Quantifying three-dimensional stand structure and its relationship with forest management and microclimate in temperate forest ecosystems

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Summary

Forest management modifies the spatial structure of forest ecosystems, which is considered to be relevant for habitat availability and biodiversity as well as several ecosystem processes and functions. Contrary to tree-attribute based measures of stand structure, laser scanning-based approaches allow to quantify the structure of forest ecosystems holistically with high detail and accuracy. In order to investigate impacts of forest management on three-dimensional stand structure and its relationship with forest microclimate, metrics and indices were developed within the frame of this work that quantify stand structure based on 3D point clouds obtained from terrestrial laser scanning.

First, the effective number of layers (ENL) was introduced as a measure to describe the vertical structure of forest stands (chapter 2). By applying diversity indices to the vertical distribution of foliage and woody components, different stand types could be differentiated based on their vertical structure and its horizontal variability. ENL values increased with increasing stand height and a more even filling of vertical layers with foliage and woody components.

Subsequently, a stand structural complexity index was developed, which is based on the fractal dimension of cross-sectional polygons through a forest stand, which were derived from single terrestrial laser scans (chapter 3). As the fractal dimension itself is a scale-independent measure to quantify object complexity, ENL was used to scale index values by taking vertical structure into account. The resulting stand structural complexity index (SSCI) intended to quantify the complexity of three-dimensional stand structure holistically, without taking individual tree attributes into account. SSCI values increased from low to high tree size variability, tree size differentiation and decreased with increasing regularity of tree spacing patterns. Moreover, the newly developed index was able to differentiate differently managed stands with different main tree species and was correlated with microclimatic variables.

Based on these findings and the hypotheses that several ecosystem processes and functions are affected by microclimatic conditions, the stand structural drivers of the diurnal temperature range (microclimatic indicator) were investigated in chapter 4. In this context, it was shown that canopy openness and a multi-layered vertical structure are the main structural drivers of the diurnal temperature range in temperate forests. The diurnal temperature range decreased with decreasing canopy openness and increasing vertical differentiation.

Ultimately, SSCI was then used to investigate impacts of forest management on stand structural complexity in temperate forest ecosystems (chapter 5). Based on subsets of 150, 1 hectare sized experimental forest research plots, representing major stand types in Central Europe, it was shown that even-aged forest management negatively impacts stand structural complexity on stand level compared to uneven-aged forest management and unmanaged forest, whereas it creates a wide variety of structural conditions on landscape scale. Moreover, tree species composition and mixing affect stand structural complexity, whereby broadleaved stands with European beech (*Fagus sylvatica*) as main trees are characterized by a significantly higher structural complexity than coniferous stands with Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*). In this context, an increasing basal area share of coniferous trees resulted in decreasing stand structural complexity. Knowing the direct structural drivers of forest microclimate from chapter 4, indirect effects of forest management on the diurnal temperate range were additionally investigated and compared between even-aged, uneven-aged and unmanaged forests. It was shown that effects of forest management on microclimatic conditions are more pronounced in even-aged forest management systems than in uneven-aged systems and unmanaged forests, mainly due to the removal of shelterwood at the end of a management cycle.

The metrics and indices introduced in this study showed a high explanatory power in order to reveal relationships between forest management, stand structure and microclimate. Beyond the use as explanatory variables for research purposes, they might be further considered to be used to monitor long-term forest development, since terrestrial laser scanning proved to be an efficient and rapid method for data acquisition.

Zusammenfassung

Waldbewirtschaftung beeinflusst und verändert die räumliche Struktur von Waldökosystemen, welche nicht nur für Habitatverfügbarkeit und Biodiversität von Bedeutung ist, sondern auch für verschiedene Ökosystemprozesse und –funktionen. Im Gegensatz zu baumbezogenen Maßen der Bestandesstruktur ermöglichen Verfahren auf Grundlage terrestrischen Laserscannings (TLS) eine holistische Quantifizierung der Bestandesstruktur in hoher Auflösung. Im Rahmen dieser Arbeit wurden Maße und Indices entwickelt, die die Bestandesstruktur auf Grundlage TLS-basierter,

dreidimensionaler Punktwolken quantifizieren, um die Effekte von Waldbewirtschaftung auf die dreidimensionale Bestandesstruktur und das Bestandesklima zu untersuchen.

Zunächst wurde die effektive Anzahl an Schichten (engl.: effective number of layers, ENL) als Maß zur Beschreibung der vertikalen Bestandesstruktur eingeführt (Kapitel 2). Durch die Anwendung von Diversitätsindizes auf die vertikale Verteilung von Laub und Holz konnten unterschiedlich bewirtschaftete Bestände anhand der Vertikalstruktur und ihrer horizontalen Variabilität unterschieden werden. Die effektive Anzahl an Schichten steigt mit zunehmender Bestandeshöhe und einer gleichmäßigeren Raumbefüllung einzelner Schichten entlang der vertikalen Achse.

Darauf aufbauend wurde ein Index zur Beschreibung der strukturellen Komplexität entwickelt (engl.: stand structural complexity index, SSCI). Dieser Index basiert auf der fraktalen Dimension von Polygonen, die einen Querschnitt durch den Bestand auf Grundlage einzelner Laserscans darstellen (Kapitel 3). Die fraktale Dimension ist ein Maß zur Quantifizierung der Komplexität von Objekten und skalenunabhängig. Zur Skalierung der fraktalen Dimension der Querschnittspolygone wurde die effektive Anzahl an Schichten herangezogen. Der daraus resultierende SSCI ermöglichte eine holistische Quantifizierung der dreidimensionalen Bestandesstruktur, ohne Einbezug individueller Baumattribute. SSCI nahm mit zunehmender Baumgrößenvariabilität und Baumgrößendifferenzierung höhere Werte, sowie mit zunehmender Gleichmäßigkeit der Baumverteilungen niedrigere Werte an. Zudem war der neu entwickelte Index in der Lage unterschiedlich bewirtschaftete Bestände mit unterschiedlichen Hauptbaumarten zu differenzieren und war darüber hinaus mit mikroklimatischen Variablen korreliert.

Auf Grundlage dieser Erkenntnisse und der Hypothese, dass verschiedene Ökosystemprozesse und -funktionen durch das Mikroklima beeinflusst werden, wurden in Kapitel 4 die Zusammenhänge zwischen verschiedenen Strukturvariablen und der mittleren, täglichen Temperaturamplitude untersucht. In diesem Zusammenhang konnte gezeigt werden, dass die Öffnung des Kronendachs (*canopy openness*) sowie eine mehrschichtige Vertikalstruktur die hauptsächlichen, strukturellen Treiber der täglichen Temperaturamplitude sind. Eine abnehmende Öffnung des Kronendaches sowie eine höhere vertikale Differenzierung der Bestandesstruktur resultierten in einer geringeren täglichen Amplitude der Lufttemperatur.

Aufbauend auf dem in Kapitel 3 entwickelten Index zur Beschreibung struktureller Komplexität (SSCI), wurde abschließend der Zusammenhang zwischen Bewirtschaftungssystem und der strukturellen Komplexität in temperaten Waldökosystemen untersucht. Auf der Grundlage von Teilmengen von 150, jeweils 1 Hektar großen experimentellen Langzeitforschungsflächen, die in Mitteleuropa vorherrschende Waldtypen repräsentieren, konnte gezeigt werden, dass Altersklassenwälder eine geringere strukturelle Komplexität auf Bestandesebene aufweisen als Plenterwälder und aus der Bewirtschaftung genommene Bestände. Allerdings entsteht durch das räumliche Nebeneinander von unterschiedlich alten Beständen im Altersklassenwald eine Vielfalt an Strukturen auf Landschaftsebene. Zudem konnte gezeigt werden, dass Baumarten-zusammensetzung und -mischung die strukturelle Komplexität beeinflussen, wobei Laubholzbestände mit Rotbuche (*Fagus sylvatica*) als Hauptbaumart durch signifikant höhere SSCI-Werte charakterisiert waren als Nadelholzbestände mit Fichte (*Picea abies*) oder Kiefer (*Pinus sylvestris*) als Hauptbaumart. In diesem Zusammenhang führte ein zunehmender Grundflächenanteil von Nadelbäumen zu einer niedrigeren strukturellen Komplexität. Mit dem Wissen über den Zusammenhang zwischen Struktur und Mikroklima aus Kapitel 4, wurden die indirekten Effekte der Waldbewirtschaftung auf die tägliche Temperaturamplitude abschließend untersucht und zwischen den Betriebsformen Altersklassenwald und Plenterwald sowie unbewirtschafteten Flächen untersucht. Es zeigte sich, dass Bewirtschaftungseffekte auf mikroklimatische Bedingungen im Altersklassenwald ausgeprägter sind als in Plenterwäldern oder unbewirtschafteten Beständen. Diese Unterschiede ließen sich hauptsächlich auf die Entnahme des Altholzschirms im Rahmen der Endnutzung zurückführen.

Table of contents

1. Introduction

1.1. Scope and background of this study

The global loss of biodiversity is associated with a decline in ecosystem functioning and human welfare (Butchart et al. 2010, Hooper et al. 2012, Cardinale et al. 2012, Crist et al. 2017). Climate change and anthropogenic disturbances are important drivers of the current biodiversity decline and alter ecosystem functions such as productivity (Liang et al. 2016, Hui et al. 2017), decomposition (Handa et al. 2014, Joly et al. 2017), and nutrient cycling (Bernal et al. 2012, Duran et al. 2017), whereby anthropogenic impacts include changes in land use or increases in land-use intensity (Durigan et al. 2017, Phillips et al. 2017, Tieskens et al. 2017). Regarding forest ecosystems, deforestation and unsustainable forest management practices are viewed as major drivers of a decline in biodiversity and ecosystem functioning (Lindenmayer et al. 2000, Barlow et al. 2016). In this context, numerous studies highlighted the functional relevance of forest structure for habitat availability and biodiversity conservation, as well as ecosystem processes and functions (e.g. Ishii et al. 2004, Kucharik et al. 2000, Ryan 2002, Ruiz-Benito et al. 2014). As more than 50% of the planet`s terrestrial biota are thriving in forest ecosystems, forests and their spatial structure play a major role in biodiversity conservation and the maintenance of ecosystem functions (Hooper et al. 2005, Latimer and Zuckerberg 2017).

With regard to biodiversity and habitat availability, it was shown that forests with heterogeneous structures promote diversity of some taxa (Mac Arthur and Mac Arthur 1961, Boncina 2000, Schall et al. 2017a). Regarding ecosystem functions, several studies suggested that structural diversity (Dănescu et al. 2016), or complexity (Hardiman et al. 2011), and/or tree species diversity (Liang et al. 2016) may promote productivity. Moreover, forests with heterogeneous structures are often associated with higher ecosystem stability and resilience against disturbances (Dobbertin 2002). An increased stability and resilience could be beneficial to the maintenance and continuity of ecosystem functions such as nutrient or water cycling. Furthermore, complex structured forests are viewed as being more adaptable to changing environmental conditions (Bolte et al. 2009, Kolström et al. 2011, Messier et al. 2015). Against this background, the functional relevance of structure has been increasingly acknowledged by public forest management administrations in Central Europe and North America and silvicultural concepts were developed that aim at increasing the heterogeneity of forest structure (Messier et al. 2012, Puettmann et al. 2015). In this context, the analysis of stand

structures is a meaningful management tool, since many management decisions are based on structural information (Mueller et al. 2000).

Forest structure – termed stand structure on stand level - is commonly defined by the spatial distribution of trees, tree species composition and diversity, and tree size variability (e.g. Pommerening 2002, v. Gadow 2012, Schall et al. 2017b). Whereas stand structure is usually used as an umbrella term that is characterized by one or more of these components, definitions can also include other ecosystem components such as deadwood (see McElhinny et al. 2005). These components are usually quantified by stand structural attributes (SSA) that intend to describe single aspects or dimensions of structure (e.g. vertical, horizontal or compositional). Several measures have been developed, proposed or used to quantify the spatial distribution of trees, tree species composition and diversity or tree size variability, or combinations of single attributes to describe structural complexity (see Fig. 1.1). Pommerening (2002), McElhinny et al. (2005), del Río et al. (2016), and Schall et al. (2017b) provide detailed reviews of stand structural measures and complexity indices. With reference to Pommerening (2002), stand structural measures can be broadly classified into position-dependent and position-independent measures of stand structure. Position-dependent measures take individual tree positions into account and describe patterns of tree spacing (e.g. Clark Evans Index of aggregation, Pielou`s index of segregation) or intermingling of tree sizes or tree species (e.g. Füldner`s index of tree size differentiation).

Position-independent measures of stand structure include stand summary measures such as stem density (N ha^{-1}), basal area (m^2 ha^{-1}), (quadratic) mean diameter at breast height (dbh; in cm) and its standard deviation or coefficient of variation, or volume (m^3) or biomass (Mg) of the growing stock. Furthermore, measures like the Shannon or Simpson-Index are frequently used to quantify species diversity (Jost 2006). Both, position-dependent and position-independent measures are based on tree attributes, such as diameter, height, position or species identity. Other options to measure stand structure include approaches to quantify structure holistically, taking the three-dimensional distribution of foliage and woody components in space into account (Pretzsch 2009, Seidel et al. 2016).

Stand structure

Spatial distribution   **Tree species diversity**   **Tree size variability**

Tree attribute based measures of forest structure   **Holistic measures of forest structure**

Position-dependent measures to characterize forest structure at stand level

Neighborhood based measures to characterize small-scale structural differences

Contagion (Füldner 1995)
Species mingling (Füldner 1995)
Size differentiation (Füldner 1995)

Clark Evans index of aggregation (Clark & Evans 1954)
Pielou`s index of segregation (Pielou 1977)
Structural complexity index (Zenner & Hibbs 2000)

Continuous functions to describe forest structure

Pair correlation function
Mark correlation function
L-, K-function (Ripley 1976)

Position-independent measures to characterize forest structure at stand level

Basal area
Stem density
Mean, SD, CV of tree diameter
Diameter distributions
Stand volume/biomass
Shannon Index
Simpson Index

Single perspective measures of forest structure

Canopy openness
Effective number of layers
Stand structural complexity index
Leaf area index/density

Multi perspective measures of forest structure

Canopy cover
Space filling
Effective number of layers
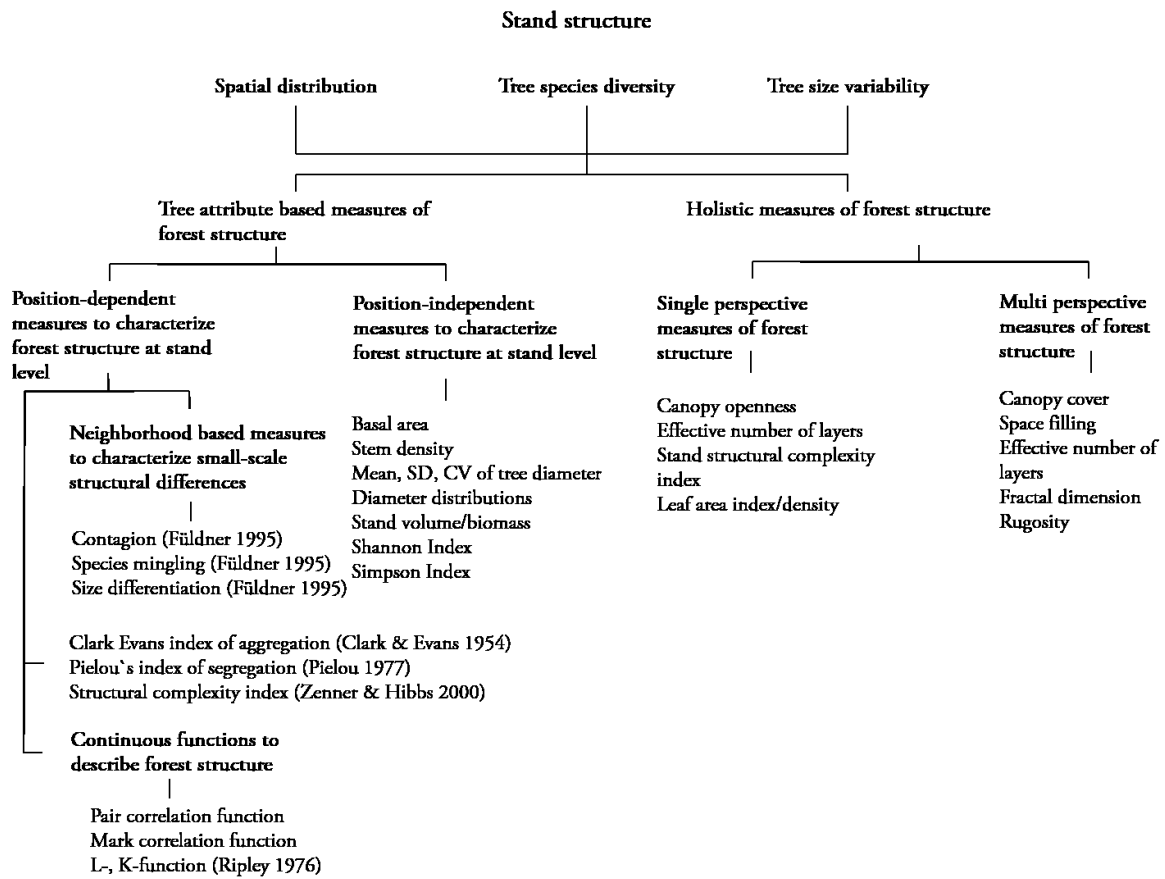Fractal dimension
Rugosity

Figure 1.1: Components and measures of stand structure (modified after Pommerening, 2002).

Here, the author introduces the category of holistic measures and differentiates between single- and multi-perspective measures (see Fig. 1.1). The main difference to conventional approaches for quantifying stand structure is that holistic approaches operate on stand level without taking individual tree attributes into account. In this context, commonly used single- and multi-perspective measures would include canopy openness or canopy cover. While canopy openness describes the sky proportion that is not covered by foliage or woody components from a single point (single-perspective), canopy cover is the percentage of ground covered by a vertical canopy projection (Jennings et al. 1999). Thus, canopy cover requires information about space that is not visible from a single point due to occlusion. Hence, the canopy needs to be assessed from several perspectives, which is why the author decided to term measures of this category as multi-perspective measures.

One focus of this study is the development and introduction of holistic single- and multi-perspective measures to quantify stand structure based on light detection and ranging (LiDAR).

For this reason, a brief introduction on LiDAR applications in forestry and forest ecology will be given in the following, before the main objectives of this work are specified in the next chapter.

Within the past 15 years, Light Detection And Ranging (LiDAR) based approaches have been increasingly used in forest ecological research. LiDAR – also termed laser scanning – is a surveying method that actively senses surfaces to capture the geometry of the sensed object or site (Vosselmann and Maas 2010). Laser scanners emit laser pulses into their surroundings, which are then reflected and/or scattered by solid surfaces and registered by the emitting device (Seidel et al. 2016). Spatial information on scanned objects is then quantified in the form of three-dimensional point clouds in Cartesian or spherical coordinates. Generally, LiDAR systems are based on two different measurement methods: phase-shift or time-of-flight sensors (Pueschel et al. 2013). Phase-shift sensors use phase differences between emitted and received laser beams to measure distances between sensor and sensed object, whereas time-of-flight sensors measure the time difference between beam emission and registration (Wulder et al. 2013). Furthermore, discrete-return and waveform-recording devices can be distinguished. Whereas discrete-return sensors are able to record a discrete number of returns (e.g. first or the last pulse return per laser beam), full waveform LiDAR systems sense the amount of returned energy in different time intervals and therefore allow for multiple return per emitted laser beam (Lim et al. 2003). LiDAR sensors may be attached to airborne (ALS), stationary (TLS) or mobile (MLS) terrestrial platforms (Lin et al. 2010). The use of ALS-systems for forestry or forest science purposes dates back to the 1980`s and they have been increasingly used to assess forest biomass and canopy metrics (Wulder et al. 2013). ALS-systems can be used to assess large forest areas by being attached to airplanes or unmanned-areal-vehicles (UAV), but may only capture a limited amount of information on trees and vegetation beneath the main canopy due to occlusion (Hilker et al. 2012). TLS-systems are commonly used to assess detailed information on single trees and were used to assess standing volume, biomass, and crown characteristics, among others (e.g. Seidel et al. 2011, Astrup et al. 2014, Bayer et al. 2014). More information about structural metrics that were derived from TLS data in forest ecosystems is discussed in chapter 2.1. Approaches to acquire TLS data can be distinguished in single- and multiple-scan approaches. Multiple-scan approaches are used to assess an object (e.g. a tree) from more than one perspective in order to fully capture the three-dimensionality of the sensed object. Multiple-scan approaches capture more information about the sensed object than a single-scan

approach, but require more time for fieldwork and post-processing. Single-scan approaches are used to assess the surrounding environment from a single perspective, which requires less intensive fieldwork and post-processing, but resulting point clouds are affected by occlusion (van der Zande et al. 2006). With regard to the classification of holistic structural measures (Fig. 1.1), metrics derived from single-scan approaches can be classified as single-perspective measures, whereas metrics derived from multiple-scan approaches can be classified as multi-perspective measures of stand structure. Information on effects of single- and multiple-scan approaches on data quality and measures that can be derived from respective approaches is discussed in chapter 2. The development of holistic single- and multi-perspective measures of stand structure based on TLS-data is the focus of chapter 2 and 3 of this study. A detailed review of other TLS applications for forestry and forest science purposes can be found in Seidel (2011) and Newnhamn et al. (2015).

1.2. Theoretical framework, hypotheses and outline

The specific structure of a forest is altered by tree growth, competition, mortality, as well as natural disturbances and forest management (Mueller et al. 2007). Forest management modifies stand structure directly through silvicultural interventions (A, Fig. 1.2), which may simplify or diversify the structural properties on tree and/or stand level (Pretzsch 2009). Thus, structure-bound ecosystem processes and functions can be indirectly affected by forest management (B, Fig. 1.2) through modifications of stand structure. Ecosystem functions are ecological processes that regulate nutrient, organic matter or energy fluxes within an ecosystem, which include processes such as primary production, nutrient cycling and decomposition, amongst others (Teuscher et al. 2015). These processes may depend on the microclimatic conditions within a forest (Parker et al. 2004, Fravolini et al. 2016). Thus, relationships between components of stand structure and ecosystem functions can be direct (C, Fig. 1.2, e.g. tree species or structural diversity can enhance productivity (Liang et al. 2016, Dănescu et al. 2016)) or indirect (E, Fig. 1.2), by being bound to microclimatic conditions that in turn may depend on stand structural properties (D, Fig. 1.2, Hardwick et al. 2015, Kovács et al. 2017). The hypothetical direct and indirect relations between stand structure, forest management, microclimate and ecosystem processes and functions are illustrated in figure 1.2.
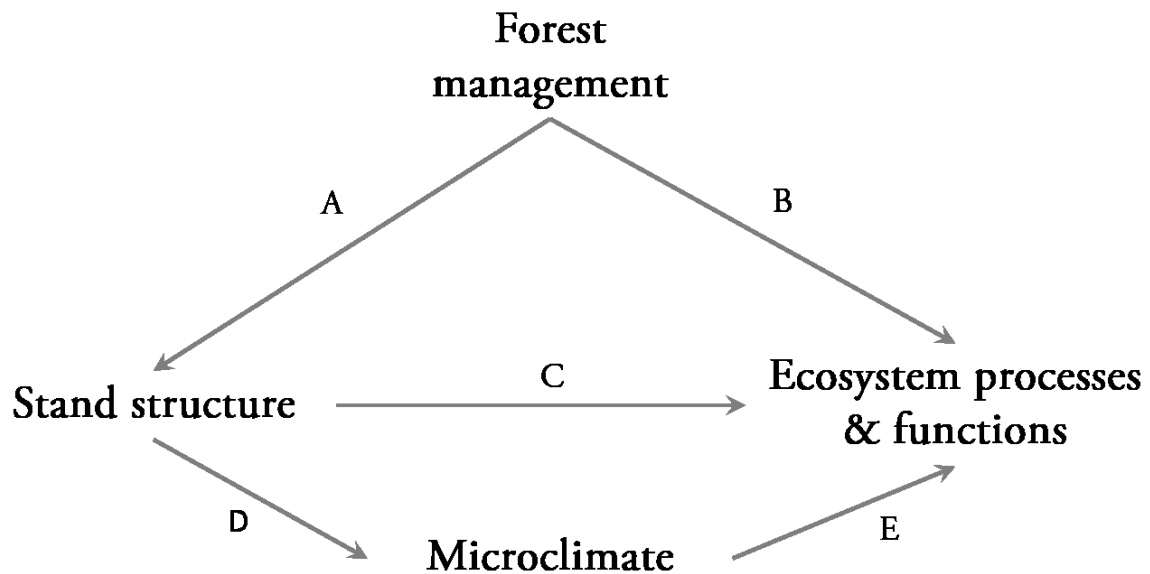
Figure 1.2: Hypothetic direct and indirect relationships between stand structure, forest management, microclimate and ecosystem processes and functions.

The objective of this study is to contribute to a better understanding of forest management impacts on biodiversity and ecosystem processes and functions (B, Fig. 1.2). A main focus is given to the development of new measures based on terrestrial laser scanning in order to quantify the 'three-dimensional nature of stand structure' (Pretzsch 2009). Using the newly developed measures, the following hypotheses shall be tested (methods and statistical analyses that were used to test these hypotheses are described in Appendix II).

(i)   Unmanaged and uneven-aged forests show a higher stand structural complexity than even-aged forests.

(ii)   Mixed species stands show a higher stand structural complexity than pure stands.

(iii)   Microclimate in unmanaged forests is characterized by lower mean diurnal temperature ranges than in managed forests.

First, a new measure of vertical structure – the effective number of layers - is introduced in chapter 2. In this context, its capability to differentiate differently managed stands is explored and its relationship with stand summary measures is tested. Moreover, approaches using different data acquisition designs and their effect on information quality are tested. Second, chapter 3 introduces a stand structural complexity index (SSCI), whereby ENL is one of two index components. Here, the newly developed SSCI is compared to tree-attribute based measures of stand structural

complexity, heterogeneity, or tree size variability and its explanatory power regarding microclimate is tested. In this context, the stand structural complexity of different stands is compared and tree species diversity as a driver of stand structural complexity is tested and discussed. Third, based on findings of chapter 3, effects of stand structure on microclimate in temperate forest ecosystems are investigated in more detail. Here, the potential of terrestrial laser scanning to provide explanatory variables for modelling approaches is further highlighted.

1.3. The Biodiversity Exploratories

This study was conducted within the frame of the Biodiversity Exploratories and funded by the German Research Foundation (DFG). The Biodiversity Exploratories are an interdisciplinary research platform for functional biodiversity research with a focus on understanding interdependencies between biodiversity of different taxa and levels, the impact of land use on biodiversity and the relevance of biodiversity for ecosystem functioning (Fischer et al. 2010). 150 long-term experimental research plots (EPs) are located in three major geographic regions, namely the Swabian Alb, the Hainich-Dün and the Schorfheide-Chorin in Germany, with 50 EPs in each exploratory. The EPs cover a gradient of forest stand types, ranging from unmanaged stands to intensively managed monocultural stands and represent dominant stand types in Central Europe regarding tree species composition and management system (Fischer et al. 2010).

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2. Effective number of layers: a new measure for quantifying three-dimensional stand structure based on sampling with terrestrial LiDAR

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Abstract

The relevance of stand structural heterogeneity for biodiversity conservation is increasingly recognized and efficient tools for its measurement are demanded. Here, we quantified three-dimensional forest structure by calculating the *effective number of layers* (ENL) for different Hill Numbers (^0D, ^1D, ^2D) as a measure of vertical structure of a subplot. We then use sampling techniques to cover the horizontal structural variability within study plots. ENL describes the vertical structure based on the occupation of 1 m wide vertical layers by tree components relative to the total space occupation of a stand. Space occupation was quantified by a voxel-model obtained from terrestrial laser scanning (TLS) on 150 forest plots in Germany. We used a single scan approach, which requires less field work and post-processing compared to multiple-scans. Single-scan derived mean ENL and its coefficient of variation successfully differentiated forest structures over a wide range of even-aged, uneven-aged and unmanaged broadleaved and coniferous stands. ENL was correlated to the stand summary measures basal area, quadratic mean diameter and stem density as well as stand age. ENL can be used to describe structural heterogeneity and proved to be efficiently assessable by TLS.

Keywords (5): voxel, TLS, canopy, structure, vertical

2.1. Introduction

The heterogeneity of forest structure is directly related to biodiversity (cf. Groom et al. 2006) and is highly influenced by forest management (Staudhammer & LeMay 2001, Mc Roberts et al. 2008, Lindenmayer et al. 2000, Gossner et al. 2014, Schulze et al. 2016). It also affects productivity (Pretzsch 1995, Bolton et al. 2013, Hardiman et al. 2013, Pretzsch et al. 2015, Miyamoto et al. 2016) as well as various other ecosystem processes and functions (Pypker et al. 2005, Dietz et al. 2006, Pretzsch 2009, Lei et al. 2009, Ruiz-Benito et al. 2013, Pretzsch et al. 2015). The demand for effective approaches to assess forest structure in order to study the relationship between forest management, forest structure and biodiversity in more detail has constantly increased. Especially in Central Europe and North America, managing forests to promote spatially more heterogeneous structures has been increasingly recognized as a measure to improve habitat quality and to support biodiversity conservation (Gustafsson et al. 2012, Pretzsch 2009, Puettmann et al. 2015, Lindenmayer et al. 2000).

The spatial structure of forest stands (stand structure) can be described by the spatial distribution of trees, tree species diversity and variations in tree dimension (Pommerening, 2002). In this context, McElhinny et al. (2005) defined structure as the "the spatial arrangement of various ecosystem components". To describe these components, measures like stem density, basal area, (quadratic) mean diameter and diameter distributions were commonly used (e.g. Bell et al. 2014, McIntyre et al. 2015). In addition, several indices have been proposed to quantify stand structure in terms of tree species diversity (e.g. Shannon-Index), species mingling and diameter differentiation (Füldner 1995, Gadow et al. 1998), patterns of horizontal tree spacing (e.g. Clark & Evans index of aggregation (1954), coefficient of segregation by Pielou (1977)), stand structural complexity (Complexity Index by Holdridge 1964, Structural Complexity Index by Zenner & Hibbs 2000, Enhanced Structural Complexity Index by Beckschäfer et al. 2013) or structural diversity (Stand Diversity Index by Jaehne & Dohrenbusch 1997, Structure index based on variance by Staudhammer & LeMay 2001). McElhinny et al. (2005) and Pommerening (2002) provided detailed reviews on indices and attributes used to quantify forest structure.

However, quantifying vertical layering to describe vertical structure is still a remaining challenge. MacArthur & MacArthur (1961) introduced *foliage height diversity* (FHD) as a measure to describe vertical stratification, which was in turn used as an indicator for habitat availability. They stratified

vertical foliage profiles into three horizontal layers, assessed foliage density within these layers and used the Shannon-Index to derive a single measure describing the vertical structure. Bird species diversity was positively correlated to FHD. So far, this approach was used in several other studies (e.g. Berger & Puettmann 2000, Sullivan et al. 2001, Tanabe et al. 2001, Montes et al. 2004, Hashimoto et al. 2004, *Canopy Shannon Index* by Stark et al. 2012). However, as FHD is dependent on the chosen stratification into layers, results of different studies are not entirely comparable or reproducible, because delineation of vertical strata differed between studies and was often arbitrary (Erdelen, 1984). Especially in uneven-aged stands, where trees of all sizes and age classes coexist, a clear delineation of layers is challenging. We agree with McElhinny et al. (2005) that FHD "appears as an ambiguous measure in the literature, because no standard method has been established for its measurement". Furthermore, its interpretation with respect to vertical structural variability is not intuitive, as high FHD values indicate an equal filling of vertical strata.

Nevertheless, the application of diversity indices to vertical profiles of forest stands appears to be useful to express vertical structure in a single number instead of functions or foliage distributions (see also Ouma et al. (2008), Treuhaft et al. (2009), Palace et al. (2016)). When applied to the total number of species in an ecosystem, the Simpson-Index and Shannon entropy were commonly used to describe species α-diversity. Based on the concepts of Hill (1974), Jost (2006) criticized how diversity indices were commonly used in ecological studies, arguing that they do not measure actual or "true diversity". He proposed a mathematical framework to convert measures of entropy, like the Shannon-Wiener index or Gini-Simpson index, into indices describing the *effective number of species*. It appears to be straightforward to apply this concept to the vertical structure of forest stands and determine the *effective number of structural layers*. When the vertical forest structure is divided into layers of 1 m thickness, the number of layers ('layer richness') approximates stand height and would be analogue to species richness (^0D). Exponential Shannon index (^1D) and inverse Simpson-Index (^2D) sensu Jost (2006) quantify the number of 'effective layers' under consideration of layer occupation. The occupation of layers by tree components (leaves and woody components) would then be analogue to the abundance of species, when using diversity indices to quantify species diversity.

In this context, terrestrial laser scanning (TLS) offers new opportunities to efficiently and rapidly assess structure and layering in forests with high resolution and accuracy, since it is an efficient tool

for obtaining highly detailed three-dimensional descriptions of structurally complex environments. TLS has been used to measure diameter at breast height, basal area, tree height, stem density, stand volume and aboveground biomass (e.g. Bienert et al. 2007, Yao et al. 2011, Liang et al. 2012, Hauglin et al. 2013, Kankare et al. 2013, Astrup et al. 2014, Seidel et al. 2012). TLS was also utilized to determine forest canopy gap fraction (Danson et al. 2007), canopy cover and structural crown properties (Fleck et al. 2007, Vockenhuber et al. 2011, Seidel et al. 2011b, Bayer et al. 2013), leaf area density or plant area volume density, vertical plant profiles as well as leaf area index (Lovell et al. 2003, Hosoi & Omasa 2006, Jupp et al. 2009, Beland et al. 2014, Calders et al. 2014, McMahon et al. 2015, Zhao et al. 2015). Furthermore, the ground-based scanning technology has been applied to model the light environment in forests (van der Zande 2010, 2011) to analyze crown plasticity and competition among tree individuals (Seidel et al. 2011b, Metz et al. 2013) as well as a means for quantifying space filling in forests (Seidel et al. 2013). It proved useful in describing the shape and size of canopy gaps (Seidel et al. 2015) and to derive taper functions for tropical trees with buttress roots (Nölke et al. 2015), as well as for mapping forest regeneration (Brolly et al. 2013). Considering the list of examples given, we support Newnham and colleagues (2015) who assessed TLS as a "disruptive technology" that "requires a rethinking of vegetation surveys".

In the past, investigations relying on TLS used various numbers of scans, ranging from one (so called single-scan approach; e.g. Astrup et al. 2014), to a combination of more than a dozen scans (multi-scan approach, e.g. Seidel et al. 2011a). Multiple-scan setups are used when a detailed assessment of the investigated space is of interest. The space of interest may be occupied be a single tree, a cohort of trees or an entire research plot. The respective area is then to be scanned from several positions to reduce the amount of occluded space in the scene and to capture the full three-dimensional extent of the object or objects of interest (see Metz et al. 2013, Kankare et al. 2013). However, assessing forest stands or single trees with multiple scans can be laborious and time consuming, as several single scans have to be merged to a single point cloud during post processing. In order to do so, artificial reference points (e.g. chessboard-targets) are to be set up in the forest, which can be challenging in dense forests or for large areas (Newnham et al 2015).

Single-scans are much more time-efficient since they do not require reference points in the scanned scene, but they are of limited usability. Some parameters, such as crown volume, cannot be reliably

extracted from a single-scan due to the incomplete representation of the trees if scanned from a single perspective. Other parameters, e.g. three-dimensional space filling or competition, can be determined from a single scan but are less accurate when compared to a multiple-scan approach (e.g. Mengesha et al. 2015, Seidel et al. 2015). This is because plant elements occlude space in the direction of the laser beam. Thus, the detectability of trees and their constituents decreases with increasing distance from the scanning position (van der Zande et al. 2011, Astrup et al. 2014, Beland et al. 2014, Zhao et al. 2015). Several studies introduced methods to correct single scan data for this shadowing effect, also called non-detection error, e.g. for stem density (Ducey & Astrup 2013), basal area (Seidel and Ammer 2014) and others. Zhao et al. (2015) introduced a method to derive foliage density profiles from single scans based on maximum likelihood estimates. Van der Zande et al. (2008) investigated how different sampling designs and laser beam densities affected shadowing (occlusion) in virtual forest stands. While pros and cons exist for both single-scan and multiple-scan approaches, determining the minimum number of scans that is necessary to achieve certain integrity in the modelled tree or plot is still a remaining challenge (Newnham et al. 2015).

Here, we set up a methodical framework to describe the three-dimensional structure of forests in terms of their effective number of layers (ENL), as a descriptor of vertical structure, and its variability across sampling points as a measure of horizontal structural variability. First, we analyze how occlusion affects the assessment of ENL in single- and multiple-scan approaches. Second, we investigate how the derived measures are related to stand summary measures like mean diameter, basal area and stem density as well as stand age. Third, we test if the application of diversity indices (with varying Hill-Numbers) facilitates a differentiation of differently structured stands. Based on the initial concept of *foliage height diversity* by MacArthur & MacArthur (1961), we aimed to provide an efficient and objective approach to quantify vertical forest structure.

2.2. Methods

2.2.1. Study sites

This study was part of the Biodiversity Exploratories, a long-term research project aiming to investigate the relationship between land-use intensity and biodiversity (Fischer et al. 2010, www.biodiversity-exploratories.de). 150 forest research plots are located in three major geographic regions across Germany; the Hainich, the Swabian Alb and the Schorfheide-Chorin (see Fig. 2.1, Tab. 2.1).

Figure. 2.1: Map of Germany with the location of the three geographic regions used in our study.

We chose beech, spruce, oak and pine as study species as they are characteristic for the specific regions (Hainich, Swabian Alb and Schorfheide, respectively) whereas the chosen management types (unmanaged, uneven-aged, even-aged) represent a range of forest management systems that are widely practiced in Central Europe. In each of the three regions we selected a subset of plots (5 to 15) from the repository of the Biodiversity Exploratories for the analysis of single- vs. multiple scan approaches (see Table 2.1, number in brackets). In the Hainich exploratory we selected 15 plots, as five plots of each management system could be selected here. Furthermore, we selected five Spruce plots in Swabian Alb and five Pine plots in Schorfheide.

Tab. 2.1: Information on main tree species, management system, and developmental stage of the selected study sites

Main tree species	Management	Management system	Developmental stage	n
European Beech[1]	managed	even-aged	thicket*	14
			pole wood	10
			immature timber	9
			mixed imm. timber	7
			mature timber	17 (5)[5]
			thicket with shelterwood	10
		uneven-aged	mature timber	13 (5)[5]
	unmanaged	(un)even-aged		25 (5)[5]
Common Oak[2]	managed	even-aged	mature timber	7
Scots Pine/E. Beech			mature timber	7
Scots Pine[4]			pole wood	4
			(im)mature timber	11 (5)[5]
Norway Spruce			immature timber	11
			mature timber	5 (5)[5]
Sum				**150**

[1]= *Fagus sylvatica* L.; [2]= *Quercus robur* L., [3]= *Picea abies* [Karst.] L.; [4]= *Pinus sylvestris* L., [5]number in brackets refer to the plots used to model the relationship between single- and multiple-scan derived values. *thickets are defined as stands where the mean diameter of the 100 largest trees is smaller than 15 cm. Main environmental characteristics of the study sites can be found in Fischer et al. (2010). For detailed information on soil properties see Solly et al. (2013).

Out of these 25 plots, we then selected nine plots to analyze the effect of different numbers of scans on occlusion. For computational reasons, this analysis had to be restricted to a small number of plots. All plots were quadratic in shape and 1600 m² (40 m by 40 m) in area. In order to investigate whether single-scan derived estimates of ENL were able to differentiate stand structures and to test how these measures are related to stand summary measures, we used all 150 plots as described in the following.

2.2.2. Terrestrial laser scanning and sampling design

We used a FARO Focus 3D terrestrial laser scanner (Faro Technologies Inc., Lake Marry, USA) for the acquisition of LiDAR data. The scanner was mounted on a tripod at 1.3 m above ground. The device was set to scan a field of view of 360° in horizontal and 305° in vertical direction with an angular step-width of 0.035°, which resulted in ~44.4 million measurements per scan.

To investigate the effect of occlusion on deriving ENL from single- and multiple-scan approaches, we used a systematic sampling design on nine 40 x 40 m plots. Each of these plots was a subplot located in the center of a 100 x 100 m plot established within the framework of the Exploratories. At first, a master scan was made in the center of the plot defining the origin of the underlying coordinate system (x, y, z). We then distributed 20 scanning position systematically over the plot. The sampling grid was oriented diagonal to the borders of the plot, in order to have four scanning positions located outside the plot. This was considered necessary to fully capture all plant-elements inside the plot. Four of the scanning positions were located at the corner points of the plot (Fig. 2.2). Whenever a stem or dense understory vegetation was present at a specific scan position, we used the nearest available position that provided sufficient space for the scanner to operate.
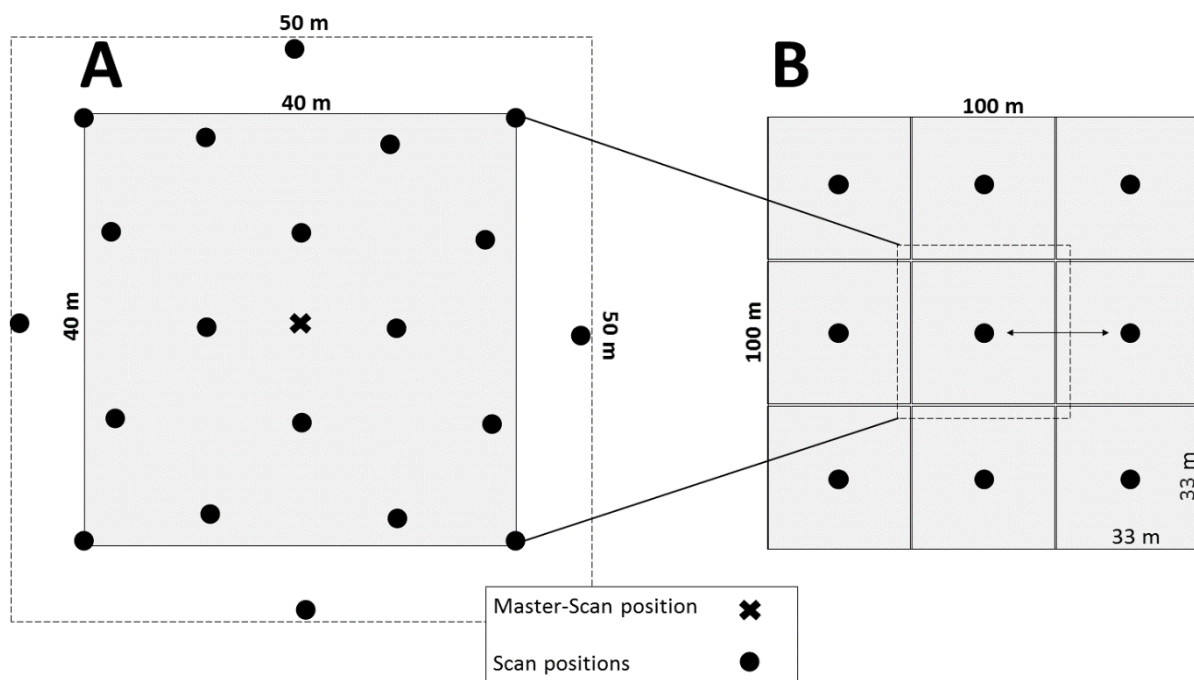

Figure. 2.2: Schematic draft of the scan design used for plots to investigate occlusion effects and the relationship between single and multiple-scan derived ENL values (A). Sampling design per forest plot with nine single-scans systematically distributed over 1 ha (B).

We referenced all scans to the master scan by distributing artificial chessboard targets in the plot before scanning. All scans were then imported to FARO Scene (Faro Technologies Inc., Lake Marry, USA) and referenced using the standard registration algorithm available in FARO Scene and semi-automatically detected the chessboard targets. We applied the software`s standard filters

to correct the point clouds for erroneous points. Finally, each scan was exported in xyz-format with the coordinates relative to the origin/master scan.

We then used a systematic sampling design at each of the 150 forest plots to calculate the effective number of layers. Here, nine single-scans were systematically distributed over each 100 x 100 m plot (Fig. 2.2B). Each scan was imported to FARO Scene (Faro Technologies Inc., Lake Marry, USA) and exported in xyz-format. ENL was calculated for each single-scan using subplots 33 x 33 x stand height [m] in size. Subplot size was limited to 33 x 33 m in horizontal extent to avoid overlap within a 1 ha plot. A subplot defines the spatial extent used to calculate measures for one single scan. Nine subplots are sampled per stand to derive stand-level information. All scans were made at wind speeds below 10 m s^{-1}.

To enable relating TLS-derived measures to stand summary measures that are usually used in forest practice to describe forest structure, we used forest inventory data that was collected between 2008 and 2010. On each of the 150 forest plots, trees with dbh ≥ 7 cm were measured for diameter at breast height (DBH) using a caliper. Additionally, tree heights were measured across the range of assessed tree dimensions to derive tree diameter-height relationships. Furthermore, we determined the age of even-aged forests using stand records. It was also possible to apply stand records to determine the age of dominating trees of unmanaged stands at Alb and Schorfheide. For unmanaged forests and selection forests in the Hainich, age of dominating trees was estimated based on diameter of the largest 30 trees per ha using diameter-age relationships derived from trees harvested nearby (Mund 2004).

2.2.3. Ray-tracing to determine occlusion

The exported point cloud (xyz-format) was then imported into a voxel array with an extent of 50 x 50 x 40 m (Fig. 2.2.A). A maximum height of 40 m was chosen as the highest stand in our dataset had a maximum tree height of around 38 m. Each cubic voxel inside the array had a side-length of 20 cm, resulting in a total of 12.5 million voxels. We applied a ray-tracing algorithm as introduced by Amanatides & Woo (1987) to each scanning position to determine whether a voxel inside the analyzed volume (array) was empty and traversed by a laser beam, filled with plant material or occluded. A laser beam can be understood as a vector. A voxel was considered to be "filled", whenever at least one laser hit was present in the voxel. A voxel was considered to be "occluded" if

a ray from the center of the voxel to the origin (scanning position) had intersected a filled voxel. All other voxels were considered "traversed" (see Fig. 2.3). By applying this procedure to each scan position, we were able to determine for each voxel inside the array whether it was traversed by a laser beam, filled or occluded from the respective perspective.
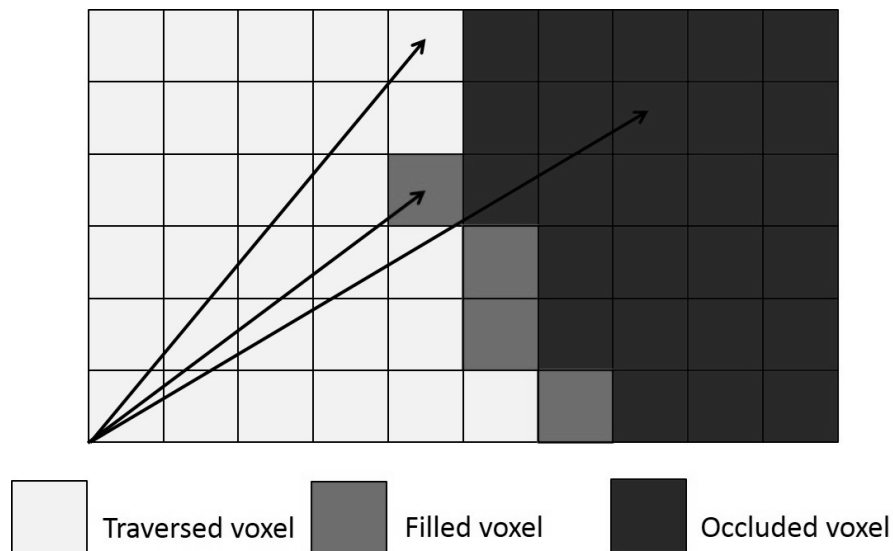

☐ Traversed voxel　■ Filled voxel　■ Occluded voxel

Figure. 2.3: 2D- visualization of a 3D-voxel array with the corresponding voxel definitions. Beam origin in the lower left corner is the beam exit point at the scanner.

We then merged the information from each scanning position to assign the attributes traversed (t), filled (f) and occluded (o) to each voxel in the array. A voxel that was occluded from all scanning positions was considered to be occluded. Any voxel that contained a laser hit, regardless of the position from which the hit was detected, was considered filled. The remaining undetermined voxels were considered traversed.

We analyzed the effect of the number of scans on occlusion, by randomly combining 1, 3, 6, 9, 12, 15, and 18 scans per plot. For each of these classes, we used 12 random combinations (sampling without replacement) for the respective number of scans out of the 20 scanning positions and applied the procedure to determine voxel types (traversed, filled, or occluded) as explained above.

2.2.4. Diversity index calculation

Effective number of layers (ENL)

With reference to the initial concept of *foliage height diversity* (FHD) we computed the *effective number of layers* (ENL) using vertical layers of 1 m thickness under consideration of their

occupation by tree components (wood and leaves). Occupation was approximated by the number of filled voxel (20 cm side-length) within each layer. Using diversity indices of different Hill-Numbers (^{0}D, ^{1}D and ^{2}D, see Hill 1972 and Jost 2006), ENL was computed as follows:

$$0D\ ENL = \sum_{i=1}^{N_{top}} p_i{}^0 \tag{2.1}$$

$$1D\ ENL = \exp\left(-\sum_{i=1}^{N_{top}} p_i * ln\, p_i\right) \tag{2.2}$$

$$2D\ ENL = 1/ \sum_{i=1}^{N_{top}} p_i^2 \tag{2.3}$$

where p_i is the proportion of filled voxels in the i_{th} vertical layer to the sum of filled voxel in the entire volume analyzed. N_{top} refers to the top stand height, and ln is the natural logarithm. ^{0}D ENL corresponds to the number of 1 m layers and thus approximates stand height (eq. 2.1). With ^{1}D ENL (exponential Shannon-Index, eq. 2.2) and ^{2}D ENL (inverse Simpson-Index, eq. 2.3), layers are weighted stronger the more they are occupied (weighing of ^{2}D ENL > that of ^{1}D ENL). Weighting results in a lower number of effective layers when compared to ^{0}D ENL. At a given number of layers both ^{1}D and ^{2}D ENL values increase with more evenly occupied layers. When considering foliage only, the natural logarithm of ^{1}D ENL equals FHD based on layers of 1 m thickness.

Stand summary measures and stand age

Stem density (N*ha^{-1}), quadratic mean diameter (d_g [cm]) and basal area (BA [m^2*ha^{-1}] were calculated as stand summary measures. The effective number of diameter classes (ENDC), was calculated based on exponential Shannon-Index (eq. 2.2) with the relative proportion of 4 cm diameter classes on a plot as p_i). At a given number of diameter classes, ENDC-value is highest when tree numbers per diameter class are equal. Stand age of forests was derived from stand records as described above.

2.2.5. Statistical analyses

All statistical computations as well as data preparation were done using the software environment R, version 3.2.0 (R Development Core Team, 2015).

To understand the occlusion effect as created by different numbers of scans in different forest types, we applied the procedure explained in chapter 2.2.1. to the three mature European Beech, Norway Spruce and Scots Pine forest stands, respectively (n = 3 for each forest type). We only used nine plots in this analysis, as the computations are very time consuming. For each class of scan numbers (1, 3, 6, 9, 12, 15, 18, 20), we calculated the percentage of occluded voxels for 12 random combinations (n = 12). Due to variance heterogeneity and non-normal distributed data we used a pairwise Wilcoxon test to test whether additional scans did or did not reduce occlusion. We compared the number of scans based on the classes with the subsequent class (one scan vs. three scans, three vs. six, six vs. nine, and so on). We used a significance level of $p < 0.05$ for all tests.

To investigate the relationship between ENL-values obtained from a single-scan and a multiple-scan point cloud, we plotted the single-scan values against the multiple-scan values. We compared the master-scan in the plot center with the results obtained from the multiple-scan approach with 20 scans distributed over the surrounding area of 40 x 40 m. We used linear regression analyses to analyze the similarity between single- (dependent variable) and multiple-scan (independent variable) approaches. Here, we used estimates of ENL obtained from the multiple-scan approach as a reference. Linear regressions were also used to model the relationship between ENL (dependent variable) and stand summary measures and stand age (independent variables). If necessary, either the dependent or independent variable was log-transformed to describe a non-linear relationship with a linear model.

2.3. Results

Occlusion within the investigated scene can be reduced significantly by using more than one scan. There is a certain variability in occluded space, when using only one or three scans on a 40 x 40 x [stand top height] m plot, which can be explained by the position of the respective scans. The more scans are made, the lower the variability of occluded space between the samples became. That means the effect of the respective scan-positions becomes less important. Even though occlusion is below

10 % for almost all plots when using six scans, we still found significant differences between the subsequent numbers of scans. A threshold where occlusion cannot be significantly reduced anymore by adding scans was found around 18 scans per 40 x 40 x [stand height] m for all plots, except for AEW11 and SEW21, where 15 scans did not show significantly higher occlusion rates than 18 or 20. Thus, using ENL-estimates obtained from the multi-scan approach as reference for each plot in the further analysis appeared reasonable.
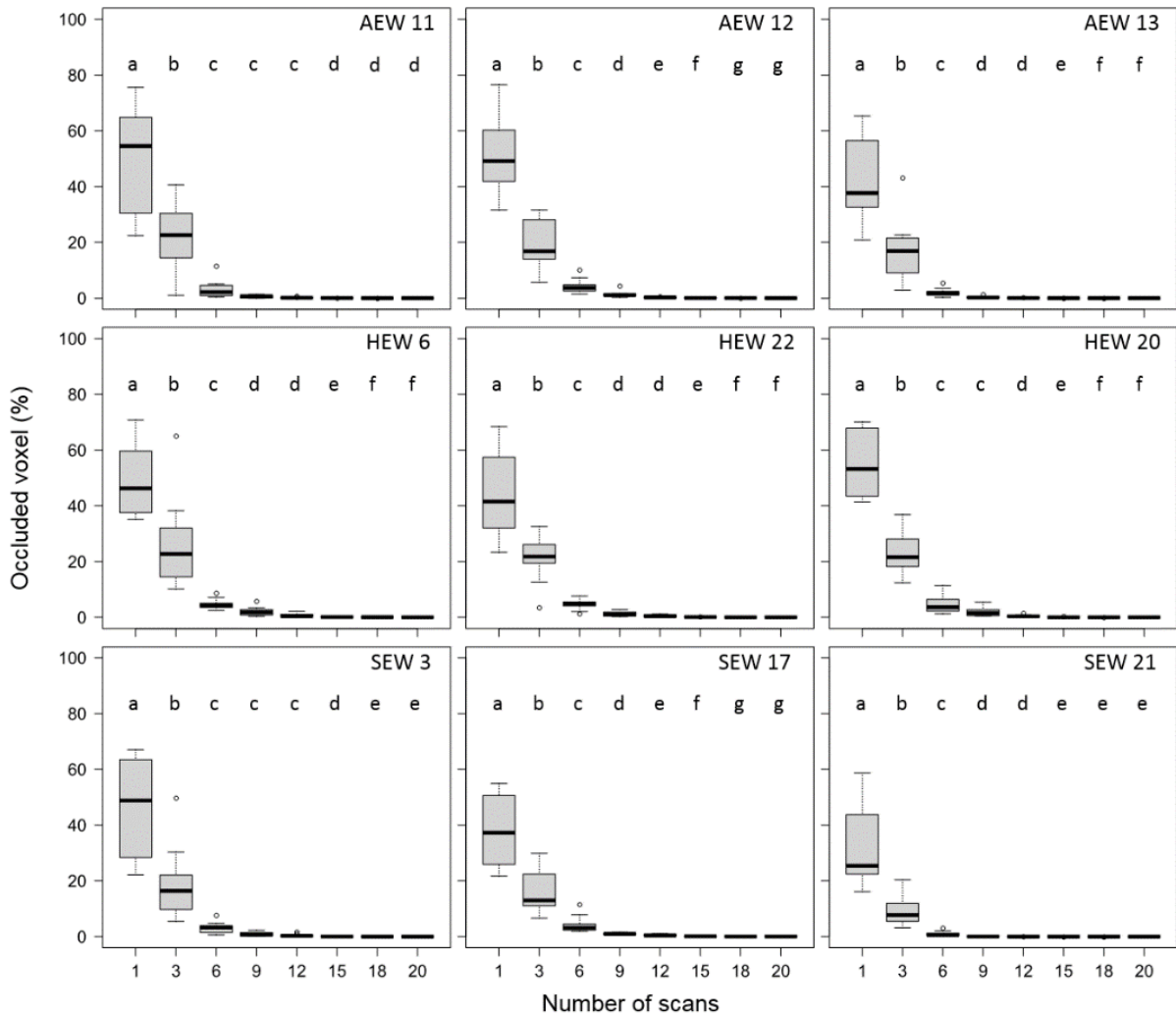

Figure. 2.4: Box-and-Whisker plots of the percentage of occluded voxels as dependent on the number of scans made per 40 x 40 x stand height (m) plot. Significant differences between subsequent numbers of scans (classes) are indicated by different letters (p< 0.05). Per class (1, 3, 6…), 12 random combinations of scan-positions were considered in the analysis (n = 12). AEW 11, 12 and 13 are mature Norway spruce plots. HEW 6, 22 and 20 are mature European Beech plots, whereas SEW 3, 17 and 21 are mature Scots Pine plots.

Deriving the number of 1 m layers (^{0}D ENL) from single-scans resulted in a slight underestimation of the true number of layers over the range of sampled stands. Deriving the effective number of layers as described by exponential Shannon (^{1}D ENL) or inverse Simpson-Index (^{2}D ENL) resulted in an overestimation of lower values and an underestimation of higher values when using single-scans (Fig. 2.5). Linear regressions explained 90% (^{0}D ENL), 80% (^{1}D ENL) and 79% (^{2}D ENL) of the total variation. The respective, relative RMSE were 5.1%, 7.54% and 9.81%.
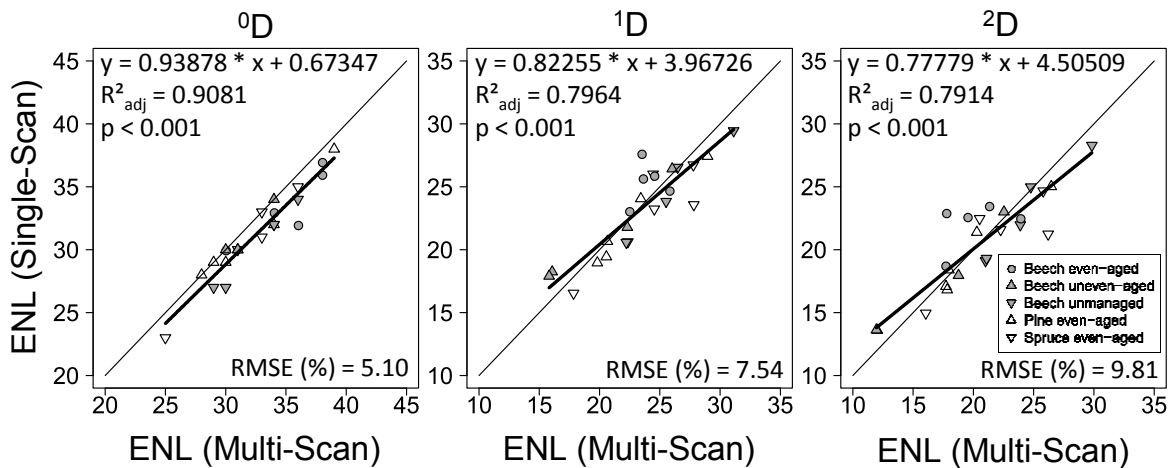

Figure. 2.5: Relationship between ENL-values (^{0}D, ^{1}D, ^{2}D) derived from single-scan vs. multiple-scan approach (reference). n = 25 in all cases.

However, with respect to the high degree of occlusion in single-scans, the relative errors of the derived ENL were rather low. Mean ENL per plot (9 scans for each of the 150 EPs) was correlated to quadratic mean diameter (d_g), basal area (BA) and stem density (N ha^{-1}). ENL followed a positive logarithmic trend over an increase in quadratic mean diameter per plot as well as with increasing effective number of diameter classes. Variation in ^{0}D ENL (~stand height) is better explained by d_g and the effective number of diameter classes than variation in ^{1}D or ^{2}D ENL. Stands with higher basal area showed a higher ENL. This relationship followed an exponential trend. Basal area explained considerably more variation in ^{2}D ENL and ^{1}D ENL than in ^{0}D. Our results showed a linear decrease in ENL with increasing stem density.
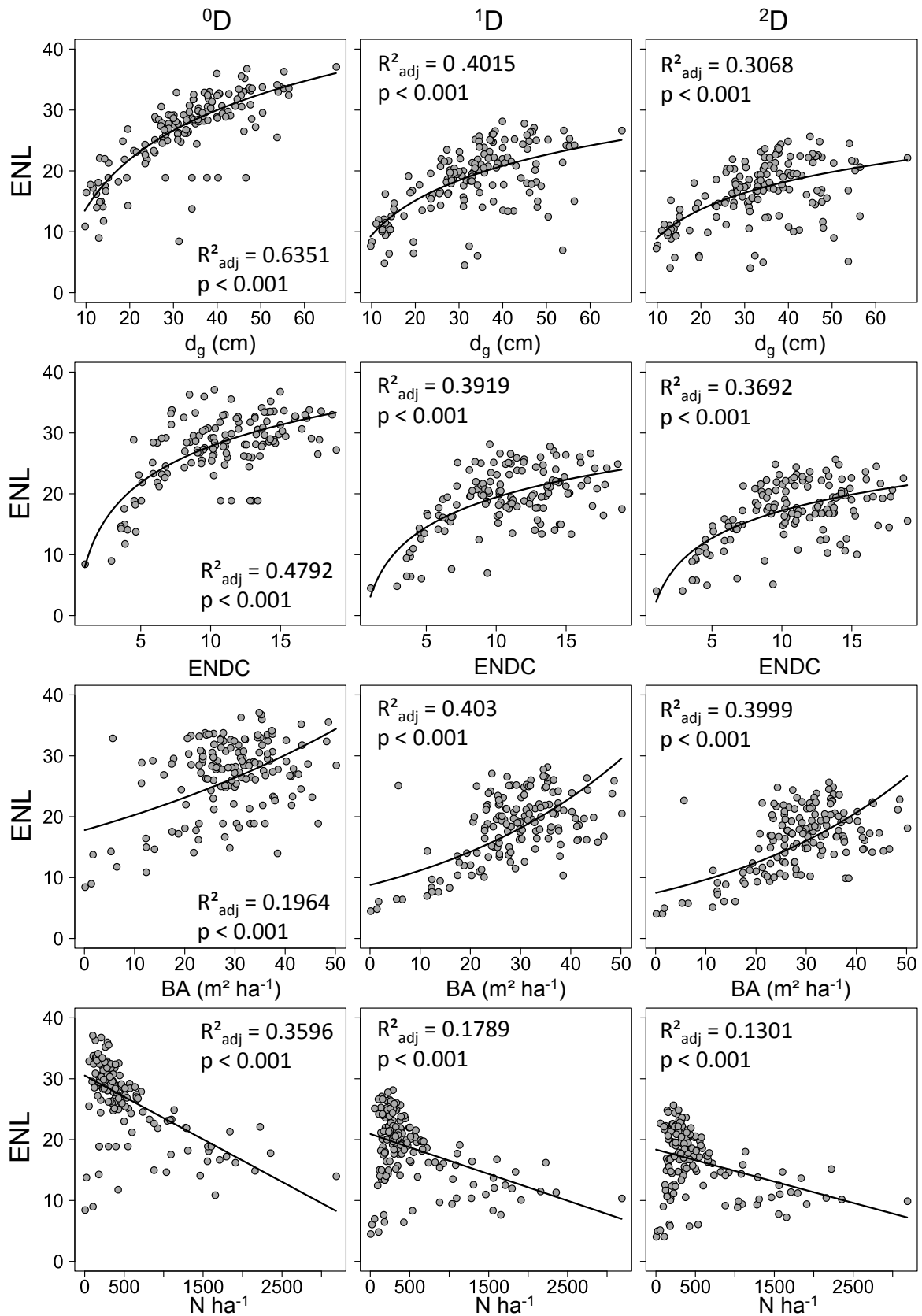
Figure 2.6: Relationship between the stand summary measure d_g (quadratic mean diameter), ENDC (effective number of diameter classes), BA (basal area), $N*ha^{-1}$ (stem density) and mean ^0D, ^1D and ^2D ENL. n = 150.

Mean ENL per plot was affected by stand age. ^{0}D ENL showed a logarithmic increase with increasing stand age whereas ^{1}D ENL and ^{2}D ENL first increased and later decreased with stand age. This relationship is best described by a parable. Furthermore, variability of ENL per plot (as expressed by the coefficient of variation (%)) was found to be slightly higher in younger stands (< 30 years) and older stands (> 130 years) for ^{0}D ENL. For ^{1}D ENL and ^{2}D ENL, the effect of a higher ENL-variability in stands older than ~130 years became more apparent.
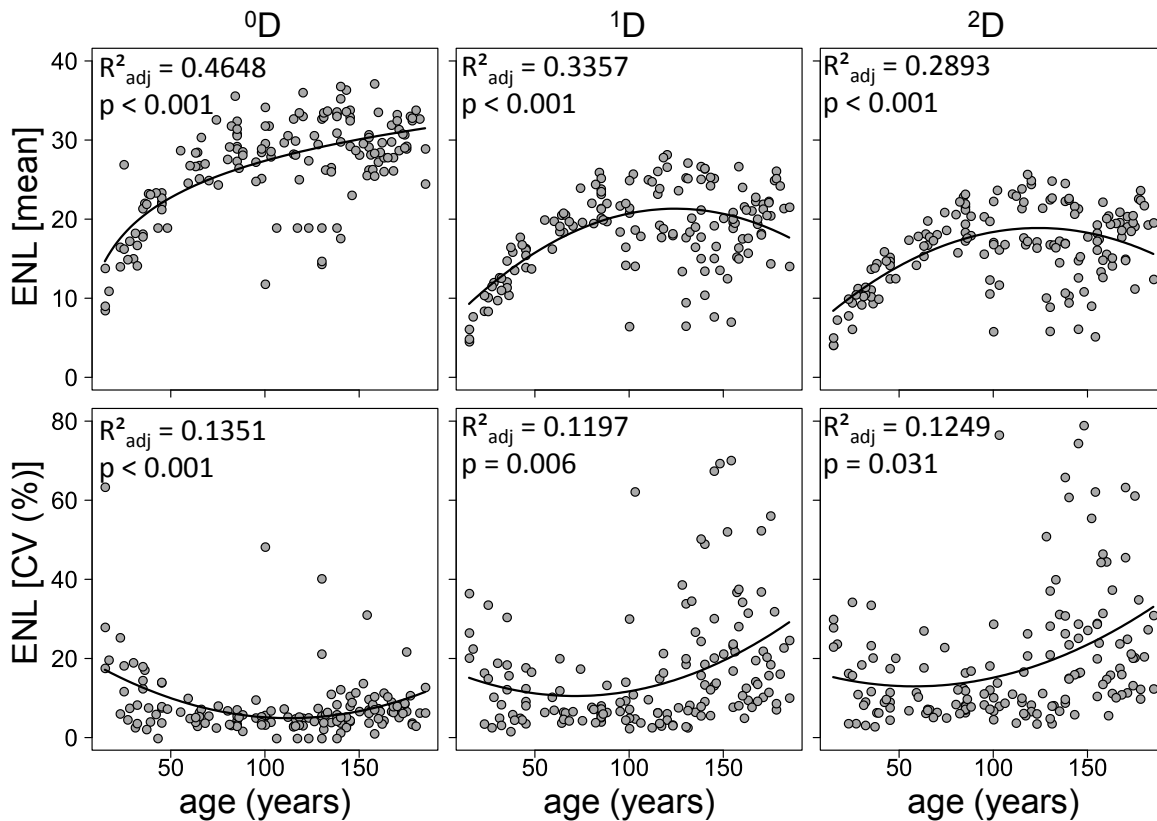

Figure. 2.7: Relationship between the stand age (years) and mean and CV (%) for ^{0}D, ^{1}D and ^{2}D ENL. n = 150.

Means and coefficients of variation (CV (%)) were used to differentiate between stand types (Fig. 2.8). The higher the Hill number was, the better the differentiation of stands. The coefficient of variation of ENL per plot reflects the horizontal structural variability of the vertical structure. Thus, stand structural heterogeneity (three-dimensional structural variability) increased from the lower left (low mean and low CV (%)) to the upper right (high mean and high CV (%)) (Fig. 2.8)
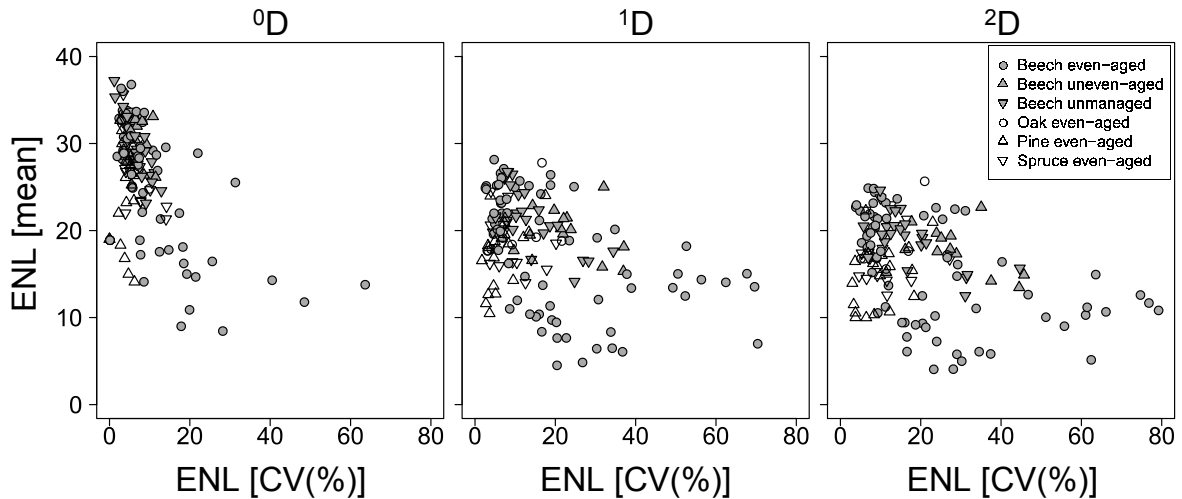
Figure. 2.8: Mean and coefficient of variation (%) of ^{0}D ENL, ^{1}D ENL and ^{2}D ENL for the investigated stand types.

2.4. Discussion

2.4.1. Occlusion

We are not aware of any study that systematically investigated the effect of different numbers of scans on occlusion in "real" forest stands. We were able to reduce occlusion rates to below 10% of all voxels by using at least six scans per 40 x 40 x stand height (m) in the forest types investigated. It is worth mentioning that the detected occlusion is further influenced by the laser beam density of the scanner and the chosen voxel size. However, we did not consider this because we wanted to know how many voxels remained occluded when using different numbers of scans, but not which effect different voxel sizes, scan settings or scanner instruments may have had. The remaining occluded space (not voxels) might be even lower, as the initial laser beam density offers a higher resolution than the voxel grid the point cloud was converted into. For computational reasons we were not able to use smaller voxel sizes.

The amount of occluded space is not only determined by the number of scans, but also by the scanning-positions (Cifuentes et al. 2008). This position-effect is indicated by the variability in occluded voxels (%) per number of scans (classes). The more scans were made, the lower the variability of occluded space between the samples was. That means the effect of the respective scan-positions becomes less important. Unfortunately, a differentiation of the underlying error sources (occlusion vs. horizontal variation in structure) was not possible based on our data. Van der Zande

et al. (2008) tested the effect of different sampling setups on occlusion in virtual forest stands. For single-scans in the plot center, they reported occlusion rates of 69.34% to 82.61% in 15 x 15 m plots. Due to different plot sizes and the fact that we investigated real stands, a direct comparison is not possible here. However, it appears that we found lower occlusion rates, which is probably the result of a higher laser beam density (here: 44.4 million vs. 6.48 million) when compared to van der Zande et al. (2008). They were able to reduce occlusion significantly by using a "Diamond" and "Corner" setup of scanning-positions, with five scans per setup. Beland et al. (2014) reported an occluded volume of about 15% when using six scans in a 20 x 20 m plot and voxel of 20 cm side-length, which is slightly higher, but within the range of what we found in our study.

2.4.2. Single vs. multiple-scan approach

ENL computed from single-scans deviates from the reference data obtained through the multiple-scan approach. The reported errors in estimation may result not only from non-detection of tree components due to occlusion but may likely also be attributed to actual structural variability within the plot, as mentioned earlier. Furthermore, when excluding the intercept of the models, which was not significant in all three cases, the regression line was nearly identical to the 1:1 line, as the slope was not significantly different from 1. Note that ENL was not dependent on total number of (theoretically) filled voxel, but on their relative frequencies per 1 m layer. Therefore, single- and multiple-scan approaches lead to similar ENL values, because single-scans seem to capture approximately the same proportion of filled voxels relative to the total amount of voxels per layer as multiple-scans do. This means that for ENL information loss in single-scans is proportional to multiple scans. Given the high level of efficiency, we argue that single-scan based estimation of ENL is reasonable for sampling larger areas, despite the RMSE of up to ~10% for ^{2}D ENL. If a more accurate estimation is required –e.g. for long-term monitoring purposes- the error can be reduced by using more than one scan per 40 x 40 m plot. Another possibility would be to work with smaller plot sizes when using single-scans. With smaller plots relative occlusion would be lower, as it increases with increasing distance from the scanner. Also, estimates of ENL would be less affected by structural variability within the investigated plot.

2.4.3. Effective number of layers, forest types and stand summary measures

ENL quantifies vertical stand structure based on the occupation of 1 m layers by tree components relative to the total space occupation inside a stand. Its values increase with increasing stand height and a more even distribution of tree components across the vertical profile. Whereas ^{0}D ENL approximates stand height (without weighing space occupation), ^{1}D ENL and ^{2}D include weighted space occupation (^{2}D ENL weighs occupied layers more than ^{1}D ENL, resulting in lower ENL-values, i.e. *effectively* filled layers). A crucial point in this context is the number and thickness of vertical layers, as it affects the resulting ENL-values. Mac Arthur & Mac Arthur (1961) used three layers to calculate *foliage height diversity* based on the foliage density within these layers. Hashimoto et al. (2014) used four and five strata to calculate FHD. Montes et al. (2004) argued that "strata must be chosen according to the characteristics of the stand (…)". However, stratification according to certain characteristics remains a somehow arbitrary assessment and hampers comparisons between the results of different studies. Generally, different approaches have been proposed for vertical stratification. Oliver & Larson (1996) proposed an A- (single emergent trees), B- (dominating canopy) and a C-Stratum (trees below the canopy; can be separated into further sub-strata). Assmann (1954) proposed three strata that are related to stand height (upper layer above 80% of maximum stand height, middle layer between 50 – 80% of maximum stand height and understory below 50% of maximum stand height). However, in each case maximum stand height is not considered, even though it can be seen as an important component of vertical structure (see also Hunter 1990). For example, when using stratification into three layers based on relative stand heights, a young stand 15 m in height with an even distribution of tree components across the profile could have the same ENL as a mature multi-layered stand of e.g. 35 m height, even though both stands obviously differ in their vertical structure. Defining layers of 1 m thickness appears to be a straightforward approach in order to integrate stand height into index calculations, as it reflects ^{0}D ENL. ^{1}D and ^{2}D ENL are then simply deductions from stand height based on relative space occupation; a stand of 35 m height with short crowns would have lower ^{1}D or ^{2}D ENL values than a stand of similar height, but with longer tree crowns.

When considering the horizontal variability of ENL per plot, structures of different stands can be differentiated. Mean and CV (%) for even-aged beech stands represent the full range of developmental stages over the rotation period. For example, plots with a high CV (%), but low

mean were mainly thickets with remaining shelterwood. Plots with a similarly low mean and a low CV (%) were thickets where the tree shelter was removed. Stands with a high mean and low CV (%) were often mature even-aged stands with low horizontal variability. Uneven-aged stands showed a higher horizontal variability of ENL than even-aged stands. ^{2}D ENL enabled a more distinct differentiation than ^{1}D ENL, as horizontal variability became more apparent. As ^{0}D ENL reflected stand height only, i.e. without consideration of layer occupation, its differentiation capability was limited.

Stark et al. (2012) introduced the *Canopy Shannon Index* to describe the vertical structure of evergreen moist forests in Amazonia. It was calculated based on the Shannon formula as used in our present study, but without the transformation to 'effective' values we performed. Stark and colleagues acquired data using airborne LiDAR and computed the index using voxels of one meter side-length. The reported values of 3.35 and 3.56 (without transformation as described in 2.2.2.), which equals 28.5 and 36.16 ^{1}D ENL, were higher than what we found in our study. This is probably due to the fact that the tropical rainforests had a higher stand height as well as a more even distribution of tree components across the profile. Palace et al. (2015) reported values of 2.78 to 3.44 for tropical old-growth forest in Costa Rica, which equals 16.12 to 31.19 ^{1}D ENL. Interestingly, Palace et al. (2016) found no significant correlations between entropy and basal area as well as mean diameter, which is contrary to what we found in this study.

Quadratic mean diameter, effective number of diameter classes, basal area and stem density explained certain proportions in the variation of mean ENL over all 150 plots sampled. With the exception of basal area, these summary measures explain a higher percentage of variation in ^{0}D ENL than in ^{1}D ENL and ^{2}D ENL. Thus, ENL ^{1}D and ^{2}D could possibly serve as additional explanatory variables to explain relationships that cannot be distinctly explained by stand summary measures. Higher mean diameter and a higher basal area per hectare are often related to taller trees and maximum stand height and thereby explain higher ENL-values. Stem density decreases with increasing mean diameter, either due to thinning and harvesting or self-thinning. The decrease in ENL with increasing stem density can thus be attributed to its relation with mean diameter and basal area. Furthermore, the effective number of diameter classes (ENDC) had a positive effect on ENL. ENDC reflects the diversity of tree sizes within a stand. This suggests that a higher diversity

of tree sizes leads to a more even occupation of layers across the vertical profile and thereby increase ENL.

Mean ^{1}D ENL and ^{2}D ENL decreased at higher stand ages after a peak at ~130 years, whereas the coefficient of variation increased. The increase in CV (%) can be attributed to the harvest of dominant trees in mature stands, creating gaps in the canopy and decreasing mean ^{1}D ENL or ^{2}D ENL, but increasing horizontal variability of ENL. Thus, ENL may reflect quite well the effect of forest management activities on stand structure.

ENL describes the vertical distribution of tree components and in combination with sampling techniques, as presented here, it can also be used to assess horizontal structural variability. However, it cannot provide information on stand density, which can also be understood as a structural component. Thus, stands of different densities can have the same ENL, because only the relative and not absolute occupation per layer is of importance (Hunter 1990). Reducing errors to derive more precise and accurate ENL-estimates from single-scans could allow for a more detailed differentiation of forest structures in combination with leaf area index.

2.4.4. Applications in forest management

Single-scan approaches show a high application potential for forest management purposes, especially for management planning as well as for monitoring purposes. Recently, several authors highlighted the efficiency of single-scan approaches with regard to estimation of stem density, stand volume or biomass and basal area (e.g. Astrup et al. 2014, Seidel & Ammer 2014). Compared to conventional inventory approaches, TLS allows for a rapid assessment of several measures with one scan. Thus, the need for intensive and time consuming field work can be reduced and data required for management planning and monitoring can be obtained more efficiently. In this context, ENL is complementary to existing methods that are also based on TLS. E.g. when biodiversity conversation is a management goal that is bound to certain stand structures, these can be monitored via ENL. The assessment of ENL can then easily be integrated in TLS-based forest inventories.

2.5. Conclusions

Multiple-scan approaches are useful when it comes to assessing forest plots if detailed information about spatial structures or individual trees is required. The advantage of a high level of information due to very low occlusion is bound to the disadvantage of a more labor- and time-intensive field work and post-processing. The introduced measure ENL could be estimated on a single-scan basis with an error ranging from 5.1 to 9.81% for the investigated forest types, depending on the Hill-Number used. ENL facilitates a distinct differentiation of three-dimensional stand structures, when its horizontal variability is taken into account. With respect to vertical structural variability, interpretation of results based on ENL-analysis is much more straightforward than based on foliage height diversity.

2.6. Acknowledgements

2.7. References

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3. Quantifying stand structural complexity and its relationship with forest management, tree species diversity and microclimate

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Abstract

Measures to describe stand structural complexity efficiently and objectively are increasingly demanded to understand the relationship between forest management, stand structure, biodiversity and ecosystem functioning. Here, we present an approach to quantify stand structural complexity based on fractal dimension derived from single terrestrial laser scans (TLS) that were made on 126 permanent forest research plots in Germany, representing major stand and management types. The newly developed SSC-index (SSCI) was positively correlated to conventional tree-based measures of stand structural complexity, tree size differentiation, diversity of tree diameters and random tree spacing patterns. Beyond that, it successfully differentiated between stand types of different main tree species and management systems. SSCI increased from low to high tree species diversity and explained microclimatic fluctuations better than conventional, tree-based measures. Given the high efficiency during data collection, TLS can be used to assess stand structural complexity for large sample sizes to provide an explanatory variable for the effects of forest management on biodiversity, productivity and ecosystem processes.

Keywords: fractal dimension, single-scan, TLS, stand structure, biodiversity

3.1. Introduction

Creating complex forest stand structures through specific management approaches has been increasingly recognized as a possibility to support ecosystem stability, adaptability and resilience as well as biodiversity and productivity (Hardiman et al. 2011, Puettmann et al. 2012, Messier et al. 2013, Zenner 2015). Especially in Central Europe and North America, the management of forests towards complex stand structures that resemble old-growth attributes was enforced in forest management policies and guidelines (Giessen et al. 2013, Messier et al. 2015, Puettmann et al. 2015). In this context, management approaches moved away from focusing on even-aged, single-species stands towards uneven-aged, multi-species stands. Such approaches aim at enhancing structural complexity, also termed 'structural heterogeneity' or 'structural diversity' (Bauhus et al. 2009, Puettmann et al. 2009, Messier et al. 2013). In order to analyze the effects of different management approaches on stand structure (even-aged vs. uneven-aged FM and pure vs. mixed stands) as well as its relation to biodiversity and ecosystem processes, measures are needed that describe structural complexity objectively and quantitatively.

Measuring structural complexity of forest ecosystems has been challenging and several measures to quantify aspects of structural complexity focused on tree-based attributes, such as tree size differentiation, diversity of diameter classes or the spatial patterns of tree positions (see Zenner & Hibbs 2000, Pommerening 2002, von Gadow et al. 2012, Beckschäfer et al. 2013). However, a widely accepted definition of stand structural complexity is lacking. McElhinny et al. (2005) provided a review on the definition and measurement of forest and woodland stand structural complexity. They defined stand structural complexity as a "measure of the number of different attributes present and the relative abundance of each of these attributes", but also pointed out that there is no "definitive suite of structural attributes". Pretzsch (2009) argued that one of the most important characteristics of forest stand structure is its three-dimensional nature. Thus, we argue that describing and defining stand structural complexity holistically in terms of the spatial, three-dimensional arrangement of tree components is reasonable (Seidel et al. 2016). It furthermore allows for an objective description of the physical forest structure without the necessity for a subjective selection of specific structural attributes.

Approaches to quantify complexity in ecology include measures of rugosity (Zenner & Hibbs 2000, Kane et al. 2010, DePreez 2015) and fractal dimension (Zeide & Pfeifer 1991, Li 2000, Silva et al.

2013). In the context of forest ecosystems, rugosity is usually used to quantify canopy roughness as a surrogate for structural complexity (e.g. Hardiman et al. 2013, Fahey et al. 2015, Zenner 2015). Structural complexity of objects was mathematically described by the fractal dimension (Mandelbrot 1975), which was also used to quantify the complexity of tree crowns (Zeide & Pfeifer 1991, Osawa 1995, Zhu et al. 2014, Dutilleul et al. 2015). A further approach to quantify stand structural complexity is based on the mean information gain index, which is a measure of pattern disorder that can be derived from digital photographs (e.g. Witté et al. 2013, Proulx & Parrot 2008).

In the present study we developed a new, fractal dimension-based method to quantify stand structural complexity based on the three-dimensional spatial arrangement of all above-ground tree components. To obtain the index components, we employed terrestrial laser scanning, which has proven to be an efficient and effective method to assess structure and dynamics of forest ecosystems with high accuracy and precision (Newnham et al. 2015, Ehbrecht et al. 2016). We investigated how stand structural complexity depends on forest management and tested the performance of our new index in differentiating conventionally determined stand structures and management types. Furthermore, we also tested the effect of tree species diversity on stand structural complexity. Finally, we investigated the effect of stand structural complexity on mean diurnal ranges of air temperature and vapor pressure deficit (VPD) in order to understand the relationship between stand structural complexity and the microclimate within stands.

3.2. Methods

This study was embedded into the Biodiversity Exploratories, which is a long-term research project investigating the relationship between land-use intensity and biodiversity (Fischer et al. 2010, www.biodiversity-exploratories.de).

3.2.1. Study sites

126 quadratic forest research plots with a side length of 100 m are located in three major geographic regions across Germany; the Hainich, the Swabian Alb and the Schorfheide-Chorin (Table 3.1, see also Appendix I, Table A1.2)). Information on environmental characteristics of the study sites was introduced in Fischer et al. (2010). The stands sampled in this study represent major Central

European forest types and management systems. Whereas plots with European beech (Fagus sylvatica L., abbr.: Fs) as main tree species are located in each of the three geographic regions, plots with Norway spruce (*Picea abies* [Karst.] L., abbr.: Pa) as main tree species are located at Swabian Alb. Scots pine (*Pinus sylvestris* L., abbr.: Ps) and Penduculate oak (*Quercus robur* L., abbr.: Qs) dominated stands are located in Schorfheide-Chorin. Management systems include even-aged and uneven-aged forest management as well as formerly managed stands, which are left unmanaged for several decades. In even-aged forest management systems, developmental stages represent different age classes, ranging from pole wood to immature and mature timber and are characterized by approximately even-sized trees (see also Röhrig et al. 2006). Uneven-aged E. beech stands are managed by single tree harvests and small-scale thinning interventions, resulting in uneven-sized tree compositions and often J-shaped diameter distributions (Röhrig et al. 2006).

Table 3.1: Main tree species, management systems, and developmental stages of the selected study stands

Main tree species	Management	Management system	Developmental stage	n
European beech[1]	managed	even-aged	pole wood	10
			immature timber	9
			mixed imm. timber	7
			mature timber	17
			mature timber	13
				25
		uneven-aged	mature timber	7
	unmanaged	(un)even-aged	mature timber	7
pedunculate oak[2]	managed	even-aged	mature timber	7
Scots pine/E. beech			mature timber	7
Scots pine[4]			(im)mature timber	4
			mature timber	11
Norway spruce			immature timber	11
			mature timber	5
Sum				126

[1]= *Fagus sylvatica* L. (abbr. Fs); [2]= *Quercus robur* L. (abbr. Qs), [3]= *Picea abies* [Karst.] L. (abbr. Pa); [4]= *Pinus sylvestris* L. (abbr. Ps). For detailed plot wise information we refer to Appendix I.

3.2.2. Terrestrial laser scanning and sampling design

The approach presented here was based on terrestrial laser scans. A point cloud of a forest scene, captured by a single laser scan, was used as an independent sample. Here, a Faro Focus 3D 120

(Faro Technologies Inc., Lake Mary, USA) laser scanner that operates based on the phase-shift technology was used. The instrument was set to scan a field of view of 90 degrees in horizontal direction (0-90 degrees over the horizon) and 360 degrees in azimuthal direction with an angular step width of 0.14065 degrees. Consequently, for a hemisphere 3.25 Mio laser beams were emitted into the forest scene and, if reflected at a vegetation element, received by the instruments detector. Maximum scan distance was defined by the instrument's limit of 120 m. Theory and mathematical formulations applied and described in the following can be used for any type of terrestrial laser scanner.
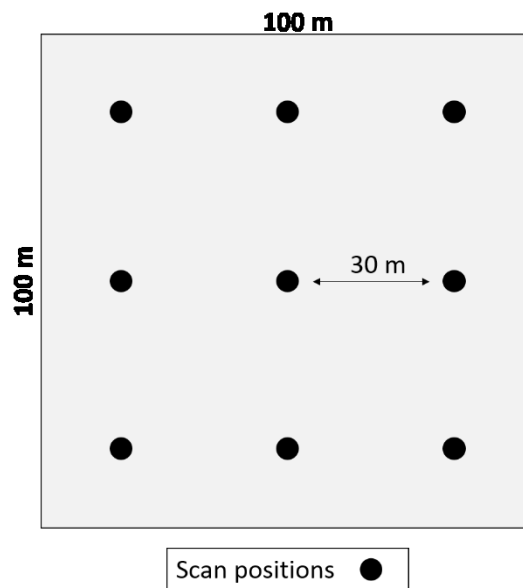

Figure 3.1: Sampling design for each 1 ha plot

TLS data acquisition can be divided into single- and multiple-scan approaches. Here, we made nine systematically distributed single-scans on each of the 126 forest research plots from June to September 2014 (Fig. 3.1). When using single scans, field work and post-processing are much faster as there is no need to register the scans to each other. For more information related to data acquisition using single- or multiple-scan approaches we refer to Ehbrecht et al. (2016).

Using Mathematica software (Wolfram Research, Champaign, USA) an algorithm was developed that calculated a single measure for each independent single-scan point cloud. This measure will be referred to as *MeanFrac* from here on and its derivation is described in the following.

First, the point cloud was split into 2560 azimuthal sectors, one for each angular direction measured by the scanner (360°/0.140625° = 2560).
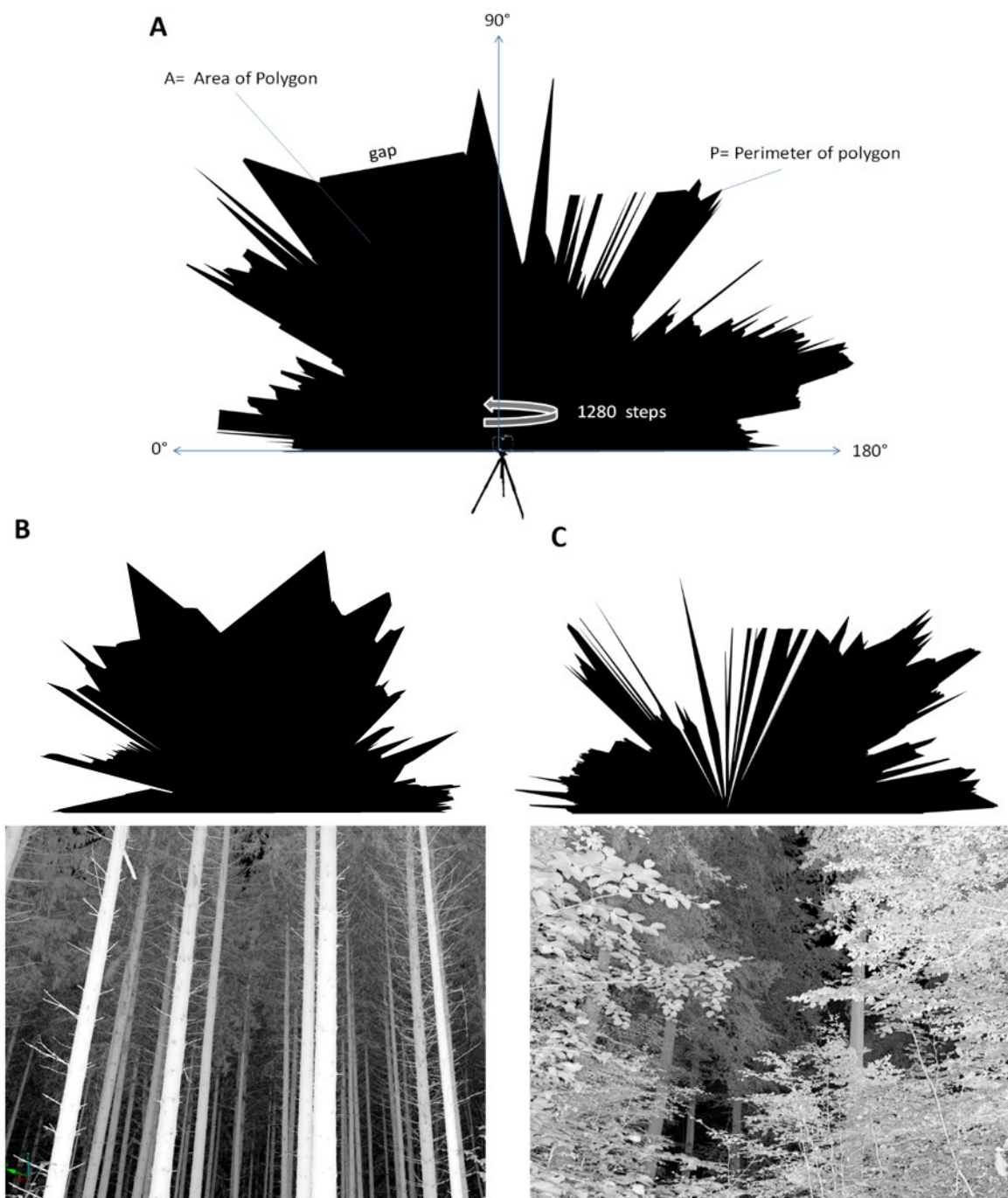
Figure 3.2: Graphical visualizations of exemplary cross-sectional polygons. (A) visualizes the way the scanner operates, (B) and (C) are examples of polygons and corresponding images from stands with low (B) and high (C) stand structural complexity, respectively.

Then, cross-sections were built based on the combination of two scanned sectors (each 0-90° in horizontal angle) that were on opposite sides of the scanner (2560 angular direction → 1280 cross-sections), e.g. 45° azimuth angle and 135° azimuth angle. Therefore, 0° horizontal angle on the

opposite site were converted into 180°, so that angles run continuously for each cross-section. Scan points of each cross-section were then sorted to run from low horizontal angle (0°) across the zenith to 180° horizontal angle on the other side of the cross-section. Based on the sorted list of horizontal angles and points' coordinates a polygon was then created for each of the 1280 cross-sections. Starting and ending at the scanners position, the polygon connects each point of a cross-section to the next point at the next horizontal angle. Since there is not always a hit or point at each horizontal angle (e.g. in case of a gap or open space), a point was then connected to the point of the next horizontal angle that contained a hit.

The fractal dimension index (FRAC) of each of the 1280 polygons was then determined based on the formula provided by McGarigal and Marks (1994):

$$FRAC = \frac{2 * \ln(0.25 * P)}{\ln(A)} \qquad (3.1)$$

with *ln* being the natural logarithm to the base e , P being the perimeter and A the area of the polygon. McGarigal and Marks stated that the fractal dimension index usually ranges from 1 to 2 when the index is calculated with the rectangle as reference (factor 0.25 in the counter). Finally, we defined *MeanFrac* as the arithmetic mean of the 1280 FRAC values per scan. In this context we have also tested the use of the vector version with a circle as reference geometry and a simple perimeter to area ratio to describe the complexity of the polygon shape. The vector based computation yields similar results as the raster based version with a rectangle as reference geometry (eq. 3.1), but has shown to have a lower capability in differentiating between stands (sensu Mc Elhinny et al. (2005)). A further limitation of simple perimeter to area ratios is its dependence on polygon size (Thenkabail 2015).

3.2.3. SSC-Index construction

The mean polygon area (A) of the cross-sections can be understood as a proxy for stand density or space occupation. Scanning in dense stands with a high space filling will result in small mean polygon areas, but not necessarily in similarly smaller perimeter lengths. Due to the high spatial resolution at which the scanner is operating (small step width), laser beams are frequently reflected from tree components that are much further away from the scanner than the average distance to a hit -even in dense stands- and thereby increasing the perimeter length. This is especially the case in

young stands with small trees or in dense spots of natural regeneration, where the size or diameter of stems and branches is small and the laser beams traverse very small gaps within the dense vegetation. That is why *MeanFrac* decreases with increasing size of the polygon area. The relationship between fractal dimension and the size of the polygon area follows a negative exponential trend (see Fig. 3.3). In fact, stand structural complexity is density-dependent because complexity depends on the existence of structural elements. The more structural elements (tree components) present, the more information is needed to fully describe stand structure in terms of the spatial arrangement of tree components. This complies with the definition of complexity provided by Puettmann et al. (2012).
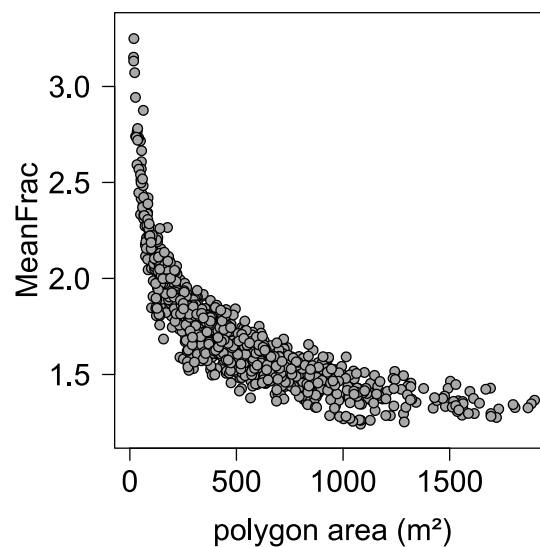

Figure 3.3: Relationship between mean fractal dimension of 1280 polygons per scan and the respective mean polygon area.

As a result, dense thickets with small branches and stems will usually show higher fractal dimension values than mature stands with large trees having larger stems and branches as well as a distinct vertical stratification. Due to the sensing with constant angular steps, larger stands, where tree to tree distances and the size of unoccupied space are larger, usually have a lower fractal dimension as computed from the cross-sections. Fractal dimension on its own is a dimensionless measure to describe the complexity of geometric objects mathematically (Mandelbrot, 1975). Hence, it cannot be used to describe forest stand structural complexity without an appropriate scaling. Without taking the vertical structure of forests for the quantification of structural complexity into account, low stands with no vertical differentiation (e.g. thickets) can have the same or even higher fractal

dimension-values than vertically heterogeneous stands with greater stand height (e.g. mature timber stands), because fractal dimension is scale-independent. To overcome this problem, we use the *effective number of layers* (ENL, see Ehbrecht et al. 2016) to scale the fractal dimension. We introduced the *effective number of layers* (ENL) as a measure of vertical stand structure that is based on single terrestrial laser scans (Ehbrecht et al. 2016). Vertical structure is stratified into layers of 1 m thickness and the number of voxel with a side-length of 20 cm inside each layer is counted. The effective number of layers was computed using the inverse Simpson-Index.

$$ENL = 1/ \sum_{i=1}^{N_{top}} p_i^2 \qquad (3.2)$$

Here, p_i is the proportion of filled voxels in the i_{th} vertical layer to the sum of filled voxel in the entire volume analyzed. N_{top} refers to the top stand height, and *ln* is the natural logarithm.

ENL is then a measure that describes vertical structure taking stand height (number of layers with 1 m thickness) and their respective occupation by tree components relative to the total space occupation into account. Increasing stand height and a more even occupation along the vertical profile result in higher values. Even though single-scans are affected by occlusion, ENL can be derived with a similarly low error as from multiple-scans (Ehbrecht et al. 2016).

As an exponent of FRAC, ENL weighs FRAC the stronger the more a stand is vertically stratified. In addition, the angular scan characteristics with fixed step width between horizontal and vertical measurements result in more jagged shapes of the polygons for smaller plant objects (see Fig. 3.2). In other words, the dimension of scanned objects (in this case: trees) does affect the *MeanFrac*-values. This means that, in contrast to fractal dimensions, scan-based estimations of *MeanFrac* are not scale independent anymore but yield smaller values for taller and wider trees. To correct for this effect we tested exponential and linear or multiplicative combinations. In order to evaluate and compare exponential and linear or multiplicative corrections, we followed Mc Elhinny et al. (2005), who stated that an index of stand structural complexity should be constructed in a way that most clearly differentiates between stands. Finally, the natural logarithm of ENL was used to scale index values to reasonable value range.

$$SSC = MeanFrac^{\ln(ENL)} \qquad (3.3)$$

Reference data

To enable a comparison between TLS-derived measures and stand structural indices, we used forest inventory data collected between 2008 and 2010. On each of the 126 forest plots, trees with dbh ≥ 7 cm were measured for diameter at breast height (DBH) using a diameter tape. Additionally, tree heights were measured across the range of assessed tree dimensions to derive tree diameter-height relationships. Furthermore, each tree`s species identity and position within a plot were recorded with coordinates relative to the plot center (x, y = 0, 0).

Based on this data we calculated conventional indices that are used to describe forest structure, in particular Zenner & Hibbs' (2000) Structural Complexity Index (SCI), Füldner`s (1995) tree size differentiation index (TD), Clark-Evans' index of aggregation (CE) (Clark & Evans 1954), and the Gini-Coefficient of tree diameters (GC_d) (Lexerød & Eid, 2006).

SCI is a measure of rugosity that describes structural complexity (Zenner & Hibbs 2000). In order to calculate SCI, based on the concept of spatial tessellation, neighboring tree tops are connected to a triangular irregular network (TIN). Dividing the sum of areas of the three-dimensional triangles (connected tree tops) by the sum of the areas of projected triangles (projected to the forest floor) yields SCI. A detailed description of index construction can be found in Zenner & Hibbs (2000).

$$SCI = \frac{surface\ area\ of\ TIN}{projected\ area\ of\ TIN} \qquad (3.4)$$

Füldner`s (1995) tree size differentiation index is a measure describing the size relations of neighboring trees. The DBH of a given tree is related to the DBH of its four nearest neighbors (the ratio of the smaller to the larger tree). The resulting ratio is then deducted from 1.

$$TDn_i = \frac{1}{n} \sum_{j=1}^{n} (1 - r_{ij}) \qquad (3.5)$$

According to Füldner (1995) and Pommerening (2002), values between $0 - 0.3$ describe a small differentiation of tree sizes, $0.3 - 0.5$ describe a medium differentiation, $0.5 - 0.7$ strong differentiation and values between 0.7 and 1 can be interpreted as very strong differentiation of tree sizes.

The Clark-Evans Index of aggregation (CE, Clark & Evans 1964) describes the horizontal arrangement of tree positions in terms of clustered (values < 1), random (values ~ 1) and regular distributions (values > 1). In this context, we interpret regular tree spacing as indication of rather homogenous and less complex structures than random patterns (Neumann & Starlinger, 2001). It is computed by relating the observed mean distance to a tree`s nearest neighbor ($r_{observed}$) to the expected mean distance ($r_{expected}$) under a random tree distribution pattern.

$$CE = \frac{r_{observed}}{r_{expected}} \tag{3.6}$$

The Gini-Coefficient is a measure of dispersion and intends to describe inequality of a distribution. When applied to tree diameter distributions it describes structural diversity and is considered to be superior to other measures that describe diversity of tree diameters (Lexerød & Eid, 2006). Values can range between 0 and 1, whereas low values indicate high equality and high values indicate high inequality of tree diameters. We used the R-package *ineq* (Zeileis 2014, version 0.2-13) to compute the Gini-Coefficient of tree diameters (GC_d).

Tree species diversity was described by the exponential Shannon-Index (Jost 2006). Here, we used the percentage of a species` basal area in relation to the total basal area as p_i.

$$\exp H` = \exp(-\sum_{i=1}^{N_{top}} p_i * ln\, p_i) \tag{3.7}$$

Measurements of temperature and vapor pressure deficit

Each research plot was equipped with a meteorological station measuring temperature (°C) and relative humidity (%) in one minute intervals at 2 m above ground (T. Nauss, personal communication, 2016). Minimum and maximum values per day were used to calculate mean diurnal ranges of temperature and vapor pressure deficit (VPD) for a three months period from

June 1st to August 31st 2014. We used the R-package *plantecophys* (Duursma 2015, Version 1.1-8) to convert relative humidity to VPD.

3.2.4. Statistics

All statistical computations were made using the software environment R, version 3.2.3 (R Development Core Team, 2016). We used linear regressions models to test the relationship between the newly developed SSC-index and stand structural indices and microclimatic variables. In order to test the relationship between tree diversity and SSCI, we used logarithmic (linear), asymptotic (non-linear) as well as power law (non-linear) regression models and selected the most appropriate model based on AIC comparison (Aikaike Information Criterion, see Appendix 1). Here, we excluded the uneven-aged stands managed under single tree selection from the analysis in order to separate management from tree diversity effects. Compared to uneven-aged stands, the even-aged stands are managed similarly. The differences between stands with different main tree species are the frequency and intensity of thinnings. However, for even-aged stands, management activities result in approximately even-sized trees and overall structure is then mainly a function of age. This is contrary to uneven-aged stands managed under single tree selection, which results in inverse J-shaped diameter distributions. Thus, in single tree selection systems, the management effect overrides a diversity effect much more than it does in even-aged stands.

3.3. Results

3.3.1. Relationship between fractal-dimension based SSCI and conventional tree-attribute based indices of stand structure

The fractal-dimension based description of stand structural complexity showed significant correlations with conventional tree-attribute based measures of stand structural complexity or heterogeneity. The new SSC-index was significantly positively correlated to Zenner & Hibbs' (2000) stand structural complexity index and Füldner's (1995) tree size differentiation index. SCI explained 22% of variance in mean SSCI over all 126 sampled plots and main tree species (Fig. 3.4). Coefficients of determination were lower for European beech dominated forests ($r^2 = 0.09$), but higher for Norway spruce ($r^2 = 0.26$) and Scots pine stands ($r^2 = 0.37$).
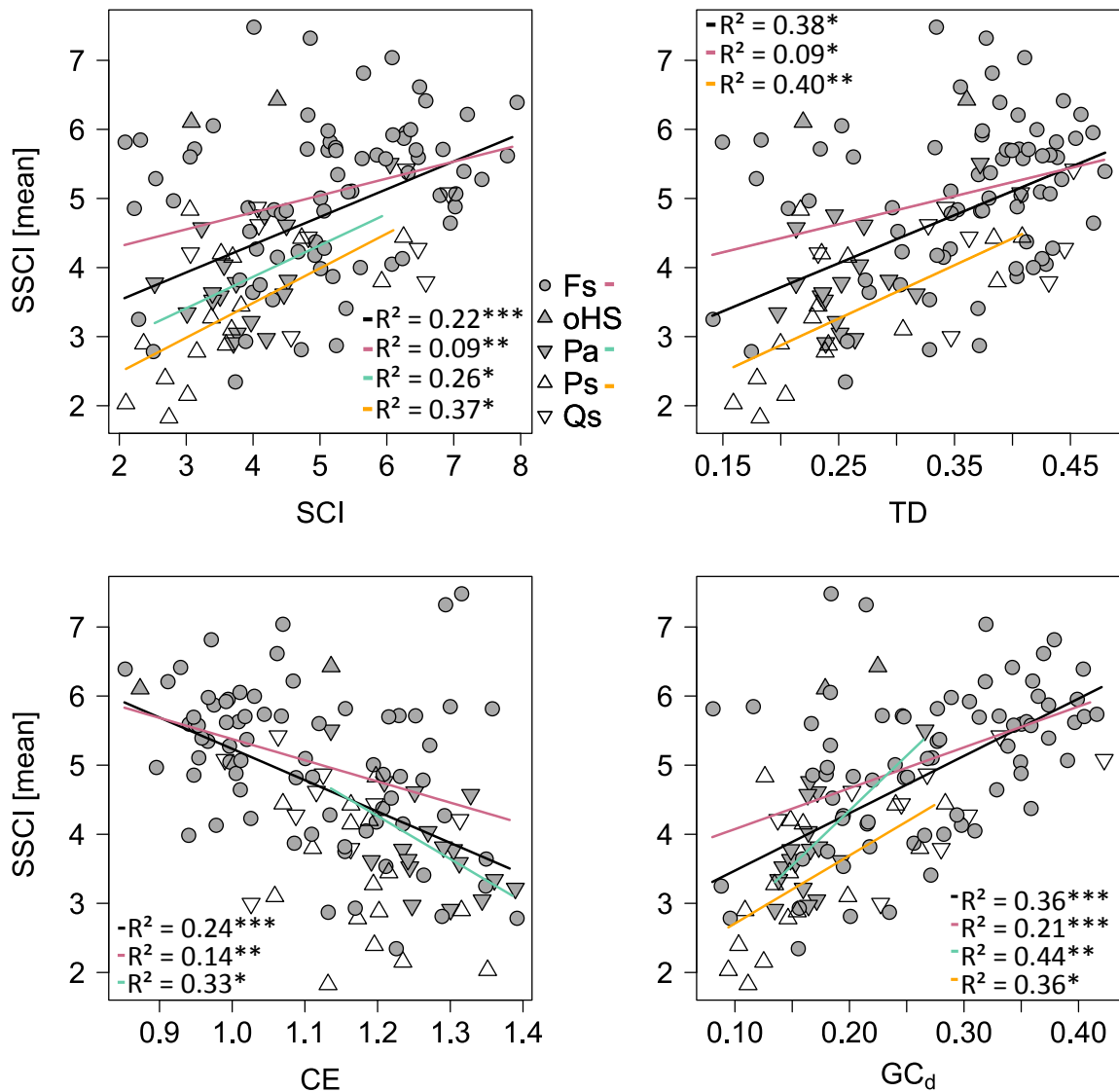
Figure 3.4: Relationship between SSCI and the Structural Complexity Index by Zenner & Hibbs (2000) SCI (*upper left*), Füldner`s (1995) tree size differentiation index (TD, *upper right*), Clark Evans index of aggregation (CE, *bottom left*), and the Gini-Coefficient of diameters (GC$_d$, *bottom right*). Regression models were computed separately for all plots (black line) and plots with E. beech (Fs, red line), N. spruce (Pa, turquoise line) or S. pine (Ps, orange line) as main tree species and plotted only when the relationship was significant at p < 0.05.

There was no significant correlation between SSCI and SCI for pedunculate oak stands. Tree size differentiation explained 38% of variance in SSCI over all plots, with lower coefficients of determination for European beech (r² = 0.09) and higher values for Scots pine (r² = 0.40). There were no significant correlations between TD and SSCI for Norway spruce and pedunculate oak (p > 0.05). Increasing regularity of stem positions lead to lower SSCI-values compared to random

stem distributions when considering all plots in the analysis (r^2 = 0.24, p < 0.001). This significant trend holds also for European beech (r^2 = 0.14, r^2 = 0.01) and Norway spruce stands (r^2 = 0.33, p < 0.05) if tested separately. Correlations between Clark-Evans Index of aggregation and SSCI were not significant for pedunculate oak and Scots pine stands (p > 0.05).

The Gini-Coefficient of tree diameters (GC_d) explained 36% of variation in SSCI over all plots (p < 0.001). There were significant correlations between the GC_d and SSCI of European beech stands (r^2 = 0.21, p < 0.001), Norway spruce stands (r^2 = 0.44, p < 0.01) and Scots pine stands (r^2 = 0.36, p < 0.05).

3.3.2. Stand structural complexity and its relationship with forest management and tree species diversity

Differently managed stands differed in stand structural complexity. Highest mean SSCI-values per plot were found in even-aged, mature European beech stands as well as in uneven-aged, single tree-selection systems, mainly comprised of European beech (Fig. 3.5). Both, even-aged, mature and unmanaged European beech stands showed a high variability in mean SSCI per 1 ha plot, whereas the highest median was found in uneven-aged stands managed by single tree-selection. Even-aged coniferous stands were on average less complex structured than the European beech stands (except for immature E. beech pure stands). Mixed stands of Scots pine and European beech had a higher mean SSCI than similarly aged pure stands of Scots pine.
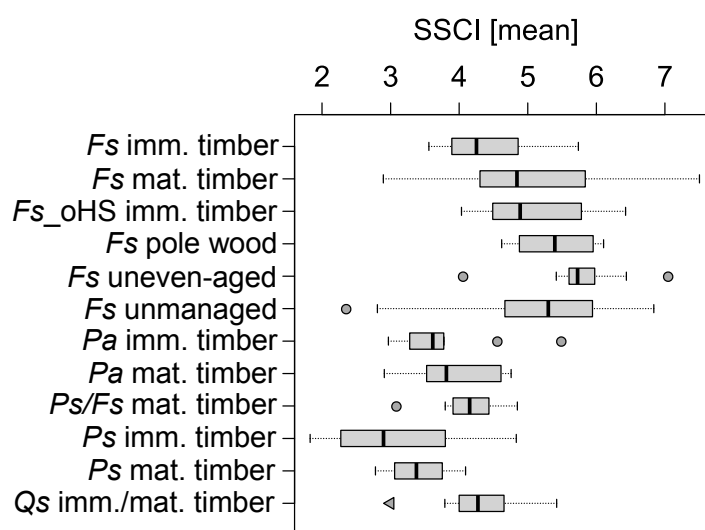

Figure 3.5: Boxplots of mean SSCI per plot for different stand types. Categories relate to developmental stages as shown in table 3.1.

SSCI increased from low to high tree species diversity (r^2_{pseudo} = 0.32 (Fig. 3.6)). The same trend holds for European beech dominated forests (r^2_{pseudo} = 0.26). The effects of tree species diversity on SSCI were not significant for Norway spruce, Scots pine or pedunculate oak dominated stands.
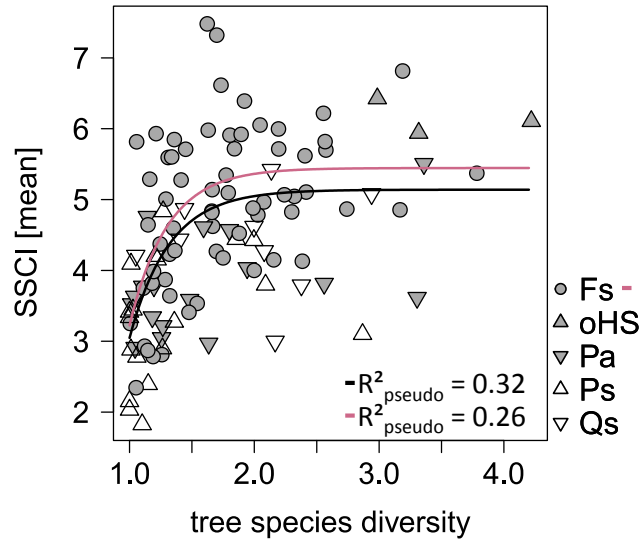

Figure 3.6: Relationship between tree species diversity (exponential Shannon Index) and mean SSCI per plot. Regression models were computed separately for all plots (black line) and plots with E. beech (Fs, red line) as main tree species. Relationships were not significant for N. spruce, S. pine and P. oak dominated plots.

3.3.3. Relationship between stand structural complexity and microclimate indicators

SSCI was significantly related to microclimatic variables in temperate forest ecosystems. The mean diurnal temperature range during the vegetation period was lower in stands with high SSCI and higher in stands with low SSCI (Fig. 3.7). Whereas SSCI explained 39% of variation in the mean diurnal temperature range (ΔT) over all 126 plots, it additionally explained 20% of the diurnal temperature range for European beech stands (p < 0.001) and 47% for Scots pine stands (p < 0.05). SSCI also affected the mean diurnal range of vapor pressure deficit (ΔhPa) within a stand (r^2 = 0.19, p < 0.001), resulting in lower diurnal ranges in stands with high SSCI. It significantly affected ΔVPD in European beech (r^2 = 0.10, p < 0.01), Scots pine (r^2 = 0.42, p < 0.05) and Norway spruce (r^2 = 0.24, p < 0.05). In this context, we also tested the explanatory power of SCI (r^2 = 0.21 for ΔT, r^2 = 0.06 for ΔVPD), TD (r^2 = 0.17 for ΔT, r^2 = 0.04 for ΔVPD), CE (r^2 = 0.14 for ΔT, r^2 = 0.06 for ΔVPD) and GC_d (r^2 = 0.22 for ΔT, r^2 = 0.06 for ΔVPD). In all cases, SSCI had a higher explanatory power than the conventional tree-based indices (data not shown).
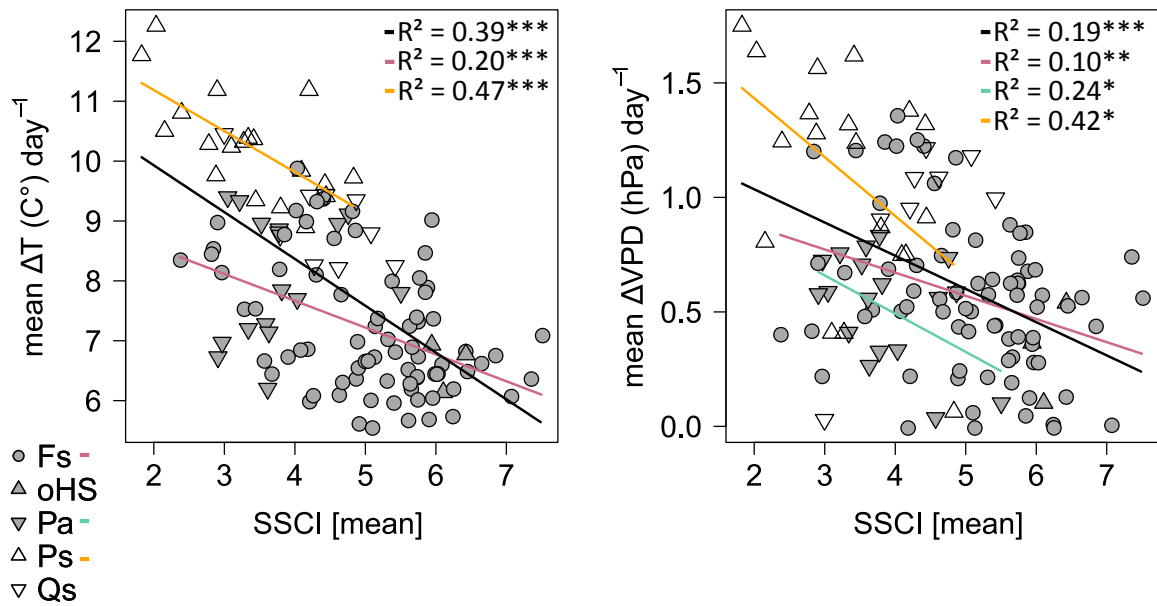
Figure 3.7: Relationship between mean SSCI per plot and mean diurnal temperature range (*left*) and mean diurnal range of vapor pressure deficit (*right*). Regression models were computed separately for all plots (black line) and plots with E. beech (Fs, red line), N. spruce (Pa, turquoise line) or S. pine (Ps, orange line) as main tree species and plotted only when the relationship was significant (p < 0.05).

3.4. Discussion

3.4.1. Relationship between fractal-dimension based SSCI and conventional tree-attribute based indices of stand structure

So far, several studies had investigated the relationship between stand structural diversity, structural heterogeneity, or structural complexity and biodiversity (e.g. Neumann & Starlinger 2001, McCleary & Mowat 2002, Ishii et al. 2004, Tews et al. 2004), or between stand structure and productivity (e.g. Lei et al. 2009, Long & Shaw 2004, Dănescu et al. 2016). The terms "structural diversity", "heterogeneity" or "complexity" are often insufficiently defined and a differentiation between them is difficult (Tews et al. 2004). Yet, they are often meant to indicate "naturalness" (Messier et al. 2013), even though not all natural forests are structurally complex. Since the index introduced here is based on fractal dimension, which is a mathematical description of object complexity, we argue that it describes rather structural complexity than heterogeneity or diversity. From a spatial point of view, SSCI describes complexity on α-level (referring to plot or stand level). The coefficient of variation of SSCI on a plot (here: nine SSCI-values per 1 ha) can then be

interpreted as small-scale variability of structural complexity. The variability of SSCI between plots could be used and interpreted as structural variability on larger scales. A multi-scale analysis should be considered in future research in order to understand scale dependencies of stand structural measures. Whereas Zenner & Hibbs` (2000) structural complexity index quantifies vertical and horizontal structure simultaneously by taking tree positioning and tree size into account, Füldner`s (1995) tree size differentiation index describes intermingling of tree sizes as an aspect of horizontal structure. Both are closely correlated to each other and intend to describe either structural complexity or structural heterogeneity on α–level (Pommerening 2002, Pretzsch 2009). The application of the Gini-Coefficient to diameter distributions (GC_d) is supposed to describe structural diversity on α–level (Lexerød & Eid, 2006). Structural complexity decreased with increasing regularity of tree spacing as indicated by the Clark-Evans index (Fig. 3.4). Our fractal-dimension based description of stand structural complexity is positively (in terms of the effect-direction) correlated to the four indices. However, even though the correlations between tree based measures and SSCI are significant, the coefficients of determination are relatively low. We assume that our index quantifies complexity holistically and with a higher spatial resolution by taking the full three-dimensional arrangement of structural elements into account, without addressing single objects. It hence describes structural complexity from a completely different perspective. Therefore, the three-dimensional TLS-based assessment of structural components goes beyond stand characterization by using one- or two-dimensional structural attributes or indices. Furthermore, our approach does not require intensive field work. However, the presence of larger gaps might negatively affect SSCI values due to shorter perimeter lengths of the polygon. Since canopy gaps are an ecological or eco-physiologically certainly important structural property of forest ecosystems, they should be considered along with SSCI when investigating certain structure-ecosystem functioning relationships.

3.4.2. Stand structural complexity and its relationship with forest management

Single tree selection systems result in uneven-aged stand structures and are commonly viewed as being structurally more diverse and complex than even-aged stands (Pommerening & Murphy 2004, Zenner et al. 2012). Indeed, the uneven-aged stands managed by single tree selection (*Plenterwald*) showed the highest median of mean SSCI-values, which is probably due to their high

degree of tree size differentiation and high diversity of tree diameters. However, except for two outliers, the variability between plots was relatively low, because single tree selection systems usually result in a high small-scale structural diversity on plot level with only small structural differences between plots. The high variability of SSCI in mature even-aged European beech stands was due to the fact that the sample included stands with a broad range of understory conditions. Understory trees led to higher SSCI-values, whereas their absence, in combination with long, branch-free stems and a single canopy layer led to lower SSCI-values (*Hallenwald*). The effect of branches on SSCI was also reflected in the differences in complexity when comparing the developmental stages 'pole wood' and 'immature timber'. In the pole wood stage, natural self-pruning was not as advanced as in the immature timber stage, which resulted in a higher plant density along the vertical profile. This increased the effective number of layers (ENL) of pole woods and thereby SSCI (Ehbrecht et al. 2016). Immature timber stands were therefore structurally less complex, as they have already developed branch-free stems. Norway spruce and Scots pine stands showed a generally lower SSCI than the European beech stands (with a few exceptions). This was probably due to differences in the structural complexity of individual tree crowns which may differ between conifers and broadleaved tree species. Zeide & Pfeifer (1991) found differences in the fractal dimension of tree crowns between dominant and intermediate trees. We assume differences in the fractal dimension of broadleaved and coniferous trees, resulting in higher structural complexity of individual crowns of European beech compared to Norway spruce or Scots pine. This is also indicated by the higher SSCI-values of Scots pine-European beech mixtures when compared to pure Scots pine stands. A similar result was found by Pretzsch et al. (2016), who examined 32 triplets comprising of pure Scots pine and European beech stands and their mixture across Europe.

SSCI increased with tree species diversity (Fig. 3.6). We assume, that differences in tree morphology between individuals of different tree species may cause higher stand structural complexity. Jucker et al. (2015) and Pretzsch et al. (2016) reported that mixed stands showed an optimized canopy packing when compared to pure stands. Mixing of tree species with different structural architectures may result in a more efficient canopy exploitation (Pretzsch 2014) and thereby leading to higher SSCI. This is in line with our assumption that stand structural complexity is, to a certain degree, density-dependent. In an earlier study canopy space filling, a measure of plant material density in the stand, was found to be affected by species identity. Actually, mixtures composed of species that

differed in their phenotype yielded higher space occupation (Seidel et al. 2013). These findings provide evidence that moving away from even-aged, mono-specific stands towards uneven-aged, multi-species stands promotes stand structural complexity.

In order to understand the effect of stand structural complexity on ecosystem functions and processes, we exemplarily investigated its effect on microclimate (Fig. 3.7). We found that diurnal ranges of temperature and vapor pressure deficit were lower in stands with higher SSCI. Structurally more complex stands usually showed a higher stand density, which might buffer the heating effect of incoming short-wave radiation as well as the cooling effect of outgoing long-wave radiation (Häckel, 2008). Other studies showed that tree diversity enhances stand transpiration, which in turn buffers fluctuations in temperature and vapor pressure deficit (Gebauer et al. 2012, Kunert et al. 2012, Forrester 2015). As tree diversity also enhanced SSCI, as shown in our data, a more stable microclimate could be due to higher tree species diversity. Jacob et al. (2010) reported increasing leaf area index values with increasing tree species diversity. Higher leaf area index values and differences in canopy characteristics of species rich stands could affect diurnal ranges of temperature and VPD. Unfortunately, we did not have LAI data available for this study to test its relationship. However, the mechanisms behind these relationships remain unclear and need to be investigated in order to better understand the effects of stand structure on microclimate.

3.5. Conclusions

α-level stand structural complexity can be objectively and efficiently quantified using single terrestrial laser scans. The new stand structural complexity index (SSCI) is based on a holistic approach to quantify the spatial arrangement of plant material in forests and proved to be able to differentiate stand structures. Its fully automatic determination and strong relationship with forest management, stand structure, and microclimate, may further encourage its application. More laboriously determined conventional, tree-based measures of stand structural complexity or structural diversity are usually based on individual objects (trees) which are described rather rudimentary (DBH, height). Hence, it is not surprising that they showed lower explanatory power for the variables investigated. However, we do not know what the most appropriate measure of stand structural complexity is, since different measures deal with different aspects of complexity. Setting up a framework that differentiates between stand structural heterogeneity, diversity or

complexity should be considered in future research. Still, we conclude that the new SSC-index introduced here offers the possibility to study relationships between stand structure, biodiversity and ecosystem functioning more objectively and detailed than conventional tree-based approaches.

3.6. Acknowledgements

3.7. References

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4. Effects of stand structure on the diurnal temperature range in temperate forest ecosystems

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Abstract

The diurnal temperature range (DTR) is an important indicator of microclimate in terrestrial ecosystems and is relevant for several ecosystem processes and functions. In order to understand relationships between forest structure and microclimate in temperate forest ecosystems, we investigated the effects of stand structure on DTR during summer and winter in 128 experimental forest plots in Germany. DTR increased linearly with increasing canopy openness, which showed to be the main structural driver of DTR, explaining 19% to 66% of variance of DTR during summer at the regional level. Across regions, 84% of variance was explained under consideration of regional climate and elevation, which alone accounted for 72% of DTR-variance. Vertical forest structure had an additional, but marginal effect on DTR, whereby an increasing effective number of canopy layers and tree size diversity resulted in decreasing DTR (R^2 = 0.86). Differences in DTR between plots of different main tree species could be attributed to differences in canopy openness, whereby tree species diversity had no significant effect on DTR. Furthermore, stand structure had no substantial effect on DTR during winter. Forest microclimate can be indirectly controlled by forest management through modifications in canopy openness. Terrestrial laser scanning (TLS) showed to be a valuable tool for modelling forest microclimate, since rapidly assessed, TLS derived measures of canopy openness and vertical structure allowed to explain 85% of variance in DTR

under consideration of geographic location and elevation, which can also be assessed by TLS with integrated GPS and altimeter.

Keywords: forest structure, microclimate, forest management, TLS

4.1. Introduction

Microclimate in forest ecosystems is not only having an impact on biodiversity (Schall et al. 2017), but also on ecosystem processes and functions including evapotranspiration, decomposition and productivity of understory vegetation (Aussenac 2000, Geiger 2013, Dahlberg 2016). The microclimatic conditions in forest stands are affected by their spatial structure (Hardwick et al. 2015, Kovács et al. 2017). An understanding of how predicted climate changes affect biodiversity and ecosystem processes and functions in forests on small spatial scales requires an understanding of stand structure-microclimate interactions (Suggitt et al. 2011, Frey et al. 2016). In this context, the diurnal temperature range (DTR) is an important indicator of climate change and variability (Karl et al. 1991, Braganza et al. 2004, Qu et al. 2014), which has decreased worldwide since the 1950`s (Dai et al. 1999). Whereas DTR is known to be mainly affected by cloud cover, water vapor and precipitation (Dai et al. 1999), effects of forest structure on the diurnal temperature range below forest canopies were hardly investigated so far (e.g. Hardwick et al. 2015). Several studies investigating forest microclimate (including DTR) focused rather on contrasting stand or land-use types or comparisons of forests with open and clear-cut sites (e.g. Luskin and Potts 2011, Dodonov et al. 2013, Meijide et al. 2015). Differences in microclimate between systems or stand types were often attributed to differences in canopy cover or openness (Porté et al. 2004, Hardwick et al. 2015), whereby closed forests were often reported to have lower daily maximum air temperature as well as diurnal temperature ranges than forest edges or open sites (e.g. Chen et al. 1993, Carlson and Groot 1997).

Generally, microclimate within terrestrial ecosystems is mainly driven by the macroclimate (Parker 1995, Aussenac 2000, Holst et al. 2004). By absorbing, transmitting and reflecting solar radiation, vegetation influences and alters the amount and intensity of radiation penetrating the canopy and thus affects energy budgets (Geiger 2013, Launiainen et al. 2016). Plant transpiration as well as interception and through-fall of precipitation affect water budgets within stands (Pypker et al.

2005, Dietz et al. 2006, Gebhardt et al. 2014). In interaction with topographic conditions (exposition, slope, aspect, etc.), these mechanisms and processes lead to microclimatic conditions within a forest that differ from those outside a forested area (Aussenac 2000).

However, little is known about how microclimate is linked to other components of stand structure than canopy closure. On the one hand, a better understanding of stand structure-microclimate relationships could enhance the understanding of forest management impacts on microclimate bound ecosystem processes and functions. Since forest management decisions are usually made on the basis of structural measures (e.g. removal of a certain share of basal area, thinning from above vs. thinning from below, minimum harvestable diameter), an improved knowledge of how microclimatic variables are related to stand structural components could be especially relevant to forest managers. On the other hand, investigating relationships between different variables of forest structure and microclimate may help to improve climate models that aim to predict climate changes on small spatial scales.

The main components of stand structure are species composition and diversity, the spatial distribution of trees or biomass as well the size variability of trees (v. Gadow 2003). Tree based measures used to quantify stand structure include spatially non-explicit summarizing metrics such as stand basal area, stem density, volume, (quadratic) mean diameter and diameter variability or indices to describe the spatial distribution of trees (e.g. Clark-Evans index of aggregation). Tree species composition and diversity are either described by the share of basal area or stem number, or by indices such as the Shannon or Simpson Index. Spatially-explicit measures of stand structure are based on neighborhood patterns, such as tree size differentiation and species intermingling (Füldner 1995), structural complexity (Zenner & Hibbs 2000) or continuous functions to describe stand structure (e.g. pair correlation functions). Reviews and evaluations of tree based structural measures and indices can be found in Pommerening (2002) as well as in Neumann and Starlinger (2001) and Staudhammer and LeMay (2001). Non-tree based measures are canopy cover, canopy openness, leaf area index and leaf area density, which are usually derived from hemispherical images. Recently, newly developed three-dimensional measures allow for a more holistic quantification of stand structure that is not based on single tree attributes and derived from terrestrial laser scanning data, such as canopy space filling, vertical layering and structural complexity (Ehbrecht et al. 2017, Juchheim et al. 2017).

In this study, we investigated relationships between stand structural variables and the mean diurnal range of air temperature (DTR) in temperate forests in Central Europe during summer and winter 2014/15. The main objective was to identify major stand structural drivers of the diurnal temperature range. Our work was guided by the following hypotheses:

(I)   Canopy openness is the main structural driver of the diurnal temperature range in forest ecosystems.

(II)   Increasing vertical stratification negatively affects the diurnal temperature range beyond canopy openness.

(III)   Main tree species and tree species diversity have an impact on the diurnal temperature range.

4.2. Methods

4.2.1. Study sites

This study was conducted within the framework of the Biodiversity Exploratories (www.biodiversity-explatories.de). The Biodiversity Exploratories are a long-term research project that aims to investigate the relationship between land-use intensity and biodiversity. Further information can be found in Fischer et al. (2010). 150 experimental research plots (EPs) were located in three major geographic regions (from here on called: exploratory), namely the Swabian Alb, Hainich-Dün and Schorfheide-Chorin (Table 4.1).

Table 4.1: Number of plots and their main tree species for each of the three exploratories

Main tree species	Swabian Alb	Hainich-Dün	Schorfheide-Chorin	Total
European beech	24	43	14	82
other hardwood species	1	3	-	4
Norway spruce	13	4	-	17
Scots pine	-	-	19	16
Oak	-	-	7	9
Sum	**38**	**50**	**40**	**128**

Out of these 150 EPs, we selected 128 EPs for which forest inventory data was available that was recorded in 2014/15. EPs located in the Swabian Alb are dominated by either European beech (*Fagus sylvatica* L.) or Norway spruce (*Picea abies* [KARST] L.), whereas plots in Hainich-Dün are

mainly E. beech stands (either pure stands or mixed stands with other hardwood species such as European ash (*Fraxinus excelsior* L.) or sycamore maple (*Acer pseudoplatanus* L.)). In Schorfheide-Chorin, plots are either dominated by E. beech, Scots pine (*Pinus sylvestris* L.) or oak species (*Quercus robur* L. or *Qurecus petraea* ((MATT.) LIEBL.) (see Table 4.1). Each plot is 100 x 100 m in size. Sampled plots included managed and unmanaged stands.

Table 4.2: Location, elevation above sea level, annual mean temperature and precipitation of the three exploratories

	Swabian Alb	Hainich-Dün	Schorfheide-Chorin
Location	SW-Germany	Central Germany	NE-Germany
Elevation a.s.l.	460 – 860 m	285 – 550 m	3 – 140 m
Mean annual temperature	6 - 7 °C	6.5 – 8 °C	8 – 8.5 °C
Mean annual precipitation	700 – 1000 mm	500 – 800 mm	500 – 600 mm

4.2.2. Assessment and computation of stand structural variables

Each tree`s diameter at breast height (DBH) was recorded if greater or equal 7 cm using a diameter tape and for each of these, individual tree position relative to the plot center ({x,y} coordinates) as well as species identity were determined.

Additionally, we made nine systematically distributed single terrestrial laser scans per plot. Here, we used a Faro Focus 3D 120 terrestrial laser scanner (Faro Technologies Inc., Lake Mary, USA) to capture a three-dimensional point clouds for each position. The laser scanner was mounted on a tripod in approximately 1.3 m above ground, covering a field of view of 360° horizontally and 300° vertically. It operates with an angular step width of 0.035°, which results in ~44.1 million measurements per scan. Plots were scanned in leaf-on conditions between June and August 2014. In a next step, we calculated tree attribute based measures and indices (inventory data) and holistic measures of stand structure (laser scans).

Basal area (BA ($m^2 ha^{-1}$)), stem density (N ha^{-1}) and canopy openness (%) were computed as stand summary measures, whereby canopy openness was derived from the terrestrial laser scans as described in Zheng et al. (2013). To describe tree size variability and diversity, we computed the coefficient of variation of DBH (DBH (CV (%)) and the effective number of height classes (HC). Based on the exponential Shannon-Index, HC is a measure of tree size diversity taking the number

of individual tree heights and their relative abundances into account. It is computed using the following formula, whereby p_i is the relative proportion of the number of trees in a certain height class relative to the total number of height classes.

$$HC = \exp(-\sum_{i=1}^{N_{top}} p_i * ln \, p_i)$$

(4.1)

ENL was also derived from the terrestrial laser scans and can be considered a measure of vertical structure, taking the number of layers with 1 m thickness (~stand height (m)) and their respective occupation by tree components relative to the total space occupation into account (see Ehbrecht et al. 2016 for details). ENL is a measure similar to HC, but it is not based on individual trees. Instead, it is based on the space occupied by trees as described by a voxel model with voxels of 20 cm side length.

$$ENL = 1/\sum_{i=1}^{N_{top}} p_i^2$$

(4.2)

For ENL the inverse Simpson-Index is used to quantify vertical structure of a given stand. Here, p_i is the share of voxels in the i_{th} vertical layer, relative to the total number of voxels in the volume analyzed. With increasing stand height and a more even filling along the vertical profile, the index value increases.

Stand structural complexity was addressed by the laser scanning-based stand structural complexity index (SSCI). Here, the fractal dimension was determined for 1280 cross-sectional polygons that were derived from each scan, whose mean (MeanFrac) was then scaled by the effective number of vertical layers (ENL, see below and eq. 4.3) according to the following formula (see Ehbrecht et al. 2017 for details).

$$SSCI = MeanFrac^{\ln(ENL)}$$

(4.3)

In an earlier study, we showed that SSCI is significantly correlated with tree attribute based measures of structural complexity, heterogeneity and diversity, such as the Gini-Coefficient of tree

diameters, Füldner's (1995) tree size differentiation or Zenner & Hibbs (2000) structural complexity index.

Tree species diversity was calculated on the basis of a species' basal area share using the exponential Shannon-Index shown in eq. (4.1).

4.2.3. Microclimatic measurements

On each plot, air temperature at 2 m above ground was measured in one minute intervals by a micrometeorological station. We calculated mean diurnal ranges (DTR) of air temperature for a period of 90 days from June to August 2014 as well as from December 2014 to February 2015. Furthermore, we calculated DTR for each of the 50 micrometeorological stations in adjacent grassland plots per exploratory. The diurnal temperature range is the difference between the daily maximum and minimum of air temperature.

4.2.4. Statistical analyses

All statistical analyses were done in the software environment R, version 3.2.3 (R Development Core Team, 2016). In a first step, we tested relationships between stand structural variables and DTR using Pearson's coefficient of correlation. This analysis was done separately for each exploratory in order to exclude effects due to regional climate. In a next step, we modelled effects of stand structure on DTR by testing each variable that showed significant correlations with a DTR in multiple linear regression models that included the exploratory as additional categorical, explanatory variable as well as its interaction with elevation above sea level. Whenever a structural variable's effect was not significant in combination with other variables tested in a multiple linear regression, it was not considered in further analyses. To test our second hypothesis, we tested stand structural variables for a significant relationship with DTR in a linear model in combination with exploratory, elevation and canopy openness. Ultimately, we ranked the most appropriate model based on AIC_c (Akaike Information Criterion). An analysis of variance was used to test differences in DTR for stands with different main tree species.

4.3. Results

4.3.1. Diurnal temperature ranges in forests and grasslands during summer and winter

From June to August 2014, mean DTR in the forest plots was 7.65 °C in the Swabian Alb, 6.65 °C in Hainich-Dün, and 9.42 °C in Schorfheide. From December 2014 to February 2015, mean DTR in the forest plots was 4.78 °C in the Swabian Alb, 3.58 °C in Hainich-Dün, and 9.42 °C in Schorfheide. Forests had a significantly lower DTR than adjacent grasslands in summer and winter in each exploratory (ANOVA, $p < 0.001$). Across the three exploratories, differences in mean DTR between forests and grasslands in winter are smaller than in summer (7.82 °C (forest) vs. 11.02 °C (grassland) in summer, 4.18 °C (forest) vs. 5.05 °C (grassland) in winter). Generally, DTR in summer is greater than in winter in the higher latitudes (Dai et al. 1999).

4.3.2. Effects of stand structure on diurnal temperature ranges in forests

Tree size diversity (HC) and variability (DBH (CV (%)), vertical stratification (ENL), stand height, stocking density (BA) and stand structural complexity (SSCI) were negatively correlated with DTR during the vegetation period in at least one exploratory (Tab. 4.3). We did not find significant correlations between tree attribute-based measures of stand structure and DTR during winter month, except for basal area in Hainich-Dün ($r = 0.55$, $p < 0.001$). Unfortunately, TLS-based measures (canopy openness, SSCI, ENL) were not available for leaf-off conditions of broadleaved stands and could hence not be tested. Moreover, there were no significant correlations between stand structural variables and mean, maximum and minimum temperature.

Table 4.3: Correlations between stand structural variables and diurnal temperature ranges in summer (Pearson`s correlation coefficient)

	Swabian Alb	Hainich-Dün	Schorfheide-Chorin
Stem density	-	- 0.32*	-
Basal area	-	- 0.48***	- 0.32*
DBH (CV (%))	-	-	- 0.43**
Canopy openness	0.60***	0.43**	0.81***
SSCI	- 0.35*	-	- 0.46**
HC	-	- 0.48**	- 0.62***
ENL	-	- 0.41**	- 0.52***
Stand height	-	- 0.38**	-
Tree species diversity	-	-	-

Canopy openness was the best predictor of DTR and explained 36% (Swabian Alb), 19% (Hainich-Dün) and 66% (Schorfheide-Chorin) of variance in DTR during the vegetation period, respectively (fig 1.). With increasing canopy openness, the diurnal temperature range became larger. Regional climate (represented by exploratory and elevation) and canopy openness explained 84% of variance in DTR (Table 4.4, rank 5), whereas regional climate alone explained 72% of variance already (Table 4.4, rank 12). Thus, the hypothesis that canopy openness is the main stand structural driver of DTR could be confirmed.
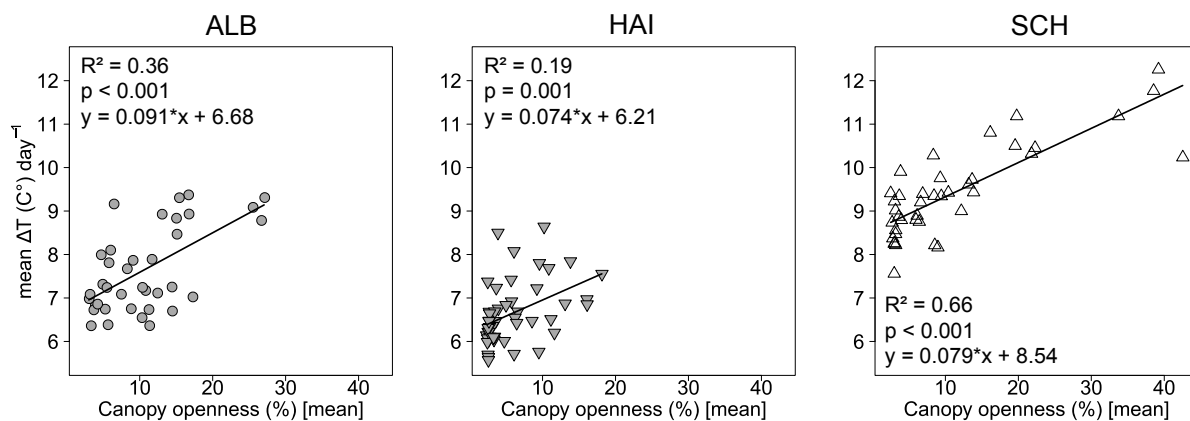
Figure 4.1: Relationship between canopy openness and mean diurnal temperature range in each exploratory.

4.3.3. Does stand structure affect DTR beyond canopy openness?

Regional climate, canopy openness and tree size diversity (HC) explained 86% of variance in DTR (Table 4.4). Similarly, ENL, stand height or basal area explained 85% of variance in DTR under consideration of regional climate and canopy openness. Thus, our second hypothesis that stand structure has an effect on DTR beyond canopy openness could be confirmed. However, the difference is marginal (Table 4.4, rank 6 vs. rank 1, 2, 3, and 4). Exploratory and elevation alone already explained 72%.

Table 4.4: Linear models explaining diurnal temperature ranges across the three exploratories.

Model (lm(DTR ~ x))	R^2_{adj}	AICc	Delta AICc	weight	rank
exploratory * elevation + openness + HC	0.858	221.443	0.000	0.89	1
exploratory * elevation + openness + ENL	0.852	226.572	5.129	0.07	2
exploratory * elevation + openness + stand height	0.849	228.827	7.384	0.02	3
exploratory * elevation + openness + BA	0.849	229.457	8.014	0.02	4
exploratory * elevation + openness	0.836	238.670	17.227	0.000	5
exploratory + openness	0.787	267.501	46.058	0.000	6
exploratory * elevation + HC	0.789	270.070	48.627	0.000	7
exploratory * elevation + BA	0.754	289.596	68.153	0.000	8
exploratory * elevation + SSCI	0.749	291.935	70.492	0.000	9
exploratory * elevation + ENL	0.747	293.205	71.762	0.000	10
exploratory * elevation + DBH (CV (%))	0.735	298.980	77.537	0.000	11
exploratory * elevation	0.723	303.310	81.867	0.000	12
exploratory + HC	0.685	317.217	95.774	0.000	13
exploratory + SSCI	0.667	324.022	102.579	0.000	14
exploratory + ENL	0.652	329.431	107.988	0.000	15
exploratory + DBH (CV (%))	0.645	331.995	110.552	0.000	16
exploratpory + stand height	0.631	336.858	115.415	0.000	17
exploratory + BA	0.629	337.524	116.080	0.000	18
exploratory	0.621	339.183	117.740	0.000	19
elevation	0.250	424.027	202.584	0.000	20

4.3.4 Effects of main tree species and tree species diversity on DTR

E. beech-dominated stands had significantly lower DTR than N. spruce-dominated stands in the Swabian Alb, whereas S. pine-dominated stands in the Schorfheide had a significantly higher DTR than E. beech and oak stands (ANOVA, $p < 0.05$, fig 2.). These significant differences could not be observed in winter. Furthermore, tree species diversity had no significant effect on DTR (data not shown).
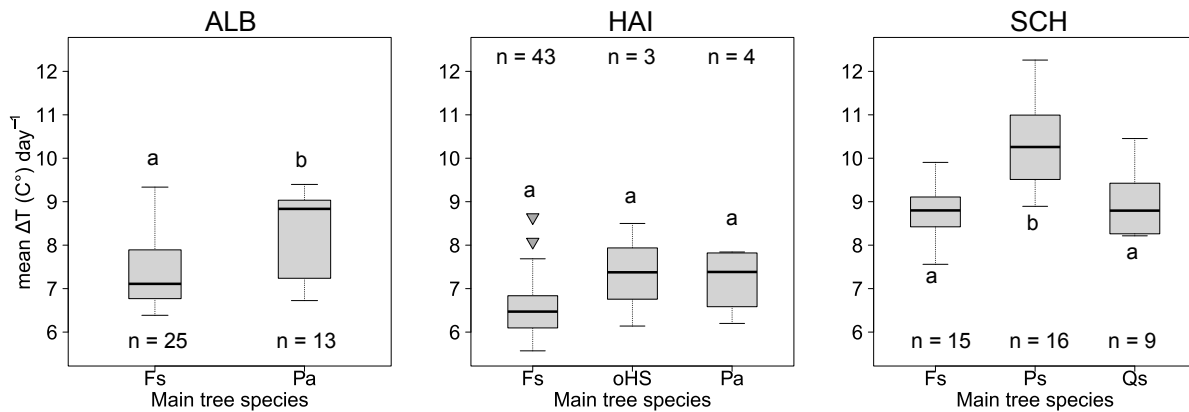
Figure 4.2: Mean diurnal temperature range in stands with different main tree species in each exploratory (Fs = *Fagus sylvatica*, Pa = *Picea abies*, Ps = *Pinus sylvestris*, Qs = *Quercus spec.*, oHS = other hardwood species).

4.4. Discussion

We found positive correlations of the mean diurnal temperature range with canopy openness across the three regions investigated. This is in line with Chen et al. (1993), who found DTR to increase from interior forest (DTR = 10.5 °C) to forest edges (DTR = 14.17 °C) to clear-cut sites (DTR = 14.75) in Douglas fir forests (*Pseudotsuga mensziesii* (MIRB.) FRANCO) in the western United States, which suggests DTR to be a function of canopy cover. Weng et al. (2007) reported that average temperatures were significantly higher in strongly thinned Japanese cedar stands (*Cryptomeria japonica* D. DON), but not in moderately or lightly thinned stands in Taiwan. Here, DTR in the thinned stands was almost comparable to pre-thinning DTR. In the tropics, Luskin and Potts (2011) found DTR to be higher in oil palm plantations compared to forests. Hardwick et al. (2015) attributed the decrease of DTR from oil palm plantation to old-growth and logged tropical forest to a decrease in leaf area index (LAI). However, this relationship was mainly driven by the low LAI of oil palm plantations and it remained open, whether this trend also holds for a LAI-gradients from logged to old-growth forests.

Generally, the question is whether a decrease in DTR with increasing canopy openness is the result of lower maximum or higher minimum air temperatures, or both. With decreasing canopy openness, the amount of incoming, short-wave solar radiation reaching the forest floor is reduced due to absorption and scattering of light by leaf surfaces during the day (Hardwick et al. 2015). These processes buffer the heating of below or within canopy air temperature (Bonan 2008). At night, emission of long-wave radiation from the ground and plant surfaces is reflected and/or

absorbed by the directly surrounding vegetation and thus 'trapped' within the stand, which probably reduces the cooling of below or within canopy air temperature (Geiger 2013). On the contrary, the upper part of the canopy cools out, since it is not covered by above-lying plant surfaces (Häckel 2016). Together, these processes could impair the diurnal temperature range. In our study, the average maximum and minimum temperatures in the grassland plots were higher, but drawing conclusions from this comparison would not be permissible, since the grassland plots in the Swabian Alb and Hainich-Dün are usually located on lower elevations than the forest plots, which results in higher maximum and minimum temperatures due to their lower altitude above sea level. However, the altitudinal range in Schorfheide-Chorin is smaller (3 – 140 m a.s.l.) and forest and grassland plots are more or less equally distributed across the altitudinal range. Here, the difference of maximum air temperatures in a forest plot compared to an adjacent grassland plot increases with decreasing canopy openness, whereby the maximum temperatures in forest plots is lower than in grassland plots (data not shown). Since this is not the case for minimum temperatures, lower maximum temperatures are likely to be the driver of a decreasing DTR with decreasing canopy openness (see also von Arx et al. 2012).

Even though the higher explanatory power of models including measures of tree size diversity (HC), vertical structure (ENL) or stand height compared to the model that included exploratory, elevation and canopy openness was marginal ($R^2 = 0.86$ or $R^2 = 0.85$ vs. $R^2 = 0.84$), these components of stand structure had a significant effect on DTR ($\Delta AIC_c = 17.23$). A higher diversity of tree heights (HC) is likely to result in a more even occupation of space by tree components along the vertical axis, which is reflected in a higher effective number of layers (ENL). Since wind speed is reduced by forest canopies (Gary 1974), movement and mixing of air masses within multi-layered stands could be reduced stronger compared to stands with a single canopy layer, depending on the distribution of biomass in the canopy (Aussenac 2000, Renaud et al. 2011). As mentioned above, upper canopy parts may cool out during the night, whereas the cooling of air temperature beneath the canopy is reduced (Geiger et al. 2013, Häckel et al. 2016). During the night, complex canopy structures in multi-layered stand could possibly impair the mixing of cool above canopy air with warmer air masses beneath the canopy, due to a reduced wind speed. However, wind speed influences latent heat fluxes, but its general influence on DTR is small (Dai et al. 1999), which could probably explain the marginal effect of vertical structure on DTR.

In an earlier study, we assumed that decreasing DTR with increasing stand structural complexity could be due to higher tree species diversity in more complex structured stands (see Ehbrecht et al. 2017), since tree species diversity enhances transpiration on stand level, which could buffer temperature fluctuations (Gebauer et al. 2012, Kunert et al. 2012, Forrester et al. 2015). However, the findings of this study do not support the hypothesis that tree species diversity has an effect on DTR. Still, we found significant differences in DTR between plots of different main tree species in Swabian Alb and Schorfheide-Chorin. Light transmission through the canopy and albedo of canopy surfaces differs between the main tree species in our study (Parker et al. 1995, Metz et al. 2013), which probably affects the heating of surfaces beneath the canopy and thus having an impact on DTR. Given the fact that we did not find significant differences between plots of different main tree species during winter suggests that the observed differences during summer are simply a function of canopy openness. E.g., the higher DTR in S. pine plots in Schorfheide-Chorin compared to E. beech forest in that region is most likely attributable to the higher canopy openness of S. pine stands.

Ultimately, we were able to explain up to 86% of variance in DTR in temperate forest ecosystems in Central Europe, but the question remains open which factors explain the remaining 14% of variance in DTR. In this study, we did not account for effects of water vapor, local topography (aspect, slope, e.g. effects of cold air drainage) and the landscape matrix surrounding the forest plots. Incorporating these factors in future studies could probably further improve the explanatory power of DTR-models. In this context, terrestrial laser scanning would offer the opportunity to rapidly assess forest stand structures and derive estimates of DTR. TLS based measures of stand structure (canopy openness and ENL) explained 85% of variance under consideration of elevation and region, which can also be assessed by laser scanners with integrated GPS. Furthermore, TLS offer the opportunity to create Digital Terrain Models (DTM) that could be integrated into models explaining forest microclimate.

4.5. Conclusions

Microclimatic conditions in temperate forest ecosystems can be controlled by forest management through modifications of canopy openness. Thus, forest management can indirectly affect air temperature bound ecosystem processes and functions by modifying stand structure. Creating

multi-layered and complex stand structures can additionally affect microclimate in forests, but canopy openness remains the major structural driver of microclimate in temperate forest ecosystems.

4.6. Acknowledgements

4.7. References

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5. Synthesis

5.1. Concluding remarks on introduced measures of stand structure

Sampling three-dimensional stand structure using single terrestrial laser scans has proved to be an efficient and objective method to quantify structure holistically. First, the effective number of layers was presented as a measure to quantify the vertical component of stand structure. Revisiting the concept of foliage height diversity by Mac Arthur and Mac Arthur (1961) and applying Jost`s (2006) transformations of diversity indices to vertical voxel distributions, ENL describes vertical stand structure as a function of stand height and the relative occupation of vertical layers by foliage and woody components (chapter 2). The more evenly vertical layers are occupied and the taller the stand, the higher the resulting ENL values will be. If a stand is completely evenly filled along the vertical axis, ENL will be equal to stand height. On the one hand, this is contra-intuitive, since an equal filling of vertical layers is intuitively not associated with higher vertical heterogeneity. On the other hand, it expresses the presence of tree crowns in several layers along the vertical axis, which is bound to a higher tree size diversity (ENL ~ HC, r = 0.47) and thus an indication of structural heterogeneity. With reference to the classification of stand structural measures (Fig. 1.1), ENL can be classified as both, a single- as well as multi-perspective measure of stand structure, since it can be derived from single- or multiple-scan point clouds.

Second, a laser scanning-based index of stand structural complexity (SSCI) was introduced, where the fractal dimension of cross-sectional polygons was used as a measure of complexity. The more `chaotic` the distribution of foliage and woody components within the three-dimensional space, the higher the resulting fractal dimension of polygons (*MeanFRAC*). Using the fractal dimension as mathematical description of object complexity requires an objective scaling in order to quantify forest structure. Since the fractal dimension itself is scale-independent, a dense thicket with small trees may have the same fractal dimension as a similarly dense forest with large trees. ENL reflects stand dimensions in terms of stand height and vertical structure and thus allowed for an appropriate scaling of the fractal dimension of cross-sectional polygons. Basically, the development of SSCI was based on the idea to mimic the way foresters or ecologist perceive stand structure when they stand at a single point in a forest and `take a look around`. SSCI was able to differentiate stand types and index values increased from regular to random tree spacing patters (CE), from low to high tree size differentiation (TD) and with increasing tree size variability (GC$_d$, but also the coefficient of

variation of tree diameters (DBH CV (%))). Furthermore, SSCI is positively correlated with tree height diversity (HC) and stand basal area variability (coefficient of variation of stand basal area based on 20 x 20 m subplots, data not shown). Overall, SSCI can be summarized as a holistic measure that quantifies structural complexity of foliage and woody components distribution in three-dimensional space without taking individual tree attributes into account (see Fig 5.1). Still, it is correlated with several tree-attribute based measures of structural heterogeneity. Observing significant correlations between SSCI and diurnal ranges of air temperature and VPD raised the question, whether this is due to a causal relationship or whether it is dependent on other factors. With reference to the classification of structural measures as shown in figure 1.1., SSCI can be classified as a single-perspective measure of stand structure.
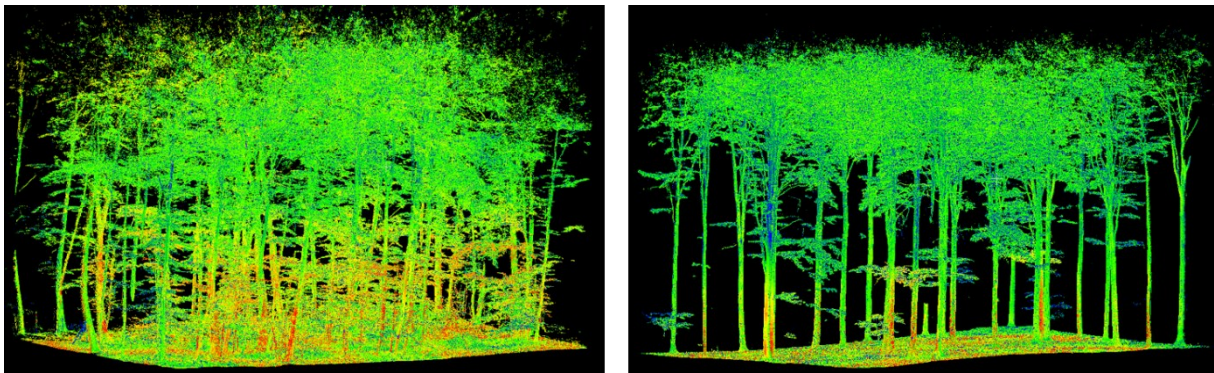
Figure 5.1: E. beech stand with high (left, SSCI = 6.1) and low stand structural complexity (right, SSCI = 2.3). Visualization is based on a point cloud that was obtained from a multiple-scan approach.

Against this background, in chapter 4 effects of stand structure on the diurnal temperature range (DTR) were investigated. Testing a set of tree-attribute based measures of stand structure and TLS-derived, holistic measures revealed that the magnitude of DTR is basically a function of canopy openness. Vertical structure, as being measured by HC or ENL, had an additional, but marginal effect on DTR. However, holistic, TLS-derived measures were able to explain up to 85% of variance in DTR, when effects of geographic location and elevation are taken into account.

Using the methods and measures developed in chapter 2 and 3, the hypotheses raised in the introduction shall be tested. Knowing the stand structural drivers of DTR in temperate forest ecosystems from chapter 4, it is further explored how DTR is affected by forest management as a driver of stand structure. Methods used to analyze differences and background information on plots that are not part of the biodiversity exploratories are introduced in appendix 2.

5.2. Are even-aged stands structurally less complex than uneven-aged or unmanaged stands?

Most studies comparing biodiversity and certain ecosystem functions in unmanaged vs. managed forests have compared selected developmental stages with unmanaged or old-growth systems (Schall et al. 2017). However, since even-aged forest management creates a spatial coexistence of different developmental stages on landscape scale, system comparisons require an incorporation of each developmental stage. Thus, the answer to the question whether even-aged stands are structurally less complex than uneven-aged or unmanaged stands is depending on the scale at which structural complexity is looked at. Analyses to investigate differences in structural complexity between different management systems were based on data from the Hainich-Dün exploratory only, since it covers all developmental stages of E. beech under even-aged forest management as well as uneven-aged and unmanaged plots. Whereas uneven-aged (UEA) and unmanaged stands (UNM) sampled in this study were structurally similarly complex, mean SSCI of even-aged forests (EA) differed significantly from UEA and UNM, and was characterized by a larger variance. EA forest management is characterized by a cycle of developmental stages from young, even-aged planting or thickets, pole wood stages, to immature and mature timber stages. The last developmental stage in even-aged E. beech management is a thicket with shelterwood. After removal of the remaining shelterwood, the management cycle starts again with the thicket stage (Burschel and Huss 2003, Röhrig et al. 2006). Structural differences between developmental stages of even-aged E. beech stands are reflected in the variance of SSCI (Fig. 5.2). Whereas thickets are characterized by low SSCI values, mainly due to a low vertical differentiation – or in other words low ENL-values -, EA forest management can also create stands with high structurally complexity. This is especially the case when final harvests are protracted over several decades. Harvesting only trees that have reached a target diameter in multiple interventions creates a heterogeneous structure on stand level, as harvested trees leave a canopy gap under which natural regeneration establishes. This practice may result in a stand structure that is characterized by an intermingling of patches of natural regeneration and patches of mature trees, creating structural complexity. UEA management is characterized by small-scale interventions, where final harvests, thinnings and natural regeneration take place on the same plot (Burschel and Huss 2003, Röhrig et al. 2006). The intermingling of trees of different ages and sizes results in a high structural complexity on plot level, but in a low diversity of structural conditions on higher scales, which is reflected in the small variance of SSCI. The unmanaged stands sampled here were all located in the Hainich National Park, and have been

left unmanaged for at least 20 years (Schall et al. 2017). Regarding their structure, they are not structurally more complex than UEA stands, but significantly more complex than EA stands. Still, their structural complexity is comparable with late developmental stages of EA stands. However, it remains open how far structural complexity in unmanaged E. beech forests develops in the long-term.
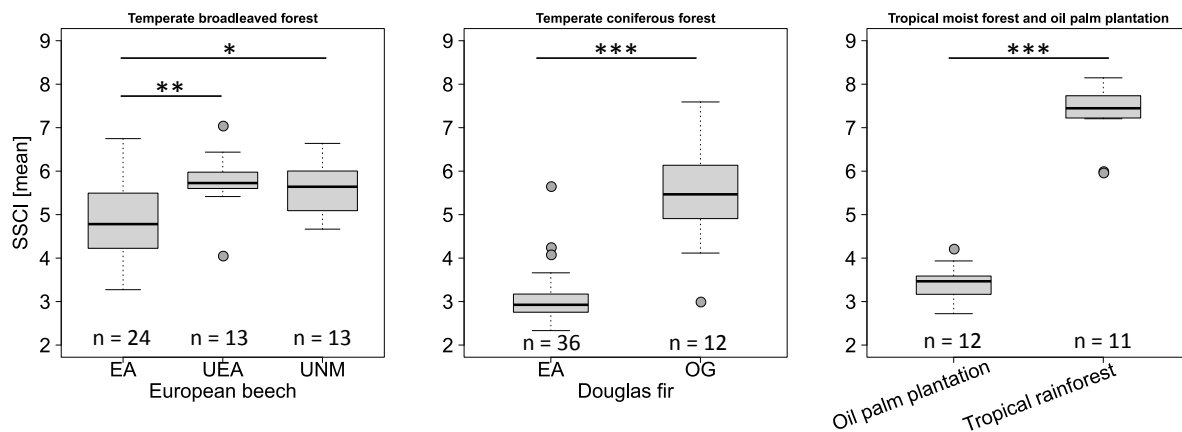

Figure 5.2: SSCI of even-aged (EA), uneven-aged (UEA) and unmanaged (UNM) E. beech stands in Hainich Dün (*left*), EA and old-growth (OG) Douglas Fir stands in Oregon, USA (*center,* Seidel et al. unpublished data), and oil palm plantations and tropical rainforest in Jambi Province, Sumatra (*right*, Zemp et al., unpublished data). Significant differences are indicated by "*" if p < 0.05, "**" if p < 0.01 and "***" if p < 0.001 (ANOVA).

Let us take a further look at the effects of management on stand structural complexity in temperate coniferous forests of the Pacific Northwest of the United States. Old-growth Douglas fir stands show a significantly higher structural complexity than stands of the same species under even-aged forest management. However, the sample of EA Douglas fir stands does not cover the full range of developmental stages, but rather immature to mature timber stages that have undergone different thinning interventions aiming at increasing structural complexity (light thinning, heavy thinning and thinning with gaps, see also Seidel et al. 2016). Still, in chapter 3 it was shown that coniferous stands are significantly less complex than broadleaved stands and it is worth to note that old-growth D. fir stands can have a structural complexity similar to unmanaged or uneven-aged broadleaved stands. With regard to land-use change in the tropics, converting tropical forests to oil palm plantations is a major threat to biodiversity (Koh et al. 2008, Lusking and Potts 2011). Despite the direct loss of species due to deforestation, mono-specific oil palm plantations are commonly viewed to support fewer species than tropical rain-forests as the naturally occurring system (Wilcove and

Koh, 2010). As expected, tropical rainforests have a much higher structural complexity than oil palm plantations (Zemp et al., unpublished data). Moreover, they have a significantly higher structural complexity than old-growth Douglas fir or unmanaged or uneven-aged E. beech forests.

5.3. Are mixed species stands characterized by a higher stand structural complexity than pure stands?

Converting coniferous pure stands to mixed stands with broadleaved trees has been practiced in Germany on vast areas overs the past two decades (Wagner 2007). Mixed stands are commonly viewed to be more resilient towards disturbances, more beneficial to biodiversity, and moreover economically more viable (Hartley 2002, Felton et al. 2010, del Río et al. 2014). Since the creation of heterogeneous stand structures is one aim of forest management administrations in Germany, which is also reflected in management and policy guidelines (Giessen et al. 2013), the question comes up if tree species mixing results in higher stand structural complexity.
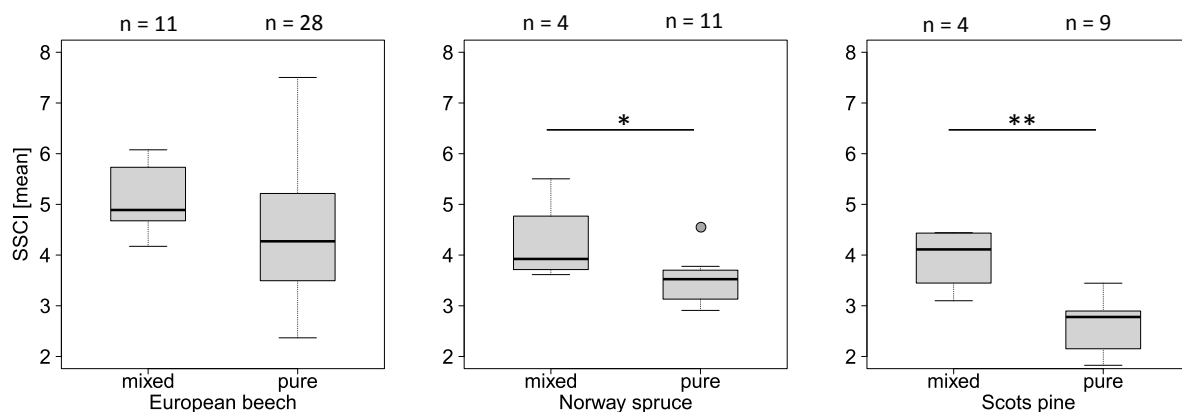
Figure 5.3: SSCI of pure and mixed stands with E. beech (*left*), N. spruce (*center*), and S. pine (*right*) as main tree species. Significant differences are indicated by "*" if p < 0.05 and "**" if p < 0.01 (ANOVA).

Comparing pure and mixed stands with E. beech, N. spruce or S. pine as main tree species revealed that mixing results in a higher stand structural complexity for N. spruce and S. pine dominated stands, but not in E. beech stands. Thus, enriching coniferous stands with broadleaved trees may increase structural complexity on stand level, but admixing E. beech with other broadleaved species had no effect on stand structural complexity. Probably, broadleaved species other than E. beech that occur in E. beech dominated stands, such as European ash or Sycamore maple, are structurally too similar on tree level to affect stand structural complexity. The structure of N. spruce or S. pine

stands in turn becomes more complex when broadleaved trees are admixed. Moreover, an increasing basal area share of coniferous trees on stand level results in decreasing stand structural complexity (Fig. 5.4).
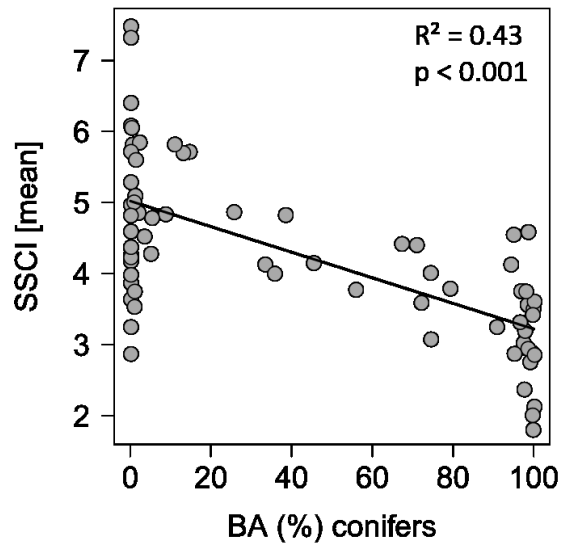
Figure 5.4: Effect of basal area share of coniferous trees on SSCI

The question whether differences in stand structural complexity between broadleaved and coniferous stands are due to differences in structural complexity of individual trees remains open and needs to be addressed in further studies.

5.4. How does forest microclimate differ between forest management systems?

From chapter 4 we already know that canopy openness is the main, direct structural driver of the diurnal temperature range. However, understanding the indirect effect of forest management on DTR is a valuable information to understand effects of different forest management systems on biodiversity, since DTR is a known driver of biodiversity in forest ecosystems (Müller et al. 2015). Since we already know that the geographic location (or exploratory) is the main non-structural driver of DTR, we only use data from Hainich-Dün exploratory in the following, because it is the sole exploratory, where even-aged and uneven-aged forest management systems as well as unmanaged forest plots occur. DTR in even-aged, uneven-aged and unmanaged forest plots did not differ significantly (Fig. 5.5). Still, unmanaged forest plots (UNM) show the lowest average

DTR compared to uneven-aged (UEA) and (EA). In even-aged forest management systems, thickets show a significantly higher DTR than other developmental stages in forests under EA management and uneven-aged and unmanaged forest plots ($p < 0.01$). Even though thickets are characterized by an overall high vegetation density, they are relatively low in height and vertically not differentiated. That means their buffering capacity regarding air temperature is low, since trees often do not form a closed canopy above 2 m height, at which the temperature sensor of the microclimatic stations is located. If one seeks to understand effects of forest management on biodiversity and ecosystem functions in even-aged forest management systems, the removal of the shelterwood made up by retention trees is a crucial point, because it is a point in time, where microclimatic conditions are significantly altered. Maintaining similar microclimatic conditions throughout the management cycle would require retaining shelterwood trees for a longer time periods, until the understory vegetation has reached a sufficient height with closed canopy.
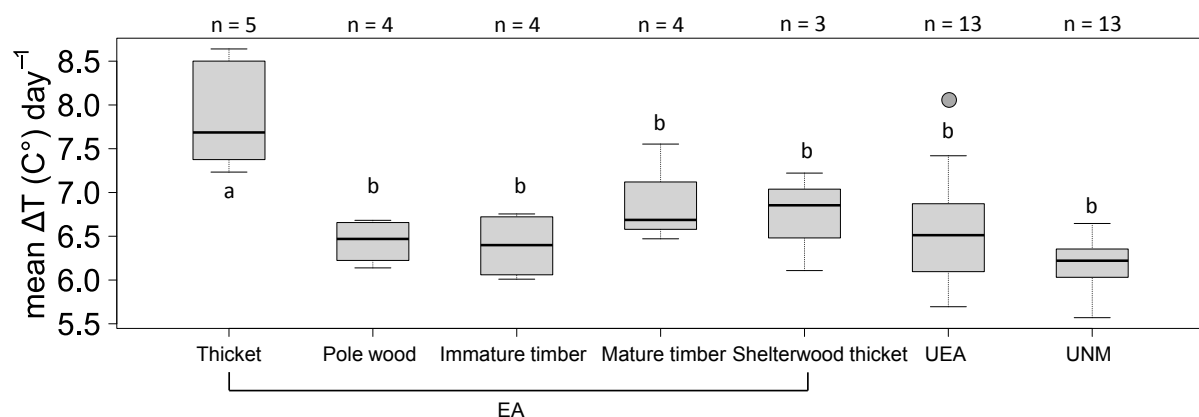
Figure 5.5: Mean diurnal temperature range in uneven-aged (UEA), unmanaged (UNM), and different developmental stages of even-aged (EA) E. beech dominated research plots in Hainich-Dün. Significant differences are indicated by different letters (ANOVA, $p < 0.01$).

5.5. Conclusions

Forest structure and its complexity can be actively controlled by forest management on different spatial scales through different approaches. The choice of tree species and tree species mixing affect structural complexity on stand level. Managed broadleaved forests are generally structurally more complex on stand level than managed coniferous stands in terms of the three-dimensional distribution of foliage and woody components, which is not necessarily the case for tree distribution

patterns and tree size variability as expressed by tree attribute-based metrics and indices. Admixing broadleaved tree species to coniferous stands may promote stand structural complexity. In turn, admixing coniferous trees to broadleaved forest may result in a lower stand structural complexity. Silvicultural measures that increase tree size variability promote structural complexity on stand level. These measures may include single tree harvests (e.g. target diameter oriented harvesting activities) in late developmental stages of even-aged management systems, but also thinning from above in earlier developmental stages. Uneven-aged forest management as well as leaving stands unmanaged for several decades result in higher structural complexity on stand level than even-aged forest management, with little variability between stands. In turn, even-aged forest management creates a variability of stand types on landscape scale and thus a range of structural conditions, ranging from stands with low to high structural complexity. Against this background, indirect effects of forest management on microclimate are more pronounced in even-aged forest management systems compared to uneven-aged and unmanaged forests. Shelterwood removal at the end of a management cycle in even-aged forest management significantly affects the radiation regime and thereby alters microclimatic conditions. For this reason, management impacts on microclimate-bound ecosystem functions might differ between even-aged and uneven-aged systems.

5.6. References

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APPENDIX I

Supplementary information:

Ehbrecht et al. 2017. Quantifying stand structural complexity and its relationship with forest management, tree species diversity and microclimate (chapter 3).

Table A1.1: Comparison of model forms to test the relationship between tree diversity and SSCI

Model	R Code	LL	df	AIC	ΔAIC
Asymptotic	nls(ssci ~ SSasymp(TreeDiversity, a, b, c))	-152.48	4	322.96	0.00
Michaelis-Menten	nls(ssci ~ SSmicmen(TreeDiversity, a, b))	-161.72	3	329.46	6.50
Logarithmic	lm(ssci ~ log(TreeDiversity)	-162.43	3	330.87	7.91
Power Law	nls2((ssci ~ a*TreeDiversity^b)	-163.57	3	333.14	10.2

Table A1.2: Information on structural characteristics, tree species richness, main tree species, age, management, developmental stage as well as SSCI and ENL for all plots (n = 126) used in this study

Plot	Stem density (N ha⁻¹)	Basal area (m² ha⁻¹)	Quadr. mean dbh (cm)	SD of mean dbh (cm)	Tree species richness	Main tree species	Age (2014)	Management	Developmental stage	SSCI	ENL
AEW01	816	41.41	25.4	6.67	12	Pa	45	EA	immature timber	3.59	14.84
AEW02	425	36	32.8	9.36	4	Pa	65	EA	immature timber	3.78	16.84
AEW03	632	44.48	29.9	8.67	4	Pa	55	EA	immature timber	3.05	17.46
AEW04	2219	29.69	13.1	3.97	5	Fs	45	EA	pole wood	4.65	15.29
AEW05	139	27.61	50.3	7.27	3	Fs	145	EA	mature timber	5.84	21.41
AEW06	374	26.48	30	11.9	7	Fs	85	EA	immature timber	5.74	21.68
AEW07	199	33.16	46.1	28.8	4	Fs	135	UNM	mature timber	6.41	14.61
AEW08	277	40.16	43	19	5	Fs	155	UNM	mature timber	5.13	19.38
AEW09	376	32.15	33	14.6	4	Fs	155	UNM	mature timber	5.37	18.34
AEW10	1077	45.32	23.2	6.51	6	Pa	38	EA	immature timber	3.22	14.49
AEW11	505	50.12	35.6	8.33	5	Pa	64	EA	mature timber	2.91	18.24
AEW12	313	36.39	38.5	9.78	2	Pa	66	EA	mature timber	3.53	17.86
AEW13	385	48.19	39.9	11.8	6	Pa	85	EA	mature timber	4.61	21.29
AEW14	299	48.56	45.5	13.4	6	Pa	84	EA	mature timber	4.76	22.94
AEW17	1836	32.84	15.1	5.85	8	Fs	35	EA	pole wood	4.62	13.79
AEW18	119	21.17	47.6	10.2	4	Fs	138	EA	mature timber	5.87	22.38
AEW19	153	23.35	44.1	16.9	3	Fs	155	EA	mature timber	5.74	16.20
AEW20	204	29.1	42.6	13.1	3	Fs	130	EA	mature timber	7.50	22.57
AEW21	182	25.71	42.4	15.8	4	oHS	140	EA	mature timber	6.43	10.40

Plot	Stem density (N ha⁻¹)	Basal area (m² ha⁻¹)	Quadr. mean dbh (cm)	SD of mean dbh (cm)	Tree species richness	Main tree species	Age (2014)	Manage-ment	Developmental stage	SSCI	ENL
AEW22	238	27.25	38.2	13	3	Fs	120	EA	immature timber	4.86	24.51
AEW23	128	22.8	47.6	16.8	3	Fs	170	EA	mature timber	5.31	15.05
AEW26	1566	19.96	12.7	4.83	12	oHS	35	EA	pole wood	5.94	11.16
AEW27	874	12.26	13.4	4.47	9	Fs	30	EA	pole wood	4.88	9.28
AEW28	552	28.6	25.7	10.2	5	Fs	65	EA	immature timber	5.72	19.89
AEW29	385	32.84	33	9.38	5	Pa	85	EA	immature timber	4.03	19.48
AEW30	583	25.15	23.4	8.46	3	Fs	75	EA	immature timber	4.81	18.70
AEW31	921	41.21	23.9	6.09	2	Pa	45	EA	immature timber	3.63	14.77
AEW32	595	25.72	23.5	6.03	4	Pa	45	EA	immature timber	3.77	12.57
AEW33	875	37.9	23.5	6.85	7	Pa	45	EA	immature timber	4.57	14.26
AEW34	732	43.09	27.4	6.63	6	Pa	59	EA	immature timber	3.34	14.29
AEW38	1792	18.68	11.5	4	8	Fs	28	EA	pole wood	5.16	11.34
AEW39	1129	29.88	18.4	7.44	5	Fs	70	EA	pole wood	5.95	18.15
AEW40	281	30.05	36.9	13	3	Fs	115	EA	mature timber	7.34	21.46
AEW41	316	28.09	33.6	10.9	4	Fs	85	EA	immature timber	4.29	23.26
AEW42	439	25.41	27.2	11.5	6	Fs	85	EA	immature timber	5.12	22.04
AEW43	278	20.47	30.6	18.7	4	Fs	145	EA	mature timber	5.93	14.87
AEW46	388	23.14	27.6	12.1	6	Fs	95	EA	immature timber	5.84	20.42
AEW47	507	30.77	27.8	9.82	5	Fs	85	EA	immature timber	4.17	18.43
AEW48	288	31.52	37.3	11.3	4	Fs	110	EA	immature timber	4.89	23.29
AEW49	197	19.24	35.3	21.8	10	Fs	185	UNM	mature timber	6.84	12.50
AEW50	160	29.84	48.7	26.4	4	Fs	160	UNM	mature timber	5.62	15.67
HEW01	278	43.3	44.5	13.1	9	Pa	82	EA	mature timber	3.81	22.31
HEW02	658	41.15	28.2	12	9	Pa	63	EA	immature timber	5.50	16.72
HEW03	651	42.58	28.9	8.03	6	Pa	68	EA	immature timber	2.97	17.40
HEW05	487	25.58	25.9	10.6	5	Fs	88	EA	immature timber	3.89	20.49
HEW06	283	35.3	39.9	11.1	4	Fs	120	EA	mature timber	3.67	24.98
HEW07	314	26.7	32.9	17.7	5	Fs	156	UEA	mature timber	5.65	17.58
HEW08	342	25.66	30.9	16.9	5	Fs	163	UEA	mature timber	5.60	14.21
HEW09	228	25.76	37.9	22.2	4	Fs	167	UEA	mature timber	5.98	19.69
HEW10	379	34.8	34.2	18.4	7	Fs	171	UNM	mature timber	5.07	20.44
HEW11	565	36.86	28.8	18.1	7	Fs	175	UNM	mature timber	5.64	19.18
HEW12	326	36.51	37.8	19.8	8	Fs	178	UNM	mature timber	5.30	23.73
HEW13	671	40.87	27.9	8.96	10	Pa	60	EA	immature timber	3.61	17.94
HEW16	1089	17.4	14.3	6.14	9	oHS	140	EA	pole wood	6.11	9.53
HEW17	1031	13.9	13.1	5.41	7	Fs	130	EA	pole wood	4.99	8.99
HEW18	1555	27.53	15	4.63	6	Fs	48	EA	pole wood	6.08	12.60
HEW19	377	35.35	34.6	12.2	3	Fs	102	EA	immature timber	4.20	23.76
HEW20	328	30.63	34.5	11.3	5	Fs	100	EA	immature timber	3.56	22.36
HEW21	289	31.99	37.5	14.5	5	Fs	115	EA	mature timber	5.03	23.95
HEW22	130	31.14	55.2	8.47	1	Fs	143	EA	mature timber	3.27	21.72
HEW26	210	27.02	40.5	23.1	3	Fs	182	UEA	mature timber	5.89	19.38

Plot	Stem density (N ha⁻¹)	Basal area (m² ha⁻¹)	Quadr. mean dbh (cm)	SD of mean dbh (cm)	Tree species richness	Main tree species	Age (2014)	Manage-ment	Developmental stage	SSCI	ENL
HEW27	256	25.59	35.7	18.9	4	Fs	167	UEA	mature timber	6.44	21.00
HEW28	207	20.71	35.7	17.7	2	Fs	155	UEA	mature timber	6.23	17.33
HEW29	247	29.08	38.7	21.6	3	Fs	171	UEA	mature timber	5.42	19.14
HEW30	401	26.15	28.8	16.8	3	Fs	168	UEA	mature timber	5.60	17.83
HEW31	363	27.35	31	19.1	6	Fs	163	UEA	mature timber	5.73	15.20
HEW32	318	24.15	31.1	19.3	6	Fs	157	UEA	mature timber	5.76	13.46
HEW33	211	35.03	46	21.9	3	Fs	177	UEA	mature timber	4.07	22.68
HEW34	453	33.99	30.9	17.1	5	Fs	168	UNM	mature timber	4.90	18.69
HEW35	572	31.69	26.6	13.9	5	Fs	161	UNM	mature timber	5.94	20.51
HEW36	509	30.18	27.5	16.1	5	Fs	158	UNM	mature timber	6.64	14.93
HEW37	283	37.41	41	20.7	3	Fs	174	UNM	mature timber	5.73	19.67
HEW38	319	33.62	36.6	21.3	6	Fs	174	UNM	mature timber	5.09	20.56
HEW39	246	33.92	41.9	22.9	6	Fs	185	UNM	mature timber	6.24	19.65
HEW40	401	38.51	35	16	7	Fs	165	UNM	mature timber	5.40	19.58
HEW41	351	31.05	33.6	18.5	5	Fs	162	UNM	mature timber	6.02	19.47
HEW42	249	31.85	40.4	20.5	5	Fs	178	UNM	mature timber	4.67	22.50
HEW45	1459	21.73	13.8	3.92	6	Fs	32	EA	pole wood	5.63	10.64
HEW46	497	35.63	30.2	9.89	4	Fs	80	EA	immature timber	4.25	20.70
HEW47	311	34.77	37.7	15.2	5	Fs	112	EA	mature timber	4.84	23.04
HEW48	184	29.81	45.4	22.1	3	Fs	170	UEA	mature timber	7.06	14.90
HEW49	280	26.22	34.5	16.7	7	Fs	150	UEA	mature timber	5.72	17.87
HEW50	495	25.59	25.7	12.2	4	Fs	146	UNM	mature timber	6.00	15.37
SEW01	1303	30.73	17.3	4.34	3	Ps	31	EA	pole wood	2.78	10.34
SEW02	1097	37.53	20.9	5.65	4	Ps	42	EA	immature timber	4.15	15.99
SEW03	384	32.72	32.9	5.98	3	Ps	63	EA	immature timber	2.39	15.42
SEW04	712	41.58	27.3	11.5	6	Ps	103	EA	mature timber	3.80	16.23
SEW05	103	23.97	54.4	29.2	3	Fs	180	EA	mature timber	4.40	21.82
SEW07	152	36.39	55.2	15.1	2	Fs	160	UNM	mature timber	2.95	20.19
SEW08	150	37.42	56.4	24.3	4	Fs	143	UNM	mature timber	3.43	20.75
SEW09	257	43.14	46.2	15.7	2	Fs	140	UNM	mature timber	2.83	22.53
SEW10	2154	28.9	13.1	3.66	1	Ps	27	EA	pole wood	3.34	10.55
SEW11	3184	38.41	12.4	3.21	2	Ps	23	EA	pole wood	4.09	10.01
SEW12	1706	27.91	14.4	4.24	1	Ps	32	EA	pole wood	3.42	11.50
SEW13	1600	46.51	19.2	4.85	2	Ps	43	EA	immature timber	3.44	14.82
SEW14	1042	37.77	21.5	4.67	1	Ps	39	EA	immature timber	2.15	10.00
SEW15	1286	35.47	18.7	4.93	2	Ps	37	EA	immature timber	2.88	13.95
SEW16	230	27.15	38.8	7.83	5	Ps	85	EA	mature timber	2.90	17.36
SEW17	347	36.41	36.6	9.58	3	Ps	100	EA	mature timber	4.20	17.16
SEW18	461	31.35	29.4	6.67	4	Ps	81	EA	immature timber	4.83	15.87
SEW19	372	27.96	30.9	6.4	5	Ps	98	EA	immature timber	1.83	10.66
SEW20	242	22.79	34.6	5.83	1	Ps	98	EA	immature timber	2.03	12.43
SEW21	428	40.15	34.6	8.31	5	Ps	74	EA	mature timber	3.27	20.96

Plot	Stem density (N ha⁻¹)	Basal area (m² ha⁻¹)	Quadr. mean dbh (cm)	SD of mean dbh (cm)	Tree species richness	Main tree species	Age (2014)	Manage-ment	Developmental stage	SSCI	ENL
SEW22	357	28.03	31.6	11.9	3	Qs	95	EA	immature timber	3.00	15.69
SEW23	401	29.29	30.5	15.8	4	Qs	116	EA	mature timber	5.42	17.75
SEW24	392	35.92	34.2	15.3	3	Qs	117	EA	mature timber	3.79	16.88
SEW25	424	27.12	28.5	12.2	4	Qs	118	EA	immature timber	4.87	17.31
SEW26	218	34.49	44.9	17.9	4	Qs	118	EA	mature timber	4.44	25.77
SEW27	297	32.98	37.6	17.9	5	Qs	130	EA	mature timber	4.27	16.88
SEW28	178	30.25	46.5	11.4	3	Qs	106	EA	mature timber	4.21	16.90
SEW29	544	33.74	28.1	13.5	7	Fs	123	EA	mature timber	4.15	17.25
SEW30	295	24.48	32.5	13.2	4	Fs	132	EA	mature timber	4.85	16.84
SEW31	285	28.56	35.7	14.2	4	Ps	88	EA	mature timber	4.43	18.03
SEW32	236	23.53	35.6	11.7	5	Ps	116	EA	mature timber	3.10	22.27
SEW33	651	37.46	27.1	12.3	3	Ps	123	EA	mature timber	4.44	16.46
SEW34	469	29.28	28.2	12.9	2	Fs	135	EA	mature timber	4.02	17.34
SEW35	180	22.77	40.1	18.4	3	Fs	138	EA	mature timber	4.30	17.06
SEW36	359	31.3	33.3	10.1	5	Fs	86	EA	immature timber	3.77	17.73
SEW37	188	30.64	45.6	14.6	4	Fs	126	EA	mature timber	4.55	21.50
SEW38	139	24.22	47.1	15.9	2	Qs	131	EA	mature timber	4.62	24.93
SEW45	165	37.29	53.6	14.6	2	Fs	100	UNM	mature timber	2.37	16.91
SEW46	98	34.76	67.2	12.2	3	Fs	158	UNM	mature timber	2.81	22.26
SEW47	151	34.45	53.9	19.7	4	Fs	138	UNM	mature timber	3.84	24.63
SEW48	357	31.64	33.6	21.9	4	Qs	173	UNM	mature timber	5.08	18.58
SEW49	187	23.36	39.9	16.8	2	Fs	98	EA	mature timber	4.01	19.84
SEW50	205	35.18	46.7	18	2	Fs	140	EA	mature timber	2.89	22.73

All plots named AEW are located in Swabian Alb, plots named HEW are located in Hainich and plots named SEW are located in Schorfheide-Chorin (see figure S1.1). Abbreviations of tree species names are Fs= *Fagus sylvatica* L. (European Beech); Qs = *Quercus robur* L. (Penduculate oak), Pa = *Picea abies* [Karst.] L. (Norway Spruce); Ps = *Pinus sylvestris* L. (Scots pine). oHs refers to other hardwood species.

APPENDIX II

Methods and statistical analyses to test main hypotheses

In the following, methods and statistical analyses used to test the hypotheses raised in chapter 1 are introduced. All statistical computations were made using the software environment R version 3.2.3 (R Development Core Team, 2016). Stand structural complexity index (SSCI) computations were made using Mathematica as described in chapter 3.

The sample used to test hypothesis (i) "Unmanaged and uneven-aged forests show a higher stand structural complexity than even-aged forests" is based on 46 EPs of the Hainich-Dün exploratory and comprises E. beech (*Fagus sylvatica*) forest of even-aged (n = 20), uneven-aged (n = 13) and unmanaged stands (n = 13). The hypothesis is tested on the basis of data from the Hainich-Dün exploratory only, because it is the sole region where each management system occurs and effects due to different main tree species and tree species mixing are excluded. Unmanaged plots on Swabian Alb include Norway spruce (*Picea abies*), whereas unmanaged plots in Schorfheide-Chorin are characterized by different a management history, which affects stand structure. Moreover, it is the only region where uneven-aged E. beech stands are found. SSCI values were the same as used in chapter 3 and are based on nine single scans per hectare.

Furthermore, data from managed and old-growth Douglas fir (*Pseudotsuga menziesii*) forests in Oregon, USA, as well as data from oil palm plantation and tropical moist forest from Jambi Province, Indonesia, was used for exemplary comparisons. The Douglas fir data was assessed by Dr. Dominik Seidel within the frame of the "Young stand thinning and diversity study", as conducted by Oregon State University, Oregon, USA (see Davis et al. (2007), Seidel et al. (2016) for more details) in the Willamette National Forest of Lane County. Here, 36 single scans were made in even-aged stands, which were established in the 1950′s and have undergone different thinning intensities (Seidel et al. 2016). Furthermore, 12 single scans were made in an old-growth Douglas fir stand in H.J. Andrew Experimental Forest. Since scans were not made based on a plot-level sampling design. Here, sample size (n) does not refer to the number of plots, but to the number of scans made. Thus, a direct comparison with data from this study is not permissive. However, a trend is still observable and reflected in the data.

The data from Jambi Province, Indonesia was assessed by Dr. Delphine Clara Zemp within the frame of the Collaborative Research Center 990 "Ecological and socio-economic functions of

tropical lowland rainforest transformation systems" (see Drescher et al. (2016) for details). Here, the author used data from 12 research plots in oil palm plantations and 11 in tropical lowland rain forest. Nine single scans were systematically distributed over each 50 x 50 m plot. Differences in stand structural complexity between management or land-use systems were tested using an ANOVA and differences were indicated by different letters if $p < 0.05$. Before, data was tested on normality using a Shapiro-Wilk test.

The sample used to test hypothesis (ii) "Mixed species stands show a higher stand structural complexity than pure stands" is based on stands with E. beech (pure: n = 28, mixed: n = 11), N. spruce (pure: n = 11, mixed: n = 4) or S. pine (pure: n = 9, mixed: n = 4) as main tree species, regardless of the exploratory. If the main tree species` basal area share was equal or above 80%, stands were considered pure stands, otherwise they were classified as mixed stands. In order to exclude effects due to uneven-aged management or no management, only even-aged stands of the developmental stages immature and mature timber were compared. Admixed tree species in E. beech stands were mainly other hardwood species such as Sycamore maple (*Acer pseudoplatanus*) or European ash (*Fraxinus excelsior*). In N. spruce stands and S. pine stands, E. beech was the most common admixed tree species. Differences in stand structural complexity between pure and mixed stands were tested using an ANOVA and differences were indicated if $p < 0.05$. Before, data was tested on normality using a Shapiro-Wilk test. Furthermore, the effect of basal area share of coniferous trees on SSCI was tested using a linear regression model. Coniferous stands that were underplanted with E. beech were excluded from both analyses. An E. beech understory has a significant effect on SSCI, but does not affect the basal area share of broadleaved and coniferous trees on stand level, because individual diameters of E. beech were below the caliper threshold of 7 cm.

The sample used to test hypothesis (iii) "Microclimate in unmanaged forests is characterized by lower mean diurnal temperature ranges than in managed forests" is based on 46 stands in Hainich-Dün with E. beech as main tree species. Here, only data from Hainich-Dün was used to exclude effects of regional climate on the diurnal temperature range (DTR, see chapter 4). DTR was computed for a period of 90 days from June to August 2014 as described in chapter 4 and is based on the same measurements. Differences in DTR between developmental stages were tested using

an ANOVA and differences were indicated by different letters if $p < 0.05$. Before, data was tested on normality using a Shapiro-Wilk test.

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Index of figures

Figure 2.4: Box-and-Whisker plots of the percentage of occluded voxels as dependent on the number of scans made per 40 x 40 x stand height (m) plot.

Figure 2.5: Relationship between ENL-values (^{0}D, ^{1}D, ^{2}D) derived from single-scan vs. multiple-scan approach (reference). n = 25 in all cases.

Figure 2.6: Relationship between the stand summary measure d_g (quadratic mean diameter), ENDC (effective number of diameter classes), BA (basal area), N*ha^{-1} (stem density) and mean ^{0}D, ^{1}D and ^{2}D ENL. n = 150.

Figure 2.7: Relationship between the stand age (years) and mean and CV (%) for ^{0}D, ^{1}D and ^{2}D ENL. n = 150.

Figure 2.8: Mean and coefficient of variation (%) of ^{0}D ENL, ^{1}D ENL and ^{2}D ENL for the investigated stand types.

Figure 3.1: Sampling design for each 1 ha plot

Figure 3.2: Graphical visualizations of exemplary cross-sectional polygons. (A) visualizes the way the scanner operates, (B) and (C) are examples of polygons and corresponding images from stands with low (B) and high (C) stand structural complexity, respectively.

Figure 3.3: Relationship between mean fractal dimension of 1280 polygons per scan and the respective mean polygon area.

Figure 3.4: Relationship between SSCI and the Structural Complexity Index by Zenner & Hibbs (2000) SCI (*upper left*), Füldner`s (1995) tree size differentiation index (TD, *upper right*), Clark Evans index of aggregation (CE, *bottom left*), and the Gini-Coefficient of diameters (GC$_d$, *bottom right*).

Figure 3.5: Boxplots of mean SSCI per plot for different stand types. Categories relate to developmental stages as shown in table 3.1.

Figure 3.6: Relationship between tree species diversity (exponential Shannon Index) and mean SSCI per plot. Regression models were computed separately for all plots (black line) and plots with E. beech (Fs, red line) as main tree species. Relationships were not significant for N. spruce, S. pine and P. oak dominated plots.

Figure 3.7: Relationship between mean SSCI per plot and mean daily temperature amplitude (*left*) and mean daily amplitude of vapor pressure deficit (*right*). Regression models were computed separately for all plots (black line) and plots with E. beech (Fs, red line), N. spruce (Pa, turquoise line) or S. pine (Ps, orange line) as main tree species and plotted only when the relationship was significant ($p < 0.05$).

Figure 4.1: Relationship between canopy openness and mean diurnal temperature range in each exploratory.

Figure 4.2: Mean diurnal temperature range in stands with different main tree species in each exploratory (Fs = *Fagus sylvatica*, Pa = *Picea abies*, Ps = *Pinus sylvestris*, Qs = *Quercus spec.*, oHS = other hardwood species).

Figure 5.1: E. beech stand with high (left, SSCI = 6.1) and low stand structural complexity (right, SSCI = 2.3). Visualization is based on a point cloud that was obtained from a multiple-scan approach.

Figure 5.2: SSCI of even-aged (EA), uneven-aged (UEA) and unmanaged (UNM) E. beech stands in Hainich Dün (*left*), EA and old-growth (OG) Douglas Fir stands in Oregon, USA (*center*), and oil palm plantations and tropical moist forest in Jambi Province, Sumatra (*right*, Zemp et al., unpublished data).

Figure 5.3: SSCI of pure and mixed stands with E. beech (*left*), N. spruce (*center*), and S. pine (*right*) as main tree species.

Figure 5.4: Effect of basal area share of coniferous trees on SSCI.

Figure 5.5: Mean diurnal temperature range in uneven-aged (UEA), unmanaged (UNM), and different developmental stages of even-aged (EA) research plots in Hainich-Dün.

Index of tables

Table 4.1: Number of plots and their main tree species for each of the three exploratories.

Table 4.2: Location, elevation above sea level, annual mean temperature and precipitation of the three exploratories.

Table 4.3: Correlations between stand structural variables and diurnal temperature ranges in summer (Pearson`s correlation coefficient).

Table 4.4: Linear models explaining diurnal temperature ranges across the three exploratories.

Declaration of honor

I hereby declare that I am the sole author of this dissertation entitled "Quantifying three-dimensional stand structure and its relationship with forest management and microclimate in temperate forest ecosystems" and that all references and data sources have been acknowledged as such. I further declare that this work has never been submitted in any form as part of any other dissertation procedure.

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Publication list

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 & Forest Meteorology, 242: 1-9

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Conference contributions

Relationships between stand structural complexity and microclimate in European beech stands revealed by TLS (Talk at SilviLaser Conference, October 2017, Blacksburg, Virginia, USA)

Quantifying stand structural complexity and its relationship with forest management, tree species diversity and microclimate (Poster presentation at the Royal Society Meeting "The terrestrial laser scanning revolution in forest ecology", February 2017, Chicheley Hall, UK)

Quantifying stand structural complexity and its relationship with forest management, tree species diversity and microclimate (Poster presentation at 13th Assembly of the Biodiversity Exploratories, Wernigerode, February 2017)

Zum Zusammenhang zwischen Bewirtschaftungsintensität und der strukturellen Komplexität von Wäldern (Poster presentation at Forstwissenschaftliche Tagung, Freiburg, September 2016)

Zum Zusammenhang zwischen der Art der Bewirtschaftung und der strukturellen Diversität von Wäldern (Talk and poster presentation at Hainich Tagung, Bad Langensalza, April 2016)

Approaches to quantify forest structure with terrestrial laser scanning (Talk and poster presentation at 12th Assembly of the Biodiversity Exploratories, Wernigerode, February 2016)

How forest management affects the structural diversity of forests (Talk and poster presentation at 11th Assembly of the Biodiversity Exploratories, Wernigerode, February 2015)

Reviewer activities for peer-reviewed journals

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Ecological Applications, Wiley

Acta Oecologica, Elsevier

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