason for the low dynamics in structural complexity and also the low variability between the forest plots (see Fig. 3a, b). In this context, it is important to keep in mind that the unmanaged stands of this study had been set aside 20 to 50 years ago only, which means that they still carry the legacy of their former management. Without disturbances that open up the canopy, they continue to grow "cathedral - like" and stay rather homogeneous, because growth conditions do not change significantly (Dieler et al., 2017). Due to the low canopy openness, establishment and growth of tree regeneration was not sufficiently promoted, resulting in nearly no change in UCI because of limited light availability (see Table 2). Although the overall stand structural complexity showed nearly no change during the 5 years, we observed an increase of ENL (see Table 2), which indicates an increase in vertical stratification within the unmanaged stands. Because of the fact that we can exclude changes of vertical stand structure due to the growth of regeneration, we assume that stand height increased due to crown enlargement of the oldest canopy trees (Rademacher et al., 2004). In the future, the structural complexity of unmanaged stands may increase with increasing stand age, when natural decay is becoming more pronounced or with the appearance of exogenous events, like storms or dying trees due to severe drought, which may create canopy gaps and thereby increase canopy openness (Hardiman et al., 2013). Unmanaged European beech forests are mainly characterized by a small - scale disturbance regime (Kucbel et al., 2010; Nagel et al., 2014). As the canopy openness in the unmanaged stands has nearly not changed from 2014 to 2019 (mean value Δ 0.91), it seems that small gaps that may occurred due to single tree mortality, were probably quickly closed by lateral crown expansion of the canopy trees (Schröter et al., 2012).

Compared to the unmanaged forests, mature even - aged and uneven - aged managed forest stands showed a significantly higher canopy openness and variability of canopy closure (see Fig. 4a), resulting from the removal of overstory trees during harvesting operations. In uneven - aged stands, Δ SSCI increased linearly with an initially higher canopy openness. In uneven - aged stands with non - uniform canopy closure, light availability for the understory vegetation was higher than in stands with a uniform canopy closure such as in even - aged or unmanaged stands. The higher the light availability was, the more the growth of young and subdominant trees was promoted (see Fig. A.1), resulting in an increase in UCI, thereby triggering the increase in SSCI (see Table 2; Fig. A.2a).

The even - aged stands showed a high variation in dynamics of structural complexity (see Table 2), since they are characterized by stands of different developmental stages, ranging from young stands, as thickets and pole woods, to immature and mature timber stands. For the different developmental stages, we observed different dynamics in structural complexity, which explains the high variability of SSCI, ENL and UCI under even - aged forest management (see Fig. 3a).

We observed high structural dynamics in even - aged thickets, which reflect in an increase in ENL and a decrease in UCI during the 5 years (see Table 2; Fig. A.2b). The higher ENL values are a result of the pronounced height growth of young trees due to an increased above- and belowground resource availability after the removal of the remaining shelterwood trees. In even - aged forest management, remaining shelterwood trees are removed after the successful establishment of regeneration, in order to enhance growth conditions of tree regeneration (Schall et al., 2018). The decrease in understory complexity of young stands (see Table 2) can be attributed to the beginning process of self - pruning (Ehbrecht et al., 2017). As part of the intraspecific competition for light, young trees showed increasingly branch - free sections of the stems Pretzsch (2019). Although, we observed a decrease in UCI for the even - aged thickets, the SSCI strongly increased during the 5 years. One explanation for that observation could be that the pronounced height growth overcompensated for less effectively occupied lower canopy layers due to the beginning process of self - pruning. In pole woods, however, it seems that the increase in height growth could not compensate the low occupation of the lower canopy layers, due to progressing self - differentiation, resulting in nearly no change in SSCI (see Table 2).

While in the younger stages, height growth and changes in vertical structure seemed to be the main driver of increases in stand structural complexity, we observed increasing Δ SSCI values with increasing understory complexity in the older immature and mature stands (see Fig. A.2a). As in the mature uneven - aged stands, the development and growth of regeneration in even - aged mature timber stands, reflected by an increase in UCI, led to an increase in SSCI (see Table 2). In this context, even - aged mature stands with a higher canopy openness (Plot no. 14 and 15, Table 1) showed a higher increase in understory complexity (and overall complexity) than mature stands with a lower canopy openness (see Fig. 3b).

Our findings on the short - term dynamics of structural complexity in even - aged, uneven - aged and unmanaged forests need to be viewed in the context of long - term dynamics of forest structure. The different developmental stages in even - aged forest management can be understood as a chrono - sequence of stand development and differences in structural complexity between these different developmental stages and reflect the dynamics of structural complexity in the long term (Stiers et al., 2018). Along this developmental trajectory, management - induced changes of light availability, as well as growth dynamics, drive changes of structural complexity on short temporal scales. Even though we did not observe decreases of structural complexity in managed forests in this study, negative effects of tree harvesting on structural complexity may generally occur, but depend on the harvesting intensity and the amount of volume or biomass removed (Asbeck and Frey 2021). Against this background, the increases in structural complexity in the stands under uneven - aged forest management need to be understood in the context of low intensity, but cyclic management interventions. While the growth of understory vegetation promoted the increase in structural complexity during the time period observed, the removal of overstory trees in a next cutting intervention may set back the stand's structural complexity to previous levels, as harvested trees of upper canopy layers reduce ENL. The resulting fluctuation around a specific level of structural complexity would then resemble the fluctuations around a certain growing stock level that is characteristic of uneven - aged forest management (O'Hara and Gersonde 2004). While managed, uneven - aged forests, and partially mature timber stages in even - aged forests, do not significantly differ in structural complexity from unmanaged forests including primary forests (Ehbrecht et al., 2017; Stiers et al., 2018), our results suggest that managed forests are characterized by more pronounced structural dynamics on short - temporal scales than unmanaged forests.

5. Conclusions

Short - term dynamics of stand structural complexity strongly depend on the developmental stage or canopy openness of the forest. Uneven - aged mature stands with higher canopy openness showed a higher increase in structural complexity than stands with lower canopy openness, resulting from the establishment and/ or growth of understory vegetation. In even - aged management systems, structural dynamics in younger stands were mainly driven by deterministic growth processes. Lowest dynamics in structural complexity were found in unmanaged forests that were set aside 20 to 50 years ago. They seem to be in the optimum phase and are characterized by a very low canopy openness due to the absence of natural disturbances. Our findings contribute to the understanding of how forest management can influence dynamics of structural complexity and therefore help to predict responses of differently managed and unmanaged beech forests to disturbances of natural and anthropogenic origin.

Funding

The work has been (partly) funded by the DFG Priority Program 1374 "Infrastructure - Biodiversity - Exploratories" (DOR 786/8–1), the Erich Ritter - Foundation (T0021/29,427/2017) and the German Research Foundation (DFG) (SE2383/7–1) provided to Dominik Seidel. The work has been funded by the DFG (German Science Foundation) Priority Program 1374 "Infrastructure - Biodiversity - Exploratories" (grant numbers Am 149/16–4 and SE2383/2–1). Field work permits were issued by the responsible state environmental offices of Baden - Württemberg, Thüringen, and Brandenburg (according to § 72 BbgNatSchG).

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We thank the managers of the three Exploratories, Kirsten Reichel - Jung, Katrin Lorenzen, Miriam Teuscher and all former managers for their work in maintaining the plot and project infrastructure; Christiane Fischer for giving support through the central office, Michael Owonibi and Andreas Ostrowski for managing the central data base, and Markus Fischer, Eduard Linsenmair, Dominik Hessenmöller, Daniel Prati, Ingo Schöning, François Buscot, Ernst - Detlef Schulze, Wolfgang W. Weisser and the late Elisabeth Kalko for their role in setting up the Biodiversity Exploratories project.

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.tfp.2022.100231.

References

Agestam, E, Ekö, PM, Nilsson, U, Welander, NT, 2003. The effects of shelterwood density and site preparation on natural regeneration of *Fagus sylvatica* in southern Sweden. For. Ecol. Manage. 176, 61–73. https://doi.org/10.1016/S0378-1127(02)00277-3.

Ammer, C, Fichtner, A, Fischer, A, Gossner, MM, Meyer, P, Seidl, R, Thomas, FM, Annighöfer, P, Kreyling, J, Ohse, B, Berger, U, Feldmann, E, Häberle, KH, Heer, K, Heinrichs, S, Huth, F, Krämer-Klement, K, Mölder, A, Müller, J, Mund, M, Opgenoorth, L, Schall, P, Scherer-Lorenzen, M, Seidel, D, Vogt, J, Wagner, S, 2018. Key ecological research questions for Central European forests. BAAE 32, 3–25. https://doi.org/10.1016/j.baae.2018.07.006.

Asbeck, T, Frey, J, 2021. Weak relationships of continuous forest management intensity and remotely sensed stand structural complexity in temperate mountain forests. Eur. J. For. Res. 140, 721–731. https://doi.org/10.1007/s10342-021-01361-4.

Assmann, E, 1961. Waldertragskunde. Organische Produktion, Struktur, Zuwachs und Ertrag von Waldbeständen. BLV Verlagsgesellschaft, München, Bonn.

Atkins, JW, Bohrer, G, Fahey, RT, Hardiman, BS, Morin, TH, Stovall, AEL., Zimmerman, N, Gough, CM, 2018. Quantifying vegetation and canopy structural complexity from terrestrial LiDAR data using the FORESTR R package. Methods Ecol. Evol. 9, 2057–2066. https://doi.org/10.1111/2041-210X.13061.

Bartsch, N, Röhrig, E, 2016. Waldökologie: Einführung für Mitteleuropa: 194 Abbildungen, Davon 129 Zeichnungen und 65 Fotos: 57 Tabellen. Springer Spektrum, Berlin Heidelberg.

Bauhus, J, Puettmann, K, Messier, C, 2009. Silviculture for old-growth attributes. For. Ecol. Manage. 258, 525–537. https://doi.org/10.1016/j.foreco.2009.01.053.

Bottero, A, Garbarino, M, Dukić, V, Govedar, Z, Lingua, E, Nagel, T.A., Motta, R, 2011. Gap-phase dynamics in the old-growth forest of Lom, Bosnia and Herzegovina. Silva Fennica 45, 875–887.

Bréda, N, Huc, R, Granier, A, Dreyer, E, 2006. Temperate forest trees and stands under severe drought: a review of ecophysiological responses, adaptation processes and long-term consequences. Ann. For. Sci. 63, 625–644. https://doi.org/10.1051/forest:2006042.

Camarretta, N, Harrison, PA, Bailey, T, Potts, B, Lucieer, A, Davidson, N, Hunt, M, 2020. Monitoring forest structure to guide adaptive management of forest restoration: a review of remote sensing approaches. New For. 51, 573–596. https://doi.org/10.1007/s11056-019-09754-5.

Canullo, R, Simonetti, E, Cervellini, M, Chelli, S, Bartha, S, Wellstein, C, Campetella, G, 2017. Unravelling mechanisms of short-term vegetation dynamics in complex coppice forest systems. Folia Geobot. 52, 71–81. https://doi.org/10.1007/s12224-016-9264-x.

Ciancio, O, Iovino, F, Menguzzato, G, Nicolaci, A, Nocentini, S, 2006. Structure and growth of a small group selection forest of calabrian pine in Southern Italy: a hypothesis for continuous cover forestry based on traditional silviculture. For. Ecol. Manage. 224, 229–234. https://doi.org/10.1016/j.foreco.2005.12.057.

Collet, C, Lanter, O, Pardos, M, 2001. Effects of canopy opening on height and diameter growth in naturally regenerated beech seedlings. Ann. For. Sci. 58, 127–134. https://doi.org/10.1051/forest:2001112.

Coumou, D, Rahmstorf, S, 2012. A decade of weather extremes. Nat. Clim. Change 2, 491–496. https://doi.org/10.1038/nclimate1452.

Dieler, J, Uhl, E, Biber, P, Müller, J, Rötzer, T, Pretzsch, H, 2017. Effect of forest stand management on species composition, structural diversity, and productivity in the temperate zone of Europe. Eur. J. For. Res. 136, 739–766. https://doi.org/10.1007/s10342-017-1056-1.

Drössler, L, Feldmann, E, Glatthorn, J, Annighöfer, P, Kucbel, S, Tabaku, V, 2016. What Happens after the Gap? - Size distributions of patches with homogeneously sized trees in natural and managed beech forests in Europe. OJF 6, 177–190. https://doi.org/10.4236/ojf.2016.63015.

Ehbrecht, M, Schall, P, Ammer, C, Fischer, M, Seidel, D, 2019. Effects of structural heterogeneity on the diurnal temperature range in temperate forest ecosystems. For. Ecol. Manage. 432, 860–867. https://doi.org/10.1016/j.foreco.2018.10.008.

Ehbrecht, M, Schall, P, Ammer, C, Seidel, D, 2017. Quantifying stand structural complexity and its relationship with forest management, tree species diversity and microclimate. Agric. For. Meteorol. 242, 1–9. https://doi.org/10.1016/j.agrformet.2017.04.012.

Ehbrecht, M, Schall, P, Juchheim, J, Ammer, C, Seidel, D, 2016. Effective number of layers: a new measure for quantifying three-dimensional stand structure based on sampling with terrestrial LiDAR. For. Ecol. Manage. 380, 212–223. https://doi.org/10.1016/j.foreco.2016.09.003.

Ehbrecht, M, Seidel, D, Annighöfer, P, Kreft, H, Köhler, M, Zemp, DC, Puettmann, K, Nilus, R, Babweteera, F, Willim, K, Stiers, M, Soto, D, Boehmer, HJ, Fisichelli, N, Burnett, M, Juday, G, Stephens, SL, Ammer, C, 2021. Global patterns and climatic controls of forest structural complexity. Nat. Commun. 12, 519. https://doi.org/10.1038/s41467-020-20767-z.

Ellenberg, H, Leuschner, C, 2010. Vegetation Mitteleuropas mit Den Alpen: in ökologischer, Dynamischer Und Historischer Sicht. UTB, Stuttgart.

Emborg, J, 1998. Understorey light conditions and regeneration with respect to the structural dynamics of a near-natural temperate deciduous forest in Denmark. For. Ecol. Manage. 106, 83–95. https://doi.org/10.1016/S0378-1127(97)00299-5.

Fahey, RT, Fotis, AT, Woods, KD, 2015. Quantifying canopy complexity and effects on productivity and resilience in late-successional hemlock–hardwood forests. Ecol. Appl. 25, 834–847. https://doi.org/10.1890/14-1012.1.

Feldmann, E, Drößler, L, Hauck, M, Kucbel, S, Pichler, V, Leuschner, C, 2018. Canopy gap dynamics and tree understory release in a virgin beech forest, Slovakian Carpathians. For. Ecol. Manage. 415–416, 38–46. https://doi.org/10.1016/j.foreco.2018.02.022.

Felipe-Lucia, MR, Soliveres, S, Penone, C, Manning, P, van der Plas, F, Boch, S, Prati, D, Ammer, C, Schall, P, Gossner, MM, Bauhus, J, Buscot, F, Blaser, S, Blüthgen, N, de Frutos, A, Ehbrecht, M, Frank, K, Goldmann, K, Hänsel, F, Jung, K, Kahl, T, Nauss, T, Oelmann, Y, Pena, R, Polle, A, Renner, S, Schloter, M, Schöning, I, Schrumpf, M, Schulze, ED, Solly, E, Sorkau, E, Stempfhuber, B, Tschapka, M, Weisser, WW, Wubet, T, Fischer, M, Allan, E, 2018. Multiple forest attributes underpin the supply of multiple ecosystem services. Nat. Commun. 9, 4839. https://doi.org/10.1038/s41467-018-07082-4.

Fenton, NJ, Simard, M, Bergeron, Y, 2009. Emulating natural disturbances: the role of silviculture in creating even-aged and complex structures in the black spruce boreal forest of eastern North America. J. For. Res. 14, 258–267. https://doi.org/10.1007/s10310-009-0134-8.

Fischer, M, Bossdorf, O, Gockel, S, Hänsel, F, Hemp, A, Hessenmöller, D, Korte, G, Nieschulze, J, Pfeiffer, S, Prati, D, Renner, S, Schöning, I, Schumacher, U, Wells, K, Buscot, F, Kalko, EKV, Linsenmair, KE, Schulze, ED, Weisser, WW, 2010. Implementing large-scale and long-term functional biodiversity research: the Biodiversity Exploratories. BAAE 11, 473–485. https://doi.org/10.1016/j.baae.2010.07.009.

Führer, E, 2000. Forest functions, ecosystem stability and management. For. Ecol. Manage. 132, 29–38. https://doi.org/10.1016/S0378-1127(00)00377-7.

Gayer, K, 1886. Der Gemischte Wald - seine Begründung und Pflege insbesondere Durch Horst- und Gruppenwirtschaft. Paul Parey Verlag, Berlin.

Glatthorn, J, Feldmann, E, Pichler, V, Hauck, M, Leuschner, C, 2018. Biomass stock and productivity of primeval and production beech forests: greater canopy structural diversity promotes productivity. Ecosyst 21, 704–722. https://doi.org/10.1007/s10021-017-0179-z.

Gough, CM, Atkins, JW, Fahey, RT, Hardiman, BS, 2019. High rates of primary production in structurally complex forests. Ecology 100. https://doi.org/10.1002/ecy.2864.

Hardiman, BS, Gough, CM, Halperin, A, Hofmeister, KL, Nave, LE, Bohrer, G, Curtis, PS, 2013. Maintaining high rates of carbon storage in old forests: a mechanism linking canopy structure to forest function. For. Ecol. Manage. 298, 111–119. https://doi.org/10.1016/j.foreco.2013.02.031.

Hédl, R, Šipoš, J, Chudomelová, M, Utinek, D, 2017. Dynamics of herbaceous vegetation during four years of experimental coppice introduction. Folia Geobot. 52, 83–99. https://doi.org/10.1007/s12224-016-9281-9.

Knoke, T, Seifert, T, 2008. Integrating selected ecological effects of mixed European beech–Norway spruce stands in bioeconomic modelling. Ecol. Model 210, 487–498. https://doi.org/10.1016/j.ecolmodel.2007.08.011.

Knuff, AK, Staab, M, Frey, J, Dormann, CF, Asbeck, T, Klein, AM, 2020. Insect abundance in managed forests benefits from multi-layered vegetation. BAAE 48, 124–135. https://doi.org/10.1016/j.baae.2020.09.002.

Korpel, S, 1995. Die Urwälder der Westkarpaten. Gustav Fischer Verlag, Stuttgart, Jena, New York.

Kovács, B, Tinya, F, Ódor, P, 2017. Stand structural drivers of microclimate in mature temperate mixed forests. Agric. For. Meteorol. 234–235, 11–21. https://doi.org/10.1016/j.agrformet.2016.11.268.

Kucbel, S, Jaloviar, P, Saniga, M, Vencurik, J, Klimaš, V, 2010. Canopy gaps in an old-growth fir-beech forest remnant of Western Carpathians. Eur. J. For. Res. 129, 249–259. https://doi.org/10.1007/s10342-009-0322-2.

Leuschner, C, Meier, IC, Hertel, D, 2006. On the niche breadth of *Fagus sylvatica*: soil nutrient status in 50 Central European beech stands on a broad range of bedrock types. Ann For Sci 63, 355–368. https://doi.org/10.1051/forest:2006016.

Madsen, P, Larsen, JB, 1997. Natural regeneration of beech (*Fagus sylvatica* L.) with respect to canopy density, soil moisture and soil carbon content. For. Ecol. Manage. 97, 95–105. https://doi.org/10.1016/S0378-1127(97)00091-1.

McElhinny, C, Gibbons, P, Brack, C, Bauhus, J, 2005. Forest and woodland stand structural complexity: its definition and measurement. For. Ecol. Manage 218, 1–24. https://doi.org/10.1016/j.foreco.2005.08.034.

Messier, C, Puettmann, KJ, 2011. Forests as complex adaptive systems: implications for forest management and modelling. Ital. J. For. Mt Environ. 249–258. https://doi.org/10.4129/ifm.2011.3.11.

Muscolo, A, Bagnato, S, Sidari, M, Mercurio, R, 2014. A review of the roles of forest canopy gaps. J. For. Res. 25, 725–736. https://doi.org/10.1007/s11676-014-0521-7.

Nagel, TA., Svoboda, M, Kobal, M, 2014. Disturbance, life history traits, and dynamics in an old-growth forest landscape of southeastern Europe. Ecol. Appl. 24, 663–679. https://doi.org/10.1890/13-0632.1.

O'Hara, KL, Gersonde, RF, 2004. Stocking control concepts in uneven-aged silviculture. Forestry 77, 131–143. https://doi.org/10.1093/forestry/77.2.131.

Parker, GG, Harmon, ME, Lefsky, MA, Chen, J, Pelt, RV, Weis, SB, Thomas, SC, Winner, WE, Shaw, DC, Frankling, JF, 2004. Three-dimensional structure of an old-growth pseudotsuga-tsuga canopy and its implications for radiation balance, microclimate, and gas exchange. Ecosystems 7. https://doi.org/10.1007/s10021-004-0136-5.

Pommerening, A, 2002. Approaches to quantifying forest structures. Forestry 75, 305–324. https://doi.org/10.1093/forestry/75.3.305.

Pretzsch, H, 2019. Grundlagen Der Waldwachstumsforschung. Springer, Berlin, Heidelberg. https://doi.org/10.1007/978-3-662-58155-1.

Pretzsch, H, 2009. Forest Dynamics, Growth and Yield: From Measurement to Model. Springer, Berlin, Heidelberg. https://doi.org/10.1007/978-3-540-88307-4.

Pretzsch, H, Biber, P, Uhl, E, Dauber, E, 2015. Long-term stand dynamics of managed spruce–fir–beech mountain forests in Central Europe: structure, productivity and regeneration success. Forestry 88, 407–428. https://doi.org/10.1093/forestry/cpv013.

Pretzsch, H, Schütze, G, 2009. Transgressive overyielding in mixed compared with pure stands of Norway spruce and European beech in Central Europe: evidence on stand level and explanation on individual tree level. Eur. J. For. Res. 128, 183–204. https://doi.org/10.1007/s10342-008-0215-9.

Primicia, I, Colomo, RA, Rodríguez, JBI, Puertas, F, Traver, C, Martínez, FJC, 2016. Influence of thinning intensity and canopy type on Scots pine stand and growth dynamics in a mixed managed forest. For syst 25, 1.

Pykälä, J, 2004. Immediate increase in plant species richness after clear-cutting of boreal herb-rich forests. Appl. Veg. Sci. 7, 29–34. https://doi.org/10.1111/j.1654-109X.2004.tb00592.x.

Rademacher, C, Neuert, C, Grundmann, V, Wissel, C, Grimm, V, 2004. Reconstructing spatiotemporal dynamics of Central European natural beech forests: the rule-based forest model BEFORE. For. Ecol. Manage. 194, 349–368. https://doi.org/10.1016/j.foreco.2004.02.022.

Schall, P, Gossner, MM, Heinrichs, S, Fischer, M, Boch, S, Prati, D, Jung, K, Baumgartner, V, Blaser, S, Böhm, S, Buscot, F, Daniel, R, Goldmann, K, Kaiser, K, Kahl, T, Lange, M, Müller, J, Overmann, J, Renner, SC, Schulze, ED, Sikorski, J, Tschapka, M, Türke, M, Weisser, WW, Wemheuer, B, Wubet, T, Ammer, C, 2018. The impact of even-aged and uneven-aged forest management on regional biodiversity of multiple taxa in European beech forests. J. Appl. Ecol. 55, 267–278. https://doi.org/10.1111/1365-2664.12950.

Schröter, M, Härdtle, W, von Oheimb, G, 2012. Crown plasticity and neighborhood interactions of European beech (*Fagus sylvatica* L.) in an old-growth forest. Eur. J. For. Res. 131, 787–798. https://doi.org/10.1007/s10342-011-0552-y.

Seidel, D, Annighöfer, P, Ammer, C, Ehbrecht, M, Willim, K, Bannister, J, Soto, DP, 2021. Quantifying understory complexity in unmanaged forests using TLS and identifying some of its major drivers. Rem. Sens. 13, 1513. https://doi.org/10.3390/rs13081513.

Seidel, D, Annighöfer, P, Ehbrecht, M, Magdon, P, Wöllauer, S, Ammer, C, 2020. Deriving stand structural complexity from airborne laser scanning data- what does it tell us about a forest? Rem. Sens. 12, 1854. https://doi.org/10.3390/rs12111854.

Seidel, D, Ehbrecht, M, Annighöfer, P, Ammer, C, 2019. From tree to stand-level structural complexity — Which properties make a forest stand complex? Agric. For. Meteorol. 278, 107699 https://doi.org/10.1016/j.agrformet.2019.107699.

Stiers, M, Annighöfer, P, Seidel, D, Willim, K, Neudam, L, Ammer, C, 2020. Quantifying the target state of forest stands managed with the continuous cover approach – revisiting Möller's "Dauerwald" concept after 100 years. Trees, Forests People 1, 100004. https://doi.org/10.1016/j.tfp.2020.100004.

Stiers, M, Willim, K, Seidel, D, Ammer, C, Kabal, M, Stillhard, J, Annighöfer, P, 2019. Analyzing spatial distribution patterns of European beech (*Fagus sylvatica* L.)

regeneration in dependence of canopy openings. Forests 10, 637. https://doi.org/10.3390/f10080637.

Stiers, M, Willim, K, Seidel, D, Ehbrecht, M, Kabal, M, Ammer, C, Annighöfer, P, 2018. A quantitative comparison of the structural complexity of managed, lately unmanaged and primary European beech (*Fagus sylvatica* L.) forests. For. Ecol. Manage. 430, 357–365. https://doi.org/10.1016/j.foreco.2018.08.039.

Tabaku, V, 2000. Struktur Von Buchen-Urwaldern in Albanien im Vergleich mit Deutschen Buchen-Naturwald-reservaten und -Wirtschaftswaldern. Disseration, Göttingen.

Willim, K, Stiers, M, Annighöfer, P, Ammer, C, Ehbrecht, M, Kabal, M, Stillhard, J, Seidel, D, 2019. Assessing understory complexity in beech-dominated forests (*Fagus sylvatica* L.) in Central Europe—From managed to primary forests. Sensors 19, 1684. https://doi.org/10.3390/s19071684.

Willim, K, Stiers, M, Annighöfer, P, Ehbrecht, M, Ammer, C, Seidel, D, 2020. Spatial patterns of structural complexity in differently managed and unmanaged beech-dominated forests in Central Europe. Rem. Sens. 12, 1907. https://doi.org/10.3390/rs12121907.

Zemp, DC, Ehbrecht, M, Seidel, D, Ammer, C, Craven, D, Erkelenz, J, Irawan, B, Sundawati, L, Hölscher, D, Kreft, H, 2019. Mixed-species tree plantings enhance structural complexity in oil palm plantations. Agric. Ecosyst. Environ. 283, 106564 https://doi.org/10.1016/j.agee.2019.06.003.

Zheng, G, Moskal, LM, Kim, S, 2013. Retrieval of effective leaf area index in heterogeneous forests with terrestrial laser scanning. IEEE Trans. Geosci. Remote Sens. 51, 777–786. https://doi.org/10.1109/TGRS.2012.2205003.