# Quantifying three-dimensional stand structure of European beech forests along a management gradient

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## List of abbreviations

| | |
|---|---|
| 3D | three-dimensional |
| ALS | Airborne laser scanning |
| a.s.l. | Above sea level |
| CBR | Carpathian Biosphere Reserve |
| CE index | Clark-Evans index |
| $D_b$ | Box dimension |
| Dbh | Diameter at breast height |
| EA | Even-aged |
| ENL | Effective number of layers |
| FM | Formerly managed |
| FRAC | Fractal dimension index |
| LiDAR | Light Detecting and Ranging |
| NNR | National Nature Reserve |
| UEA | Uneven-aged |
| UM | Unmanaged |
| PF | Primary forest |
| rSPf | relative space filling |
| SSCI | Stand structural complexity index |
| TLS | Terrestrial laser scanning |
| UCI | Understory complexity index |

## Summary

Forest structure is of functional importance for ecosystem stability and resilience, as well as for numerous other ecosystem functions and services. In this context, a high structural complexity can have a positive effect on diverse functions and services. Silvicultural management has the potential to negatively or positively affect forest structure and its complexity. In order to investigate the relationship between silvicultural management and forest structure, one first has to quantify forest structure and its complexity.

To do so, various 3D measures based on terrestrial laser scanning data were used to quantify forest structure and structural complexity along a management gradient. The main objective of the thesis was to investigate the impact of different management systems on the structure of European forests and to compare them with formerly managed and primary forests. As beech (*Fagus sylvatica* L.) is the natural dominating tree species in Europe, beech-dominated forests were selected for this study.

First, the understory complexity index (UCI) was introduced as a measure to describe the structural complexity of the forest understory (chapter 2). The UCI is based on the fractal dimension of a cross-sectional horizontal polygon, which represents the forest understory between 0.8 and 1.5 m. It is a density-dependent measure. Forest stands with advanced tree regeneration, as e.g. thickets, showed high UCI values compared to forest stands with a lower regeneration density. Comparing different management systems and forest types, the results revealed that the understory complexity was either large during the early phases of stand development or when the senescence of trees has largely proceeded, as found in beech primary forests.

The second research aim of the study was to investigate, how structural complexity express itself in terms of the spatial distribution and density of plant material and how forest management influences these structural attributes (chapter 3). For that purpose, the structural complexity, as well as the density and spatial distribution of plant material within different forest strata of differently managed and unmanaged beech forests were quantified. The results showed that forest strata with a rather high structural complexity were characterized by a rather high density and a random to regular distribution of plant material. This could be observed for the primary beech forests and uneven-aged beech stands. Forest strata with a low structural complexity, as found in formerly managed forests, showed in contrast a rather low density and a clustered distribution of plant material. It can be assumed that structural complexity increases with increasing density and increasing homogeneity of the spatial distribution of plant material within a forest stand.

Finally, the focus was on analyzing the influence of the understory complexity and vertical heterogeneity on the overall stand structural complexity of beech-dominated forests. The sub-study (chapter 4) on short-term dynamics of structural complexity revealed for uneven-aged stands that an increase of the understory complexity lead to an increase in the overall stand structural complexity. In this context, the initial canopy openness positively influenced the development of a complex understory and thus the overall structural complexity. Whereas in the younger, even-aged beech stands, an increase of vertical stratification positively influenced the stand structural complexity. In summary, short-term dynamics of stand structural complexity strongly depend on the developmental stage or canopy openness of the forest.

This thesis not only contributes to the understanding of structural complexity and its relationship with other structural attributes, but also provides information on structural characteristics of different forest types. Managed and primary beech forests can be quite similar in terms of structural complexity. Especially, single-tree selection cutting seems to be a useful management approach for creating a complex stand structure. Furthermore, the thesis particularly highlighted the structural importance of the forest understory for the development of a complex stand structure. Therefore, management interventions could especially focus on the creation of complex understory structures, especially in early developmental stages, if an enhancement of structural complexity is desired. Lastly, the study demonstrated the wide range of potential applications of terrestrial laser scanning data for forest structure analysis.

# Zusammenfassung

Die Waldstruktur beeinflusst nicht nur die Stabilität und Resilienz von Waldökosystemen, sondern auch zahlreiche andere Ökosystemfunktionen und -dienstleistungen. In diesem Kontext, kann sich strukturelle Komplexität positiv auf diverse Waldfunktionen und - dienstleistungen auswirken. Die waldbauliche Bewirtschaftung hat das Potenzial Waldstruktur und ihre Dynamik sowohl negativ als auch positiv zu beeinflussen. Um die Zusammenhänge zwischen waldbaulicher Bewirtschaftung und Strukturveränderungen sowie den damit verbundenen ökosystemaren Funktionen und Leistungen zu untersuchen, bedarf es einer Quantifizierung der Waldstruktur und ihrer Komplexität.

Zu diesem Zweck wurde mittels diverser 3D Maße, die auf der Grundlage von terrestrischen Laserscanning-Daten generiert wurden, die Waldstruktur sowie ihre Komplexität entlang eines Bewirtschaftungsgradienten quantifiziert. Ziel war es, den Effekt unterschiedlicher Managementstrategien auf die Struktur europäischer Wälder zu untersuchen und diese mit ehemals bewirtschafteten und Primärwäldern zu vergleichen. Da die Buche (*Fagus sylvatica* L.) die natürlich dominierende Baumart in Europa ist, wurden für diese Studie buchendominierte Wälder ausgewählt.

Zunächst wurde der understory complexity index (UCI) als Maß zur Beschreibung der strukturellen Komplexität der unteren Bestandesschicht vorgestellt (Kapitel 2). Der UCI basiert auf der fraktalen Dimension eines horizontalen Querschnittspolygons, das die untere Bestandesschicht zwischen 0,8 und 1,5 m darstellt. Waldbestände mit fortgeschrittener Baumverjüngung, wie z. B. Dickungen, wiesen im Vergleich zu Waldbeständen mit einer geringeren Verjüngungsdichte hohe UCI-Werte auf. Der Vergleich verschiedener Bewirtschaftungssysteme und Waldtypen ergab, dass die Komplexität des Unterwuchses entweder in den frühen Phasen der Bestandesentwicklung groß ist oder in der Terminalphase, welche in Buchenurwäldern zu finden sein kann.

Das zweite Forschungsziel der Studie war zu untersuchen, wie sich die strukturelle Komplexität in der räumlichen Verteilung und Dichte des Pflanzenmaterials wiederspiegelt und wie die Waldbewirtschaftung diese strukturellen Merkmale beeinflusst. Zu diesem Zweck wurden die strukturelle Komplexität sowie die Dichte und räumliche Verteilung des Pflanzenmaterials in verschiedenen Waldschichten von unterschiedlich bewirtschafteten und unbewirtschafteten Buchenwäldern quantifiziert. Die Ergebnisse zeigten, dass Waldschichten mit einer hohen strukturellen Komplexität durch eine hohe Dichte und eine zufällige bis regelmäßige Verteilung des Pflanzenmaterials gekennzeichnet waren. Dies konnte für die Primärwälder und die ungleichaltrigen Buchenbestände beobachtet werden. Waldschichten mit einer geringen strukturellen Komplexität, wie sie in ehemals bewirtschafteten Wäldern zu finden waren, wiesen dagegen eine eher geringe Dichte und eine geklumpte Verteilung des Pflanzenmaterials auf.

Es kann daher davon ausgegangen werden, dass die strukturelle Komplexität mit zunehmender Dichte und zunehmender Homogenität der räumlichen Verteilung des Pflanzenmaterials zunimmt.

Schließlich wurde untersucht, welchen Einfluss die Komplexität des Unterwuchses und die vertikale Heterogenität auf die strukturelle Bestandeskomplexität haben. Die Teilstudie (Kapitel 4) zur kurzfristigen Dynamik der strukturellen Komplexität ergab für ungleichaltrige Bestände, dass eine Zunahme der Komplexität des Unterwuchses zu einer Zunahme der strukturellen Komplexität des Gesamtbestandes führt. In diesem Zusammenhang wirkte sich die initiale Kronendachöffnung positiv auf die Entwicklung eines komplexen Unterwuchses und damit auf die strukturelle Gesamtkomplexität aus. In den jüngeren, gleichaltrigen Buchenbeständen hingegen wirkte sich eine Zunahme der vertikalen Schichtung positiv auf die strukturelle Komplexität der Bestände aus. Zusammenfassend lässt sich sagen, dass die kurzfristige Dynamik der strukturellen Komplexität stark vom Entwicklungsstadium bzw. der Offenheit des Kronendachs abhing.

Diese Arbeit trägt nicht nur zum Verständnis von struktureller Komplexität und ihrer Beziehung zu anderen strukturellen Merkmalen bei, sondern liefert auch Informationen über die Strukturmerkmale verschiedener Waldtypen. Bewirtschaftete Wälder und Primärwälder können sich hinsichtlich ihrer strukturellen Komplexität durchaus ähneln. Insbesondere die selektive Einzelbaumentnahme scheint ein effektiver Managementansatz zu sein, um eine komplexe Bestandsstruktur zu schaffen. Darüber hinaus verdeutlicht diese Arbeit, dass der Unterwuchs für die Entwicklung einer komplexen Bestandsstruktur einen wesentlichen Beitrag leistet. Daher könnten sich Bewirtschaftungsmaßnahmen besonders auf die Schaffung komplexer Unterholzstrukturen konzentrieren, vor allem in frühen Entwicklungsstadien, wenn eine Erhöhung der strukturellen Komplexität angestrebt wird. Schließlich zeigt die Studie das breite Spektrum möglicher Anwendungen von terrestrischen Laserscanning-Daten für die Waldstrukturanalyse.

# Chapter 1 Introduction

## 1.1 Background of the study

Forests ecosystems are influenced by natural disturbances (like e.g. drought, wind, fire) and environmental conditions (e.g. $CO_2$ concertation, temperature, nutrient and water supply) (Pretzsch 2009). A stable and resilient forest has the ability to respond to environmental influences and recover after disturbances (Koontz et al. 2020). Forests are dynamic ecosystems, which are shaped by disturbances and their responses towards them (White and Jentsch 2001). Global environmental changes influence the dynamics of forests, as they may lead to increasingly frequent and intense natural disturbances and also change the abiotic conditions during the recovery process (Buras et al. 2020, Trumbore et al. 2015, Zscheischler and Seneviratne 2017). These environmental changes often occur with direct anthropogenic drivers such as forest management, which may negatively or positively affect the capacity of forests to recover from disturbances (Lenton et al. 2008, Reyer et al. 2015). It remains unclear, whether forest ecosystems have the capacity to resist, recover or adapt to the changing disturbance regimes (Bauhus et al. 2017, Reyer et al. 2015). However, an increase in severity and frequency of disturbances has the potential to reduce the recovery of forests (Buma and Wessman 2011).

In this context, several studies highlighted the functional importance of forest structure for ecosystem stability and resilience, as well as for numerous other ecosystem functions and services (Brang et al. 2014, Dobbertin 2002, Jactel et al. 2005). Forest structure (also called stand structure or structure at stand-level), refers mainly to the abundance and distribution of trees and their attributes (e.g. foliage, stems, crowns, branches) and the spatial interactions (Gadow et al. 2012, Pretzsch 2009, Schall et al. 2018b). As forests are open systems, forest structure cannot be seen as a static construct, but is shaped by disturbances and recovery processes. Regeneration, growth and mortality of tree individuals shape forest structure and in return the modified forest structure determines environmental factors, as e.g. light availability that influence the establishment of regeneration and growth of tree individuals (Pretzsch 2019). Thus, there is an interrelation between forest structure, resource availability and stand growth. Due to differences in disturbances and dynamics, each forest ecosystem has a specific forest structure that comprises particular structural attributes. A list with structural attributes that can be used in order to describe forest structure is provided by McElhinny et al. (2005). In general, structural attributes mainly describe the (relative) abundance, richness, size variation or spatial variation of trees and their components. Stand basal area, tree species diversity, tree size diversity are common structural attributes used in order to describe forest structure (Del Río et al. 2016, Gadow et al. 2012). The combination of different structural attributes and their spatial interactions within a forest stand represent the structural complexity of the stand (McElhinny et al. 2005, Pretzsch 2009). The more structural attributes and information are needed to characterize a forest stand, the more complex is its structure (Pukkala and von Gadow 2012, Witté et al. 2013). European primary forests for instance, are known for their high structural complexity, as they comprise a high number of structural attributes, especially old-growth attributes, e.g. the presence of emerging trees, a high spatial heterogeneity of tree and gap distribution or the presence of an advanced regeneration layer (Bauhus et al. 2009, Hobi et al. 2015b, Kucbel et al. 2010, Nagel et al. 2010, Wirth et al. 2009). In contrast, an even-aged pure stand, with even tree sizes and tree heights, would be characterized by a low structural complexity (Witté et al. 2013). I.e., if one refers to the structural complexity of a forest, one considers a forest as an entity instead of focusing on single structural attributes.

Complex forest structures that are characterized by a high heterogeneity of structural attributes, have the potential to enhance the resistance against disturbances, as e.g. windstorms, and promote the recovery after disturbances (Bauhus et al. 2017). Moreover, structural heterogeneity is positively associated with various other ecosystem functions and services (Gadow et al. 2012, Kint et al. 2004), as e.g. biodiversity (Brang 2005, Gustafsson et al. 2012, Mulwa et al. 2012), productivity (Glatthorn et al. 2018, Gough et al. 2019, Hardiman et al. 2011), regulating microclimate (Ehbrecht et al. 2019, Kovács et al. 2017), health and recreation (Wirth et al. 2009).

Because of the knowledge of the functional relevance of structural heterogeneity or complexity, management strategies that reduce structural complexity, have been questioned in the recent decades (Fenton et al. 2009, Messier and Puettmann 2011, Puettmann et al. 2015). At the same time, the concept ‘management for complexity’ was increasingly applied in forest management, also in Central Europe (Brang et al. 2014, Camarretta et al. 2019, Messier et al. 2013, Puettmann et al. 2009). As a consequence, uneven-aged management systems gained in importance, as they create heterogeneous stand structures (Mizunaga et al. 2010, Schütz 2002). Against this background, the clear-cut management system in Central Europe has been more and more replaced by uneven-aged management systems or even-aged management systems that follow retention tree approaches (Diaci et al. 2017, Mizunaga et al. 2010, Schall et al. 2018a).

European primary forests are known for their heterogeneous structure and are therefore important references for forest management that aims to promote structural complexity. In Europe, nearly no primary forests are left due to historical deforestation and forest exploitation (Kaplan et al. 2009, Potapov et al. 2017). Schnitzler et al. (2014) identified 1.4 % of Europe’s landscape as untouched, primary forests. Some of the most iconic beech primary forests can be found in countries of Eastern Europe, like e.g. Uholka-Shyrokyi Luh in Ukraine or Izvoarele Nerei in Romania (Sabatini et al. 2018, Veen et al. 2010). Most of these primary forests are under protection, but in some areas harvesting activities can still be observed due to a lack of an efficient protection on the part of the government as well as due to a consensus on protection strategies (Knorn et al. 2013, Sabatini et al. 2020, Wesołowski 2005). So, there is a certain possibility that some parts of remaining European primary forests may disappear in the future. Thus, current research on primary forest structure and its dynamics are of crucial importance. As disturbances play a key role in structural dynamics, many studies have been conducted on the disturbance regime of European primary forests (Feldmann et al. 2018, Kucbel et al. 2010, Nagel et al. 2014, Schelhaas et al. 2003, Trotsiuk et al. 2012). These forests are mainly affected by small-scale disturbances, which also result in a heterogeneous, uneven forest structure over a small spatial scale (Hobi et al. 2015a, Rademacher et al. 2004, Trotsiuk et al. 2012). The main driver of small-scale disturbances in European forests is single tree mortality due to senescence during the decay phase (Kucbel et al. 2010, Rugani et al. 2013). The decay phase is besides the growth phase and optimum phase, the terminal stage in the natural developmental cycle of forests (Korpel 1995, Meyer et al. 2003).

In managed beech stands, the natural development cycle is interrupted due to a rotation period of about 120 - 140 years (Bauhus et al. 2009, Boncina 2000). As a consequence, the latest developmental phases, as e.g. the decay phase, is often missing in managed forests, because the single tree mortality as a result of senescence is not given. Hence, the main disturbance agents that shape forest structure in managed stands are harvest and thinning interventions (Schall and Ammer, 2013). In order to generate small-scale structural heterogeneity, management systems have the possibility to imitate natural disturbances with regard to the frequency and intensity, still having timber production as one of the major goals of forest management in mind. For example, the uneven-aged management uses a low intensity and small-scale felling regime in order to imitate natural disturbances at the stand-level (Diaci et al. 2017, Pommerening and Murphy, 2004, Schütz 2002). Other management strategies to enhance structural complexity may focus on structural attributes besides spatial heterogeneity, as e.g. on the promotion of deadwood (Martikainen et al. 2000, Stiers et al. 2018). Despite the utilization of management interventions, there is also the possibility to set forests aside in order to facilitate the development of complex or heterogenous forest structures (Sabatini et al. 2020). The conservation approach has been increasingly applied since 1950 (McGrath et al. 2015). The idea behind this approach is that managed and unmanaged forests are declared as protected areas, so that natural dynamics can establish. Passive protection areas have various designations, like e.g. strict forest reserve, abandoned, formerly managed, lately unmanaged, unmanaged in national parks (Bouget et al. 2014). In order to evaluate active and passive approaches of “management for complexity”, two basic research steps have to be considered in advance. First, forest structure and its complexity have to be become measurable. Detailed information on how structural complexity can be quantified and the advantages and disadvantages of structural complexity measures will be discussed in the chapter 1.3. In the second step, the target state of structural complexity has to be quantified and described. Forest managers need information on structural characteristics and structural dynamics of highly complex forests to imitate them. Therefore, measuring structural complexity of primary forests is of crucial importance. At the same time, structural complexity of differently managed and formerly managed forest stands has to be quantified in order to understand, how forest management affects structural complexity and its dynamics. As beech (*Fagus sylvatica* L.) is the naturally dominating tree species in Central Europe, managed and unmanaged beech forests were chosen for this study. Therefore, the following chapter will provide some information on distribution, characteristics and forest management implementation of European beech.

## 1.2 Beech (*Fagus sylvatica* L.) forests in Central Europe

Without human disturbances, Central European forests would be mainly dominated by beech (Bohn et al. 2000). During the Bronze Age (ca. 5500 - 2500 BC) beech began to expand and was the dominant tree species in natural forests of Central Europe around 2000 - 500 BC (Rademacher et al. 2004). Due to historical land use and deforestation in the past 2000 years, natural beech forests widely disappeared (Rademacher et al. 2004). Many of them were converted into farmland and later into coniferous forests, as it was the case in north-eastern Germany and northern Poland (Ellenberg 2009). During the last decades, a comeback of beech was increasingly observed in some regions of Europe due to a second conversion of Scots pine forests back to deciduous forests and due to the natural expansion of beech (Fritz et al. 2006). Today, beech forms the potential natural vegetation mainly in Central and Western Europe, as well as in Southern European mountain regions, e.g. in the Carpathians, where some of the last beech primary forests can be found (see chapter 1.1) (Bolte et al. 2007, Ellenberg and Leuschner 2010, Sabatini et al. 2018).

Leuschner et al. (2006) describes beech as ‘the most successful plant species in Central Europe`. In the largest parts of its natural distribution area, beech forms mono-specific forest stands (Leuschner et al. 2006). Beech is known for its tolerance towards a broad range of climatic and edaphic conditions (Peters, 1997, Rademacher et al. 2004). Its occurrence is not limited by soil acidity, soil nutrition or humus type and it grow nearly on all sediments, if sufficient drainage is ensured (Peters 1997). However, beech shows the best growth performance on moderately moist, base-rich calcareous cambisols (Leuschner et al. 2006). Beech-dominated stands prefer a temperate climate with mild winters and moist summer conditions and are sensitive towards summer droughts (Aranda et al. 2000, Bolte et al. 2016, Geßler et al. 2007). In the year 2018, beech showed severe signs of drought stress in European forests (BMEL 2019, Brun et al. 2020, Buras et al. 2020, NW-FVA, 2019, Schuldt et al. 2020). Furthermore, beech is known for its shade tolerance and is thus able to regenerate and grow under limited light conditions (Collet et al. 2001, Emborg et al. 2000, Schuldt et al. 2020). Compared to other tree species, like e.g. spruce, beech is rather wind-firm at the stand-level and is characterized by a high crown plasticity (Feldmann et al. 2018, Schütz 2006).

In the context of European silvicultural management, beech-dominated forest stands typically provide a lower income to silviculturists than comparable stands of coniferous species (e.g. *Picea abies*, *Pseudotsuga menziesii*) (Möhring et al. 2008). Therefore, native beech forests were generously transformed into mono-specific coniferous forests or were admixed with conifer species in the past (Bauhus et al. 2017). However, it has turned out that the transformation of natural vegetation may lead to a loss of biodiversity and reduces the resistance against natural disturbances, as e.g. windstorms, drought and insect outbreaks (Hagge et al. 2019, Spiecker 2003). Today, modern silviculture aims to promote multifunctional forests, which guarantee, besides timber production, other ecosystem services and functions, as e.g. biological diversity, temperature regulation, stability and resilience regeneration ability and vitality (Felipe-Lucia et al. 2018, Messier et al. 2013). Therefore, the conversion of coniferous-dominant stands into stable, site-adapted, mixed or broadleaved stands was promoted during the recent decades in Central Europe (Pach et al. 2018, Rumpf and Petersen 2008, Spiecker 2003). In this context, beech-dominated forest stands have gained in relevance for the current forest management in Central Europe. In 2012, beech forests covered around 15.43 % of the forest area in Germany and in the context of near-natural forest management, one can expect a further increase of forest area covered by beech (BMEL 2018).

## 1.3 The three-dimensionality of forest structure and its measurement

Conventional measures of stand structure can be time-consuming and expensive to assess and monitor (Zenner and Hibbs 2000). Especially, if multi-temporal measurements have to be conducted in order to observe structural dynamics. Additionally, conventional measures often ignore the three-dimensionality of forest structure and its complexity (Pretzsch 1997). The three-dimensionality of forest structure is an important measure, as it represents the spatial interaction of tree individuals within a forest stand (Pretzsch 2009). It describes forest patterns and processes that are *per se* three-dimensional, but have conventionally been limited to one or two dimensions in order to be comprehensible (Chen and Bradshaw 1999). Thanks to modern remote sensing techniques, the three-dimensionality of objects can today be captured. In order to capture three-dimensional (3D) forest structure, Light Detection And Ranging (LiDAR) was used in the framework of this study. The use of LiDAR is an efficient alternative compared to traditional measures, as it can provide 3D information on forest structure at a high temporal and spatial resolution (Beland et al. 2019, Calders et al. 2020). Therefore, the application of active LiDAR sensors increased in forest ecological research during the recent years (Lim et al. 2003, QingWang et al. 2017, Sačkov et al. 2019). LiDAR systems work by using laser beams to detect the geometry of a sensed object in space (Beland et al. 2019). Generally, there are two ranging approaches: time-of-flight and phase-shift sensors. Time-of-flight sensors measure the time that passes between the emission and the arrival of the reflection of a discrete outgoing laser beam. Measurements with a phase-shift sensor are based on the same concept as the time-of-flight approach, but emit a continuous signal (Calders et al. 2020). Each laser return is captured and saved with the corresponding angle of observation and the position and orientation of the sensor (El-Sheimy 2009). The captured spatial information on scanned objects is shown as a 3D point cloud in spherical or cartesian coordinates and can be afterwards processed by visual interpretations or automatic approaches (Brolly et al. 2013). LiDAR sensors can be attached to different platforms. Beland et al. (2019) identified five main platform types, namely airborne laser scanning (ALS), unmanned Aerial Vehicle (UAV) laser scanning, terrestrial laser scanning (TLS) from a solid platform and mobile laser scanning (MLS) from a moving platform. These platform types show different characteristics concerning spatial resolution, occlusion and coverage (Beland et al. 2019). While ALS has the ability to describe relatively large forest areas and mainly provide detailed spatial information about the upper canopy of a forest, TLS has the ability to create fine scale visualizations of the distribution of plant material within a forest stand, especially under the upper canopy layer (Donager et al. 2018, El-Sheimy 2009, Li et al. 2017, Seidel et al. 2021, 2020). For this study, TLS was used in order to capture 3D forest structure. More details on the used TLS instrument, as well as on the scanner settings are described in chapter 1.5. TLS systems are commonly used to get highly detailed information on single trees in order to assess tree volume (Hackenberg et al. 2014), tree and crown architecture (Barbeito et al. 2017, Dorji et al. 2019, Seidel et al. 2011) and timber quality (Höwler et al. 2019), just to name a few. TLS is also increasingly used, when it comes to describing the forest's understory e.g. in terms of biomass (Li et al. 2021), regeneration density (Brolly et al. 2013) and species composition (Torralba et al. 2018).

In the recent years, a lot of research has been conducted in order to develop measures of structural complexity for forests based on TLS. Especially, holistic measures that consider stand structure as an entity are currently of great interest for forest ecology and management. This is not surprising, as these measures offer great opportunities for research on forest structure and its relationship with ecosystem functions and processes. Holistic measures of structural complexity are useful to reveal relationships between structural complexity and, e.g. productivity (Hardiman et al. 2011), forest management (Ehbrecht et al. 2017, Stiers et al. 2018), and (micro-) climate (Ehbrecht et al. 2021, 2019, Kovács et al. 2017, Seidel et al. 2021). Another advantage of holistic measures of forest structure is that there is no need to choose between single structural attributes to describe stand structure. Nevertheless, there is no universal measure to quantify stand structural complexity, as there are different interpretations of the term 'complexity'. While e.g. the canopy structural complexity (CSC) refers to the horizontal and vertical variance of vegetation density throughout the canopy, the box dimension ($D_b$) and the stand structural complexity index (SSCI) describe the geometric complexity of plant material within a forest stand based on the fractal dimension approach (Atkins et al. 2018, Ehbrecht et al. 2017, Mandelbrot, 1975, Seidel et al. 2019). For this study, the $D_b$ and the SSCI were used to quantify structural complexity, as it allows an objective, mathematical description of the distribution of all plant elements within the 3D space (Ehbrecht et al. 2017, Frey et al. 2019).

While holistic approaches of quantifying structural complexity are useful for comparing structure of different forest stands or investigating the relationship between forest structure and ecosystem functions, they do not provide the necessary in-depth understanding of the structural components that are needed for forest ecologists and forest managers to understand and emulate the intended structures and processes behind it (Camarretta et al. 2019). Especially, ecologists need structural information at much finer scales, e.g. when information is needed on structural attributes that are associated with patterns of habitat use (Chen and Bradshaw 1999, Payer and Harrison 2003). The information gap about structural characteristics is strengthened when one has not seen the forest stand described by the holistic measure by her-or himself. In this case, one does not have the knowledge about the structural attributes that are responsible for e.g. a high structural complexity. Even if the researcher her- or himself have seen the forest stand, she or he can rather guess than know, which structural attributes are responsible for the high structural complexity. Moreover, many forest ecology studies rely on mixed data that include structural information of varying dimensions and scales (Chen and Bradshaw 1999).

## 1.4 Thesis objectives and research questions

The main objective of the study was to investigate the impacts of forest management on the stand structure and structural complexity of European beech forests in comparison with unmanaged primary forests and with a specific focus on:

- Understory complexity
- Structural complexity in regard to the spatial distribution and density of plant material
- Temporal dynamics of structural complexity

The findings of the study may contribute to develop a deeper understanding of the relationship between forest management and different aspects of structural compelxity and associated ecosystem fucntions and services. Different 3D measures were used in combination in order to answer the following research questions:

i. Can managed beech forests have a similar understory complexity as primary beech forests?

ii. Do beech forests with a high structural complexity show a different spatial distribution and density of plant material compared to beech forests with a low structural complexity?

iii. How does silvicultural management affect dynamics of structural complexity in beech forests?

Figure 1.1 provides an overview of the investigated structural attributes that were considered to address the research objectives of the study. The arrows represent the interrelationships between the structural attributes, as well as the relationship between stand structural complexity and the considered structural attributes.

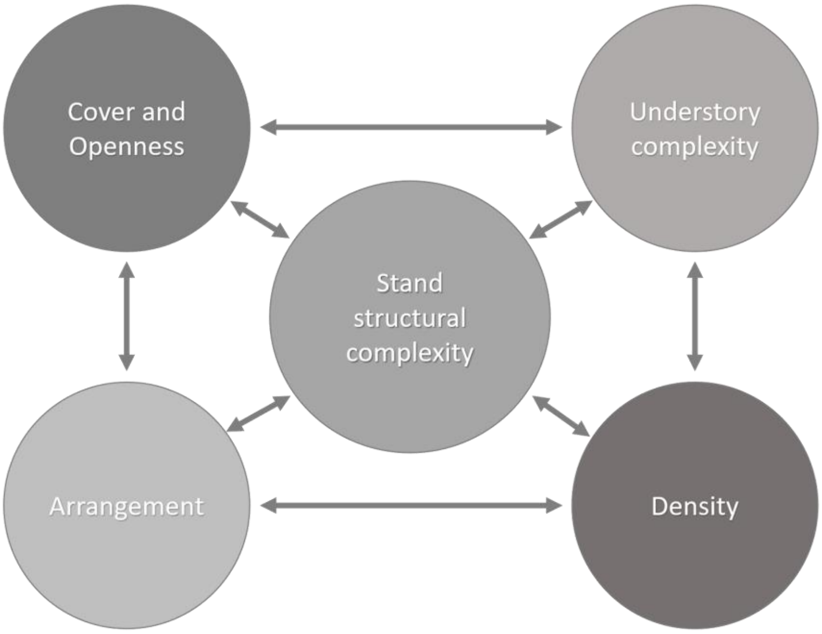

**Figure 1.1:** *Different structural attributes (Cover and Openness, Understory complexity, Density and Arrangement) and their interrelationships, as well as their relationship with overall structural complexity*

In order to quantify the understory complexity of forests, the understory complexity index (UCI) was developed and introduced in chapter 2. In this regard, the effect of regeneration density on the UCI was investigated. Furthermore, we quantified the impact of different management systems on the UCI and compared the understory complexity between differently managed and unmanaged European beech forests. In chapter 3, the structural complexity within forest stands was analyzed and characterized regarding its spatial distribution and density of plant material. For that purpose, the structural complexity for different forest strata was quantified by using the box dimension ($D_b$). The spatial arrangement of plant material within different forest layers was determined by using the Clark-Evans Index. The space filling (SPf) was used to determine the vegetation density within the forest strata. This was done for differently managed and unmanaged European beech forests, in order to examine the effect of management on structural complexity of different forest strata and their structural characteristics. In chapter 4, short-term dynamics of structural complexity were quantified in differently managed and unmanaged European beech stands. Here, the focus was on analyzing, how changes in understory complexity (UCI) and in the effective number of layers (ENL) affected dynamics of the overall stand structural complexity (SSCI). Furthermore, the relationship between the overall stand structural complexity (SSCI) or respectively the understory complexity (UCI) and canopy openness was investigated.

## 1.5 Conceptional framework, material and methods

The first sub-study (chapter 2) and the second sub-study (chapter 3) were mainly realized under the project „Strukmana“ funded by the Dr. Erich-Ritter Stiftung. The project aimed to gain a deeper understanding of forest structure and its modification through silvicultural management along a gradient of management intensity. The third sub-study (chapter 4) was primarily conducted within the framework of the Biodiversity Exploratories and funded by the German Research Foundation (DFG). The Biodiversity Exploratories serve as an open research platform for scientific collaborations across Germany, which provides the necessary infrastructure to address questions about biodiversity change due to e.g. land use and to assess the impact of these changes on ecosystem functions (Fischer et al. 2010).

### 1.5.1 Study sites

The locations of the chosen European beech forests can be found on Figure 1.2. The considered forest stands cover a gradient of management intensity. Managed (un)even-aged forest stands were selected in Reinhausen (1), Hannoversch Münden (2), Lübeck (3), Ebrach (4) and the Hainich-Dün region (5). Additionally, lately unmanaged forest stands were chosen in the National Parks Hainich (5) and Kellerwald-Edersee (6), as well as primary forests in the nature reserves Rožok (7) and Uholka (8). All considered managed and lately unmanaged forest stands were located in Germany, whereas the unmanaged primary forest Rožok was located in Slovakia and the primary forest Uholka in Ukraine (see Figure 1.2). Detailed information on the environmental conditions of the eight study sites can be found in the following chapters 2 - 4.

To ensure the comparability of our results, all selected forest stands were either pure European beech forests or beech-dominated forests with a minimum beech share of 66 % in basal area. Furthermore, forest stands with terrain as plain as possible were selected, in order to have a low variability in terrain conditions. To ensure the comparability between the managed forests, the here considered managed stands have not been affected by management interventions for at least two years.

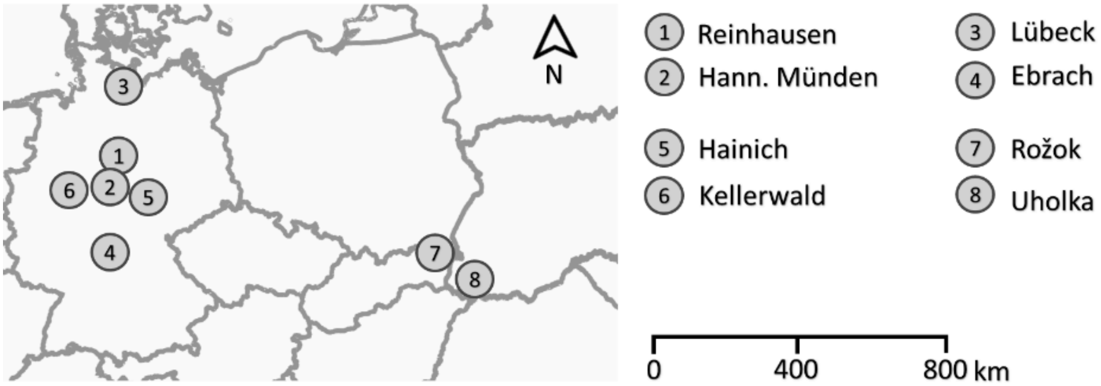

**Figure 1.2:** *Locations of the studied beech forests in Germany (1 - 6), Slovakia (7) and Ukraine (8).*

### 1.5.2 TLS and data processing

The 3D structure of the investigated forest stands was captured by using a Faro Focus 3D terrestrial laser scanner (Faro Technologies Inc., Lake Marry, USA), which operates based on the phase-shift technology. It covered a field of view of 300° (vertically) x 360° (horizontally). An angular resolution of 0.035° was set, resulting in a resolution of 10,240 points per 360° rotation and hence about 44 million measurements per scan.

During the measurements, the laser scanner was positioned on a tripod at 1.30 m, in accordance with breast height (see Figure 1.3). By avoiding stems and dense vegetation in close distance to the laser scanner, enough operational space was ensured. Detailed information about the product details and used scanner settings during the measurements can be found in the following chapters.The spatial information on the forest stands was saved in a 3D point cloud in the hardware specific format and then imported into the hardware specific software Faro Scene (Faro Technologies Inc., Lake Mary, USA). Here, the software's standard filters were applied to each 3D point cloud in order to eliminate erroneous and dark points. The filtered point clouds were then exported in the more universal file format (.xyz).

For the study, two different 3D point cloud types were used. The single-scan 3D point cloud is generated from a single-scan that showed the forest stand from the scanner's perspective. Here, the point cloud is characterized by an incomplete representation of plant material, because vegetation elements occlude space in the laser beam’s direction. Therefore, the visibility of plant material decreases with increasing distance from the scanner position (Astrup et al. 2014, Zhao et al. 2015).

**Figure 1.3:** *Faro Focus 3D terrestrial laser scanner installed on a tripod 1.3 m above ground. An example of the used chessboard targets lies next to the laser scanner. The targets were attached to stems and served as reference points, when multiple scans were merged into one point cloud.*

Due to the shadowing-effect, the usability of single-scan point clouds for structural analyses is limited (Ehbrecht et al. 2016). While some 3D measures, such as SSCI, canopy openness or canopy rugosity can be delivered from single-scans, other measures such as space filling or competition should be rather calculated using a multiple-scan point cloud, in order to have a complete and detailed forest image (Seidel et al. 2015). Some of the main advantages of the single-scan approach are the low field and post-processing efforts. Therefore, it is a popular scan method, which was utilized in numerous recent studies in order to capture 3D forest structure (Ehbrecht et al. 2021, Juchheim et al. 2020, Xia et al. 2015, Zemp et al. 2019). Here, the single-scan approach was used in the first and third sub-study. Detailed information on the sampling design of both studies can be found in chapter 2.2.2 and chapter 4.2.2.

For the second sub-study (chapter 3) 3D point clouds based on the multi-scan approach were used. Basically, this scan method is utilized, if a detailed, high quality 3D image of an object is needed (Zande et al. 2008). Here, multiple laser measurements are conducted in order to capture a forest stand from many different perspectives (Juchheim et al. 2017, Metz et al. 2013, Stiers et al. 2020, Tomșa et al. 2021). This had the effect that laser beams enter the forest stand from different angles and directions, which in turn increased the probability that all vegetation elements were fully captured by the laser scanner. The sampling design used in the multi-scan approach is described in chapter 3.2.2. The conducted multiple-scans were imported into Faro Scene (Faro Technologies Inc., Lake Mary, USA) and merged into one detailed 3D point cloud.

For the spatial co-registration of the single point clouds, artificial chessboard targets (see Figure 1.3) were used, which were installed systematically within the forest stand before scan start.

Based on the 3D point clouds, different 3D measures were generated in order to describe stand structure. The single-scan point clouds were used to calculate the UCI, which is introduced in the first sub-study (chapter 2), as well as SSCI, ENL and canopy openness (chapter 4). Based on the multi-scan point clouds, we computed SPf and $D_b$ in order to determine structural complexity and vegetation density within different forest strata (chapter 3).

## 1.6 References

Aranda, I., Gil, L., Pardos, J.A. (2000). Water relations and gas exchange in *Fagus sylvatica* L. and *Quercus petraea* (Mattuschka) Liebl. in a mixed stand at their southern limit of distribution in Europe. Trees, 14, 344-352. https://doi.org/10.1007/s004680050229.

Astrup, R., Ducey, M.J., Granhus, A., Ritter, T., von Lüpke, N. (2014). Approaches for estimating stand-level volume using terrestrial laser scanning in a single-scan mode. Canadian Journal of Forest Research,666-676. https://doi.org/10.1139/cjfr-2013-0535.

Atkins, J.W., Bohrer, G., Fahey, R.T., Hardiman, B.S., Morin, T.H., Stovall, A.E.L., (…), Gough, C.M. (2018). Quantifying vegetation and canopy structural complexity from terrestrial Li DAR data using the FORESTR R package. Methods in Ecology and Evolution, 9, 2057-2066. https://doi.org/10.1111/2041-210X.13061.

Barbeito, I., Dassot, M., Bayer, D., Collet, C., Drössler, L., Löf, M., (…), Pretzsch, H. (2017). Terrestrial laser scanning reveals differences in crown structure of *Fagus sylvatica* in mixed vs. pure European forests. Forest Ecology and Management, 405, 381-390. https://doi.org/10.1016/j.foreco.2017.09.043.

Bartsch, E., Lüpke, von B., N., Röhrig (2020). Waldbau auf ökologischer Grundlage. Verlag Eugen Ulmer, Stuttgart.

Bauhus, J., Forrester, D.I., Gardiner, B., Jactel, H., Vallejo, R., Pretzsch, H. (2017). Ecological Stability of Mixed-Species Forests. *In* Mixed-Species Forests: Ecology and Management. Springer, Berlin, Heidelberg. https://doi.org/10.1007/978-3-662-54553-9_7.

Bauhus, J., Puettmann, K., Messier, C. (2009). Silviculture for old-growth attributes. Forest Ecology and Management, 258, 525-537. https://doi.org/10.1016/j.foreco.2009.01.053.

Beland, M., Parker, G., Sparrow, B., Harding, D., Chasmer, L., Phinn, S., (…), Strahler, A. (2019). On promoting the use of lidar systems in forest ecosystem research. Forest Ecology and Management, 450, 117484. https://doi.org/10.1016/j.foreco.2019.117484.

BMEL - Bundesministerium für Ernährung und Landwirtschaft (2018). Der Wald in Deutschland-Ausgewählte Ergebnisse der dritten Bundeswaldinventur. https://www.bmel.de/DE/Wald-Fischerei/Waelder/_texte/Waldzustandserhebung.html (accessed 4.3.21).

BMEL - Bundesministerium für Ernährung und Landwirtschaft (2019). Ergebnisse der Waldzustandserhebung 2018. https://www.bmel.de/DE/Wald-Fischerei/Waelder/texte/Waldzustandserhebung.html (accessed 6.4.21).

Bohn, U., Gollub, G., Hettwer, Ch., Neuhäuslová, Z., Raus, Th., Schlüter, H. (2000). Karte der natürlichen Vegetation Europas / Map of the Natural Vegetation of Europe. Bundesamt für Naturschutz, Münster. https://is.muni.cz/el/1431/podzim2012/Bi9420/um/Bohn_etal2004_Map-Nat-Veg-Europe.pdf (accessed 12.6.21).

## Chapter 1

Bolte, A., Czajkowski, T., Cocozza, C., Tognetti, R., de Miguel, M., Pšidová, (…), Müller, J. (2016). Desiccation and Mortality Dynamics in Seedlings of Different European Beech (*Fagus sylvatica* L.) Populations under Extreme Drought Conditions. Frontiers in Plant Science,7. https://doi.org/10.3389/fpls.2016.00751.

Bolte, A., Czajkowski, T., Kompa, T. (2007). The north-eastern distribution range of European beech - a review. Forestry: An International Journal of Forest Research, 80, 413-429. https://doi.org/10.1093/forestry/cpm028.

Boncina, A. (2000). Comparison of structure and biodiversity in the Rajhenav virgin forest remnant and managed forest in the Dinaric region of Slovenia: Structure and biodiversity of forests in Slovenia. Global Ecology and Biogeography, 9, 201-211. https://doi.org/10.1046/ j.1365-2699.2000.00155.x.

Bouget, C., Parmain, G., Gilg, O., Noblecourt, T., Nusillard, B., Paillet, (…), Gosselin, F. (2014). Does a set-aside conservation strategy help the restoration of old-growth forest attributes and recolonization by saproxylic beetles? Animal Conservation, 17, 342-353. https://doi.org/10.1111/acv.12101.

Bradshaw, R.H.W. (2004). Past anthropogenic influence on European forests and some possible genetic consequences. Forest Ecology and Management, Dynamics and Conservation of Genetic Diversity in Forest Ecology, 197, 203-212. https://doi.org/10.1016/j.foreco.2004.05.025.

Brang, P. (2005). Virgin forests as a knowledge source for central European silviculture: Reality or myth? Forest Snow and Landscape Research, 79, 19-32. https://www.dora.lib4ri.ch/wsl/islandora/object/wsl:15327.

Brang, P., Spathelf, P., Larsen, J.B., Bauhus, J., Boncina, A., Chauvin, (…), Svoboda, M. (2014). Suitability of close-to-nature silviculture for adapting temperate European forests to climate change. Forestry, 87, 492-503. https://doi.org/10.1093/forestry/cpu018.

Brolly, G., Király, G., Czimber, K. (2013). Mapping Forest Regeneration from Terrestrial Laser Scans. Acta Silvatica et Lignaria Hungarica, 9, 135-146. https://doi.org/10.2478/aslh-2013-0011.

Brun, P., Psomas, A., Ginzler, C., Thuiller, W., Zappa, M., Zimmermann, N.E. (2020). Large-scale early-wilting response of Central European forests to the 2018 extreme drought. Global Change Biology, 26, 7021-7035. https://doi.org/10.1111/gcb.15360.

Buma, B., Wessman, C.A. (2011). Disturbance interactions can impact resilience mechanisms of forests. Ecosphere, 2, art64. https://doi.org/10.1890/ES11-00038.1.

Buras, A., Rammig, A., Zang, C.S. (2020). Quantifying impacts of the 2018 drought on European ecosystems in comparison to 2003. Biogeosciences, 17, 1655-1672. https://doi.org/10.5194/bg-17-1655-2020.

Calders, K., Phinn, S., Ferrari, R., Leon, J., Armston, J., Asner, G.P., Disney, M. (2020). 3D Imaging Insights into Forests and Coral Reefs. Trends in Ecology & Evolution, 35, 6-9. https://doi.org/10.1016/j.tree.2019.10.004.

Camarretta, N., Harrison, P.A., Bailey, T., Potts, B., Lucieer, A., Davidson, N., Hunt, M. (2019). Monitoring forest structure to guide adaptive management of forest restoration: a review of remote sensing approaches. New Forests, 51, 573-596. https://doi.org/10.1007/s11056-019-09754-5.

Chen, J., Bradshaw, G.A. (1999). Forest structure in space: a case study of an old growth spruce-fir forest in Changbaishan Natural Reserve, PR China. Forest Ecology and Management, 120, 219-233. https://doi.org/10.1016/S0378-1127(98)00543-X.

Clark, P.J., Evans, F.C. (1954). Distance to nearest neighbor as a measure of spatial relationships in populations. Ecology, 35, 445-453. https://doi.org/10.2307/1931034.

Collet, C., Lanter, O., Pardos, M. (2001). Effects of canopy opening on height and diameter growth in naturally regenerated beech seedlings. Annals of Forest Science, 58, 127-134. https://doi.org/10.1051/forest:2001112.

Del Río, M., Pretzsch, H., Alberdi, I., Bielak, K., Bravo, F., Brunner, (…), Bravo-Oviedo, A. (2016). Characterization of the structure, dynamics, and productivity of mixed-species stands: review and perspectives. European Journal of Forest Research, 135, 23-49. https://doi.org/10.1007/s10342-015-0927-6.

Diaci, J., Rozenbergar, D., Fidej, G., Nagel, T.A. (2017). Challenges for uneven-aged silviculture in restoration of post-disturbance forests in Central Europe: A synthesis. Forests, 8, 378. https://doi.org/10.3390/f8100378.

Dobbertin, M. (2002). Influence of stand structure and site factors on wind damage comparing the storms Vivian and Lothar. Forest Snow and Landscape Research, 77, 187-205.

Donager, J.J., Sankey, T.T., Sankey, J.B., Meador, A.J.S., Springer, A.E., Bailey, J.D. (2018). Examining forest structure with terrestrial lidar: Suggestions and novel techniques based on comparisons between scanners and forest treatments. Earth and Space Science, 5, 753-776. https://doi.org/10.1029/2018EA000417.

Dorji, Y., Annighöfer, P., Ammer, C., Seidel, D. (2019). Response of beech (*Fagus sylvatica* L.) trees to competition - New insights from using fractal analysis. Remote Sensing, 11, 2656. https://doi.org/10.3390/rs11222656.

Drößler, L. (2006). Struktur und Dynamik von zwei Buchenurwäldern in der Slowakei. Dissertation. Göttingen.

Ehbrecht, M., Schall, P., Ammer, C., Fischer, M., Seidel, D. (2019). Effects of structural heterogeneity on the diurnal temperature range in temperate forest ecosystems. Forest Ecology and Management, 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. Agricultural and Forest Meteorology, 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. Forest Ecology and Management, 380, 212-223. https://doi.org/10.1016/j.foreco.2016.09.003.

Ehbrecht, M., Seidel, D., Annighöfer, P., Kreft, H., Köhler, M., Zemp, D.C., (…), Ammer, C. (2021). Global patterns and climatic controls of forest structural complexity. Nature Communications, 12, 519. https://doi.org/10.1038/s41467-020-20767-z.

Ellenberg, H. (2009). Vegetation ecology of Central Europe. Cambridge University Press, Cambridge.

Ellenberg, H., Leuschner, C. (2010). Vegetation Mitteleuropas mit den Alpen: in ökologischer, dynamischer und historischer Sicht. Uni-Taschenbücher, Stuttgart.

El-Sheimy, N. (2009). Emerging MEMS IMU and its impact on mapping applications. Presented at the Photogrammetric Week 2009, Stuttgart. https://phowo.ifp.uni-stuttgart.de/publications/phowo09/220El-Sheimy.pdf (accessed 4.12.21).

Emborg, J., Christensen, M., Heilmann-Clausen, J. (2000). The structural dynamics of Suserup Skov, a near-natural temperate deciduous forest in Denmark. Forest Ecology and Management, 126, 173-189. https://doi.org/10.1016/S0378-1127(99)00094-8.

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. Forest Ecology and Management, 415-416, 38-46. https://doi.org/10.1016/j.foreco.2018.02.022.

Felipe-Lucia, M.R., Soliveres, S., Penone, C., Manning, P., van der Plas, F., Boch, S., (…), Allan, E. (2018). Multiple forest attributes underpin the supply of multiple ecosystem services. Nature Communications, 9, 4839. https://doi.org/10.1038/s41467-018-07082-4.

Fenton, N.J., 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. Journal of Forest Research, 14, 258-267. https://doi.org/10.1007/s10310-009-0134-8.

Fischer, M., Bossdorf, O., Gockel, S., Hänsel, F., Hemp, A., Hessenmöller, D., (…), Weisser, W.W., (2010). Implementing large-scale and long-term functional biodiversity research: The Biodiversity Exploratories. Basic and Applied Ecology, 11, 473-485. https://doi.org/10.1016/j.baae.2010.07.009.

Franklin, J.F., Van Pelt, R. (2004). Spatial aspects of structural complexity in old-growth forests. Journal of Forestry, 102, 22-28. https://doi.org/10.1093/jof/102.3.22.

Frey, J., Joa, B., Schraml, U., Koch, B. (2019). Same viewpoint different perspectives-A comparison of expert ratings with a TLS derived forest stand structural complexity index. Remote Sensing, 11. https://doi.org/10.3390/rs11091137.

Fritz, P., Weber, D., Jenssen, M. (2006). Ökologischer Waldumbau in Deutschland: Fragen, Antworten, Perspektiven. Ökom-Verlag, München.

Gadow, K. v., Zhang, C.Y., Wehenkel, C., Pommerening, A., Corral-Rivas, J., Korol, M, (…), Zhao, X.H. (2012). Forest Structure and Diversity. *In* Continuous Cover Forestry, Managing Forest Ecosystems. Springer, Dordrecht. https://doi.org/10.1007/978-94-007-2202-6_2.

Geßler, A., Keitel, C., Kreuzwieser, J., Matyssek, R., Seiler, W., Rennenberg, H. (2007). Potential risks for European beech (*Fagus sylvatica* L.) in a changing climate. Trees, 21, 1-11. https://doi.org/10.1007/s00468-006-0107-x.

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. Ecosystems, 21, 704-722. https://doi.org/10.1007/s10021-017-0179-z.

Gough, C.M., Atkins, J.W., Fahey, R.T., Hardiman, B.S. (2019). High rates of primary production in structurally complex forests. Ecology ,100. https://doi.org/10.1002/ecy.2864.

Gustafsson, L., Baker, S.C., Bauhus, J., Beese, W.J., Brodie, A., Kouki, J, (…) Franklin, J.F. (2012). Retention forestry to maintain multifunctional forests: A world perspective. BioScience, 62, 633-645. https://doi.org/10.1525/bio.2012.62.7.6.

Hagge, J., Leibl, F., Müller, J., Plechinger, M., Soutinho, J.G., Thorn, S. (2019). Reconciling pest control, nature conservation, and recreation in coniferous forests. Conservation Letters 12, e12615. https://doi.org/10.1111/conl.12615.

Hardiman, B.S., Bohrer, G., Gough, C.M., Vogel, C.S., Curtis, P.S. (2011). The role of canopy structural complexity in wood net primary production of a maturing northern deciduous forest. Ecology, 92, 1818-1827. https://doi.org/10.1890/10-2192.1.

Hobi, M.L., Commarmot, B., Bugmann, H. (2015a). Pattern and process in the largest primeval beech forest of Europe (Ukrainian Carpathians). Journal of Vegetation Science, 26, 323-336. https://doi.org/10.1111/jvs.12234.

Hobi, M.L., Ginzler, C., Commarmot, B., Bugmann, H. (2015b). Gap pattern of the largest primeval beech forest of Europe revealed by remote sensing. Ecosphere, 6, art76. https://doi.org/10.1890/ES14-00390.1.

Höwler, K., Vor, T., Seidel, D., Annighöfer, P., Ammer, C. (2019). Analyzing effects of intra- and interspecific competition on timber quality attributes of *Fagus sylvatica* L.-from quality assessments on standing trees to sawn boards. European Journal of Forest Research, 138, 327-343. https://doi.org/10.1007/s10342-019-01173-7.

Jactel, H., Brockerhoff, E., Duelli, P. (2005). A test of the Biodiversity-Stability Theory: Meta-analysis of tree species diversity effects on insect pest infestations, and re-examination of responsible factors. *In* Forest Diversity and Function: Temperate and Boreal Systems, Ecological Studies. Springer, Berlin, Heidelberg. https://doi.org/10.1007/3-540-26599-6_12.

Juchheim, J., Ammer, C., Schall, P., Seidel, D. (2017). Canopy space filling rather than conventional measures of structural diversity explains productivity of beech stands. Forest Ecology and Management, 395, 19-26. https://doi.org/10.1016/j.foreco.2017.03.036.

Juchheim, J., Ehbrecht, M., Schall, P., Ammer, C., Seidel, D. (2020). Effect of tree species mixing on stand structural complexity. Forestry: An International Journal of Forest Research, 93, 75-83. https://doi.org/10.1093/forestry/cpz046.

Kaplan, J.O., Krumhardt, K.M., Zimmermann, N. (2009). The prehistoric and preindustrial deforestation of Europe. Quaternary Science Reviews, 28, 3016-3034. https://doi.org/10.1016/j.quascirev.2009.09.028.

Kenderes, K., Mihok, B., Standovar, T. (2008). Thirty years of gap dynamics in a Central European beech forest reserve. Forestry, 81, 111-123. https://doi.org/10.1093/forestry/cpn001.

Kint, V., Robert, D.W., Noël, L. (2004). Evaluation of sampling methods for the estimation of structural indices in forest stands. Ecological Modelling, 180, 461-476. https://doi.org/10.1016/j.ecolmodel.2004.04.032.

Knorn, J., Kuemmerle, T., Radeloff, V.C., Keeton, W.S., Gancz, V., Biriş, I.-A, (…), Hostert, P. (2013). Continued loss of temperate old-growth forests in the Romanian Carpathians despite an increasing protected area network. Environmental Conservation, 40, 182-193. https://doi.org/10.1017/S0376892912000355.

Koontz, M.J., North, M.P., Werner, C.M., Fick, S.E., Latimer, A.M. (2020). Local forest structure variability increases resilience to wildfire in dry western U.S. coniferous forests. Ecology Letters, 23, 483-494. https://doi.org/10.1111/ele.13447.

Korpel, Š. (1995). Die Urwälder der Westkarpaten: 39 Tabellen. Gustav Fischer, Stuttgart.

Kottek, M., Grieser, J., Beck, C., Rudolf, B., Rubel, F. (2006). World Map of the Köppen-Geiger climate classification updated. Meteorologische Zeitschrift, 15, 259-263. https://doi.org/10.1127/0941-2948/2006/0130.

Kovács, B., Tinya, F., Ódor, P. (2017). Stand structural drivers of microclimate in mature temperate mixed forests. Agricultural and Forest Meteorology, 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. European Journal of Forest Research, 129, 249-259. https://doi.org/10.1007/s10342-009-0322-2.

Lenton, T.M., Held, H., Kriegler, E., Hall, J.W., Lucht, W., Rahmstorf, S., Schellnhuber, H.J. (2008). Tipping elements in the Earth’s climate system. PNAS, 105, 1786-1793. https://doi.org/10.1073/pnas.0705414105.

Leuschner, C., Meier, I.C., 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. Annals of Forest Science, 63, 355-368. https://doi.org/10.1051/forest:2006016.

Li, S., Wang, T., Hou, Z., Gong, Y., Feng, L., Ge, J. (2021). Harnessing terrestrial laser scanning to predict understory biomass in temperate mixed forests. Ecological Indicators, 121, 107011. https://doi.org/10.1016/j.ecolind.2020.107011.

Li, W., Niu, Z., Chen, H., Li, D. (2017). Characterizing canopy structural complexity for the estimation of maize LAI based on ALS data and UAV stereo images. Null, 38, 2106-2116. https://doi.org/10.1080/01431161.2016.1235300.

Lim, K., Treitz, P., Wulder, M., St-Onge, B., Flood, M. (2003). LiDAR remote sensing of forest structure. Progress in Physical Geography: Earth and Environment, 27, 88-106. https://doi.org/10.1191/0309133303pp360ra.

Mandelbrot, B.B. (1975). Stochastic models for the Earth’s relief, the shape and the fractal dimension of the coastlines, and the number-area rule for islands. Proceedings of the National Academy of Sciences, 72, 3825-3828. https://doi.org/10.1073/pnas.72.10.3825.

Martikainen, P., Siitonen, J., Punttila, P., Kaila, L., Rauh, J. (2000). Species richness of Coleoptera in mature managed and old-growth boreal forests in southern Finland. Biological Conservation, 94, 199-209. https://doi.org/10.1016/S0006-3207(99)00175-5.

McElhinny, C., Gibbons, P., Brack, C., Bauhus, J. (2005). Forest and woodland stand structural complexity: Its definition and measurement. Forest Ecology and Management, 218, 1-24. https://doi.org/10.1016/j.foreco.2005.08.034.

McGrath, M.J., Luyssaert, S., Meyfroidt, P., Kaplan, J.O., Bürgi, M., Chen, Y., (…), Schelhaas, M.-J., Valade, A. (2015). Reconstructing European forest management from 1600 to 2010. Biogeosciences, 12, 4291-4316. https://doi.org/10.5194/bg-12-4291-2015.

Messier, C., Puettmann, K.J. (2011). Forests as complex adaptive systems: implications for forest management and modelling. L’Italia Forestale e Montana, 249-258. https://doi.org/10.4129/ifm.2011.3.11.

Messier, C., Puettmann, K.J., Coates, K.D. (2013). Managing Forests as Complex Adaptive Systems: Building Resilience to the Challenge of Global Change. Routledge, Oxon.

Metz, J., Seidel, D., Schall, P., Scheffer, D., Schulze, E.-D., Ammer, C. (2013). Crown modeling by terrestrial laser scanning as an approach to assess the effect of aboveground intra- and interspecific competition on tree growth. Forest Ecology and Management, 310, 275-288. https://doi.org/10.1016/j.foreco.2013.08.014.

Meyer, P., Tabaku, V., v. Lupke, B. (2003). Die Struktur albanischer Rotbuchen Urwälder - Ableitungen für eine naturnahe Buchenwirtschaft. Structural Characteristics of Albanian Beech (*Fagus sylvatica* L.) Virgin Forests - Deductions for Semi-Natural Forestry. Forstwissenschaftliches Centralblatt, 122, 47-58. https://doi.org/10.1046/j.1439-0337.2003.02041.x.

Mizunaga, H., Nagaike, T., Yoshida, T., Valkonen, S. (2010). Feasibility of silviculture for complex stand structures: designing stand structures for sustainability and multiple objectives. Journal of Forest Research, 15, 1-2. https://doi.org/10.1007/s10310-009-0177-x.

Möhring, B., Leefken, G., Gutsche, C. (2008). Economic valuation of beech forests. *In* Ergebnisse Angewandter Forschung zur Buche. Beiträge aus Der Nordwestdeutschen Forstlichen Versuchsanstalt. NW-FVA.

Mulwa, R.K., Böhning- Gaese, K., Schleuning, M. (2012). High bird species diversity in structurally heterogeneous farmland in Western Kenya. Biotropica, 44, 801-809. https://doi.org/10.1111/j.1744-7429.2012.00877.x.

Nagel, T.A., Svoboda, M., Kobal, M. (2014). Disturbance, life history traits, and dynamics in an old-growth forest landscape of southeastern Europe. Ecological Applications, 24, 663-679. https://doi.org/10.1890/13-0632.1.

Nagel, T.A., Svoboda, M., Rugani, T., Diaci, J. (2010). Gap regeneration and replacement patterns in an old-growth *Fagus-Abies* forest of Bosnia-Herzegovina. Journal of Plant Ecology, 208, 307-318. https://doi.org/10.1007/s11258-009-9707-z.

NLF - Niedersächsische Landesforsten (2018): Entscheidungshilfen zur Behandlung und Entwicklung von Buchenbeständen. https://www.nw-fva.de/fileadmin/user_upload/Verwaltung/Publikationen/Merkblaetter/Bu_Nds_Entscheidungshilfen_zur_Behandlung_und_Entwicklung_von_Buchenbestaenden.pdf (accessed 6.5.21).

NW-FVA - Nordwestdeutsche Forstliche Versuchsanstalt (2019). Komplexe Schäden an Rotbuche (*Fagus sylvatica*) und Auswirkungen des trockenen und heißen Sommers 2018 auf ältere Bestände. Waldschutzinfo, 06. Waldschutzinfo_06-2019_Komplexe_Schaeden_ an_Buche.pdf (nw-fva.de) (accessed 21.6.21).

Pach, M., Sansone, D., Ponette, Q., Barreiro, S., Mason, B., Bravo-Oviedo, Andres, Löf, M., Bravo, F., (…), Corona, P. (2018). Silviculture of Mixed Forests: A European Overview of Current Practices and Challenges. *In* Dynamics, Silviculture and Management of Mixed Forests, Managing Forest Ecosystems. Springer International Publishing, Cham. https://doi.org/10.1007/978-3-319-91953-9_6.

Payer, D.C., Harrison, D.J. (2003). Influence of forest structure on habitat use by American marten in an industrial forest. Forest Ecology and Management, 179, 145-156. https://doi.org/10.1016/S0378-1127(02)00517-0.

Peters, R. (1997). Beech Forests. Springer Netherlands, Dordrecht.

Pommerening, A., Murphy, S.T. (2004). A review of the history, definitions and methods of continuous cover forestry with special attention to afforestation and restocking. Forestry: An International Journal of Forest Research, 77, 27-44. https://doi.org/10.1093/forestry/77.1.27.

Potapov, P., Hansen, M.C., Laestadius, L., Turubanova, S., Yaroshenko, A., Thies, C, (…), Esipova, E. (2017). The last frontiers of wilderness: Tracking loss of intact forest landscapes from 2000 to 2013. Science Advances, 3, e1600821. https://doi.org/10.1126/sciadv.1600821.

Pretzsch, H. (2019). Grundlagen der Waldwachstumsforschung. Springer Berlin Heidelberg, 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. (1997). Analysis and modeling of spatial stand structures. Methodological considerations based on mixed beech-larch stands in Lower Saxony. Forest Ecology and Management, 97, 237-253. https://doi.org/10.1016/S0378-1127(97)00069-8.

Puettmann, K.J., Coates, K.D., Messier, C.C. (2009). A critique of silviculture: managing for complexity. Island Press, Washington, DC.

Puettmann, K.J., Wilson, S.M., Baker, S.C., Donoso, P.J., Drössler, L., Amente, G, (…) Bauhus, J. (2015). Silvicultural alternatives to conventional even-aged forest management - what limits global adoption? Forest Ecosystems, 2, 8. https://doi.org/10.1186/s40663-015-0031-x.

Pukkala, T., von Gadow, K. (2012). Continuous Cover Forestry, Managing Forest Ecosystems. Springer Netherlands, Dordrecht.

QingWang, L., ShiMing, L., ZengYuan, L., LiYong, F., KaiLong, H. (2017). Review on the applications of UAV-based LiDAR and photogrammetry in forestry. Scientia Silvae Sinicae, 53, 134-148.

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. Forest Ecology and Management, 194, 349-368. https://doi.org/10.1016/j.foreco.2004.02.022.

Reyer, C.P.O., Brouwers, N., Rammig, A., Brook, B.W., Epila, J., Grant, R.F., (…), Villela, D.M. (2015). Forest resilience and tipping points at different spatio-temporal scales:

approaches and challenges. Journal of Ecology, 103, 5-15. https://doi.org/10.1111/1365-2745.12337.

Rugani, T., Diaci, J., Hladnik, D. (2013). Gap Dynamics and Structure of Two Old-Growth Beech Forest Remnants in Slovenia. PLoS ONE, 8, e52641. https://doi.org/10.1371/journal.pone.0052641.

Rumpf, H., Petersen, R. (2008). Forest conversion to beech in consideration of its ecological demands. *In* Ergebnisse Angewandter Forschung zur Buche. Beiträge aus der Nordwestdeutschen Forstlichen Versuchsanstalt, Göttingen.

Sabatini, F.M., Burrascano, S., Keeton, W.S., Levers, C., Lindner, M., Pötzschner, F., (…), Kuemmerle, T. (2018). Where are Europe's last primary forests? Diversity and Distributions, 24, 1426-1439. https://doi.org/10.1111/ddi.12778.

Sabatini, F.M., Keeton, W.S., Lindner, M., Svoboda, M., Verkerk, P.J., Bauhus, J., (…), Kuemmerle, T. (2020). Protection gaps and restoration opportunities for primary forests in Europe. Diversity and Distributions, 26, 1646-1662. https://doi.org/10.1111/ddi.13158.

Sačkov, I., Scheer, Ľ., Bucha, T. (2019). Predicting forest stand variables from airborne LiDAR data using a tree detection method in Central European forests. Central European Forestry Journal, 65, 191-197. https://doi:10.2478/forj-2019-0014.

Sarkar, N., Chaudhuri, B.B. (1994). An efficient differential box-counting approach to compute fractal dimension of image. IEEE Transactions on Systems, Man, and Cybernetics, 24, 115-120. https://doi.org/10.1109/21.259692.

Schall, P., Ammer, C. (2013). How to quantify forest management intensity in Central European forests. European Journal of Forest Research, 132, 379-396. https://doi.org/10.1007/s10342-013-0681-6.

Schall, P., Gossner, M.M., Heinrichs, S., Fischer, M., Boch, S., Prati, D., (…), Ammer, C. (2018a). The impact of even-aged and uneven-aged forest management on regional biodiversity of multiple taxa in European beech forests. Journal of Applied Ecology, 55, 267-278. https://doi.org/10.1111/1365-2664.12950.

Schall, P., Schulze, E.-D., Fischer, M., Ayasse, M., Ammer, C. (2018b). Relations between forest management, stand structure and productivity across different types of Central European forests. Basic and Applied Ecology, 32, 39-52. https://doi.org/10.1016/j.baae.2018.02.007.

Schelhaas, M.-J., Nabuurs, G.-J., Schuck, A. (2003). Natural disturbances in the European forests in the 19th and 20th centuries. Global Change Biology, 9, 1620-1633. https://doi.org/10.1046/j.1365-2486.2003.00684.x.

Schnitzler, A. (2014). Towards a new European wilderness: Embracing unmanaged forest growth and the decolonisation of nature. Landscape and Urban Planning, 126, 74-80. https://doi.org/10.1016/j.landurbplan.2014.02.011.

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

Schuldt, B., Buras, A., Arend, M., Vitasse, Y., Beierkuhnlein, C., Damm, A., (…), Kahmen, A. (2020). A first assessment of the impact of the extreme 2018 summer drought on Central European forests. Basic and Applied Ecology, 45, 86-103. https://doi.org/10.1016/j.baae.2020.04.003.

Schütz, J. (2002). Silvicultural tools to develop irregular and diverse forest structures. Forestry: An International Journal of Forest Research, 75, 329-337. https://doi.org/10.1093/forestry/75.4.329.

Schütz, J.-P. (2006). Modelling the demographic sustainability of pure beech plenter forests in Eastern Germany. Annals of Forest Science, 63, 93-100. https://doi.org/10.1051/forest:2005101.

Seidel, D. (2018). A holistic approach to determine tree structural complexity based on laser scanning data and fractal analysis. Ecology and Evolution, 8, 128-134. https://doi.org/10.1002/ece3.3661.

Seidel, D., Annighöfer, P., Ammer, C., Ehbrecht, M., Willim, K., Bannister, J., Soto, D.P. (2021). Quantifying understory complexity in unmanaged forests using TLS and identifying some of its major drivers. Remote Sensing, 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? Remote Sensing, 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? Agricultural and Forest Meteorology, 278, 107699. https://doi.org/10.1016/j.agrformet.2019.107699.

Seidel, D., Hoffmann, N., Ehbrecht, M., Juchheim, J., Ammer, C. (2015). How neighborhood affects tree diameter increment - New insights from terrestrial laser scanning and some methodical considerations. Forest Ecology and Management, 336, 119-128. https://doi.org/10.1016/j.foreco.2014.10.020.

Seidel, D., Leuschner, C., Müller, A., Krause, B. (2011). Crown plasticity in mixed forests-Quantifying asymmetry as a measure of competition using terrestrial laser scanning. Forest Ecology and Management, 261, 2123-2132. https://doi.org/10.1016/j.foreco.2011.03.008.

Spiecker, H. (2003). Silvicultural management in maintaining biodiversity and resistance of forests in Europe-temperate zone. Journal of Environmental Management, Maintaining Forest Biodiversity, 67, 55-65. https://doi.org/10.1016/S0301-4797(02)00188-3.

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 and 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. Forest Ecology and Management, 430, 357-365. https://doi.org/10.1016/j.foreco.2018.08.039.

Stinglwagner, G., Haseder, I., Erlbeck, R. (2016). Das Kosmos Wald & Forst-Lexikon, Kosmos, Stuttgart.

Tomșa, V.R., Curtu, A.L., Niță, M.D. (2021). Tree shape variability in a mixed oak forest using terrestrial laser technology: Implications for mating system analysis. Forests, 12, 253. https://doi.org/10.3390/f12020253.

Torralba, J., Crespo-Peremarch, P., Ruiz, L.A. (2018). Assessing the use of discrete, full-waveform LiDAR and TLS to classify Mediterranean forest species composition. Revista de Teledetección, 0, 27-40. https://doi.org/10.4995/raet.2018.11106.

Trotsiuk, V., Hobi, M.L., Commarmot, B. (2012). Age structure and disturbance dynamics of the relic virgin beech forest Uholka (Ukrainian Carpathians). Forest Ecology and Management, 265, 181-190. https://doi.org/10.1016/j.foreco.2011.10.042.

Trumbore, S., Brando, P., Hartmann, H. (2015). Forest health and global change. Science, 349, 814. https://doi.org/10.1126/science.aac6759.

Veen, P., Fanta, J., Raev, I., Biriş, I.-A., de Smidt, J., Maes, B. (2010). Virgin forests in Romania and Bulgaria: results of two national inventory projects and their implications for protection. Biodiversity Conservation, 19, 1805-1819. https://doi.org/10.1007/s10531-010-9804-2n.

Wesołowski, T. (2005). Virtual conservation: How the European Union is turning a blind eye to its vanishing primeval forests. Conservation Biology, 19, 1349-1358. https://doi.org/10.1111/j.1523-1739.2005.00265.x.

White, P.S., Jentsch, A. (2001). The Search for generality in studies of disturbance and ecosystem dynamics. *In* Progress in Botany: Genetics Physiology Systematics Ecology, Progress in Botany. Springer, Berlin, Heidelberg. https://doi.org/10.1007/978-3-642-56849-7_17.

Wirth, C., Gleixner, G., Heimann, M. (2009). Old-Growth Forests: Function, Fate and Value - an Overview. *In* Old-Growth Forests: Function, Fate and Value, Ecological Studies. Springer, Berlin, Heidelberg. https://doi.org/10.1007/978-3-540-92706-8_1.

Witté, I., Kneeshaw, D., Messier, C. (2013). Do partial cuts create forest complexity? A new approach to measuring the complexity of forest patterns using photographs and the mean information gain. The Forestry Chronicle, 89, 340-349. https://doi.org/10.5558/tfc2013-064.

Xia, S., Wang, C., Pan, F., Xi, X., Zeng, H., Liu, H. (2015). Detecting stems in dense and homogeneous forest using single-scan TLS. Forests, 6, 3923-3945. https://doi.org/10.3390/f6113923.

Zande, D.V. der, Jonckheere, I., Stuckens, J., Verstraeten, W.W., Coppin, P. (2008). Sampling design of ground-based lidar measurements of forest canopy structure and its effect on shadowing. Canadian Journal of Remote Sensing, 34, 526-538. https://doi.org/10.5589/m08-070.

Zemp, D.C., Ehbrecht, M., Seidel, D., Ammer, C., Craven, D., Erkelenz, J., (…), Kreft, H. (2019). Mixed-species tree plantings enhance structural complexity in oil palm plantations. Agriculture, Ecosystems & Environment, 283, 106564. https://doi.org/10.1016/j.agee.2019.06.003.

Zenner, E.K., Hibbs, D.E. (2000). A new method for modeling the heterogeneity of forest structure. Forest Ecology and Management, 129, 75-87. https://doi.org/10.1016/S0378-1127(99)00140-1.

Zhao, K., García, M., Liu, S., Guo, Q., Chen, G., Zhang, X., Zhou, Y., Meng, X. (2015). Terrestrial lidar remote sensing of forests: Maximum likelihood estimates of canopy profile, leaf area index, and leaf angle distribution. Agricultural and Forest Meteorology, 209-210, 100-113. https://doi.org/10.1016/j.agrformet.2015.03.008.

Zscheischler, J., Seneviratne, S.I. (2017). Dependence of drivers affects risks associated with compound events. Science Advances, 3, e1700263. https://doi.org/10.1126/sciadv.1700263.

# Chapter 2

## Chapter 2 Assessing understory complexity in beech-dominated forests (*Fagus sylvatica* L.) in Central Europe - from managed to primary forests

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### Abstract

Understory vegetation influences several ecosystem services and functions of European beech (*Fagus sylvatica* L.) forests. Despite this knowledge on the importance of understory vegetation, it is still difficult to measure its three-dimensional characteristics in a quantitative manner. With the recent advancements in terrestrial laser scanning (TLS), we now have the means to analyze detailed spatial patterns of forests. Here, we present a new measure to quantify understory complexity. We tested the approach for different management types, ranging from traditionally and alternatively managed forests and national parks in Germany to primary forests of Eastern Europe and the Ukraine, as well as on an inventory site with more detailed understory reference data. The understory complexity index (UCI) was derived from point clouds from single scans and tested for its relationship with forest management and conventional inventory data. Our results show that advanced tree regeneration is a strong driver of the UCI. Furthermore, the newly developed index successfully measured understory complexity of differently managed beech stands and was able to distinguish scanning positions located on and away from skid-trails in managed stands. The approach enables a deeper understanding of the complexity of understory structures of forests and their drivers and dependents.

**Keywords:** understory structure; management intensity; regeneration; *Fagus sylvatica* L.; primary forests; terrestrial laser scanning; Carpathian Biosphere Reserve

## 2.1 Introduction

The understory, i.e. “all vegetation growing under an overstory” (Helms 1998, p. 192) is an important functional and structural component of temperate forests. Understory vegetation influences ecosystem functions, such as nutrient cycling (Kimmins 2004) or biodiversity of stands (Thomas et al. 1999). Moreover, it interacts with animal communities (Augusto et al. 2003), e.g. by serving as food source or shelter, and may impact the future composition of tree species (Antos 2009). The understory of primary temperate forests is characterized by the presence of advanced regeneration, vertical heterogeneity and the development of secondary crowns by trees not yet reaching the overstory (Bauhus et al. 2009). In the few remaining beech (*Fagus sylvatica* L.) primary forests in Europe, a high density of natural regeneration as well as a multi-layered understory structure has been observed (Commarmot et al. 2005, Kucbel et al. 2010, Trotsiuk et al. 2012).

Recent studies have shown that understory vegetation contributes notably to the stand structure of a forest. Ehbrecht et al. (2017) observed an increase in the overall three-dimensional stand structural complexity due to the presence of dense understory vegetation, such as thickets with shelterwood trees. An essential part of modern silvicultural practices in Europe is to emulate complex structures as found in primary forests (Gustafsson et al. 2012, Nagel et al. 2013). To do so, we need quantitative information on the different elements of the structure of primary forests to serve as a reference (Brang 2005, Feldmann et al. 2018, Nagel et al. 2013).

Previous research has mainly focused on single attributes such as shrub cover (Berger and Puettmann 2000, Spies and Franklin 1991), shrub height (Drößler 2006, Feldmann et al. 2018, Nagel et al. 2013) or understory richness (Sullivan et al. 2001). Such understory attributes were used to emphasize the influence of understory vegetation on the overall structure of a forest. Hinsely et al. (2009) found that understory “density” has a crucial impact on the provision of resources and habitats for birds in temperate forests of Europe. For example, Anderson and Meikle (2006) revealed that an increase in the “presence” of understory vegetation had a positive effect on the relative abundance of mice (*Peromyscus leucopus*) in temperate deciduous forests.

With the ecological and functional importance of understory structures in mind, a quantitative measure of understory complexity is needed. Here, we define understory complexity as an integrative measure of the three-dimensional, architectural and spatial arrangement of all plant organs in the understory of a given forest at a given point in time.

Recently, new options of measuring stand structural attributes by 3D reality capturing were successfully used to quantify the spatial arrangement of plant material in forests (Ehbrecht et al. 2017, Palace et al. 2016, Seidel et al. 2016). Brolly et al. (2013) showed that terrestrial laser scanning (TLS) has the ability to quantify tree regeneration. However, the potential of using 3D data for an assessment of forest understory was little explored so far. In this study, we developed a new method to quantify the structural complexity of forest understories based on TLS. We hypothesized (i) that the understory complexity index is driven by young tree regeneration. By this, attributes that can be expected to be related to reductions of structural complexity, such as skid-trails, should be detectable. Furthermore, we hypothesize (ii) that beech-dominated forests of different management types differ in the complexity of understory structure.

## 2.2 Material and methods

### 2.2.1 Study sites

To address hypothesis (i) we used tree regeneration data from an inventory that was conducted in mixed broadleaf-coniferous even-aged stands in the region of Waake (administrative district of Göttingen, Lower Saxony, Germany). The site, from here on named “inventory site” is located between 220 and 400 m above sea level (a.s.l.). To address hypothesis (ii) we investigated the understory in a series of beech-dominated forests across a gradient of management intensity, ranging from traditionally managed forests in Germany to primary forests in Slovakia and Ukraine (Stiers et al. 2018). A detailed description of the location of the study sites and important characteristics can be found in Figure 2.1 and Table 2.1. To ensure comparability, we determined certain selection criteria for our study plots at the sites. All plots were located in forest stands with a minimum beech share of 66 % in basal area. Furthermore, the last management intervention was to date back two or more years.

For each management type (traditionally managed, alternatively managed, national park (formerly managed forest), primary forest), we chose two geographical locations (Figure 2.1). Traditionally managed forests were selected in Lower Saxony State Forest in the forest districts of Hannoversch Münden and Reinhausen, respectively. Sites with alternative management (see explanation of ‘alternative’ below) were selected in the Northern German lowlands (Lübeck) and in the lower mountains of the Steigerwald, Bavaria (Ebrach), respectively. Two sites were placed in beech-dominated forests of the National Parks ‘Hainich’ and ‘Kellerwald-Edersee’. Finally, two sites were chosen from primary beech forests located in the Carpathian Mountains, where the largest remnants of primeval forests can be found in Europe (Sabatini et al. 2018). We selected ‘Rožok’, a National Nature Reserve (NNR) in the Slovakian Republic and the primary forest Uholka-Shyroky Luh (Ukraine), which is a part of the Carpathian Biosphere Reserve (CBR) (Table 2.1). In addition to the site pairs according to the management type, a further site was used in Waake. This site was also considered to be traditionally managed, with the advantage that regeneration inventory data was also available for this site.

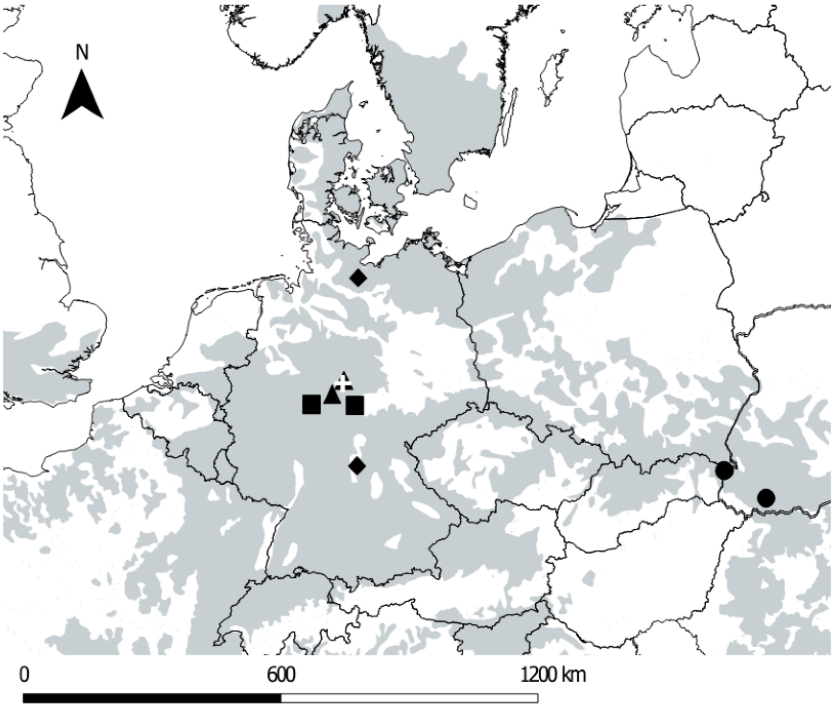

**Figure 2.1:** *Distribution of Fagus sylvatica L. in Central Europe (grey area) and location of studied beech forests (▲= Traditionally managed, ♦ = Alternatively managed, ■ = National Parks, ● = Primary forests). Source of species distribution map: <http://www.euforgen.org>). The white + indicates the location of the inventory study site used for the young tree regeneration inventory (Waake, near Göttingen).*

Apart from the lowland sites in Lübeck (40 - 90 m a.s.l), all study areas in Germany are located in the lower mountain ranges (190 - 635 m a.s.l.). The sites in the Western Carpathians were located highest, with 580 - 840 m a.s.l. The climatic conditions at all our study sites are considered temperate after the Köppen Geiger classification (Kottek et al. 2006). Annual mean temperature ranges from 6.5 °C to 8.5 °C and annual precipitation varies between 600 and 1407 mm.

**Table 2.1:** *Information on location and basic environmental conditions of the study sites. For each management type, we chose two study sites. For each study site of the management type "Traditional" and "Alternative", the age classes "0 - 20", "21 - 40", "41 - 80", "81 - 120" were considered.*

| Country | Management type | Study sites | Mean temperature (°C) | Precipitation (mm $y^{-1}$) | Elevation (m a.s.l.) | Age class (years) |
|---|---|---|---|---|---|---|
| Germany | Traditional | Waake (inventory site) | 7.5 | 750 | 220 - 400 | 0 - 20,<br>21 - 40,<br>41 - 80,<br>81 - 120,<br>121 - 190 |
| Germany | Traditional | Hann. Münden | 6.5 - 7.5 | 750 - 1050 | 270 - 410 | 0 - 20,<br>21 - 40,<br>41 - 80,<br>81 - 120 |
| | | Reinhausen | 8 | 740 | 190 - 310 | |
| | Alternative | Ebrach | 7 - 8 | 850 | 320 - 480 | 0 - 20,<br>21 - 40,<br>41 - 80,<br>81 - 120 |
| | | Lübeck | 8 - 8.5 | 625 - 725 | 40 - 90 | |
| | National Park | Kellerwald | 6 - 8 | 600 - 800 | 540 - 635 | ~ 180 |
| | | Hainich | 7 - 8 | 600 - 800 | 330 - 380 | ~ 180 |
| Slovakia | Primary forest | Rožok | 6 - 7 | 780 | 580 - 745 | ~ 220 |
| Ukraine | | Uholka | 7 | 1407 | 700 - 840 | ~ 350 |

The four different management intensities correspond to four different management types that represent a gradient in management intensity (Table 2.2). Management in traditionally managed forests sites Reinhausen and Hannoversch Münden is based on the "Guidelines of beech forest management in Lower Saxony, Germany" (NLF). These forests are characterized by a thinning cycle of 5 to 10 years during which up to three competitors per target tree are removed. Target trees are harvested when they have reached a target diameter of at least 65 cm at breast height (1.3 m). In the alternatively managed forest sites, the thinning frequencies and intensities are lower, so thinning cycles are longer and less competitors are removed during the rotation period. Also, the share of trees growing beyond the mentioned target diameter is larger. In Lübeck, a further objective is to increase the growing stock by ceasing silvicultural activities within stand ages of 30 - 80 years. Finally, the forest districts Ebrach and Lübeck aim for a higher amount of coarse woody debris compared to Reinhausen and Hannoversch Münden.

No management for at least two decades characterizes the sites in the National Parks Hainich and Kellerwald-Edersee, while the primary forests Uholka and Rožok have developed without a forest management concept (Brang 2005).

To allow an appropriate comparison of the managed systems with the unmanaged systems, we took the different age classes occurring in managed stands into account. These ranged from thickets (0 - 20 years) with shelterwood trees to mature timber stands (81 - 120 years) (Table 2.1). The mature stands in National Park Hainich had an average age of 180 years, which is comparable to the range of mean ages reported for the stands in the National Park Kellerwald-Edersee (174 - 194 years). The primary beech forests in Uholka and Rožok can be described as uneven-aged stands (Kucbel et al. 2012, Trotsiuk et al. 2012), which are mainly characterized by continuous, small-scale regeneration processes (Hobi et al. 2015a, Korpel 1995, Trotsiuk et al. 2012). However, the average age of the mature trees in Rožok was 180 - 230 years (Korpel, 1995), whereas the mean age of mature trees in Uholka was estimated to be 350 years (Trotsiuk et al. 2012). For details on the primary beech forests of Rožok and Uholka, the interested reader is referred to Kucbel et al. (2012) and Commarmot et al. (2005).

**Table 2.2:** *Degree of intervention for traditionally managed, alternatively managed beech forests, National Parks and primary forests.*

| Management type | Degree of intervention |
|---|---|
| Traditional | Yield-orientated with thinning cycles of 5 to 10 years and removal of up to 3 competitors per intervention; target-diameter harvest |
| Alternative | Compared to traditional forestry, lower thinning and harvesting frequencies and intensities + additional management goals |
| National Park | Unmanaged for 20 - 30 years |
| Primary forest | Unmanaged, no or minimal human impact |

## 2.2.2 Terrestrial laser scanning and sampling design

A Faro Focus 3D 120 Terrestrial Laser Scanner (Faro Technologies Inc., Lake Mary, USA) was used on all sites. The instruments provide data with a ranging error of ± 2 mm and a range noise between 0.3 and 2.2 mm depending on the reflectivity of the objects. All scans were conducted during dry weather conditions and with wind speeds below 10 m*s-1. The scanner was always aligned horizontally (< 5 °) using its internal electronic level. The scanner was mounted on a standard tripod at breast height (1.3 m), ensuring enough space for the scanner to operate (0.6 m of clearance in all directions during scanning). For a field of view of 300° (vertically) x 360° (horizontally), an angular resolution of 0.035° was used during scanning, resulting in ~ 44.4 million measurements per scan. During the scans, the scanner's standard filters (Clear Contour- and Clear Sky-filter) were applied.

In the region of Waake, we used 71 sample points from an inventory of tree regeneration, which were located on a systematic grid (100 m x 100 m) covering a total of 171.4 hectares. At each sample point of the inventory site, all juvenile trees (≥ 1.30 m height, < 7 cm DBH) located inside the circular 10 m² plot area were counted. We conducted one single scan between October and November 2017 at the center of each of 73 plots. Trees within the plots were still partially foliaged.

For all other sites (4 management types x 2 sites) we scanned at 30 sample points on a systematic grid (82 m x 82 m) in an area of about 20 hectares each (Figure 2.2). These scans were conducted between May and September 2017. A buffer-distance of 20 m to neighboring forest stands, forest edges and roads was respected during scanning to avoid edge effects. For all managed stands we recorded, which scans were located on skid-trails or away from skid-trails (Figure 2.3).

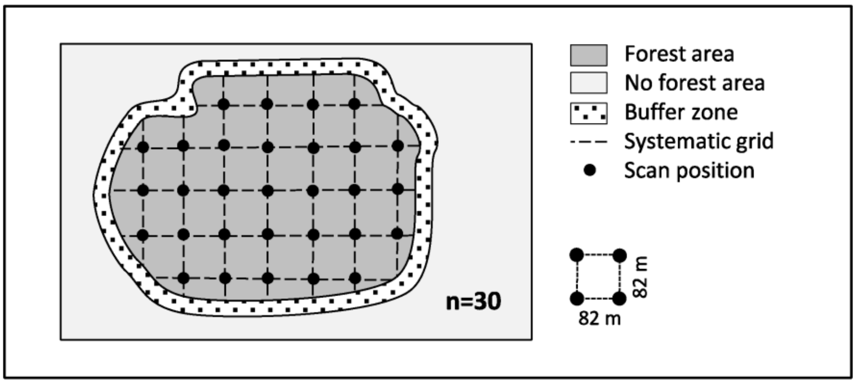

**Figure 2.2:** *Sampling design for an exemplary plot (Forest area = ~ 20 ha).*

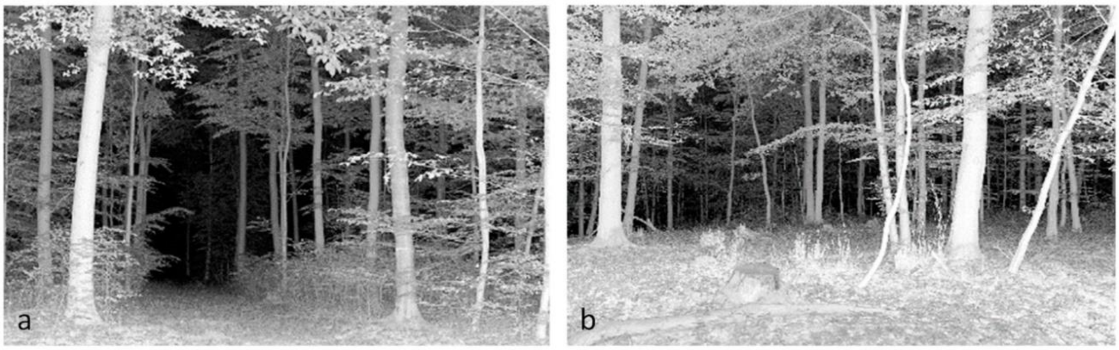

**Figure 2.3:** *Exemplary locations of measurements on skid-trails (a) and away from skid-trails (b).*

### 2.2.3 Construction of an understory complexity index

Each of the 30 single scans per plot generated a three-dimensional point cloud representing all detected hits in the vicinity of the scanner (120 m range) as xyz-coordinates. Each scan was imported to Faro Scene® Software (Faro Technologies Inc., Lake Marry, USA) and subsequently filtered using the software's standard filter (Dark Scan Points, Outlier) as recommended by the manufacturer. In a last step, the point cloud of each scan was exported as xyz-file (Cartesian coordinates).

Each point cloud in .xyz format was than imported to Mathematica® software (Wolfram Research, Champaign, USA) to compute the understory complexity index, from here on called UCI, based on a newly developed algorithm described in the following. First, in order to limit the extent of the analysis to the area in the proximity of the measurement site, we reduced the point clouds to hits within 15 m horizontal distance of the scanner. This should also reduce the effects of shadowing which increase with distance. Then, to normalize the spatial density of the raw data, we homogenized the point cloud resolution further by using voxels (volumetric pixel) with an edge length of 1 cm. Voxeled point clouds are also less prone to measurement errors, like e.g. beam divergence (Cifuentes et al. 2014, Van der Zande et al. 2006). To account for uneven terrain, we then calculated digital terrain models from each scan using the lowermost hits in a 10 cm xy-resolution of the initial point cloud, keeping the original 1 cm resolution for the z-values (height). Based on the lowermost hit at each ‘xy-cell’ we interpolated the digital terrain model to the 1 cm resolution of the voxeled point cloud. Using the ground-level height from the digital terrain model we then calculated normalized heights of each voxel by correcting it with the terrain level height at the xy-position of the voxel.

As the UCI was intended to describe the understory, we selected all voxels located between 0.8 and 1.8 m height (0.5 m below and above the scanner). We decided to use the lower boundary of 0.8 m for this ‘layer’ as we wanted to exclude larger herb and shrub layer vegetation, which is most dominant below 0.8 m. We also wanted to reduce influences of lying deadwood on the data. The upper boundary of 1.8 m was chosen to have as little crown material from overstory trees as possible affecting the data.

All points of the resulting horizontal ‘slice’ were projected onto a horizontal plane. To do so, the height values (z-value) were set to zero (vertical projection). Then the x- and y- coordinates were transformed into polar coordinates and sorted according to their azimuth angle using a resolution of 1° for further standardization. During this step, only the first hit in each direction was used for further processing. Then we reconverted the polar coordinates to Cartesian coordinates, which we finally used to generate a polygon connecting all points.

Based on the formula introduced by McGarigal and Marks (1995) the fractal dimension index (FRAC) for the polygon of each single-scan was calculated:

$$\mathrm{FRAC} = (2 * \ln(0.25 * \mathrm{P}))/\ln(\mathrm{A}) \tag{1}$$

*With ln being the natural logarithm to the base e, P being the perimeter and A the area of the polygon (see also Ehbrecht et al. 2017).*

FRAC is as a measure of shape complexity (cf. McGarigal and Marks 1995) and we used it to characterize the degree of complexity of the polygons, each representing hits within the horizontal cross-section through the stand, as visible from the specific location of the scanner. This FRAC-value is the final result of the processing chain of the UCI.

In its construction, the UCI makes use of a similar approach as the stand structural complexity index (SSCI) introduced by Ehbrecht et al. (2017). While the SSCI used multiple vertical cross-sections through a single scan point cloud (see Ehbrecht et al. 2017 for further detail on the method) we used a single horizontal cross-section to derive the UCI as explained above (Figure 2.4). We argue that due to its construction the UCI increases with increasing number and distributional irregularity of plant objects in the understory. We determined the UCI for all scans made in the eight study sites as well as on the site where we conducted the young tree inventory.

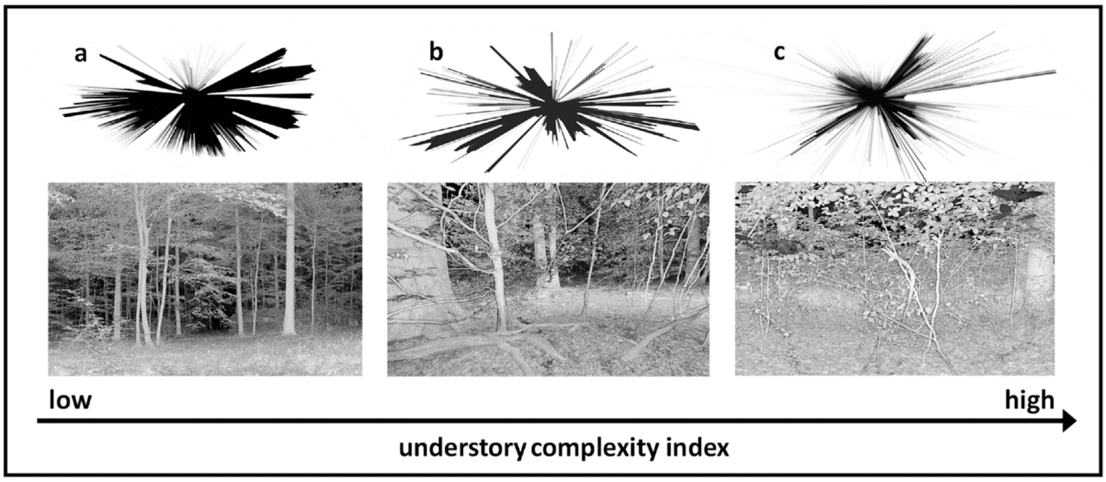

**Figure 2.4:** *Exemplary horizontal cross-sectional polygons and corresponding images of stands with a low (a), intermediate (b) and high UCI value (c).*

### 2.2.4 Statistics

The statistical analyses were conducted with the software environment R, version 3.3.3 (R Development Core Team 2017). To determine differences in understory complexity depending on the presence of tree regeneration, skid-trails and for different management types and study areas, we used the non-parametric Kruskal-Wallis test, because normal distribution and homogeneity of variance could not be assumed. As Post-hoc analysis, we used the Wilcoxon rank sum test with Bonferroni corrected p-value. Both tests were conducted at the alpha-level 0.05.

## 2.3 Results

### 2.3.1 Effect of tree regeneration and skid-trails on the UCI

The dataset of tree regeneration was used to verify the performance of the UCI with regard to the presence of understory regeneration. On scan locations with tree regeneration (Figure 2.5 a), the median UCI (2.55) is significant higher (a), than the median UCI (1.87) on scan locations without tree regeneration (b). In the managed beech stands (Figure 2.5 b), the median UCI (2.07) of scan locations on skid-trails (b) is significant lower than the UCI median value (2.47) of the samples taken off skid-trails (a).

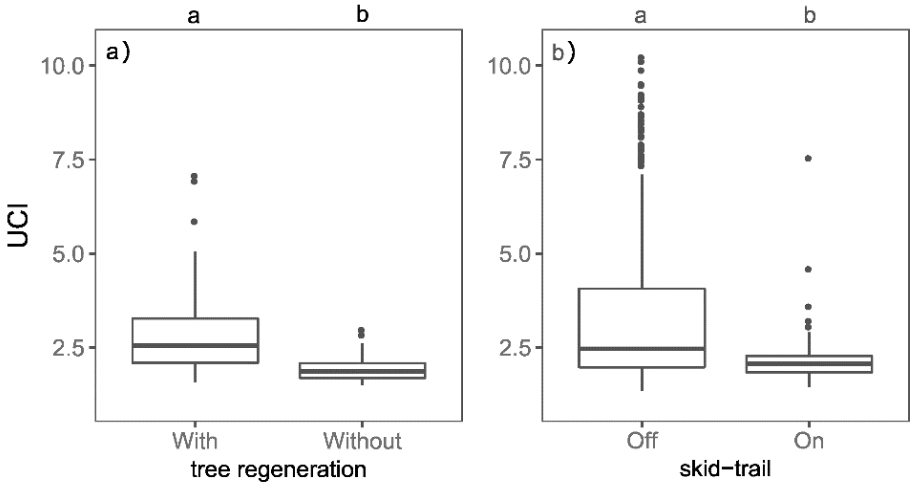

**Figure 2.5:** *a) Box- and Whisker plots of the understory complexity index (UCI) in dependence of the presence of tree regeneration in the inventory plots. The letters a and b (p < 0.05) indicate significant differences between samples with and without tree regeneration. Sample sizes were: with tree regeneration (n = 27), without tree regeneration (n = 44). b) Box- and Whisker plots of the understory complexity index (UCI) in dependence of the presence of skid-trails in the managed beech stands. The letters a and b (p < 0.05) indicate significant differences between samples, in which we measured on skid-trails and off skid-trails. Sample sizes were: on skid-trails (n = 54), off skid-trails (465).*

### 2.3.2 UCI of beech stands with regard to different management types

UCI differed for the investigated managed (Figure 2.6 a) and unmanaged (Figure 2.6 b) beech stands. With focus on the managed study sites (Figure 2.6 a), the median UCI values of the traditionally managed forest sites (Hann. Münden = 2.77, Reinhausen = 3.39) are significant higher (a) than the UCI median of the alternatively managed forest sites (Ebrach = 2.30, Lübeck = 2.12). Within the management type “Traditional” and “Alternative”, no significant in the median UCI could be found between the study locations, respectively differences (Hann. Münden = Reinhausen and Ebrach = Lübeck). Considering the different age classes of the managed forests (Table 2.3), we observed a decreasing trend of the median UCI from thickets with mature overstory trees (0 - 20) to immature timber stands (41 - 80) in traditionally managed forest sites and mature timber stands (81 - 120) in alternatively managed forest sites. Looking at the median UCI of the unmanaged study sites (Figure 2.6 b), there is an increasing trend from the National Parks Hainich (1.83) and Kellerwald (1.98) over the primary forests Rožok (2.22) to Uholka (3.56), even though only Uholka differed significantly (b) from the other unmanaged sites (Hainich = Kellerwald = Rožok < Uholka). Within the unmanaged forest sites, Uholka had the highest UCI.

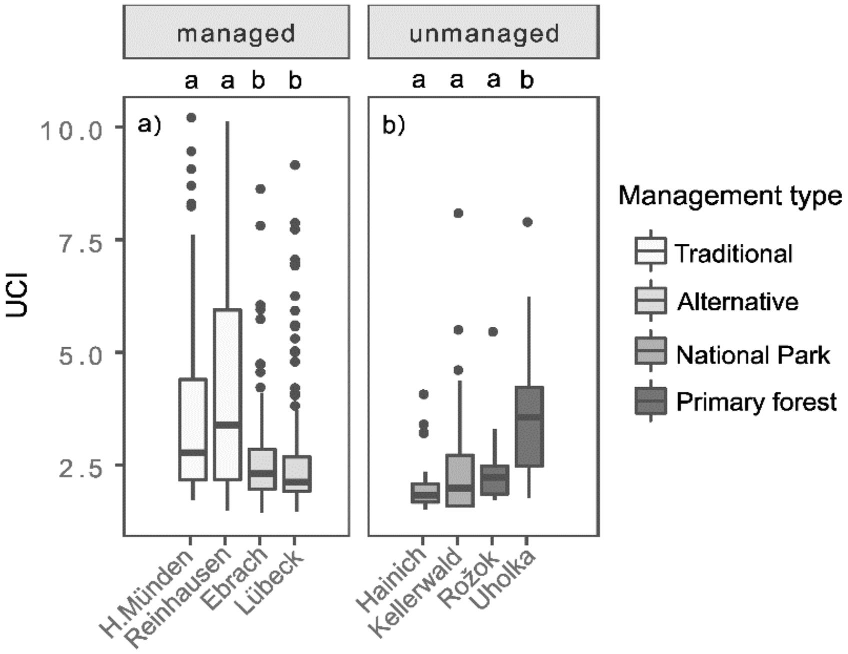

**Figure 2.6:** *a) Box-and-Whisker plots showing the understory complexity index (UCI) values for all managed study sites. The letters a and b indicate significant differences in the medians between the traditionally managed and the alternatively manaegd study sites at p < 0.05. Sample size for managed study sites were: Hann. Münden (n = 120), Reinhausen (n = 120), Ebrach (n = 120), Lübeck (n = 120). b) Box-and-Whisker plots showing the understory complexity index (UCI) values for all unmanaged study sites. The letters a and b indicate significant differences in the medians between the study sites of the national parks and the primary forests at p < 0.05. Sample size for unmanaged study sites were: Hainich (n = 30), Kellerwald (n = 30), Rožok (n = 30), Uholka (n = 30). Different colors represent the different management types.*

**Table 2.3:** *Descriptive statistics of understory complexity index (UCI) for each management type and age class. Different letters indicate significant differences between the age classes at p < 0.05.*

| Management type | Age class | mean | median | minimum | maximum | standard deviation | variance | coefficient of variation (%) |
|---|---|---|---|---|---|---|---|---|
| Traditional | all | 3.89 | 2.91 | 1.49 | 10.23 | 2.24 | 5.02 | 57.53 |
| | 0 - 20 | 6.05 | $6.47^{e}$ | 1.76 | 10.23 | 2.51 | 6.31 | 41.54 |
| | 21 - 40 | 4.06 | $3.93^{a}$ | 2.11 | 8.67 | 1.62 | 2.63 | 39.88 |
| | 41 - 80 | 2.25 | $2.10^{bc}$ | 1.67 | 7.64 | 0.77 | 0.59 | 34.17 |
| | 81 - 120 | 3.25 | $2.47^{ba}$ | 1.49 | 9.52 | 1.73 | 2.99 | 53.30 |
| Alternative | all | 2.67 | 2.22 | 1.44 | 9.18 | 1.35 | 1.82 | 50.40 |
| | 0 - 20 | 4.18 | $3.73^{a}$ | 1.91 | 9.18 | 1.85 | 3.42 | 44.25 |
| | 21 - 40 | 2.34 | $2.31^{b}$ | 1.78 | 3.41 | 0.33 | 0.11 | 14.16 |
| | 41 - 80 | 2.13 | $2.02^{cd}$ | 1.48 | 3.52 | 0.41 | 0.17 | 19.24 |
| | 81 - 120 | 2.05 | $1.84^{cd}$ | 1.44 | 6.10 | 0.74 | 0.55 | 36.07 |
| National Park | ~180 | 2.26 | $1.86^{cd}$ | 1.34 | 8.11 | 1.15 | 1.33 | 50.93 |
| Primary forest | all | 2.96 | 2.47 | 1.72 | 7.92 | 1.31 | 1.71 | 44.18 |
| | ~220 | 2.34 | $2.22^{bcd}$ | 1.72 | 5.48 | 0.73 | 0.53 | 31.19 |
| | ~350 | 3.60 | $3.56^{a}$ | 1.77 | 7.92 | 1.47 | 2.16 | 40.78 |

## 2.4 Discussion

### 2.4.1 Important drivers of understory complexity

Prior studies have shown a relationship between understory density or understory diversity and biodiversity (Berger and Puettmann 2000, Fuller 2001, Hinsley et al. 2007). This indicates the importance of the understory structure and its precise and objective description based on quantitative information. We introduced the UCI to allow for an objective, solely mathematically way of assessing understory complexity. When interpreting the results, one has to consider that in our study, the mean UCI of all plot-based single scans describe understory complexity on stand scale (α-level) only.

Our results showed that there is a significant higher UCI (a) on our inventory plots with tree regeneration compared to the inventory plots without regeneration (Figure 2.5 a). This finding indicates that regeneration is a strong driver of the UCI (hypothesis (i)). The UCI also proved to be sensitive to skid trails. There is a significant lower UCI of samples measured on skid-trails compared to samples measured off skid-trails (Figure 2.5 b). Skid-trails are usually cleared of regeneration and other vegetation and show therefore lower UCI values.

The observed importance of tree regeneration for the UCI is consistent with the findings of Ehbrecht et al. (2017), who already observed that the structural complexity of entire stands increased with overall tree density (trees with DBH > 7 cm). Consequently, an increase in the density of plants seems to have an increasing effect on both, overall stand and understory structural complexity. Despite the higher UCI values with the presence of regeneration, it is worth noting that our data also showed a certain variation in UCI values measured on skid-trails with no juvenile tree present (Fig. 2.5 b). So, as one would expect, tree regeneration is not the only driver of the UCI. In general, according to McElhinny et al. (2005), structural complexity “involves the interaction between a number of different attributes”. Therefore, it is likely that in addition to regeneration density the UCI is driven by other understory attributes, like understory species richness (Sullivan et al. 2001), shrub height (Berger and Puettmann 2000) or architecture, as well as the overall diameter distribution of the trees.

### 2.4.2 Effects of different management intensities on the UCI

Our study showed that UCI differed for different management types, so hypothesis (ii) could be confirmed. In Central Europe, thinning is an essential part of forest management (Daume and Robertson 2000) resulting in important structural differences during forest development. Accordingly, thinning and harvest frequencies, timing and intensities, varied in the investigated beech plots and are likely the main causes of the observed differences. In our study, highest median UCI was found in even-aged thickets with mature overstory trees (Table 2.3). To initiate this developmental phase about 30 % of the growing stock was harvested in one intervention (Schall et al. 2018) and remaining overstory trees have continuously been removed over the least 30 years.

In the stands between 21 and 40 years, the branch-free section of the stems become more dominant and the tree crowns, which generally increase the complexity due to the presence of tiny irregular structures such as leaves and twigs, were only partly located in the layer that was considered for the UCI. The effect of the absence of crown elements on the UCI can be seen in the immature timber stands (age class ’41 - 80’). Here, stems are mainly branchless in the height layer relevant to determine UCI (0.8 - 1.8 m).

During the last decades, single-tree selection (target diameter harvest) as regeneration form has gained increasing importance in traditional forest management (Schall et al. 2018). This approach ultimately results in small uneven-aged regeneration patches across the whole forest stand, as opposed to shelterwood systems aiming at regenerating an expanded area homogeneously and even-aged. In any case, the beech stands between 81 and 120 years considered here, are mainly being regenerated through single-tree selection, whereby many of these stands were not being regenerated thoroughly yet, which explains why the UCI mainly was still rather low in this age class.

Reduced thinning and harvesting frequencies and intensities, as conducted in beech stands referred to as alternative management type here, also resulted in significantly lower UCI values (Figure 2.6 a; Table 2.3). Presumably, this can also be explained by the higher canopy densities, resulting in a weaker development of the understory, due to the lack of light. The effects of varying canopy densities on the growth of saplings is well documented (Agestam et al. 2003, Ammer 1996, Modrý et al. 2004).

In the investigated unmanaged forest sites, we found an increasing trend in UCI from the National Parks to the primary forests, even if we could not find significant differences between the UCI median values of both National Parks and the primary forest Rožok (Figure 2.6 b). The comparatively low UCI values for the National Parks can be explained by the fact that management was ceased in these forests at the peak of what can be referred to as a “vault-like” forest structure (German: “Hallenwälder”), characterizing the optimal phase of beech forests, when canopy densities are high and trees still comparably vital. So, in this stage the beech stands of both National Parks were characterized by a single canopy layer and pronounced shade in the understory (canopy cover regularly higher than 90 %; see for example Vockenhuber et al. (2011)). In the year of measurement, this condition was still relatively pronounced at both study sites in the National Parks due to a low age-induced mortality and the absence of high severity disturbance events (Holzwarth et al. 2013). Therefore, a comprehensive regeneration layer could not develop yet (Berger and Puettmann 2000, Firm et al. 2009, Meyer et al. 2003), which was represented by the low UCI values found here.

Interestingly, our results showed significant differences between the median UCI values in both primary forests. Gaps from the senescence of single trees or small tree groups are the most prominent initiators of regeneration in primary European beech forests (Hobi et al. 2015a, Korpel 1995, Rugani et al. 2013, Trotsiuk et al. 2012). With an estimated mean age of ~ 220 years of the mature trees, the sampled stand in Rožok appeared to still be in the transition from optimum phase to senescence and decay phase (Stiers et al. 2018). The general absence of gaps was presumably also the reason here, why a pronounced understory was missing in the parts of the Rožok primary forest we sampled, again, resulting in a low median UCI. Compared to Rožok, the sampled stands in the primary forest Uholka were comprised of a higher average age of the overstory trees and showed a significantly higher UCI median (Table 2.3). Apparently, the decay phase was more advanced in these stands, characterized by a higher abundance of canopy gaps and corresponding understory development, compared to Rožok (Hobi et al. 2015b). As a result of several small and medium sized gaps (Diaci et al. 2012, Kucbel et al. 2010, Nagel et al. 2010) earlier studies detected large regeneration stocks (Nagel et al. 2013), which is also reflected in our higher UCI values. However, not only the density of natural regeneration, but also the heterogeneity of different heights of the saplings and young trees are crucial drivers of UCI. Due to continuous, small-scale disturbance events (Trotsiuk et al. 2012), in several European primary beech forests different age classes of natural regeneration coexist (Commarmot et al. 2005, Drößler 2006, Feldmann et al. 2018, Nagel et al. 2013). This resulted in heterogeneous understory structures as observed in virgin beech forests in Uholka

(Feldmann et al. 2018) and may also contribute to high complexity of the understory measured by the UCI.

Generally, understory development is not only a question of age but also of browsing pressure through ungulates like roe deer and red deer (Modrý et al. 2004). At least for Uholka, Hobi et al. (2015a) recorded low browsing damage. For Rožok no recent information is available. However, varying ungulate densities can hence also affect the understory structure and with this, the values of our UCI.

## 2.5 Conclusions

The aim of the presented study was to examine the possibilities to record and measure the complexity of understory forest structure objectively and efficiently using terrestrial laser scans. The suggested understory complexity index (UCI) has proven to yield plausible results distinguishing a variety of stand situation and allows quantitatively comparing these with one another, as presented here for beech forests.

Because of the fact that we found significant lower UCI values on scan locations without tree regeneration than on scan locations with tree regeneration, we conclude that the presence of young, established trees is a strong driver for the UCI. The significant lower UCI values measured on skid-trails, without vegetation around the scanner position, support this assumption.

The observed significant differences in the UCI between traditionally and alternatively managed stands and between the national parks and the primary forest Uholka show that the UCI is able to distinguish the understory structure of differently managed forest sites. In addition, the significant differences between the different age classes show that the UCI is capable of differentiating understory complexity of the investigated even-aged stands. Coevally, these results support empirical findings. In the investigated managed beech-dominated stands, the structural complexity of the understory is either large during the early phases of stand development (even-aged thickets with mature overstory trees, see age class 0 - 20) or when the senescence of trees has largely proceeded, as in the primary forest Uholka (age class ~350), initiating the understory development.

Analyzing the influence of additional understory-related attributes on UCI, such as the presence of large shrubs, effects of understory species richness or the diameter variability of the overstory trees may be an important future research task, next to the comparison of forests dominated by different tree species (e.g., conifer forest vs. deciduous forest; early successional vs. late successional forests).

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## 2.7 References

Agestam, E., Ekö, P.-M., Nilsson, U., Welander, N.T. (2003). The effects of shelterwood density and site preparation on natural regeneration of *Fagus sylvatica* in southern Sweden. Forest Ecology and Management, 176, 61-73. https://doi.org/10.1016/S0378-1127(02)00277-3.

Ammer, C. (1996). Konkurrenz um Licht - zur Entwicklung der Naturverjüngung im Bergmischwald. Forstliche Forschungsberichte München, 158, Frank, München.

Anderson, C.S., Meikle, D.B. (2006). Annual changes in structural complexity of understory vegetation and relative abundance of Peromyscus leucopus in fragmented habitats. Acta Theriologica, 51, 43-51. https://doi.org/10.1007/BF03192654.

Antos, J.A., 2009. Understory plants in temperate forests, in: Lund, H.G., Owens, J.N. (Eds.), Forests and Forest Plants. EOLSS Publishers/ UNESCO, Oxford, United Kingdom, pp. 262-279.

Augusto, L., Dupouey, J.-L., Ranger, J. (2003). Effects of tree species on understory vegetation and environmental conditions in temperate forests. Annals of Forest Science, 60, 823-831. https://doi.org/10.1051/forest:2003077.

# Chapter 2

Bauhus, J., Puettmann, K., Messier, C. (2009). Silviculture for old-growth attributes. Forest Ecology and Management, 258, 525-537. https://doi.org/10.1016/j.foreco.2009.01.053

Berger, A.L., Puettmann, K.J. (2000). Overstory composition and stand structure influence herbaceous plant diversity in the mixed aspen forest of Northern Minnesota. The American Midland Naturalist, 143, 111-125. https://doi.org/10.1674/0003-0031(2000)143[0111:OCASSI]2.0.CO;2.

Brang, P. (2005). Virgin forests as a knowledge source for central European silviculture: Reality or myth? Forest, Snow and Landscape Research, 79 (1-2), 19-32.

Brolly, G., Király, G., Czimber, K. (2013). Mapping Forest Regeneration from Terrestrial Laser Scans. Acta Silvatica et Lignaria Hungarica, 9, 135-146. https://doi.org/10.2478/aslh-2013-0011.

Cifuentes, R., Van der Zande, D., Farifteh, J., Salas, C., Coppin, P. (2014). Effects of voxel size and sampling setup on the estimation of forest canopy gap fraction from terrestrial laser scanning data. Agricultural and Forest Meteorology, 194, 230-240. https://doi.org/10.1016/j.agrformet.2014.04.013.

Commarmot, B., Bachofen, H., Bundziak, Y., Bürgi, A., Shparyk, Y., Sukhariuk, D., Viter, R., Zingg, A. (2005). Structures of virgin and managed beech forests in Uholka (Ukraine) and Sihlwald (Switzerland): a comparative study. Forest, Snow and Landscape Research, 79 (1-2),45-56.

Daume, S., Robertson, D. (2000). A heuristic approach to modelling thinnings. Silva Fennica, 34 (3). https://doi.org/10.14214/sf.628.

Diaci, J., Adamic, T., Rozman, A. (2012). Gap recruitment and partitioning in an old-growth beech forest of the Dinaric Mountains: Influences of light regime, herb competition and browsing. Forest Ecology and Management, 285, 20-28. https://doi.org/10.1016/j.foreco.2012.08.010

Drößler, L. (2006). Struktur und Dynamik von zwei Buchenurwäldern in der Slowakei. Dissertation. Göttingen.

Ehbrecht, M., Schall, P., Ammer, C., Seidel, D. (2017). Quantifying stand structural complexity and its relationship with forest management, tree species diversity and microclimate. Agricultural and Forest Meteorology, 242, 1-9. https://doi.org/10.1016/j.agrformet.2017.04.012.

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.

Forest Ecology and Management, 415-416, 38-46. https://doi.org/10.1016/j.foreco.2018.02.022.

Firm, D., Nagel, T.A., Diaci, J. (2009). Disturbance history and dynamics of an old-growth mixed species mountain forest in the Slovenian Alps. Forest Ecology and Management, 257, 1893-1901. https://doi.org/10.1016/j.foreco.2008.09.034.

Fuller, R.J. (2001). Responses of woodland birds to increasing numbers of deer: a review of evidence and mechanisms. Forestry, 74, 289-298. https://doi.org/10.1093/forestry/74.3.289.

Gustafsson, L., Baker, S.C., Bauhus, J., Beese, W.J., Brodie, A., Kouki, J., (…), Franklin, J.F. (2012). Retention forestry to maintain multifunctional forests: A world perspective. BioScience, 62, 633-645. https://doi.org/10.1525/bio.2012.62.7.6.

Helms, J.A. (1998). The dictionary of forestry. Society of American Foresters, Bethesda, MD.

Hinsley, S., Hill, R., Fuller, R., Bellamy, P., Rothery, P. (2009). Bird species distributions across woodland canopy structure gradients. Community Ecology, 10, 99-110. https://doi.org/10.1556/ComEc.10.2009.1.12.

Hinsley, S.A., Carpenter, J.E., Broughton, R.K., Bellamy, P.E., Rothery, P., Amar, A., Hewson, C.M., Gosler, A.G. (2007). Habitat selection by Marsh Tits Poecile palustris in the UK: Habitat selection by Marsh Tits. Ibis, 149, 224-233. https://doi.org/10.1111/j.1474-919X.2007.00691.x.

Hobi, M. L., Commarmot, B., Bugmann, H. (2015a). Pattern and process in the largest primeval beech forest of Europe (Ukrainian Carpathians). Journal of Vegetation Science, 26, 323-336. https://doi.org/10.1111/jvs.12234.

Hobi, M.L., Ginzler, C., Commarmot, B., Bugmann, H. (2015b). Gap pattern of the largest primeval beech forest of Europe revealed by remote sensing. Ecosphere, 6(5), 76. https://doi.org/10.1890/ES14-00390.1.

Holzwarth, F., Kahl, A., Bauhus, J., Wirth, C. (2013). Many ways to die - partitioning tree mortality dynamics in a near-natural mixed deciduous forest. Journal of Ecology, 101, 220-230. https://doi.org/10.1111/1365-2745.12015.

Kimmins, J.P., 2004. Forest ecology: a foundation for sustainable forest management and environmental ethics in forestry, Prentice Hall, Upper Saddle River, N.J.

Korpel, Š., 1995. Die Urwälder der Westkarpaten: 39 Tabellen. Gustav Fischer, Stuttgart.

Kottek, M., Grieser, J., Beck, C., Rudolf, B., Rubel, F. (2006). World Map of the Köppen-Geiger climate classification updated. Meteorologische Zeitschrift, 15, 259-263. https://doi.org/10.1127/0941-2948/2006/0130.

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

Kucbel, S., Saniga, M., Jaloviar, P., Vencurik, J. (2012). Stand structure and temporal variability in old-growth beech-dominated forests of the northwestern Carpathians: A 40-years perspective. Forest Ecology and Management, 264, 125-133. https://doi.org/10.1016/j.foreco.2011.10.011.

McElhinny, C., Gibbons, P., Brack, C., Bauhus, J. (2005). Forest and woodland stand structural complexity: Its definition and measurement. Forest Ecology and Management, 218, 1-24. https://doi.org/10.1016/j.foreco.2005.08.034.

McGarigal, K., Marks, B.J. (1995). Spatial pattern analysis program for quantifying landscape structure. General Technical Report, PNW-GTR-351, US Department of Agriculture, Forest Service, Pacific Northwest Research Station, 1-122.

Meyer, P., Tabaku, V., v. Lupke, B. (2003). Die Struktur albanischer Rotbuchen-Urwälder - Ableitungen für eine naturnahe Buchenwirtschaft. Structural Characteristics of Albanian Beech (*Fagus* sylvatica L.) Virgin Forests - Deductions for Semi-Natural Forestry. Forstwissenschaftliches Centralblatt, 122, 47-58. https://doi.org/10.1046/j.1439-0337.2003.02041.x.

Modrý, M., Hubený, D., Rejšek, K. (2004). Differential response of naturally regenerated European shade tolerant tree species to soil type and light availability. Forest Ecology and Management, 188, 185-195. https://doi.org/10.1016/j.foreco.2003.07.029.

Nagel, T., Zenner, E., Brang, P. (2013). Research in old-growth forests and forest reserves: implications for integrated forest management. *In* Integrative Approaches as an Opportunity for the Conservation of Forest Biodiversity. European Forest Institute, Joensuu, pp. 44-50.

Nagel, T.A., Svoboda, M., Rugani, T., Diaci, J. (2010). Gap regeneration and replacement patterns in an old-growth *Fagus-Abies* forest of Bosnia-Herzegovina. Plant Ecology, 208, 307-318. https://doi.org/10.1007/s11258-009-9707-z.

NLF - Niedersächsische Landesforsten (2018): Entscheidungshilfen zur Behandlung und Entwicklung von Buchenbeständen. (accessed 05.06.20). https://www.nw-fva.de/fileadmin/user_upload/Verwaltung/Publikationen/Merkblaetter/Bu_Nds_Entscheidungshilfe_zur_Behandlung_und_Entwicklung_von_Buchenbestaenden.pdf.

Palace, M., Sullivan, F.B., Ducey, M., Herrick, C. (2016). Estimating Tropical Forest Structure Using a Terrestrial Lidar. PLoS ONE, 11, e0154115. https://doi.org/10.1371/journal.pone.0154115.

Rugani, T., Diaci, J., Hladnik, D. (2013). Gap Dynamics and Structure of Two Old-Growth Beech Forest Remnants in Slovenia. PLoS ONE, 8, e52641. https://doi.org/10.1371/journal.pone.0052641.

Sabatini, F.M., Burrascano, S., Keeton, W.S., Levers, C., Lindner, M., Pötzschner, F., (…), Kuemmerle, T. (2018). Where are Europe’s last primary forests? Diversity and Distributions, 24, 1426-1439. https://doi.org/10.1111/ddi.12778.

Schall, P., Gossner, M.M., Heinrichs, S., Fischer, M., Boch, S., Prati, D., (…), Ammer, C. (2018). The impact of even-aged and uneven-aged forest management on regional biodiversity of multiple taxa in European beech forests. Journal of Applied Ecology, 55, 267-278. https://doi.org/10.1111/1365-2664.12950.

Seidel, D., Ehbrecht, M., Puettmann, K. (2016). Assessing different components of three-dimensional forest structure with single-scan terrestrial laser scanning: A case study. Forest Ecology and Management, 381, 196-208. https://doi.org/10.1016/j.foreco.2016.09.036.

Spies, T.A., Franklin, J.F. (1991). The structure of natural young, mature, and old-growth Douglas-fir forests in Oregon and Washington. *In* Wildlife and Vegetation of Unmanaged Douglas-Fir Forests. USDA Forest Service, Portland.

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. Forest Ecology and Management, 430, 357-365. https://doi.org/10.1016/j.foreco.2018.08.039.

Sullivan, T.P., Sullivan, D.S., Lindgren, P.M.F. (2001). Stand structure and small mammals in young lodgepole pine forest: 10-year result after thinning. Ecological Applications, 11, 1151-1173. https://doi.org/10.1890/1051-0761(2001)011[1151:SSASMI]2.0.CO;2.

Thomas, S.C., Halpern, C.B., Falk, D.A., Liguori, D.A., Austin, K.A (1999). Plant diversity in managed forests: Understory response to thinning and fertilization. Ecological Applications, 9, 864-879. https://doi.org/10.1890/10510761(1999)009[0864:PDIMFU]2.0.CO;2.

Trotsiuk, V., Hobi, M.L., Commarmot, B. (2012). Age structure and disturbance dynamics of the relic virgin beech forest Uholka (Ukrainian Carpathians). Forest Ecology and Management, 265, 181-190. https://doi.org/10.1016/j.foreco.2011.10.042.

Van der Zande, D., Hoet, W., Jonckheere, I., van Aardt, J., Coppin, P. (2006). Influence of measurement set-up of ground-based LiDAR for derivation of tree structure. Agricultural and Forest Meteorology, 141, 147-160.https://doi.org/10.1016/j.agrformet.2006.09.007.

Vockenhuber, E.A., Scherber, C., Langenbruch, C., Meißner, M., Seidel, D., Tscharntke, T. (2011). Tree diversity and environmental context predict herb species richness and cover in Germany’s largest connected deciduous forest. Perspectives in Plant Ecology, Evolution and Systematics, 13, 111-119. https://doi.org/10.1016/j.ppees.2011.02.004.

# Chapter 3

## Chapter 3 Spatial patterns of structural complexity in differently managed and unmanaged beech-dominated forests in Central Europe

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### Abstract

One of the main goals of modern silviculture is to emulate the structural complexity of old-growth forests. In this context, it is of advantage to identify a target state of structural complexity at the stand-level and to analyze the spatial characteristics that led to the desired complexity of forest structures in primary forest references. In this study, we used 3D forest scenes captured by terrestrial laser scanning (TLS) to identify spatial patterns of structural complexity of differently managed and unmanaged European forests dominated by beech (*Fagus sylvatica* L.). We scanned in managed even-aged and uneven-aged stands, as well as in formerly managed forests (National Parks) and primary forests. For three different forest strata, representing the understory, the midstory, and the overstory of a forest stand, we determined the structural complexity mathematically using fractal analysis. Beyond that, we analyzed the density, as well as the horizontal and vertical distribution of plant material. For all three forest strata, we observed differences in structural complexity between the different forest types. Within the lower and middle strata, the investigated primary forests showed a random to regular distribution of plant material, as well as a complex understory structure as a result of pronounced natural decay. Compared to the primary forests, the managed uneven-aged stands showed quite similar spatial patterns of distribution of plant material, but on average a higher space occupation in the lower and middle forest stratum. Our results suggest that single tree or group selection cutting is a useful management tool to imitate old-growth structures of undisturbed beech-dominated forests.

# Chapter 3

**Keywords:** stratification; canopy layer; box dimension; *Fagus sylvatica* L.; primary forest; fractal analysis; terrestrial laser scanning; management gradient; Carpathian Biosphere Reserve

## 3.1 Introduction

Creating complex forest structures is one of the main objectives of modern forest management and is becoming increasingly popular, especially in Central Europe and North America (Brang et al. 2014, Messier et al. 2013, Puettmann et al. 2009, Schütz 2002). This management goal is of interest, because structural complexity can be positively associated with several ecosystem services and functions (Gadow et al. 2012, Kint et al. 2004), including biodiversity (Brang 2005, Gustafsson et al. 2012, Pommerening 2002), forest productivity (Glatthorn et al. 2018, Gough et al. 2019, Messier et al. 2013, Pretzsch et al. 2015), nutrient cycling (Ellison et al. 2005), and habitat heterogeneity (Franklin and Van Pelt 2004). A complex forest structure is also expected to support ecosystem stability, resilience, and adaptability towards changes in environmental conditions (Ehbrecht et al. 2019, Parker et al. 2004).

The few remaining primary forests that can be found in Central Europe are characterized by what is referred to as old-growth forest structure (Sabatini et al. 2018). They combine structural attributes, such as dense natural regeneration, the presence of secondary crowns, and a high variation of crown structure that all result in complex spatial arrangements within the forest (Bauhus et al. 2009, Commarmot et al. 2005, Kucbel et al. 2010, Trotsiuk et al. 2012). Considering the vertical and horizontal dimension, structural complexity manifests itself in multiple canopy layers and an irregular horizontal distribution of tree components, consisting of irregularly distributed canopy gaps and dense understory vegetation patches (Franklin and Van Pelt 2004).

So far, in order to promote structural complexity, the management focus is more on uneven-aged, multi-layered forest stands, instead of even-aged, single-layered stands. In terms of enhancing the horizontal structure, the creation of differently sized and distributed canopy gaps proved to be an efficient management approach (Schütz 2002). It is yet largely unknown whether these measures result in structures that are also typical for primary forests. In order to imitate complex structures of primary forests, we first need to make their characteristic structures measurable and reproducible. Despite approaches to quantify complexity without 3D measurements, such as the structural complexity index (SCI) (Zenner and Hibbs 2000), the mean information gain index (MIG) (Witté et al. 2013), or the arc-chord ratio (ACR) rugosity index (Du Preez 2015), terrestrial laser scanning (TLS) has shown to be an efficient and effective method allowing for an accurate and precise assessment of three-dimensional forest structure (Atkins et al. 2018, Ehbrecht et al. 2016, Seidel et al. 2016). In combination with methods for quantifying complexity, such as fractal analysis (Mandelbrot 1975), the structural complexity of forests can be assessed mathematically. The approach can also be utilized to quantify the complexity of tree foliage (Boudon et al. 2006), tree crowns (Dutilleul et al. 2015, Jonckheere et al. 2006, Zhu et al. 2014), entire tree architecture (Dorji et al. 2019, Seidel, 2018) and stand structure (Seidel et al. 2019, Zemp et al. 2019) by using three-dimensional (3D) point clouds derived from TLS. Several studies used this approach to characterize and compare the structural complexity of European temperate forests along a management gradient (Ehbrecht et al. 2017, Stiers et al. 2018, Willim et al. 2019). Ehbrecht et al. (2017) showed that forests with a high stand structural complexity are characterized by a high tree size differentiation, high diversity of tree diameters, and random patterns of tree spacing. Stiers et al. (2018) found a significantly higher stand structural complexity in primary European beech forests than in formerly managed (20 - 30 years of no management) and presently managed beech stands.

While we are now able to quantify the structural complexity of forests, we still lack a clear picture of the spatial patterns of structural complexity at the stand-level (Camarretta et al. 2019). After identifying the target structural complexity at the stand-level, e.g., by taking the structural complexity of an old-growth forest as a reference, it is also crucial to identify the structural characteristics of such a reference that resulted in a given complexity. This is because many different configurations of plant material in a forest may result in similar levels of structural complexity, but the forests may differ largely in where the key strata or zones of complexity can be found, e.g., complex understory versus complex overstory.

Therefore, it is important to not only quantify the level of stand structural complexity, but also to study the spatial arrangement of plant material that leads to a given structural complexity. From a management perspective, it is also important to know how structural complexity and its characteristics differ among differently managed forests, formerly managed forests, and primary forests. Therefore, the primary aim of this paper is to contribute to the understanding of spatial patterns of structural complexity in such forests. To do so, structural complexity needs to be quantified at the stand-level but also for smaller entities. We calculated the box dimension ($D_b$) as an estimate of the fractal dimension for three different forest strata of 3D forest scenes, representing the under-, mid- and overstory of a forest stand. We analyzed the density, as well as the horizontal and vertical distribution of plant material, in order to examine spatial patterns of structural complexity. Specifically, the following research questions were addressed:

(i) Do differently managed beech-dominated forests differ in the complexity of their lower, middle, and upper forest stratum?

(ii) Are differences in the structural complexity of different forest strata characterized by differences in the density and distribution of plant material?

## 3.2 Materials and methods

### 3.2.1 Study sites

We studied different European beech (*Fagus sylvatica* L.) forest sites in Germany, Slovakia, and the Ukraine. The location of all study sites can be found in Figure 3.1.

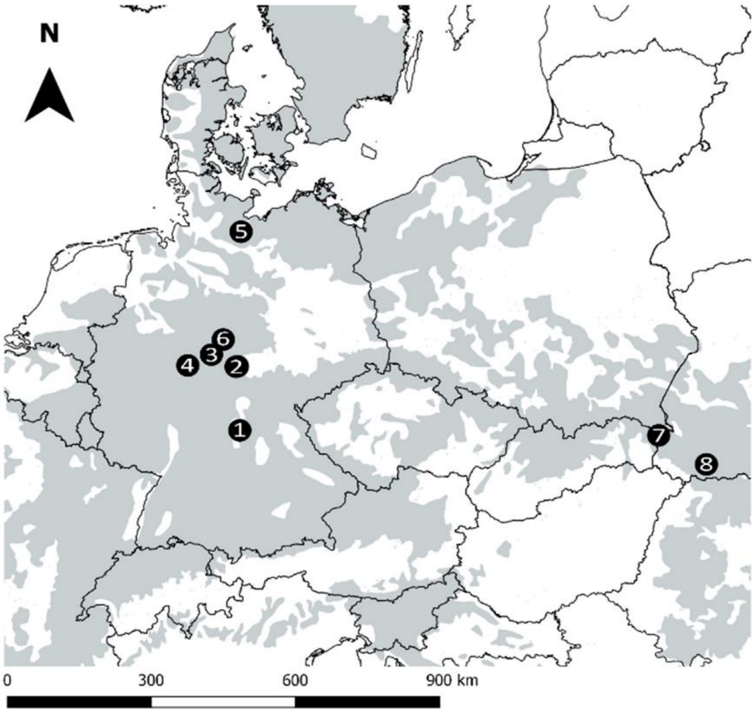

**Figure 3.1:** *Natural distribution area of Fagus sylvatica L. in Central Europe (gray area) and location of the study sites. Each number represents one study site (1 = Ebrach, 2 = Hainich-Dün, 3 = Hann. Münden, 4 = Kellerwald, 5 = Lübeck, 6 = Reinhausen, 7 = Rožok and 8 = Uholka. Source of species distribution map: http://www.euforgen.org. (modified after Willim et al. 2020).*

All study sites were pure beech stands or beech-dominated stands with a minimum share of beech of 66 % in basal area. The managed stands are in the developmental phase of mature timber and at least 81 years of age (see Table 3.1). We tried to figure out the documented ages of the managed and unmanaged stands. However, this was only possible in forest stands of the Biodiversity Exploratories, as well as for the managed stands in Ebrach, Hann. Münden, Lübeck and Reinhausen, where current data was available. In the formerly managed National Parks, we had information about the stand age at that time when management was ceased, e.g., 30 years ago. Therefore, it was possible to calculate the age during data collection. Only in the primary forests, we had to rely on estimates from other studies.

**Table 3.1:** *Information on the basic environmental conditions of the study sites (MAT = mean annual temperature; MAP = mean annual precipitation). For each study site, we chose four study plots. For the Hainich-Dün region, we considered additional study plots (*), which were part of the Biodiversity Exploratories. Number (No.) of study plots for each forest type were: even-aged (EA): n = 12, uneven-aged (UEA): n = 8, formerly managed (FM): n = 11 and primary forest (PF): n = 8.*

| Location | Study Sites | MAT (°C) | MAP (mm) | Elevation (m a.s.l.) | Forest Type | Age (Years) | No. of Plots |
|---|---|---|---|---|---|---|---|
| Germany | Ebrach | 7 - 8 | 850 | 320 - 480 | UEA | 111 | 4 |
| | Hainich | 6.5 - 8 | 500 - 800 | 285 - 550 | UEA<br>FM | 160 - 186<br>150 - 182 | 4 *<br>4 + 3 * |
| | Hann. Münden | 6.5 - 7.5 | 750-1050 | 270 - 410 | EA | 81 | 4 |
| | Kellerwald | 6 - 8 | 600 - 800 | 540 - 635 | FM | 184 | 4 |
| | Lübeck | 8 - 8.5 | 625 - 725 | 40 - 90 | EA | 131 | 4 |
| | Reinhausen | 8 | 740 | 190 - 310 | EA | 98 | 4 |
| Slovakia | Rožok | 6 - 7 | 780 | 580 - 745 | PF | ~220 | 4 |
| Ukraine | Uholka | 7 | 1407 | 700 - 840 | PF | ~350 | 4 |

All our study sites have temperate climatic conditions after the Köppen Geiger classification (Kottek et al. 2006). Annual mean temperature varies between 6.0 and 8.0 °C. Annual precipitation ranges from 500 to 1407 mm. Except for Lübeck (40 - 90 m above sea level; abbreviation: a.s.l.), all study sites in Germany are located in the lower mountain ranges (190 - 1000 m a.s.l.). The study sites in the Western Carpathians are located highest, with 580 - 840 m (a.s.l). A detailed description of the environmental conditions of the study sites, as well as information about the number of plots per study sites are given in Table 3.1.

The chosen forest sites represent different forest types in Central Europe. They consist of even-aged, uneven-aged, formerly managed, and unmanaged beech stands. Even-aged managed stands are located in the forest districts of Hannoversch Münden and Reinhausen (Lower Saxony State Forest). In these stands, management is based on the "Guidelines of beech forest management in Lower Saxony, Germany" (NLF). This forest type is mainly characterized by a rather yield-orientated management. It is based on a thinning cycle of about five to 10 years. Around an age of 120 to 140 years, trees that have reached a certain target diameter are harvested (Stiers et al. 2019). Further, even-aged stands were selected in the forest districts of Lübeck (Northern German Lowlands). These stands are characterized by reduced thinning and harvesting frequencies and intensities, as well as by a high growing stock. Formerly managed beech stands were selected in the National Parks "Hainich" and "Kellerwald-Edersee". Both study sites underwent no management interventions for at least two to three decades (Willim et al. 2019). In addition to the above-mentioned stands, we considered uneven-aged and formerly managed stands in the Hainich-Dün region (marked by a *, Table 3.1) that are part of the Biodiversity-Exploratories (www.biodiversity-exploratories.de), which is a long-term research project that aims at investigating the impacts of management on biodiversity and ecosystem processes (Fischer et al. 2010). Further uneven-aged stands were recorded in Ebrach (Bavaria). The management of the uneven-aged stands is characterized by single-tree harvests of high frequency but low intensity (Bartsch et al. 2020). Interventions are mainly focused on the overstory trees (≥ 50 cm in diameter at breast height; see Schall et al.(2018a)). The two investigated primary forests of the Carpathian Mountains (Sabatini et al. 2018) showed no signs of silvicultural disturbance (Brang 2005). Rožok is a National Nature Reserve (NNR) in the Slovakian Republic near the Ukraine Border. The second primary forest Uholka is located in Uholka-ShyrokyLuh (Ukraine), which is part of the Carpathian Biosphere Reserve (CBR). In Rožok, the average age of mature trees was 180 to 230 years (Korpel, 1995). We assumed a conservative mean age of about 220 years for Rožok (see Table 3.1). The mean age of dominant trees in Uholka was estimated to be 350 years (Trotsiuk et al. 2012). For details on the primary beech forests of Rožok and Uholka, the interested reader is referred to Kucbel et al. (2010) and Commarmot et al. (2005).

### 3.2.2 Terrestrial laser scanning and sampling design

We used terrestrial laser scanning to measure the three-dimensional structure of each stand. In order to collect data of forest stands in leaf-on condition, measurements were done in the vegetation period (May to August), with all species being fully foliaged. Within the framework of the Biodiversity Exploratories, scans were conducted in 2014. All other scans were taken in 2017 and 2018. All scans were conducted at wind speeds below 10 m × $s^{-1}$ and during dry weather conditions.

Before scanning in the field, four sample plots were randomly placed in an area of about 20 hectares within each forest site using QGIS software (Quantum GIS Development Team 2017). Additionally, we selected a subset of seven sample plots from the repository of the Biodiversity Exploratories. Within the Biodiversity Exploratory project, an area of 45 × 45 m was considered for data acquisition. For the data collection in 2017/2018, we scanned an area of 50 × 50 m. The scans were based on the multi-scan approach (Juchheim et al. 2017). Before scanning, chessboard targets were distributed in order to enable a spatial co-registration. To cover the vegetation in detail and from multiple perspectives, 30 - 80 scans were systematically distributed across the plot. However, the exact number and position of the scans depended on the understory density and heterogeneity. We conducted more scans in plots with dense understory compared to plots with lower understory density. Nevertheless, even with a large number of scans per plot, there is still the possibility that occlusion affected the measured spatial complexity, resulting in an underestimation of the real complexity. However, Ehbrecht et al. (2016) showed that with more than 18 scans per plot (40 × 40 m), a threshold that we always met, occlusion cannot be significantly reduced anymore.

The scans were performed with a Faro Focus 3D laser scanner (Faro Technologies Inc., Lake Mary, FL, USA). In the year 2018, additionally, the Faro Focus M70 (Faro Technologies Inc) was used, depending on which model was available. Before scanning, it was ensured that both scanners had the same scan settings and used identical standard filters during the scan process (Clear Contour- and Clear Sky-filter).

In the field, the scanners were placed on a tripod at breast height (1.30 m above ground). Both instruments covered a field of view of 300° (vertically) × 360° (horizontally). During scanning, an angular resolution of 0.035° was used, resulting in a resolution of 10,240 points per 360°.

All scans were imported into the Faro Scene Software (Faro Technologies Inc). Dark scan points (with low reflectance) and erroneous points (e.g., split beams) were eliminated using the software's standard filters. Then, all individual scans conducted within one plot were co-registered, so that at the end, one three-dimensional (3D) point cloud is representing one plot.

### 3.2.3 Data processing

Then, raw point clouds were imported into Mathematica® software (Wolfram Research, Champaign, IL, USA). In order to normalize the spatial density of the point clouds, they were voxelized based on 20 × 20 × 20 cm voxels (volumetric pixels). We decided to choose this voxel size for several reasons. If the voxel size is chosen too small, it would be possible that occlusion effects result in artificial gaps in the voxel model. Additionally, tree trunks may appear as hollow cylinders instead of solid objects, which would lead to an underestimation of space filling by plant material (Seidel et al. 2013). While larger voxel sizes have proven to be a solid method to compensate occlusion, they can lead to an overestimation of the effective space filling, because smaller gaps are missed (Ehbrecht et al. 2016). By using larger voxel sizes, there is also the risk that structural heterogeneity cannot be recorded in detail. Since we know that a voxel size of 20 cm side length is a trustful size in order to minimize occlusion effects and preserve detailed information on forest structure at the same time, we decided on this voxel length (Béland et al. 2014, Ehbrecht et al. 2016).

Filled voxels contained at least one laser hit, whereas empty voxels had no laser hits. To exclude uneven terrain, we corrected the topography based on a digital terrain model calculated from the voxelized point cloud using the lowermost hits. Then, the ground-level height from the digital terrain model was used to calculate normalized heights for each voxel. To do so, each voxel was corrected with the terrain level height at the voxel's xy-position. Out of the voxelized, slope-corrected point clouds, we extracted a predefined extent (40 m × 40 m × stand height). In order to reduce the influences of terrain points, shrubs, grasses, and dead wood on the data, we eliminated all voxels below 1 m stand height. The stand height of each individual 3D forest stand was defined as the uppermost height stratum, in which at least one voxel was present,

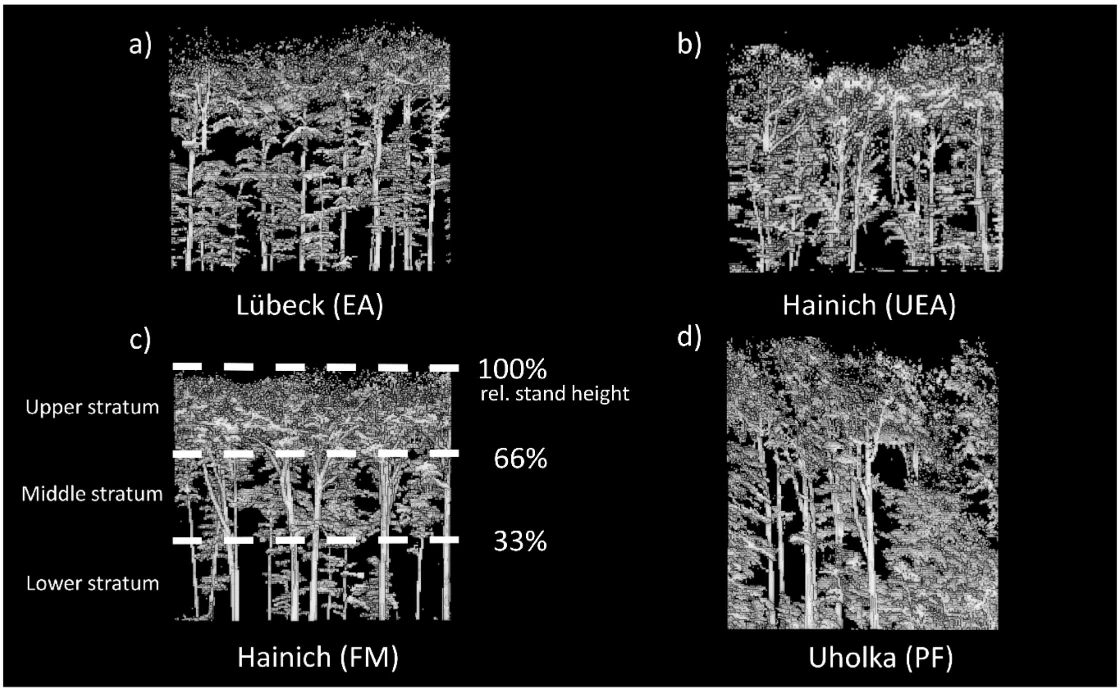

**Figure 3.2:** *Side views of transects gained of voxelized (20 × 20 × 20 cm) 3D forest stands representing different forest types: An even-aged (EA) forest stand in Lübeck (**a**), a managed uneven-aged (UEA) and formerly managed (FM) forest stand in Hainich (**b**,**c**) and an unmanaged primary forest (PF) in Uholka (**d**). The relative stand height (100 %) was defined as the uppermost stand stratum in which at least one voxel could be found. The three main forest strata were lower forest stratum (≤33 % of the relative stand height), middle forest stratum (34 - 66 % of the relative stand height), and the upper forest stratum (67 - 100 % of relative stand height).*

and it was considered as 100 % (relative heights). The absolute stand height was defined as the z-value of the highest voxel in the uppermost layer minus 1 m. To quantify the complexity of the forest structures, we used the box dimension ($D_b$) that is used to describe the fractal dimension of objects (Mandelbrot, 1975). $D_b$ was calculated as the slope of the fitted straight line through a scatterplot of log (n) over log (1/r). In this context, log () is the natural logarithm and n is the number of boxes with the size r needed to enclose all points in a 3D point cloud. Details on this method when applied to trees or forest stands can be found in Seidel et al. (2018) and Sarkar and Chaudhuri (1994).

We calculated the $D_b$ for three horizontal forest strata of each 3D point cloud. Based on the classification of the International Union of Forest Research Organizations (IUFRO), we defined the lower stratum as the lowest 33 %, the middle stratum between 34 % and 66 %, and the upper stratum from 67 % to 100 % of our predefined stand height (Clark and Evans 1954, Stinglwagner et al. 2016) (see Figure 3.2).

To determine the density and spatial patterns of the vegetation, we imported the voxelized, slope-corrected 3D point clouds into the software R (version 3.4.2; R Development Core Team, 2017 Vienna, Austria). We divided each point cloud into 20 horizontal strata, each 5 % of the total stand height in thickness. We used the relative space filling rSPf [%] as a measure of density and calculated it for each stratum. The calculation of the rSPf [%] was based on the method described in Juchheim et al. (2017). rSPf [%] describes the percentage of space that is filled with voxels that contained vegetation hits. To calculate rSPf [%], the volume of all filled voxels within a stratum was determined and set in relation to the stratum's total volume.

To describe spatial patterns of the vegetation, we calculated the Clark-Evans index (CE index) of aggregation (Clark and Evans 1954) using the package ('spatstat'). Before the calculation, we projected the 20 horizontal strata onto a plane by setting the height value (z-value) of each voxel to zero (vertical projection). Subsequently, we extracted duplicate voxels. We used the index as a measure of horizontal point patterns of individual voxels in the area of the previously extracted horizontal strata. It is based on the distance from a voxel to its nearest neighbor and defined as:

$$R = \bar{r}A / \bar{r}E \tag{1}$$

With $\bar{r}A$ being the mean observed distance from randomly selected voxel to their nearest neighbors and $\bar{r}E$ being the expected mean distance between nearest neighbors, if a random distribution (Poisson distribution) is assumed. The ratio $R$ expresses the degree to which $\bar{r}A$ approaches or departs from $\bar{r}A$. R values range between 0 (maximum clumping) and 2.1491 (strictly regular, hexagonal pattern). Values equal to 1 indicate random voxel patterns. Based on this range, one can coarsely distinguish between clustered ($R$ < 1) and more regular ($R$ > 1) voxel patterns. To avoid edge bias on the aggregation index, the Donnelly edge correction was applied (Donnelly 1978, Pommerening and Stoyan 2006).

### 3.2.4 Statistics

Statistical analyses were done with the software R, version 3.6.3 (R Development Core Team, 2020, Vienna, Austria). Before determining differences in $D_b$ for the different forest types, we tested for normal distribution and homogeneity of variance (Shapiro-Wilk test for normality; Levene test for homogeneity of variance). If the data met the conditions for parametric tests, we used the ANOVA to test for differences in $D_b$ between the different forest types. After applying the ANOVA, we used the Tukey HSD (honestly significant difference) test for post-hoc comparisons. In case normal distribution and homogeneity of variance could not be assumed, we used the non-parametric Kruskal-Wallis test to determine differences in $D_b$ for the different forest types. For post-hoc analysis, we applied the Wilcoxon rank sum test. We used a significance level of $p < 0.05$ for all tests.

## 3.3 Results

### 3.3.1 $D_b$ of the lower, middle, and upper forest stratum of differently managed and unmanaged beech-dominated stands

We found significant differences in $D_b$ of all three forest strata between the different forest types (see Figure 3.3 a - c). The highest median of the $D_b$ was found in the lower forest stratum of the primary forests. It was significantly higher than those of the lower forest strata in the even-aged ($p = 0.014$) and formerly managed stands ($p < 0.001$), but equal to the uneven-aged stands ($p = 0.139$) (see Figure 3.3 a). Considering the middle forest stratum, we found significant differences in $D_b$ between the managed even-aged and the formerly managed stands ($p < 0.001$) (see Figure 3.3 b).

In the upper forest stratum, $D_b$ was significantly lower in the primary forests than in the even-aged ($p = 0.0011$) and formerly managed beech stands ($p = 0.007$), but we found no significant differences between the $D_b$ of the primary forests and the uneven-aged managed stands ($p = 0.236$) (see Figure 3.3 c). We also observed that the $D_b$ of the upper forest stratum in the formerly managed stands did not differ significantly from the managed, even-aged beech stands ($p = 0.887$) (see Figure 3.3 c). Compared to the even-aged stands, the uneven-aged stands showed significantly lower $D_b$ in the upper forest stratum ($p = 0.012$). Considering the lower forest stratum of the managed even-aged stands, lowest $D_b$ was observed in the forest district Reinhausen (98 years) (see Table 3.2).

Considering the unmanaged forests, Rožok showed highest $D_b$ in the middle forest stratum (see Table 3.2). For the upper forest stratum of the managed stands, highest $D_b$ was found in Lübeck (131 years) (see Table 3.2). Furthermore, we observed lowest $D_b$ for the upper stratum of the managed uneven-aged stands in Hainich-Dün (see Table 3.2). Looking at the upper forest stratum, there were decreasing $D_b$ median values from the formerly managed stands (150 - 184 years) over the primary forests Rožok (approximately 220 years) to Uholka (approximately 350 years) (see Table 3.2).

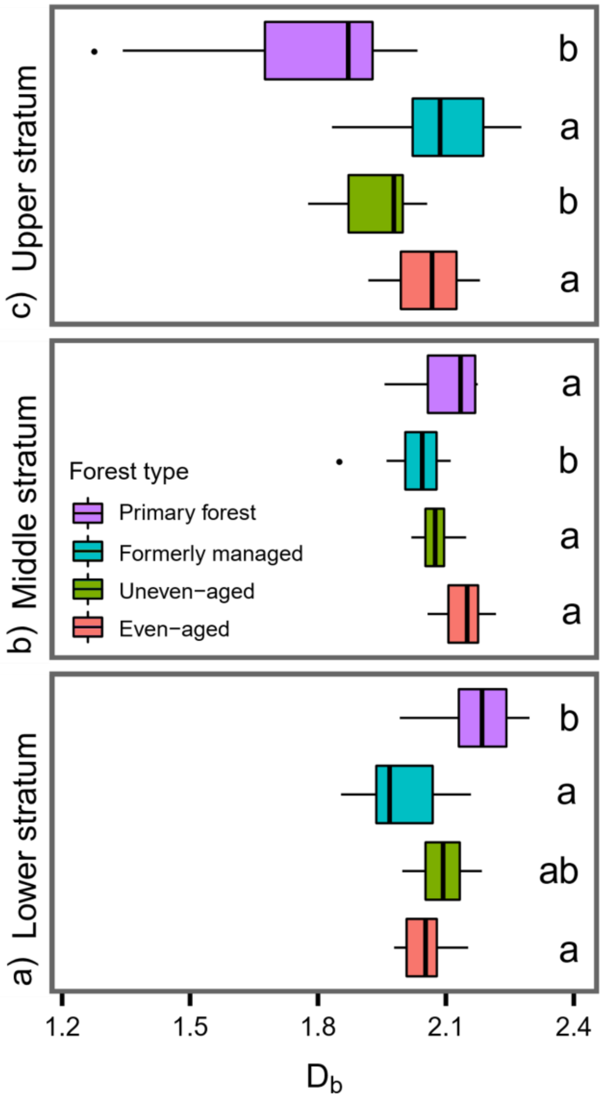

**Figure 3.3:** *Box-and-whisker plots showing the box dimension ($D_b$) for the lower (**a**), middle (**b**), and upper forest stratum (**c**) depending on the forest types. The different letters indicate significant differences between the different forest types at $p < 0.05$. Sample sizes for the different forest types were even-aged managed (EA): n = 12, uneven-aged managed (UEA): n = 8, formerly managed (FM): n = 11, and primary forest (PF): n = 8. Black horizontal lines indicate the median.*

### 3.3.2 Spatial patterns and density of vegetation in differently managed and unmanaged beech-dominated stands within the lower, middle, and upper forest strata

#### Lower forest stratum (≤ 33 % of relative stand height)

We found highest rSPf [%] mean values within the lower forest stratum of the primary forest Uholka (rSPf [%] = 9.55) and the uneven-aged forest stands in the Hainich-Dün region (rSPf [%] = 8.85) (see Table 3.2). The uneven-aged stands and the primary forests showed a tendency towards random to regular horizontal vegetation patterns within the entire lower forest stratum (CE index mean values > 1, see Figure 3.4 a), although Rožok showed lower mean values of the CE index when compared to Uholka (see Table 3.2). Compared to the primary forests and the uneven-aged stands, the even-aged managed and formerly managed stands showed, on average, clustered horizontal vegetation patterns within the entire lower forest stratum (see Figure 3.4 a).

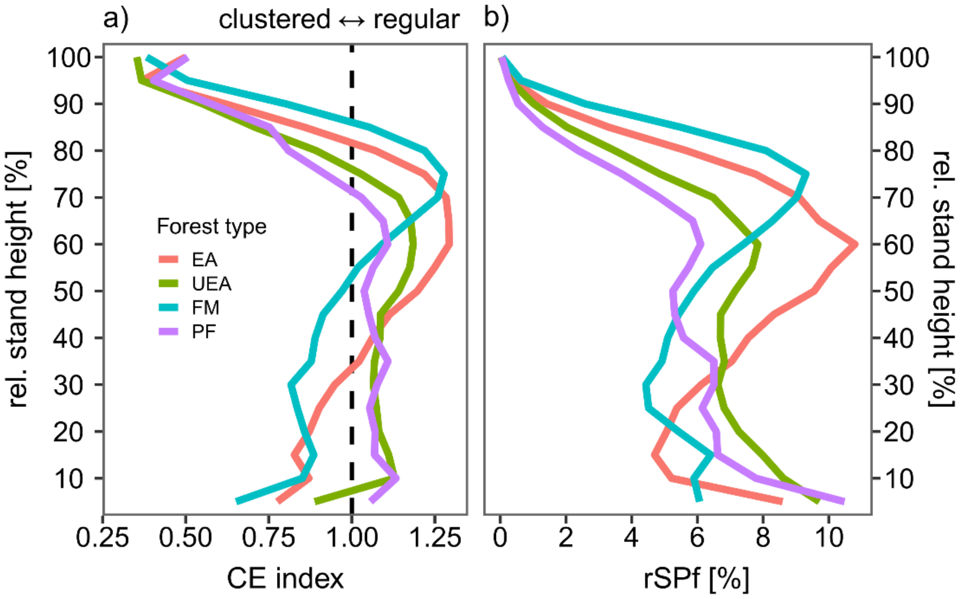

**Figure 3.4:** ***(a)*** *Line plots showing the mean values of the Clark-Evans index (CE index) calculated for forest strata of 5 % thickness each in the different forest types. Values > 1 indicate regular spatial patterns, while values < 1 tend to more clustered patterns. Values = 1 indicate random patterns; (****b****) Line plots showing the mean values of relative space filling (rSPf %) calculated for forest strata of 5 % thickness each in the different forest types. Sample size per 5 % height layer for different forest types was: even-aged (EA): n = 12, uneven-aged (UEA): n = 8, formerly managed (FM): n = 11, and primary forest (PF): n = 8.*

### Middle forest stratum (34 - 66 % of rel. stand height)

Within the middle layer, the lowest rSPf [%] mean value was found in the primary forest Uholka (see Table 3.2). We found highest rSPf [%] mean values in the even-aged stands (see Figure 3.4 b; Table 3.2: Reinhausen = 9.69 and Hann. Münden = 10.51). Especially between 50 % and 65 % of total stand height, even-aged stands showed higher rSPf [%] and mean values of CE index than the remaining forest types (see Figure 3.4 a, b). Compared to the other forest types, the formerly managed stands showed lowest mean values of the CE index (see Figure 3.4 a; Table 3.2). Up to a relative stand height of 50 %, they showed more clustered vegetation patterns (mean values < 1) compared to the remaining forest types (mean values > 1) (see Figure 3.4 a).

**Upper forest stratum (67 - 100 % rel. stand height)**

From 75 % to 95 % of relative stand height, rSPf [%] and mean values of the CE index were constantly decreasing (see Figure 3.4 a, b). The even-aged and formerly managed stands showed up to 90 % of relative stand height, constantly higher rSPf [%], and higher mean values of the CE index than the uneven-aged stands and primary forests (see Table 3.2). The primary forests showed a quite similar trend of rSPf [%] and CE index as observed for the uneven-aged stands, with Uholka having the lowest rSPf [%] mean values (see Figure 3.4 a, b; Table 3.2).

## 3.4 Discussion

### 3.4.1 Spatial patterns of structural complexity of the lower, middle, and upper stratum of different forest types

The managed (EA, UEA) and unmanaged (FM, PF) forests considered here comprise different stand ages (see Table 3.1), resulting in a certain variability in $D_b$, rSPf [%], and CE index (see Table 3.2). Within the lower, middle, and upper forest strata of the differently managed stands, we observed differences in the structural complexity, density, and horizontal distribution of plant material. In general, forest strata with a significantly higher $D_b$ (see Figure 3.3 a - c) showed comparably high CE index and rSPf [%] mean values (see Figure 3.4 a, b). Therefore, it seems that forest strata with a higher $D_b$ are characterized by a high density and random to regular distribution of plant material. This pattern can be observed in the example of the lower stratum of the uneven-aged stands and primary forests (see Figure 3.3 a; Figure 3.4 a). In contrast, forest strata with a significantly lower $D_b$ (see Figure 3.3 a - c) are also characterized by lower CE index and rSPf [%] mean values (see Figure 3.4 a, b). In this case, forest strata with a low $D_b$ were more likely to show clustered distribution patterns, as well as a lower occupation by plant material, as it can be exemplarily observed for the middle stratum of the formerly managed stands (see Figure 3.3 b; Figure 3.4 b). However, our observations are in line with the assumption that structural complexity is, to a certain degree, density-dependent (Ehbrecht et al. 2017, Seidel et al. 2019), because the spatial arrangement of structure depends on the existence of plant material. This dependency can be pretty well observed in Figure 3.4, when comparing the vertical profile of rSPf [%] and the CE index.

Canopy gaps have a direct impact on the spatial patterns of crown plant material (Franklin and Van Pelt 2004). In mature, even-aged stands, canopy gaps were created through target diameter harvests. Assuming that trees that have reached their target diameter are regularly distributed across the stand, canopy openings of the remaining canopy trees do also largely follow an even distribution (Schall et al. 2018, Schütz 2002). Therefore, the remaining upper canopy plant material in the even-aged stands (70 - 80 % of relative stand height) tended to a more regular horizontal distribution (CE index mean values > 1; see Figure 3.4 a).

Due to thinning from above, the remaining midstory trees of the managed even-aged stands were kept alive. This resulted in comparably high rSPf [%] and CE index mean values in the middle forest stratum, as can be found in the forest districts Reinhausen and Hann. Münden (see Table 3.2). The positive effect of thinning from above on the rSPf [%] of the middle forest stratum (50 - 60 % relative stand height) in beech-dominated stands was also observed by Juchheim et al. (2017). Due to a certain variation of tree heights and crown dimensions in the even-aged stands, plant material between 50 % and 65 % of relative stand height showed a more regular distribution pattern, while young regeneration growing in canopy gaps as well as stems of midstory trees appeared rather clustered in the lower layer (see Figure 3.4 a, Table 3.2).

Compared to the even-aged stands, we observed a significantly lower $D_b$ for the upper forest stratum of the uneven-aged stands (see Figure 3.3 c). One management goal in terms of creating an uneven-aged stand is a noticeable reduction of canopy closure (Schütz 2002). Especially in beech-dominated uneven-aged forests, single to group selection is a common management tool to open up the canopy (Schall et al. 2018, Schütz 2002). Interventions are mainly focused on the overstory trees > 50 cm diameter at breast height (Schall et al. 2018). This would explain the lower rSPf [%] mean values in the uneven-aged managed stands compared to the even-aged stands (see Figure 3.4 b), resulting in a more clustered plant material of the upper canopy that is comparable to that of primary forests (see Figure 3.4 a). The constant reduction of canopy closure in the upper layer of uneven-aged stands resulted in a regular vertical and horizontal distribution of dense plant material within the lower and middle forest stratum. We observed higher rSPf [%] and CE index mean values up to 30 % of relative stand height, compared to the majority of the even-aged stands (see Figure 3.4 a, b). Canopy gaps in unmanaged forests in Central Europe are caused by the mortality of single trees due to senescence, decay, and exogenous events, such as storms and snow falls (Kucbel et al. 2010, Nagel et al. 2014, Schelhaas et al. 2003). In the upper forest stratum of the unmanaged forests under study, we found a significantly higher $D_b$ in the formerly managed stands than in the primary forests (see Figure 3.3 c). The formerly managed beech stands showed a dense and regular distributed canopy structure between 75 % and 90 % of relative stand height (Figure 3.4 a, b). These results can be explained by the fact that management in the formerly managed stands was ceased during their optimal phase, which the majority of the forests still seemed to be in (decay phase has not begun yet). Even if single trees might have collapsed or have been outcompeted by neighboring trees and left small gaps, these were quickly closed by the lateral crown expansion of neighboring beech trees due to their high crown plasticity (Emborg et al. 2000, Feldmann et al. 2018, Schröter et al. 2012).

**Table 3.2:** *Box dimension (Db), relative space filling (rSPf %), Clark-Evans index (CE), and the height limits (m) of the lower, middle, and upper forest stratum of the forest stands in the different study sites (mean ± standard deviation). Mean Db is defined as the arithmetic mean of the Db values calculated for the lower, middle, and upper forest stratum of each forest stand within the different study sites. Mean rSPf [%] and mean CE is defined as the arithmetic mean of the rSPf [%] and CE values calculated for 5 % high forest strata within the lower, middle, and upper layer of each forest stand in the different study sites. Sample sizes for even-aged (EA) managed study sites were: Hann. Münden (n = 4), Lübeck (n = 4), and Reinhausen (n = 4). Sample sizes for uneven-aged (UEA) managed study sites were: Ebrach (n = 4), Hainich-Dün (n = 4). Sample sizes for formerly managed (FM) study sites were: Hainich-Dün (n = 7), Kellerwald (n = 4). Sample sizes for Primary forests (PF) were: Rožok (n = 4) and Uholka (n = 4).*

| | Lower Stratum | | | | Middle Stratum | | | | Upper Stratum | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Study Site** | **$D_b$** | **rSPf (%)** | **CE** | **Height Limits (m)** | **$D_b$** | **rSPf (%)** | **CE** | **Height Limits (m)** | **$D_b$** | **rSPf (%)** | **CE** | **Height Limits (m)** |
| Ebrach (UEA) | 2.14 ± 0.05 | 7.04 ± 1.80 | 1.06 ± 0.15 | Min: 1<br>Max: 12.1 ± 0.6 | 2.10 ± 0.04 | 5.55 ± 0.91 | 1.07 ± 0.07 | Min: 12.1 ± 0.6<br>Max: 24.3 ± 1.89 | 1.99 ± 0.01 | 2.41 ± 2.24 | 0.76 ± 0.31 | Min: 24.3 ± 1.89<br>Max: 35.7 ± 2.15 |
| Hainich (UEA) | 2.05 ± 0.04 | 8.85 ± 1.37 | 1.07 ± 0.05 | Min: 1<br>Max: 11.15 ± 0.93 | 2.05 ± 0.02 | 8.21 ± 1.16 | 1.16 ± 0.08 | Min: 11.15 ± 0.93<br>Max: 23.56 ± 0.61 | 1.89 ± 0.10 | 2.83 ± 1.50 | 0.72 ± 0.14 | Min: 23.56 ± 0.61<br>Max: 33.9 ± 2.75 |
| (FM)) | 1.96 ± 0.09 | 4.61 ± 2.22 | 0.78 ± 0.16 | Min: 1<br>Max: 11.73 ± 0.3 | 2.01 ± 0.08 | 5.45 ± 1.42 | 0.92 ± 0.13 | Min: 11.73 ± 0.3<br>Max: 22.45 ± 1.88 | 2.13 ± 0.13 | 6.28 ± 2.04 | 1.03 ± 0.14 | Min: 22.45 ± 1.88<br>Max: 35.8 ± 0.92 |
| Hann. Münden (EA) | 2.05 ± 0.05 | 6.76 ± 4.23 | 0.87 ± 0.15 | Min: 1<br>Max: 11.4 ± 0.51 | 2.16 ± 0.05 | 10.51 ± 2.75 | 1.22 ± 0.15 | Min: 11.4 ± 0.51<br>Max: 22.9 ± 1.09 | 2.07 ± 0.05 | 4.42 ± 4.01 | 0.8 ± 0.41 | Min: 22.9 ± 1.09<br>Max: 33.55 ± 1.59 |
| Kellerwald (FM) | 2.06 ± 0.10 | 7.12 ± 4.95 | 0.89 ± 0.26 | Min: 1<br>Max: 10.15 ± 0.41 | 2.07 ± 0.02 | 6.51 ± 1.60 | 1.05 ± 0.11 | Min: 10.15 ± 0.41<br>Max: 20.5 ± 0.82 | 2.01 ± 0.12 | 3.58 ± 3.3 | 0.86 ± 0.34 | Min: 20.5 ± 0.82<br>Max: 29.9 ± 1.25 |
| Lübeck (EA) | 2.09 ± 0.05 | 6 ± 2.39 | 0.92 ± 0.21 | Min: 1<br>Max: 11.85 ± 0.71 | 2.10 ± 0.05 | 6.80 ± 2.54 | 1.08 ± 0.19 | Min: 11.85 ± 0.71<br>Max: 23.83 ± 1.31 | 2.10 ± 0.10 | 4.62 ± 4.16 | 0.96 ± 0.40 | Min: 23.83 ± 1.31<br>Max: 35.15 ± 2.16 |
| Reinhausen (EA) | 2.02 ± 0.03 | 4.77 ± 2 | 0.80 ± 0.07 | Min: 1<br>Max: 11.6 ± 0.49 | 2.17 ± 0.02 | 9.69 ± 2.61 | 1.22 ± 0.17 | Min: 11.6 ± 0.49<br>Max: 23.25 ± 0.89 | 1.99 ± 0.07 | 2.79 ± 3.08 | 0.8 ± 0.37 | Min: 23.25 ± 0.89<br>Max: 34.15 ± 1.48 |
| Rožok (PF) | 2.10 ± 0.08 | 5.14 ± 3.38 | 0.87 ± 0.19 | Min: 1<br>Max: 14.5 ± 0.48 | 2.15 ± 0.03 | 6.71 ± 2.04 | 1.11 ± 0.17 | Min: 14.5 ± 0.48<br>Max: 29.1 ± 0.90 | 1.92 ± 0.08 | 2.57 ± 2.88 | 0.7 ± 0.39 | Min: 29.1 ± 0.90<br>Max: 42.85 ± 1.43 |
| Uholka (PF) | 2.25 ± 0.04 | 9.55 ± 2.61 | 1.28 ± 0.15 | Min: 1<br>Max: 15.3 ± 0.5 | 2.05 ± 0.10 | 4.80 ± 2.66 | 1.07 ± 0.24 | Min: 15.3 ± 0.5<br>Max: 30.75 ± 0.91 | 1.59 ± 0.34 | 1.15 ± 1.57 | 0.68 ± 0.30 | Min: 30.75 ± 0.91<br>Max: 45.3 ± 1.35 |

The shading effect of the pronounced closure of the upper forest stratum led to a reduction in tree numbers in the midstory due to competition and a successive self-pruning of lower branches. This in turn resulted in lowest $D_b$ median for the middle forest stratum (see Figure 3.4 b). We also observed a lower rSPf [%] and lower CE index mean values compared to the primary forests (see Figure 3.4 a, b). At the same time, a substantial regeneration layer could not develop yet, which was indicated by the low $D_b$ values for the lower forest stratum (see Figure 3.3 a; Table 3.2). Therefore, trunks had the main influence on the horizontal distribution of plant material in the lower and middle stratum. For that reason, the formerly managed stands showed, on average, clustered patterns of plant material in the lower and middle forest stratum (see Figure 3.4 a).

For the upper forest stratum of the unmanaged forests, we observed decreasing $D_b$ median values from the formerly managed stands (150 - 184 years) over the primary forest Rožok (approximately 220 years) to the primary forest Uholka (approximately 350 years) (see Table 3.1; Table 3.2). Compared to the formerly managed forests, the decay phase is more pronounced in old-growth forests and characterized by a larger number of small gaps (< 200 $m^2$) and a few larger gaps (Drößler 2006, Hobi et al. 2015b, 2015a, Kenderes et al. 2008, Meyer et al. 2003, Nagel et al. 2010). Stiers et al. (2019) recorded small gaps for some of the primary forest stands investigated here (< 200 $m^2$). Since we observed lower mean values of rSPf [%] in Uholka than in Rožok (see Table 3.2), we assume that the canopy of Uholkas' primary forests contains more and/or larger gaps. Therefore, one possible explanation for the low mean values of $D_b$ in Uholka's upper layer could be the absence of plant material as a result of decay. However, the upper stratum of primary forests is not always organized in a single stratum, but it is sometimes dominated by a few giant trees emerging from a more closed stratum underneath. The emergent layer is characterized by a lower space occupation compared to the layer underneath. This resulted in the low box dimension values, which are, in extreme cases, close to 1 due to the presence of a few tree tops of giant trees reaching out of the "stand". Considering the other forest stands, the vertical layering of the upper stratum was more homogenous with no emergent trees.

Due to the large canopy openings, resulting in low rSPf [%] values in the upper forest stratum in Uholka (see Table 3.2), pronounced understory vegetation could establish. This explains the high rSPf [%] within the lower stratum (see Table 3.2). The different heights and crown dimensions of young and more advanced regeneration trees resulted in a pronounced vertical distribution of regularly distributed vegetation patches (see Figure 3.4 a, b). The density of natural regeneration, as well as the heterogeneity of different heights of regeneration trees, resulted in a significantly higher $D_b$ for the lower forest stratum, compared to the one of the formerly managed forests (see Figure 3.3 a). In addition, other understory attributes, such as shrub height (Berger and Puettmann 2000) and understory species richness (Sullivan et al. 2001) were additional drivers for the high $D_b$ of Uholka's lower stratum. Commarmot et al. (2005)

found a rather sparse occupation of the middle forest stratum of the primary forest in Uholka. This result corresponds well with our observations. With a focus on the middle forest stratum, we found the lowest rSPf [%] in Uholka (see Table 3.2). One explanation for this observation may be that suppressed beech strongly responds to increased light conditions, growing quickly through the midstory. When interpreting the space filling in the middle layer of Uholka, one has to consider the maximum height limit (in meter) of this stratum (see Table 3.2). The middle stratum of both primary forests ranged from about 15 to 30 m. Due to this fact, the middle stratum of the investigated primary forest could be affected by a high age-induced mortality of mature trees.

In general, there is likely greater light availability in the middle and lower stratum with lower complexity in the upper stratum. However, a recent study conducted on the same sites as used in our study showed that light availability is not as important for the development of the understory of beech forest as reported for stands dominated by more light-demanding species (Stiers et al. 2019).

### 3.4.2 Methodical considerations

In order to account for the different stand heights, we chose relative heights to ensure the comparability of the different forest strata. This approach was also chosen in order to avoid empty upper strata of forest stands that are lower in height, which would be the case for fixed strata heights.

The definition of the three major forest strata used in our study is based on the IUFRO classification, which was also used in several other studies (Hobi et al. 2015b, Rugani et al. 2013, von Oheimb et al. 2005): lower stratum < 1/3 stand height; middle stratum 1/3 - 2/3 stand height; and upper stratum (> 2/3 stand height) (Leibundgut 1956). In our study, the stand height was defined as the uppermost layer, where at least one voxel could be found.

To ensure the comparability of the results, we deliberately selected stands in the mature timber stage. The majority of the investigated forest stands were characterized by a quite similar stand height. For these stands (managed and formerly managed stands), the stand heights varied between a minimum of 29.9 m and a maximum of 35.8 m (see Table 3.2). Therefore, the forest strata of these stands showed a rather low variation in thickness. However, if there are forest stands, which are considerably higher than the remaining forest stands, the use of relative heights showed limitations (Parker and Brown, 2000). In this study, the stand height of the investigated primary forests varied between 42.85 and 45.3 m, which was due to the presence of emerging trees. As a result, the strata of the primary forests showed a higher thickness compared to the smaller stands. These limitations have to be considered when evaluating and interpreting results.

## 3.5 Conclusions

The main goal of the current study was to determine the spatial characteristics of structural complexity within differently managed and unmanaged beech-dominated forests.

Our study showed that terrestrial laser scanning data can be used to quantify the structural complexity of single forest stratums. The considered beech-dominated primary forests are characterized by a complex forest structure in the lower forest stratum, resulting in significantly higher $D_b$ values for the lower forest stratum, compared to the even-aged stands.

Furthermore, it was possible to identify differences in density and the spatial distribution of plant material within differently managed and unmanaged forest stands. Both primary forests studied here showed a random to regular distribution of plant material within the lower stratum and middle forest stratum, but on average a lower space occupation for the middle stratum compared to the managed forest stands. This finding may have implications for the forest management. Our results clearly showed that management for uneven-aged stands leads to a quite similar spatial distribution of plant material, as observed for the primary forests. Management in beech-dominated forest that aims for increased structural complexity (taking primary forests as a reference) could focus on a promotion of complex understory structures, which can be achieved by creating larger canopy openings through single and group cuttings and the subsequent establishment of regeneration. Additionally, the reduction of vegetation density within the middle forest stratum could be considered.

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### Author Contributions

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## 3.7 References

Atkins, J.W., Bohrer, G., Fahey, R.T., Hardiman, B.S., Morin, T.H., Stovall, (…), Gough, C.M. (2018). Quantifying vegetation and canopy structural complexity from terrestrial LiDAR data using the FORESTR R package. Methods in Ecology and Evolution, 9, 2057-2066. https://doi.org/10.1111/2041-210X.13061.

Bartsch, N., Röhrig, E., von Lüpke, B. (2020). Waldbau auf ökologischer Grundlage, Eugen Ulmer KG, Stuttgart (Hohenheim).

Bauhus, J., Puettmann, K., Messier, C. (2009). Silviculture for old-growth attributes. Forest Ecology and Management, 258, 525-537. https://doi.org/10.1016/j.foreco.2009.01.053.

Béland, M., Widlowski, J.-L., Fournier, R.A. (2014). A model for deriving voxel-level tree leaf area density estimates from ground-based LiDAR. Environmental Modelling & Software, 51, 184-189. https://doi.org/10.1016/j.envsoft.2013.09.034.

Berger, A.L., Puettmann, K.J. (2000). Overstory Composition and Stand Structure Influence Herbaceous Plant Diversity in the Mixed Aspen Forest of Northern Minnesota. The American Midland Naturalist, 143, 111-125. https://doi.org/10.1674/0003-0031(2000)143[0111:OCASSI]2.0.CO;2.

Boudon, F., Godin, C., Pradal, C., Puech, O., Sinoquet, H. (2006). Estimating the fractal dimension of plants using the two-surface method: an analysis based on 3d-digitized tree foliage. Fractals, 14, 149-163. https://doi.org/10.1142/S0218348X06003179.

Brang, P. (2005). Virgin forests as a knowledge source for central European silviculture: Reality or myth? Forest, Snow and Landscape Research 79, 19-32.

Brang, P., Spathelf, P., Larsen, J.B., Bauhus, J., Boncina, A., Chauvin, C., (…), Svoboda, M. (2014). Suitability of close-to-nature silviculture for adapting temperate European forests to climate change. Forestry, 87, 492-503. https://doi.org/10.1093/forestry/cpu018.

Camarretta, N., Harrison, P.A., Bailey, T., Potts, B., Lucieer, A., Davidson, N., Hunt, M. (2019). Monitoring forest structure to guide adaptive management of forest restoration: a review of remote sensing approaches. New Forests, 51, 573-596. https://doi.org/10.1007/s11056-019-09754-5.

Clark, P.J., Evans, F.C. (1954). Distance to Nearest Neighbor as a Measure of Spatial Relationships in Populations. Ecology, 35, 445-453. https://doi.org/10.2307/1931034.

Commarmot, B., Bachofen, H., Bundziak, Y., Bürgi, A., Shparyk, Y., Sukhariuk, D., Viter, R., Zingg, A. (2005). Structures of virgin and managed beech forests in Uholka (Ukraine) and Sihlwald (Switzerland): a comparative study. Forest, Snow and Landscape Research 79, 45-76.

Donnelly, K., 1978. Simulation to determine the variance and edge-effect of total nearest neighbor distance. Simulation methods in archeology. *In* Simulation methods in archaeology, Cambridge University Press, Cambridge.

Dorji, Y., Annighöfer, P., Ammer, C., Seidel, D. (2019). Response of beech (*Fagus sylvatica* L.) trees to competition-New insights from using fractal analysis. Remote Sensing, 11, 2656. https://doi.org/10.3390/rs11222656.

Drößler, L. (2006). Struktur und Dynamik von zwei Buchenurwäldern in der Slowakei (Dissertation). Göttingen.

Du Preez, C. (2015). A new arc-chord ratio (ACR) rugosity index for quantifying three-dimensional landscape structural complexity. Landscape Ecology, 30, 181-192. https://doi.org/10.1007/s10980-014-0118-8.

Dutilleul, P., Han, L., Valladares, F., Messier, C. (2015). Crown traits of coniferous trees and their relation to shade tolerance can differ with leaf type: a biophysical demonstration using computed tomography scanning data. Frontiers in Plant Science, 6. https://doi.org/10.3389/fpls.2015.00172.

Ehbrecht, M., Schall, P., Ammer, C., Fischer, M., Seidel, D. (2019). Effects of structural heterogeneity on the diurnal temperature range in temperate forest ecosystems. Forest Ecology and Management, 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. Agricultural and Forest Meteorology, 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. Forest Ecology and Management, 380, 212-223. https://doi.org/10.1016/j.foreco.2016.09.003.

Ellison, A.M., Bank, M.S., Clinton, B.D., Colburn, E.A., Elliott, K., Ford, C.R., (…), Webster, J.R. (2005). Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. Frontiers in Ecology and the Environment, 3, 479-486. https://doi.org/10.1890/1540-9295(2005)003[0479:LOFSCF]2.0.CO;2.

Emborg, J., Christensen, M., Heilmann-Clausen, J. (2000). The structural dynamics of Suserup Skov, a near-natural temperate deciduous forest in Denmark. Forest Ecology and Management, 126, 173-189. https://doi.org/10.1016/S0378-1127(99)00094-8.

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. Forest Ecology and Management, 415-416, 38-46. https://doi.org/10.1016/j.foreco.2018.02.022.

Fischer, M., Bossdorf, O., Gockel, S., Hänsel, F., Hemp, A., Hessenmöller, D., (…), Weisser, W.W. (2010). Implementing large-scale and long-term functional biodiversity research: The Biodiversity Exploratories. Basic and Applied Ecology, 11, 473-485. https://doi.org/10.1016/j.baae.2010.07.009.

Franklin, J.F., Van Pelt, R. (2004). Spatial aspects of structural complexity in old-growth forests. Journal of Forestry, 102, 22-28. https://doi.org/10.1093/jof/102.3.22.

Gadow, K. v., Zhang, C.Y., Wehenkel, C., Pommerening, A., Corral-Rivas, J., Korol, M., (…), Zhao, X.H. (2012). Forest Structure and Diversity, *In* Continuous Cover Forestry, Managing Forest Ecosystems. Springer, Dordrecht. https://doi.org/10.1007/978-94-007-2202-6_2.

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. Ecosystems, 21, 704-722. https://doi.org/10.1007/s10021-017-0179-z.

Gough, C.M., Atkins, J.W., Fahey, R.T., Hardiman, B.S. (2019). High rates of primary production in structurally complex forests. Ecology, 100. https://doi.org/10.1002/ecy.2864.

Gustafsson, L., Baker, S.C., Bauhus, J., Beese, W.J., Brodie, A., Kouki, J., (…), Franklin, J.F. (2012). Retention forestry to maintain multifunctional forests: A world perspective. BioScience, 62, 633-645. https://doi.org/10.1525/bio.2012.62.7.6.

Hobi, M.L., Commarmot, B., Bugmann, H. (2015a). Pattern and process in the largest primeval beech forest of Europe (Ukrainian Carpathians). Journal of Vegetation Science, 26, 323-336. https://doi.org/10.1111/jvs.12234.

## Chapter 3

Hobi, M.L., Ginzler, C., Commarmot, B., Bugmann, H. (2015b). Gap pattern of the largest primeval beech forest of Europe revealed by remote sensing. Ecosphere, 6, 1-5. https://doi.org/10.1890/ES14-00390.1.

Jonckheere, I., Nackaerts, K., Muys, B., van Aardt, J., Coppin, P. (2006). A fractal dimension-based modelling approach for studying the effect of leaf distribution on LAI retrieval in forest canopies. Ecological Modelling, 197, 179-195. https://doi.org/10.1016/j.ecolmodel.2006.02.036.

Juchheim, J., Ammer, C., Schall, P., Seidel, D. (2017). Canopy space filling rather than conventional measures of structural diversity explains productivity of beech stands. Forest Ecology and Management, 395, 19-26. https://doi.org/10.1016/j.foreco.2017.03.036.

Kenderes, K., Mihok, B., Standovar, T. (2008). Thirty years of gap dynamics in a central European beech forest reserve. Forestry, 81, 111-123. https://doi.org/10.1093/forestry/cpn001.

Kint, V., Robert, D.W., Noël, L. (2004). Evaluation of sampling methods for the estimation of structural indices in forest stands. Ecological Modelling, 180, 461-476. https://doi.org/10.1016/j.ecolmodel.2004.04.032.

Korpel, Š. (1995). Die Urwälder der Westkarpaten: 39 Tabellen. Gustav Fischer, Stuttgart.

Kottek, M., Grieser, J., Beck, C., Rudolf, B., Rubel, F. (2006). World Map of the Köppen-Geiger climate classification updated. Meteorologische Zeitschrift, 15, 259-263. https://doi.org/10.1127/0941-2948/2006/0130.

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

Leibundgut, H. (1956). Empfehlungen für die Baumklassenbildung und Methodik bei Versuchen über die Wirkung von Waldpflegemassnahmen. Presented at the IUFRO, Oxford, United Kingdom, pp. 92-94.

Mandelbrot, B.B. (1975). Stochastic models for the Earth’s relief, the shape and the fractal dimension of the coastlines, and the number-area rule for islands. Proceedings of the National Academy of Sciences, 72, 3825-3828. https://doi.org/10.1073/pnas.72.10.3825.

Messier, C., Puettmann, K.J., Coates, K.D. (2013). Managing forests as complex adaptive systems: Building resilience to the challenge of global change. Routledge.

Meyer, P., Tabaku, V., v. Lupke, B. (2003). Die Struktur albanischer Rotbuchen-Urwälder - Ableitungen für eine naturnahe Buchenwirtschaft. Structural Characteristics of Albanian Beech (*Fagus sylvatica* L.) Virgin Forests - Deductions for Semi-Natural Forestry. Forstwissenschaftliches Centralblatt, 122, 47-58. https://doi.org/10.1046/j.1439-0337.2003.02041.x.

Nagel, T.A., Svoboda, M., Kobal, M. (2014). Disturbance, life history traits, and dynamics in an old-growth forest landscape of southeastern Europe. Ecological Applications, 24, 663-679. https://doi.org/10.1890/13-0632.1.

Nagel, T.A., Svoboda, M., Rugani, T., Diaci, J. (2010). Gap regeneration and replacement patterns in an old-growth *Fagus-Abies* forest of Bosnia-Herzegovina. Plant Ecology, 208, 307-318. https://doi.org/10.1007/s11258-009-9707-z.

NLF - Niedersächsische Landesforsten (2018): Entscheidungshilfen zur Behandlung und Entwicklung von Buchenbeständen. (accessed 05.06.20). https://www.nw-fva.de/fileadmin/user_upload/Verwaltung/Publikationen/Merkblaetter/Bu_Nds_Entscheidungshilfe_zur_Behandlung_und_Entwicklung_von_Buchenbestaenden.pdf.

Parker, G.G., Brown, M.J. (2000). Forest Canopy Stratification-Is It Useful? The American Naturalist ,155, 473-484. https://doi.org/10.1086/303340.

Parker, G.G., Harmon, M.E., Lefsky, M.A., Chen, J., Pelt, R.V., Weis, S.B., Thomas, S.C., Winner, W.E., Shaw, D.C., Frankling, J.F. (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.

Pommerening, A., Stoyan, D. (2006). Edge-correction needs in estimating indices of spatial forest structure. Canadian Journal of Forest Research, 36, 1723-1739. https://doi.org/10.1139/x06-060.

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.

Puettmann, K.J., Coates, K.D., Messier, C.C. (2009). A critique of silviculture: managing for complexity. Island Press, Washington, DC.

Rugani, T., Diaci, J., Hladnik, D. (2013). Gap dynamics and structure of two old-growth beech forest remnants in Slovenia. PLoS ONE, 8, e52641. https://doi.org/10.1371/journal.pone.0052641.

Sabatini, F.M., Burrascano, S., Keeton, W.S., Levers, C., Lindner, M., Pötzschner, F., (…),Kuemmerle, T. (2018). Where are Europe’s last primary forests? Diversity and Distributions, 24, 1426-1439. https://doi.org/10.1111/ddi.12778.

Sarkar, N., Chaudhuri, B.B. (1994). An efficient differential box-counting approach to compute fractal dimension of image. IEEE Transactions on Systems, Man, and Cybernetics, 24, 115-120. https://doi.org/10.1109/21.259692.

Schall, P., Gossner, M.M., Heinrichs, S., Fischer, M., Boch, S., Prati, D., (…), Ammer, C. (2018). The impact of even-aged and uneven-aged forest management on regional biodiversity of multiple taxa in European beech forests. Journal of Applied Ecology, 55, 267-278. https://doi.org/10.1111/1365-2664.12950.

Schelhaas, M.-J., Nabuurs, G.-J., Schuck, A. (2003). Natural disturbances in the European forests in the 19th and 20th centuries. Global Change of Biology, 9, 1620-1633. https://doi.org/10.1046/j.1365-2486.2003.00684.x.

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

Schütz, J. (2002). Silvicultural tools to develop irregular and diverse forest structures. Forestry: An International Journal of Forest Research, 75, 329-337. https://doi.org/10.1093/forestry/75.4.329.

Seidel, D. (2018). A holistic approach to determine tree structural complexity based on laser scanning data and fractal analysis. Ecology and Evolution, 8, 128-134. https://doi.org/10.1002/ece3.3661.

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

Seidel, D., Ehbrecht, M., Puettmann, K. (2016). Assessing different components of three-dimensional forest structure with single-scan terrestrial laser scanning: A case study. Forest Ecology and Management, 381, 196-208. https://doi.org/10.1016/j.foreco.2016.09.036.

Seidel, D., Leuschner, C., Scherber, C., Beyer, F., Wommelsdorf, T., Cashman, M.J., Fehrmann, L. (2013). The relationship between tree species richness, canopy space exploration and productivity in a temperate broad-leaf mixed forest. Forest Ecology and Management, 310, 366-374. https://doi.org/10.1016/j.foreco.2013.08.058.

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. Forest Ecology and Management, 430, 357-365. https://doi.org/10.1016/j.foreco.2018.08.039.

Stinglwagner, G., Haseder, I., Erlbeck, R. (2016). Das Kosmos Wald & Forst-Lexikon, Kosmos, Stuttgart.

Sullivan, T.P., Sullivan, D.S., Lindgren, P.M.F. (2001). Stand structure and small mammals in young lodgepole pine forest: 10-year result after thinning. Ecological Applications, 11, 1151-1173. https://doi.org/10.1890/1051-0761(2001)011[1151:SSASMI]2.0.CO;2.

Trotsiuk, V., Hobi, M.L., Commarmot, B. (2012). Age structure and disturbance dynamics of the relic virgin beech forest Uholka (Ukrainian Carpathians). Forest Ecology and Management, 265, 181-190. https://doi.org/10.1016/j.foreco.2011.10.042.

von Oheimb, G., Westphal, C., Tempel, H., Härdtle, W. (2005). Structural pattern of a near-natural beech forest (*Fagus sylvatica*) (Serrahn, North-east Germany). Forest Ecology and Management, 212, 253-263. https://doi.org/10.1016/j.foreco.2005.03.033.

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.

Witté, I., Kneeshaw, D., Messier, C. (2013). Do partial cuts create forest complexity? A new approach to measuring the complexity of forest patterns using photographs and the mean information gain. The Forestry Chronicle, 89. https://doi.org/10.5558/tfc2013-064.

Zemp, D.C., Ehbrecht, M., Seidel, D., Ammer, C., Craven, D., Erkelenz, J., (…), Kreft, H. (2019). Mixed-species tree plantings enhance structural complexity in oil palm plantations. Agriculture, Ecosystems & Environment, 283, 106564. https://doi.org/10.1016/j.agee.2019.06.003.

Zenner, E.K., Hibbs, D.E. (2000). A new method for modeling the heterogeneity of forest structure. Forest Ecology and Management, 129, 75-87. https://doi.org/10.1016/S0378-1127(99)00140-1.

Zhu, J., Wang, X., ChenJunqi, Huang, H., Yang, X. (2014). Estimating fractal dimensions of tree crowns in 3-D space based on structural relationships. The Forestry Chronicle, 90. https://doi.org/10.5558/tfc2014-035.

# Chapter 4 Short-term dynamics of structural complexity in differently managed and unmanaged European beech forests

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## 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.

**Keywords:** *Fagus sylvatica* L.; TLS, stand structural complexity index (SSCI); disturbance; forest structure; forest dynamics; forest management

## 4.1 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 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.

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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 stand´s 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).

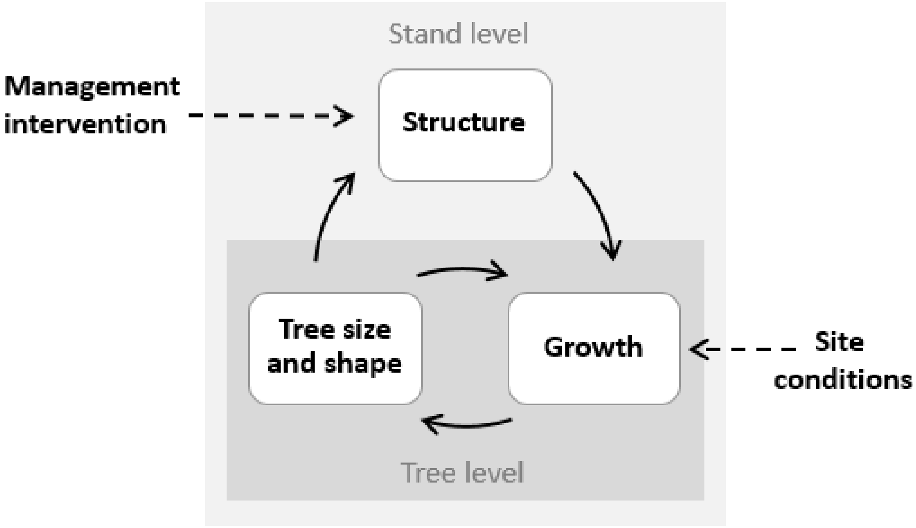

**Figure 4.1:** *Feedback loop modified after Pretzsch (2009), showing the relationship between stand structure, growth conditions, tree size and shape, with management intervention and site conditions as external factors.*

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 forests 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.

## 4.2 Methods

### 4.2.1 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 x 100m (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 Tab. 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 (≤ 1000 m2) 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 (1990), 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.

**Table 4.1:** *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 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 |

### 4.2.2 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.

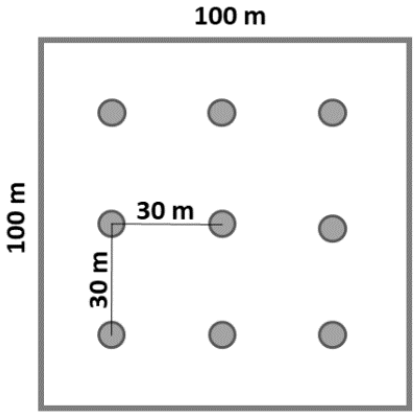

**Figure 4.2:** *Sample design for each 100 x 100 m (1 ha) plot. Grey circles represent the scan positions within the plot.*

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 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 x 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.

### 4.2.3 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 $p < 0.05$ 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 $p < 0.01$.

## 4.3 Results

### 4.3.1 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 Tab. 2) in SSCI. Moreover, all unmanaged forest stands showed a low variability of dynamics in SSCI (standard deviation of SSCI ± 6.61 %; see Tab. 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 Tab. 2). For the uneven - aged forests, SSCI increased on average by 17.79 % (see Tab. 2) from 2014 to 2019. In contrast to the unmanaged forests, we observed a quite high variability in dynamics of SSCI (± 24.52; see Tab. 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).

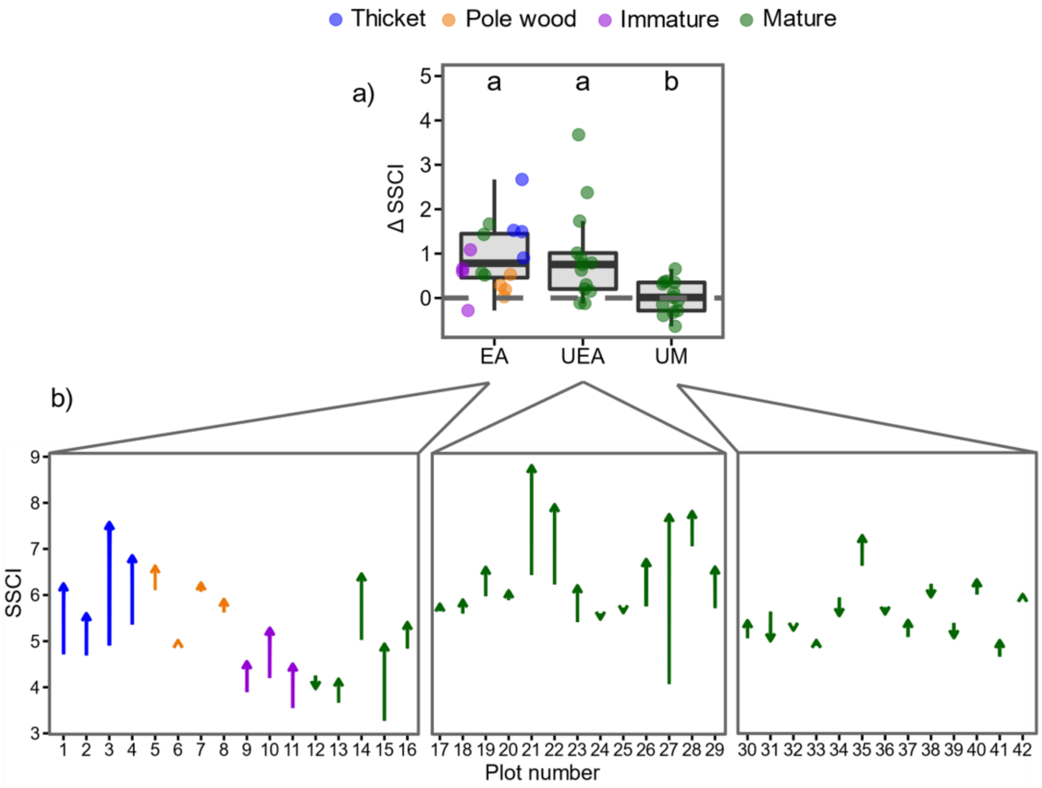

**Figure 4.3:** *Dynamics of stand structural complexity (SSCI) in different forest management types: EA = Even-aged (n = 16), UEA = Uneven-aged (n = 13) and UM = Unmanaged (n = 13). Different colors represent different developmental stages. a) Box-and-whisker plots showing Δ SSCI for the different forest 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.*

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 Tab. 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 Tab. 2).

We observed different dynamics of UCI and ENL for the different forest management types and developmental stages (see Tab. 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 Tab. 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 Tab. 2). ENL, in contrast, increased in the younger stages during the 5 years (see Tab. 2). In thickets ENL increased on average by 75.58 %, whereas in pole wood ENL increased by 29.06 %.

**Table 4.2:** *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 |

### 4.3.2 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).

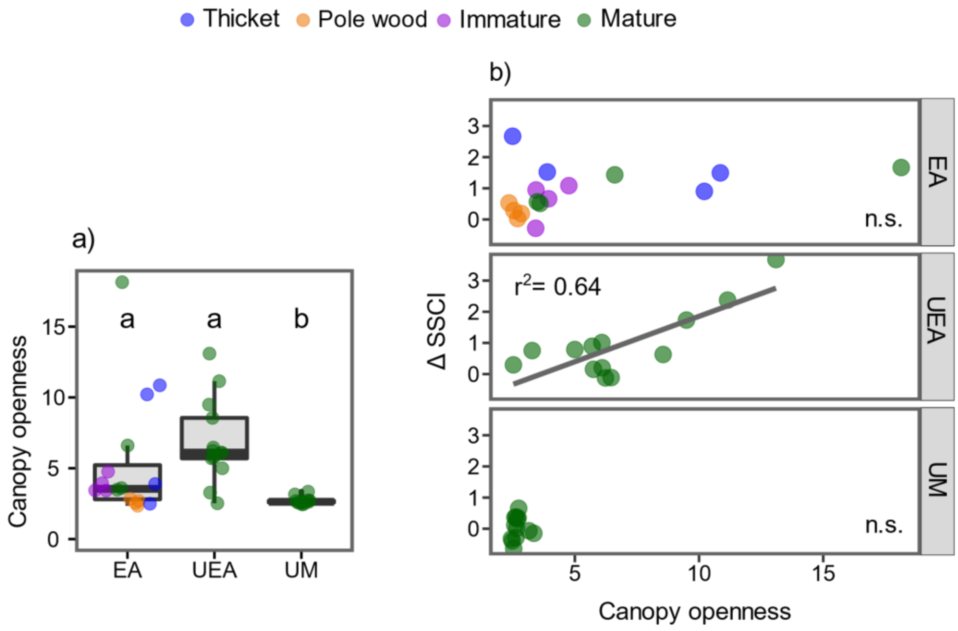

**Figure 4.4:** *Canopy openness for different forest management types and its relationship with dynamics of stand structural complexity (Δ SSCI). The different forest management types are: EA = Even-aged (n = 16), UEA = Uneven-aged (n = 13) and UM = Unmanaged (n = 13). Different colors represent different 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.".*

## 4.4 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 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 Tab. 2). Although the overall stand structural complexity showed nearly no change during the 5 years, we observed an increase of ENL (see Tab. 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 ∆ 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 Tab. 2; Fig. A.2a).

The even - aged stands showed a high variation in dynamics of structural complexity (see Tab. 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 Tab. 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 Tab. 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 Tab. 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 ∆ 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 Tab. 2). In this context, even - aged mature stands with a higher canopy openness (Plot no. 14 and 15, Tab. 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.

## 4.5 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.

## 4.6 Acknowledgements

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## 4.7 References

Agestam, E., Ekö, P.-M., Nilsson, U., Welander, N.T. (2003). The effects of shelterwood density and site preparation on natural regeneration of *Fagus sylvatica* in southern Sweden. Forest Ecology and Management, 176, 61-73. https://doi.org/10.1016/S0378-1127(02)00277-3.

Ammer C., Fichtner A., Fischer A., Gossner M. M., Meyer P., Seidl R., (…), Wagner S. (2018). Key ecological research questions for Central European forests. Basic and Applied Ecology, 32, 3-25. https://doi.org/10.1016/j.baae.2018.07.006.

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Ammer, C., Stimm, B., Mosandl, R., (2008). Ontogenetic variation in the relative influence of light and belowground resources on European beech seedling growth. Tree Physiology, 28, 721-728. https://doi.org/10.1093/treephys/28.5.721.

Asbeck, T., Frey, J. (2021). Weak relationships of continuous forest management intensity and remotely sensed stand structural complexity in temperate mountain forests. European Journal of Forest Research, 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, J.W., Bohrer, G., Fahey, R.T., Hardiman, B.S., Morin, T.H., Stovall, A.E., (…), Gough, C.M. (2018). Quantifying vegetation and canopy structural complexity from terrestrial LiDAR data using the FORESTR R package. Methods in Ecology and Evolution, 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. Forest Ecology and Management, 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. Annals of Forest Science, 63, 625-644. https://doi.org/10.1051/forest:2006042.

Camarretta, N., Harrison, P.A., 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 Forests, 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. Forest Ecology and Management, 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. Annals of Forest Science, 58, 127-134. https://doi.org/10.1051/forest:2001112.

Coumou, D., Rahmstorf, S. (2012). A decade of weather extremes. Nature Climate 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. European Journal of Forest Research, 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. Forest Ecology and Management, 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. Agricultural and Forest Meteorology, 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. Forest Ecology and Management, 380, 212-223. https://doi.org/10.1016/j.foreco.2016.09.003.

Ehbrecht, M., Seidel, D., Annighöfer, P., Kreft, H., Köhler, M., Zemp, D.C, (…), Ammer, C. (2021). Global patterns and climatic controls of forest structural complexity. Nature Communications, 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. Forest Ecology and Management, 106, 83-95. https://doi.org/10.1016/S0378-1127(97)00299-5.

Fahey, R.T., Fotis, A.T., Woods, K.D. (2015). Quantifying canopy complexity and effects on productivity and resilience in late-successional hemlock-hardwood forests. Ecological Applications, 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. Forest Ecology and Management, 415-416, 38-46. https://doi.org/10.1016/j.foreco.2018.02.022.

Felipe-Lucia, M.R., Soliveres, S., Penone, C., Manning, P., van der Plas, F., Boch, S., (…), Allan, E. (2018). Multiple forest attributes underpin the supply of multiple ecosystem services. Nature Communications, 9, 4839. https://doi.org/10.1038/s41467-018-07082-4.

Fenton, N.J., 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. Journal of Forest Research, 14, 258-267. https://doi.org/10.1007/s10310-009-0134-8.

Fischer, M., Bossdorf, O., Gockel, S., Hänsel, F., Hemp, A., Hessenmöller, D., (…), Weisser, W.W. (2010). Implementing large-scale and long-term functional biodiversity research: The Biodiversity Exploratories. Basic and Applied Ecology, 11, 473-485. https://doi.org/10.1016/j.baae.2010.07.009.

Führer, E. (2000). Forest functions, ecosystem stability and management. Forest Ecology and Management, 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. Ecosystems, 21, 704-722. https://doi.org/10.1007/s10021-017-0179-z.

Gough, C.M., Atkins, J.W., Fahey, R.T., Hardiman, B.S. (2019). High rates of primary production in structurally complex forests. Ecology, 100. https://doi.org/10.1002/ecy.2864.

Hardiman, B.S., Gough, C.M., Halperin, A., Hofmeister, K.L., Nave, L.E., Bohrer, G., Curtis, P.S. (2013). Maintaining high rates of carbon storage in old forests: A mechanism linking canopy structure to forest function. Forest Ecology and Management, 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. Ecological Modelling, 210, 487-498. https://doi.org/10.1016/j.ecolmodel.2007.08.011.

Knuff, A.K., Staab, M., Frey, J., Dormann, C.F., Asbeck, T., Klein, A.-M. (2020). Insect abundance in managed forests benefits from multi-layered vegetation. Basic and Applied Ecology, 48, 124-135. https://doi.org/10.1016/j.baae.2020.09.002.

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

Kovács, B., Tinya, F., Ódor, P. (2017). Stand structural drivers of microclimate in mature temperate mixed forests. Agricultural and Forest Meteorology, 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. European Journal of Forest Research, 129, 249-259. https://doi.org/10.1007/s10342-009-0322-2.

Leuschner, C., Meier, I.C., 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. Annals of Forest Science, 63, 355-368. https://doi.org/10.1051/forest:2006016.

Madsen, P., Larsen, J.B. (1997). Natural regeneration of beech (*Fagus sylvatica* L.) with respect to canopy density, soil moisture and soil carbon content. Forest Ecology and Management, 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. Forest Ecology and Management, 218, 1-24. https://doi.org/10.1016/j.foreco.2005.08.034.

Messier, C., Puettmann, K.J. (2011). Forests as complex adaptive systems: implications for forest management and modelling. Italian Journal of Forest and Mountain Environments, 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. Journal of Forestry Research, 25, 725-736. https://doi.org/10.1007/s11676-014-0521-7.

Nagel, T.A., Svoboda, M., Kobal, M. (2014). Disturbance, life history traits, and dynamics in an old-growth forest landscape of southeastern Europe. Ecological Applications, 24, 663-679. https://doi.org/10.1890/13-0632.1.

O'Hara, K.L., Gersonde, R.F. (2004). Stocking control concepts in uneven-aged silviculture. Forestry, 77, 131-143. https://doi.org/10.1093/forestry/77.2.131.

Parker, G.G., Harmon, M.E., Lefsky, M.A., Chen, J., Pelt, R.V., Weis, S.B., Thomas, S.C., Winner, W.E., Shaw, D.C., Frankling, J. (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. (2005). Stand density and growth of Norway spruce (Picea abies (L.) Karst.) and European beech (*Fagus sylvatica* L.): evidence from long-term experimental plots. European Journal of Forest Research, 124, 193-205. https://doi.org/10.1007/s10342-005-0068-4.

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. European Journal of Forest Research, 128, 183-204. https://doi.org/10.1007/s10342-008-0215-9.

Primicia, I., Colomo, R.A., Rodríguez, J.B.I., Puertas, F., Traver, C., Martínez, F.J.C. (2016). Influence of thinning intensity and canopy type on Scots pine stand and growth dynamics in a mixed managed forest. Forest systems, 25, 1.

Pykälä, J. (2004). Immediate increase in plant species richness after clear-cutting of boreal herb-rich forests. Applied Vegetation Science, 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. Forest Ecology and Management, 194, 349-368. https://doi.org/10.1016/j.foreco.2004.02.022.

Schall, P., Gossner, M.M., Heinrichs, S., Fischer, M., Boch, S., Prati, D., (…), Ammer, C. (2018). The impact of even-aged and uneven-aged forest management on regional biodiversity of multiple taxa in European beech forests. Journal of Applied Ecology, 55, 267-278. https://doi.org/10.1111/1365-2664.12950.

Schelhaas, M.-J., Nabuurs, G.-J., Schuck, A. (2003). Natural disturbances in the European forests in the 19th and 20th centuries. Global Change Biology, 9, 1620-1633. https://doi.org/10.1046/j.1365-2486.2003.00684.x.

Schröter, M., Härdtle, W., von Oheimb, G. (2012). Crown plasticity and neighborhood interactions of European beech (*Fagus sylvatica* L.) in an old-growth forest. European Journal of Forest Research, 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, D.P. (2021). Quantifying understory complexity in unmanaged forests using TLS and identifying some of its major drivers. Remote Sensing, 13, 1513. https://doi.org/10.3390/rs13081513.

Seidel, D., Annighöfer, P., Ehbrecht, M., Magdon, P., Wöllauer, S. and Ammer, C. (2020). Deriving stand structural complexity from airborne laser scanning data- what does it tell us about a forest? Remote Sensing, 12, 1854. doi: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? Agricultural and Forest Meteorology, 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 and 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. Forest Ecology and Management, 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.

Widenfalk, O., Weslien, J. (2009). Plant species richness in managed boreal forests-Effects of stand succession and thinning. Forest Ecology and Management, 257, 1386-1394. https://doi.org/10.1016/j.foreco.2008.12.010.

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. Remote Sensing, 12, 1907. https://doi.org/10.3390/rs12121907.

Zemp, D.C., 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. Agriculture, Ecosystems & Environment, 283, 106564. https://doi.org/10.1016/j.agee.2019.06.003.

Zheng, G., Moskal, L.M., Kim, S. (2013). Retrieval of effective leaf area index in heterogeneous forests with terrestrial laser scanning. IEEE Transactions on Geoscience and Remote Sensing, 51, 777-786. https://doi.org/10.1109/TGRS.2012.2205003.

## 4.8 Appendix

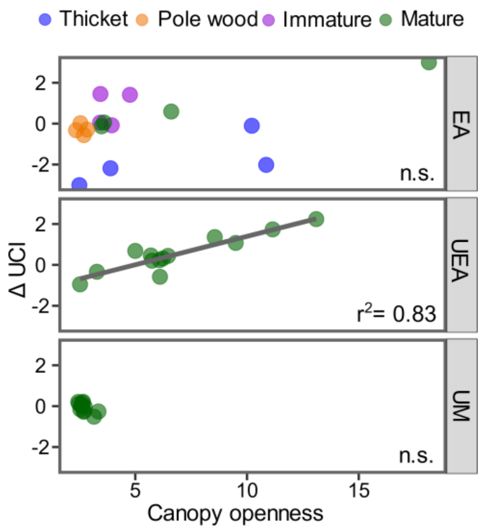

***Figure A.4.1:*** *Relationship between canopy openness measured in 2014 and dynamics of understory complexity (Δ UCI). The different forest management types are: EA = Even-aged (n = 16), UEA = Uneven-aged (n = 13) and UM = Unmanaged (n = 13). Different colors represent different developmental stages. Non-significant relationships are marked by the abbreviation “n.s.”.*

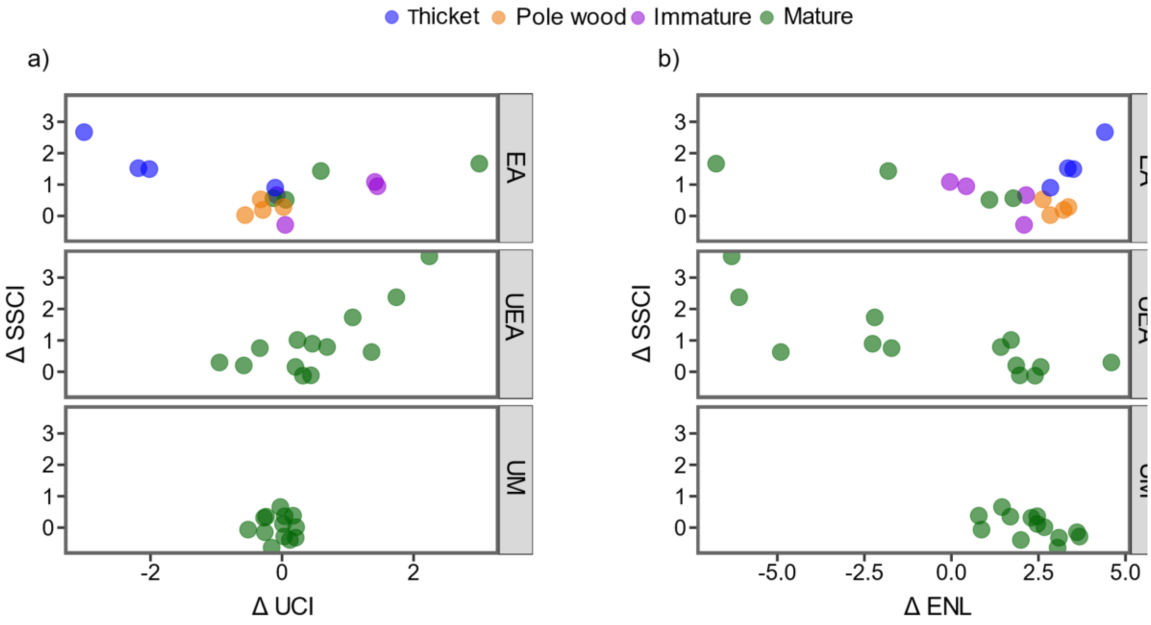

***Figure A.4.2:*** *a) Relationship between dynamics of understory complexity (Δ UCI) and dynamics of stand structural complexity (Δ SSCI). b) Relationship between dynamics of effective number of layers (Δ ENL) and dynamics of Δ SSCI. The different forest management types are: EA = Even-aged (n = 16), UEA = Uneven-aged (n = 13) and UM = Unmanaged (n = 13).*

# Chapter 5

## Chapter 5 Synthesis

Considering the main objectives and research questions of the overall study:

i. Can managed beech forests have a similar understory complexity as primary beech forests?

ii. Do beech forests with a high structural complexity show a different spatial distribution and density of plant material compared to beech forests with a low structural complexity?

iii. How does silvicultural management affect dynamics of structural complexity in beech forests?

the main findings of the three sub-studies (chapter 2, chapter 3, chapter 4) are summarized and discussed in the following. Furthermore, the main methodological approaches with a special focus on the fractal dimension are introduced and evaluated in terms of their suitability (chapter 5.1), before the methodological limitations of the studies are introduced and discussed (chapter 5.5).

### 5.1 Methodological approaches to quantify structural complexity within forest stands

In theory, fractal geometry tries to quantify the irregularity of geometric shapes (Mandelbrot 1975). For this reason, fractal geometry was increasingly used in order to describe complex surfaces of natural objects, as e.g. rivers, mountains and also vegetation (Zeide 1991). Also, in forest ecology, the potential of fractal geometry has been discovered to describe forest structure and diverse structural attributes (Boudon et al. 2006, Seidel 2018, Dorji et al. 2019, Jonckheere et al. 2006, Zhu et al. 2014). The fractal dimension (FD) serve as measure of structural complexity that can be applied at different spatial scales. In chapter 2, the FD was used to develop the understory complexity index (UCI) that describes the structural complexity of the forest understory. Basically, the UCI is based on the fractal dimension of cross-sectional horizontal polygons, which were derived from a 1 m thick layer (0.8 - 1.8 m) of a voxelized single-scan point cloud (see Figure 2.4). Here, the FD reflects the shape complexity of the created polygons, which in turn reflects the structural complexity of the understory structure. The single steps of the UCI construction can be viewed in detail in chapter 2. This particular forest layer was chosen to concentrate on tree regeneration as the main driver of understory complexity. However, shrubs and herbs, as well as deadwood, were excluded for the most part and the influence of overstory trees and their leaves on the UCI was mostly reduced. Whether the UCI can be calculated for vegetation below 0.5 m above the ground needs to be tested in further studies. The FD approach to determine structural complexity is quite similar to the one of the stand structural complexity index (SSCI) introduced by Ehbrecht et al. (2017). The main differences between both measures are that for the calculation of the SSCI, multiple, vertical cross-sectional polygons are used instead of one horizontal polygon. Like the SSCI, the UCI can be interpreted as a holistic measure that describes vegetation structure as an entity. It reflects the spatial complexity of the captured understory vegetation between 0.8 m and 1.8 m of a 3D forest scene. The UCI was able to quantify the understory complexity of different forest types and it also proved useful for the assessment of climatic effects on the understory complexity (Seidel et al. 2021). As the UCI refers to the forest layer between 0.8 m and 1.8 m, the use of this index is limited to a certain layer of the forest's understory. However, the development of new indices based on 3D forest scenes is generally associated with methodological progress in the field of TLS and forest ecology. It gives us a better understanding of 3D forest data, allowing us to address new research questions and to answer old ones that could not be addressed so far.

Instead of deriving the shape complexity of polygons, the FD can be also derived by using the box-counting method. This method was used in chapter 3 to determine the structural complexity of different forest strata (lower stratum < 1/3 stand height, middle stratum 1/3 - 2/3 stand height and upper stratum > 2/3 stand height) based on voxelized, multi-scan based 3D point clouds. The box-counting fractal dimension ($D_b$) is an efficient method to measure the spatial arrangement of complex objects. It was successfully used for the analysis of digital binary raster images. Jonckheere et al. (2006) applied the $D_b$ to hemispherical photographs to quantify the spatial complexity of 2D forest canopy. Seidel et al. (2019a, 2019b) and Stiers et al. (2020) used the $D_b$ to determine the fractal dimension of three-dimensional objects, as e.g. trees and forest structure at the stand-level. Applied on 3D forest structure, the $D_b$ describes the number of boxes that are needed to enclose all structural objects in a forest stand. It is calculated as the slope of the fitted straight line through a scatterplot of log (n) over log (1/r). Here, log () is the natural logarithm and n /r is the number of boxes with the size r needed to enclose all points in a 3D point cloud (see chapter 3.3). Our study showed that the $D_b$ approach can be successfully applied in order to calculate the fractal dimension of forest strata and thus can be used as a tool to quantify the structural complexity of certain spatial areas within a forest stand.

## 5.2 Understory complexity in European beech forests along a gradient of management intensity

The first research question (i) was whether the investigated managed beech forests show a similar understory complexity to the primary beech forests. The results of the study clearly indicate that uneven-aged management may result in understory structures that are comparable to beech primary forests (see Figure 5.1, Figure 3.3 a, Figure 3.4 a). However, it has to be mentioned in this context that not all beech primary forests in Europe are characterized by a highly complex understory structure at the stand-level. Our results showed that the beech primary forests in Rožok for instance, showed both, for the UCI and for the $D_b$ lower values in the lower stratum than the primary forest in Uholka (see Figure 2.6, Table 3.2). In general, primary beech forests, where a pronounced decay phase has established, are characterized by a heterogeneous vertical and horizontal understory structure, as it was the case in several investigated stands in Uholka (Commarmot et al. 2005, Sabatini et al. 2015, Trotsiuk et al. 2012). The investigated forest stands in Rožok in contrast, seemed to be in the optimum phase or either in the transition between late optimum phase and decay phase. Unmanaged beech stands, which are in the optimum phase are rather characterized by an understory with a low structural complexity (Boncina, 2000, Commarmot et al. 2005, Firm et al. 2009, Meyer et al. 2003). This can not only be observed for the forest stands in Rožok, but also for the formerly managed stands in the Hainich-Dün region, which are most likely also in the optimum phase (Stiers et al. 2018).

Even though the here investigated managed uneven-aged forests showed a quite similar understory complexity to the primary forests, there are in general structural differences between both forest types. The beech primary forest in Uholka is characterized by a comparably high stand volume. In 2005, Commarmot et al. (2005) measured a mean standing volume of 770 $m^3$/ha (min 421 $m^3$/ha, max 1042 $m^3$/ha) in Uholka. In general, the stand volume in primary beech forests of the Western Carpathians never decreases below 400 $m^3$/ha (Korpel 1995). In contrast, the uneven-aged management system usually aims a standing volume between 360 - 400 $m^3$/ha (Hessenmöller et al. 2012). Also, with regard to the diameter distribution, there are probably differences between managed uneven-aged beech forests and beech primary forests. Uholka was characterized by a predominantly even distribution of trees over a diameter range between 30 - 80 cm, what is typical for beech primary forests (Korpel 1995). Additionally, large trees up to 132.6 cm in diameter were found (Commarmot et al. 2005). Compared to the diameter distribution of beech primary forest, the model diameter distribution of managed uneven-aged beech forests in the Hainich, mainly differs in two points. On the one hand, a smaller number of large trees per ha (> 100 cm in dbh) can be found in uneven-aged beech stands managed by single-tree selection. On the other hand, a higher number of trees around 30 cm can be observed in managed uneven-aged stands (Commarmot et al. 2005, Hessenmöller et al.2012). Beech primary forests tend to have a slight decline around 30 cm in dbh, what was also indicated by the results of the second sub-study (see Figure 3.4 b, between 33 - 66 % stand height). Another structural attribute that is missing in uneven-aged beech forests managed under single-tree selection, but is present in beech primary forests, is the high amount of deadwood (Bauhus et al. 2009, Commarmot et al. 2005).

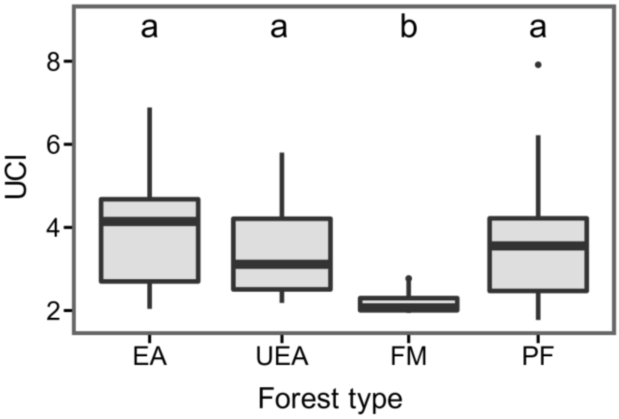

**Figure 5.1:** *Box- and whisker plots showing the understory complexity index (UCI) values for different forest types: EA = Even-aged (n = 16), UEA = Uneven-aged (n = 13), FM = Formerly managed (n = 13), PF = Primary forest (n = 30). Letters indicate significant differences at $p < 0.05$.*

Comparing the different forest types, we found no significant differences for the UCI between the even-aged (EA) and the uneven-aged (UEA) (see Figure 5.1). One explanation for this observation could be that the even-aged management system results in forest stands of different developmental phases, which also contains dense thickets that are characterized by high UCI values (see Table 2.3). Another explanation could be that the regeneration form of the uneven-aged management system also gained in importance in traditional forest management (Schall et al. 2018). Therefore, some mature stands of the even-aged management system may show advanced understory structures that are comparable to those of the uneven-aged management system (see Figure 3.3 a, Table 4.2).

Comparing the different forest types, the lowest UCI values were found for the formerly managed stands, now unmanaged stands in the Hainich-Dün region (see Figure 5.1, Figure 2.6, Table 4.2). Here, it seems that in the formerly managed stands a pronounced regeneration layer has not established yet. However, the unmanaged primary forest in Uholka showed a complex regeneration structure, resulting in significantly higher UCI values compared to formerly managed forests.

As the UCI only quantifies the structural complexity between 0.8 m and 1.8 m, it seems reasonable to use further approaches to determine the structural complexity of the entire lower forest stratum. The results of the second sub-study (Chapter 3) go in line with the results founded in the first sub-study (chapter 1) and in Figure 5.1. The formerly managed stands showed within the entire lower forest stratum a lower structural complexity than the managed forests and the unmanaged primary forests due to a lack of young and advanced regeneration.

## 5.3 Characteristics of structural complexity regarding the spatial distribution and density of plant material

Another main objective of the study was to investigate whether beech forests with a high structural complexity show a different spatial distribution and density of plant material compared to beech forests with a low structural complexity (ii). The results of the second sub-study (chapter 3) showed exemplary at different forest strata that a high structural complexity showed a different distribution and density of plant material than forest strata with a low structural complexity. Forest strata with a rather high $D_b$ were characterized by a rather high density and a random to regular distribution of plant material. This could be observed for the primary beech forests and the uneven-aged beech stands (see Figure 3.3, Figure 3.4). Forest strata with a low $D_b$, as e.g. the lower and middle forest stratum of the formerly managed forests, showed in contrast a rather low density and a clustered distribution of plant material (see Figure 3.3, Figure 3.4). Thus, it seems that $D_b$ increases with increasing density and increasing homogeneity of the spatial distribution of plant material within the forest strata. Our results showed that vegetation density can be a driver of structural complexity (see Figure 2.5), what could be confirmed by several other studies (Marsden et al. 2002, Seidel et al. 2019b, Stiers et al. 2020, Zeide 1991). However, it has to mentioned that an increase in vegetation density only results in an increase in $D_b$, when the additional plant material contributes to the overall homogeneous arrangement.

Our results are in accordance to findings of other studies, which observed a low fractal dimension for objects that are characterized by irregularities resulting in clumped structures and an increasing fractal dimension with increasing regularity, as theoretically demonstrated in Figure 5.2 (Dibble and Thomaz 2009, Jonckheere et al. 2006, Kaye 1994).

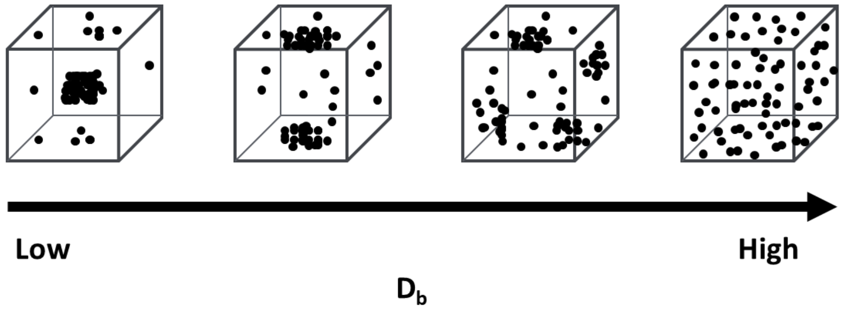

**Figure 5.2:** *Theoretical development of the $D_b$ with an increasing regular distribution of objects within a 3D space.*

Transferred to the stand-level that would mean that a forest stand with a high $D_b$ would be characterized by an evenly distributed, dense vegetation within the 3D space. Indeed, Stiers et al. (2020) found high $D_b$ values for beech-dominated uneven-aged and primary forests, which showed a vertically and horizontally homogeneous distribution of dense plant material. In contrast, forest stands with a low $D_b$ showed indeed low space filling values and a heterogeneous distribution of plant material (Stiers et al. 2020).

In general, the $D_b$ is a useful approach to describe structural complexity of forest stands in terms of the arrangement of plant material. However, the three-dimensional arrangement of vegetation is one of several characteristics of structural complexity. Besides, arrangement, canopy openness and vegetation density, as well as the variability of individual tree structures was used in several studies to determine the structural complexity of forests (Atkins et al. 2018, Gough et al. 2019, Hardiman et al. 2013, 2011). Here, the canopy rugosity was used in order to describe the horizontal and vertical variance of vegetation density throughout the canopy. Forest stands that have a high variability in vegetation density show high canopy rugosity values, as it can be observed in an exemplary primary forest stand in Uholka (see Figure 5.3 b). Forest stands that show a low variability in vegetation structure, so a rather homogeneous distribution of plant material within the stand, are characterized by low canopy rugosity values, like observed for the exemplary uneven-aged stand in Figure 5.3 a. In summary, it is important to keep in mind that there is not one single method to determine the structural complexity of forest stands, because there is no ultimate definition of structural complexity. Therefore, the choice of suitable methods for its assessment remains challenging to a certain extent and needs to be targeted towards the ecosystem function or service in focus (Camarretta et al. 2019).

## 5.4 Effect of silvicultural management on dynamics of structural complexity in European beech forests

The overall study also addressed the research question, how silvicultural management affects dynamics of structural complexity in European beech forests (iii). The management systems considered here differed in thinning and harvesting frequencies, intensities and timing, resulting in different canopy structures at different spatial scales, which regulated short-term and long-term structural dynamics.

Understory complexity and thus also overall structural complexity started to increase in the older immature and mature stands, when management interventions are increasing (see Table 2.3). In the context of even-aged management, reduced thinning and harvesting frequencies and intensities led to a weaker development of understory vegetation, as it could be observed for the alternatively managed beech stands (see Table 2.3).

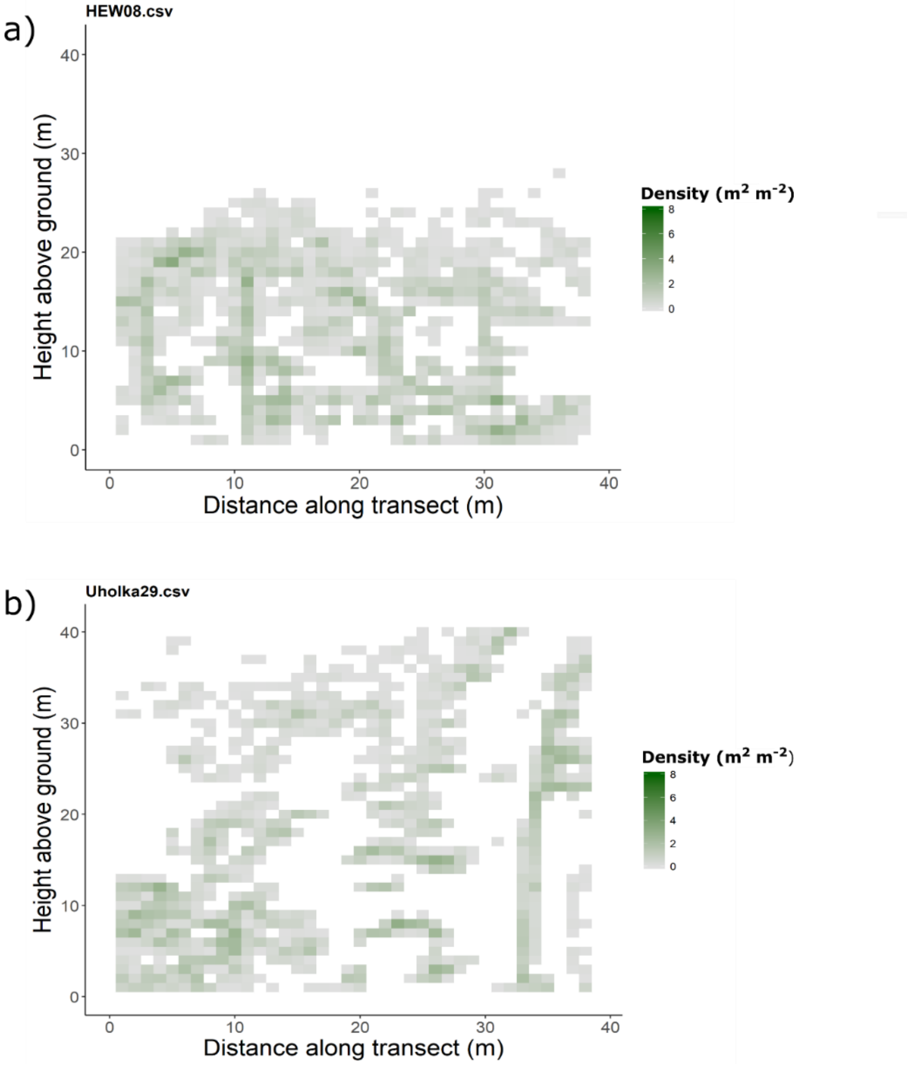

**Figure 5.3:** *Side-profile of an uneven-aged beech stand in the Hainich-Dün region* ***(a)*** *and a beech primary forest in Uholka* ***(b)*** *showing the distribution of vegetation density within the forest stand. The canopy rugosity was 11.70 for transect a) and 46.09 for transect b). Side-profiles and canopy rugosity values were calculated using the R package forestr (Atkins et al. 2018).*

In contrast to the even-aged forest system, uneven-aged management avoids bigger biomass fluctuations at the long-term (Pretzsch 2009). Therefore, continuous interventions of rather low intensity are used and mainly focus on bigger overstory trees (> 50 cm diameter at breast height, see Schall et al. (2018)), resulting in a comparable canopy structure as found for the beech primary forests (see Figure 3.3 c). The continuous removal of overstory trees simulates the natural mortality of the biggest and oldest trees within a primary forest (Pretzsch 2019). Thus, uneven-aged forest management can be seen as an emulation of natural dynamics, resulting in forest stands that are characterized by complex, uneven-aged structures, as they can be found in European beech primary forests (see Figure 3.3 a -c).

At the short-term, management interventions generally had a positive effect on structural dynamics of beech stands (see Figure 4.4 a). Within five years, the majority of the managed (un) even-aged stand showed an increase stand structural complexity. While in the younger stands, the height growth seemed to be the main driver of increasing structural complexity (see Figure A.4.2 b), in the older stands the development and growth of regeneration was mainly responsible for the increase in overall structural complexity (see Figure A.4.2 a). The latter was strongly influenced by the canopy openness, as it could be observed for the uneven-aged stands (see Figure A.4.1).

## 5.5 Limitations of the study

The results of the conducted study provide information about structural characteristics of unmanaged and managed European forests with beech as dominant tree species. Therefore, the findings on the impact of forest management on different aspects of structural complexity cannot be transferred to mixed forests or to forest stands with another dominating tree species in Europe.

For the first and second sub studies (chapter 2 and chapter3), beech forests of three European countries were chosen, which showed slight differences regarding their environmental conditions (e.g. in climate, soil, terrain). We cannot exclude that these environmental differences affected the observed differences in structural complexity to a certain extent (see also Ehbrecht et al. 2021).

Within the frame of this study, two different single-scan approaches were used (see chapter 2.2.2, chapter 4.2.2). In the first sub-study (chapter 2), one forest plot with an area of 20 ha was captured by 30 systematically distributed sample points. For further statistical analyses, one scan was considered as one sample. Thus, the coefficient of variation represents the variability of the UCI within the forest plot. Because only one forest plot was considered for each study site, the variability of the understory structure at larger scales could not been determined. In the second sub-study (chapter 4), a smaller area (1 ha) was considered as one forest plot, in which nine scans were conducted. In contrast to the first sub-study (chapter 2), the values of the structural measures, which were generated for each of the nine scans, were aggregated to one mean value for further statistical analyses. Therefore, a more robust estimate of structural complexity per forest plot was used, while in the first study the structural complexity values rather represent the specific structural conditions of the scan locations. Furthermore, it was possible to determine the variability of structural complexity at a larger-scale, because several forest plots were considered in each study site.

One main methodological limitation of the second sub-study (chapter 3) was the use of relative stand heights for comparing different forest strata. This approach seems useful in order to compare different strata of forests that do not show large differences in stand height. If forest stands are considerably higher than the remaining forest stands, as it was the case between the considered primary forests and the (formerly) managed stands, the use of relative heights clearly showed its limitation. Here, another methodological approach could have been more appropriate for a comparison of different forest strata. For example, instead of using absolute or relative heights, one could use specific structural, functional or environmental conditions (e.g. light conditions) to define forest strata. This would have the advantage that forest strata would not be fixed to the vertical profile (Parker and Brown 2000).

Another limitation of the second sub-study was the small sample size for the different forest types, which was owed to the time-consuming multi-scan approach. For future research projects on quantifying forest structure based on laser scanning, the application of a mobile scanner (MLS) should be considered in order to capture forest structure. Compared to TLS, MLS can capture much larger forest areas in less time and with the same or very similar resolution (Bauwens et al. 2016, Bienert et al. 2018).

TLS measurements were especially difficult to perform in very dense beech regeneration. Here, two methodological factors had to be considered. Firstly, scan locations with very dense beech regeneration had to be avoided in order to ensure the scanner’s operability. Therefore, it is possible that the investigated forest stands are partly characterized by an even higher understory complexity than found in results. Secondly, TLS measurements at locations with dense beech regeneration have as consequence that the field of view of the scanner is limited. The surrounding vegetation intercepts a large part of the laser beams, which means that plant material lying behind it can only be captured to a limited extent. This applies to both the horizontal and vertical axis of a forest stand. Therefore, occlusion effects have to be considered by interpreting the results, especially for the structural characterization of the lower understory and the canopy structure of forests.

## 5.6 Conclusions and remarks on the structural importance of understory complexity

This study showed that 3D forest scenes captured by TLS are versatile to quantify different aspects of structural complexity and their interrelations. Furthermore, the present study contributed to the understanding of how highly complex forests, as e.g. primary beech forests, are structurally characterized, as well as to the question, how different types of forest management affect dynamics of structural complexity of European beech forests. Our study has demonstrated that the lower understory of a forest is a major structural component that influences structural complexity and its dynamics. Furthermore, a complex understory structure can be also seen as preliminary stage of overall structural complexity and may contain many structural attributes that are characteristic for old-growth structures, e.g. vertical and horizontal heterogeneity, dense regeneration, or a high variation in branch systems (Bauhus et al. 2009, Donato et al. 2012). Primary beech forests that have a high stand structural complexity (see Stiers et al. 2018), are characterized by a high understory complexity, which is created by the presence of young and advanced beech regeneration of varying heights and positions. Therefore, one main focus of “management for complexity” should be the creation of complex structures in the lowest forest stratum. Uneven-aged management that aims to simulate natural dynamics, results in quite similar understory structures, as can be found in primary forests. Thus, this management approach can be evaluated as a promising strategy to enhance understory complexity at the long-term and thus positively influence stand structural complexity. With the focus on beech-dominated forests, a main goal of uneven-aged management should be the creation of canopy gaps of different shapes and sizes in different temporal intervals and intensities, because regular distributed canopy gaps created by single-tree harvests may be quickly closed by surrounding overstory trees due to lateral crown expansion (Feldmann et al. 2018, Schütz et al. 2016).

Furthermore, the study contributed to the understanding of how structural complexity changes with progressing succession of beech forests; from stand initiation over stem exclusion to understory re-initialization due to gap formation. We observed high dynamics of understory complexity in the early-successional stages, due to a high growth response of beech regeneration on the canopy release. Without external disturbances, this even-aged, single-layered forest structure determines dynamics of structural complexity over decades, as it firstly leads during the self-pruning and self-thinning phase to a decrease of understory complexity and then to a stagnation of understory dynamics (see formerly managed stands) until the decay phase establishes (see primary forests in Uholka) or harvest interventions start (see (un) even-aged mature stands). Based on these findings, mainly two conclusions can be drawn in the context of “management for complexity”. Traditional forest management, e.g. shelterwood system, does not *per se* lead to low levels of structural complexity. The most critical developmental phases with low structural complexity are the early- and mid-successional stages, with beginning canopy closure. If the enhancement of structural complexity is desired, management interventions could also focus more on early developmental stages, instead of only focusing on the creation of late-successional structures in mature stands, as it was already thematized in further studies.

A further main conclusion of our study is that passive management, as e.g. setting forest stands that are in optimum phase aside in order to establish complex structures may last several decades in European beech forests, what can also be attributed to the longevity of beech. If an acceleration of the establishment of complex structures is desired, the creation of canopy gaps of different sizes and shapes before ceasing management could be a possible approach, to promote understory dynamics at the short-term (Stiers et al. 2018). In forests, which have been affected by a stand-replacing disturbance event, a modulation of the conventional forest development (stand initiation over stem exclusion to understory re-initialization due to gap formation) could be considered in order to promote complex understory structures (Donato et al. 2012). This would reduce the dependence on the establishment of late-successional stages to create complex understory structures. Here, further studies are needed to evaluate, which approaches could be suggested for managed and unmanaged European forests, especially with beech being the dominant tree species to create early-seral structural complexity.

## 5.7 References

Atkins, J.W., Bohrer, G., Fahey, R.T., Hardiman, B.S., Morin, T.H., Stovall, A.E.L., (…), Gough, C.M. (2018). Quantifying vegetation and canopy structural complexity from terrestrial Li DAR data using the FORESTR R package. Methods of Ecology and Evolution, 9, 2057-2066. https://doi.org/10.1111/2041-210X.13061.

Bauhus, J., Puettmann, K., Messier, C. (2009). Silviculture for old-growth attributes. Forest Ecology and Management, 258, 525-537. https://doi.org/10.1016/j.foreco.2009.01.053.

Bauwens, S., Bartholomeus, H., Calders, K., Lejeune, P. (2016). Forest inventory with terrestrial LiDAR: A comparison of static and hand-held mobile laser scanning. Forests, 7, 127. https://doi.org/10.3390/f7060127.

Bienert, A., Georgi, L., Kunz, M., Maas, H.G., Von Oheimb, G. (2018). Comparison and combination of mobile and terrestrial laser scanning for natural forest inventories. Forests, 9, 395. https://doi.org/10.3390/f907039.

Boncina, A. (2000). Comparison of structure and biodiversity in the Rajhenav virgin forest remnant and managed forest in the Dinaric region of Slovenia. Global Ecology and Biogeography, 9, 201-211. https://doi.org/10.1046/j.1365-2699.2000.00155.x.

Boudon, F., Godin, C., Pradal, C., Puech, O., Sinoquet, H. (2006). Estimating the fractal dimension of plants using the two-surface method: An analysis based on 3d-digitized tree foliage. Fractals, 14, 149-163. https://doi.org/10.1142/S0218348X06003179.

Camarretta, N., Harrison, P.A., Bailey, T., Potts, B., Lucieer, A., Davidson, N., Hunt, M. (2019). Monitoring forest structure to guide adaptive management of forest restoration: A review of remote sensing approaches. New Forests, 51, 573-596. https://doi.org/10.1007/s11056-019-09754-5.

Commarmot, B., Bachofen, H., Bundziak, Y., Bürgi, A., Shparyk, Y., Sukhariuk, D., (…), Zingg, A. (2005). Structures of virgin and managed beech forests in Uholka (Ukraine) and Sihlwald (Switzerland): A comparative study. Forest, Snow and Landscape. Research, 79, 45-56.

Dibble, E.D., Thomaz, S.M. (2009). Use of fractal dimension to assess habitat complexity and its influence on dominant invertebrates inhabiting tropical and temperate macrophytes. Journal of Freshwater Ecology, 24, 93-102. https://doi.org/10.1080/02705060.2009.9664269.

Donato, D.C., Campbell, J.L., Franklin, J.F. (2012). Multiple successional pathways and precocity in forest development: can some forests be born complex? Journal of Vegetation Science, 23, 576-584. https://doi.org/10.1111/j.1654-1103.2011.01362.x.

Dorji, Y., Annighöfer, P., Ammer, C., Seidel, D. (2019). Response of beech (*Fagus sylvatica* L.) trees to competition - New Insights from Using Fractal Analysis. Remote Sensing ,11, 2656. https://doi.org/10.3390/rs11222656.

Ehbrecht, M., Schall, P., Ammer, C., Seidel, D. (2017). Quantifying stand structural complexity and its relationship with forest management, tree species diversity and microclimate. Agricultural and Forest Meteorology, 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. Forest Ecology and Management, 380, 212-223. https://doi.org/10.1016/j.foreco.2016.09.003.

Ehbrecht, M., Seidel, D., Annighöfer, P., Kreft, H., Köhler, M., Zemp, D.C., (…), Ammer, C. (2021). Global patterns and climatic controls of forest structural complexity. Nature Communications, 12, 519. https://doi.org/10.1038/s41467-020-20767-z.

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. Forest Ecology and Management, 415-416, 38-46. https://doi.org/10.1016/j.foreco.2018.02.022.

Firm, D., Nagel, T.A., Diaci, J. (2009). Disturbance history and dynamics of an old-growth mixed species mountain forest in the Slovenian Alps. Forest Ecology and Management, 257, 1893-1901. https://doi.org/10.1016/j.foreco.2008.09.034.

Gough, C.M., Atkins, J.W., Fahey, R.T., Hardiman, B.S. (2019). High rates of primary production in structurally complex forests. Ecology, 100. https://doi.org/10.1002/ecy.2864.

Hardiman, B.S., Bohrer, G., Gough, C.M., Vogel, C.S., Curtis, P.S. (2011). The role of canopy structural complexity in wood net primary production of a maturing northern deciduous forest. Ecology, 92, 1818-1827. https://doi.org/10.1890/10-2192.1.

Hardiman, B.S., Gough, C.M., Halperin, A., Hofmeister, K.L., Nave, L.E., Bohrer, G., Curtis, P.S. (2013). Maintaining high rates of carbon storage in old forests: A mechanism linking canopy structure to forest function. Forest Ecology and Management, 298, 111-119. https://doi.org/10.1016/j.foreco.2013.02.031.

Hessenmöller, D., Fritzlar, D., Schulze, E. D. (2012). Die Buchenplenterwälder in Thüringen. Allgemeine Forstzeitschrift für Waldwirtschaft und Umweltvorsorge, 12, 4-7.

Jonckheere, I., Nackaerts, K., Muys, B., van Aardt, J., Coppin, P. (2006). A fractal dimension-based modelling approach for studying the effect of leaf distribution on LAI retrieval in forest canopies. Ecological Modelling, 197, 179-195. https://doi.org/10.1016/j.ecolmodel.2006.02.036.

Kaye, B.H. (1994). A random walk through fractal dimensions. VCH, Weinheim, New York.

Korpel, Š. (1995). Die Urwälder der Westkarpaten: 39 Tabellen. Gustav Fischer, Stuttgart.

Mandelbrot, B.B. (1975). Stochastic models for the Earth's relief, the shape and the fractal dimension of the coastlines, and the number-area rule for islands. Proceedings of the National Academy of Sciences, 72, 3825-3828. https://doi.org/10.1073/pnas.72.10.3825.

Marsden, S.J., Fielding, A.H., Mead, C., Hussin, M.Z. (2002). A technique for measuring the density and complexity of understorey vegetation in tropical forests. Forest Ecology and Management, 165, 117-123. https://doi.org/10.1016/S0378-1127(01)00653-3.

Meyer, P., Tabaku, V., v. Lupke, B. (2003). Die Struktur albanischer Rotbuchen-Urwalder - Ableitungen fur eine naturnahe Buchenwirtschaft. Structural Characteristics of Albanian Beech (*Fagus sylvatica* L.) Virgin Forests - Deductions for Semi-Natural Forestry. Forstwissenschaftliches Centralblatt, 122, 47-58. https://doi.org/10.1046/j.1439-0337.2003.02041.x.

Muscolo, A., Bagnato, S., Sidari, M., Mercurio, R. (2014). A review of the roles of forest canopy gaps. Journal of Forestry Research, 25, 725-736. https://doi.org/10.1007/s11676-014-0521-7.

Parker, G.G, Brown, M.J. (2000) Forest canopy stratification - Is it useful? The American Naturalist,155,473-84. https://doi.org/10.1086/303340.

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.

Sabatini, F.M., Burrascano, S., Lombardi, F., Chirici, G., Blasi, C. (2015). An index of structural complexity for Apennine beech forests. iForest - Biogeosciences and Forestry, 8, 314. https://doi.org/10.3832/ifor1160-008.

Schall, P., Ammer, C. (2013). How to quantify forest management intensity in Central European forests. European Journal of Forest Research, 132, 379-396. https://doi.org/10.1007/s10342-013-0681-6.

Schall, P., Gossner, M.M., Heinrichs, S., Fischer, M., Boch, S., Prati, D., (…), Ammer, C. (2018). The impact of even-aged and uneven-aged forest management on regional biodiversity of multiple taxa in European beech forests. Journal of Applied Ecology, 55, 267-278. https://doi.org/10.1111/1365-2664.12950.

Schütz, J.-P., Saniga, M., Diaci, J., Vrška, T. (2016). Comparing close-to-nature silviculture with processes in pristine forests: lessons from Central Europe. Annals of Forest Science, 73, 911-921. https://doi.org/10.1007/s13595-016-0579-9.

Seidel, D. (2018). A holistic approach to determine tree structural complexity based on laser scanning data and fractal analysis. Ecology and Evolution, 8, 128-134. https://doi.org/10.1002/ece3.3661.

Seidel, D., Annighöfer, P., Stiers, M., Zemp, C.D., Burkardt, K., Ehbrecht, M., (…), Ammer, C. (2019a). How a measure of tree structural complexity relates to architectural benefit-to-cost ratio, light availability, and growth of trees. Ecology and Evolution, 9, 7134-7142. https://doi.org/10.1002/ece3.5281.

Seidel, D., Ehbrecht, M., Annighöfer, P., Ammer, C. (2019b). From tree to stand-level structural complexity — Which properties make a forest stand complex? Agricultural and Forest Meteorology, 278, 107699. https://doi.org/10.1016/j.agrformet.2019.107699.

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

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 and People, 1, 100004. https://doi.org/10.1016/j.tfp.2020.100004.

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. Forest Ecology and Management, 430, 357-365. https://doi.org/10.1016/j.foreco.2018.08.039.

Trotsiuk, V., Hobi, M.L., Commarmot, B. (2012). Age structure and disturbance dynamics of the relic virgin beech forest Uholka (Ukrainian Carpathians). Forest Ecology and Management, 265, 181-190. https://doi.org/10.1016/j.foreco.2011.10.042.

## Chapter 5

Zeide, B. (1991). Fractal geometry in forestry applications. Forest Ecology and Management, 46, 179-188. https://doi.org/10.1016/0378-1127(91)90230-S.

Zenner, E.K., Peck, J.E., Hobi, M.L., Commarmot, B. (2015). The dynamics of structure across scale in a primaeval European beech stand. Forestry, 88, 180-189. https://doi.org/10.1093/forestry/cpu042.

Zhu, J., Wang, X., ChenJunqi, Huang, H., Yang, X. (2014). Estimating fractal dimensions of tree crowns in 3-D space based on structural relationships. The Forestry Chronicle, 90. https://doi.org/10.5558/tfc2014-035.

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## Declaration of honor

I declare that I independently prepared this dissertation entitled “Quantifying three-dimensional stand structure of European beech forests along a management gradient” and that I did not use any literature or resources other than those indicated. I further declare that the digital version is identical with the printed version in content and wording.

Additionally, I confirm that this dissertation has never been submitted in any form as part of any other dissertation procedure.

Göttingen, 30.10.2021