

# Forest Structure and Structural Dynamics of Virgin Beech Forests in Slovakia

DISSERTATION

for the award of the degree “Doctor of Philosophy” (Ph.D.) of the Georg-August-Universität Göttingen

within the doctoral program “Biodiversity and Ecology”  
of the Georg-August University School of Science (GAUSS)

submitted by

**Eike Feldmann**

from Hannover

Göttingen, 2018

### **Thesis Committee**

Christoph Leuschner

(Plant Ecology and Ecosystems Research, Albrecht-von-Haller Institute, Georg-August University Göttingen)

Markus Hauck

(Applied Vegetation Ecology, Institute of Forest Sciences, Albert-Ludwigs University Freiburg)

Christian Ammer

(Silviculture and Forest Ecology of the Temperate Zones, Burckhardt Institute, Georg-August University Göttingen)

### **Members of the Examination Board**

#### **Reviewer:**

Christoph Leuschner

(Plant Ecology and Ecosystems Research, Albrecht-von-Haller Institute, Georg-August University Göttingen)

#### **Second Reviewer:**

Markus Hauck

(Applied Vegetation Ecology, Institute of Forest Sciences, Albert-Ludwigs University Freiburg)

### **Further members of the Examination Board**

Christian Ammer

(Silviculture and Forest Ecology of the Temperate Zones, Burckhardt Institute, Georg-August University Göttingen)

Dirk Hölscher

(Tropical Silviculture and Forest Ecology, Burckhardt Institute, Georg-August University Göttingen)

Erwin Bergmeier

(Vegetation and Phytodiversity Analysis, Albrecht-von-Haller Institute, Georg-August University Göttingen)

Mathias Waltert

(Conservation Biology, Johann-Friedrich-Blumenbach Institute, Georg-August University Göttingen)

**Date of the oral examination: 01.11.2018**



## Abstract

European beech (*Fagus sylvatica* L.) forests gain a special interest in Central Europe. The highly competitive species would most likely achieve dominance within a wide range of site conditions. Understanding the natural structure and dynamics of beech forests is of great importance for forest ecosystem research from both a conservation and management perspective. Today, there are only few remnants of virgin beech forests and our knowledge on their structure and especially on structural dynamics is poor. This thesis focuses on gap dynamics processes, their effect on stand structure and the analytical description of stand structures in terms of forest development stages in virgin beech forests.

Canopy gap formation is suggested being the main driver of structural processes in natural beech forests. However, information on spatio-temporal change of gap pattern, released understory structures and their reaction to canopy release are scarce. In the virgin beech forest Kyjov a repeated gap inventory was conducted to quantify differences in gap size frequency and fraction over a 10-year interval (2003–2013). Further, the percentage cover of understory trees and regeneration were estimated in 2013. Gap fraction decreased significantly from 13.6% in 2003 to 8.2% in 2013. Within 10 years the mean rate of gap closure was  $> 80\%$ . Saplings and trees in lower canopy layers formed a heterogeneous understory in large parts of recently formed gaps. The results indicate considerable variation in disturbance intensity in the past decades. The prevalent heterogeneous tree understory guarantees a high resilience to canopy disturbance.

The effects of gap formation on the regeneration process are fundamental for understanding forest dynamics. There are only a few studies from temperate virgin forests on gap regeneration and its natural dynamics over time and results are partly contradictory. The regeneration structure was studied in understory gaps of variable size and age, and under closed-canopy conditions in the Kyjov forest. Further, spatial differences in regeneration structure and height growth within a gap and in the gap periphery were analyzed. Sapling density and cumulative biomass were significantly higher in understory gaps than under the closed canopy. Sapling density was positively affected by high direct radiation but low diffuse radiation intensities, resulting in pronounced spatial differences in sapling density across a gap. Sapling shoot length growth was positively affected by higher levels of diffuse radiation and increased sapling size, while direct radiation was not influential. The results suggest that regeneration in small gaps most likely ends in a suppressed heterogeneous understory while in gaps  $\geq 100 \text{ m}^2$ , regeneration may be capable even at low plant densities to fill the gap center, often forming a rapidly growing cohort-like regeneration layer.

It is suggested that in natural temperate forests gap induced regeneration processes imprint on forest structure in the way that trees establish on the approximate gap area and close the gap over time. This assumption lacks an empirical basis. To verify this assumption neighboring trees of similar size were assigned to tree groups on a continuous 12 ha plot in the Kyjov forest and the group size-frequency of such homogeneous patches was analyzed across diameter classes. The number of tree groups (cohorts) in a particular diameter class decreased exponentially as group size increased. Compared to random distributions, the Kyjov forest exhibited a more clumped distribution especially for small trees. The frequency distribution patterns for group sizes are similar to those for gap sizes reported from the same stand and many others. Even though a direct comparison (number of trees vs. m<sup>2</sup>) is not possible, the results indicate that gap initiated tree groups may persist through the forest cycle.

Researchers defined a succession of forest development stages to explain the diversity of structures encountered in beech-dominated virgin forests. However, existing methods based on empirical stand structural data fail to display structural development comprehensively. A novel approach for determining the extension of development stages is proposed. The Development Stage Index ( $I_{DS}$ ) assigns living and dead trees to the Initial, Optimum and Terminal stage according to their DBH (7–39 cm, 40–69 cm and  $\geq 70$  cm, respectively) and quantifies their extension by means of stem density and basal area. It was applied to 40 spaced sample plots (500 m<sup>2</sup> each) in three beech virgin forests in East Slovakia (Kyjov, Havešová and Stuižca; 120 plots in total). Based on thorough stand structural analyses in the three virgin beech forests, it is demonstrated that  $I_{DS}$  is a promising tool for quantifying the proportion of the three stages on different scales, visualizing the complex mixing of stages and analyzing dynamic changes in old-growth forest structure. The results from the Kyjov forest derived by the  $I_{DS}$  are in large agreement with the conclusions on how gap dynamics shape forest structure in this forest. This suggests that it might be possible to infer on past forest dynamics by analyzing stand structure with the  $I_{DS}$ .

TABLE OF CONTENTS

<b>1</b>	<b>General Introduction</b>	1
1.1	Why are beech forests of particular interest?	1
1.2	Why is it important to study the structure of virgin forests?	2
1.3	The study of structure and structural dynamics in beech virgin forests	2
1.4	Research objectives and approaches	5
1.5	References	7
<b>2</b>	<b>Canopy gap dynamics and tree understory release in a virgin beech forest, Slovakian Carpathians</b>	11
	Abstract	11
2.1	Introduction	12
2.2	Methods	15
2.2.1	Study site	15
2.2.2	Gap definition	15
2.2.3	Field methods	16
2.2.4	Data analysis	17
2.3	Results	19
2.3.1	Canopy gap area, frequency and size distribution	19
2.3.2	Gap development	20
2.3.3	Structure and development of released tree understory	22
2.4	Discussion	23
2.4.1	Can gap fractions detected in beech forests be generalized?	23
2.4.2	Gap size frequency and gap area	24
2.4.3	Gap closure and the legacy of past disturbance	26
2.4.4	Gap effects on understory structure	27
2.5	Conclusions	30
2.6	Appendix	31
2.7	References	32
<b>3</b>	<b>Regeneration dynamics following the formation of understory gaps in a Slovakian beech virgin forest</b>	37
	Abstract	37
3.1	Introduction	38
3.2	Methods	41
3.2.1	Study site	41
3.2.2	Study design	42
3.2.3	Field methods	42
3.2.4	Data analysis	43
3.3	Results	45
3.3.1	Comparison of gaps with closed-canopy conditions	46
3.3.2	Spatial differences in regeneration structure	46
3.3.2.1	Sapling density	46
3.3.2.2	Shoot length growth and sapling height	48
3.3.2.3	Sapling biomass	50
3.4	Discussion	51
3.4.1	Comparing beech regeneration in gaps and closed-canopy patches	51
3.4.2	The role of gaps for beech regeneration	52
3.5	Conclusions	56
3.6	Appendix	58
3.7	References	59
<b>4</b>	<b>What Happens after the Gap? — Size Distributions of Patches with Homogeneously Sized Trees in Natural and Managed Beech Forests in Europe</b>	65
	Abstract	65
4.1	Introduction	66
4.1.1	Background of the study	66
4.1.2	Silvicultural research in natural beech forests in Europe	67

TABLE OF CONTENTS

4.2	Material and methods	69
4.2.1	Study sites	69
4.2.2	Data sampling	70
4.2.3	Data analysis and determination of tree groups	70
4.3	Results	72
4.3.1	Diameter distributions	72
4.3.2	Tree group frequencies in the natural forest	73
4.3.3	Tree group frequencies in the managed forests	75
4.3.4	Exponential fits and sensitivity analyses	76
4.4	Discussion	76
4.4.1	Natural forest structure and dynamics	76
4.4.2	Comparing managed and natural stands	77
4.4.3	Limitations of the presented method	78
4.5	Conclusions	79
4.6	Appendix	81
4.7	References	83
<b>5</b>	<b>A novel empirical approach for determining the extension of forest development stages in temperate old-growth forests</b>	<b>87</b>
	Abstract	87
5.1	Introduction	88
5.2	Methods	90
5.2.1	Study sites	90
5.2.2	Data collection	91
5.2.3	The Forest Development Stage Index ( $I_{DS}$ )	92
5.2.4	Calculation of $I_{DS}$	94
5.2.5	Data analysis	95
5.3	Results	96
5.3.1	Stand structural characteristics	96
5.3.2	Characterizing stand structure by the Development Stage Index $I_{DS}$	97
5.3.3	Spatial extension of development stages	100
5.3.4	Sensitivity analysis of the classification scheme	101
5.3.5	Visualizing the mingling of stages in the study plots	101
5.4	Discussion	103
5.4.1	Plot number and plot size requirements in old-growth forest studies	103
5.4.2	Quantifying forest structure with the Development Stage Index $I_{DS}$	103
5.4.3	Distribution and abundance of development stages	105
5.4.4	Deadwood as an old-growth forest attribute	107
5.4.5	$I_{DS}$ as a proxy for further stand structural characteristics	109
5.5	Conclusions	110
5.6	Appendix	111
5.7	References	114
<b>6</b>	<b>Synthesis</b>	<b>119</b>
6.1	Effects of gap dynamics on stand structure	119
6.2	Stand structure and development stages	123
6.3	Implications for forest ecosystem conservation, restoration and close-to-nature forest management	126
6.4	References	129
	<b>Curriculum Vitae</b>	<b>132</b>





# 1<sup>st</sup>

## CHAPTER

### GENERAL INTRODUCTION

#### 1.1 Why are beech forests of particular interest?

Central Europe has a relatively limited set of deciduous tree species when compared to other temperate regions. One species - European beech (*Fagus sylvatica* L.) - plays an outstanding role within the region, as due to a high shade tolerance coupled with a high plasticity in growth development it is very competitive and often forms monospecific stands, or beech is at least found codominant among few other species (Leuschner and Ellenberg, 2017). The glacial distribution of European beech was limited to a few scattered refugia, mainly in South and South-East Europe (Magri et al., 2008). While the beech populations increased slowly and to a moderate extent in the South, in Central Europe they increased quickly and extensively replaced mixed oak forests and spruce forests due to a climate favorable for the competitiveness of beech (Burschel and Huss, 2003; Magri et al., 2008). Under the current climatic conditions European beech would most likely achieve dominance within a wide range of site conditions in large parts of Central Europe and beyond (Peters, 1997; Bohn et al., 2003; Giesecke et al., 2007). Even though it is forecasted that the species will be regionally threatened by climate change, especially at the southern margin of its occurrence, it would potentially still be widely distributed in Central Europe (e.g. Kramer et al., 2010). However, during the past centuries intensive deforestation activities, often followed by reforestation with coniferous monocultures, have put the share of beech forests within the region far below its potential (Leuschner and Ellenberg, 2017). Silvicultural practices, such as retention forestry, lead to even-aged and homogeneous stand structures in most remaining beech forests. Remnants of beech-dominated virgin forests (*sensu* Hunter, 1990; also primeval or primary forests) are extremely rare and can only be found

in the east and southeast of Central Europe (Parviainen, 2005; Veen et al., 2010). Some of them are endangered by commercial activities (Veen et al., 2010).

## **1.2 Why is it important to study the structure of virgin forests?**

Virgin forests are forest stands with no indication of human management impact and a discrete development over several tree generations (Hunter, 1990). Their physical structure is shaped by the long-term interactions of climate, soil conditions and tree species feedback (White and Jentsch, 2001). With the prospect of climate change and global biodiversity loss, a profound understanding of their structure and dynamics is of great importance for forest ecosystem research from both a conservation and management perspective (Leuschner and Ellenberg, 2017). The structures found in these forests are thought of as being well adapted to abiotic factors and having developed a better resistance and/or resilience to extreme events like windstorms (Bauhus et al., 2013). They generally contain higher average volume of stock (living and dead) when compared to managed forests and there are indications that they have a positive effect on forest productivity (Glatthorn et al., 2018). Further, virgin forests host the local biodiversity that is adapted to the specific structures and partly depends on structural elements (or combinations of these) which are rarely found in adequate quality or quantity in managed forests (Lindenmayer and McCarthy, 2002; Frank et al., 2009). Various important questions of forest ecology can only be answered in virgin forests, as management activities can imprint on forest structure for centuries (e.g. Tabaku, 2000).

## **1.3 The study of structure and structural dynamics in beech virgin forests**

Silvicultural research in European beech virgin forests began in the middle of the 18<sup>th</sup> century, when they still covered large areas on the Balkan Peninsula, in the Dinaric Alps and the Carpathian Mountains (Fröhlich, 1954; Müller, 1929), and has shaped today's notion about the structure and dynamics of these forests (Brang, 2005). The increasingly detailed analyses of corresponding stands in eastern and south-eastern Europe has provided important data about volume of stock, the proportion of deadwood and structural diversity of natural beech forests (e.g. Leibundgut, 1993; Korpel, 1995; Commarmot et al., 2013). Strong spatial heterogeneity in stand structure seems a general feature that is reflected in a considerable variation in tree canopy layering, stem density, diameter distributions, volume of stock and the proportion of deadwood.

Understanding the structural dynamics, i.e. the processes that shaped these heterogeneous forest structures, has always been a major objective in beech virgin forest research. The diversity of structures encountered in beech-dominated virgin forests was traditionally explained by applying the plausible theoretical concept of the ‘forest development cycle’ introduced by Watt (1947). It describes the structural dynamics of natural forests driven by demographic processes and the action of external disturbances, and repeats itself with the formation of a new generation. In order to quantify the horizontal variability of forest structure and to draw conclusions on the driving factors of change, researchers defined a succession of forest development stages (sometimes further divided into different development phases) and their occurrence was mapped as a texture of patches. Applications of this procedure evolved from expert decisions (Neumann, 1979; Leibundgut, 1993; Korpel, 1995) into more objective and repeatable methods based on empirical stand structural data (Meyer, 1999; Tabaku, 2000; Emborg et al., 2000; Grassi et al., 2003; Kral et al., 2010, 2016). However, the results from repeated inventories raised doubts about the ability of the existing approaches to comprehensively display structural development (Christensen, 2007; Kral et al., 2018) and thus their explanatory value in general seems questionable. A reason might be the focus on dominant structural elements and the associated assumption of a uniform appearance and behavior at a chosen spatial scale (patch size). Within these patches the heterogeneity in stand structure as the most important stand characteristic (Pretzsch, 2009) is largely ignored.

A different approach in the study of structural dynamics, that rigorously follows the basic idea of Watt (1947), is the study of ‘gap dynamics’ (e.g. Yamamoto, 2000). When canopy trees die they leave gaps in the canopy and these gaps get then filled by other trees. Studies on gap dynamics mainly focus on the disturbance regime and the gap-induced regeneration process. Thus, they cover only a sequence in the forest cycle. However, as this sequence is supposed to constitute the generational turnover it is of high significance in the study of forest structural dynamics. A better understanding might help as guidance to the question what scale should be best addressed in this research discipline, and to development strategies in close-to-nature management and forest ecosystem restoration (Seymour et al., 2002).

In the recent past several authors studied gap fraction and gap size-frequencies in European beech-dominated virgin forests (Tabaku and Meyer, 1999; Zeibig et al., 2005; Dröbner and von Lüpke, 2005; Nagel and Svoboda, 2008; Kenderes et al., 2009; Kucbel et al., 2010; Bottero et al., 2011; Petritan et al., 2013). These studies report considerable differences in gap fraction between the corresponding forest stands (3–19%). Gap size-frequency distributions of canopy gaps generally showed an exponential decline in the number of gaps with increasing gap size.

Hence, most gaps in beech forests resulted from the mortality of single or a few trees and ranged in size from  $< 100$  to several hundred  $m^2$ . Nevertheless, large gaps up to several thousand  $m^2$  were found as well in some of the studied forest stands and they accounted for a large fraction of the total gap area (Dröbner and von Lüpke, 2005; Nagel and Svoboda, 2008).

According to Leibundgut (1993), the beech virgin forests of the Balkan Peninsula, the Dinaric Alps and the Carpathian Mountains are so similar in structure and dynamics that they are well comparable to one another. However, thorough analysis of diameter distributions from a set of beech-dominated virgin forests revealed that there are deviations between the stands in this general characteristic (Westphal et al., 2006) which might be associated with differences in the local disturbance regime. The high variation in gap fractions found in the different studied stands is a strong indicator that such differences do exist. While early studies suggested that beech virgin forests are in a structural equilibrium condition at the stand scale (e.g., 30 ha; Korpel, 1995), more recent dendroecological studies in beech-dominated virgin forests indicate a high variability in the frequency and intensity of disturbances (e.g. Nagel et al., 2014) which would explain the strong differences in gap fractions reported. However, studies on the temporal development of gap fraction and gap size-frequency are rare and both low variation (Kenderes et al., 2009) or high variation (Splechtna and Gratzner, 2005) in disturbance intensity have been reported.

The size development of gaps over time, i.e. gap formation, gap expansion or gap closure, is driven by processes of tree growth and population dynamics, which are not well understood in virgin forests. As for the process of gap closure, the distinction between lateral crown expansion of adjacent trees and vertical ingrowth from lower layers is crucial for the interpretation of gap dynamics, as only the latter is connected with a generational turnover in the canopy.

The structure of the released tree understory (from seedlings to sub-canopy trees) is supposed to play an important role in this process. There are only few studies on gap regeneration in (mixed) beech virgin forests and they reported that gaps most often released advanced regeneration of spatially heterogeneous structure (Diaci et al., 2005; Rozenbergar et al., 2007; Kucbel et al., 2010; Nagel et al., 2010). Even though it is undisputed that canopy gaps influence tree understory dynamics, this relationship has rarely been quantified. It was indicated that there are spatial differences in the development of regeneration within gaps, associated with the unequal distribution of light and variable preconditions for establishment, that are further influenced by gap size (Rozenbergar et al., 2007).

## 1.4 Research objectives and approaches

The overarching objectives of this doctoral thesis are to conclusively describe and analyze the structure of beech-dominated virgin forests and to progress our understanding of the dynamics that shape forest structure. The first part of the thesis (Chapter 2–4) addresses the processes that naturally shape beech forest structure by means of gap dynamics. For this reason a repeated inventory of canopy gaps (2003 and 2013) was conducted in the beech virgin forest Kyjov in the Vihorlat Mountains in eastern Slovakia (Chapter 2). It was based on an earlier inventory by Dröbner and von Lüpke (2005) which represents one of the pioneering works on gap dynamics and disturbance patterns in European temperate broadleaf forests. The repeated inventory allows to quantify changes in gap fraction and gap size-frequency distribution and to assess the size development of individual gaps and the relevant processes. The second inventory was accomplished by an extensive evaluation of the released tree understory structures (Chapter 2), and a detailed assessment of regeneration structure and growth development in a subset (understory gaps) of the canopy gaps mapped in 2013 (Chapter 3). In an accompanying study (chapter 4) the structure of the Kyjov forest and two differently managed stands was studied by analyzing the extent of patches with relatively homogeneous tree dimensions (tree groups or cohorts) which are proposed to have a similar background in initiation and development. Size distributions of such tree groups are meant to illustrate general stand dynamic patterns, from the initiation to the terminal phase.

The following questions in the field of gap dynamics research, which arose from recent studies in temperate virgin forests, are addressed in the first part of the thesis:

- Is there a temporal variation in disturbance patterns (gap fraction and gap size-frequency) in the Kyjov forest? (Chapter 2)
- How do canopy gaps develop in size following disturbance and what is the importance of different processes involved in gap closure (horizontal ingrowth vs. vertical gap filling) in dependence of gap size? (Chapter 2)
- Do canopy gaps release advanced tree understory, and if so, how is it structured? (Chapter 2 and 3)
- Do canopy gaps have a significant impact on regeneration development of shade tolerant beech? (Chapter 3)
- Are there spatial differences in regeneration development related to gap geometry and gap size? (Chapter 3)

- Is the size-frequency pattern of canopy gaps reflected in stand structure in terms of tree groups, which would indicate that canopy gaps condition the general stand dynamic patterns, from the initial to the terminal stage? (Chapter 4)

While there is no doubt about the validity of the forest development cycle as a theoretical concept, current methods for the determination of developmental stages or phases seem unable to coherently display forest structural changes with time (see above). Hence, in the second part of the thesis (Chapter 5) a novel approach was developed that classifies forest structure in terms of forest development stages by using empirical data on easy-to-measure parameters and considers complex mixing of trees in different life history stages. The approach was further meant to be applicable at different scales to accommodate different types of forest inventory data. Three Slovakian beech virgin forests in the Eastern Carpathians (Kyjov, Havešová and Stučica) were selected as test systems and forest structure was studied on a total of 118 spaced research plots of 500 m<sup>2</sup>. The approach intends to quantify the proportions of three commonly recognized development stages (Initial, Optimum and Terminal) at plot, stand and landscape levels. The information is supposed to allow conclusions on vertical structure and its spatial variation in a forest stand and thus on the character of the disturbance regime as driver to generational turnover. The following ecological questions are addressed in the second part of the thesis:

- Do development stages form homogeneously structured patches or is structure rather heterogeneous at the plot level, due to overlap and small-scale mingling of stages?
- Are the studied forests in structural equilibrium at the stand scale?
- Are there structural differences between the three beech virgin forests?

In chapter 6 the studies are synthesized to draw a comprehensive picture of forest dynamics in the beech-dominated virgin forests. Further, this chapter addresses questions and issues that should be the focus of future research.

## 1.5 References

- Bauhus, J., Puettmann, K. J., Kühne, C., 2013. Close-to-nature forest management in Europe: does it support complexity and adaptability of forest ecosystems, in: Messier, C., Puettmann, K. J., Coates, K. D. (Eds.), *Managing forests as complex adaptive systems: building resilience to the challenge of global change*. Routledge, London, New York. 187–213.
- Bohn, U., Neuhäusl, R., Gollub, R., Hettwer, C., Neuhäuslova, Z., Schlüter, H., Weber H., 2003. Karte der natürlichen Vegetation Europas. Teil 1: Erläuterungstext. Landwirtschaftsverlag, Münster.
- Bottero, A., Garbarino, M., Dukić, V., Govedar, Z., Lingua, E., Nagel, T. A., Motta, R., 2011. Gap-Phase Dynamics in the Old-Growth Forest of Lom, Bosnia and Herzegovina. *Silva Fennica*, 45(5), 875–887.
- Brang, P., 2005. Virgin forests as a knowledge source for central European silviculture: reality or myth. *Forest, Snow and Landscape Research*, 79(1/2), 19–32.
- Burschel, P., Huss, J., 2003. Grundriß des Waldbaus – Ein Leitfaden für Studium und Praxis. Ulmer Verlag, Stuttgart.
- Christensen, M., Emborg, J., Busse Nielsen, A., 2007. The forest cycle of Suserup Skov – revisited and revised. *Ecological Bulletins*, 52, 33–42.
- Commarmot, B., Brändli, U.-B., Hamor, F., Lavnyy, V. (Eds.), 2013. Inventory of the largest virgin beech forest of Europe. A Swiss-Ukrainian scientific adventure. Birmensdorf, Swiss Federal Research Institute WSL; L'viv, Ukrainian National Forestry University, Rakhiv, Carpathian Biosphere Reserve.
- Dröbler, L., Lüpke, B., 2005. Canopy gaps in two virgin beech forest reserves in Slovakia. *Journal of Forest Science*, 51, 446–457.
- Diaci, J., Rozenbergar, D., Boncina, A., 2005. Interactions of light and regeneration in Slovenian Dinaric Alps: patterns in virgin and managed forests. *Forest, Snow and Landscape Research*, 79(1/2), 154–160.
- Emborg, J., Christensen, M., Heilmann-Clausen, J., 2000. The structural dynamics of Suserop Skov, a near natural temperate deciduous forest in Denmark. *Forest Ecology and Management*, 126, 173–179.
- Frank, D., Finckh, M., Wirth, C., 2009. Impacts of Land Use on Habitat Functions of Old-Growth Forests and their Biodiversity, in: C. Wirth, G. Gleixner, M. Heimann (Eds.), *Old-Growth Forests: Function, Fate and Value*, Ecological Studies, Analysis and Synthesis, 207. Springer-Verlag Berlin Heidelberg, Berlin, Heidelberg. 429–450.
- Fröhlich, J., 1954. *Urwaldpraxis. 40jährige Erfahrungen und Lehren*. Berlin, Radebeul.
- Giesecke, T., Hickler, T., Kunkel, T., Sykes, M. T., Bradshaw, R. H., 2007. Towards an understanding of the Holocene distribution of *Fagus sylvatica* L. *Journal of biogeography*, 34(1), 118–131.
- Glatthorn, J., Feldmann, E., Pichler, V., Hauck, M., Leuschner, C., 2018. Biomass stock and productivity of primeval and production beech forests: greater canopy structural diversity promotes productivity. *Ecosystems*, 21(4), 704–722.
- Grassi, G., Minotta, G., Giannini, R., Bagnaresi, U., 2003. The structural dynamics of managed uneven-aged conifer stands in the Italian eastern Alps. *Forest Ecology and Management*, 185, 225–237.
- Hunter Jr., M. L., 1990. *Wildlife, forests and forestry: Principles of managing forests for biological diversity*. Englewood Cliffs, New Jersey: Prentice-Hall.
- Kenderes, K., Král, K., Vrška, T., Standovar, T., 2009. Natural Gap Dynamics in a European Mixed Beech-Spruce-Fir Old-Growth Forest. *Ecoscience*, 16(1), 39–47.
- Korpel, Š., 1995. *Die Urwälder der Westkarpaten*. Gustav Fischer Verlag, Stuttgart.
- Král, K., Vrška, T., Hort, L., Adam, D., Šamonil, P., 2010. Developmental phases in a temperate natural spruce-fir-beech forest. Determination by a supervised classification method. *European Journal of Forest Research*, 129, 339–351.
- Král, K., Shue, J., Vrška, T., Gonzalez-Akre, E. B., Parker, G. G., McShea, W. J., McMahon, S. M., 2016. Fine-scale patch mosaic of developmental stages in Northeast American secondary temperate forests: the European perspective. *European Journal of Forest Research*, 135, 981–996.

- Král, K., Daněk, P., Janík, D., Krůček, M., Vrška, T., 2018. How cyclical and predictable are Central European temperate forest dynamics in terms of development phases? *Journal of Vegetation Science*, 29(1), 84–97.
- Kucbel, S., Jaloviari, P., Saniga, M., Vencurik, J., Klimaš, V., 2010. Canopy gaps in an old-growth fir-beech forest remnant of Western Carpathians. *European Journal of Forest Research*, 129, 249–259.
- Kramer, K., Degen, B., Buschbom, J., Hickler, T., Thuiller, W., Sykes, M. T., de Winter, W., 2010. Modelling exploration of the future of European beech (*Fagus sylvatica* L.) under climate change—range, abundance, genetic diversity and adaptive response. *Forest Ecology and Management*, 259(11), 2213–2222.
- Leibundgut, H., 1993. Europäische Urwälder - Wegweiser zur naturnahen Waldwirtschaft. Paul Haupt.
- Leuschner, C., Ellenberg, H., 2017. Ecology of Central European Forests. Vegetation Ecology of Central Europe, Vol. I., Springer Nature, Cham.
- Lindenmayer, D., McCarthy, M. A., 2002. Congruence between natural and human forest disturbance: a case study from Australian montane ash forests. *Forest Ecology and Management*, 155(1-3), 319–335.
- Magri, D., 2008. Patterns of post-glacial spread and the extent of glacial refugia of European beech (*Fagus sylvatica*). *Journal of Biogeography*, 35(3), 450–463.
- Meyer, P., 1999. Bestimmung der Waldentwicklungsphasen und der Texturdiversität in Naturwäldern. *Allgemeine Forst- und Jagdzeitung*, 170, 203–211.
- Müller, K. M., 1929. Aufbau, Wuchs und Verjüngung der südosteuropäischen Urwälder, Hannover: Schaper.
- Nagel, T. A., Svoboda, M., 2008. Gap disturbance regime in an old-growth Fagus–Abies forest in the Dinaric Mountains, Bosnia–Herzegovina. *Canadian Journal of Forest Research*, 38, 2728–2737.
- Nagel, T. A., Svoboda, M., Rugani, T., Diaci, J., 2010. Gap regeneration and replacement patterns in an old-growth Fagus–Abies forest of Bosnia–Herzegovina. *Plant Ecology*, 208(2), 307–318.
- Nagel, T. A., Svoboda, M., Kobal, M., 2014. Disturbance, life history traits, and dynamics in an old-growth forest landscape of southeastern Europe. *Ecological Applications*, 24 (4), 663–679.
- Neumann, M., 1979. Bestandesstruktur und Entwicklungsdynamik im Urwald Rothwald/NÖ und im Urwald Čorkova Uvala/Kroatien. PhD thesis, Univ. f. Bodenkultur, Wien.
- Parviainen, J., 2005. Virgin and natural forests in the temperate zone of Europe. *Forest, Snow and Landscape Research*, 79(1/2), 9–18.
- Peters, R., 1997. Beech Forests. *Geobotany*, 24, Springer.
- Petritan, A. M., Nuske, R. S., Petritan, I. C., Tudose, N. C., 2013. Gap disturbance patterns in an old-growth sessile oak (*Quercus petraea* L.)–European beech (*Fagus sylvatica* L.) forest remnant in the Carpathian Mountains, Romania. *Forest Ecology and Management*, 308, 67–75.
- Pretzsch, H., 2009. Forest Dynamics, Growth and Yield. Springer, Berlin, Heidelberg.
- Rozenberger, D., Mikac, S., Anić, I., Diaci, J., 2007. Gap regeneration patterns in relationship to light heterogeneity in two old-growth beech–fir forest reserves in South East Europe. *Forestry*, 80(4), 431–443.
- Seymour, R. S., White, A. S., deMaydenadier, P. G., 2002. Natural disturbance regimes in northeastern North America - evaluating silvicultural systems using natural scales and frequencies. *Forest Ecology and Management*, 155(1), 357–367.
- Splechtna, B. E., Gratzner, G., 2005. Natural disturbances in Central European forests: approaches and preliminary results from Rothwald, Austria. *Forest, Snow and Landscape Research*, 79, 57–67.
- Tabaku, V., Meyer, P., 1999. Lückenmuster albanischer und mitteleuropäischer Buchenwälder unterschiedlicher Nutzungsintensität. *Forstarchiv*, 70, 87–97.



- Tabaku, V., 2000. Struktur von Buchen-Urwäldern in Albanien im Vergleich mit deutschen Buchen-Naturwaldreservaten und -Wirtschaftswäldern. Cuvillier Verlag, Göttingen, 206 pp.
- Veen, P., Fanta, J., Raev, I., Biriş, I. A., de Smidt, J., Maes, B., 2010. Virgin forests in Romania and Bulgaria: results of two national inventory projects and their implications for protection. *Biodiversity and Conservation*, 19(6), 1805–1819.
- Watt, A. S., 1947. Pattern and Process in the Plant Community. *Journal of Ecology*, 35, 1–22.
- Westphal, C., Tremer, N., von Oheimb, G., Hansen, J., von Gadow, K., Härdtle, W., 2006. Is the reverse J-shaped diameter distribution universally applicable European virgin beech forests? *Forest Ecology and Management*. 223, 75–83.
- White, P. S., Jentsch, A., 2001. The search for generality in studies of disturbance and ecosystem dynamics. In *Progress in Botany*, pp. 399–450. Springer, Berlin, Heidelberg.
- Yamamoto, S. I., 2000. Forest gap dynamics and tree regeneration. *Journal of forest research*, 5(4), 223–229.
- Zeibig, A., Diaci, J., Wagner, S., 2005. Gap disturbance patterns of a *Fagus sylvatica* virgin forest remnant in the mountain vegetation belt of Slovenia. *Forest, Snow and Landscape Research*, 79, 69–80.



# 2<sup>ND</sup>

## CHAPTER

### CANOPY GAP DYNAMICS AND TREE UNDERSTORY RELEASE IN A VIRGIN BEECH FOREST, SLOVAKIAN CARPATHIANS

Eike Feldmann, Lars Drößler, Markus Hauck, Stanislav Kucbel,  
Viliam Pichler, Christoph Leuschner

Forest Ecology and Management 415 (2018), 38–46

#### Abstract

Canopy gaps play a crucial role for forest dynamics processes, as they largely determine light transmission to lower canopy strata, thereby controlling the turnover of tree individuals in the stand. Even though their functional importance is undisputed, quantitative data on the rate of gap creation and gap closure, and the temporal change in gap size distribution patterns in temperate virgin forests are scarce. We used a repeated inventory (line-intercept sampling) of gap size frequency and fraction in a virgin beech (*Fagus sylvatica*) forest in the Slovakian Carpathians over a 10-year interval (2003–2013) to test the hypotheses that (i) disturbance intensity and thus gap creation and gap closure rate change only little over time, (ii) gaps persist or even expand, until they are filled primarily by vertical ingrowth of trees from lower strata, and (iii) gap creation promotes the height growth of released saplings and sub-canopy trees. In the 2003 and 2013 inventories, 37 and 30 gaps > 20 m<sup>2</sup> size were mapped along a total of 3217 m transect line investigated. The large majority of gaps was < 100 m<sup>2</sup> in size; large gaps > 500 m<sup>2</sup> were very rare. Gap fraction decreased significantly from 13.6% in 2003 to 8.2% in 2013 (associated with a reduction in mean gap size from 261 to 96 m<sup>2</sup>), indicating considerable variation in disturbance intensity in the past decades. Before 2003, both large gaps (probably caused by wind throw) and small gaps (from dying trees) have been formed, while only small

gaps developed in the period 2003–2013. Small gaps were closed within a few years through rapid horizontal canopy expansion of neighboring beech trees, while vertical gap filling through ingrowth of lower canopy layers and regeneration was the dominant process in larger gaps. Saplings and trees in lower canopy layers formed a heterogeneous understory in large parts of recently formed gaps and responded to this process with increased height growth. We conclude that, despite considerable variation in disturbance intensity over time, this beech virgin forest responds to gap formation with high resilience through rapid lateral canopy expansion in small gaps and ingrowth of saplings and sub-dominant tree layers in larger gaps.

**Keywords:** canopy gap; gap dynamics; disturbance intensity; European beech; gap filling; regeneration

## 2.1 Introduction

In the prospect of climate change and global biodiversity loss, understanding the structure and dynamics of virgin forests is of great importance for forest ecosystem research from both a conservation and management perspective (Leuschner and Ellenberg, 2017). Various questions of forest ecology can only be answered in virgin forests, as management activities can imprint on forest structure for centuries (e.g. Tabaku, 2000). When investigating the structural dynamics of natural forests, the study of the disturbance regime is of high significance, as it largely determines the turnover of tree individuals in the canopy. The disturbance regime of forest ecosystems is characterized by several, partly interacting factors, including the type of disturbance, its magnitude, frequency and size, as well as the spatio-temporal dispersion of disturbances (Frelich, 2002; Nagel et al., 2007; White and Jentsch, 2001). Similar to many temperate forests in eastern Asia and North America (e.g. Coates and Burton, 1997), forests of European beech (*Fagus sylvatica* L.) are mainly exposed to small-scale disturbances (Peters, 1997) while medium and large-scale disturbance events are rare and most often related to wind throw (Peters, 1997; Schelhaas et al., 2003). Small-scale disturbances result in canopy gaps of < 100 to several hundred m<sup>2</sup> size that drive the forest cycle through their control on light transmission to the lower strata (Whitmore, 1989). Adjacent and formerly suppressed trees as well as seedlings and saplings in gaps benefit from the reduction in competition intensity. Further, gaps are an important habitat for many woodland plant and animal species (Coates and Burton, 1997; Lachat et al. 2016; Muscolo et al., 2014). Emulating natural gap dynamics in forestry offers opportunities for close-to-nature management and forest ecosystem restoration (Seymour et al., 2002), notably in beech-dominated forests (e.g. Nagel and Svoboda, 2008; Schütz et al., 2016). Several authors have studied canopy gaps in beech-dominated virgin forests in the recent past.

Approaches using terrestrial methods reported gap areas ranging from 3 to 19% (Bottero et al., 2011; Drößler and von Lüpke, 2005; Kenderes et al., 2009; Kucbel et al., 2010; Nagel and Svoboda, 2008; Petritan et al., 2013; Tabaku and Meyer, 1999; Zeibig et al., 2005), whereas remote sensing approaches found canopy gap percentages of 1% (Garbarino et al., 2012) or even less (Hobi et al., 2015a). However, these remote sensing approaches are constrained by only identifying those gaps that do not contain tree regeneration. Irrespective of the method applied, size-frequency distributions of canopy gaps generally show an exponential decline in the number of gaps with increasing gap size. This means that most gaps in beech forests result from the mortality of single or a few trees. Nevertheless, large gaps, if they are present, can account for a large fraction of the total gap area (Bottero et al., 2011; Kucbel et al., 2010; Nagel and Svoboda, 2008; Zeibig et al., 2005).

Early studies on the stand structure of beech virgin forests suggested that these forests are in a structural equilibrium condition at the stand scale (e.g., 30 ha; Korpel, 1995). In contrast, dendroecological studies in beech-dominated virgin forests indicate a high variability in the frequency and intensity of disturbances (e.g. Nagel et al., 2014). Time series of aerial photographs from beech forests covering a few decades document both, low variation (Kenderes et al., 2009) or high variation (Splechtna and Gratzner, 2005) in disturbance intensity. Both scenarios seem plausible against the background of variation in local climate and site conditions, and they are not necessarily contradictory, as return intervals of high intensity disturbances might be longer than a few decades.

Change in gap area over time with gap formation, gap expansion or gap closure is driven by processes of tree growth and population dynamics, which are not well understood in virgin forests. Some terrestrial studies in virgin beech forests described a successive expansion of canopy gaps, driven apparently through the death of bordering trees as indicated by snags in different stages of decay ('gap makers') (Drößler and von Lüpke, 2005; Nagel and Svoboda, 2008; Bottero et al., 2011). These findings suggest that gaps may destabilize the bordering stand through mechanical damage, exposure to wind, or direct sunlight overheating the bark. In contrast, Tabaku and Meyer (1999) found gaps to be formed only by single disturbance events. In an old-growth beech-sugar maple forest in Ohio (USA), Runkle (2013) observed tree mortality over 32 years; tree mortality was not higher in the trees neighboring a gap than in the canopy trees in the closed stand. As for the process of gap closure, the distinction between lateral crown expansion of adjacent trees and vertical ingrowth from lower layers is crucial for the interpretation of gap dynamics, as only the latter is connected with a generational turnover in the canopy. The structure and species composition of formerly suppressed tree layers is

supposed to play an important role in the process of gap closure. Studies on gap regeneration in (mixed) beech virgin forests reported a high presence of advanced regeneration (Nagel et al., 2010; Kucbel et al., 2010; Diaci et al., 2012). Even though it is undisputed that canopy gaps influence tree understory dynamics, this relationship has rarely been quantified.

In this case study, we conducted a repeated inventory of canopy gaps (2003 and 2013) in a virgin beech forest in the Carpathians. Our study bases on an earlier inventory by Drößler and von Lüpke (2005) that was conducted in 2003, representing one of the pioneering works on gap dynamics and disturbance patterns in European temperate broadleaf forests. As far as we know, our analysis represents the first ground-based repeated inventory of canopy gaps in a virgin beech forest. We addressed several questions in the field of canopy gap dynamics research, which arose from recent studies in temperate virgin forests.

Studies in virgin forests of *F. sylvatica* document a high variability in gap fraction among different stands. It is not yet clear whether this variation is caused by (i) the use of different inventory methods and gap definitions, (ii) regional differences in disturbance frequency and intensity, or (iii) possible temporal variation in disturbance frequency and intensity. With the repeated inventory approach, factors (i) and (ii) can be excluded, allowing us to focus on the temporal variation in canopy structure. Our work was guided by three hypotheses:

(H1) Based on the observation that large-scale, stand-replacing disturbances are rare in the climate of eastern-central Europe and old-growth forest may develop a dynamic equilibrium state in the long intervals between two external disturbance events (Korpel, 1995), we hypothesized that in the period between two large-scale events, the imprint of disturbance on stand structure should remain relatively constant over time, resulting in similar gap formation and gap closure rates on the stand scale. For our 10-yr observation period we thus predict similar total gap areas and gap size patterns for the 2003 and 2013 inventories.

(H2) Conclusions on the size development of gaps, once formed, are vague and different trends have been reported. The importance of different processes behind gap closure, i.e. horizontal ingrowth or vertical gap filling, in beech virgin forests has not been quantified yet. To test the general assumption, that gaps induce the turnover of tree-generations in the canopy, we formulated the hypothesis that gaps persist or expand, until they are filled mainly by vertical ingrowth of trees from lower layers into the upper canopy.

(H3) By addressing the assumed response of sub-canopy layers to gap formation we hypothesized

that gap formation and the associated increase in light transmission to lower strata promote the development of the understory via two pathways, (i) facilitation of the establishment of new seedlings which increases the regeneration layer cover, and (ii) the release of existing advanced regeneration from competition through the upper canopy, causing a shift in canopy density towards taller sub-canopy layers.

## 2.2 Methods

### 2.2.1 Study site

The study was conducted in the virgin forest reserve Kyjov at 700–820 m a.s.l. in the Vihorlat Mountains in the eastern Slovakian Carpathians (48°53' N, 22°06' E). The forest reserve covers an area of 53 ha on a north- to north-east-facing slope (21% mean inclination). Mean annual temperature ranges from 5.2 to 5.7 °C and mean annual precipitation from 950–1000 mm in the sloping terrain with 120 m altitudinal distance (Kucbel et al., 2012). The bedrock is andesite, on which Dystric Cambisols with good water-holding capacity have developed. The forest community was assigned to the Fagetum dentarietosum glandulosae beech forest association. European beech was the dominant tree species, which formed almost pure stands (99% of the tree individuals) in the reserve with a small share of sycamore (*Acer pseudoplatanus* L.), Norway maple (*Acer platanoides* L.), common ash (*Fraxinus excelsior* L.), and wych elm (*Ulmus glabra* L.). Stand height was approximately 30 m. According to local foresters (personal communication), stand-replacing disturbances have not occurred during the last 60 years in this mountainous forest region, which is made accessible since about 1950. As a consequence, records from the more distant past do not exist.

### 2.2.2 Gap definition

As this study is a gap inventory repeating an earlier investigation of Drößler and von Lüpke (2005) in the year 2003 in the same forest, we largely adopted the method and gap definition used in that study. Canopy gaps were defined as openings in the canopy layer that were caused by the death of canopy trees. The maximum height of the vegetation, which filled the gap, was allowed to reach up to 2/3 of stand height. Thus, the canopy was considered to be closed, if tree height exceeded 20 m, corresponding to a diameter at breast height (DBH)  $\geq 20$  cm in this stand (see Fig. 1 in Drößler and von Lüpke, 2005). In our inventory, we only counted gaps of a minimum size of 20 m<sup>2</sup>, since smaller gaps were thought to hardly affect the radiation regime

of the lower strata. The data of Drößler and von Lüpke (2005), which also include smaller gaps, were adapted to this definition. Therefore, the values calculated for 2003 differ slightly from those reported in their publication.

### 2.2.3 Field methods

Gaps were mapped in 2003 by Drößler and von Lüpke (2005) and in 2013 by us using the same method. Mapping was done in a rectangular grid of transect lines using line-intercept sampling as proposed by Runkle (1992). A 100-m distance to the nearest reserve border was realized when placing the grid, in order to avoid edge effects. Grid spacing was approximately 82.5 m x 82.5 m and the total transect length (sum of transect lines,  $L$ ) was 3217 m, covering an area of about 30 ha. By using a grid with perpendicular orientation of transect lines and a similar sampling distance on both axes, we reduced possible bias in sampling that might result from a possible systematic orientation of noncircular gaps, e.g. due to wind throw (van Wagner, 1968; de Vries, 1986). We are aware of the discussion on probable sampling bias that might be caused by using segmented line transects and having multiple intersections (e.g. Affleck et al., 2005; Gregoire and Valentine, 2003). A gap was mapped if it was crossed by a transect line. The section of a gap ( $l$ ) along the transect line was measured with a measuring tape and subsequently used to calculate gap fraction (see below). If the gap had a more or less elliptical shape, gap size was estimated by placing an ellipse on the crossing lines using the longest and the perpendicular widest diameter as axes (Runkle, 1992). If the shape was more “irregular”, we precisely plumbed several points in the outline of the bordering canopy using a canopy mirror and measured their distance to a fixed point at the approximate gap center. Connecting the points with a line gave a rough projection of the gap in form of a polygon, and gap area was then calculated accordingly.

A gap that was crossed by a transect line in 2003, but not so in 2013, usually would not be mapped again. However, for being able to examine the fate of individual gaps, these gaps were mapped in 2013 as well, but they were not included in the calculation of gap size frequency and area in 2013. The processes that putatively led to the formation, extension or reduction of a gap in the 10-yr period, were also noted in the field. Concerning a reduction in gap size between 2003 and 2013, we distinguished between the horizontal crown expansion of neighboring trees and vertical gap closure by the height growth of former sub-canopy trees. We defined an ‘expanded gap area’ as the area enclosed by the stems bordering the gap and determined the cover percentage of sub-canopy tree layers (understory) of < 20 m in height (corresponding to DBH < 20 cm) in this area. Sub-canopy trees were grouped into three height classes (< 2 m, 2–9 m, 10–19 m, see Table 2.1). In cases of medium-sized trees (ca. 10 m in height) which



could not be assigned to height classes through expert decision, the exact height of the trees was measured with a Vertex IV height meter (Haglöf Sweden AB, Långsele, Sweden).

*Table 2.1:* Categorization of tree layers according to tree height (left) and of gap size classes by gap area (right) as used in the text.

Tree layer	Tree height	Gap size class	Area
(1) canopy layer	$\geq 20$ m	small	$< 100$ m <sup>2</sup>
(2) middle layer	10 – 19 m	medium	100 – 499 m <sup>2</sup>
(3) lower layer	2 – 9 m	large	500 – 999 m <sup>2</sup>
(4) regeneration layer	$< 2$ m	very large	$\geq 1000$ m <sup>2</sup>

#### 2.2.4 Data analysis

The representative proportion of forest area that was occupied by a single gap ( $g_i$ ) was calculated as the quotient of gap length on the transect line ( $l_i$ ) and total transect length ( $L$ ) as

$$g_i = \frac{l_i}{L}$$

The total gap fraction ( $G$ ) in the forest was then calculated by summing over all  $g_i$  values of the  $n$  gaps in the forest:

$$G = \frac{1}{L} \sum_{i=1}^n l_i$$

Gap frequency, i.e. the number of gaps per forest area, cannot simply be derived from gap counts along the transect lines, since large gaps possess a higher probability to be hit than small gaps and thus are likely to be overrepresented, when using the line-intercept method (De Vries, 1986). Instead, we used a correction method proposed by Drößler and von Lüpke (2005) that was already applied to the 2003 survey in Kyjov forest: For every gap  $i$ , a correction factor  $c_i$  was calculated as the quotient of the intercept of gap  $i$  ( $l_i$ ) and the summed interceptions of all gaps on the transects, divided by the quotient of the area of gap  $i$  ( $A_i$ ) and the summed gap area of all

gaps (or multiplied with the reciprocal of these, as in the equation below).  $c_i$  is then obtained as

$$c_i = \frac{l_i \sum_{i=1}^n A_i}{\left(\sum_{i=1}^n l_i\right) A_i}$$

Subsequently, the percental frequency  $p_i$  of each gap was calculated:

$$p_i = \frac{c_i}{\sum_{i=1}^n c_i}$$

The results of the line-intercept sampling are reported by means of summary statistics and by plotting the gap size-frequency and gap size-fraction distributions. Gap frequency and gap fraction were expressed as gaps per ha and gap area in percent of forest area, respectively, to enable a comparison of the 2003 and 2013 data in a quantitative way. Furthermore, the gaps were grouped into four size classes (Table 2.1). In Table 2.A1, gap frequency and gap fraction are also presented in 100 m<sup>2</sup> size classes to allow for a better comparison with other published data sets.

Since the initial study of Dröbler and von Lüpcke (2005) was not planned as a repeated inventory, data documentation was performed following a different standard of accuracy, which is limiting the potential for advanced data analysis. One shortcoming is that the grid of line transects from the 2003 survey cannot be assigned to the 2013 data in full detail, because multiple interceptions of a gap with more than one grid segment had been summed without noting the lengths along the individual segments. To compare the gap fractions of the two sampling years, we segmented the grid at locations, where definitely no canopy gaps existed at the two sampling dates. This resulted in 10 transect sections of different length, for which the gap fraction weighted by transect length could be compared with a paired Wilcoxon signed-rank test.

In a second line of analysis, we investigated the temporal development of gap size. Any gap that changed its size within the period 2003–2013 was treated as a case in the sample. Increases in gap area through gap formation and size expansion are contrasted with reductions in gap area due to gap closure using a paired Wilcoxon signed-rank test.

For all gaps that were crossed by line transects in 2003 and decreased in size thereafter (including those not crossed by line transects anymore in 2013), we reported the relative rate of gap closure in dependence on gap size in 2003. The dominant process of gap closure (horizontal vs. vertical ingrowth, see above) was assessed in the field. We modeled the probability of vertical gap closure through the establishment of the next tree generation in the canopy in dependence of initial gap size, applying a GLM with binomial errors using the “glm()” function (R Core Team, 2016). As the distribution of gap size was highly right-skewed, the data were log-transformed prior to analysis.

The cover percentages of sub-canopy tree layers were compared between gaps of different gap age (i.e., old gaps already existing in 2003 and new gaps formed after 2003). As the data were not normally distributed (Kolmogoroff-Smirnow test), we used the Wilcoxon rank-sum test for comparing the means. We plotted the cover of sub-canopy trees (all layers combined and that of separate layers) against log-transformed gap size to explore relationships among these parameters for old and new gaps separately. The fit and significance of correlations was analyzed by calculating Pearson’s correlation coefficient ( $r$ ). All analyses were done with the R statistical software (R Core Team, 2016) using a confidence level of 0.95 throughout.

## 2.3 Results

### 2.3.1 Canopy gap area, frequency and size distribution

The number of gaps  $> 20 \text{ m}^2$  mapped along the transect lines was 37 in 2003 and 30 in 2013. The gap density calculated under application of the correction factor ( $c_i$ ) tended to be higher in 2013 ( $8.6 \text{ ha}^{-1}$ ) than in 2003 ( $5.2 \text{ ha}^{-1}$ ), but this difference was not significant ( $p = 0.28$ , paired Wilcoxon signed-rank test). Mean gap size decreased from 261 to  $96 \text{ m}^2$  in the 10-year period (difference not significant), while gap fraction declined from 13.6% to 8.2% ( $p = 0.02$ ).

The frequency of gaps decreased exponentially with increasing size in 2003 and 2013 (Fig. 2.1), but the slope of the decay function was steeper in 2013. Gaps  $< 100 \text{ m}^2$  were nearly twice as abundant in 2013 than in 2003; medium-sized gaps ( $100\text{--}499 \text{ m}^2$ ) had a roughly 50% higher frequency in 2013. The ratio reversed for large ( $500\text{--}999 \text{ m}^2$ ) and very large gaps ( $> 1000 \text{ m}^2$ ) that were mapped in 2003 (reaching a maximum of  $4415 \text{ m}^2$ ), but nearly all had disappeared in 2013. The size of the largest gap mapped in 2013 was  $951 \text{ m}^2$ .

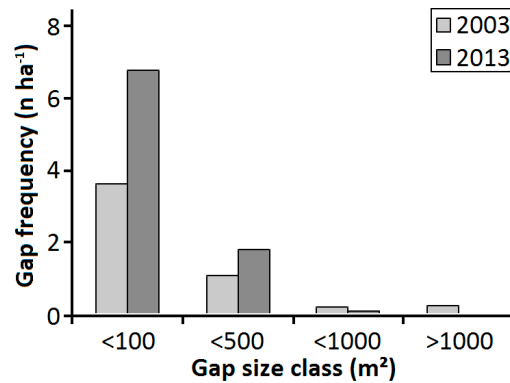


Figure 2.1: Gap size-frequency. Frequency of canopy gaps according to size class (< 100 m<sup>2</sup> = small, 100–500 m<sup>2</sup> = medium, 500–1000 m<sup>2</sup> = large, > 1000 m<sup>2</sup> = very large) in 2003 (light grey) and 2013 (dark grey) derived by line intercept sampling on 3217 m of investigated transect lines in Kyjov forest.

The gap area distribution in size classes (Fig. 2.2) shows that in 2003, about half of the total gap area was contributed by gaps > 1000 m<sup>2</sup>, while small gaps < 100 m<sup>2</sup> accounted for only 13% of the gap area. In 2013, 44% of the gap area referred to the size class < 100 m<sup>2</sup> and nearly all of the remainder to the 100–499 m<sup>2</sup> class, while gaps larger than 500 m<sup>2</sup> contributed only with 2%.

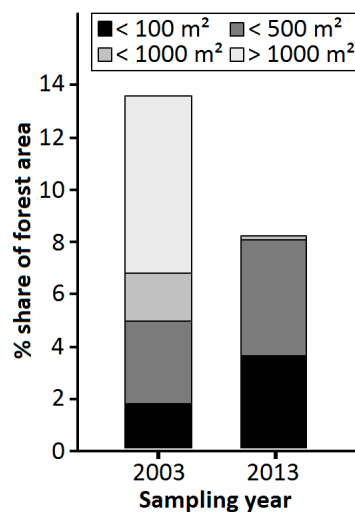


Figure 2.2: Gap size-fraction. Contribution of gaps of four different size classes (< 100 m<sup>2</sup> = small, 100–500 m<sup>2</sup> = medium, 500–1000 m<sup>2</sup> = large, > 1000 m<sup>2</sup> = very large) to total gap area in Kyjov forest in 2003 and 2013 in absolute percent points. Note the overall smaller gap area in 2013.

### 2.3.2 Gap development

From the 37 gaps registered in 2003, 15 were still present on the transect lines in 2013 (two

of them had split into two or three smaller gaps). The gap fraction contributed by gaps formed prior to 2003 (old gaps) had decreased from 13.6% in 2003 to 5.4% in 2013 (referring to the 15 old gaps that persisted). In the 10 years since the first inventory, 12 new gaps have been formed, accounting for 2.8% of the forest area. Thus, in 2013, two thirds of the gap area referred to gaps formed prior to 2003. Gap area created between 2003 and 2013 ranged mainly in the smallest size class (62%) and gap size did not exceed 500 m<sup>2</sup>. In this 10-yr period, significantly larger gap areas were closed along the transect lines than were newly formed ( $p < 0.001$ ; paired Wilcoxon signed-rank test). When taking gap frequency into account, the areas, that were affected by gap closure, were still significantly larger than those areas affected by gap expansion and formation ( $p$ -value = 0.04; Wilcoxon signed-rank test), indicating that the newly formed small and medium-sized gaps did not compensate for the reduction in gap area in the large gaps. This resulted in an overall decrease in gap area and a strong decrease in mean gap size.

The development of gap size was assessed for all 37 gaps that were mapped in 2003 (i.e. including also the gaps that were no longer crossed by transect lines in 2013). The vast majority of gaps decreased in size between 2003 and 2013. In 6 gaps, the death of adjacent trees caused gap expansion, but 4 out these 6 gaps nevertheless decreased in size, since gap closure was more vigorous than expansion. Most of the small gaps (77%) had vanished in 2013, and about 25% of medium-sized and large gaps (up to 892 m<sup>2</sup> in size) were completely closed as well. The velocity of gap closure (percent size reduction in 10 years relative to gap size in 2003) decreased with increasing gap size for small gaps, but it reached a quasi-constant rate at around 80% closure in the 10 years for gaps larger than ca. 200 m<sup>2</sup> (Fig. 2.3). While horizontal gap closure via crown expansion of bordering trees was the most likely closure process in the smallest gaps, the probability of vertical gap closure via upward growth of lower beech strata increased with logarithmized gap size, as demonstrated with a GLM (black continuous line in Fig. 2.3). Gaps larger than 500 m<sup>2</sup> had a probability > 90% that the gap was partly closed by vertical ingrowth within 10 years. Due to their high proportion in gap area in 2003, the closure of large gaps through upward growth of lower strata contributed most to the reduction in total gap area in Kyjov forest between 2003 and 2013.

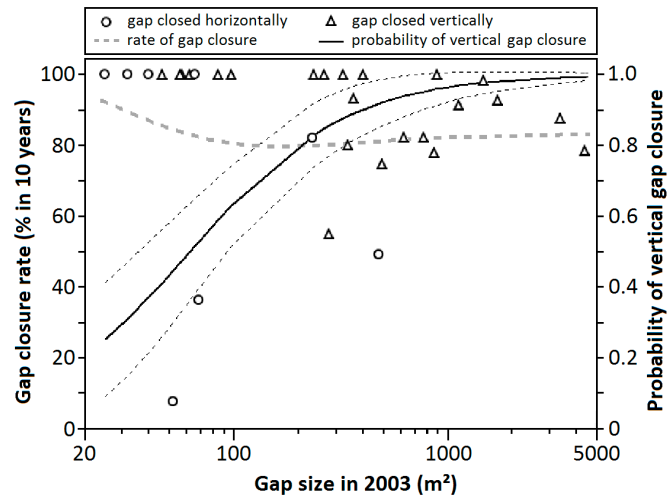


Figure 2.3: Gap size development and closure processes. Relative reduction in gap size during 10 years (2003–2013) in percent of gap size in 2003 for all 31 gaps that showed a gap size reduction in this period. Circles mark gaps in which gap closure mainly occurred via lateral crown expansion of adjacent tall canopy trees (horizontal gap closure) while triangles stand for gaps in which upward growth of understory trees (< 20 m) led to gap closure. The grey dotted line indicates the dependence of relative gap size closure on gap size in 2003 (non-parametric LOESS smoother function), the black continuous line shows the relative probability of gap closure via upward growth of lower tree strata (vertical gap closure) in dependence on gap size (GLM with binomial error ranges).

### 2.3.3 Structure and development of released tree understory

The cover of sub-canopy layers was investigated in 23 old (including old gaps not crossed by the transect lines in 2013) and 12 new gaps (Fig. 2.4). Beech sub-canopy trees of up to 19 m in height were abundant in all gaps studied, with a mean total cover of 61%. Admixed species (*Acer pseudoplatanus*, *Acer platanoides*, *Fraxinus excelsior* and *Ulmus glabra*) had only a negligible share in sub-canopy layers cover (< 1%). While total cover and the cover of the middle layer were found to be quite similar for old and new gaps, there was a greater regeneration layer cover in the new gaps, but a higher cover of the lower layer in the older gaps (Wilcoxon test,  $p < 0.05$ ), indicating a shift in canopy density towards taller sub-canopy layers and thus, a gap-induced height growth trend.

When cover of sub-canopy layers was plotted against the log-transformed gap size for new and old gaps separately, there was a significant positive correlation between log gap size and total cover of sub-canopy layers in old gaps ( $r = 0.43$ ,  $p = 0.04$ ) (the cover of the lower layer, but not of the middle and regeneration layer, also increased with gap size;  $r = 0.50$ ,  $p = 0.02$ ). In new gaps, no significant corresponding trends were found.

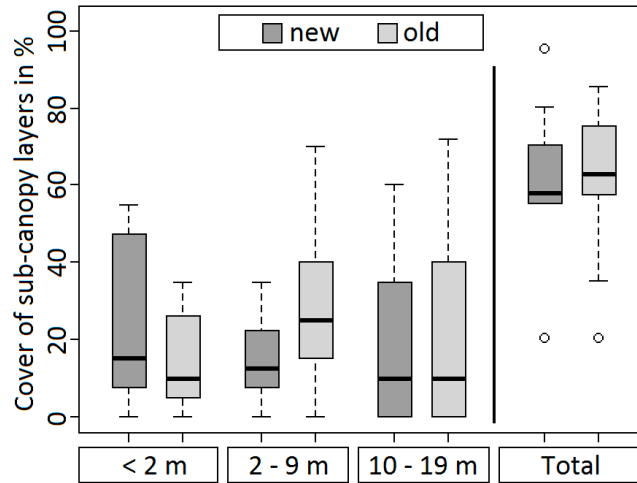


Figure 2.4: Cover of sub-canopy layers. Cover of beech (in %) in old gaps (created before 2003) and young gaps (created in 2003–2013) according to vegetation height (three layers: (< 2 m = regeneration layer, 2–10 m = lower layer, 10–20 m = middle layer) and total cover of sub-canopy layers (all three layers combined). Cover is expressed in percent of the expanded gap area (stem bases as the border). Box-whisker plots with median (thick line), 25- and 75-percentiles (box) and extremes not exceeding the 1.5fold of the interquartile range (whiskers). Dots mark extreme data points beyond 1.5 times the IQR.

## 2.4 Discussion

### 2.4.1 Can gap fractions detected in beech forests be generalized?

For beech-dominated virgin forests in Central and Southeastern Europe, highly variable gap fractions in the range of 3 to 19% have been reported in the literature. Our means for the Kyjov forest (13.6% in 2003, 8.2% in 2013) are well within this range. The quite large variation in gap fraction among the beech forests across Europe can be explained by a complex of site-specific preconditions (e.g. topography, soil type and moisture regime) that influence a forest stand's vulnerability to disturbances (Foster and Boose, 1992; Hanewinkel, 2015; Holeska et al., 2009; Mayer et al., 2005; White and Jentsch, 2001). Furthermore, there are regional differences in the frequency and intensity of disturbance events. The existing gap fraction data still await an overarching analysis on the causes of regional variation in gap size and frequency in a given forest community. Another important cause of the high variability in gap fraction can be seen in the lack of a standard definition of canopy gaps, as differences in the criteria to map gaps strongly affect the results (Dröbler and von Lüpke, 2005; Nagel and Svoboda, 2008; Van der Meer et al., 1994). This complicates any evaluation of differences and similarities in the disturbance regimes of different woodland regions and forest communities.

Using the same sampling method and gap definition as in the earlier inventory of Dröbner and von Lüpke (2005), we found a significant decrease in average gap fraction within only 10 years, evidencing high temporal dynamics of gap fraction in this *Fagus sylvatica* virgin forest. A period of putatively high disturbance intensity prior to 2003 was followed by a period of much lower disturbance intensity in the period 2003–2013. The opposite trend was described by Splechtna and Gratzner (2005) for a spruce-fir-beech virgin forest in Austria, where the gap fraction increased from 3.3 to 13.8% within 34 years (1962–1996). In contrast to these two studies with highly variable gap fraction over time, Kenderes et al. (2009) found gap fraction (9 to 11%) and gap frequency distribution to be very stable over a 33-year period (1971–2004) in a mixed beech virgin forest reserve in Czech Republic. Dröbner and von Lüpke (2005) found in the beech virgin forest Havešová in eastern Slovakia a gap fraction similar to that in nearby Kyjov forest in 2003, but information on temporal change does not exist. These different findings suggest that regional climate and disturbance regimes and also topography and physiography exert a large influence on the temporal dynamics of gap formation. Results from case studies can thus be generalized only with great caution.

Our findings from Slovakia match the conclusion from dendroecological studies in European beech-dominated virgin forests that disturbance intensity can vary in this region over decades and possibly even over centuries (Firm et al., 2009; Nagel et al., 2007, 2014; Samonil et al., 2013; Splechtna et al., 2005; Trotsiuk et al., 2012). Yet, dendroecological studies are rarely suited to conclude on the spatial distribution of canopy gaps and their temporal dynamics (Splechtna et al., 2005). Thus, this approach leaves high uncertainty with respect to the disturbance agents. A high gap fraction could result from a severe windstorm when it affected a large continuous forest patch (as is often concluded), but it could also be due to increased mortality caused by drought stress (Lakatos and Molnár, 2009), pests or air pollution (Diaci et al., 2011), affecting individual trees and resulting in many small gaps. For example, Bottero et al. (2011) reported from a mixed beech-spruce-fir forest the highest gap fraction observed so far (19%) for beech-dominated forests. But in this forest only a small proportion of large gaps did exist and hints on extensive disturbance events were lacking. White and Jentsch (2001) use the terms of ‘discrete disturbance’ and ‘diffuse disturbance’ to describe this difference.

#### **2.4.2 Gap size frequency and gap area**

Exponential decay functions describe the gap size frequency distribution in Kyjov forest in both sampling years well (Fig. 2.1). The disturbance regime of temperate beech forests (and other forest communities) driven by gap dynamics is composed of more or less deterministic



endogenous small-scale disturbances (notably tree senescence) and stochastic exogenous disturbances (e.g. windthrow), with the probability of occurrence of the latter decreasing with the increase of affected area. Drößler et al. (2016) showed that this pattern has imprinted on the structure of the Kyjov virgin beech forest, as the frequency of cohorts, i.e. neighboring trees of similar dimension, decreases exponentially with increasing cohort size. The exponential gap size frequency distribution has changed over the 10 observation years. The shift was very subtle when frequency was expressed in relative terms, but it became obvious in the absolute number of gaps of different sizes. The absolute frequency of small gaps has nearly doubled and that of medium-sized gaps increased as well within the 10-year period, while large and very large gaps mostly vanished. However, due to a high overall variability, these changes in the frequency distribution did not lead to a significantly altered total gap number, but to a change in the cumulative gap area between the two sampling years. The distinct trade-off between gap size and gap frequency in this forest demands for a separate investigation of the impact of gap size and gap numbers on forest dynamics. Despite their low numbers, Nagel and Svoboda (2008) suggested for larger gaps a possibly greater overall influence on forest dynamics than for the abundant small gaps. The shift in dominance from more frequent large gaps in 2003 (63% of total gap area), caused by extensive disturbances, to small and medium-sized gaps in 2013 (44 and 54%, respectively), with the formation of new gaps mainly limited to the smallest size class, suggests that the disturbance intensity must have been lower in 2003–2013 than in the years prior to 2003. We assume that one or more severe windstorms affected the stand before 2003, creating several larger gaps. They were accompanied by numerous endogenous disturbance events ('background mortality'), i.e. the death of single senescent trees or individuals weakened by pathogen attack, a process that continued in the following 10-year period. This is at least partly contradicting our first hypothesis, in which we postulated a relatively low temporal variation in disturbance intensity and thus a quasi steady-state in the formation and disappearance of canopy gaps in this virgin forest.

Even though Central Europe is less exposed than eastern North America and eastern Asia to migrating cyclones from the subtropics with high destruction potential (Peters, 1997), there are reports of large-scale disturbance events ( $> 1500 \text{ m}^2$ ) affecting a considerable proportion of some beech-dominated old-growth forests in Central and southeastern Europe (Drößler and von Lüpke, 2005; Nagel and Svoboda, 2008; Kucbel et al., 2010). Other studies found evidence of large-scale disturbances, but they were rare and related only to a small proportion of the total gap area (Kenderes et al., 2009; Petritan et al., 2013), or the authors only mentioned their occurrence without quantifying their role (e.g., Nagel and Diaci, 2006). This suggests that the intensity of disturbances, which likely characterized the period prior to 2003 in Kyjov, is not exceptionally

high in the disturbance history of Central European beech forests. In Havešová, another virgin beech forest reserve in the Slovakian Carpathians close to our study site, a storm threw the vast majority of trees in an 8.3 ha patch in May 2014 (personal observation), confirming that not only spruce or other shallow-rooted trees, but also beech-dominated virgin forests are affected by large-scale, stand-replacing disturbances in this region. The occurrence of stand-replacing disturbances in the Carpathian region in the past has been mentioned by other authors as well (Hobi et al., 2015a; Kucbel et al., 2010, 2012), suggesting that the largest gaps found in Kyjov in 2003 (up to 4500 m<sup>2</sup>) must in fact be considered as relatively small, when placed in a broader spatial context. On the other hand, several studies in virgin beech forests found no large-scale disturbances at all, or only a small proportion of large gaps in total gap area (Tabaku and Meyer, 1999; Zeibig et al., 2005; Bottero et al., 2011). These findings would match our observations from the 2013 inventory. Thus, the gap pattern recorded by us in Kyjov in the two different sampling years is representative for a fairly broad range of disturbance intensities reported in the literature for temperate forests.

### **2.4.3 Gap closure and the legacy of past disturbance**

As the gap formation rate (2.8 percentage points of stand area in 10 years) was significantly lower than the rate of gap closure (8.2 percentage points), total gap area decreased from 2003 to 2013. In 2013, only 40% of the total gap area recorded in 2003 was still present. Nevertheless, gaps older than 10 years still had a share of about 62% in the number and 65% in the total area of gaps that were mapped in 2013. These gaps represent a legacy of former disturbance events and are no measure of the disturbance intensity in the period 2003–2013. Nonetheless, their fate is of great importance with respect to the forest's resilience to disturbance.

In accordance with Runkle (1992), Dröbner and von Lüpke (2005) interpreted the occurrence of gap makers in various stages of decay as a sign of secondary gap expansion or the coalescence of several gaps in their inventory of 2003, in a similar manner as was also suggested by other authors (Nagel and Svoboda, 2008; Kucbel et al., 2010). In 2013, however, we found that old gaps rarely showed signs of expansion, but most of them rather had experienced a strong decrease in size. In these gaps, lateral closure by crown expansion of neighboring trees was the dominant process when they were small, whereas vertical ingrowth from lower layers became increasingly important with increasing gap size. Beech is known for its capacity to rapidly expand its crown, when light is available (Roloff, 1986; Peters, 1997). Our second hypothesis (H2) is thus confirmed for large gaps, even though these gaps were not stable due to vivid lateral ingrowth of branches. For small and medium-sized gaps, however, H2 has to be rejected, as

in both categories lateral gap closure occurred at rapid speed, and certain gaps disappeared in the 10-year period entirely. Our findings are in line with conclusions of Kucbel et al. (2010) suggesting a gap's importance for regeneration development is increasing with its size. The different processes taking place in large and small gaps are explicable by the effect of gap size on gap closure rates (through the growth of lateral branches) and the promotion of sub-canopy trees. Both, the time needed for gap closure by adjacent trees and the light availability in the gap, which promotes juvenile growth, are proportional to effective gap diameter (e.g. Canham et al., 1990, Čater et al., 2014). How rapid beech can close gaps is demonstrated by the observations of Madsen and Hahn (2008), who found medium-sized gaps (180–470 m<sup>2</sup>) cut into a 110-year old beech stand to be nearly closed after 3 to 4 years.

The high share of old gaps in the total gap area mapped in 2013 demonstrates that past disturbances have a strong impact on observations made years later. To address this problem, Runkle (1992) proposed to estimate the gap age through the decay stage of gap makers, the age of regeneration or dendroecological data. Employing these methods, some gaps in European beech-dominated forests were estimated at ages of 50 years and more (Drössler and von Lüpke, 2005; Kucbel et al., 2010) with maximal ages of 140 years (Bottero et al., 2011). Contrasting these high estimates with the rapid gap closure observed in Kyjov raises some doubt on these numbers, at least for our study area. Yet, processes like gap closure and expansion, the re-opening of closed gaps and the coalescence of neighboring gaps are hard to reconstruct in the retrospective. Shade-tolerant tree species like *Fagus sylvatica* may tolerate low-light periods under a closed canopy for a relatively long time; thus no direct inference from sapling or tree age on gap age is possible. In addition, the duration of deadwood decay is not only species-specific, but also varies strongly with the macroclimate (Přivětivý et al., 2016) and the microclimatic conditions (Harmon et al., 1986), which also weakens their indicative value for gap age. Further, we encountered several beech trees with advanced decay along the stem, while still possessing an intact crown. The decay stage of many of the gap makers that died in the 2003–2013 period, would wrongly have suggested that they had died several decades earlier, which was not the case.

#### **2.4.4 Gap effects on understory structure**

In beech-dominated virgin forests, the understory from the sapling to the pole-sized stage has been characterized by a clumped spatial distribution in close association with the presence of canopy gaps (Janík et al., 2016; Nagel et al., 2006). In the Kyjov forest, beech trees in sub-canopy layers were recorded on the expanded gap area of all gaps and occurred with similar mean total cover (about 60%) in older (> 10 years) and new gaps of various sizes. In many

gaps, more than one sub-canopy layer was present in the 1–19 m height range, indicating the coexistence of several beech cohorts in vertical layering that must have established in several periods with favorable light conditions. However, a characteristic feature is a large variation in understory cover and structure in the different gaps (Fig. 2.4). Canopy gaps in other beech-dominated virgin forests have been reported to release multiple sub-canopy layers as well (Bottero et al., 2011; Diaci et al., 2005; Diaci et al., 2012; Garbarino et al., 2012; Nagel et al., 2010; Rozenberger et al., 2007), whereas for forest reserves with past management history, gaps are often described as having a single regeneration cohort of more or less the same height (e.g. Diaci et al., 2005; Emborg, 1998; Kenderes et al., 2008). Thus, the sub-canopy structure seems to differ between virgin forests and stands with management history, even if the human impact relates to the distant past. Therefore, observations on gap-induced understory dynamics and dependent ecosystem processes (such as nutrient leaching and nitrogen mineralization; Bartsch, 2000) are applicable to other forest ecosystems only with great care.

The impressive rate of gap closure is partly a consequence of the rapid growth of pole-sized young beech trees, which can fill a gap within a few years. Indeed, we found cohorts of pole-sized young beeches (middle layer) in 60% of the gaps formed between 2003 and 2013 that must have established long before gap formation, offering an explanation for the rapid gap closure observed in larger old gaps for the period 2003–2013. On the long run, the released understory as a whole (from saplings to pole-sized trees) is of crucial importance, as it determines the potential for vertical gap closure. This is especially true for larger gaps, where the potential for lateral gap closure is limited, as is the arrival of new seedlings.

In a beech-fir virgin forest in Bosnia-Herzegovina, Nagel et al. (2010) found the regeneration structure in gaps not to differ from that in systematically placed research plots, which covered a wide range of canopy conditions, due to a high presence of advance regeneration across the whole forest. The authors suggested that gaps do primarily alter the development of advanced regeneration, rather than promoting the establishment of new offspring. Our results are in line with this suggestion, as total cover of sub-canopy layers was similar in old and newly formed gaps in Kyjov; yet the lower sub-canopy layers (< 2 and 2–9 m in height) differed in their cover in these two distinct gap types. Janík et al. (2016) found beech saplings under closed canopy conditions to grow up to a stem diameter of 4 cm, and then requiring canopy disturbance to advance to larger size classes. Our data suggest that gap formation had a large effect on sapling height growth in their early development stages, as expressed by the shift from small-sized regeneration (< 2 m) in the new gaps (recorded in 2013) to the dominance of larger saplings (2–9 m) in the older gaps (established before 2003). The positive relation between gap size and the cover of lower tree

layer (2–9 m) in older gaps further documents that the growth conditions improve with increasing gap size also for shade-tolerant species such as beech. This corresponds well with the increase in light intensity with increasing gap size (Canham et al., 1990; Coates and Burton, 1997; Vilhar et al., 2015) and it matches the observation that shifts in the cover of sub-canopy layers, as well as vertical gap filling, mainly happened in medium to large gaps ( $> 100 \text{ m}^2$ ).

Our results only partly support our hypothesis H3, as the comparison of old and new gaps evidences a positive gap effect on the vertical growth of the lower sub-canopy layers ( $< 2$  and 2–9 m). However, we obtained no clear signs for a promotion of seedling establishment through gap creation, since total understory cover was similar in old and new gaps. In a Slovenian virgin beech forest, Diaci et al. (2012) recorded in the first years after gap formation increasing sapling numbers ( $\leq 20$  cm in height), indicating an important role of gap formation for the establishment of *F. sylvatica* seedlings. The sapling density decreased in the subsequent years and the population of young beeches shifted to a larger size class, in a similar manner as was observed in Kyjov. Thus, for studying the effect of gap formation on the establishment of beech regeneration, it seems necessary to count young tree individuals in the period immediately after gap formation.

Our results also highlight a methodological issue relevant for forest dynamics research, which is related to the definition of a gap. Part of the gap area mapped by us would not have been classified as a gap by approaches, which consider the canopy to be closed when tree height is  $1/3$  (e.g. Hobi et al., 2015b) or half (e.g. Nagel and Svoboda, 2008) the stand height. An even smaller gap fraction would be seen by the remote sensing approaches of Garbarino et al. (2012) and Hobi et al. (2015a) that rely on detecting more or less bare ground conditions. All the mentioned approaches may miss part of the gaps in the upper canopy, which play an important role for the turnover of tree individuals and canopy strata in virgin forests. A key issue in the search for a more generally accepted definition of canopy gaps is the question, from what height, relative to stand height, a tree should be assigned to the (main) canopy. This threshold is separating the dominant upper canopy layer from all subordinate strata including the understory layers. As there are species-specific differences in growth characteristics, it is necessary to develop specific definitions for different forest types.

## 2.5 Conclusions

The profound change in gap patterns observed between 2003 and 2013 in the Kyjov virgin beech forest highlights the high value of repeated stand structural inventories for better comprehending the disturbance regime and dynamics of natural forests. Our data indicate a marked change in disturbance intensity in this short period of 10 years only. Prior to 2003, exogenous disturbances, most likely one or more windstorms, must have affected this montane beech forest by throwing several to many neighboring canopy trees, part of them probably vital trees, forming large gaps. In the following decade, the canopy largely recovered from these disturbances due to rapid lateral crown expansion and vertical ingrowth of beeches from sub-canopy layers; the latter process of vertical canopy filling increased in importance with increasing gap size. In addition to these large-scale exogenous disturbances, a considerable number of small-scale endogenous disturbances ('background mortality') was observed, caused by the death of single weakened or senescent trees that often damage a few neighbors when crushing down. These events seem to occur more or less constantly in virgin beech forests, facilitating the establishment and persistence of populations of advanced regeneration and sub-canopy trees, which were nearly omnipresent under open and closed canopy conditions in the Kyjov forest. This bank of seedlings, saplings and pole sized trees guarantees a high resilience of the ecosystem to larger exogenous disturbances. In turn, large disturbances strongly facilitate the growth of established sub-canopy layers and thus promote their later access to the upper canopy. Even if strong disturbances strike the studied virgin beech forest ecosystem has a high potential to recover without change in the tree species composition.

As a case study, our results represent one stepping stone in the search for a more general understanding of disturbance dynamics in natural beech forests. A longer time span of canopy structural data and the inclusion of dendrochronological information are needed for characterizing the disturbance regime in the study area. Repeated inventories from other pure beech and beech-dominated virgin forests would help to assess regional and site-specific differences in forest dynamics.

**Acknowledgements:** The project was funded by the Stemmler Foundation and the support is gratefully acknowledged. We also like to thank the Ministry of Defense of the Slovak Republic for the permits to conduct the study. For statistical advices we like to thank Roman Link and Lutz Fehrmann.

## 2.6 Appendix

*Table 2.A1:* The frequency and cumulative fraction (share in forest area) of gaps according to gap size classes of 100 m<sup>2</sup> in the 2003 and 2013 inventories.

Gap size class (m <sup>2</sup> )	2003	2013	2003	2013
	n ha <sup>-1</sup>	n ha <sup>-1</sup>	% of area	% of area
20-99	3.61	6.77	1.79	3.64
100-199	0.25	0.73	0.38	0.97
200-299	0.42	0.22	1.08	0.50
300-399	0.19	0.80	0.65	2.72
400-499	0.23	0.07	1.08	0.30
500-599				
600-699	0.05		0.33	
700-799	0.01		0.03	
800-899	0.17		1.45	
900-999		0.01		0.13
1000-1099				
1100-1199	0.03		0.37	
1200-1299				
1300-1399				
1400-1499	0.05		0.69	
1500-1599				
1600-1699				
1700-1799	0.07		1.19	
3300-3399	0.09		3.11	
4400-4499	0.03		1.40	
Sum	5.20	8.60	13.56	8.24

## 2.7 References

- Affleck, D.L., Gregoire, T.G., Valentine, H.T., 2005. Design unbiased estimation in line intersect sampling using segmented transects. *Environmental and Ecological Statistics*, 12(2), 139-154.
- Bartsch, N., 2000. Element release in beech (*Fagus sylvatica* L.) forest gaps. *Water, Air and Soil Pollution*, 122(1-2), 3-16.
- Bottero, A., Garbarino, M., Dukic, V., Govedar, Z., Lingua, E., Nagel, T.A., Motta, R., 2011. Gap-phase dynamics in the old-growth forest of Lom, Bosnia and Herzegovina. *Silva Fennica*, 45(5), 875-887.
- Canham, C.D., Denslow, J.S., Platt, W.J., Runkle, J.R., Spies, T.A., White, P.S., 1990. Light regimes beneath closed canopies and tree-fall gaps in temperate and tropical forests. *Canadian Journal of Forest Research*, 20, 620-631.
- Čater, M., Diaci, J., Roženbergar, D., 2014. Gap size and position influence variable response of *Fagus sylvatica* L. and *Abies alba* Mill. *Forest Ecology and Management*, 325, 128-135.
- Coates, K.D., Burton, P.J., 1997. A gap-based approach for development of silvicultural systems to address ecosystem management objectives. *Forest Ecology and Management*, 99(3), 337-354.
- Diaci, J., Rozenbergar, D., Anic, I., Mikac, S., Saniga, M., Kucbel, S., Visnjic, C., Ballian, D., 2011. Structural dynamics and synchronous silver fir decline in mixed old-growth mountain forests in Eastern and Southeastern Europe. *Forestry*, 84(5), 479-491.
- Diaci, J., Adamic, T., Rozman, A., 2012. Gap recruitment and partitioning in an old-growth beech forest of the Dinaric Mountains: Influences of light regime, herb competition and browsing. *Forest Ecology and Management*, 285, 20-28.
- Dröbfler, L., von Lüpke, B., 2005. Canopy gaps in two virgin beech forest reserves in Slovakia. *Journal of Forest Science*, 51, 446-457.
- Drössler, L., Feldmann, E., Glatthorn, J., Annighöfer, P., Kucbel, S., Tabaku, V., 2016. What Happens after the Gap?—Size Distributions of Patches with Homogeneously Sized Trees in Natural and Managed Beech Forests in Europe. *Open Journal of Forestry*, 6(03), 177.
- Emborg, J., 1998. Understorey light conditions and regeneration with respect to the structural dynamics of a near-natural temperate deciduous forest in Denmark. *Forest Ecology and Management*, 106(2), 83-95.
- Firm, D., Nagel, T.A., Diaci, J., 2009. Disturbance history and dynamics of an old-growth mixed species mountain forest in the Slovenian Alps. *Forest Ecology and Management*, 257(9), 1893-1901.
- Foster, D.R., Boose, E.R., 1992. Patterns of forest damage resulting from catastrophic wind in central New England, USA. *Journal of Ecology*, 80, 79-98.
- Frelich, L.E., 2002. Forest dynamics and disturbance regimes: studies from temperate evergreen-deciduous forests. Cambridge University Press.
- Garbarino, M., Mondino, E.B., Lingua, E., Nagel, T.A., Dukić, V., Govedar, Z., Motta, R., 2012. Gap disturbances and regeneration patterns in a Bosnian old-growth forest: a multispectral remote sensing and ground-based approach. *Annals of Forest Science*, 69(5), 617-625.
- Gregoire, T.G., Valentine, H.T., 2003. Line intersect sampling: Ell-shaped transects and multiple intersections. *Environmental and Ecological Statistics*, 10(2), 263-279.
- Hanewinkel, M., Albrecht, A., Schmidt, M., 2015. Können Windwurfschäden vermindert werden? Eine Analyse von Einflussgrößen. *Schweizerische Zeitschrift für Forstwesen*, 166(3), 118-128.
- Harmon, M.E., Franklin, J.F., Swanson, F.J., Sollins, P., Gregory, S.V., Lattin, J.D., Anderson, N.H., Cline, S.P., Aumen, N.G., Sedell, J.R., Lienkaemper, G.W., Cromack Jr., K., Cummins, K.W., 1986. Ecology of coarse woody debris in temperate ecosystems. *Advances in Ecological Research*, 15, 133-302.



- Hobi, M.L., Ginzler, C., Commarmot, B., Bugmann, H., 2015a. Gap pattern of the largest primeval beech forest of Europe revealed by remote sensing. *Ecosphere*, 6(5), 1-15.
- Hobi, M.L., Commarmot, B., Bugmann, H., 2015b. Pattern and process in the largest primeval beech forest of Europe (Ukrainian Carpathians). *Journal of Vegetation Science*, 26(2), 323-336.
- Holeksa, J., Saniga, M., Szwagrzyk, J., Czerniak, M., Staszyńska, K., Kapusta, P., 2009. A giant tree stand in the West Carpathians - An exception or a relic of formerly widespread mountain European forests? *Forest Ecology and Management*, 257(7), 1577-1585.
- Hunter Jr., M.L., 1990. Wildlife, Forests, and Forestry. Principles of Managing Forests for Biological Diversity. Prentice Hall.
- Janík, D., Král, K., Adam, D., Hort, L., Samonil, P., Unar, P., Vrska, T., McMahon, S., 2016. Tree spatial patterns of *Fagus sylvatica* expansion over 37 years. *Forest Ecology and Management*, 375, 134-145.
- Kenderes, K., Mihók, B., Standovár, T., 2008. Thirty years of gap dynamics in a Central European beech forest reserve. *Forestry*, 81(1), 111-123.
- Kenderes, K., Král, K., Vrska, T., Standovár, T., 2009. Natural gap dynamics in a Central European mixed beech-spruce-fir old-growth forest. *Ecoscience*, 16 (1), 39-47.
- Korpel, Š., 1995. Die Urwälder der Westkarpaten. Gustav Fischer Verlag, Stuttgart.
- Kucbel, S., Jaloviar, P., Saniga, M., Vencurik, J., Klimaš, V., 2010. Canopy gaps in an old-growth fir-beech forest remnant of Western Carpathians. *European Journal of Forest Research*, 129(3), 249-259.
- Kucbel, S., Saniga, M., Jaloviar, P., Vencurik, J., 2012. Stand structure and temporal variability in old-growth beech-dominated forests of the northwestern Carpathians: A 40-years perspective. *Forest Ecology and Management*, 264, 125-133.
- Lachat, T., Chumak, M., Chumak, V., Jakoby, O., Müller, J., Tanadini, M., Wermelinger, B., 2016. Influence of canopy gaps on saproxylic beetles in primeval beech forests: a case study from the Uholka-Shyrokyi Luh forest, Ukraine. *Insect Conservation and Diversity*, 9(6), 559-573.
- Lakatos, F., Molnár, M., 2009. Mass mortality of beech (*Fagus sylvatica* L.) in South-West Hungary. *Acta Silvatica et Lignaria Hungarica*, 5, 75-82.
- Leuschner, C., Ellenberg, H., 2017. Ecology of Central European Forests. Vegetation Ecology of Central Europe, Vol. I. Springer Nature, Cham.
- Madsen, P., Hahn, K., 2008. Natural regeneration in a beech-dominated forest managed by close-to-nature principles - a gap cutting based experiment. *Canadian Journal of Forest Research*, 38(7), 1716-1729.
- Mayer, P., Brang, P., Dobbertin, M., Hallenbarter, D., Renaud, J. P., Walthert, L., Zimmermann, S., 2005. Forest storm damage is more frequent on acidic soils. *Annals of Forest Science*, 62(4), 303-311.
- Muscolo, A., Bagnato, S., Sidari, M., Mercurio, R., 2014. A review of the roles of forest canopy gaps. *Journal of Forestry Research*, 25(4), 725-736.
- Nagel, T.A., Diaci, J., 2006. Intermediate wind disturbance in an old-growth beech-fir forest in southeastern Slovenia. *Canadian Journal of Forest Research*, 36(3), 629-638.
- Nagel, T.A., Svoboda, M., Diaci, J., 2006. Regeneration patterns after intermediate wind disturbance in an old-growth *Fagus-Abies* forest in southeastern Slovenia. *Forest Ecology and Management*, 226(1), 268-278.
- Nagel, T.A., Levanic, T., Diaci, J., 2007. A dendroecological reconstruction of disturbance in an old-growth *Fagus-Abies* forest in Slovenia. *Annals of Forest Science*, 64(8), 891-897.
- Nagel, T.A., Svoboda, M., 2008. Gap disturbance regime in an old-growth *Fagus-Abies* forest in the Dinaric Mountains, Bosnia-Herzegovina. *Canadian Journal of Forest Research*, 38(11), 2728-2737.

- Nagel, T.A., Svoboda, M., Rugani, T., Diaci, J., 2010. Gap regeneration and replacement patterns in an old-growth Fagus–Abies forest of Bosnia–Herzegovina. *Plant Ecology*, 208(2), 307-318.
- Nagel, T.A., Svoboda, M., Kobal, M., 2014. Disturbance, life history traits, and dynamics in an old-growth forest landscape of southeastern Europe. *Ecological Applications*, 24(4), 663-679.
- Peters, R., 1997. Beech Forests. Geobotany, 24. Springer, Dordrecht. 170 pp.
- Petritan, A.M., Nuske, R.S., Petritan, I.C., Tudose, N.C., 2013. Gap disturbance patterns in an old-growth sessile oak (*Quercus petraea* L.)–European beech (*Fagus sylvatica* L.) forest remnant in the Carpathian Mountains, Romania. *Forest Ecology and Management*, 308, 67-75.
- Přívětivý, T., Janík, D., Unar, P., Adam, D., Král, K., Vrška, T., 2016. How do environmental conditions affect the deadwood decomposition of European beech (*Fagus sylvatica* L.)? *Forest Ecology and Management*, 381, 177-187.
- R Core Team, 2016. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.
- Roloff, A., 1986. Morphology of crown development in European beech with regard to possibly new modifications. *Ber Forschungszent Waldokosysteme Goettingen* 18, 177 pp.
- Rozenbergar, D., Mikac, S., Anić, I., Diaci, J., 2007. Gap regeneration patterns in relationship to light heterogeneity in two old-growth beech–fir forest reserves in South East Europe. *Forestry*, 80(4), 431-443.
- Runkle, J.R., 1992. *Guidelines and sample protocol for sampling forest gaps* (Vol. 283). Portland: US Department of Agriculture, Forest Service, Pacific Northwest Research Station.
- Runkle, J.R., 2013. Thirty-two years of change in an Ohio beech-maple forest. *Ecology*, 95(5), 1165-1175.
- Šamonil, P., Doleželová, P., Vašíčková, I., Adam, D., Valtera, M., Král, K., Janík, D., Šebková, B., 2013. Individual-based approach to the detection of disturbance history through spatial scales in a natural beech-dominated forest. *Journal of Vegetation Science*, 24(6), 1167-1184.
- Schelhaas, M.J., Nabuurs, G.J., Schuck, A., 2003. Natural disturbances in the European forests in the 19th and 20th centuries. *Global Change Biology*, 9(11), 1620-1633.
- Schütz, J.P., Saniga, M., Diaci, J., Vrška, T., 2016. Comparing close-to-nature silviculture with processes in pristine forests: lessons from Central Europe. *Annals of Forest Science*, 73(4), 911-921.
- Seymour, R.S., White, A.S., 2002. Natural disturbance regimes in northeastern North America - evaluating silvicultural systems using natural scales and frequencies. *Forest Ecology and Management*, 155(1), 357-367.
- Splechtna, B.E., Gratzner, G., Black, B.A., 2005. Disturbance history of a European old-growth mixed-species forest - A spatial dendro-ecological analysis. *Journal of Vegetation Science*, 16(5), 511-522.
- Splechtna, B. E., Gratzner, G., 2005. Natural disturbances in Central European forests: approaches and preliminary results from Rothwald, Austria. *Forest, Snow and Landscape Research*, 79, 57-67.
- Tabaku, V., 2000. Struktur von Buchen-Urwäldern in Albanien im Vergleich mit deutschen Buchen-Naturwaldreservaten und -Wirtschaftswäldern. Cuvillier Verlag, Göttingen, 206 pp.
- Tabaku, V., Meyer, P., 1999. Lückenmuster albanischer und mitteleuropäischer Buchenwälder unterschiedlicher Nutzungsintensität. *Forstarchiv* 70, 87–97.
- Trotsiuk, V., Hobi, M.L., Commarmot, B., 2012. Age structure and disturbance dynamics of the relic virgin beech forest Uholka (Ukrainian Carpathians). *Forest Ecology and Management*, 265, 181-190.
- de Vries, P. G., 1986. *Sampling Theory for Forest Inventory* (pp. 242-279). Springer, Berlin, Heidelberg.
- Van Wagner, C.E., 1968. The line intersect method in forest fuel sampling. *Forest Science*, 14(1), 20-26.

- 
- Van der Meer, P.J., Bongers, F., Chatrou, L., Riéra, B., 1994. Defining canopy gaps in a tropical rain forest: effects on gap size and turnover time. *Acta Ecologica*, 15(6), 701-714.
- Vilhar, U., Roženbergar, D., Simončič, P., Diaci, J., 2015. Variation in irradiance, soil features and regeneration patterns in experimental forest canopy gaps. *Annals of Forest Science*, 72(2), 253-266.
- White, P.S., Jentsch, A., 2001. The search for generality in studies of disturbance and ecosystem dynamics. In *Progress in Botany* (pp. 399-450). Springer, Berlin, Heidelberg.
- Whitmore, T.C., 1989. Canopy gaps and the two major groups of forest trees. *Ecology*, 70(3), 536-538.
- Zeibig, A., Diaci, J., Wagner, S., 2005. Gap disturbance patterns of a *Fagus sylvatica* virgin forest remnant in the mountain vegetation belt of Slovenia. *Forest Snow and Landscape Research*, 79(1/2), 69-80.



# 3<sup>rd</sup>

## CHAPTER

### REGENERATION DYNAMICS FOLLOWING THE FORMATION OF UNDERSTORY GAPS IN A SLOVAKIAN BEECH VIRGIN FOREST

Eike Feldmann, Jonas Glatthorn, Christian Ammer, Christoph Leuschner

Prepared manuscript

#### Abstract

The frequency and size of canopy gaps largely determine light transmission to lower canopy strata, controlling structuring processes in the understory and the turnover of tree individuals in the canopy. However, quantitative data from temperate virgin forests on the structure of regeneration in gaps in relation to light availability and its natural dynamics over time are scarce.

We studied the structure and height growth of tree regeneration (height  $\geq 0.5$  m) by means of sapling density, shoot length growth and cumulative biomass in 17 understory gaps (29 to 931 m<sup>2</sup> in size) in a beech (*Fagus sylvatica* L.) virgin forest in the Slovakian Carpathians, and compared the gaps with the regeneration under closed-canopy conditions. Spatial differences in regeneration structure and growth rate within a gap and in the gap periphery were analyzed in their dependence on the relative intensities of direct-beam and diffuse radiation (high vs. low), which are largely determined by gap geometry. We tested the hypotheses that (i) the density and cumulative biomass of saplings are higher in gaps than in closed-canopy patches, (ii) the position in a gap influences the density and height growth of the saplings, and (iii) the height growth of saplings increases with gap size.

Sapling density and biomass were significantly higher in understory gaps than under the closed canopy. General linear models revealed that sapling density was positively affected by high

direct radiation but low diffuse radiation intensities, resulting in pronounced spatial differences in sapling density across a gap. In contrast, sapling shoot length growth was positively affected by higher levels of diffuse radiation and also depended on sapling size, while direct radiation intensity was not influential. In conclusion, beech regeneration in small gaps ( $< 100 \text{ m}^2$ ) is in this virgin forest largely confined to gap positions receiving high quantities of both, direct and diffuse radiation. Within a few years, the saplings will face light limitation due to lateral canopy closure, resulting in a highly heterogeneous understory structure in former small gaps. In larger gaps ( $\geq 100 \text{ m}^2$ ), regeneration typically develops in all gap positions, and existing advanced regeneration may be capable even at low plant densities to rapidly fill the gap center, often forming a rapidly growing cohort-like regeneration layer. Thus, gaps of different sizes imprint on the resulting canopy structure in different ways, enhancing spatial heterogeneity.

**Keywords:** direct sunlight, diffuse light, *Fagus sylvatica*, gap age, gap size, sapling biomass, sapling density, sapling growth rate

### 3.1 Introduction

Understanding the natural dynamics of forests and the resulting structural change is a major focus of forest ecological research, as forest structure has a large influence on the energy and matter fluxes in the stand. Knowledge about forest dynamics processes may also serve as guidance for the development of close-to-nature forest management strategies and forest conservation and restoration efforts.

Tree regeneration is a fundamental process which drives forest dynamics. Except for very dry and nutrient-poor soils, seedling establishment and sapling growth in the forest interior are largely controlled by light availability (Ricard et al., 2003). The structural attribute which largely controls radiation transmission to the understory is the degree of canopy closure in the upper tree layer. Due to species differences in light requirement for regeneration and in the canopy structure of adult trees, the relation between canopy closure, light transmission and regeneration success is highly variable among forest types and also depends on the disturbance regime. How canopy structural change affects the regeneration layer, is not well understood for most forest communities. Moreover, this relationship likely differs considerably among tree species, and a more general picture for temperate forests has not yet emerged.

Large parts of Central Europe would be covered by European beech (*Fagus sylvatica* L.), if man had not destroyed the natural forest cover in the last millennia. This species often forms monospecific stands, or it is co-dominant together with a few other tree species (Leuschner and

Ellenberg, 2017). Beech forest ecosystems are therefore of special interest to forest ecology, conservation and management in Europe.

Even though a variety of factors influencing the regeneration process of beech have been identified (Wagner et al., 2010), a strong dependence on light availability has been documented for both, seedling establishment and sapling growth (Burschel and Schmalz, 1965; Szwagrzyk et al., 2001; Collet and Chenost, 2006; Petritan et al., 2007, 2009). As a highly shade-tolerant tree species, seedlings, saplings and understory trees of beech can endure long periods of low light and suppression by the upper canopy, during which ontogenetic development is greatly retarded (Leuschner and Ellenberg, 2017). As a consequence, the presence of beech regeneration may be uncoupled from the actual light regime, rather reflecting the growing conditions of the past. This may be the reason why beech saplings have been found to be nearly omnipresent in beech virgin forests, even though stem density and canopy cover vary largely in space (Leibundgut, 1993; Korpel, 1995; Drößler and von Lüpke, 2006; Nagel et al., 2010; Motta et al., 2011; Petritan et al., 2012; Hobi et al., 2015a). When the suppressed saplings (which often are termed ‘advanced regeneration’) are released by disturbance from the competitive pressure of the overstory and light levels increase, they benefit from a developed root system and advanced height growth in the understory, overtopping lower seedling layers, leading to competitive superiority over newly recruited seedlings.

The disturbance regime of natural beech forests in Central and southern Europe is characterized by local biotic and abiotic events, which typically create only small canopy gaps (Peters, 1997), while medium and large-scale disturbances are rare and most often related to wind throw (Peters, 1997; Schelhaas et al., 2003). Quite a number of detailed studies on gap frequency and gap formation in beech-dominated virgin forests have been published since the late 1990s (Tabaku and Meyer, 1999; Drößler and von Lüpke, 2005; Zeibig et al., 2005; Splechna and Gratzner, 2005; Nagel and Svoboda, 2008; Kenderes et al., 2009; Kucbel et al., 2010; Bottero et al., 2011; Petritan et al., 2013; Hobi et al., 2015b; Feldmann et al., 2018a). From these studies, it is visible that the gap size frequency distribution in beech old-growth forests is generally best described by exponential decay functions, i.e. the frequency of gaps decreases with increasing size, and small gaps caused by the mortality of single or a few trees occur most often. However, gap area, which largely determines the ground area to be colonized by tree offspring, is disproportionate to the frequency of gaps of a given size (Zeibig et al., 2005; Nagel and Svoboda, 2008; Kucbel et al., 2010; Bottero et al., 2011; Feldmann et al., 2018a).

The importance of the different gap size categories for forest dynamics does not only depend on

their share in total gap area, but also on their specific effect on the dynamics of the understory vegetation. Gap size and gap geometry are main determinants of the quantity of light reaching the understory and how light intensity varies across the gap and its immediate vicinity in the stand (Wiedemann, 1927; Canham et al., 1990; Coates and Burton, 1997; Wagner, 1999; Diaci, 2002; Madsen and Hahn, 2008; Vilhar et al., 2015). The great variability of light intensities encountered by seedlings and saplings in gaps of different sizes certainly influences seedling establishment success and sapling growth, determining the future development of the considered forest patch and, in mixed stands, the competitive interaction of different tree species (Runkle, 1989; Whitmore, 1989).

It has been argued that the physiology of beech offspring and beech regeneration dynamics fit well the light regime which is created by canopy gaps in beech-dominated natural forests (Wagner et al., 2010). Yet, the regeneration layer has been studied only rarely in the gaps of beech-dominated virgin forests. The existing studies document a generally high spatial heterogeneity in the regeneration layer, i.e. sapling density and sapling height differ largely across a single gap and also between gaps of different sizes, and they suggest that gaps in most cases release already established advanced regeneration (Diaci et al., 2005; Rozenbergar, 2007; Nagel et al., 2010; Feldmann et al., 2018a). This seems to be different from the majority of ‘natural’ forests with management history, where gaps generally do not release advanced regeneration or, if so, only a relatively homogeneous cohort-like regeneration layer is released (e.g., Diaci, 2005; Kenderes et al., 2008).

An extensive gap survey in a mixed beech-Silver fir (*Abies alba*)-Norway spruce (*Picea abies*) virgin forest in Bosnia revealed for the beech-dominated regeneration layer no differences in structure between gaps differing in size (Nagel et al., 2010). Even more surprising, the authors found no differences in the regeneration layer between gaps and average stand conditions, suggesting that no direct link between gap creation and the regeneration process does exist in this primeval forest. This would further imply that gap-induced structural patterns have only a small influence on stand structure, if human influence is absent. In contrast to these findings, studies in European beech and beech-Silver fir virgin forests reported that gap formation had a significant influence on seedling and sapling density and sapling growth and that growth rate increased with the size of the gap (Diaci et al., 2005; Rozenbergar, 2007; Feldmann et al., 2018a). Rozenbergar (2007) observed that seedling establishment after gap formation was generally more successful in the periphery of the gap, while seedling and sapling height growth was greater in the gap interior.

The present study utilizes a detailed regeneration survey in 17 canopy gaps of variable size and



in 32 plots under closed canopy in the beech virgin forest reserve ‘Kyjov’ in the Carpathians of eastern Slovakia. The time of gap formation could be assigned either to the period 2003–2013 (= ‘new gaps’) or to prior to 2003 (= ‘old gaps’). In the gaps, radiation penetration to the level of the regeneration layer (defined here as  $\leq 3$  m maximum height) occurred in most of the studied gap area.

Main study goals were (i) to search for differences in the structure of the regeneration layer between gaps and forest patches with closed canopy, testing the observation of Nagel et al. (2010) for broader validity, (ii) to investigate differences in sapling density and height growth in gaps differing in age, (iii) to analyze the spatial distribution of saplings and sapling growth in a gap in relation to local variation in the light regime, and (iv) to elucidate the effect of gap size on the spatial regeneration patterns in a gap.

We explicitly tested three hypotheses:

H1: Gaps stimulate the height growth of beech seedlings and saplings through higher radiation intensities with the consequence that the density and cumulative biomass of saplings of  $\geq 0.5$  m in height is higher in gaps than in closed-canopy patches of the stand.

H2: The position in the gap and the related variation in radiation intensity influence both, the establishment success of beech seedlings after gap formation and the height growth of seedlings and saplings. The older the gap, the more heterogeneous is the spatial distribution of sapling density and biomass in a gap.

H3: Since gap size must have a positive effect on average radiation intensity in the gap, average sapling growth rate should increase with gap size.

## 3.2 Methods

### 3.2.1 Study site

The study was conducted in the virgin forest reserve Kyjov in the Vihorlat Mountains in eastern Slovakia (48°53′ N, 22°06′ E) at 700–820 m a.s.l.. This strict forest reserve covers an area of 53 ha on a north- to north-east-facing slope. The mean annual temperature is 5.2–5.7 °C and the mean annual precipitation is 950–1000 mm along the elevation range. Dystric Cambisols with good water-holding capacity have developed from andesite as bedrock (Korpel, 1995; Dröbler and von Lüpke, 2006). The dominant plant community is a Fagetum dentarietosum glandulosae association. European beech (*Fagus sylvatica* L.) is the dominating tree species

which forms almost pure stands (99% of stems) with little admixture of sycamore maple (*Acer pseudoplatanus* L.), Norway maple (*Acer platanoides* L.), common ash (*Fraxinus excelsior* L.) and wych elm (*Ulmus glabra* L.). The stand structure is highly heterogeneous vertically and horizontally at small scale (Drößler and Meyer, 2006; Feldmann et al., 2018b); the height of the dominant trees is approximately 30 m.

### 3.2.2 Study design

In the Kyjov forest, canopy gaps were sampled by the line-intercept method in 2003 (Drößler and von Lüpke, 2005) and 2013 (Feldmann et al., 2018a). Using the same transect lines in both surveys allowed assigning gap formation either to the time before 2003 (old gaps) or to the period 2003–2013 (new gaps). In the second inventory, the cover of sub-canopy tree layers (< 20 m in height) was visually estimated on the expanded gap area, i.e. the area enclosed by the stems bordering the gap, for all 34 canopy gaps mapped in this survey. Many of the gaps had a complex vertical structure of different layers of tree regeneration. In order to study the response of tree regeneration to gap formation in the upper canopy, we selected a subset of gaps that guaranteed relatively comparable initial conditions in terms of tree understory structure and allowed for conducting the measurements described below. We choose only gaps where tree regeneration had not exceeded an approximate maximum height of 3 m at the time of release, i.e. gap closure was in a relatively early stage. This criterion meets broadly the definition of an understory gap given by Brokaw (1982), i.e. “a ‘hole’ extending through all levels down to an average height of two m above ground”. We further excluded gaps where the light regime at the gap edge was obviously influenced by a neighboring gap. These selection criteria were fulfilled by 17 gaps located in the entire study area of Kyjov forest with gap size ranging from 29 to 931 m<sup>2</sup>. Eleven of these gaps were formed prior to 2003 (old gaps) and six in the period between 2003 and 2013 (new gaps). The decay stages of tree trunks in the new gaps that once had created the gaps (gapmakers; data not shown), indicate that at least five of the six disturbances dated back more than five years.

The study is accomplished by data on the density of saplings (height  $\geq 0.5$  m and DBH < 7 cm) on 32 plots under closed canopy that was available from a systematic forest structure inventory conducted by Glatthorn et al. (2018) in Kyjov forest.

### 3.2.3 Field methods

In all gaps, a transect of 2 m width was placed from North to South passing through the approximate gap center and extending by 10 m beyond the projected gap edge in both directions

in order to cover the full range of light intensities encountered by tree regeneration in the gaps (Fig. 3.1). The belt transect was divided into adjacent squares of 4 m<sup>2</sup> size. In each square, the density of tree saplings was determined in four height classes (50–149 cm, 150–299 cm, 300–699 cm and  $\geq 700$  cm, if DBH was  $< 7$  cm).

Additionally, on one dominant or co-dominant sapling per quadrant, the shoot length growth during the last three years was determined by measuring the distances between bud scars along the leading shoot. Squares with ingrowing leaf layers from trees outside the plot or groups of larger pole-sized trees within the plot were excluded from the analysis, as the light regime of these plots differed largely from that of plots with small-sized regeneration.

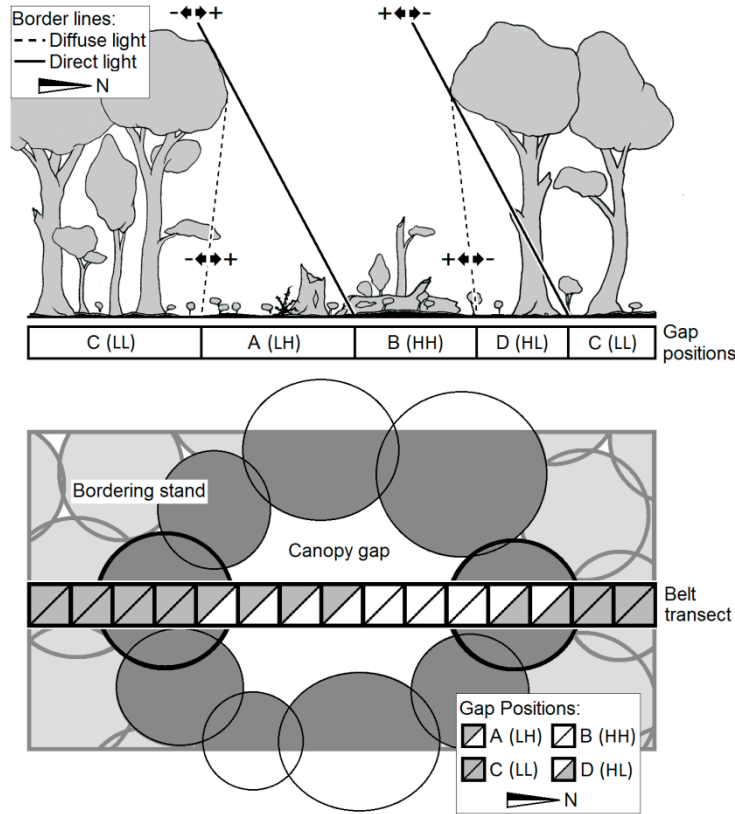
In order to compare the regeneration in gaps with that under closed canopy conditions, we also investigated the regeneration layers on 32 plots located under closed canopy. Tree saplings were counted in four height classes ( $< 50$  cm, 50–149 cm, 150–299 cm,  $> 300$  cm) along transects of each 13 m<sup>2</sup> size (2 m x 6.5 m).

### 3.2.4 Data analysis

We first analyzed the differences between the structure of the regeneration in the gaps and under closed-canopy conditions addressing H1 by comparing the density and the cumulative biomass of saplings  $\geq 0.5$  m tall on the ‘closed stand’ plots ( $n = 32$ ) to that on the gap plots ( $n = 17$ ). To do this comparison on similar plot areas, we confronted the closed-canopy plots, with an area of 13 m<sup>2</sup>, with the data from the gaps of which the three squares closest to the approximate gap center with a total area of  $4 \text{ m}^2 \times 3 = 12 \text{ m}^2$  were chosen. Since the data were not normally distributed (K-S test), we used the non-parametric Wilcoxon rank-sum test to test for significant differences between plots in gaps and under closed canopy.

Second, we tested for differences in the regeneration structure at different locations within a gap and in the immediate surrounding (‘gap periphery’) by adopting a conceptual scheme proposed by Diaci (2002). This scheme subdivides the area of a gap and its direct neighborhood into the four light intensity and quality classes A to D according to the relative intensity (high or low) of direct and diffuse radiation received on the ground that are closely related to gap geometry (see Fig. 3.1 and Table 3.1). We re-labeled the four classes into *LH* (A), *HH* (B), *LL* (C) and *HL* (D) to indicate the relative intensity of direct-beam radiation (first letter) and diffuse radiation (second letter) with *H* for relatively high and *L* for relatively low (for example, *HH* stands for relatively high direct and diffuse radiation). These microsites with contrasting light regimes may be linked to spatial variation in other ecological factors such as precipitation, soil

moisture, temperature, humus decomposition rate, and seed dispersal that are in part caused by gap geometry (Diaci, 2002; Čater et al., 2014).



*Figure 3.1:* Vertical (a) and horizontal (b) projection of a schematic canopy gap. The sketches illustrate the categorical zonation of the relative intensities of direct and diffuse radiation along a south-north-directed belt transect and the location of four classes of radiation input on the forest floor (C = low direct and low diffuse (LL), A = low direct and high diffuse (LH), B = high direct and high diffuse (HH), D = high direct and low diffuse (HL)) according to the conceptual model of Diaci (2002) (labelling modified).

*Table 3.1:* Definition of four light regime classes in a gap (A-D) according to the relative availability of direct and diffuse radiation after Diaci (2002).

Gap position	Direct radiation	Diffuse radiation	Symbol
A	low	high	(LH)
B	high	high	(HH)
C	low	low	(LL)
D	high	low	(HL)

The structure of the tree regeneration along transects was analyzed for sapling density and estimated cumulative sapling biomass per ground area using the allometric equation proposed for beech saplings by Annighöfer et al. (2016). Sapling biomass per ground area was used as a proxy for estimating the space filling by beech regeneration in the quadrants, combining information on plant density and height in a single biomass number. Clearly, this parameter is only a rough measure of biomass, which should only be used for relative comparisons, as calculations solely base on the mean height of the sapling size classes.

The effects of gap size, gap age (old: formed prior to 2003; new: formed between 2003 and 2013) and position in the gap and the associated light regime (high or low direct radiation, high or low diffuse radiation) on the presence of seedlings and saplings were analyzed with generalized linear mixed-effects model using the `glmer()` function of the R statistical software (R Core Team, 2016). We used the logarithm of gap size in the model calculations to reduce the influence of rare large gaps and to account for an assumed asymptotic effect of gap size on light availability at the ground.

In the subsequent analysis, we used only squares which contained saplings to model sapling density and sapling biomass in dependence on gap size, gap age and position in the gap with a linear mixed effects model using the `lme()` function (R Core Team, 2016). Squares without saplings were dropped.

To explore the effects of sapling size, sapling density and gap position (as a proxy for the relative availability of direct and diffuse radiation) in gaps of variable size on sapling shoot length growth, we further modeled mean annual shoot length growth during three years (2012 to 2014) in dependence on these five variables with a linear mixed effects model using the `lme()` function. Again, we used log gap size in the model calculations. To test for the significance of influencing factors in the different models, ANOVAS were performed using a confidence level of  $p \leq 0.05$  throughout.

### 3.3 Results

The tree regeneration on the gap plots and the plots in the closed-canopy stand consisted nearly exclusively of beech seedlings and saplings. Since other species occurring in the forest (sycamore maple, Norway maple, common ash and wych elm) were present in only negligible numbers, they were not counted separately. A dense cover of herbal vegetation was rarely present and thus was not specifically addressed as a factor influencing regeneration dynamics in the Kyjov forest. On the inventory plots, browsing by herbivores in winter was surveyed in

spring 2014 (unpublished data). Accordingly, only 4% of the seedlings < 0.5 m height and 9% of the beech saplings < 1.5 m height were found to be damaged. We thus assume that browsing is not an important factor for beech sapling vitality and survival in this forest.

### 3.3.1 Comparison of gaps with closed-canopy conditions

The density of saplings ( $\geq 0.5$  m height) was about five times higher in gaps (mean: 10147 ha<sup>-1</sup>) than in the closed stand (mean: 1923 ha<sup>-1</sup>,  $p < 0.001$ ) (Fig. 3.2). The difference was even greater when regarding the cumulative sapling biomass per ground area (means: 513 g m<sup>-2</sup> in gaps vs. 79 g m<sup>-2</sup> in the closed stand,  $p < 0.001$ ).

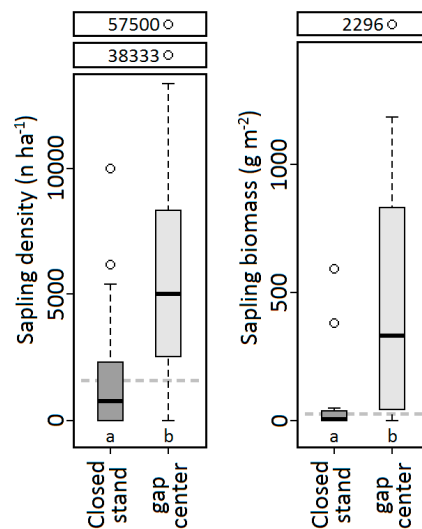


Figure 3.2: Density of saplings ( $\geq 0.5$  m) and cumulative sapling biomass in closed-canopy plots and gap plots (only gaps with regeneration layer < 3 m height at the time of gap formation). Box-whisker plots with median (thick black line), 25- and 75-percentiles (box) and extremes not exceeding the 1.5fold of the interquartile range (whiskers). Dots mark extreme data points beyond 1.5 times the IQR.  $N = 17$  plots in gaps and 32 plots under closed canopy. The dashed grey line marks the median values of samples containing 48 plots  $\acute{a}$  13 m<sup>2</sup> selected by random in the forest (including gap and closed-canopy plots). Different letters below the boxes indicate significant differences between the groups (Wilcoxon rank-sum test).

### 3.3.2 Spatial differences in regeneration structure

#### 3.3.2.1 Sapling density

Squares in the light regime classes *HH* and *HL*, which receive direct radiation, contained saplings more frequently (91% of all squares) than squares hit only by diffuse radiation (classes *LH* and *LL*; 71%). Moreover, the GLM indicates that sapling density in canopy gaps and their

immediate surroundings is promoted by the presence of direct radiation, i.e. the success of beech seedling establishment increases (Table 3.2). According to the model, low intensities of diffuse radiation, as they occur in the gap periphery, had a positive effect on sapling density, and not the expected higher light levels. Unexpected is also that sapling density was independent of gap size and gap age.

*Table 3.2:* Summary of ANOVA results on the influence of higher levels of direct or diffuse radiation, gap size, gap age, and sapling height and density on sapling density, height growth and biomass per ground area in the sample of 229 plots (squares of 4 m<sup>2</sup> size) in gaps according to GLMs. Arrows indicate the direction of the influence (↑ = positive, ↓ = negative); significance level: n.s. = not significant:  $p > 0.05$ , ‘\*’:  $p \leq 0.05$ , ‘\*\*’:  $p \leq 0.01$  and ‘\*\*\*’:  $p \leq 0.001$ . Factors that were not considered in the respective model are marked by -.

Response variables	Influencing factors					
	direct radiation	diffuse radiation	gap size	gap age	sapling height	sapling density
Sapling density	↑ *	↓ *	n.s.	n.s.	—	—
Shoot height growth	n.s.	↑ ***	↑ *	—	↑ ***	n.s.
Sapling biomass	↑ **	n.s.	↑ ***	↑ **	—	—

In accordance with the model results, sapling density was lowest in class *LH* squares (low direct but high diffuse radiation; Fig. 3.3). It was somewhat higher in gap position *LL* and peaked in squares exposed to direct radiation (*HH* and *HL*), which had significantly higher densities than class *LH* squares (Wilcoxon rank-sum test;  $p < 0.01$ ). Gap size and gap age were not found to have a significant effect on sapling density, and thus, these factors were not included in the diagram. Fig. 3.A1 in the appendix considers sapling density in its relation to gap size and gap age.

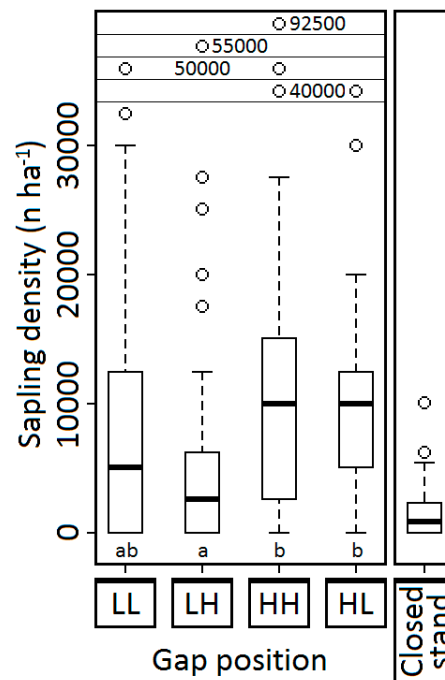


Figure 3.3: Sapling density in squares at different position in the gap. The four gap positions are characterized by the availability of different relative intensities of direct and diffuse radiation (high = H, low = L; first letter for direct and second for diffuse radiation; see Table 3.1 and Figure 3.1) following Diaci (2002). The density values of closed-canopy plots are displayed at the right for comparison (32 belt transects á 13 m<sup>2</sup> total area). Box-whisker plots with median (thick line), 25- and 75-percentiles (box) and extremes not exceeding the 1.5fold of the interquartile range (whiskers). Dots mark extreme data points beyond 1.5 times the IQR.

### 3.3.2.2 Shoot length growth and sapling height

According to the mixed model, the measured shoot length growth of saplings (recorded in 189 plants) was largely determined by the initial size of the plants and the availability of diffuse radiation (Table 3.2), while the intensity of direct radiation was not influential. Gap size had also a positive influence. The plant size influence is displayed by the generally accelerating height growth of saplings with increasing plant height, the role of diffuse light in the generally higher growth rate in the patches receiving high diffuse light intensities (classes *LH* and *HH*) and in the generally higher growth rate in medium- than small-sized gaps (Fig. 3.4). While we either found no change or even a decrease in height growth rate with increasing sapling size from < 1.5 to 3 m in small gaps (< 100 m<sup>2</sup>), growth rate increased with plant size more continuously in medium-size gaps (≥ 100 m<sup>2</sup>).



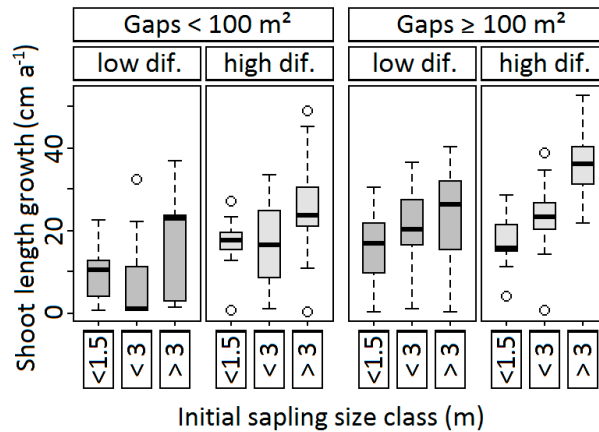


Figure 3.4: Shoot length growth of saplings in squares exposed to different levels of diffuse radiation (relatively low: dark grey; relatively high: light grey) in gaps of two size categories (< 100 m<sup>2</sup> and ≥ 100 m<sup>2</sup>). Box-whisker plots with median (thick line), 25- and 75-percentiles (box) and extremes not exceeding the 1.5fold of the interquartile range (whiskers). Dots mark extreme data points beyond 1.5 times the IQR.

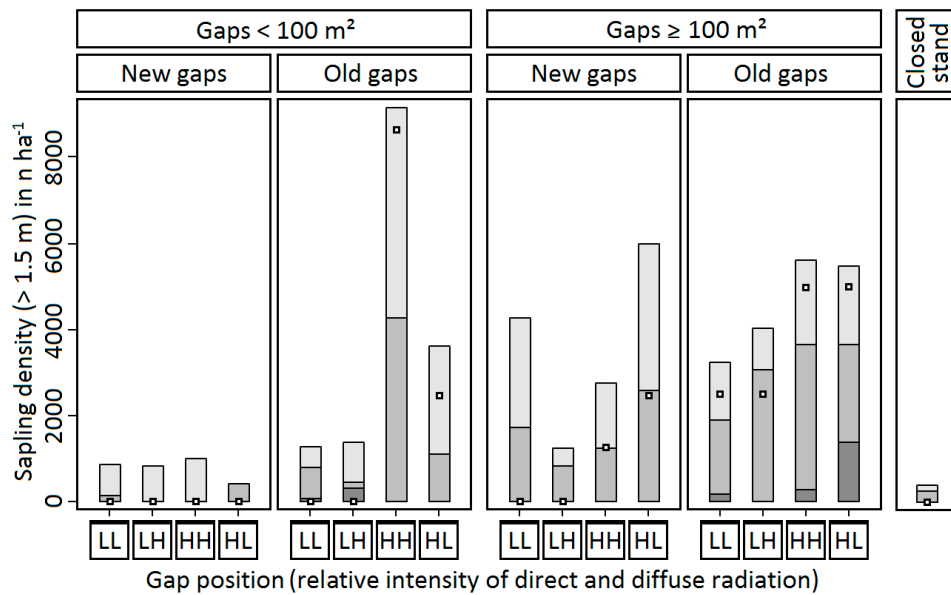


Figure 3.5: Abundance of saplings of three height classes (light grey = 1.5 m–2.99 m, mid grey = 3 m–6.99 m, dark grey ≥ 7 m) in squares of different relative light exposure (first letter for direct and second for diffuse radiation; high = H, low = L; see Table 3.1 and Figure 3.1) differentiated by gap size and gap age (before 2003: old; between 2003 and 2013: new). The median values across height classes are indicated by the small squares. Only saplings > 1.5 m height considered. For further explanations see Fig. 3.3.

In new small gaps  $< 100 \text{ m}^2$ , only few saplings exceeded the height of 1.5 m and most squares lacked saplings of larger size classes at all (Fig. 3.5). In old small gaps (formed before 2003), the density was only slightly higher, when the light classes with no direct sunlight (*LH* and *LL*) are considered, even though some saplings had already reached the larger size classes ( $\geq 3 \text{ m}$  and  $\geq 7 \text{ m}$ ). Squares with high direct and diffuse light (class *HH*) had a very high density of large saplings and the proximity of mean and median value indicates that this was a rather general trend. In class *HL* (only high direct light) in old gaps, the density was much lower, but exceeded the corresponding value in new gaps strongly, reflecting vigorous ingrowth.

In medium-sized gaps ( $\geq 100 \text{ m}^2$ ), the density of saplings with greater height was generally higher than in small gaps, in particular in the old gaps. This was particularly striking in the light class *LL* and also *LH* without direct light, which apparently profited from the larger gap size. Nevertheless, the squares with direct light (classes *HH* and *HL*) had nearly twice as large median densities as the *LH* and *LL* classes in old gaps. The position of the mean far above the median shows that the samples in new gaps are characterized by a few squares with exceptionally high densities of large saplings.

### 3.3.2.3 Sapling biomass

Sapling biomass per ground area was significantly higher in squares with high direct radiation compared to low direct radiation, and it increased with gap size and gap age, while no influence of the level of diffuse light (high or low) was found (see Table 3.2).

The cumulative sapling biomass in small new gaps was at a low level, not very different from that under closed-canopy, irrespective of the square's position in the gap (Fig. 3.6). The higher sapling density found in squares receiving high intensities of direct radiation (classes *HH* and *HL*) was poorly reflected in sapling biomass. In old small gaps, however, median sapling biomass showed a distinct peak in class *HH* (high direct and diffuse radiation). In *HL* with high direct but low diffuse radiation, biomass was much smaller, and it remained close to zero in *LH* and *LL* with only diffuse radiation.

In medium-sized new gaps, median values were very low in classes *LL* and *LH*, increased slightly toward *HH* and peaked at a much higher level in class *HL*. In old gaps of medium size, sapling biomass was at a comparably high level already in low-light conditions (*LL*), reached a somewhat higher median in squares receiving high diffuse radiation (*LH* and *HH*), and peaked at twice this value in squares receiving high direct, but low diffuse radiation (*HL*). Especially in the medium-sized gaps, variation of sapling biomass among squares was generally high in all four light classes.

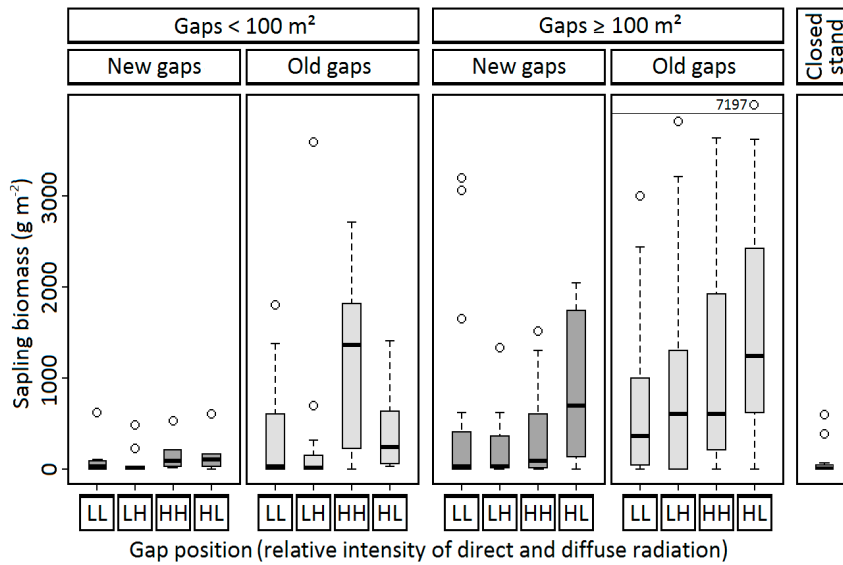


Figure 3.6: Sapling biomass in squares at different position in a gap that formed between 2003 and 2013 (new gaps; dark grey) or prior to 2003 (old gaps; light grey) presented for small (< 100 m<sup>2</sup>) and medium-sized gaps (≥ 100 m<sup>2</sup>). The four gap positions are characterized by the availability of different relative intensities of direct and diffuse radiation (high = H, low = L; first letter for direct and second for diffuse radiation; see Table 3.1 and Figure 3.1) following Diaci (2002). The density values of closed-canopy plots are displayed at the right for comparison (32 belt transects á 13 m<sup>2</sup> area). Box-whisker plots with median (thick line), 25- and 75-percentiles (box) and extremes not exceeding the 1.5fold of the interquartile range (whiskers). Dots mark extreme data points beyond 1.5 times the IQR.

## 3.4 Discussion

### 3.4.1 Comparing beech regeneration in gaps and closed-canopy patches

In our study, the density and cumulative biomass of saplings ≥ 0.5 m height was significantly higher in ‘understory gaps’, i.e. gaps allowing radiation penetration to at least 3 m above ground, than in closed-canopy patches ( $p < 0.001$ , Wilcoxon rank-sum test). This clearly demonstrates that the regeneration structure in this virgin forest was affected by gap formation, in support of the first hypothesis. Positive gap effects on regeneration have been observed in many forest types from the boreal zone to the tropics (Runkle, 1989; Whitmore, 1989), and they should be especially strong in light-demanding tree species. One would expect that highly shade-tolerant late-successional species such as beech are less dependent on gap formation, and very large gaps might even inhibit the development of shade-tolerant tree saplings, which thrive best in semi-shade (Turner, 2001, Leuschner and Ellenberg, 2017). The evidence from beech-dominated virgin forests on the role of canopy gaps for the regeneration process is indeed contradictory. While

some authors found, similar to the recent study, gaps to have a positive effect on the establishment and growth of beech offspring (Diaci et al., 2005; Rozenbergar, 2007; Feldmann et al., 2018a), others detected no explicit gap influence on the structure of the regeneration (Nagel et al., 2010). The latter finding suggests that beech saplings are capable of tolerating the shade cast by the nearly closed canopy in natural beech forests, which is characteristic for large parts of the stand. This is not only a consequence of the well-studied high physiological shade tolerance of *Fagus sylvatica* seedlings and saplings (e.g., Petritan et al., 2007; Swagrzyk et al., 2001; Leuschner and Ellenberg, 2017), but also reflects the fact that canopy gaps increase the light levels on the ground on a much larger area than just in the projected gap area (Canham, 1988). Calculations show that the cumulative expanded canopy gap area, i.e. the area of the stand approximately influenced by gap formation, comprised more than a quarter to half (29–55%) of the total area of beech-dominated virgin forests, even though cumulative gap area itself covered only about 13–16% (Dröbner and von Lüpke, 2005; Nagel and Svoboda, 2008; Petritan et al., 2013).

However, there may be other reasons related to methodology, why Nagel et al. (2010) were unable to detect a significant gap effect on the structure of the regeneration. These authors used a relatively broad gap definition in terms of the regeneration layer, including also gaps that are filled by larger saplings and young trees ( $> 3$  m). If a broader gap definition is used which considers both ‘understory gaps’ and ‘canopy gaps’, the average gap becomes more similar in its light regime to the closed-canopy stand, as the presence of larger saplings and understory trees decreases light transmission to the ground and effectively reduces the number of surviving saplings in lower strata. If we had included canopy gaps with such large saplings and understory trees, it is likely that the statistical difference to the closed-canopy plots would have been weakened or even lost. Further, Nagel et al. (2010) did not compare gaps with the closed-canopy stand, but with average stand conditions, which also include gap-affected plots. This implies circular reasoning and additionally reduces the probability for statistical differences.

### 3.4.2 The role of gaps for beech regeneration

When an understory gap is created and light levels become more favorable for beech offspring, newly established seedlings usually meet an already existing seedling and sapling population that managed to persist at low density under closed-canopy conditions. According to the shoot length growth data from Kyjov forest, small seedlings that established prior to gap formation, and many younger saplings from post-disturbance colonization events must even in new gaps have reached or exceeded the height threshold ( $\geq 0.5$  m) used here to count them as saplings, and not seedlings ( $< 0.5$  m). We found in newly formed understory gaps an equally low median

sapling biomass in most gap positions (Fig. 3.3) which differed only slightly from that of closed-stand conditions, suggesting that there were no eminent differences in pre-disturbance regeneration structure that would have affected the results markedly.

The GLM revealed a significant effect of both direct and diffuse radiation intensity on sapling density, though in opposite direction. While seed germination seems not to depend on light availability in European beech (Ammer et al., 2002; Swagrzyk et al., 2001), radiation intensity has frequently been reported to be a key factor determining the survival and development of seedlings and saplings (Ammer, 1996; Minotta and Pinzauti, 1996; Collet et al., 2001; Swagrzyk et al., 2001; Petritan et al., 2007, 2009). Small saplings of 0.5–1.5 m height showed a median shoot length growth rate of 11–18 cm a<sup>-1</sup> in the gaps in Kyjov, which is in the range of growth rates recorded for beech saplings under 9–15% relative light intensity by Petritan et al. (2007). At such light intensities, beech is capable of forming stable seedling banks, as observed in a mixed beech-fir-spruce forest in Poland (Swagrzyk et al., 2001). In accordance, median sapling density was higher in all gap positions than in the closed stand.

Our GLM results suggest that the direct and diffuse radiation components may act differently on seedling establishment and early survival on the one side, and on sapling growth and survival on the other side. Significantly higher sapling densities were observed in the light regime classes *HH* and *HL* with high direct radiation as compared to class *LH* with high diffuse radiation, suggesting a dominant effect of direct light intensity on sapling density in support of the first part of our second hypothesis (H2). In contrast, high amounts of diffuse radiation seem to promote sapling growth but not seedling establishment and survival. This is evidenced by the observation that sapling shoot length growth was higher in gap positions with high than low levels of diffuse radiation, while the GLM does not show a positive effect of elevated levels of diffuse radiation on sapling density. Thus, the process of seedling establishment and early survival seems to depend largely on the intensity of direct radiation. Seedling survival and the associated sapling density could also depend on competition for light in dense sapling populations. However, our sapling density data suggest that plant densities were in most cases < 1 m<sup>-2</sup> and thus too low to result in significant competition. Only in gap position *HL*, median sapling density exceeded 1 m<sup>-2</sup> already in new gaps and competition may have resulted in thinning processes in certain gaps, reducing plant density.

The apparently opposing effects of direct and diffuse radiation components on sapling density in our study suggest that other factors than light likely are influencing seedling density, establishment and survival as well. The observed positive influence of a low diffuse light level on sapling density may be due to seed dispersal effects, as beech seeds are dispersed only within

small distance to the source tree through barochory and zoochory, and seed density is typically by far higher below fruiting trees than at more distant locations, e.g. in gaps with higher light intensity (Karlsson, 2001; Wagner et al., 2010). That this spatial effect of seed availability imprints on the spatial pattern of tree regeneration in gaps was shown in several studies in previously managed beech forests (Mihók et al., 2005; Mountford et al., 2006; Vilhar et al., 2015). Interestingly, gap size did not influence sapling density negatively in our study. This suggests that gap diameters did not exceed critical distance thresholds, which would hamper the colonization of gap centers by beech seedlings.

The significant positive effect of direct-beam radiation intensity on sapling density may perhaps relate more to associated thermal effects than to the influence of radiation itself. Notably, air temperature close to the ground and soil surface temperature are typically higher in gap positions which receive high light intensities (Bartsch and Röhrig, 2016), and these reach maxima when direct sunlight hits the spot (Anderson, 1964). A warmer soil surface could positively affect germination and early seedling development (Harper, 1977), especially at relatively cool sites as in Kyjov forest. Elevated soil surface temperatures could also increase the N mineralization rate in the organic layer (Scharenbroch and Bockheim, 2008), which may facilitate seedling survival on acid, relatively nutrient-poor soils. Finally, more rapid decomposition in the warmer gap positions (*HH* and *HL*) could result in thinner organic layers, which represent an improved seedbed and favor early seedling survival (Ammer et al., 2002; Röhrig et al., 2006). A lower thickness of the organic layer along with a higher density of beech regeneration in gap positions receiving direct sunlight (*HH* and *HL*) was observed in a Slovenian beech-fir forest (Vilhar et al., 2015).

The overall effect of gap age (< 10 or > 10 years) on sapling density was not significant in our sample. However, the higher sapling densities in gaps compared to closed-stand conditions suggest that a considerable number of beech seedlings must have established in the first months or years after gap formation, especially in gap positions *HH* and *HL*. This colonization event likely was missed in our study due to the choice of the observation intervals. Further, the subsequent temporal development of sapling density was not consistent across gap positions (Fig. 3.A1) with either increases, decreases or no change in density. Therefore, a significant gap age effect did not appear in our data. The observed trends in sapling density between new and old gaps may well be interpreted as an expression of interacting effects of seed dispersal (high in *LL* and *HL*), seedling establishment success (high in *HH* and *HL*) and competition (reduced density in *HL* in old gaps).

Main determinants of the shoot length growth of seedlings and saplings were the actual size

of the plants and, to a lesser extent, the relative amount of diffuse radiation, which is related to gap size (Vilhar et al., 2015, Coates and Burton, 1997). This confirms hypotheses H3 and H2. Positive effects of increased levels of diffuse radiation on shoot length growth of beech regeneration have frequently been observed (e.g., Collet et al., 2001, Collet and Chenost, 2006; Petritan et al., 2009; but see Annighöfer, 2018). In other studies that applied the conceptual model of Diaci (2002) for separating light classes, higher growth rates in gap positions receiving relatively high diffuse radiation have been reported as well (Rozenbergar et al., 2007; Bilek et al., 2014). Thus, our findings are well in agreement with the results of experiments and also field observations on the light response of tree sapling growth. That shoot length growth depends on plant size and thus on ontogeny agrees also with earlier observations (Collet and Chenost, 2006), even though this factor is rarely addressed. The growth data indicate that only in the periphery of small gaps, light intensity fell below a certain critical level, which strongly hampered the height growth especially of medium-sized saplings (1.5–2.99 m tall).

In contrast to diffuse light, we did not find a significant stimulation of sapling growth rate by elevated levels of direct light. This may result from the known sensitivity of young beeches to extended periods of excess radiation, which may cause photoinhibition (e.g., Einhorn et al., 2004) and the formation of small, more xerophytic leaves (Petritan et al., 2009). Yet, radiation intensity matters: Short episodes of higher direct light intensity, as they occur in sunflecks, can contribute much to the carbon gain of understory plants, as was shown by gas exchange measurements for beech regeneration (Chazdon and Pearcy, 1991; Rees, 1999). Beech seedlings and saplings have a remarkable potential to adapt to the elevated light levels, which are found in gap positions receiving direct light (Čater et al., 2014). It is not known whether part of the additional carbohydrate gain is invested, e.g., belowground, or in increased diameter growth.

How successful beech is regenerating in gaps of different sizes and ages, may best be deduced from data on sapling biomass per ground area, as they reflect both plant density and growth rate. Although we have only biomass estimates and no harvest data, they demonstrate that the regeneration success in small gaps (< 100 m<sup>2</sup>) is clearly highest in gap position *HH* with high direct and diffuse radiation. In the other gap positions, either the establishment (and thus sapling density) or growth rate was apparently limited by low direct light or diffuse light.

In medium-sized gaps, sapling biomass reached higher values in most gap positions (except for *HH*) than in small gaps, probably due to higher levels of diffuse radiation that promoted shoot length growth even in the gap periphery. Here, saplings in the smallest recorded size class (0.5–1.5 m) grew in height at relatively similar rates in all gap positions. Consequently, in these larger gaps, the density of seedlings established prior to, or shortly after, gap formation

largely determined sapling biomass, while subsequently colonizing seedlings (which appeared mainly in *HH* and *LL*) contributed only to a minor extent. Thus, early colonizing advanced saplings dominated space filling and the rather low sapling density in gap position *LH* (median density in new medium gaps:  $0.5 \text{ m}^{-2}$ ) seems to be sufficient to fill the area without any time lag. The biomass data also suggest that competition between saplings is playing a decisive role for sapling survival only in later phases of regeneration development, while seedling densities are generally too low for lateral interaction in the early phase of gap filling. In peripheral gap positions (*LL* and *HL*), lateral canopy closure and increasing sapling heights and leaf areas in the gap interior (*LH* and *HH*) will likely hamper the development of the saplings in the medium term.

### 3.5 Conclusions

European beech is one of the most shade-tolerant temperate tree species that is capable of establishing a vital regeneration layer under the sparse light of a nearly closed canopy with only ca. 5–10% of incident light (Swagrzuk et al., 2001, Leuschner and Ellenberg, 2017). However, gaps nevertheless play an important role for the density and growth of the beech offspring in beech virgin forests, even though the majority of gaps are smaller than  $100 \text{ m}^2$ , gap area accounts for only about 10% (3 to 19%) of stand area, and gap formation in many cases does promote the growth of an already existing tree understory rather than facilitating the establishment of new seedlings (Feldmann et al., 2018a). This is partly because the gap effect reaches well beyond the projected gap area into the closed-canopy stand. Our study showed marked spatial differences in sapling density and height growth within the gaps and across gaps of different size, which seem to depend on variation in the light regime and seed availability. However, other abiotic factors such as temperature or nitrogen availability could additionally have an effect on this pattern. Experimental approaches are needed to disentangle the influence of these often correlated environmental factors on beech regeneration in gaps.

A major result of our detailed regeneration mapping is that gap microsites exposed to different intensities of direct and diffuse light seem to influence sapling density and growth in different ways. It appears that direct light in most cases promotes seedling and sapling density of beech, while growth promotion of existing saplings is generally higher under elevated levels of diffuse light, and not direct light. We interpret these findings as support for the validity of the conceptual model of gap microsites proposed by Diaci (2002).

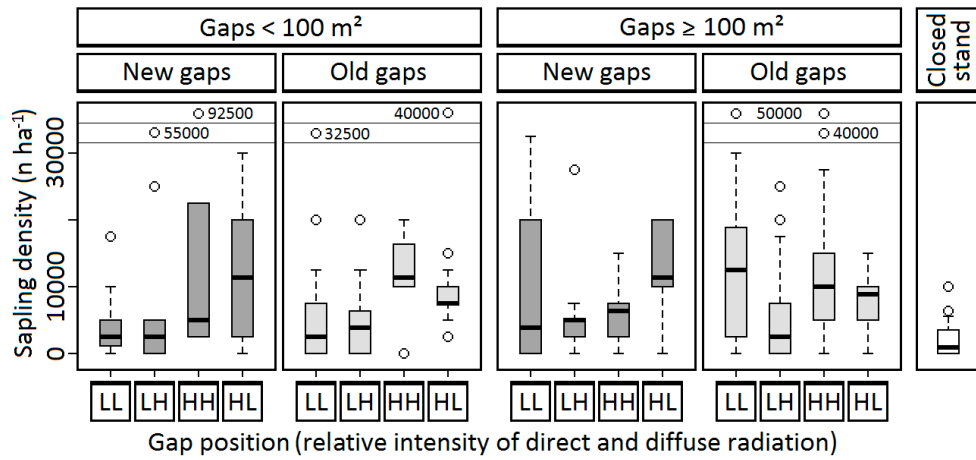
There is indication from the following observations that the detected spatial pattern in gap regeneration will change over longer time spans (decades) and that it should be only poorly



reflected in the structure of the canopy of the next tree generation. Small gaps  $< 100 \text{ m}^2$  are often closed by lateral expansion of adjacent beech trees (Feldmann et al., 2018a) and only very few released understory trees may be able to grow into the canopy within the relatively short period of higher light availability. Thus, the area of former small gaps will in the stand usually be associated with quite heterogeneous lower canopy layers, a pattern that may increase the resilience of the forest in the face of future disturbances. In medium-sized gaps  $\geq 100 \text{ m}^2$ , in contrast, the density of advanced regeneration seems in most cases to be sufficient to completely fill the gap area, even when the rate of post-disturbance colonization is low, as is typically the case in gap position *LH*. A few saplings in the gap interior (gap positions *LH* and *HH*) will likely manage to grow into the canopy, while in the gap periphery (gap positions *LL* and *HL*) sapling growth sooner or later will be suppressed by the cover of trees bordering the gap. Nearly equal current plant sizes and growth rates of the dominant saplings in gap positions *LH* and *HH* suggest that the successful individuals will reach the canopy layer more or less at the same time and form a relatively homogeneous, cohort-like canopy patch that is filling the former gap. However, the high variability in sapling density and growth suggests that other ecological factors might affect regeneration development as well, and understory gaps in beech virgin forests could follow very individual development paths. This may render it difficult to reach at a fully mechanistic understanding of gap dynamics in beech virgin forests.

**Acknowledgements:** The project was funded by the Stemmler Foundation and the support is gratefully acknowledged. We like to thank the Ministry of Defense of the Slovak Republic for the permits to conduct the study. For organizational and technical support, we also like to thank Viliam Pichler and his working group at the Technical University of Zvolen.

### 3.6 Appendix



*Figure 3.A1:* Sapling density in squares at different position in a gap that formed between 2003 and 2013 (new gaps; dark grey) or prior to 2003 (old gaps; light grey) presented for small (< 100 m<sup>2</sup>) and medium-sized gaps (≥ 100 m<sup>2</sup>). The four gap positions are characterized by the availability of different relative intensities of direct and diffuse radiation (high = H, low = L; first letter for direct and second for diffuse radiation; see Table 3.1 and Figure 3.1) following Diaci (2002). The density values of closed-canopy plots are displayed at the right for comparison (32 belt transects á 13 m<sup>2</sup> size). Box-whisker plots with median (thick line), 25- and 75-percentiles (box) and extremes not exceeding the 1.5fold of the interquartile range (whiskers). Dots mark extreme data points beyond 1.5 times the IQR.

### 3.7 References

- Ammer, C., 1996. Konkurrenz um Licht - Zur Entwicklung der Naturverjüngung im Bergmischwald. Forstliche Forschungsberichte München, 158, 198 pp.
- Ammer, C., Mosandl, R., El Kateb, H., 2002. Direct seeding of beech (*Fagus sylvatica* L.) in Norway spruce (*Picea abies* [L.] Karst.) stands — effects of canopy density and fine root biomass on seed germination. *Forest Ecology and Management*, 159(1-2), 59-72.
- Anderson, M. C., 1964. Studies of the woodland light climate: I. The photographic computation of light conditions. *Journal of Ecology*, 52(1), 27-41.
- Annighöfer, P., Ameztegui, A., Ammer, C., Balandier, P., Bartsch, N., Bolte, A., Coll, L., Collet, C., Ewald, J., Frischbier, N., Gebereyesus, T., Haase, J., Hamm, T., Hirschfelder, B., Huth, F., Kändler, G., Kahl, A., Kawaletz, H., Kuehne, C., Lacoite, A., Lin, N., Löf, M., Malagoli, P., Marquier, A., Müller, S., Promberger, S., Provendier, D., Röhle, H., Sathornkich, J., Peter Schall, P., Scherer-Lorenzen, M., Schröder, J., Seele, C., Weidig, J., Christian Wirth, C., Heino Wolf, H., Wollmerstädt, J., Mund, M., 2016. Species-specific and generic biomass equations for seedlings and saplings of European tree species. *European Journal of Forest Research*, 135(2), 313-329.
- Annighöfer, P., 2018. Stress relief through gap creation? Growth response of a shade tolerant species (*Fagus sylvatica* L.) to a changed light environment. *Forest Ecology and Management*, 415, 139-147.
- Bartsch, N., Röhrig, E., 2016. Waldökologie. Springer Spektrum, Berlin, Heidelberg.
- Bílek, L., Remes, J., Podrazsky, V., Rozenbergar, D., Diaci, J., Zahradník, D., 2014. Gap regeneration in near-natural European beech forest stands in Central Bohemia—the role of heterogeneity and micro-habitat factors. *Dendrobiology*, 71, 59-71.
- Bottero, A., Garbarino, M., Dukic, V., Govedar, Z., Lingua, E., Nagel, T. A., Motta, R., 2011. Gap-phase dynamics in the old-growth forest of Lom (Bosnia-Herzegovina). *Silva Fennica*, 45, 875-887.
- Brokaw, N. V. L., 1982. The definition of treefall gap and its effect on measures of forest dynamics. *Biotropica*, 14(2), 158-160.
- Burschel, P., Schmalz, J., 1965. Die Bedeutung des Lichtes für die Entwicklung junger Buchen. *Allgemeine Forst und Jagdzeitung*, 136, 193–210.
- Canham, C. D., 1988. An index for understory light levels in and around canopy gaps. *Ecology*, 69(5), 1634-1638.
- Canham, C. D., Denslow, J. S., Platt, W. J., Runkle, J. R., Spies, T. A., White, P. S., 1990. Light regimes beneath closed canopies and tree-fall gaps in temperate and tropical forests. *Canadian Journal of Forest Research*, 20(5), 620-631.
- Čátek, M., Diaci, J., Rozenbergar, D., 2014. Gap size and position influence variable response of *Fagus sylvatica* L. and *Abies alba* Mill. *Forest Ecology and Management*, 325, 128-135.
- Chazdon, R. L., Pearcy, R. W., 1991. The importance of sunflecks for forest understory plants. *Bioscience*, 41(11), 760-766.
- Coates, K.D., Burton, P.J., 1997. A gap-based approach for development of silvicultural systems to address ecosystem management objectives. *Forest Ecology and Management*, 99(3), 337-354.
- Collet, C., Lanter, O., Pardos, M., 2001. Effects of canopy opening on height and diameter growth in naturally regenerated beech seedlings. *Annals of Forest Science*, 58(2), 127-134.
- Collet, C., Chenost, C., 2006. Using competition and light estimates to predict diameter and height growth of naturally regenerated beech seedlings growing under changing canopy conditions. *Forestry*, 79(5), 489-502.
- Diaci, J., 2002. Regeneration dynamics in a Norway spruce plantation on a silver fir-beech forest site in the Slovenian Alps. *Forest Ecology and Management*, 161(1-3), 27-38.
- Diaci, J., Rozenbergar, D., Boncina, A., 2005. Interactions of light and regeneration in Slovenian Dinaric Alps: patterns in virgin and managed forests. *Forest, Snow and Landscape Research*, 79(1/2), 154-160.

- Drößler, L., von Lüpke, B., 2005. Canopy gaps in two virgin beech forest reserves in Slovakia. *Journal of Forest Science*, 51, 446-457.
- Drößler, L., von Lüpke, B., 2006. Bestandesstruktur, Verjüngung und Standortfaktoren in zwei Buchenurwald-Reservaten der Slowakei. *Allgemeine Forst und Jagdzeitung*, 178, 121-135.
- Drößler, L., Meyer, P., 2006. Waldentwicklungsphasen in zwei Buchen-Urwaldreservaten in der Slowakei. *Forstarchiv*, 77, 155-161.
- Einhorn, K. S., Rosenqvist, E., Leverenz, J. W., 2004. Photoinhibition in seedlings of *Fraxinus* and *Fagus* under natural light conditions: implications for forest regeneration. *Oecologia*, 140(2), 241-251.
- Feldmann, E., Drößler, L., Hauck, M., Kucbel, S., Pichler, V., Leuschner, C., 2018a. Canopy gap dynamics and tree understory release in a virgin beech forest, Slovakian Carpathians. *Forest Ecology and Management*, 415, 38-46.
- Feldmann, E., Glatthorn, J., Hauck, M., Leuschner, C., 2018b. A novel empirical approach for determining the extension of forest development stages in temperate old-growth forests. *European Journal of Forest Research*, 137(3), 321-335.
- Glatthorn, J., Feldmann, E., Pichler, V., Hauck, M., Leuschner, C., 2018. Biomass stock and productivity of primeval and production beech forests: greater canopy structural diversity promotes productivity. *Ecosystems*, 21(4), 704-722.
- Harper, J. L., 1977. Population Biology of Plants. Academic Press, London, UK.
- Hobi, M. L., Commarmot, B., Bugmann, H., 2015a. Pattern and process in the largest primeval beech forest of Europe (Ukrainian Carpathians). *Journal of Vegetation Science*, 26(2), 323-336.
- Hobi, M. L., Ginzler, C., Commarmot, B., Bugmann, H., 2015b. Gap pattern of the largest primeval beech forest of Europe revealed by remote sensing. *Ecosphere*, 6(5), 1-15.
- Karlsson, M., 2001. Natural regeneration of broadleaved tree species in southern Sweden. *Acta Univ. Agric. Svec. Silvustria*, 196, Alnarp/Sweden.
- Kenderes, K., Mihók, B., Standovár, T., 2008. Thirty years of gap dynamics in a Central European beech forest reserve. *Forestry*, 81(1), 111-123.
- Kenderes, K., Král, K., Vrška, T., Standovár, T., 2009. Natural gap dynamics in a Central European mixed beech-spruce-fir old-growth forest. *Ecoscience*, 16(1), 39-47.
- Korpel, Š., 1995. Die Urwälder der Westkarpaten. Gustav Fischer Verlag, Stuttgart.
- Kucbel, S., Jaloviari, P., Saniga, M., Vencurik, J., Klimaš, V., 2010. Canopy gaps in an old-growth fir-beech forest remnant of Western Carpathians. *European Journal of Forest Research*, 129(3), 249-259.
- Leibundgut, H., 1993. Europäische Urwälder - Wegweiser zur naturnahen Waldwirtschaft. Paul Haupt, Bern.
- Leuschner, C., Ellenberg, H., 2017. Ecology of Central European Forests. Vegetation Ecology of Central Europe, Vol. I. Springer Nature, Cham.
- Madsen, P., Hahn, K., 2008. Natural regeneration in a beech-dominated forest managed by close-to-nature principles—a gap cutting based experiment. *Canadian Journal of Forest Research*, 38(7), 1716-1729.
- Mihók, B., Gálhidy, L., Kelemen, K., Standovár, T., 2005. Study of gap-phase regeneration in a managed beech forest: relations between tree regeneration and light, substrate features and cover of ground vegetation. *Acta Silv. Lign. Hung.*, 1, 25-38.
- Minotta, G., Pinzauti, S., 1996. Effects of light and soil fertility on growth, leaf chlorophyll content and nutrient use efficiency of beech (*Fagus sylvatica* L.) seedlings. *Forest Ecology and Management*, 86(1-3), 61-71.

- Motta, R., Berretti, R., Castagneri, D., Dukić, V., Garbarino, M., Govedar, Z., Lingua, E., Maunaga, Z., Meloni, F., 2011. Toward a definition of the range of variability of central European mixed Fagus – Abies – Picea forests: the nearly steady-state forest of Lom (Bosnia and Herzegovina). *Canadian Journal of Forest Research*, 41(9), 1871-1884.
- Mountford, E. P., Savill, P. S., Bebb, D. P., 2006. Patterns of regeneration and ground vegetation associated with canopy gaps in a managed beechwood in southern England. *Forestry*, 79(4), 389-408.
- Nagel, T.A., Svoboda, M., 2008. Gap disturbance regime in an old-growth Fagus-Abies forest in the Dinaric Mountains, Bosnia-Herzegovina. *Canadian Journal of Forest Research*, 38(11), 2728-2737.
- Nagel, T.A., Svoboda, M., Rugani, T., Diaci, J., 2010. Gap regeneration and replacement patterns in an old-growth Fagus-Abies forest of Bosnia-Herzegovina. *Plant Ecology*, 208(2), 307-318.
- Peters, R., 1997. Beech Forests. *Geobotany*, 24. Springer, 170 pp.
- Petritan, A. M., Von Lüpke, B., Petritan, I. C., 2007. Effects of shade on growth and mortality of maple (*Acer pseudoplatanus*), ash (*Fraxinus excelsior*) and beech (*Fagus sylvatica*) saplings. *Forestry*, 80(4), 397-412.
- Petritan, A. M., von Lüpke, B., Petritan, I. C., 2009. Influence of light availability on growth, leaf morphology and plant architecture of beech (*Fagus sylvatica* L.), maple (*Acer pseudoplatanus* L.) and ash (*Fraxinus excelsior* L.) saplings. *European Journal of Forest Research*, 128(1), 61-74.
- Petritan, A. M., Biris, I. A., Merce, O., Turcu, D. O., Petritan, I. C., 2012. Structure and diversity of a natural temperate sessile oak (*Quercus petraea* L.)–European Beech (*Fagus sylvatica* L.) forest. *Forest Ecology and Management*, 280, 140-149.
- Petritan, A. M., Nuske, R. S., Petritan, I. C., Tudose, N. C., 2013. Gap disturbance patterns in an old-growth sessile oak (*Quercus petraea* L.)–European beech (*Fagus sylvatica* L.) forest remnant in the Carpathian Mountains, Romania. *Forest Ecology and Management*, 308, 67-75.
- R Core Team, 2016. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.
- Rees, U., 1999. Lichtflecken und ihre Bedeutung für die CO<sub>2</sub>-Aufnahme junger Buchen (*Fagus sylvatica* L.) im Unterwuchs eines Buchenwaldes. Ph D thesis, Univ. Goettingen. 155 p.
- Ricard, J. P., Messier, C., Delagrangé, S., Beaudet, M., 2003. Do understory sapling respond to both light and below-ground competition?: a field experiment in a north-eastern American hardwood forest and a literature review. *Annals of Forest Science*, 60(8), 749-756.
- Röhrig, E., Bartsch, N., von Lüpke, B., 2006. *Waldbau auf ökologischer Grundlage*. Ulmer, Stuttgart.
- Rozenberger, D., Mikac, S., Anić, I., Diaci, J., 2007. Gap regeneration patterns in relationship to light heterogeneity in two old-growth beech–fir forest reserves in South East Europe. *Forestry*, 80(4), 431-443.
- Runkle, J. R., 1989. Synchrony of regeneration, gaps, and latitudinal differences in tree species diversity. *Ecology*, 70(3), 546-547.
- Scharenbroch, B. C., Bockheim, J. G., 2008. The effects of gap disturbance on nitrogen cycling and retention in late-successional northern hardwood–hemlock forests. *Biogeochemistry*, 87(3), 231-245.
- Schelhaas, M.J., Nabuurs, G.J., Schuck, A., 2003. Natural disturbances in the European forests in the 19th and 20th centuries. *Global Change Biology*, 9(11), 1620-1633.
- Splechtna, B. E., Gratzner, G., 2005. Natural disturbances in Central European forests: approaches and preliminary results from Rothwald, Austria. *Forest, Snow and Landscape Research*, 79, 57-67
- Szwagrzyk, J., Szewczyk, J., Bodziarczyk, J., 2001. Dynamics of seedling banks in beech forest: results of a 10-year study on germination, growth and survival. *Forest Ecology and Management*, 141(3), 237-250.

- Tabaku, V., Meyer, P., 1999. Lückenmuster albanischer und mitteleuropäischer Buchenwälder unterschiedlicher Nutzungsintensität. *Forstarchiv*, 70, 87–97.
- Turner, I. M. (2001). *The ecology of trees in the tropical rain forest*. Cambridge University Press, Cambridge.
- Vilhar, U., Roženberger, D., Simončič, P., Diaci, J., 2015. Variation in irradiance, soil features and regeneration patterns in experimental forest canopy gaps. *Annals of Forest Science*, 72(2), 253-266.
- Wagner, S., 1999. Ökologische Untersuchungen zur Initialphase der Naturverjüngung in Eschen-Buchen-Mischbeständen. Schriften aus der Forstlichen Fakultät der Universität Göttingen und der Niedersächsischen Forstlichen Versuchsanstalt, 129.
- Wagner, S., Collet, C., Madsen, P., Nakashizuka, T., Nyland, R. D., Sagheb-Talebi, K., 2010. Beech regeneration research: from ecological to silvicultural aspects. *Forest Ecology and Management*, 259(11), 2172-2182.
- Whitmore, T. C. (1989). Canopy gaps and the two major groups of forest trees. *Ecology*, 70(3), 536-538.
- Wiedemann, E., 1927. Über den künstlichen gruppenweisen Voranbau von Tanne und Buche. *Allgemeine Forst und Jagdzeitung*, 103, 433-452.
- Zeibig, A., Diaci, J., Wagner, S., 2005. Gap disturbance patterns of a *Fagus sylvatica* virgin forest remnant in the mountain vegetation belt of Slovenia. *Forest, Snow and Landscape Research*, 79(1/2), 69-80.







# 4<sup>th</sup>

## CHAPTER

### WHAT HAPPENS AFTER THE GAP? — SIZE DISTRIBUTIONS OF PATCHES WITH HOMOGENEOUSLY SIZED TREES IN NATURAL AND MANAGED BEECH FORESTS IN EUROPE

Lars Drößler, Eike Feldmann, Jonas Glatthorn, Peter Annighöfer,  
Stanislav Kucbel, Vath Tabaku

Open Journal of Forestry 6 (2016), 177–190

#### Abstract

A novel but simple approach for describing stand structure in natural and managed forests driven by small-scaled disturbances is introduced. A primeval beech forest reserve in Slovakia and two beech stands in Germany with different management histories were studied, and their forest stand texture was analysed in terms of tree coordinates, stem diameter, and crown radius. Neighbouring trees of similar size with estimated contact of their crowns were assigned to tree groups. The study goal was to estimate the number and size of such homogeneous patches. In all cases, the number of tree groups in a particular diameter class decreased exponentially as group size increased. Single trees were predominant. Compared to simulated random tree distributions, the natural stand exhibited a more clumped distribution of small trees and more regular distribution of larger ones. The natural forest generally had smaller groups than the managed even aged stand, but the smallest group sizes were found in the uneven-aged selection forest. The simple analytical approach provided new spatial insights into neighbourhood relations of trees. The continuous scale from single trees to larger tree groups is an important achievement compared to other analytical methods applied in this field. The findings may even indicate a certain degree of self-organization in natural forests. Due to the limitations

associated with each method or statistical models, a joint consideration of 1) gap dynamics, 2) forest developmental stages, and 3) size classes of homogeneous tree groups is recommended. Relevant to forest practitioners, the size class distributions enhance an understanding of the complex stand structures in natural forests and therewith support an emulation of natural forest dynamics in managed beech forests.

**Keywords:** forest structure, natural forest dynamics, tree neighbourhood relationships, close-to-nature management, *Fagus sylvatica*, Central Europe

## 4.1 Introduction

### 4.1.1 Background of the study

Forest ecosystems are complex and adaptive, with the ability to adjust and react to changing conditions (Messier et al., 2014). For instance, light and microclimate influence various processes in beech forest ecosystems, affecting their regeneration performance and growth of individual trees (Madsen and Larson, 1997; Wagner, 1999; Bartsch et al., 2002; Pretzsch, 2009). These processes are also influenced by other factors such as stand structure. Because natural stand structures provide certain advantages in terms of resilience and genetic adaptability, they are increasingly regarded as a viable option for the management of beech stands (Finkeldey and Ziehe, 2004; Röhrig et al., 2006; Brumme and Khanna, 2009). The paradigm of “Close-to-Nature Forest Management” (CNFM) was developed to exploit these benefits. CNFM is widely used in Central Europe and can be implemented in conjunction with a wide range of silvicultural methods focusing on single trees and tree groups (Duncker et al., 2012; Brang et al., 2014; Bauhus et al., 2014). However, it is impossible to perfectly reproduce natural forest structures in a managed stand since by definition, natural forest is not managed (Leibundgut, 1993).

*F. sylvatica* would be the dominant species in large parts of Central Europe in the absence of human influence (Ellenberg, 1996). Due to the human impact, however, only a small proportion of Central European forests are remnant natural beech forests. In this study, we compare two managed beech stands in Germany to one of the closest remaining natural beech forest reserves below 800 m elevation: the reserve Kyjov in Slovakia. The purpose of the study was to enhance the understanding of forest dynamics in beech ecosystems by determining frequency distributions of patches (tree groups) with neighbouring trees of similar size. Another aim was to support forest managers who want to develop natural stand structures and wilderness-like

areas (i.e. the Sihlwald near Zurich in Switzerland, or the National Park Hainich in Germany).

The following section provides an overview of established methods for analysing stand structure and dynamics of natural European beech forests. Later, the novel approach for describing and comparing the aggregation of similarly-sized trees in forests is presented.

#### **4.1.2 Silvicultural research in natural beech forests in Europe**

Natural stand structures have been of interest to foresters since the late 19<sup>th</sup> century (see Brang, 2005 for an overview). Older studies described both more heterogeneous and homogeneous types of stand structure in natural beech forests (Fröhlich, 1925; Müller, 1929; Gehrhardt, 1923). More recent studies emphasized the prevalence of heterogeneous stand structures (Tabaku, 2000; Meyer et al., 2003; Commarmot et al., 2005). Smith et al. (1997) defined the internal forest structure in terms of tree species composition, age classes, stand layers, and diameter distributions. Helms (1998) distinguished between vertical and horizontal forest structures. The horizontal structure of the forest is the spatial arrangement of its vertical structures, i.e. the forest texture. Later structural analyses also considered the abundance of dead wood or other micro-habitats (e.g., Winter and Brambach, 2011).

To analyze the forest texture (as one aspect of horizontal structure on the patch scale), development stages and phases have been defined in terms of typical stand structures (Leibundgut, 1993; Korpel, 1995; Meyer, 1999). For example, Neumann (1979), Leibundgut (1993) and Korpel (1995) identified and mapped developmental stages in the forest. Later, other methods were developed to ensure that the results of structure analyses were reproducible (Meyer, 1999; Tabaku, 2000; Dröbner and Meyer, 2006). However, all of these methods failed at identifying true borders between developmental stages because they assigned development stages and phases to defined forest patches of certain size using relatively coarse rasters. This may bias the estimation of the area of each stage, especially for smaller units. In addition, the raster approach can fail to detect overlapping stages (Korpel, 1995; Dröbner and Meyer, 2006), as shown by Grassi et al. (2003). A more advanced mapping of developmental phases in a natural spruce-fir-beech forest was presented (Kral et al., 2010), which also included dead trees. In addition, irregular patches (usually 400–1100 m<sup>2</sup> in size) with spatially distinct stand characteristics (tree number, standing volume, deadwood) were indicated by statistical models (Kral et al., 2014).

Direct information about the area and spatial distribution of initial development phases can be gained from canopy gap studies (e.g. Runkle, 1992; Zeibig et al., 2005; Nuske, 2006) or extensive dendrochronological studies (Šamonil et al., 2013). Terrestrial gap surveys typically

use measurements of tree heights or diameters at breast height (DBH) to distinguish between gaps and adjacent stands (Runkle, 1992). DBH data were also analysed by Tabaku and Meyer (1999), who created stand maps based on modelled tree crowns and identified canopy gaps in beech forests based on the absence of trees of  $\geq 7$  cm DBH. Drößler and von Lüpke (2005) used higher DBH thresholds in a similar way (20 and 30 cm, respectively) to study gaps in the upper canopy layer.

If the initial gap stage is defined using such thresholds, subsequent developmental stages could be estimated by focusing on particular size classes of trees. Neighbouring trees of approximately the same size could then be regarded as groups representing one stage of development. This idea is similar to that presented by Grassi et al. (2003), who distinguished between developmental stages on the basis of tree height and growth-related parameters. Although it is difficult to equalize diameter and development stage (Piovesan et al., 2005; Kral et al., 2010; Trotsiuk et al., 2012; Šebkova et al., 2012), we followed this idea to gain more insights into the interactions of fine-scale neighbourhood processes and coarser-scale forest dynamics. Thereby, we went beyond the scope of conventional forest structure indicators and sophisticated point pattern correlations (von Gadow et al., 2012) that oversimplified forest structure from a management point of view. Especially the flexibility to summarize exponentially decreasing numbers of patches with increasing patch size was desired when the presented simple analytical method was developed.

The goal of this study was to identify tree groups and describe their size in terms of the number of individuals belonging to a group. Study objects were forests of different management intensity. Main objective was to determine how frequently trees of particular size classes are aggregated in groups. Hopefully, size distributions of such tree groups could point out general stand dynamic patterns, from the initiation to the terminal phase. Also, comparisons of individual-based stand structure between natural and managed forests (especially those managed in a “close to nature” fashion) could be made. Finally, the comparison of observed and randomized tree distributions could link ecological field studies better with hypothetical spatio-temporal models (Gratzer et al., 2004).

Since the abundance of canopy gaps in natural beech forests decreases exponentially with increasing gap size (Zeibig et al., 2005; Drößler, 2006), we hypothesized that the number of tree groups within a given size class would decrease exponentially with increasing group size. We also hypothesized that the spatial arrangement of tree groups would not be random. In addition to these two hypotheses, we addressed management history and cutting regime by assessing their effect on the size distribution of tree groups.

## 4.2 Material and methods

### 4.2.1 Study sites

The stand characteristics and structure of the examined stands were already chosen in two extensive studies that documented the structures of beech forest stands with different management intensity (Tabaku, 2000; Drößler, 2006). Within these studies, field data were collected in the Kyjov natural forest reserve in eastern Slovakia, in an uneven-aged single-tree selection stand (Plenterwald) in Bleicherode, and in an even-aged stand in Stauffenburg managed by target diameter cutting. The latter two stands are both located in central Germany. Stand sizes ranged from 22 to 50 ha. The basal area proportion of European beech was 99% in Kyjov and Bleicherode, and 97% in Stauffenburg. The stand top height in Stauffenburg was 38 m at an age of 166 years. The top heights in Kyjov and Bleicherode were estimated to be 30 m and 33.5 m, respectively. All three sites were moist-mesic and fertile. The uneven-aged stand at Bleicherode has been managed by single-tree selection for more than 140 years. In Stauffenburg, the trees have been harvested on reaching a target diameter (Table 4.1) for several decades. The Kyjov reserve is one of the last remaining natural beech forests in central Europe at sub-montane elevation, and one of the closest to the German study sites. Its altitude is 400 m greater than that of the German sites (Table 4.1), and it has not been subjected to any silvicultural management. Korpel (1995) reported an annual periodic increment of  $6.5 \text{ m}^3 \text{ ha}^{-1}$ , ranging from 3 to  $12 \text{ m}^3 \text{ ha}^{-1} \text{ a}^{-1}$  depending on the developmental phase. Tabaku (2000) and Drößler (2006) describe also forest floor vegetation, soil conditions, and other features of the studied stands.

Table 4.1: Site and stand characteristics of the studied stands in Slovakia (Kyjov) and Germany (Bleicherode, Stauffenburg).

	Kyjov	Bleicherode	Stauffenburg
<b>Latitude</b>	48°51'	51°16'	51°21'
<b>Longitude</b>	22°01'	10°20'	10°05'
<b>Altitude</b>	700 - 800 m	420 - 440 m	300 - 350 m
<b>Mean annual precipitation</b>	750 - 800 mm	650 - 730 mm	780 - 900 mm
<b>Mean annual temperature</b>	6°C	7°C	7.5°C
<b>Base rock</b>	Andesite	Limestone	Sandstone
<b>Soil type</b>	Cambisol	Leptosol	Cambisol
<b>Top stand height</b>	30 m	33.5 m	38.4 m
<b>Stand age</b>	uneven	uneven	166 yrs.
<b>Harvest method</b>	Never managed	Single-tree selection	Target diameter cutting
<b>Study plot size</b>	12 ha	7.5 ha	7.25 ha
<b>Total no. trees (DBH ≥ 7 cm)</b>	3871	1887	663

#### 4.2.2 Data sampling

One representative plot covering 7–12 ha was established in the centre of each stand. The plots in Bleicherode and Stauffenburg were measured by Tabaku (2000) in 1997. The plot in Kyjov was measured in autumn 2003. The measuring procedure and the methods applied were identical during all measurements. All living trees with a diameter at breast height (DBH)  $\geq 7$  cm were recorded in each study stand. The coordinates of these trees were measured by distance and angle from a 31.25 m grid, and their DBH values were calipered. The tree heights and 8 crown radii per tree were measured for 30 - 60 trees covering the DBH range in each stand. Established correlations between DBH and mean crown radius were used to assign a circular crown to every tree (see Tabaku, 2000; Dröbler, 2006).

#### 4.2.3 Data analysis and determination of tree groups

DBH distributions were calculated for each of the three stands on the basis of 4 cm wide DBH classes. In order to identify tree groups containing trees of similar size, all trees were assigned to DBH classes with widths of 10 cm. In addition, for a sensitivity analysis of the results, tree

groups were also defined on the basis of DBH classes with widths of 20 cm.

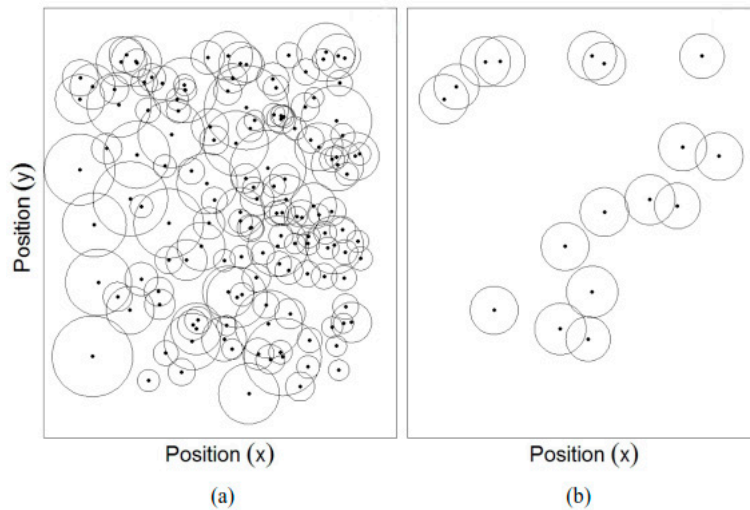


Figure 4.1: A section of one of the crown maps used in the analysis ((a): all trees  $\geq 7$  cm DBH; (b): trees of DBH class 37–47 cm)

Maps showing the spatial arrangement of trees in a given size class and their allotted crowns were used to identify tree groups (Fig. 4.1). All trees having a crown contact with a neighbouring tree of the same size class were considered to be part of the same group as the contacted tree. Thus, each group represents a collection of similarly sized trees in which the mean crown radius is used as a boundary limit for defining neighbouring and non-neighbouring trees (i.e. trees whose crowns do and do not touch, respectively). Finally, the frequency of these differently sized groups was determined and exponential regression models were fit to the frequency data. In addition, a random distribution of the recorded tree diameters over the sample area was simulated and compared to the tree group frequencies observed in reality. In 1000 simulations the spatial position of each tree was changed by randomly assigning new x- and y-coordinates to each tree within the borders of the original stands. Total stem count and DBH distributions stayed the same. Borders of the 95% confidence intervals of group frequencies were determined by the 0.025 and 0.975 quantiles of the group size frequency distributions of the simulations.

The bootstrap Kolmogorov-Smirnoff two-sample test was used to identify statistically significant differences between the tree group frequencies in the natural stand and the managed stands. Significant differences between the tree distributions of the simulations and the empirically observed stands were identified by means of the Kolmogorov-Smirnoff statistic  $D$ .  $D$  was calculated for each of the 1000 simulated and the empirical stands by comparing

their distribution functions with the distribution function of the arithmetic mean of all of the simulations. The p-value was determined by the fraction of simulated stands with a D-value higher than the one of the respective empirical stand. All tests were performed with a confidence level of 0.95. Tree group frequency comparisons were performed for each DBH class separately.

In addition, sensitivity analyses were conducted. The sensitivity of the results to variation in the definition of crown size was tested by increasing the crown diameters used to define neighbouring trees by 10% and 20%. Secondly, instead of the total sample area, 20 systematic sample plots (62.5 m · 62.5 m) within the original data from Kyjov were tested to assess edge effects and to facilitate comparison of the results obtained to those presented for a different forest reserve (Drößler, 2006).

## **4.3 Results**

### **4.3.1 Diameter distributions**

The largest tree observed in this work was growing in the natural forest and had a DBH of 121 cm. Fig. 4.2 shows that in the natural forest, trees in the first two DBH classes were the most abundant, and that the number of trees in each class declined exponentially with increasing DBH after the second class. However, the rate of decline was relatively modest on going from 30 to 110 cm DBH. In managed forests, the diameter range was smaller and the maximum observed DBH values were 87 and 74 cm for the uneven- and even-aged stand, respectively. The even-aged stand exhibited the bell-shaped DBH distribution typical of such management regimes, with diameters ranging from 26–74 cm and a mean DBH of around 50 cm. The uneven-aged managed stand was characterized by a more even decline in tree number with increasing tree size compared to the unmanaged forest, with a very steep decline from 12 to 24 cm and a fairly steady number of trees having DBH values of 40 to 65 cm (Fig. 4.2).



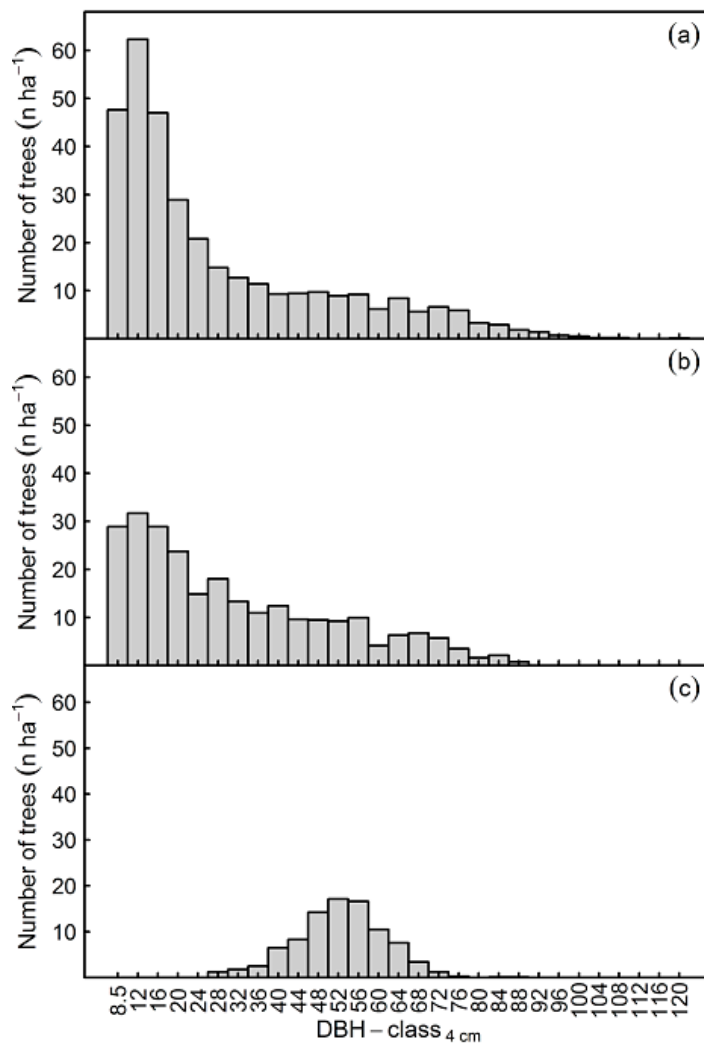


Figure 4.2: Diameter distributions in (a) the natural forest Kyjov; (b) the uneven-aged managed forest Bleicherode; and (c) the even-aged managed forest Stauffenburg.

### 4.3.2 Tree group frequencies in the natural forest

31% of the measured trees had no neighbouring trees belonging to the same DBH class. Single trees (representing the smallest group size) dominated the group size distributions, and in general there was an exponential decline in the number of groups as the group size increased for all DBH classes. For example, 258 single trees, 99 two-tree groups, and 15 large groups with 15–36 trees were identified for the smallest DBH class in Kyjov (Fig. 4.3(a)). Larger DBH classes contained fewer tree groups. The 77–86.9 cm DBH class included 54 single trees, 10 two-tree groups, and two groups with three trees (Fig. 4.3(i)).

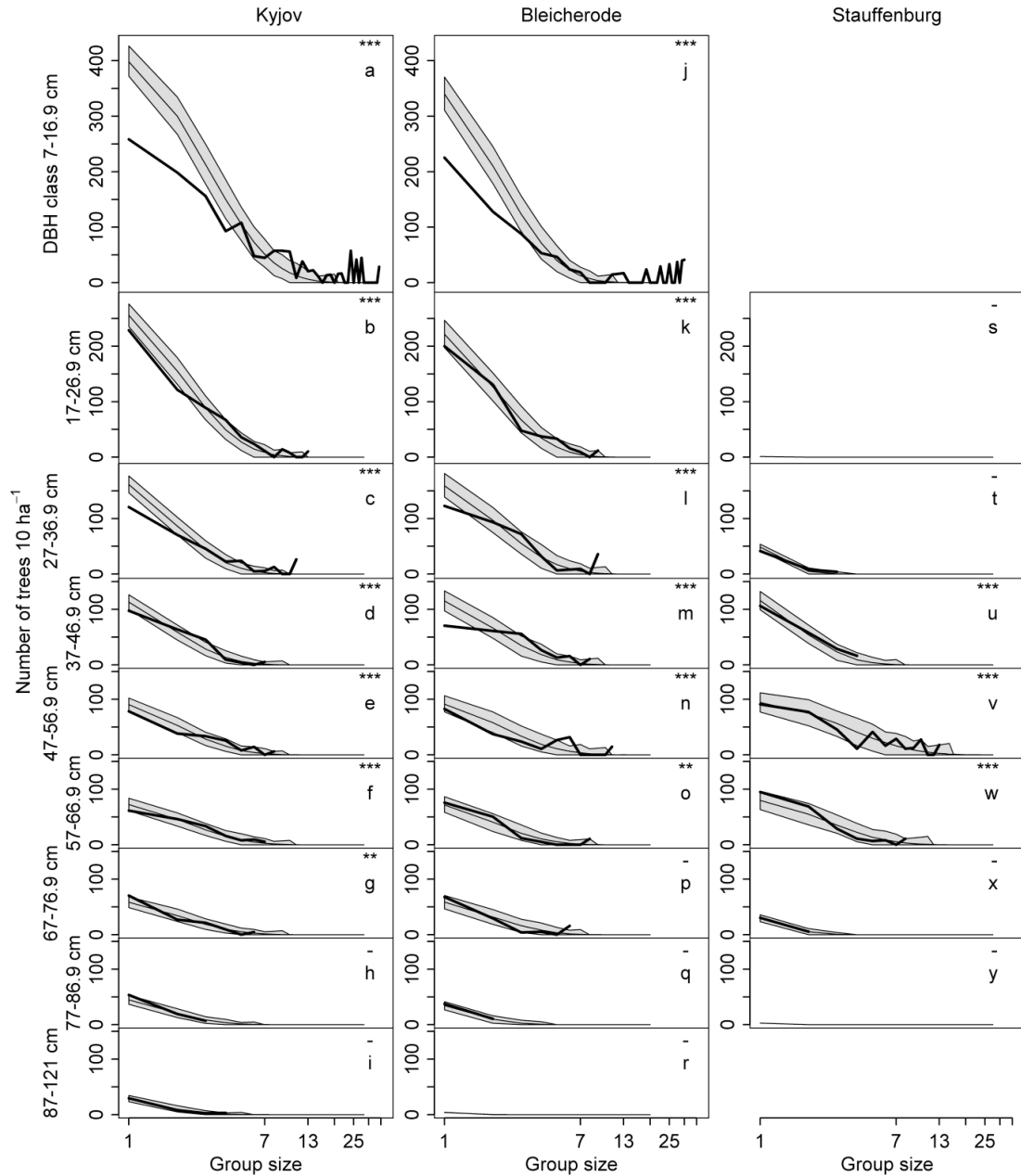


Figure 4.3: Observed (black line) and expected (grey) group size distributions for different DBH classes in Kyjov ((a)–(i)), Bleicherode ((j)–(r)) and Stauffenburg ((s)–(y)). The y-axis shows the number of trees in groups of the same size, for an imaginary forest compartment of 10 ha size. The logarithmic x-axis indicates the group size which is determined by groups of trees with crown contact. The observed empirical distributions were compared to random distributions of trees (with 95% confidence interval highlighted in grey). The star symbols denote statistically significant differences at 90, 95, 99 and 99.9% confidence levels (“.”, “\*”, “\*\*”, “\*\*\*”). For sample sizes of less than 50 no significances are given (“-”).

Trees in smaller DBH classes occurred more often in groups than was observed in simulated random spatial tree distributions (Fig. 4.3(a)–(c)). We found statistically significant differences between the actual and random distributions of smaller DBH classes (Fig. 4.3(a)–(e)), but not for the largest classes with the fewest trees. Trees in the larger classes were more likely to occur as single trees than would be expected based on a random distribution. However, the differences were not significant for neither of the DBH class widths (10 or 20 cm) or the enlarged crown radii in the sensitivity analysis.

### 4.3.3 Tree group frequencies in the managed forests

In the managed stands, the number of groups also decreased exponentially with group size. Across all DBH classes, the proportion of single trees (32%) in the uneven-aged single-tree selection stand was comparable to that in the natural forest. The smallest DBH class (7–17 cm) in the uneven-aged stand contained 215 single trees, 57 two-tree groups and seven larger groups with 15–31 trees, meaning that the number of single trees in this class was somewhat lower than in the natural forest whereas the number of larger groups was greater (Fig. 4.3(a) and Fig. 4.3(j)). The group size distributions for this DBH class in the single tree selection stand differed significantly from the natural forest, as was the case for all other DBH classes except the 27 to 37 cm and the 67 to 77 cm classes. For tree sizes below 57 cm DBH, the selection stand contained fewer small tree groups than would be expected from a random distribution. Differences were significant except for the 27 to 37 cm class where the p-value was 0.09. Larger trees with a DBH above 57 cm seemed to occur slightly more often in smaller groups and less often in bigger groups compared to the random stands. However, differences were only significant for the 67 to 77 cm class in the sensitivity analysis with enlarged crown radii. One major difference between these two stands was the narrower DBH range of the latter. In addition, the managed stands contained fewer trees and tree groups than the natural forest. Single frequency values of tree groups per size class are shown in the appendix (Table 4.A1 and Table 4.A2) for those two study stands. Across all 10 cm wide DBH classes, the single-tree selection stand was broadly similar to that of the unmanaged forest, compared to the even-aged stand.

The tree size distribution for the even aged stand did not differ significantly from that for the random distributions (Fig. 4.3(s)–(y)). Beside its general lack of small and very large trees, the even-aged stand also exhibited group numbers that declined exponentially with increasing group size. Contrary to the findings in the other two stands, the 47–57 cm DBH class contained most of the trees and the largest groups. Within the 10 ha study plot, this class was represented by 91 single trees, 39 two-tree groups, and 11 groups with minimum seven trees of this size per group (Fig. 4.3(v)).

### 4.3.4 Exponential fits and sensitivity analyses

The exponential regression function  $f(x) = \lambda \cdot e^{-\lambda x}$  ( $x$  = number of trees per group) was fitted to the three empirical tree group size distributions presented in Fig. 4.3, yielding  $R^2$  values of  $> 0.8$ . Lower  $R^2$  values only occurred when the exponential function was not flexible enough to follow the steep decline of small groups and the flat distribution of large groups. Lambda values of the fitted functions ranged from -0.1 to -1.2.

Increasing the crown radii used to define the neighbourhood of each tree by 20% reduced the number of single trees for all size classes and stands by one third, and increased the number of large tree groups. In the natural forest, the number of single trees in the smallest DBH class (7–17 cm) decreased from 26 to 15 trees per ha while the number of large groups with more than 15 trees rose from one to two per ha.

An analysis of 20 separated systematic sample plots of 0.4 ha each in Kyjov yielded virtually identical group size frequencies to those observed in the initial analysis of a single large 12 ha plot; one difference was that the maximum number of large tree groups in large DBH classes decreased slightly.

## 4.4 Discussion

### 4.4.1 Natural forest structure and dynamics

Earlier studies by Zeibig et al. (2005) and Dröbner and von Lüpke (2005) described steep exponential declines in the size distributions of canopy gaps in natural beech forests in Europe. The size and shape of canopy gaps influences the initial conditions that govern future stand development. Canopy gaps give rise to tree groups and determine the future stand structure (Oliver and Larsen, 1996; Muscolo et al., 2014). In addition, closed and open canopies are associated with different stand structures, depending on the stand history (former gaps) and other factors (Schütz and Saniga, 2011). Concerning former gap sizes, Šamonil et al. (2013) determined disturbance events dendrochronologically in a beech-dominated forest reserve and reported autocorrelations within ranges of 0–30 m, and rarely exceeding 60 m.

Our results indicate that neighbouring trees of different sizes dominate the heterogeneous stand structure of natural beech forests. Interestingly, the number of more homogeneously structured stand sections decreased exponentially as their size increased. The number of groups declined exponentially (and in some cases, even more rapidly, exhibiting a reversed J-shaped decline)

with increasing group size. The same pattern has been observed in a similar study conducted in a second natural forest reserve in Slovakia even though the initial agents of disturbance (uprooting versus wind-break) were different (Drößler and von Lüpke, 2005). Such a pattern may be typical for natural beech forests in central Europe, but further studies at other locations would be required to answer this question.

More insights into natural stand dynamics were obtained by comparing the observed group distributions with randomly simulated distributions. Whereas small trees were actually more likely to be aggregated into groups, very large trees were less extensively grouped. The latter indicates the tendency that very large trees are more regularly distributed than randomly. Such a finding could even be interpreted as an indication of a self-organizing process which is on debate in ecological theory (Levin, 2005; Solé and Bascompte, 2006). A more regular distribution of the largest trees would also facilitate small disturbances because larger trees are more prone to such events than smaller ones (Schütz and Saniga, 2011).

The low frequency of small groups of trees with low diameter indicated a somewhat coarser forest texture than in the random distribution. Large groups of small trees are more frequent than random, also indicating a coarse (homogeneous) structure. However, due to the small maximum size of such groups (covering less than 0.1 ha, with interspersed larger trees), this finding does not contradict with our previous conclusion of the dominance of heterogeneous stand structures. But our findings revealed a more complex stand structure than described by average patch sizes.

#### **4.4.2 Comparing managed and natural stands**

Diameter distributions make it possible to assess the stand structure of natural and managed forests with relatively little effort (Burschel and Huss, 1997; Schütz, 2001). The DBH distributions of the three study stands reflected the differences in tree sizes between the stands completely and would provide a useful management guide for tree removals in the managed stands. However, they did not provide spatial information such as neighbourhood relationships between trees. If a closer imitation of complex natural stand structures is desired, information about this relationship would be crucial. The method presented herein could potentially support the development of more natural stand structures in managed forests.

The decrease in group numbers with increasing group size was observed in all stands, but the numbers and the decline were different. For example, the number of groups containing at least four trees of DBH 50–64 cm in the even-aged stand in Stauffenburg was twice that in the natural forest. The single-tree selection stand in Bleicherode more closely reproduced the

observed natural stand structures. Only small differences between the number of large trees and the maximum size of tree groups were revealed. This finding demonstrates that different heterogeneous horizontal stand structures can be achieved by adequate forest management.

As mentioned in the introduction, existing quantitative methods for identifying different developmental stages in forests are mainly based on rasterization. We suggest that tree groups in beech forests develop via multiple pathways and can change their spatial arrangement over time (for example, disturbances and diameter differentiation may split a tree group). Consequently, it may be best to combine multiple methods in order to more accurately describe the complex process of forest development in natural and managed forests. For example, in previous studies different raster types were used and compared to determine the developmental stages of natural stands or the three study stands examined in this work (Tabaku, 2000; Drößler and Meyer, 2006; Kral et al., 2014). The tree group size distributions identified in this investigation are broadly consistent with those identified using the earlier raster-based approach.

Furthermore, the success in achieving “close-to-nature” conditions could also be assessed by other indicators of forest structure, biodiversity or ecological complexity (see Zenner and Hibbs, 2000; Pommerening, 2002; Parrott, 2010; Winter and Brambach, 2011; von Gadow et al., 2012).

#### **4.4.3 Limitations of the presented method**

The method is time consuming because tree coordinates are required over study areas large enough to feature trees from all of developmental stages. Therefore, rare large-scale disturbances are difficult to address with this method (Drößler and von Lüpke, 2005). Moreover, trees of the same size may have very different ages because beech can tolerate long periods of suppression (Piovesan et al., 2005; Kral et al., 2010; Šebkova et al., 2012) and respond strongly after release even at high ages (Leibundgut, 1993; Korpel, 1995; Schütz, 2001). This may complicate the application of the cohort concept in beech stands. However, Trotsiuk et al. (2012) found a good correlation between DBH and age ( $R^2 = 0.8$ ) in a natural beech forest reserve in Ukraine. In addition, it requires huge resources to determine the age of trees on such large areas, while tree sizes provide sufficient guidance for the management of uneven-aged forests (Schütz, 2001). Nevertheless, the probability of finding neighbour trees of the same size with precisely the same age in uneven-aged forest is not high, especially in older stages (Shimatani and Kubota, 2011). Therefore, a group of trees of the same size class is not equal to a cohort sensu Oliver and Larson (1996) or others. In this respect, the even-aged stand Stauffenburg illustrates how

one large single cohort can be divided into different tree groups (Fig. 4.3, see Drößler, 2006, for single frequency values) or developmental stages (Tabaku, 2000), due to self-differentiation processes of trees.

Another drawback of the method is the large proportion of overlapping tree crowns in tree groups of different tree size classes. Drößler and Meyer (2006) found a ratio of 186% between crown coverage (area sum of single trees) and stand area in Kyjov. Furthermore, the crown size-based definition of neighbourhood and DBH classes affects the calculation of group sizes. However, steep exponential declines of group observations with increasing group size were found for all DBH classes even in cases where enlarged radii were used to define neighbouring trees.

The exclusion of dead trees and coarse woody debris from this study ignored the possibility to explore other important links to previous forest dynamics, which can improve the relation between the evaluated forest structure and assumed disturbance history (Koop and Hilgen, 1987).

Lastly, climate and soil conditions have effects on forest structure and dynamics. The natural forest stand examined in this work was several hundred kilometres away from the managed stands, and so may have rather different climatic conditions and soil. Unfortunately, this was unavoidable – the Slovakian reserves are the closest natural stands of pure beech forest to the managed sites representing locations at sub-montane elevation. Beech forest is presumed to be the natural vegetation in the absence of human interference at sub-montane and colline elevation in Germany (Bohn et al., 2003). It is worth noting in this context that the study conducted at a second reserve in Slovakia with a different soil type yielded similar results to those reported herein for Kyjov (Drößler, 2006).

## 4.5 Conclusions

We provide a method for describing complex stand structures that may result from close-to-nature forest management which aims to simulate natural forest processes, to emulate natural disturbances and to increase structural diversity (Otto, 1994; Larsen, 2012). The results are based on quantitative measurements and enable comparisons to references from natural forests. Although the method generates images that can be used by managers who are aiming to develop natural stand structures, the frequency distributions of tree groups is not equal to forest developmental stages! In fact, the method is developed to complement the existing methods for studying stand structure and development.

Our results support the findings of other authors (Korpel, 1995; Tabaku, 2000; Meyer et al., 2003; Chernyavskyy, 2005; Commarmot et al., 2005) who concluded that the structure of natural beech forests was heterogeneous. Although homogeneously structured patches occur and cover areas of 400–1100 m<sup>2</sup> (as indicated by Kral et al., 2014), they cover only a smaller proportion of the total forest area than heterogeneously structured stand sections characterized by the interspersed of smaller patches.

The results strongly support our two hypotheses: A mix of single trees dominated in different size classes in all three types of stands, and the number of tree groups decreased exponentially with increasing group size. Also, we revealed a tendency for large, single trees in natural forest to be more regularly distributed over the whole stand as suggested by random distributions.

**Acknowledgements:** We are grateful to Prof. M. Saniga, Prof. B. von Lüpke and Dr. P. Jaloviar for their help. We thank DFG, TC4F, the Stemmler foundation (Project: Biodiversity and ecology of beech forests in Slovakia), and the Southern Swedish forest research centre for financial support.



## 4.6 Appendix

Table 4.A1: Natural forest Kyjov: Number of tree groups on 10 ha (total tree number is 3226 trees). Trees in each group belong to one DBH class. Grouping criterion is the estimated crown contact (see section 2.3).

Group size (Number of trees per group)	DBH classes [cm]									Total number of trees in that group size
	7-16.9	17-26.9	27-36.9	37-46.9	47-56.9	57-66.9	67-76.9	77-86.9	≥ 87	
1	258.4	228.8	120.8	97.6	78.4	61.6	70.4	53.6	29.6	999
2	99.2	60.8	35.2	32.0	19.2	23.2	13.6	9.6	4.0	594
3	52.0	29.6	15.2	15.2	11.2	11.2	7.2	2.4	0.8	434
4	23.2	16.8	5.6	2.4	6.4	4.0	2.4		0.8	246
5	21.6	7.2	4.8	0.8	1.6	1.6				188
6	8.0	4.0	0.8		2.4	1.6	0.8			106
7	6.4	1.6	0.8	0.8		0.8				73
8	7.2		1.6		0.8					77
9	6.4	1.6								72
10	5.6	0.8								64
11	0.8		2.4							35
12	3.2									38
13	1.6	0.8								31
14	1.6									22
15	0.8									12
16										
17	0.8									14
18	0.8									14
19										
20	0.8									16
21	0.8									17
22										
23										
24	2.4									58
25										
26	1.6									42
27										
28	1.6									45
29										
30										
31										
32										
33										
34										
35										
36	0.8									29

Table 4.A2: Selection forest stand Bleicherode (Plenterwald): Number of tree groups on 10 ha (total tree number is 2516 trees). Trees in each group belong to one DBH class. Grouping criterion is the estimated crown contact (see section 2.3).

Group size (Number of trees per group)	DBH classes [cm]								Total number of trees in that group size
	7-16.9	17-26.9	27-36.9	37-46.9	47-56.9	57-66.9	67-76.9	≥ 77	
1	214.7	184.0	145.3	78.7	78.7	61.3	34.7		797.3
2	57.3	44.0	58.7	30.7	32.0	25.3	1.3		498.7
3	30.7	8.0	33.3	16.0	9.3	5.3			308.0
4	10.7		14.7	13.3	5.3				176.0
5	6.7	1.3	9.3	6.7	2.7	2.7			146.7
6	4.0		4.0	6.7	5.3	4.0			144.0
7			2.7	4.0		1.3			56.0
8			1.3	1.3	1.3				32.0
9	1.3		1.3	2.7	2.7				72.0
10					1.3				13.3
11	2.7								29.3
12	1.3								16.0
13	1.3		1.3						34.7
14									
15				1.3					20.0
16									
17	1.3								22.7
18									
19									
20									
21									
22									
23									
24									
25	1.3								33.3
26									
27	1.3								36.0
28									
29	1.3								38.7
30									
31	1.3								41.3

## 4.7 References

- Bartsch, N., Bauhus, J., Vor, T., 2002. Effects of Group Selection and Liming on Nutrient Cycling in an European Beech Forest on Acidic Soil. In A. Dohrenbusch, N. Bartsch (Eds.), *Forest Development* (pp. 109-142). Springer, Berlin.
- Bauhus, J., Puettmann, K. J., Kühne, C., 2014. Close-to-Nature Forest Management in Europe—Does It Support Complexity and Adaptability of Forest Ecosystems? In C. Messier, K. J. Puettmann, K. D. Coates (Eds.), *Managing Forests as Complex Adaptive Systems* (p. 353). Routledge, London, New York.
- Bohn, U., Neuhäusl, R., Gollub, G., Hettwer, C., Neuhäulovala, Z., Schlüter, H., Weber, H., 2003. Karte der natürlichen Vegetation Europas. Landwirtschaftsverlag, Münster.
- Brang, P., 2005. Virgin Forests as a Knowledge Source for Central European Silviculture: Reality or Myth? *Forest, Snow and Landscape Research*, 79, 19-32.
- Brang, P., Spathelf, P., Larsen, J. B., Bauhus, J., Boncina, A., Chauvin, C., Drössler, L., Garcia-Guemes, C., Heiri, C., Kerr, G., Lexer, M. J., Mason, B., Mohren, F., Mühlethaler, U., Nocentini, S., Svoboda, M., 2014. Suitability of Close-to-Nature Silviculture for Adapting Temperate European Forests to Climate Change. *Forestry*, 87, 492-503.
- Brumme, R., Khanna, P. K., 2009. *Functioning and Management of European Beech Ecosystems*. Springer, Berlin.
- Burschel, P., Huss, J., 1997. *Grundriß des Waldbaus*. Parey, Berlin.
- Chernyavskyy, M., 2005. The Dynamics of Virgin Beech Forests in the Ukrainian Carpathians. In F. D. Hamor, B. Commarmot (Eds.), *Natural Forests in the Temperate Zone of Europe—Values and Utilisation* (pp. 100-108). Rakhiv: Carpathian Biosphere Reserve and Birmensdorf: Swiss Federal Research Institute WSL.
- Commarmot, B., 2005. Structures of Virgin and Managed Beech Forests in Uholka (Ukraine) and Sihlwald (Switzerland): A Comparative Study. *Forest, Snow and Landscape Research*, 79, 45-56.
- Dröbler, L., 2006. *Struktur und Dynamik von zwei Buchenurwäldern in der Slowakei*. Ph.D Thesis, University of Göttingen.
- Dröbler, L., von Lüpke, B., 2005. Canopy Gaps in Two Virgin Beech Forest Reserves in Slovakia. *Journal of Forest Science*, 51, 446-457.
- Dröbler, L., Meyer, P., 2006. Waldentwicklungsphasen in zwei Buchen-Urwaldreservaten in der Slowakei. *Forstarchiv*, 77, 155-161.
- Duncker, P. S., Barreiro, S. M., Hengeveld, G. M., Lind, T., Mason, W. L., Ambrozy, S., Spiecker, H., 2012. Classification of Forest Management Approaches: A New Conceptual Framework and Its Applicability to European Forestry. *Ecology and Society*, 17, 51.
- Ellenberg, H., 1996. *Vegetation Mitteleuropas mit den Alpen*. Ulmer, Stuttgart.
- Finkeldey, R., Ziehe, M., 2004. Genetic Implications of Silvicultural Regimes. *Forest Ecology and Management*, 197, 231-244.
- Fröhlich, J., 1925. Aus dem südosteuropäischen Urwalde. *Forstwissenschaftliches Centralblatt*, 47, 199-206.
- Gehrhardt, E., 1923. Ueber Urwaldungen in den Karpathen. *Forstliche Wochenschrift Silva*, 11, 361-363.
- Grassi, G., Minotta, G., Giannini, R., Bagnaresi, U., 2003. The Structural Dynamics of Managed Uneven-Aged Conifer Stands in the Italian Eastern Alps. *Forest Ecology and Management*, 185, 225-237.
- Gratzer, G., Canham, C., Dieckmann, U., Fischer, A., Iwasa, Y., Law, R., Lexer, M. J., Sandmann, H., Spies, T. A., Splachtna, B., Szwagrzyk, J., 2004. Spatio-Temporal Development of Forests—Current Trends in Field Methods and Models. *Oikos*, 107, 3-15.
- Helms, J. A., 1998. *The Dictionary of Forestry*. CABI, Wallingford.

- Koop, H., Hilgen, P., 1987. Forest Dynamics and Regeneration Mosaic Shifts in Unexploited Beech (*Fagus sylvatica*) Stands at Fontainebleau (France). *Forest Ecology and Management*, 20, 135-150.
- Korpel, S., 1995. Die Urwälder der Westkarpaten. Gustav Fischer Verlag, Stuttgart, Jena, New York.
- Kral, K., Valtera, M., Janik, D., Samonil, P., Vrska, T., 2014. Spatial Variability of General Stand Characteristics in Central European Beech-Dominated Natural Stands—Effects of Scale. *Forest Ecology and Management*, 328, 353-364.
- Kral, K., Vrska, T., Hort, L., Adam, D., Samonil, P., 2010. Developmental Phases in a Temperate Natural Spruce-Fir-Beech Forest: Determination by a Supervised Classification Method. *European Journal of Forest Research*, 129, 339-351.
- Larsen, J. B., 2012. Close-to-Nature Forest Management: The Danish Approach to Sustainable Forestry. In J. M. Garcia, J. J. D. Casero (Eds.), *Sustainable Forest Management—Current Research*. InTechOpen.
- Leibundgut, H., 1993. Europäische Urwälder: Wegweiser zur naturnahen Waldwirtschaft. Haupt, Bern, Stuttgart.
- Levin, S. A., 2005. Self-Organization and the Emergence of Complexity in Ecological Systems. *BioScience*, 55, 1075-1079.
- Madsen, P., Larsen, J. B., 1997. Natural Regeneration of Beech (*Fagus sylvatica* L.) with Respect to Canopy Density, Soil Moisture and Soil Carbon Content. *Forest Ecology and Management*, 97, 95-105.
- Messier, C., Puettmann, K. J., Coates, K. D., 2014. *Managing Forests as Complex Adaptive Systems* (353 p). Routledge, London, New York.
- Meyer, P., 1999. Bestimmung der Waldentwicklungsphasen und der Texturdiversität in Naturwäldern. *Allgemeine Forst- und Jagdzeitung*, 170, 203-211.
- Meyer, P., Tabaku, V., von Lüpke, B., 2003. Die Struktur albanischer Rotbuchen-Urwälder—Ableitungen für eine naturnahe Buchenwirtschaft. *Forstwissenschaftliches Centralblatt*, 122, 47-58.
- Müller, K. M. (1929). *Aufbau, Wuchs und Verjüngung der südosteuropäischen Urwälder*. Schaper, Hannover.
- Muscolo, A., Bagnato, S., Sidari, M., Mercurio, R., 2014. A Review of the Roles of Forest Canopy Gaps. *Journal of Forestry Research*, 25, 725-736.
- Neumann, M., 1979. Bestandesstruktur und Entwicklungsdynamik im Urwald Rothwald/NÖ und im Urwald Čorkova Uvala/Kroatien. Ph.D Thesis, BOKU Vienna.
- Nuske, R. S., 2006. A Retrospective Study of Canopy Gap Dynamics of a European Beech Stand. Proceedings of the International Workshop “3D Remote Sensing in Forestry”, Vienna, 14-15 February 2006, 40-44.
- Oliver, C. D., Larson, B. C., 1996. *Forest Stand Dynamics* (update edition). John Wiley, New York.
- Otto, H. J., 1994. *Waldökologie* (391 p). Ulmer, Stuttgart.
- Parrott, L., 2010. Measuring Ecological Complexity. *Ecological Indicators*, 10, 1069-1076.
- Piovesan, G., Di Filippo, A., Alessandrini, A., Biondi, F., Schirone, B., 2005. Structure, Dynamics and Dendroecology of an Old-Growth *Fagus* Forest in the Apennines. *Journal of Vegetation Science*, 16, 13-28.
- Pommerening, A., 2002. Approaches to Quantifying Forest Structures. *Forestry*, 75, 305-324.
- Pretzsch, H., 2009. *Forest Dynamics, Growth and Yield* (664 p). Springer, Berlin.
- Röhrig, E., von Lüpke, B., Bartsch, N., 2006. *Waldbau auf ökologischer Grundlage*. Ulmer, Stuttgart.
- Runkle, J. R., 1992. *Guidelines and Sample Protocol for Sampling Forest Gaps* (44 p). General Technical Report PNW-GTR-283, Portland, OR: US Department of Agriculture Forest Service.

- Šamonil, P., Dolezelova, P., Vasickova, I., Adam, D., Valtera, M., Kral, K., Janik, D., Sebkova, B., 2013. Individual-Based Approach to the Detection of Disturbance History through Spatial Scales in a Natural Beech-Dominated Forest. *Journal of Vegetation Science*, 24, 1167-1184.
- Schütz, J.-P., 2001. Der Plenterwald und weitere Formen strukturierter und gemischter Wälder. Parey, Berlin.
- Schütz, J.-P., Saniga, M., 2011. Modelling the Risks of Natural Stand Closure Release with Ageing in Pure Beech (*Fagus sylvatica*) and Spruce (*Picea abies*) Stand. *Annals of Forest Science*, 68, 1105-1114.
- Shimatani, I. K., Kubota, Y., 2011. The Spatio-Temporal Forest Patch Dynamics Inferred from the Fine-Scale Synchronicity in Growth Chronology. *Journal of Vegetation Science*, 22, 334-345.
- Smith, D. M., Larson, B. C., Kelty, M. J., Ashton, P. M. S., 1997. The Practice of Silviculture. John Wiley and Sons, New York.
- Solé, R. V., Bascompte, J., 2006. Self-Organization in Complex Ecosystems. Princeton University Press, Princeton, NJ.
- Tabaku, V., 2000. Struktur von Buchen-Urwäldern in Albanien im Vergleich mit deutschen Buchen-Naturwaldreservaten und -Wirtschaftswäldern. Ph.D Thesis, University of Göttingen, Göttingen.
- Trotsiuk, V., Hobi, M. L., Commarmot, B., 2012. Age Structure and Disturbance Dynamics of the Relic Virgin Beech Forest Uholka (Ukrainian Carpathians). *Forest Ecology and Management*, 265, 181-190.
- von Gadow, K., Zhang, C. Y., Wehenkel, C., Pommerening, A., Corral-Rivas, J., Korol, M., Myklush, S., Hui, G. Y., Kiviste, A., Zhao, X. H., 2012. Forest Structure and Diversity. In T. Pukkala, von Gadow, K. (Eds.), Continuous Cover Forestry, Managing Forest, Ecosystems 23 (2nd ed., pp. 29-83). Springer, Dordrecht.
- Wagner, S., 1999. Ökologische Untersuchungen zur Initialphase der Naturverjüngung in Eschen-Buchen-Mischbeständen. Schriften aus der Forstlichen Fakultät der Universität Göttingen und der Niedersächsischen Forstlichen Versuchsanstalt. Band 129. Sauerländer, J D, Frankfurt.
- Winter, S., Brambach, F., 2011. Determination of a Common Forest Life Cycle Assessment Method for Biodiversity Evaluation. *Forest Ecology and Management*, 262, 2120-2132.
- Zeibig, A., Diaci, J., Wagner, S., 2005. Gap Disturbance Patterns of a *Fagus sylvatica* Virgin Forest Remnant in the Mountain Vegetation Belt of Slovenia. *Forest, Snow and Landscape Research*, 79, 69-80.
- Zenner, E. K., Hibbs, D. E., 2000. A New Method for Modeling the Heterogeneity of Forest Structure. *Forest Ecology and Management*, 129, 75-87.



# 5<sup>th</sup>

## CHAPTER

### A NOVEL EMPIRICAL APPROACH FOR DETERMINING THE EXTENSION OF FOREST DEVELOPMENT STAGES IN TEMPERATE OLD-GROWTH FORESTS

Eike Feldmann, Jonas Glatthorn, Markus Hauck, Christoph Leuschner

*European Journal of Forest Research* 137 (2018), 321–335.

#### Abstract

In the analysis of old-growth forest dynamics, the continuous process of tree ageing and forest structural change is split up into several distinct forest development stages. The criteria for distinguishing the stages vary among the different approaches. In most of them, vertical canopy heterogeneity is only coarsely addressed, and horizontal forest structure is quantified at spatial scales far exceeding the size of conventional forest inventory plots. In order to describe and analyze the complex mosaic structure of temperate old-growth forests with objective and quantitative measures in the context of forest inventories, we propose the Forest Development Stage Index  $I_{DS}$ . It employs two easily measured stand structural parameters (stem density and basal area) for quantifying the abundance of trees in three conventionally recognized tree diameter classes (premature: < 40 cm; mature: 40–70 cm; over-mature:  $\geq$  70 cm) in plots of 500 m<sup>2</sup> size, systematically distributed in the forest. This allows quantifying the spatial extension of the Initial, Optimum and Terminal stages of forest development at plot, stand and landscape levels. Based on thorough stand structural analyses in three virgin beech (*Fagus sylvatica*) forests in Slovakia, we demonstrate that  $I_{DS}$  is a promising tool for (i) quantifying the proportion of the three stages on different scales, (ii) visualizing the complex mixing of stages, and

(iii) analyzing dynamic changes in old-growth forest structure. We conclude that the Forest Development Stage Index has potential to improve the empirical foundation of forest dynamics research and to allow this discipline to proceed to more rigorous hypothesis testing.

**Keywords:** Forest Development Stage Index, forest dynamics, *Fagus sylvatica*, forest structure, old-growth forest, deadwood

## 5.1 Introduction

The forest development cycle is a theoretical concept to describe the structural dynamics of natural forests driven by demographic processes and the action of external disturbances, which repeats itself with the formation of a new generation (Watt, 1947; Remmert, 1991). Forest dynamics processes can take place on different spatial scales, from the single tree to the stand level (Oliver and Larson, 1996). What spatial scale is the most appropriate for study depends on the disturbance regime and tree species composition, both of which vary with climate and soil conditions (Peters, 1997; Kral et al., 2010a). North-American conceptual models generally concentrate on forest succession following relatively frequent large-scale disturbances that peak in a steady-state or dynamic equilibrium (which can last for quite long) before another disturbance resets the system (Franklin et al., 2002). In Europe, where large-scale disturbances are less frequent and forests are often formed by late successional tree species, concepts were developed to describe the spatial pattern and processes in the anticipated status of dynamic equilibrium at the stand level. Král et al. (2016) found the European conceptual model to be applicable to late-successional forests in North America as well, indicating some similarities in structural dynamics.

For describing the temporal dynamics of stand development in old-growth forests, most researchers split up the continuous process of tree ageing and forest structural change into distinct forest development stages, which sometimes were further divided into different development phases. Verbal descriptions of development stages or phases in European temperate forests are given by e.g. Leibundgut (1993), Korpel (1995), Meyer (1999), Tabaku (2000) and Kral et al. (2010 b). The categories were traditionally defined by expert decision. They were used to map the occurrence of different development stages or phases in old-growth forest landscapes in order to quantify the horizontal variability of forest structure and to draw conclusions on the driving forces of change (e.g. Neumann, 1979; Leibundgut, 1993; Korpel, 1995). Even though the distinction of development stages is a subjective process, it may allow comparing stand-level dynamics across different forest communities and biomes, if the criteria for stage



identification are sufficiently comparable across studies.

More recently, methods based on empirical stand structural data have been developed, which help to make the distinction of forest development stages or phases more objective and repeatable (Meyer, 1999; Tabaku, 2000; Emborg et al., 2000; Grassi et al., 2003; Kral et al., 2010b, 2016). While the required amount and quality of data differs, all such approaches allow the unambiguous assignment of forest plots to certain development stages or phases.

The information quality of stand structural data largely depends on the chosen spatial scale and this does also apply to the outcome of development stage categorizations (Commarmot et al., 2005; Kral et al., 2010a; Winter and Brambach, 2011; Zenner et al., 2014). The smallest possible unit is a single tree with its ontogenetic development and associated change in height and stem diameter. Information on these tree dimensional data has frequently been used in the study of natural forest dynamics (Emborg et al., 2000; Grassi et al., 2003; Kral et al., 2010b, 2016; Peck et al., 2015; Peterken, 1996; Tabaku, 2000; Winter and Brambach, 2011; Zenner et al., 2016). All the afore-mentioned approaches are based on selected structural features, among them the diameter or height of the largest trees, canopy cover, regeneration cover, or the amount of deadwood. The identification of development stages is mostly done on the plot level (156.25 to 500 m<sup>2</sup>) by determining which structural feature seems to have the strongest indicative value, while ignoring less obvious structural properties. This puts strong emphasis on a single ‘structural master factor’ in the classification process, while information about other stand characteristics is lost. Thus, these approaches implicitly assume structural uniformity at the chosen spatial scale (Pretzsch, 2009), while heterogeneity in stand structure in a patch as a characteristic of primeval forests is largely ignored. One consequence of such approaches is that end-life stages tend to be mapped more often than early ones (e.g. Zenner et al., 2016), and the forest appears more homogeneous than it really is. Further, Christensen et al. (2007) showed that the focus on only the dominant structural elements can result in misleading conclusions on how forest structure changes with time. In reality, the tree individuals in a patch of old-growth forest often differ in age and size and represent different ontogenetic phases, even in small plots of only 156.25 m<sup>2</sup> size. Thus, stages or phases might intermingle horizontally as well as vertically even in forest patches not exceeding the size of one or two trees. Korpel (1995) also observed that different stages and phases frequently overlapped in space and time in Slovakian virgin forests, and only his Optimum stage was found to occur in more or less pure form. Similar observations were made by Grassi et al. (2003) and Drößler and Meyer (2006). Paluch (2007) emphasized the spatially highly variable vertical stratification in the canopy of a natural beech-fir forest.

Thus, it seems desirable to advance the structural classification approach towards a concept that views tree populations as the sum of all tree individuals and allows conclusions on the development stage which dominates the patch, but provides information on subdominant structures as well. Further progress would be achieved, if the approach facilitated the assessment of development stages on different spatial scales. This would allow the application on various data sets including standardized forest structure inventories, which are often conducted in plots of 500–1000 m<sup>2</sup> size that are placed randomly or systematically in the stand (e.g. Commarmot et al., 2013; Meyer et al., 2001). To do so would further restrict the input data to parameters that are widely available.

Here, we propose a method for quantifying the extension of three commonly recognized forest development stages ('Initial', 'Optimum' and 'Terminal') on the plot level in temperate old-growth forests using empirical data on tree size and stem density. We select true virgin forests (sensu Hunter, 1990) of *Fagus sylvatica* L. in the western Carpathians as test systems. The proposed approach aims at defining forest development stages by objective criteria, allowing to compare the dynamics of different forest stands and communities and providing a solid data base for the multivariate analysis of stand structure. As criteria for development stage distinction, we choose easy-to-measure parameters and express them in relative terms in order to account for large structural differences between forest communities and biomes. The approach is therefore not restricted to our test systems, but could be adapted for use in other forest types with different structure and environmental conditions as well.

## 5.2 Methods

### 5.2.1 Study sites

Since our study addresses the dynamics of natural forests, and management activities often imprint on forest structure for centuries (e.g. Tabaku, 2000), we selected true virgin forests for study, for which no forest management is known for the past 500 years or so. We studied three beech-dominated (*Fagus sylvatica*) forests at montane elevation in the Carpathians of eastern Slovakia which are protected as National Nature Reserves, two of them listed in UNESCO's World Heritage. They represent some of the last remnants of temperate broad-leaved virgin forest in the western Carpathians, where they still covered extended areas in the early 20<sup>th</sup> century. While the reserves Havešová (HA) and Kyjov (KY) are pure beech stands, Stučica (ST) contains a considerable proportion (11% by stem numbers) of silver fir (*Abies alba*). However,

all three stands belong to the *Fagetum dentariosum glandulosae* forest community (Bohn et al., 2003). The physiography of the three forests is summarized in Table 5.1. Some basic stand structural characteristics are given in Table 5.3.

*Table 5.1:* Physiography of the three study sites in eastern Slovakia. Due to the sloping terrain, ranges are given for altitude, precipitation and temperature. 1 - mean annual precipitation and mean annual temperature.

	<b>Havešová</b>	<b>Kyjov</b>	<b>Stužica</b>
<b>Altitude</b>	550 – 650 m a.s.l.	700 – 820 m a.s.l.	700 – 950 m a.s.l.
<b>Precipitation<sup>1</sup></b>	800 – 850 mm	950 – 1000 mm	900 – 1200 mm
<b>Mean temperature<sup>1</sup></b>	6.0 – 6.5 °C	5.2 – 5.7 °C	4.0 – 5.0 °C
<b>Parent material</b>	Carpathian flysh	Andesite	Carpathian flysh
<b>Soil type (FAO/WRB)</b>	Eutric Cambisol	Dystric Cambisol	Eutric Cambisol
<b>Aspect</b>	South to east	North to east	South-east to south-west
<b>Slope</b>	15.8°	11.9°	12.9°
<b>Plant community</b>	Fagetum dentariosum glandulosae association		

### 5.2.2 Data collection

In every stand, we installed each 40 circular plots of 500 m<sup>2</sup> size (25.24 m in diameter) arranged on the nodes of rectangular grids. The grid spacing was 65 m in Kyjov, 100 m in Stužica and 140 m in Havešová. Different spacing had to be chosen so that the 40 plots could be accommodated within each of the stands and no plot was within a 100 m distance to the nearest reserve border. As ST is comparably large and hosts different forest types (Korpel, 1995), we concentrated our study on an area of approximately 70 ha in the south-east of the reserve. Two of the 40 plots in ST close to the stand edge were subsequently excluded from the analysis, as it turned out that they may have been affected by forest management activities in the early 20<sup>th</sup> century. In every plot, we mapped all living and dead trees with diameter at breast height (DBH)  $\geq 7$  cm and recorded their DBH. Lying deadwood was also measured if the stump was located in the plot. Every dead tree trunk was assigned to one of five decay classes, adopting the classification system of Meyer et al. (2001) that agrees well with the systems proposed by Hunter (1990), Nagel and Svoboda (2008) and others. On every plot the height of three tree individuals of the main tree species (beech in Kyjov and Havešová, beech and fir in Stužica) and of all individuals of the less abundant tree species was recorded with a Vertex IV height meter (Haglöf Sweden AB, Långsele, Sweden). The volume of living trees was then calculated according to Petráš

and Pajtk (1991) and for dead trees we applied a reduction factor in dependence on their decay class, as proposed by Meyer et al. (2001). All trees were inspected for the occurrence of microhabitats formed by bark injury or the bracket fungus, and cavities at the stem base and the upper stem and signs of necrosis on the trunk. Tree saplings > 1.5 m in height (termed ‘advanced regeneration’) were counted in two belt transects of each 13 m<sup>2</sup> area per plot.

### 5.2.3 The Forest Development Stage Index ( $I_{DS}$ )

In temperate broad-leaved old-growth forests, plots of 500 m<sup>2</sup> size typically contain tree individuals of variable age and dimension, which from an ontogenetic perspective, may be assigned to different forest development stages. Even in monospecific stands, the forest structure in a plot of this size can be quite heterogeneous. Groups of trees of different age and dimensions may occur in close neighborhood to each other and identified development stages thus may overlap through vertical canopy stratification. To account for this heterogeneity, we introduced the Development Stage Index  $I_{DS}$ , which is derived from measured tree dimensional data. It calculates the relative extension of development stages in a plot and allows assigning a plot to a prevailing stage by identifying the stage with largest extension.

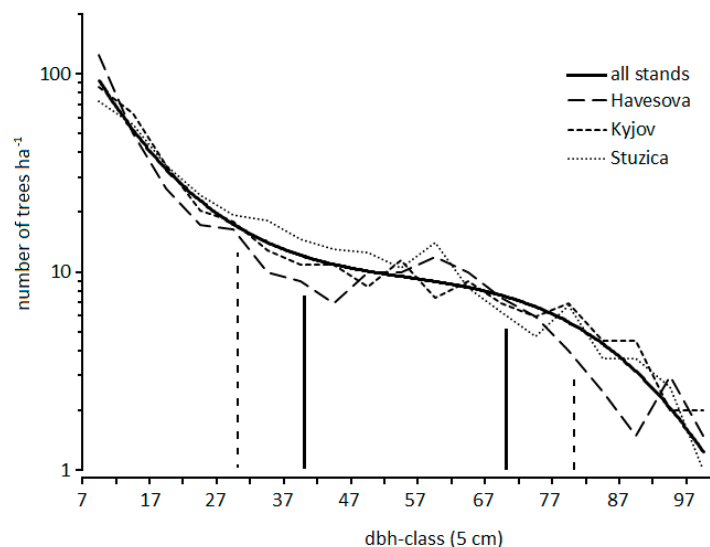


Figure 5.1: Semi-logarithmic stem diameter-density distribution curve of living trees (N ha<sup>-1</sup>) per 5 cm DBH-class for the three forest stands (dashed lines) and a fitted line (continuous), representing a third degree-polynomial function calculated on the mean of the three stands across the DBH-classes. The continuous vertical lines mark the locations of the thresholds set for the assignment of trees to the three stages ‘Initial’, ‘Optimum’ and ‘Terminal’. The dashed vertical lines mark the altered thresholds in the sensitivity analysis

Stem diameter was used as the principal criterion for assigning a tree or tree group to one of the three development stages ‘Initial’, ‘Optimum’ or ‘Terminal’. The DBH thresholds were chosen by approximating points that enclose a section of the mean stem diameter-density distribution curve of the three virgin forests with low curve steepness (Fig. 5.1). According to Goff and West (1975) the beginning and end points of such a section (bench marks) indicate transitions between three distinct phases in the tree life cycle in temperate old-growth forests of shade-tolerant North American tree species. The resulting DBH-classes and their main characteristics are given in Table 5.2.

*Table 5.2:* Assignment of trees to ontogenetic phases (premature, mature, over-mature) according to the three DBH-classes proposed in this study, with a short characterization of the respective phase. The corresponding phases given by Goff and West (1975) are indicated in brackets.

DBH-class	Ontogenetic phase	Characterization
$7 \leq \text{DBH} < 40 \text{ cm}$	Premature phase (understory phase)	slow growth and high mortality
$40 \leq \text{DBH} < 70 \text{ cm}$	Mature phase (vigorous overstory phase)	rapid growth and low mortality
$70 \text{ cm} \leq \text{DBH}$	Over-mature phase (senescent overstory phase)	reduced growth and increased mortality

These diameter thresholds largely fit to a categorization of tree dimensions often used in silviculture (e.g. Röhrig et al., 2006). For simplicity, the premature trees in a plot were subsequently assigned to the Initial development stage, mature trees to the Optimum stage, and over-mature trees to the Terminal stage of forest development (Fig. 5.2). Dead trees have until recently influenced the structure of the living stand and still are imprinting on the recent stand structure through competitive effects that were exerted by the now dead trees in the past. To include dead trees in the  $I_{DS}$  thus can help to understand the stand development in the more recent past. Therefore, not only live trees were considered in the calculation of  $I_{DS}$ , but dead trees as well to account for their contribution to forest structure and space filling. We used the same DBH-based classification as above, assuming that mortality is to a considerable extent caused by community-level processes characteristic for the considered life-history phase (Holzwarth et al., 2013). With proceeding decay, dead trees were reduced in their count and for calculating basal area by applying specific reduction factors for the five wood decay classes (DC) (DC 1 = 1.0, DC 2 = 0.95, DC 3 = 0.85, DC 4 = 0.7 and DC 5 = 0.5). Thus, deadwood represents a structural memory of the recent past in the  $I_{DS}$  score that is fading with increasing wood decay. This procedure considers that the space once occupied by the live tree is increasingly filled by

neighbors and recently established individuals. Beech logs up to class DC 5 are present in the stands for about 35 years (Müller-Using and Bartsch, 2009; Prívětivý et al., 2016); according to Lombardi et al. (2008) beech and fir logs decompose at similar rates.

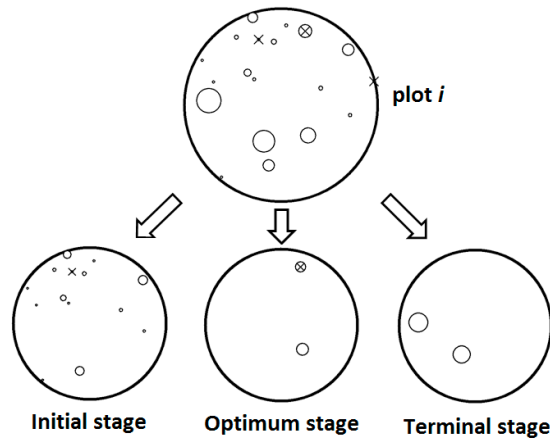


Figure 5.2: Scheme illustrating the assignment of stems of variable diameter in an exemplary 500 m<sup>2</sup>-plot to the three development stages (Initial, Optimum and Terminal) using the DBH categories 7–39 cm, 40–69 cm and ≥ 70 cm as selection criteria. Thus, the plot contains elements of all three stages

The relative importance of trees of these three diameter categories in a plot was quantified through their abundance in terms of stem number ( $N$ ) and basal area ( $BA$ ) to account for tree size differences. To solely rely on  $BA$  as a measure of ‘natural stocking density’ (Assmann, 1961) is not sufficient here. Trees at the lower end of a size class have a low  $BA$  but can reach high  $N$ ; the opposite is valid for trees at the upper end of the class. Both dimension measures were expressed in relative terms using forest patches with more or less exclusive presence of one of these tree size classes as a reference (see Table 5.4).

### 5.2.4 Calculation of $I_{DS}$

For all plots  $i$ , the summed number of trees ( $N_{DSi}$ ) and the summed basal area ( $BA_{DSi}$ ) in the respective stages ( $DS$ ) were calculated. To define the highest achievable tree number, which a given diameter category or development stage may reach in a plot ( $N_{DSref}$ ), we identified the plots with the highest tree number ( $N_{DSmax}$ ) in that stage in the three forest stands and averaged over these maximum densities:

$$N_{DSref} = \frac{\sum N_{DSmax}}{3}$$

The same was done for the parameter basal area:

$$BA_{DSref} = \frac{\sum BA_{DSmax}}{3}$$

The index value  $I$  of a given development stage  $DS$  ( $I_{DS}$ ) in plot  $i$  was then calculated as the summed quotients of actual tree number ( $N_{DSi}$ ) to potential maximum tree number ( $N_{DSref}$ ), and actual basal area ( $BA_{DSi}$ ) to potential maximum basal area ( $BA_{DSref}$ ) in this diameter category:

$$I_{DSi} = \left( \frac{N_{DSi}}{N_{DSref}} + \frac{BA_{DSi}}{BA_{DSref}} \right)$$

with  $DS$  being the Initial (*Ini*), Optimum (*Opt*) or Terminal (*Ter*) stage.

The stage with the highest index score is per definitionem the dominating development stage in that plot. Dominance refers only to abundance and not to interactions between trees of different diameters. A main purpose of the  $I_{DS}$  score is to measure the complex structural mixing of the three development stages on the plot level. The relative proportion of  $I_{DS}$  scores of the three stages informs more about the current structural composition of the stand than about the stages conditions and the development potential. However, it can also be used to infer on processes of dynamic structural change, when repeated surveys with the index are conducted.

### 5.2.5 Data analysis

The index  $I_{DS}$  was used for two purposes, (i) to generate data on the relative abundance of the three development stages in the individual plots and the forest stands, and (ii) to identify the most extended (or ‘dominant’) stage in a plot. This data can be used for mapping principal forest structural categories in old-growth forests, and they served for calculating the relative extension of previously defined development stages in the three primeval forests. As a measure of structural heterogeneity (and not species diversity) in the sample plots, we calculated Shannon’s diversity index ( $H'$ ) and evenness with the relative stage extension data of the three stages in the plot. In the calculations, we assigned zero values to stages that were currently not present on a plot; the calculation of evenness was done with reference to conditions with equal abundance of all three stages in a plot.

There is the possibility that the  $I_{DS}$  approach works only in the frame of the DBH classes and

plots sizes which exist in the studied forests. To explore whether alterations of the proposed  $I_{DS}$  index to modification in the chosen DBH classes and plot size lead to unexpected results which might be in conflict with the underlying assumptions and thus challenge the validity of the index, we conducted a sensitivity analysis. We tested for the effect (i) of altered DBH thresholds used for distinguishing the tree diameter classes, and (ii) of different plot sizes on the  $I_{DS}$  values calculated for the plots. In these runs, the DBH thresholds were shifted from 40 to 30 cm and from 70 to 80 cm, and plot size was reduced from 500 to 156.25 m<sup>2</sup>.

We further analyzed relationships between the development stage index  $I_{DS}$  and selected structural characteristics of the trees and stands, notably:

- the number of live, dead and all trees ( $N_p$ ,  $N_d$  and  $N_{tot}$ )
- the  $BA$  of live, dead and all trees ( $BA_p$ ,  $BA_d$  and  $BA_{tot}$ )
- the volume of live, dead and total wood ( $V_p$ ,  $V_d$  and  $V_{tot}$ )
- the density of advanced regeneration ( $REG$ ), and
- the number of microhabitats ( $HAB$ )

The three stands were compared for significant differences in their structural characteristics. If this was the case, then further analyses were performed separately for the three stands. We performed correlation analyses for the  $I_{DS}$  scores of the three stages, and for their relative proportions ( $I_{DS}/I_{Total}$ ) on the plots. The first may better indicate stage-specific density effects and the latter effects of apparent structural complementarity among the stages. The fit and significance of correlations was analyzed by performing Pearson's product-moment correlation. After stratification of the plots by assigning them to the prevailing development stage, the three development stages were tested for significant differences in the above-mentioned structural characteristics. As the data for stands and stratified stages did not fit to normal distribution, a Mann-Whitney U-test was employed. All analyses were done with R software version 3.2.2 (R Core Team, 2015) using a confidence level of 0.95 throughout. The p-values for multiple testing were adjusted by the Bonferroni-Holm method.

## 5.3 Results

### 5.3.1 Stand structural characteristics

The three virgin forests had similar mean densities of live trees and nearly equal basal areas



(Table 5.3), while the number of dead trees increased in the sequence  $KY < HA < ST$  (HA and ST significantly different from KY). The difference in total tree density (live and dead) was also small between the stands. There was no significant difference in the volume of aboveground wood biomass and dead wood volume among the three stands, but the volume of live and dead wood taken together was ~20% smaller in KY than in HA and ST (difference significant). The density of advanced regeneration (height > 1.5 m) was highest in ST, but the stands differed not significantly in this respect.

Stand		$N_l$	$N_d$	$N_{tot}$	$BA_l$	$BA_d$	$BA_{tot}$	$V_l$	$V_d$	$V_{tot}$	$REG$	$HAB$	$pFIR^*$
		(N ha <sup>-1</sup> )			(m <sup>2</sup> ha <sup>-1</sup> )			(m <sup>3</sup> ha <sup>-1</sup> )			(N ha <sup>-1</sup> )	(N ha <sup>-1</sup> )	%
HA	mean	334	<b>60</b>	394	33.8	11.4	45	664	168	<b>831</b>	2346	<b>161</b>	0
	SD	±126	±45b	±153	±12.5	±10.5	±12.4	±292	±172	±293b	±2781	±78a	0
KY	mean	329	<b>43</b>	372	35.3	11.7	47	536	123	<b>659</b>	2279	<b>133</b>	0
	SD	±91	±36.5a	±98	±13.1	±8.8	±10.6	±219	±104	±178a	±4027	±89a	0
ST	mean	329	<b>71</b>	400	36.0	13.4	49.4	634	177	<b>811</b>	3269	<b>241</b>	11.6
	SD	±114	±43.9b	±131.9	±11.6	±9.3	±10.9	±250	±126	±223b	±4254	±129b	±10.2

Table 5.3: Stand-level means ( $\pm$  standard deviation) of 12 structural characteristics of the virgin forests Havešová (HA), Kyjov (KY) and Stučica (ST) for the each 40 plots of 500 m<sup>2</sup> per stand. All parameters are given on a hectare basis.  $N_l$ ,  $N_d$ ,  $N_{tot}$  – number of live, dead and all stems (live + dead)  $\geq 7$  cm DBH,  $BA_l$ ,  $BA_d$ ,  $BA_{tot}$  – cumulative basal area of live, dead and total stems,  $V_l$ ,  $V_d$ ,  $V_{tot}$  – volume of live, dead and all stems,  $REG$  - density of larger tree saplings > 1.5 m in height,  $HAB$  - number of microhabitats in stems, and  $pFIR$  - proportion of silver fir stem in the plots (\*only in Stučica). Parameters with significant differences between stands are indicated by different small letters and are printed in bold.

The volume of aboveground wood biomass increased from the Initial to the Optimum stage (Fig. 5.A2 in the Supplement). Between the Optimum and the Terminal stage, it remained stable in the HA and KY forests, but increased in the ST stand. When deadwood is added to obtain total wood volume, all stands showed increasing volumes from the Initial to the Terminal stage. Among the plots of a development stage, wood volume generally varied greatly.

### 5.3.2 Characterizing stand structure by the Development Stage Index $I_{DS}$

The minimum number of trees found on a 500 m<sup>2</sup>-plot was  $n = 7$ . All plots contained trees of two, and often three, different stem diameter classes. Thus, the same plot was often assignable to two or more development stages. Ninety-nine percent of the plots contained trees assignable to the

Initial stage (7–40 cm DBH), 98% trees of the Optimum stage (40–70 cm), and 88% contained over-mature trees (> 70 cm) assignable to the Terminal stage. In the KY stand, over-mature trees were present in 98% of the plots, indicating a relatively even distribution of large trees across the stand. Even though mean stem density and basal area were not significantly different between the three stands, the observed maximum  $N$  and  $BA$  values in the respective stages differed between the HA, KY and ST forests (Table 5.4).  $N_{Ini}$  and  $BA_{Ter}$  reached exceptionally high maxima in certain HA plots, but much lower peak values in KY (except for  $BA_{Ini}$ ). With the means of the stage-specific maxima being used as a reference, the relative stem density and basal area values of the three stages (0.31 to 0.47, mostly in the range 0.35–0.44) were remarkably similar in the three stands (supplemental Table 5.A1). The calculated  $I_{DS}$  scores reached very similar proportions of  $I_{Ini}$ ,  $I_{Opt}$  and  $I_{Ter}$  in  $I_{Total}$  (the summed indices of all three stages) regarding all 118 plots, but varied to some extent in their means (Table 5.6) and distribution (Fig. 5.A1 in the Supplement) between the three stands. As follows from the logics of the  $I_{DS}$  score approach, we found significant negative correlations between the  $I_{DS}$  score of a single stage with the summed scores of the respective two other stages ( $I_{Ini}$ :  $r = -0.43$ ,  $p < 0.001$ ;  $I_{Opt}$ :  $r = -0.55$ ,  $p < 0.001$ ;  $I_{Ter}$ :  $r = -0.64$ ,  $p < 0.001$ ).

Table 5.4: Maximum values of stem number ( $N_{max}$ ) and basal area ( $BA_{max}$ ) in the DBH classes of three forest development stages in the three stands (presented as  $n\ ha^{-1}$  and  $m^2\ ha^{-1}$ ; consider the effect of the reduction factors for the different decay classes on the calculated values). The means over all three stands are also given. The latter were used as a reference for expressing the calculated extension of a stage in a plot in relative terms.

Stand	Initial stage		Optimum stage		Terminal stage	
	$N_{max}$	$BA_{max}$	$N_{max}$	$BA_{max}$	$N_{max}$	$BA_{max}$
HA	967	17.89	180	43.17	94	74.97
KY	476	20.84	174	37.10	80	46.37
ST	687	20.22	180	44.49	104	52.63
<b>mean</b>	<b>710</b>	<b>19.65</b>	<b>178</b>	<b>41.59</b>	<b>93</b>	<b>57.99</b>

As expected,  $I_{DS}$  was closely related to various plot-level structural attributes such as the basal area and wood volume of the living trees (Table 5.5). This relation was positive for  $I_{Ter}$  and  $I_{Opt}$  but negative for  $I_{Ini}$ , as trees of the latter stage profit from a reduced biomass of the older and larger trees. A close negative relation was also found between the  $I_{Ini}$  score and the abundance of tree saplings > 1.5 m ( $REG$ ), reflecting that dense stands of young trees generally suppress the offspring most effectively. A strong correlation ( $r: 0.87$ – $0.94$ ) exists between the  $I_{DS}$  scores of the three stages and their corresponding proportions ( $I_{DS}/I_{Total}$ ) in a plot. Accordingly, we found similar tendencies for the relations between the stages proportions and the structural attributes (Table 5.5). The Initial

stage on the one hand and the Optimum and Terminal stages on the other revealed significant differences in the structural parameters ( $N_p$ ,  $BA_p$ ,  $BA_{tot}$ ,  $V_l$ ) (Table 5.A2 in the Supplement).

Table 5.5: Pearson's r and significance level (p-value) of the correlation between 11 stand structural characteristics and the abundance of the three development stages (Initial, Optimum, Terminal) in the three stands as expressed by the  $I_{DS}$  scores and the relative proportion ( $I_{DS}/I_{Total}$ ) of the three stages ( $N_p$ ,  $N_d$  and  $N_{tot}$  = number of live, dead and all trees,  $BA_p$ ,  $BA_d$ ,  $BA_{tot}$  = basal area of live, dead and all trees,  $V_p$ ,  $V_d$  and  $V_{tot}$  = volume of live, dead and total wood,  $REG$  = density of advanced regeneration). Significant correlations are marked by bold print. For convenience, the three stands are analyzed separately only in the case of  $N_d$  and  $V_{tot}$  with significantly different means between the stands.

Structural attributes	Initial stage				Optimum stage				Terminal stage				
	$I_{ini}$		proportion <sub>ini</sub>		$I_{opt}$		proportion <sub>opt</sub>		$I_{ter}$		proportion <sub>ter</sub>		
	r	p-value	r	p-value	r	p-value	r	p-value	r	p-value	r	p-value	
$N_p$ (N/ha)	<b>0,84</b>	<b>&lt;0,001</b>	<b>0.64</b>	<b>&lt;0.001</b>	0,11	0,25	-0,07	0,452	<b>-0,28</b>	<b>0,002</b>	<b>-0.40</b>	<b>&lt;0.001</b>	
HA	<b>0,69</b>	<b>&lt;0,001</b>	<b>0.53</b>	<b>&lt;0.001</b>	-0,14	0,4	-0,21	0,194	-0,13	0,423	-0,21	0,203	
$N_d$ (N/ha)	KY	0,27	0,092	0,24	0,14	-0,06	0,728	-0,05	0,757	-0,02	0,921	-0,14	0,384
ST	<b>0,50</b>	<b>0,001</b>	<b>0.40</b>	<b>0.013</b>	0,22	0,181	0,13	0,435	<b>-0,40</b>	<b>0,014</b>	<b>-0.39</b>	<b>0.019</b>	
$N_{tot}$ (N/ha)	<b>0,89</b>	<b>&lt;0,001</b>	<b>0.67</b>	<b>&lt;0.001</b>	0,11	0,243	-0,06	0,49	<b>-0,31</b>	<b>&lt;0,001</b>	<b>-0.43</b>	<b>&lt;0.001</b>	
$BA_p$ (m <sup>2</sup> /ha)	<b>-0,22</b>	<b>0,019</b>	<b>-0.54</b>	<b>&lt;0.001</b>	<b>0,37</b>	<b>&lt;0,001</b>	0,14	0,157	<b>0,44</b>	<b>&lt;0,001</b>	<b>0.26</b>	<b>0.004</b>	
$BA_d$ (m <sup>2</sup> /ha)	0,12	0,201	0,11	0,244	-0,15	0,102	-0,17	0,064	0,11	0,223	0,08	0,38	
$BA_{tot}$ (m <sup>2</sup> /ha)	-0,13	0,15	<b>-0.49</b>	<b>&lt;0.001</b>	<b>0,27</b>	<b>0,003</b>	0,01	0,93	<b>0,57</b>	<b>&lt;0,001</b>	<b>0.35</b>	<b>&lt;0.001</b>	
$V_p$ (m <sup>3</sup> /ha)	<b>-0,33</b>	<b>&lt;0,001</b>	<b>-0.61</b>	<b>&lt;0.001</b>	<b>0,31</b>	<b>&lt;0,001</b>	0,11	0,223	<b>0,50</b>	<b>&lt;0,001</b>	<b>0.34</b>	<b>&lt;0.001</b>	
$V_d$ (m <sup>3</sup> /ha)	0,06	0,514	0,05	0,577	-0,15	0,102	-0,17	0,060	0,16	0,089	0,12	0,176	
HA	<b>-0,42</b>	<b>0,008</b>	<b>-0.65</b>	<b>&lt;0.001</b>	0,20	0,217	-0,06	0,730	<b>0,74</b>	<b>&lt;0,001</b>	<b>0.54</b>	<b>&lt;0.001</b>	
$V_{tot}$ (m <sup>3</sup> /ha)	KY	-0,23	0,16	<b>-0.66</b>	<b>&lt;0.001</b>	<b>0,40</b>	<b>0,011</b>	0,16	0,31	<b>0,60</b>	<b>&lt;0,001</b>	<b>0.38</b>	<b>0.017</b>
ST	<b>-0,38</b>	<b>0,02</b>	<b>-0.70</b>	<b>&lt;0.001</b>	0,10	0,544	-0,09	0,60	<b>0,70</b>	<b>&lt;0,001</b>	<b>0.54</b>	<b>&lt;0.001</b>	
$REG$ (N/ha)	<b>-0,24</b>	<b>0,01</b>	<b>-0.23</b>	<b>0.013</b>	0,06	0,533	0,05	0,575	0,11	0,228	0,12	0,199	
$HAB$ (N/ha)	-0,17	0,058	<b>-0.31</b>	<b>&lt;0.001</b>	<b>0,25</b>	<b>0,007</b>	0,15	0,102	<b>0,19</b>	<b>0,037</b>	0,08	0,341	

### 5.3.3 Spatial extension of development stages

The  $I_{DS}$  score allows quantifying the extension of different development stages in the forest, either through the relative extension of the stage in the total investigated plot area or via the proportion of all plots that are dominated by that stage. As shown by the box plots in supplemental Fig. 5.1, the  $I_{DS}$  scores characterizing the abundance of the three stages vary largely among the plots, reflecting small-scale heterogeneity in the stands. Structural differences between the three forests become visible when comparing the median values (supplemental Fig. 5.A1) and arithmetic means (Table 5.6) of the  $I_{Ini}$ ,  $I_{Opt}$  and  $I_{Ter}$  scores of the three stands. The Terminal stage with over-mature trees is more widely distributed in the KY forest (34% of the total plot area), while the ST forest has a greater presence of the Optimum and Initial stages in its plots (present on 34 and 39%, respectively); in contrast, the Terminal stage occurs in ST on only 28% of the area (Table 5.6).

*Table 5.6:* Mean extension of the three development stages in the plots of the three stands as expressed by the  $I_{DS}$  index (i.e. the summed quotients of actual tree number,  $N_{DS}$  to potential maximum tree number,  $N_{DSref}$ , and actual basal area,  $BA_{DS}$  to potential maximum basal area,  $BA_{DSref}$ , in the respective DBH category) (means and standard deviation of  $I_{Ini}$ ,  $I_{Opt}$ ,  $I_{Ter}$ , and  $I_{Total}$ , n = 40 plots in HA and KY, n = 38 in ST, 118 plots in total). The percentage share of the Initial, Optimum and Terminal stages (proportion of  $I_{DS}$  in  $I_{Total}$ ) in the three stands is given in brackets.  $I_{Total}$  is the summed extension of the three stages in a plot. The mean evenness of the three stages in the plots is also given (1.0 = all stages occur at equal abundance).

Stand	$I_{Ini}$			$I_{Opt}$			$I_{Ter}$			$I_{Total}$		evenness	
	mean	SD	%	mean	SD	%	mean	SD	%	mean	SD	mean	SD
HA	0.75	±0.39	(35%)	0.78	±0.46	(35%)	0.66	±0.46	(30%)	2.19	±0.43	0.84	±0.15
KY	0.72	±0.31	(33%)	0.73	±0.47	(32%)	0.76	±0.41	(35%)	2.21	±0.46	0.88	±0.12
ST	0.81	±0.35	(34%)	0.94	±0.47	(39%)	0.66	±0.51	(27%)	2.41	±0.43	0.85	±0.15
All stands	0.76	±0.35	(34%)	0.81	±0.47	(35%)	0.69	±0.46	(31%)	2.27	±0.45	0.85	±0.14

A similar picture emerges when the proportion of plots dominated by a given stage is compared among the three forests: The ST forest has a lower frequency of the Terminal stage (dominant in 32% of the plots), which is more widespread in the KY and HA forests (35 and 38%; Table 5.7). While plots dominated by the Terminal stage prevail in the HA forest, the most frequent plots in ST are those dominated by the Optimum stage. The KY forest ranges between HA and ST with respect to the dominance of Optimum and Terminal phase.

Table 5.7: Proportion of plots (in %) dominated by one of the three development stages in the three stands (n = 40 plots in HA and KY, n = 38 in ST, 118 plots in total).

Stand	Initial	Optimum	Terminal
HA	30.0	32.5	37.5
KY	30.0	35.0	35.0
ST	28.9	39.5	31.6
All	29.7	35.6	34.7

### 5.3.4 Sensitivity analysis of the classification scheme

Shifting the DBH thresholds for the premature tree class from 7–40 cm in the original scheme to 7–30 cm and that of the over-mature tree class from > 70 to > 80 cm increased the DBH range of the trees which are included in the Optimum (> 30 to ≤ 70 cm) stage with the result that the mean  $I_{Opt}$  score increased in the three stands by 21%, while the mean scores of the Initial and Terminal stages ( $I_{Ini}$  and  $I_{Ter}$ ) decreased by 4 and 18% compared to the original scheme. Thirty-one instead of 13% of the plots contained no trees assignable to the over-mature DBH category (Terminal stage). When reducing the plot size from 500 to 156.25 m<sup>2</sup>, still more than 95% of the plots contained two or more trees (median: n = 5.5). The number of plots, in which only two development stages were present, strongly increased from 19 to 81 of 118; 16 plots contained just a single stage (in most cases the Initial). Thus, smaller plots resulted in less spatial overlap of the three development stages, but the average proportion of the three development stages in the total investigated plot area remained similar to that derived for the 500 m<sup>2</sup>-plots.

### 5.3.5 Visualizing the mingling of stages in the study plots

We used ternary graphical plots to visualize for our 118-plot sample the variable mixing of trees assignable to the three development stages. For every plot, the  $I_{DS}$  scores of the three stages were expressed in percent of the summed three  $I_{DS}$  values of that plot (=  $I_{Total}$ ) along three axes from 0 to 100%, which define the contribution of the Initial, Optimum and Terminal stage to the  $I_{Total}$  score (see Fig. 5.3 for ternary plots of the HA, KY and ST stands, and the pooled plots of all stands). The majority of plots was located in moderate distance to the center of the graph, where the three stages contribute equally to  $I_{Total}$  (by about 33%); this is also expressed by the evenness of the three  $I_{DS}$  scores which reaches high means in all three stands (Table 5.6). Plots with high percentages of  $I_{Ini}$ ,  $I_{Opt}$  and  $I_{Ter}$ , and low percentages of  $I_{Ini}$  and  $I_{Opt}$ , are rare. In contrast, plots with low or zero scores of  $I_{Ter}$  were present in all three forests ( $I_{Ter}$  was zero in 12% of the 118 plots). The HA forest differed from the other two stands in that many plots were located

left of the plot center at higher  $I_{Ter}$  scores, while the ST plots were more frequent right of the center towards lower  $I_{Ter}$  scores. The 40 KY plots showed the most even distribution across the ternary plot, reflecting the relatively balanced proportions of stages on the stand level (Table 5.6) in this forest.

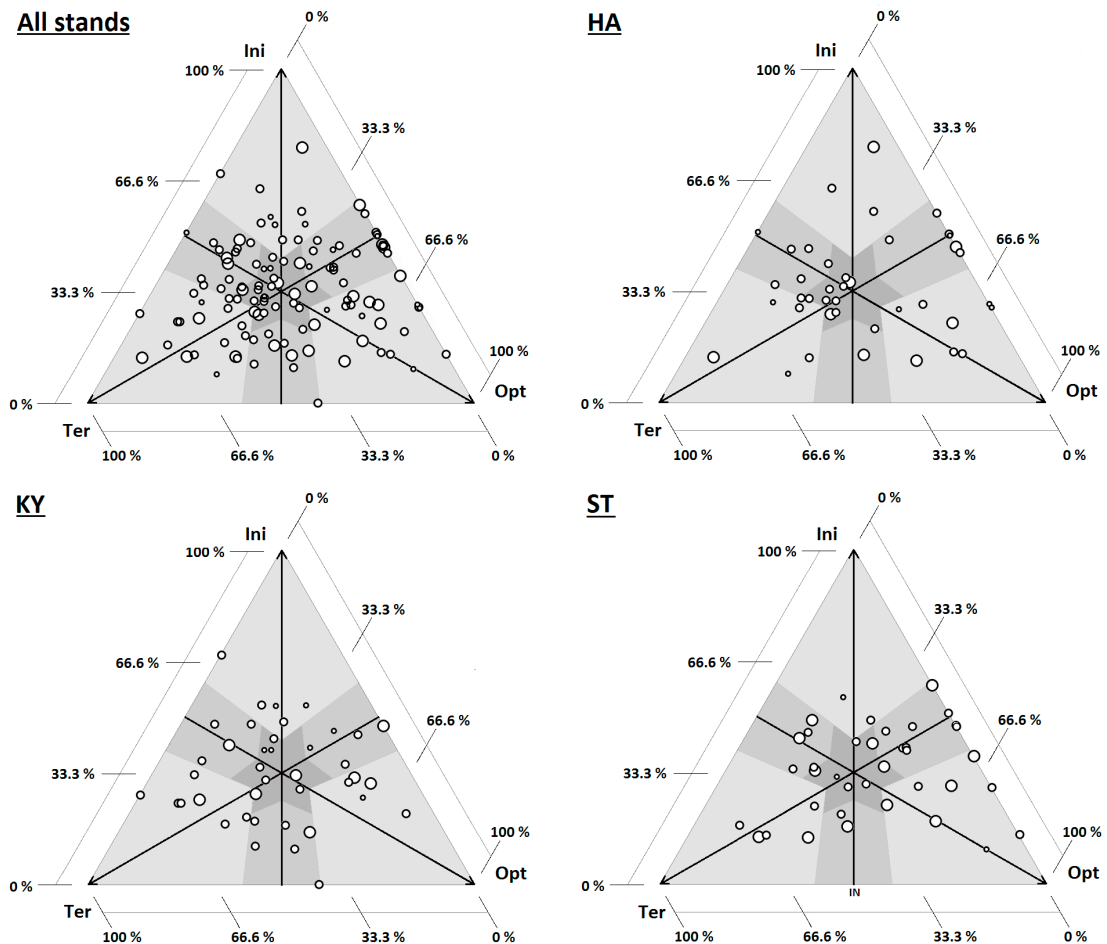


Figure 5.3: Ternary diagrams visualizing the relative importance of the Initial, Optimum and Terminal stage in the 40 (or 38) plots in the stands HA, KY and ST and in all plots pooled (all stands). The relative importance of a stage is expressed by its  $I_{DS}$  score related to the plot  $I_{Total}$  (the summed  $I_{DS}$  scores of all three stages in a plot). The three arrows in the diagram indicate the position of a plot along the 0-100% axes for the Initial stage (upper corner of triangle), the Optimum stage (lower right corner) and the Terminal stage (lower left corner). Plots located in the dark grey area have a relatively similar share of all three stages (no stage exceeds the other two in terms of stem numbers and basal area more than 1.5 fold). In the medium grey zone, two stages exceed the other one more than 1.5 fold. In the light grey zone, a single stage exceeds both other stages more than 1.5 fold. The size of the circles gives the size of the total index score  $I_{Total}$  of the plot (small: < 1.8, medium: 1.8–2.6, large: > 2.6), indicating the total density of stages

## 5.4 Discussion

### 5.4.1 Plot number and plot size requirements in old-growth forest studies

Plot numbers and plot size determine the information quality available when studying forest stand structure. In the long term absence of stand-level disturbances, primary forests typically develop towards horizontally and vertically diverse ‘old-growth’ structures (Franklin et al., 2002, Bauhus et al., 2009). In forests with high structural heterogeneity the coefficient of variation of many structural characteristics tends to increase with decreasing plot size (Kral et al., 2010a). This inflates the minimum number of sample plots required for reliably estimating the spatial variability of the stand structure at small plot sizes. According to the approach given by Kral et al. (2010a), our 118 plots well exceed the minimum plot number needed for reliably estimating total basal area ( $n = 27$ ) and total tree number ( $n = 49$ ).

Plot size depends on the type of information sought in the study. A meaningful spatial scale in the study of beech forest dynamics may be defined by gap size (Dröbner and Meyer, 2006). Spies and Franklin (1996) also use the term “shifting-gap phase” for their last phase in forest developmental succession. Most canopy gaps in beech old-growth forests result from the death of single trees or small groups of trees (Bottero et al., 2011; Dröbner and von Lüpke, 2005; Kenderes et al., 2009; Kucbel et al., 2010; Tabaku and Meyer, 1999; Zeibig et al., 2005) with a size of  $< 100 \text{ m}^2$  being most frequent, while stand-replacing disturbances (e.g., Hobi et al., 2015; Kucbel et al., 2012) seem to be rare in European beech forests. Analyzing spatial tree distribution in the Kyjov virgin beech forest, Dröbner et al. (2016) found gap size patterns to be reflected in stand structure throughout the entire forest development cycle. Single trees were the most frequent “group size” suggesting to collect information with a spatial grain size of a single tree in studies on beech forest dynamics. Since sample plots must be larger than this minimum grain size to conclude on stand structure and structural interactions, plot dimensions should exceed the area covered by a single tree, i.e. approximately  $150 \text{ m}^2$  for a beech canopy tree (Meyer, 1999). When studying the vertical stratification of canopies, even larger plots should be picked. We followed Lombardi et al. (2015) who assumed a plot size of  $500 \text{ m}^2$  to be adequate for quantifying old-growth structural indicators in European temperate forests.

### 5.4.2 Quantifying forest structure with the Development Stage Index $I_{DS}$

The introduced Development Stage Index  $I_{DS}$  is based on the grouping of trees into three diameter classes that are then referred to as ontogenetic development phases. Goff and West (1975) also divided the life cycle in old growth forests of shade-tolerant North American tree species into

three distinct phases, an understory phase of slow growth and high mortality, a vigorous canopy phase of relatively rapid growth and low mortality, and an older canopy phase of reduced growth and increased mortality. These authors associate the transitions between these phases with the bench marks in the inclination of the polynomial curve fitted to the tree diameter-density distribution, which has a rotated sigmoidal shape. This curve reflects the initial exponential decline in stem numbers (understory phase), that turns into a subsequent plateau with relatively stable stem numbers (vigorous canopy phase) and is then followed by an increasing decline at high DBH values (senescent overstory phase). The diameter-density distributions in our three stands also fit to this curve type, as has also been reported from other beech-dominated virgin forests (e.g. Alessandrini et al., 2011; Westphal et al., 2006). This suggested to adopt the criteria formulated by Goff and West (1975) for distinguishing between the three ontogenetic phases in our study. We used this DBH-based classification also for standing dead trees, assuming that mortality is to a considerable extent caused by community-level processes characteristic for the considered life-history stage (Holzwarth et al., 2013).

One may argue that describing the forest development cycle by distinguishing only three stages, as proposed here, must represent an over-simplification of forest structure and a loss of information compared to other approaches which used more stages (e.g. disintegration, gap, regeneration and plenter phases or stages; Kral et al., 2016; Tabaku, 2000). However, the results obtained from our analysis with the  $I_{DS}$  scores clearly demonstrate that the areal mingling of only three development stages results in complex patterns (e.g. Fig. 5.3). These patterns correspond to a diversity of forest structures and thus facilitate the interpretation of structural dynamics of primeval forests, in particular when applied in repeated surveys.

The calculation of  $I_{DS}$  scores requires referencing to tree density ( $N$ ) and basal area ( $BA$ ) data of plots which are dominated mostly or exclusively by that development stage. Since the Terminal stage forms extended patches only in old-growth forests, our approach is applicable only to forest stands with a long continuity of natural development, but not to stands with higher human impact. Yet, transferring  $I_{DS}$  reference values derived from virgin forests to other forests of the same species and site characteristics seems feasible. This is indicated by the only moderate variation in  $N_{max}$  values (found in the Optimum and Terminal stage) and  $BA_{max}$  values (found in the Initial and Optimum Stage) of a development stage among the three Slovakian beech forests. Considerable variation in  $N_{max}$  and  $BA_{max}$  values was only observed in plots, where either stem number (as found in  $N_{maxIni}$ ) or DBH were exceptionally large (as seen in  $BA_{maxTer}$ ). Recorded differences in the stem density and basal area maxima likely are caused by the sampling design with plot numbers probably still being too small to reliably detect the  $N$  and  $BA$  maxima in these



forests, as the whole-stand means of tree density and basal area were not different between the three forests. To account for this possible shortcoming, we averaged over the  $N_{max}$  and  $BA_{max}$  values of the three forests, when calculating the stem density and basal area reference.

$I_{DS}$  is a mixed index which expresses the effects of both tree abundance and tree size on the spatial extension of a development stage in the forest. This is important as the cover of the Initial stage is mostly determined by the number of trees ( $N$ ), while it is  $BA$  that largely determines cover in the Optimum stage, when stand thinning is completed. In the Terminal stage, dying trees reduce stem density, a process which typically is not compensated by the basal area growth of the remaining trees; thus  $N$  achieves a larger influence on cover again. Combining both measures ensures that  $I_{DS}$  can be used to estimate the extension of all three development stages. Highly significant negative correlations between the  $I_{DS}$  scores of the three stages are an expression of the fact that the different demographic populations of beech in a stand compete for canopy space.

As expected, the  $I_{DS}$  index was sensitive to the choice of DBH class ranges in our run with altered DBH thresholds. If a diameter class is narrowed, this class represents a shorter period in the forest cycle and the forest area assignable to the corresponding forest development stage must decrease. From diameter frequency plots of beech old-growth forests, it appears that the chosen 40 and 70 cm class limits are justified because they roughly correspond to demographic bench marks in the life cycle of a beech tree. The nearly equal abundance found for the three development stages in the pooled plots of the three Slovakian virgin forests also underpins this judgment. Certainly, other tree species may require defining different DBH thresholds. While plot size alters the size of  $I_{DS}$  and  $I_{Total}$  values in the plots, it appears to be less influential on the calculated proportion of the development stages at the stand level. This indicates that the  $I_{DS}$  index is applicable to different plot sizes and thus to different types of forest inventory data, while the proportion of forest area assigned to the three stages is largely unaffected. In contrast, the development stage classification approach proposed by Tabaku (2000) is highly sensitive to plot size: raising plot size from 156.25 to 500 m<sup>2</sup> caused large changes in the proportion of phases identified in the stands we studied (Table 5.A3 in the Supplement), as well as in the Ukrainian beech virgin forest of Uholka (compare Peck et al., 2015 and Zenner et al., 2016). The greatest changes were visible in the large extension of the ‘plenter phase’, which is a surrogate for high spatial heterogeneity.

### 5.4.3 Distribution and abundance of development stages

We found roughly similar frequencies (about 30–36%) of the Initial, Optimum and Terminal stages across our 118 plots, irrespective of the calculation approach used (proportion of the stage-specific  $I_{DS}$  in  $I_{Total}$  vs. proportion of plots dominated by a certain stage). Under the assumption of a landscape-scale quasi-equilibrium state of the studied virgin forests, the relatively balanced distribution of indices evidences similar spatial extensions of the three development stages in the forest suggesting that the DBH classes were well chosen. Since growth and development of shade-tolerant trees are often retarded in the understory, the extension of a forest development stage, however, is not a good indicator for the duration of a given stage in a tree's life cycle. In fact, dendroecological data indicate that beech trees are often spending much longer time spans in the Initial stage than in the other two stages (Trotsiuk et al., 2012).

Different development stage definitions in other classification approaches can lead to largely deviating results. For example, the approach of Tabaku (Dröbner and Meyer, 2006; Tabaku, 2000; Zenner et al., 2016) applied to primeval beech forests results in a much larger proportion of phases corresponding to our Terminal stage (nearly 50%), while only about 17 and 12% were assigned to phases related to our Initial and Optimum stage, respectively. This is caused by a focus on attributes with association to late developmental stages (deadwood and large trees), while information on other structural elements such as lower canopy strata is not considered. A considerable proportion of the plots had been characterized as the 'plenter phase', which has no direct equivalent in our classification system and has been criticized for being a synonym for small-scale spatial heterogeneity without logical order in the forest dynamics cycle (Winter and Brambach, 2011). According to this approach, the abundance of development stages is highly unbalanced in all six beech primeval forests, to which it was applied (see Zenner et al., 2016). On our plots, we see the same tendency when the approach of Tabaku is used (supplementary Table 5.A3). This suggests that all investigated beech primeval forests in eastern-central and south-eastern Europe should shift in the next decades from the terminal and decay phases to early development phases at large parts of their area. We assume that this is a consequence of methodology rather than an overarching ecological phenomenon of beech forest dynamics in our time. Kral et al. (2010b) proposed another classification approach, which yielded more balanced proportions of the stages, but the results varied considerably during the study period of 30 years (Kral et al., 2014). Analysis of the  $I_{DS}$  data in our study shows that all three stages coexist in the plots of 500 m<sup>2</sup> size, demonstrating high spatial heterogeneity in the three Slovakian virgin forests. This seems to contrast with reports of other authors on the occurrence of relatively homogeneous patches in European old-growth forests (e.g. Müller, 1929 and Leibundgut, 1982, 1993). A

possible explanation is that these authors studied forests in which past large-scale disturbances created extensive forest patches with cohort-like structure. We rarely encountered the exclusive presence of one single development stage on larger areas, as has been described by Korpel (1995) for Slovakian virgin forests. In fact, only very few of our 118 plots reached high proportions ( $> 70\%$  of  $I_{Total}$ ) for any of the three stages, or alternatively low proportions ( $< 10\%$ ) for the Initial or Optimum stages. The high evenness of the three stages in the plots ( $> 0.84$  in all stands) is another expression of the high small-scale heterogeneity, which has been addressed in earlier old-growth forest studies by introducing the term ‘plenter structure’ (Tabaku, 2000). The standard deviation of  $I_{DS}$  in Table 5.6, which varied from 43 to 77% of the mean in the three forests, expresses differences between the forests in terms of the degree of structural heterogeneity. Deviation from equality in the abundance of Initial, Optimal and Terminal stage plots (as in the Havešová (HA) and Stučica (ST) forests) may indicate past disturbance events such as windstorms that may affect a forest on the stand-scale (e.g. Nagel et al., 2014).

From the ternary plots, different stand-level structural patterns become visible for the three studied primeval forests. These patterns likely are providing information on past disturbance regimes and environmental heterogeneity at the stand level, but in the absence of repeated inventory data, any interpretation must remain speculative. However, a remarkable outcome is that many study plots are localized relatively close to the center of the ternary plot in all three forests, suggesting that the degree of small-scale mixing of the three stages is indeed high with frequent stage overlap within a plot. The graphical presentation of canopy structural heterogeneity in a ternary plot is a promising tool, which allows visualizing the complex mixing of life history stages in temperate old-growth forests and enables interpreting the underlying dynamic processes. Application to repeated inventory data might help understanding structural self-organization processes in the canopy, as they become visible in changing study plot positions over time in the ternary plot.

#### 5.4.4 Deadwood as an old-growth forest attribute

Deadwood adds largely to the conservation value of old-growth forests due to its importance for xylobiontic organisms and cavity-nesting birds (e.g. Begehold et al., 2015; Müller and Büttler, 2010; Winter and Brambach, 2011). It is also a valuable structural attribute in assessments of the old-growth character of forests (e.g. Bauhus et al., 2009) and a decisive structural feature in the definition of development phases and stages (e.g. Tabaku, 2000). The  $I_{DS}$  index associates deadwood objects with the different forest development stages through diameter, assigning thin deadwood to the Initial stage and thick dead logs to the Terminal stage. High deadwood

numbers and volumes increase the  $I_{DS}$  score. This approach has not been used before, since deadwood then partly loses its indicator value for forest development phases or stages. We share the opinion on the important role of deadwood as a characteristic structural attribute of old-growth forests and its high value in conservation matters. However, tree death is in many cases related to processes characteristic for the specific life history stage and thus the diameter class of the tree (Holzwarth et al., 2013). Furthermore, in forest dynamics, the death of a tree in the first place implies a release of growing space and the associated availability of resources (light, water and nutrients) to the surrounding trees. The still important role of deadwood in the  $I_{DS}$  may become visible in particular, when the index is applied to repeated inventory data, because deadwood decay gradually decreases the  $I_{DS}$  score of the respective stage. For example, if a storm kills all Terminal stage trees in a plot, where this stage was dominant, 10 years later the  $I_{Ter}$  score will decrease considerably by the decline in  $N_{Ter}$  and  $BA_{Ter}$ , while other individuals that survived will profit from the released growing space and react with increased growth. Thus, the  $I_{DS}$  score of the respective stages will increase. The consideration of deadwood in the calculation of the score causes the index to react only slowly to structural changes caused by tree mortality. Therefore, the  $I_{DS}$  score is best applied in long-term observational studies. Yet, deadwood in its role as a structural memory of the past can improve the understanding of interactions among the different stages and may help tracking stage transitions in the forest that happened in past decades.

Incorporating deadwood abundance in the index allows searching for structural interdependencies by means of correlation analysis. Earlier studies have frequently reported a negative correlation between deadwood volume and live wood mass (e.g., Kral et al., 2010a; Holeska et al., 2009). The  $I_{DS}$  score, however, incorporates deadwood volume (through  $BA_d$ ) and the number of deadwood objects (through  $N_d$ ), both of which may change independently across development stages. We observed a positive relation between  $I_{Ini}$  and  $N_d$ , probably reflecting the outcome of self-thinning processes in this stage. Dead trees in the Initial stage are of small size and do only marginally influence  $BA_d$  and  $V_d$ . As the Initial stage usually follows the Terminal stage with gradual stand decay (or large-scale disturbance) and typically is lasting much longer than the period of deadwood decomposition, deadwood volume and numbers often vary largely (see also Kral et al., 2010b and Tabaku, 2000). While deadwood amount passed through a minimum in the Optimum stage with typically lowest mortality (Korpel, 1995), a significant negative relation between the number of dead logs ( $N_d$ ) and the  $I_{Opt}$  score did not exist in our data (negative trends in the HA and KY stands, but positive relation in ST with presence of fir).

In our DBH-based definition, the Terminal stage covers a time span from “growing old” to

“replacement by young trees”, resembling the definition of the “breakdown stage” proposed by Kral et al. (2010b). While our definition is not necessarily related to the presence of dead trees, other classification approaches define distinct disintegration phases or decay stages (Jaworski and Podlaski, 2007; Korpel, 1995; Tabaku, 2000), which may result in higher deadwood amounts in this phase. While we found only a non-significant tendency towards higher deadwood amounts with higher  $I_{Ter}$  scores, this index showed a significant positive relation to deadwood volume ( $r = 0.25$ ,  $p = 0.006$ ), when only coarse woody debris of low to medium decay ( $> 20$  cm DBH, decay class  $\leq 3$ ) was considered. This substrate is of higher value for xylobionts (Schuck et al., 2004). For  $I_{Ini}$  and  $I_{Opt}$ , such a relation was not found, which indicates that the over-mature trees of the Terminal stage indeed are largely determining the deadwood amount.

#### 5.4.5 $I_{DS}$ as a proxy for further stand structural characteristics

From the correlation analyses, it is evident that the  $I_{DS}$  scores, and likewise the stages proportions, can provide further information on stand structure in old-growth forest plots (see Table 5.5). As expected, higher  $I_{Ini}$  scores generally stand for higher stem densities also in plots that are dominated by the respective other development stages, while a higher  $I_{Ter}$  score indicates smaller overall tree densities. Higher  $I_{Opt}$  and  $I_{Ter}$  scores stand for higher cumulative basal areas in the plot, while higher  $I_{Ini}$  values relate to smaller basal areas. The same is true for the volume of aboveground woody biomass. Interestingly, a higher frequency of microhabitats (such as cavities in the stem and bark injury) is indicated not only by higher  $I_{Ter}$  scores but also by higher  $I_{Opt}$  values. A similar abundance of microhabitats in the Optimum and Terminal stages (see Table 5.A2 in the Supplement) may suggest that microhabitats relevant for xylobionts are created in virgin beech forests well before the trees are reaching over-mature size. One explanation is the generally higher stem density in the Optimum than Terminal stage, which may outweigh the lower specific frequency of microhabitat occurrence. Another explanation could be that falling dead trees are damaging younger, vital neighbors, which is prevented in managed forests. Since we registered only the density of microhabitats, but did not assess their quality, it may however be that the Terminal stage with its very old and large trees does possess habitats of greater value for xylobionts than do exist in the Optimum stage.

High  $I_{Ini}$  scores are also indicators of a reduced density of tree saplings  $> 1.5$  m height, probably because they are suppressed by a dense cover of young trees. Thus, in these montane virgin beech forests, regeneration is highest in the Optimum and Terminal stages, but is largely suppressed in the Initial stage, which allows the next beech generation to develop only after the trees of the Initial stage have grown tall. As the  $I_{DS}$  scores of the three stages correlate positively with the

$I_{Total}$  score (r: 0.22–0.49), the latter is also associated with stand structural characteristics that are strongly correlated with one or more  $I_{DS}$  scores.

## 5.5 Conclusions

The proposed  $I_{DS}$  index can be viewed as an important step toward the goal to describe and analyze the complex mosaic structure of temperate old-growth forests with objective and quantitative measures. The index bases on two easily measured variables, which serve as suitable proxies for quantifying the spatial extension of life history stages from the Initial to the Terminal stage. The index seems to be relatively robust against variation in plot size, but is sensitive to altered classification schemes of the development stages. The  $I_{DS}$  score allows interpreting stand development from the plot to the landscape scale. On the plot level,  $I_{DS}$  scores provide information on the mixing of tree populations of different demographic position, allowing conclusions on vertical structure and its spatial variation in the forest and thus on the character of the disturbance regime. At the stand and landscape scale, mean  $I_{DS}$  values can give hints on past major disturbances, visible through deviation from equilibrium conditions. Displaying  $I_{DS}$  scores in ternary graphical plots allows visualizing spatial variation in the mixing of development stages. This approach can also facilitate the comparison of different forests in terms of canopy structure and function. Further, when the ternary plot is applied to repeat-inventory data, dynamic changes in stand structure can be analyzed. Finally, the improved empirical data base generated by introducing the  $I_{DS}$  score may enable more rigorous hypothesis testing in forest dynamics research. In future studies, the  $I_{DS}$  index should be applied to other beech old-growth forests, repeat-inventory data and further structurally different forest types. This may require modifying the index by altering the DBH thresholds, including other or additional structural variables, and extending the set of stem density and basal area data, which are needed as a reference.

**Acknowledgements:** The support by the Stemmler Foundation is gratefully acknowledged. We are also grateful to the Poloniny National Park authority, the local forest administrations and the Ministry of Defence of the Slovak Republic for the permits to conduct the study and for technical support during the fieldwork. For organizational and technical support we also like to thank Viliam Pichler and his working group at the Technical University of Zvolen. Many thanks for assistance in the field to Matthias Steckel. We thank two anonymous reviewers for highly useful comments and suggestions on the manuscript.

## 5.6 Appendix

Table 5.A1: Stem density ( $N$ ) and basal area ( $BA$ ) of trees assignable to the Initial ( $Ini$ ), Optimum ( $Opt$ ) or Terminal ( $Ter$ ) stages in the three stands, expressed as fraction of the maximum stem density and basal area observed in the respective stages and stands (means of each 40 plots in HA and KY and of 38 plots in ST).

Stand	Initial stage		Optimal stage		Terminal stage	
	$N_{Ini}$	$BA_{Ini}$	$N_{Opt}$	$BA_{Opt}$	$N_{Ter}$	$BA_{Ter}$
HA	0.40	0.36	0.38	0.39	0.34	0.32
KY	0.36	0.36	0.36	0.37	0.40	0.35
ST	0.37	0.44	0.47	0.47	0.36	0.31
All stands	0.38	0.38	0.41	0.41	0.37	0.33

Table 5.A2: Stand structural characteristics of plots dominated by the Initial ( $n = 35$ ; 12 in HA, 12 in KY and 11 in ST), Optimum ( $n = 42$ ; 13 in HA, 14 in KY and 15 in ST) and Terminal stages ( $n = 41$ ; 15 in HA, 14 in KY and 12 in ST) in the three stands. The stage reaching the highest  $I_{DS}$  score in a plot was considered as the 'dominant' stage in that plot. Significant differences between the stages are indicated by different small letters and bold print (Mann-Whitney U-test,  $p < 0.05$ ).

		Initial stage		Optimum stage		Terminal stage	
		mean	SD	mean	SD	mean	SD
$N_i$ ( $N\ ha^{-1}$ )		<b>396</b>	$\pm 121b$	<b>326</b>	$\pm 99a$	<b>280</b>	$\pm 81a$
	HA	80	$\pm 69.8$	47.7	$\pm 22.9$	54.7	$\pm 23.6$
$N_d$ ( $N\ ha^{-1}$ )	KY	53.3	$\pm 34$	35.7	$\pm 26.4$	41.4	$\pm 44.4$
	ST	90.9	$\pm 44.6$	72	$\pm 45.5$	50	$\pm 30$
$N_{tot}$ ( $N\ ha^{-1}$ )		<b>470</b>	$\pm 158c$	<b>379</b>	$\pm 104b$	<b>329</b>	$\pm 85a$
$BA_i$ ( $m^2\ ha^{-1}$ )		<b>26.3</b>	$\pm 8.7a$	<b>38.3</b>	$\pm 12b$	<b>39.2</b>	$\pm 12b$
$BA_d$ ( $m^2\ ha^{-1}$ )		14.4	$\pm 10$	10.2	$\pm 8.1$	12.1	$\pm 10$
$BA_{tot}$ ( $m^2\ ha^{-1}$ )		<b>40.7</b>	$\pm 9.3a$	<b>48.5</b>	$\pm 10.4b$	<b>51.3</b>	$\pm 12b$
$V_i$ ( $m^3\ ha^{-1}$ )		<b>424</b>	$\pm 184a$	<b>659</b>	$\pm 239b$	<b>721</b>	$\pm 255b$
$V_d$ ( $m^3\ ha^{-1}$ )		183	$\pm 135$	124	$\pm 110$	164	$\pm 162$
	HA	<b>659</b>	$\pm 126a$	<b>849</b>	$\pm 313ab$	<b>954</b>	$\pm 303b$
$V_{tot}$ ( $m^3\ ha^{-1}$ )	KY	<b>482</b>	$\pm 115a$	<b>726</b>	$\pm 153b$	<b>742</b>	$\pm 131b$
	ST	688	$\pm 181$	779	$\pm 164$	965	$\pm 235$
REG ( $N\ ha^{-1}$ )		1495	$\pm 1899$	2756	$\pm 3431$	3443	$\pm 4879$
HAB ( $N\ ha^{-1}$ )		543	$\pm 321$	678.6	$\pm 426$	658.5	$\pm 327$

Table 5.A3: The percentage share of development stages of the  $I_{DS}$  (first row) and the associated development phases derived by the Tabaku (2000) method (second row) are displayed for the pooled plots of the three stands ( $n = 118$ ). For the Tabaku method the share is given for the separate phases and as the sum of the phases theoretically covered by the  $I_{DS}$  stages. The multilayered Plenter phase has no direct equivalent in the  $I_{DS}$  approach as structural heterogeneity is seen simply as a mixture of stages.

stage ( $I_{DS}$ )	phase (Tabaku)	156.25 m <sup>2</sup>			500 m <sup>2</sup>		
		Tabaku	$I_{DS}$	Tabaku	$I_{DS}$	Tabaku	$I_{DS}$
Initial	Establishment	5,8		0			
	early Optimum	15	20,8	36	0,8	0,8	34,0
Optimum	mid Optimum	5		0			
	late Optimum	2,5	7,5	32,1	0,8	0,8	35,3
	Terminal	21,7		20			
Terminal	Decay	11,7		10,8			
	Gap	0	33,3	31,9	0	30,8	30,7
	Regeneration	0		0			
	Plenter	38,3	38,3	67,5	67,5		

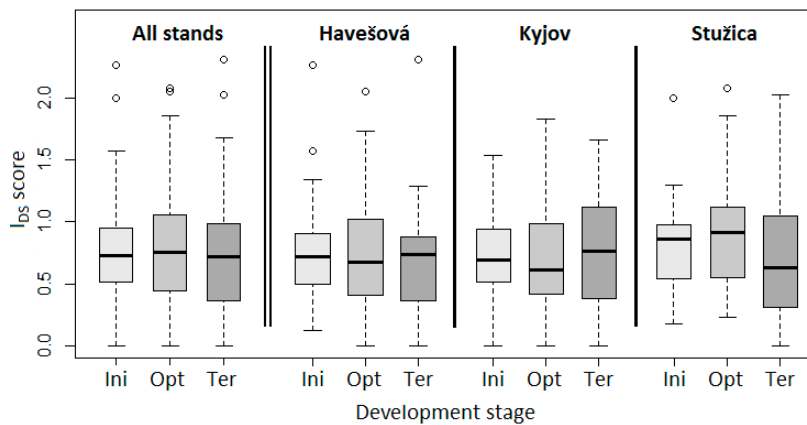


Figure 5.A1: Box-whisker plots with median (thick line), 25- and 75-percentiles (box) and extremes not exceeding the 1.5fold of the interquartile range (whiskers) of the  $I_{DS}$  scores of the three development stages in the plots in Havesova, Kyjov and Stuzica and for all stands pooled. Dots mark extreme data points beyond 1.5 times the IQR



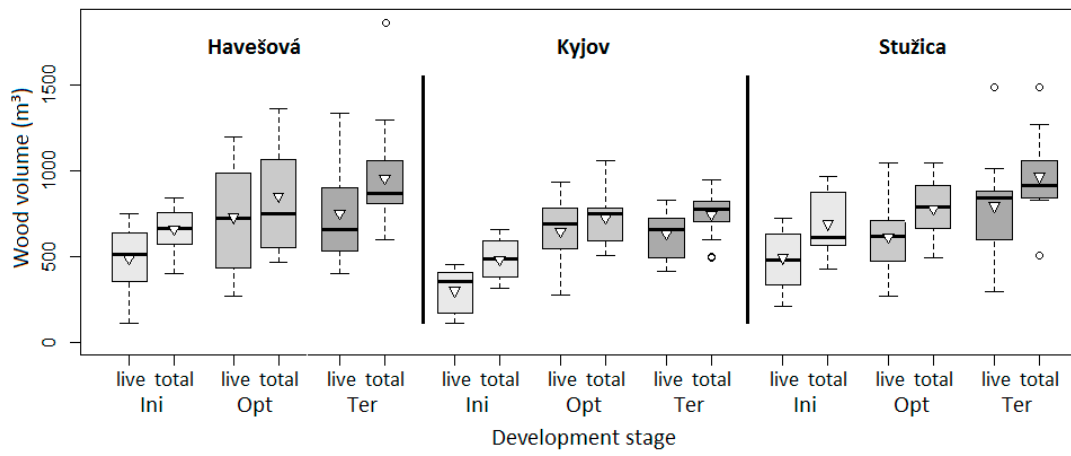


Figure 5.A2: Wood volume (aboveground wood biomass or total aboveground wood mass including deadwood) in plots assigned to the Initial, Optimum or Terminal stage according the highest  $I_{DS}$  score. Box-whisker plots with median (thick line), 25- and 75-percentiles (box) and extremes not exceeding the 1.5fold of the interquartile range (whiskers). Dots mark extreme data points beyond 1.5 times the IQR

## 5.7 References

- Alessandrini, A., Biondi, F., Di Filippo, A., Ziaco, E., Piovesan, G., 2011. Tree size distribution at increasing spatial scales converges to the rotated sigmoid curve in two old-growth beech stands of the Italian Apennines. *Forest Ecology and Management*, 262, 1950–1962.
- Assmann, E., 1961. *Waldertragskunde*. BLV Verlagsgesellschaft, München, Bonn, Wien.
- Bauhus, J., Puettmann, K., Messier, C., 2009. Silviculture for old-growth attributes. *Forest Ecology and Management*, 258, 525–537.
- Begehold, H., Rzanny, M., Flade, M., 2015. Forest development phases as an integrating tool to describe preferences of breeding birds in lowland beech forests. *Journal of Ornithology*, 156, 19–29.
- Bohn, U., Neuhäusl, R., Gollub, R., Hettwer, C., Neuhäuslova, Z., Schlüter, H., Weber H., 2003. Karte der natürlichen Vegetation Europas. Teil 1: Erläuterungstext. Landwirtschaftsverlag, Münster.
- Bottero, A., Garbarino, M., Dukić, V., Govedar, Z., Lingua, E., Nagel, T.A., Motta, R., 2011. Gap-Phase Dynamics in the Old-Growth Forest of Lom, Bosnia and Herzegovina. *Silva Fennica*, 45 (5), 875–887.
- Christensen, M., Emborg, J., Busse Nielsen, A., 2007. The forest cycle of Suserup Skov – revisited and revised. *Ecological Bulletins*, 52, 33–42.
- Commarmot, B., Bachofen, H., Bundziak, Y., Bürgi, A., Ramp, B., Shparyk, Y., Sukhariuk, D., Viter, R., Zingg, A., 2005. Structures of virgin and managed beech forests in Uholka (Ukraine) and Sihlwald (Switzerland): a comparative study. *Forest, Snow and Landscape Research*, 79, 45–56.
- Commarmot, B., Brändli, U.-B., Hamor, F., Lavnyy, V. (Eds.), 2013. Inventory of the largest virgin beech forest of Europe. A Swiss-Ukrainian scientific adventure. Birmensdorf, Swiss Federal Research Institute WSL; L'viv, Ukrainian National Forestry University, Rakhiv, Carpathian Biosphere Reserve.
- Drößler, L., Lüpke, B., 2005. Canopy gaps in two virgin beech forest reserves in Slovakia. *Journal of Forest Science*, 51, 446–457.
- Drößler, L., 2006. Struktur und Dynamik von zwei Buchenurwäldern in der Slowakei. Ph.D Thesis, Georg August University, Göttingen.
- Drößler, L., Meyer, P., 2006. Waldentwicklungsphasen in zwei Buchen-Urwaldreservaten in der Slowakei. *Forstarchiv*, 77, 155–161.
- Drössler, L., Feldmann, E., Glatthorn, J., Annighöfer, P., Kucbel, S., Tabaku, V., 2016. What Happens after the Gap? - Size Distributions of Patches with Homogeneously Sized Trees in Natural and Managed Beech Forests in Europe. *Open Journal of Forestry*, 6, 177–190.
- Emborg, J., Christensen, M., Heilmann-Clausen, J., 2000. The structural dynamics of Suserop Skov, a near natural temperate deciduous forest in Denmark. *Forest Ecology and Management*, 126, 173–179.
- Franklin, J.F., Spies, T.A., Van Pelt, R., Carey, A.B., Thornburgh, D.A., Berg, D.R., Lindenmayer, D.B., Harmon, M.E., Keeton, W.S., Shaw, D.C., Bible, K., Chen, J., 2002. Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. *Forest Ecology and Management*, 155, 399–423.
- Goff, F.G., West, D., 1975. Canopy-understorey interaction effects on forest population structure. *Forest Science*, 21, 98–108.
- Grassi, G., Minotta, G., Giannini, R., Bagnaresi, U., 2003. The structural dynamics of managed uneven-aged conifer stands in the Italian eastern Alps. *Forest Ecology and Management*, 185, 225–237.
- Hobi, M.L., Ginzler, C., Commarmot, B., Bugmann, H., 2015. Gap pattern of the largest primeval beech forest of Europe revealed by remote-sensing. *Ecosphere*, 6, 1–15.
- Holeksa, J., Saniga, M., Szwagrzyk, J., Czerniak, M., Staszyńska, K., Kapusta, P., 2009. A giant tree stand in the

- western Carpathians - an exception or a relic formerly widespread mountain European forests? *Forest Ecology and Management*, 257, 1577–1585.
- Holzwarth, F., Kahl, A., Bauhus, J., Wirth, C., 2013. Many ways to die – partitioning tree mortality dynamics in a near-natural mixed deciduous forest. *Journal of Ecology*, 101, 220–230.
- Hunter Jr., M.L., 1990. Wildlife, forests and forestry: Principles of managing forests for biological diversity. Englewood Cliffs, New Jersey: Prentice-Hall.
- Jaworski, A., Podlaski, R., 2007. Structure and dynamics of selected stands of primeval character in the Pieniny National Park. *Dendrobiology*, 58, 25–42.
- Kenderes, K., Král, K., Vrška, T., Standovar, T., 2009. Natural Gap Dynamics in a European Mixed Beech-Spruce-Fir Old-Growth Forest. *Ecoscience*, 16(1), 39–47.
- Korpel, Š., 1995. Die Urwälder der Westkarpaten. Gustav Fischer Verlag, Stuttgart.
- Král, K., Janík, D., Vrška, T., Adam, D., Hort, L., Unar, P., 2010a. Local variability of stand structural features in beech dominated natural forests of Central Europe: implications for sampling. *Forest Ecology and Management*, 260, 2196–2203.
- Král, K., Vrška, T., Hort, L., Adam, D., Šamonil, P., 2010b. Developmental phases in a temperate natural spruce-fir-beech forest. Determination by a supervised classification method. *European Journal of Forest Research*, 129, 339–351.
- Král, K., Valtera, M., Janík, D., Šamonil, P., Vrška, T., 2014. Spatial variability of general stand characteristics in central European beech-dominated natural stands – Effects of scale. *Forest Ecology and Management*, 328, 353–364.
- Král, K., Shue, J., Vrška, T., Gonzalez-Akre, E.B., Parker, G.G., McShea, W.J., McMahon, S.M. 2016. Fine-scale patch mosaic of developmental stages in Northeast American secondary temperate forests: the European perspective. *European Journal of Forest Research*, 135, 981–996.
- Kucbel, S., Jaloviari, P., Saniga, M., Vencurik, J., Klimaš, V., 2010. Canopy gaps in an old-growth fir-beech forest remnant of Western Carpathians. *European Journal of Forest Research*, 129, 249–259.
- Kucbel, S., Saniga, M., Jaloviari, P., Vencurik, J., 2012. Stand structure and temporal variability in old-growth beech-dominated forests of the northwestern Carpathians: A 40-years perspective. *Forest Ecology and Management*, 264, 125–133.
- Leibundgut, H., 1982. Europäische Urwälder der Bergstufe. Paul Haupt, Bern.
- Leibundgut, H., 1993. Europäische Urwälder - Wegweiser zur naturnahen Waldwirtschaft. Paul Haupt, Bern.
- Lombardi, F., Cherubini, P., Lasserre, B., Tognetti, R., Marchetti, M., 2008. Tree rings used to assess time since death of deadwood of different decay classes in beech and silver fir forests in Central Apennines (Molise, Italy). *Canadian Journal of Forest Research*, 38, 821–833.
- Lombardi, F., Marchetti, M., Corona, P., Merlini, P., Chirici, G., Tognetti, R., Burrascano, S., Alivernini, A., Puletti, N., 2015. Quantifying the effect of sampling plot size on the estimation of structural indicators in old-growth forest stands. *Forest Ecology and Management*, 346, 89–97.
- Meyer, P., 1999. Bestimmung der Waldentwicklungsphasen und der Texturdiversität in Naturwäldern. *Allgemeine Forst- und Jagdzeitung*, 170, 203–211.
- Meyer, P., Ackermann, J., Balcar, P., Boddenberg, J., Detsch R., Förster, B., Fuchs, H., Hoffmann, B., Keitel, W., Kölbl, M., Köthke, C., Koss, H.; Unkrig, J., Weber, J., Willig, J., 2001. Untersuchungen der Waldstruktur und ihrer Dynamik in Naturwaldreservaten. Arbeitskreis Naturwälder. Bund-Länder-Arbeitsgemeinschaft Forsteinrichtung. IHW-Verlag.
- Müller, K.M., 1929. Aufbau, Wuchs und Verjüngung der südosteuropäischen Urwälder, Hannover, Schaper.

- Müller, J., Büttler, R., 2010. A review of habitat thresholds for dead wood: a baseline for management recommendations in European forests. *European Journal of Forest Research*, 129, 981–992.
- Müller-Using, S., Bartsch, N., 2009. Decay dynamic of coarse and fine woody debris of (*Fagus sylvatica* L.) forest in Central Germany. *European Journal of Forest Research*, 128, 287–296.
- Nagel, T.A., Svoboda, M., 2008. Gap disturbance regime in an old-growth *Fagus–Abies* forest in the Dinaric Mountains, Bosnia-Herzegovina. *Canadian Journal of Forest Research*, 38, 2728–2737.
- Nagel, T.A., Svoboda, M., Kobal, M., 2014. Disturbance, life history traits, and dynamics in an old-growth forest landscape of southeastern Europe. *Ecological Application*, 24 (4), 663–679.
- Neumann, M., 1979. Bestandesstruktur und Entwicklungsdynamik im Urwald Rothwald/NÖ und im Urwald Čorkova Uvala/Kroatien. PhD thesis, Univ. f. Bodenkultur, Wien.
- Oliver, C.D., Larson, B.C., 1996. *Forest Stand Dynamics*. Wiley, New York.
- Paluch, J.G., 2007. The spatial pattern of a natural European beech (*Fagus sylvatica* L.) – silver fir (*Abies alba* Mill.) forest: a patch mosaic perspective. *Forest Ecology and Management*, 253, 161–170.
- Peck, J.E., Zenner, E.K., Hobi, M.L., Commarmot, B., 2015. Should reference conditions be drawn from a single 10 ha plot? Assessing representativeness in a 10,000 ha old-growth European beech forest? *Restoration Ecology*, 23, 927–935.
- Peterken, G.F., 1996. *Natural Woodland Ecology and Conservation in Northern Temperate Regions*. Cambridge University Press.
- Peters, R., 1997. *Beech Forests*. *Geobotany*, 24, Springer.
- Petráš, R., Pajtík, J., 1991. Sústava Česko-slovenských objemových tabuliek drevín. *Lesnícky Časopis*, 37, 49–56.
- Pretzsch, H., 2009. *Forest Dynamics, Growth and Yield*. Springer, Berlin, Heidelberg.
- Prívětivý, T., Janík, D., Unar, P., Adam, D., Král, K., Vrška, T., 2016. How do environmental conditions affect the deadwood decomposition of European beech (*Fagus sylvatica* L.)? *Forest Ecology and Management*, 381, 177–187.
- Remmert, H., 1991. The mosaic-cycle concept of ecosystems—an overview, in: Remmert, H. (Ed.), *The mosaic-cycle concept of ecosystems*, Springer Berlin Heidelberg, pp. 1–21.
- Röhrig, E., Lüpke, B., Bartsch, N., 2006. *Waldbau auf ökologischer Grundlage*. Ulmer, Stuttgart.
- Schuck, A., Meyer, P., Menke, N., Lier, M., Lindner, M., 2004. Forest biodiversity indicator: Deadwood – A proposed approach towards operationalising the MCPFE indicator, in: Marchetti, M. (Ed.), *Monitoring and indicators of forest biodiversity in Europe – From ideas to operationality*, European Forest Institute, EFI proc. 51, pp. 49–77.
- Spies, T.A., Franklin, J.F., 1996. The diversity and maintenance of old-growth forests. In: Szaro, R.C., Johnson, D.W. (Eds), *Biodiversity in Managed Landscapes: Theory and Practice*. Oxford, New York, pp. 296–314
- Tabaku, V., 2000. Struktur von Buchen-Urwäldern in Albanien im Vergleich mit deutschen Buchen-Naturwaldreservaten und -Wirtschaftswäldern. Cuvillier Verlag, Göttingen, 206 pp.
- Tabaku, V., Meyer, P., 1999. Lückemuster albanischer und mitteleuropäischer Buchenwälder unterschiedlicher Nutzungsintensität. *Forstarchiv* 70, 87–97.
- Trotsiuk, V., Hobi, M.L., Commarmot, B., 2012. Age structure and disturbance dynamics of the relic virgin beech forest Uholka (Ukrainian Carpathians). *Forest Ecology and Management*, 265, 181–190.
- Watt, A.S., 1947. Pattern and Process in the Plant Community. *Journal of Ecology*, 35, 1–22.

- 
- Westphal, C., Tremer, N., von Oheimb, G., Hansen, J., von Gadow, K., Härdtle, W., 2006. Is the reverse J-shaped diameter distribution universally applicable European virgin beech forests? *Forest Ecology and Management*, 223, 75 – 83.
- Winter, S., Brambach, F., 2011. Determination of a common forest life cycle assessment method for biodiversity evaluation. *Forest Ecology and Management*, 262, 2120–2132.
- Zeibig, A., Diaci, J., Wagner, S., 2005. Gap disturbance patterns of a *Fagus sylvatica* virgin forest remnant in the mountain vegetation belt of Slovenia. *Forest, Snow and Landscape Research*, 79, 69–80.
- Zenner, E.K., Peck, J.E., Hobi, M.L., Commarmot, B., 2015. The dynamics of structure across a primeval European beech stand. *Forestry*, 88, 180–189.
- Zenner, E.K., Peck, J.E., Hobi, M.L., Commarmot, B., 2016. Validation of a classification protocol: meeting the prospect requirement and ensuring distinctiveness when assigning forest development phases. *Applied Vegetation Science*, 19, 541-552.



# 6<sup>th</sup>

## CHAPTER SYNTHESIS

Forest structure and structuring processes, i.e., tree growth, regeneration and mortality, are mutually dependent and closely linked to various ecosystem functions (von Gadow et al. 2012). The study of forest dynamics, which describes the underlying physical and biological forces that shape and change a forest ecosystem, therefore, is a key discipline in forest ecological research. The scarce remnants of beech (*Fagus sylvatica* L.) virgin forests in east and southeast of Central Europe (Parviainen, 2005; Veen et al., 2010) present an outstanding opportunity to study and compare the natural structure of beech forests and the underlying long-term dynamics. Yet few of the existing remnants have been studied and our knowledge on structures and dynamics in these forests is still limited. Valuable long-term observations, that partly date back more than half a century (e.g., Korpel, 1995), are scarce and most of them rather represent case studies that focused on specific structural conditions. Thus, researchers are largely limited to infer temporal forest dynamics by the analysis of forest structure at a given time. This thesis is focused on some key aspects in linking forest structure and forest dynamics processes and the results may serve as guidance in the advancement of close-to-nature forest management strategies and forest conservation and restoration efforts.

### **6.1 Effects of gap dynamics on stand structure**

Canopy gaps drive the forest cycle through their control on light transmission to the lower strata (Whitmore, 1989). Consequently, the size of canopy gaps is a meaningful spatial scale in the study of forest structure and dynamics in beech forests (Watt, 1947; Drößler and Meyer, 2006). The temporal variation in the frequency of differently sized gaps is relevant to infer the importance of the respective size categories in long-term forest dynamics.

The first study presented in this thesis (chapter 2) revealed that in the Kyjov forest there was a rather continuous formation of numerous small (< 100 m<sup>2</sup>) and several medium sized gaps

(< 500 m<sup>2</sup>), while only few large gaps (up to 4500 m<sup>2</sup>) were formed by events that seem rare on a temporal scale (e.g., severe windstorms). There are studies from other beech-dominated virgin forests indicating similar spatio-temporal pattern in gap formation (Nagel et al., 2014; Splechtna and Gratzner, 2005; but see Kenderes et al., 2009). The contribution of large gaps to the total gap area in Kyjov, however, was disproportionately high. They covered slightly more area in the year 2003 than small and medium gaps did together in both gap inventories (2003 and 2013). Even though it is uncertain when larger gaps will be formed the next time, the results show that gaps  $\geq 500$  m<sup>2</sup> play an important role in the structural dynamics of this forest stand.

It was shown that canopy gaps may affect forest structure at multiple scales. Knowledge on the process of gap filling and its imprint on forest texture through the life cycle is important for the interpretation of forest structure and for predicting structural dynamics.

In chapter 3 the regeneration structure and development in understory gaps was analyzed. The study indicates that gaps have strong positive effects on beech regeneration establishment and growth development exceeding the projected gap area, as it was found by others (Rozenbergar et al., 2007; Diaci et al., 2012). Despite significant spatial differences in plant density, the findings suggest that regeneration might develop a relatively homogeneous canopy within the area projected by medium and large gaps ( $\geq 100$  m<sup>2</sup>) and apparently form classic tree cohorts (Oliver and Larsen, 1996). Assuming such homogeneous behavior in regeneration development, in chapter 4, tree cohorts were defined being ‘neighboring trees of similar dimension’ and the cohort size-frequency relationship was studied for a continuous set of dbh classes on a 12 ha research plot in the Kyjov forest. Across the DBH classes (10 cm width, 7–97 cm) the relationship approximated steep exponential decay functions, i.e., the frequency decreased strongly with increasing cohort size, and differed significantly from random tree distributions in terms of a more intense clustering of trees of similar dimension. A comparable curve progression was found for gap size-frequency distributions in Kyjov (chapter 2) and many other beech-dominated forests. This could suggest that gap dynamics in beech virgin forests follow a rather simple developmental pathway as it was proposed in the early descriptions of patch dynamics (Watt, 1947; Remmert, 1991) – i.e. death of canopy trees initiates tree regeneration at the approximate area and some of these trees grow into the canopy and close the gap. However, the size-frequencies of gaps and cohorts cannot be directly compared as cohort size was defined by the number of trees and not by the area they covered.

Actually, the area of gaps was not found to be constant but considerably reduced by lateral crown expansion of the trees bordering the gap (chapter 2). Accordingly, light transmission was reduced, especially at the former gap edge. Many small gaps were completely closed by



this process within 10 years. Tree regeneration in small gaps and at the edges of larger gaps might endure the following period of low light and suppression by the upper canopy due to the high shade-tolerance of beech (Leuschner and Ellenberg, 2017). These saplings are in a favorable position when disturbance forms a canopy gap in striking distance the next time. However, constant progress in ontogenetic development, and thus the formation of a cohort that consists of trees of similar dimensions, seems only possible in larger gaps, but on an area that is considerably smaller than was the initial gap size. In a period of higher disturbance intensity, processes such as gap size expansion and the coalescence of gaps that rarely occurred in the period 2003–2013, could become more important. These would release the advanced regeneration from suppression that could remain a part of the cohort in the gap interior, if the release happens within a short period (few decades). Otherwise it would constitute a new (retarded) cohort.

Furthermore, a cohort-wise development would rely on a relatively homogeneous initial regeneration structure as it is realized in understory gaps. In fact, such conditions were found in less than half of the gaps encountered in Kyjov (chapter 2). Nearly all gaps (> 90%) released larger saplings (height > 3 m) and sub-canopy trees in some part of their extent (mean cover = 33% in new gaps) that likely represent legacies of former small or medium gaps. Only in few cases (19%) there was a strong dominance of a single released understory layer. Thus, even though gaps were found to initiate the establishment of tree regeneration (chapter 3), in large parts of the gap area in Kyjov a rather heterogeneous structured understory was released, which is a rather general finding in beech-dominated virgin forests (Diaci et al., 2005; Rozenbergar et al., 2007; Nagel et al., 2010; Bottero et al., 2011). This understory secures a high degree of resilience to canopy disturbance, as can be seen by the intense vertical gap filling within 10 years reported in chapter 2. In gaps containing such diverse understory the light distribution pattern, and thereby the growth responses among different vertical canopy strata, can be assumed to be very complex. Based on the current observations, the trends in the gap-driven development of stand structure in Kyjov can be summarized as follows: The frequent death of single weakened or senescent trees, that may damage a few neighbors when crashing down, results in small and medium sized gaps. These size categories may soon become closed by lateral ingrowth from neighboring trees. They mainly facilitate the development and persistence of regeneration patches and small-scale vertical and horizontal heterogeneity in stand structure. On occasion, individual released understory trees gain access to the canopy. Infrequent large gaps allow for vital and continuous growth. A generational turnover in the canopy seems obligatory here. They might cause the emergence of cohorts that dominate stand structure on a larger scale, but only if they meet understory gap conditions at a considerable portion of gap area.

This comprehensive model of forest dynamics in Kyjov relies on conclusions from the intensive study of several key aspects to this process. However, there are important questions that were not fully answered or raised by the study and should be in the focus of future research.

- An outstanding issue is to learn more about the relationship between disturbance intensity and frequency. The repeated inventory represents only a glimpse of the canopy development in this forest where a tree's life may last longer than 200 years (Korpel, 1995). The survey should be continued with periodical reports on changes in the canopy.
- As there are several regional and site-specific factors that influence the disturbance regime in a forest (chapter 2, 4.1), the findings from Kyjov represent only a stepping stone on the way to derive generality in natural dynamics of beech forests. Similar long-term studies from other beech-dominated virgin forests are needed to evaluate the influence of the individual factors. These should also address the released tree understory, as it is relevant for the resilience to disturbances and might differ with site conditions. The potential for repetition of previous inventories, as performed in chapter 2, should be considered, to promote progress in evaluating temporal changes.
- Detailed information on the speed (measured in  $\text{m a}^{-1}$ ) of lateral crown expansion of mature beech trees (and a possible limit in range) would be desirable. Such knowledge could help to better estimate the perspectives of structural development.
- Many gaps were found to release a heterogeneous structured understory. In such gaps the light distribution pattern and thereby the growth response of the tree understory, i.e., seedlings, saplings and sub-canopy trees, can be assumed to be very complex. Due to the high abundance of such structures in the Kyjov forest, it is important to understand their development following canopy release. The evaluation of growth development in the released understory is laborious, as it requires a high spatial resolution. Novel techniques like terrestrial laser scanning (e.g., Seidel et al., 2011) might prove most suitable in documenting the development in the different understory layers.
- The availability of direct sunlight had a positive influence on the density of beech saplings. The cause of this effect could not be clearly attributed to a certain process (chapter 3). To better understand this effect requires studying the development in seedling density and growth right after gap formation under consideration of various environmental conditions and processes linked to direct sunlight (e.g., temperature and mineralization rate). Additional laboratory experiments seem helpful in evaluating the single factors influence.

- Both theoretical reflections (Tilman, 1982) and also experimental results (Wagner, 1999), suggest a complementary use of resources, which ultimately means that the light availability needed for survival and growth can decrease with an increase in nutrient availability and/or soil moisture at the site. This could reasonably alter the regeneration dynamics, especially through its effect on sapling survival in low light conditions, and thus affect forest dynamics itself in dependence of site conditions. Other factors, such as root competition from mature trees (Bauhus, 2009), that was at most subordinate to gap regeneration dynamics in the Kyjov forest (highest values for sapling density and biomass were found in the gap periphery), might also become more important under poor water and/or nutrient availability.

## 6.2 Stand structure and development stages

The concept of forest development stages has a long tradition in the description of stand structure and structural dynamics in Central Europe. However, the existing approaches for classifying different stages of stand development seem incapable of displaying structural changes in a comprehensive way (Christensen, 2007; Kral et al., 2018). Hence, their explanatory value in the description and analysis of forest stand structure and dynamics seems questionable. Likely, the problem is a strong emphasis on ‘structural master factors’ that determine the development stage and implicitly assume structural uniformity and thus, a collective development at the chosen spatial scale. The proposed development stage index  $I_{DS}$  (chapter 5) is a new approach to objectively quantify the spatial extension of three forest development stages (Initial, Optimum and Terminal) at different scales. It mainly differs from the existing approaches in two aspects: i) It incorporates multiple levels of mixing of life history stages on the observational scale used, and ii) dead trees are not per se attributed to a Decay or Terminal stage, but account for different stages depending on their dimension. Thereby, the  $I_{DS}$  provides information on variable mixing of tree populations in different demographic positions (stages) by only relying on a very confined set of input data. A great benefit is that the mixing of stages can be continuously displayed by ternary graphical plots.

The three development stages had a relatively balanced mean spatial extension (27–39%) in the three virgin beech forests studied, which suggests that they are not far from so called ‘structural equilibrium condition’ at the stand scale. It turned out that the development stages rarely occur in strong areal dominance and there is a high variation in the mixing of stages on circular plots of 500 m<sup>2</sup> or even smaller (156 m<sup>2</sup>). This reveals that by ignoring subdominant structures, the existing approaches largely blanked out a very characteristic feature that is highly relevant to future structural development.

If intense and diverse mixing of stages is rather the rule than the exception, one may argue if the concept of development stages makes sense in these forests. But when the structures found in the Kyjov forest are regarded against the background of gap dynamics, which means going back to the roots of the forest cycle concept (Watt, 1947), there is a lot of conformity.

Canopy gaps occurred, ranging in size from 24 to 4415 m<sup>2</sup>, which shows structural development can be affected at very different scales. Frequent endogenous small-scale disturbances were found to drive the structuring processes on a considerable proportion of the forest area in Kyjov. Tree development supposedly takes very individual pathways here, depending on the time interval until the next canopy opening and its size. Dendroecological studies on beech trees grown in virgin forests strongly support this assumption (Trotsiuk et al., 2012; Nagel et al., 2014; Hobi et al., 2015). As a result, trees in multiple life history stages may occur in direct proximity to one another. In accordance, the degree of small-scale mixing of trees in the Initial (7–39 cm DBH), Optimum (40–69 cm dbh) and Terminal ( $\geq 70$  cm DBH) stages was indeed high in the Kyjov forest with frequent stage overlap within a plot of 500 m<sup>2</sup> (chapter 5).

In larger gaps, newly establishing cohorts might obtain a higher degree of areal dominance, which is presumably correlated with gap size. However, when exceeding a certain scale, some (rather low) level of structural heterogeneity seems obligatory. The frequency of canopy gaps decreased exponentially with increasing gap size but rare large gaps affected comparably large areas on a spatio-temporal scale. Thus, more extensive patches of less heterogeneous structure could also be expected on a considerable portion of forest area in the Kyjov forest. That a single stage dominated over the others was found on many plots, but their number decreased exponentially with increasing factor of dominance (i.e., the difference between the highest  $I_{DS}$  value and the closest of the respective other two  $I_{DS}$  values). There were no plots with an exclusive presence of a single stage.

Altogether, the structures encountered on the inventory plots in Kyjov, as described by means of the  $I_{DS}$ , are very consistent with the trends described for structural development driven by gap dynamics in this forest. The development stage index ( $I_{DS}$ ) thus seems an appropriate tool to comprehensively describe and analyze forest structure in terms of forest dynamics in this forest. The general functioning of gap induced structural processes, i.e., small gaps promote vertical heterogeneity while larger gaps may cause more homogeneously structured patches, can be anticipated to be roughly similar in other beech-dominated virgin forests. Thus, it seems valid to interpret forest dynamics by analyzing stand structure applying the  $I_{DS}$  in these forests as well. Looking at the ternary graphical plots (chapter 5, Fig. 5.3) this notion would suggest that, despite a relatively balanced mean areal presence of the three development stages in the

studied forest stands, there are also some differences in forest dynamics, as the stands revealed different patterns in plot locations. Assuming that endogenous disturbances cause small-scale heterogeneity and with increasing disturbance intensity (i.e., increasing gap size) the resulting structure becomes increasingly homogenized, a research plot's distance to the center of the ternary plot (that represents maximum heterogeneity) could be interpreted as a gradual indicator for the intensity of past disturbance. In the long-term absence of more intense exogenous disturbances, endogenous small-scale disturbances would drive structural development that should tend towards positions close to the center (attractor). Consequently, the pattern is largely determined by the frequency and intensity of exogenous disturbances.

According to this interpretation scheme, Havešová and Stučica would have experienced more severe disturbances than Kyjov, as in these stands there are more plots at rather eccentric locations. The clumped occurrence of sample plots, e.g. left of the center in the ternary plot for the Havešová forest (Fig. 5.3), might indicate that a disturbance event caused damage at the stand scale.

So far, the interpretation of the ternary plots remains speculative. Similar structures may originate from different pathways of stand development. However, at least for Kyjov, the interpretation seems substantiated by the results on gap dynamics in this forest (chapter 2 and 3). There are two major issues regarding the validation of the development stage index as a conclusive tool for the interpretation of forest dynamics: i) The application of the  $I_{DS}$  on repeated inventory data would inform about structural developmental pathways and could provide information on structural self-organization in beech-dominated forests. Further, ii) the  $I_{DS}$  could be adapted to be applicable on continuous stand structural datasets (moving window, focal filtering). This would inform on spatial pattern in stand structure and allow for mapping of the horizontal texture of development stages. A combination, i.e. repeated inventory data from a continuous area (several hectare), would be most suitable.

Yet the application of the  $I_{DS}$  is limited to our test systems, as the index relies on reference values for stand density that were specifically generated for these forest stands. However, the impact of site conditions, and also that of different tree species, on maximum stand density is consistent across tree-dimensions and causes parallel shifts towards higher or lower densities in even-aged stands (Reineke, 1933; Pretzsch and Biber, 2005). This indicates that the application of the reference values to other forests would only affect the absolute values of the stages  $I_{DS}$ , but not the relative proportions in a plot or in a stand. The general applicability of the reference values, and a potential adjustment of these, need to be evaluated to allow for a broad implementation of the  $I_{DS}$  as a tool in the analysis of forest structure and dynamics.

### **6.3 Implications for forest ecosystem conservation, restoration and close-to-nature forest management**

As it is pointed out in chapter 2, several regional and site-specific factors might influence the disturbance regime. Further, they may affect the regeneration dynamics in gaps and below canopy. Thus, the structuring processes and stand structures described in this thesis are not absolutely transferable to beech forests growing under different abiotic conditions. However, the apparently high resemblance in stand structures of the three virgin beech forests studied indicate that there is a certain degree of generality to these findings, at least across the variation in sites we encountered. Leibundgut (1993), who had himself visited many beech-dominated virgin forests across Europe covering a broad range of site-conditions, perceived structure and dynamics in these forests to be relatively similar to one another. Seeing that valid data for comparison is rare one cannot deny the general usefulness of such a respected expert opinion, even though this largely subjective assessment was partly challenged (concerning subtle details) in a previous section.

The beech virgin forests Havešová, Kyjov and Stučica were all characterized by a highly diverse stand structure in the majority of plots and at the stand level. The relatively intense mixing of trees in different life history stages that was found in most plots can be linked to several beneficial functions. It guarantees high resilience to exogenous disturbances (chapter 2) and the continuous provision of certain habitat structures such as deadwood and veteran trees within small distances, which is of special importance to some comparably immobile species. A positive effect of small-scale structural diversity on forest productivity was also evidenced for the studied stands (Glatthorn et al., 2018). Thus, creating and sustaining similar structures seems highly desirable. However, a main emphasis on small-scale structural diversity in close-to-nature forest management and forest restoration has been criticized, as the establishment of more light-demanding tree species and certain rare animal and plant species rely on more extensive canopy openings that are largely prevented (e.g., Röhrig et al., 2006; Schall et al., 2018).

The findings from this thesis show that the occurrence of more homogeneously structured patches is also typical in virgin beech forests. They seem to base on spatio-temporally dispersed disturbances that affect larger scales and would provide habitat for these species. At the stand scale such events may hold off for longer periods (probably several decades). Thus, dependent species can be assumed to show either a high mobility (by movement or seed dispersal), or they may endure long periods of unfavorable conditions (by longevity of adults or by forming seedbanks), or both.

Common ash, wych elm, Norway maple and sycamore maple, e.g., were nearly absent in the advanced regeneration of the three studied virgin forests, but they were present in the canopy in low numbers and seedlings of these species were frequently encountered. This indicates that suitable conditions for establishment, that guarantee continuance of these tree species populations, must have occurred at sufficient frequency in the past. The scarcity of admixed tree species in the canopy layer largely has to be attributed to the rare occurrence of larger disturbances and not to overly high (i.e. unnatural) browsing pressure by ungulates. Most of these canopy trees grew up in a time when the study sites were embedded in a virgin forest landscape that likely contained balanced populations of ungulates and predators. Their presence in the forest matrix likely ensures high resilience of the forest ecosystem to more severe disturbances that affect larger areas and could not rapidly be recolonized by beech with its limited seed dispersal. Yet, the role of large gaps and stand replacing disturbances in beech forest dynamics is not well understood, due to their rare occurrence in space and time.

Emulating the size-frequency pattern of canopy disturbances found in virgin forests was proposed for forest ecosystem restoration and close-to-nature forest management (Seymour et al., 2002; Dröbler and von Lüpke, 2005; Nagel and Svoboda, 2008). According to Nagel and Svoboda (2008) the silvicultural models that could be combined to a flexible management strategy are ‘single-tree selection’, ‘group selection’ and ‘irregular shelterwood cuttings’. The conclusions presented in this thesis largely agree with this. The occasional formation of larger openings (up to small clear cuts) would account for more light demanding species and should be added to the strategy, but not dominate it.

The trends for regeneration development in the Kyjov forest (chapter 3) suggest that small gaps (< 100 m<sup>2</sup>) do not allow for good sapling growth over longer periods. Further, the growth morphology of saplings might be negatively affected (Rozenbergar and Diaci, 2014). These findings raise doubt on the suitability of small gaps in the management of beech forests for commercial purposes or for a progressive conversion of even aged stands towards a vertically heterogeneous structure, at least under comparable dystic site conditions. A frequent expansion to avoid such negative consequences would be costly. In large gaps, that provide good growth conditions for longer time periods, however, the density of saplings might be insufficient to properly recover the area and problems with competing herbaceous plants might occur. A good trade off that accounts for a sufficient density of saplings and good and continuous growth could be archived by initial irregular shelterwood cutting followed by gap cuttings between 500 to a few thousand m<sup>2</sup>. However, if the recruitment of more light-demanding tree species is desired a prior shelterwood cutting should only cover a part of the later gap or be suspended.

The initial structure of a forest stand must always be considered in planning interventions. In chapter 4, it was found that the structural constitution of the uneven aged single tree selection forest was relatively similar to that in large parts of the Kyjov forest, and adjustment towards less heterogeneous structures in parts of such a stand seems easily induced. In contrast, the structure of the even aged stand was very different, and to achieve vertical and horizontal heterogeneity seems complex and would take a long time. Deviating approaches (e.g., Dodson et al., 2012) might prove useful to convert the structure of individual forests towards a higher degree of naturalness. The proposed  $I_{DS}$  enables us to quantify and display stand level structural heterogeneity that might serve as a major stand structural attribute in evaluating the success of forest structure restoration efforts or in the assessment of the ‘naturalness’ of beech forests.



## 6.4 References

- Bauhus, J., Puettmann, K., Messier, C., 2009. Silviculture for old-growth attributes. *Forest Ecology and Management*, 258, 525–537.
- Bottero, A., Garbarino, M., Dukić, V., Govedar, Z., Lingua, E., Nagel, T. A., Motta, R., 2011. Gap-Phase Dynamics in the Old-Growth Forest of Lom, Bosnia and Herzegovina. *Silva Fennica*, 45(5), 875–887.
- Christensen, M., Emborg, J., Busse Nielsen, A., 2007. The forest cycle of Suserup Skov – revisited and revised. *Ecological Bulletins*, 52, 33–42.
- Diaci et al., 2005 Diaci, J., Rozenbergar, D., Boncina, A., 2005. Interactions of light and regeneration in Slovenian Dinaric Alps: patterns in virgin and managed forests. *Forest, Snow and Landscape Research*, 79(1/2), 154–160.
- Dodson, E. K., Ares, A., Puettmann, K. J., 2012. Early responses to thinning treatments designed to accelerate late successional forest structure in young coniferous stands of western Oregon, USA. *Canadian Journal of Forest Research*, 42(2), 345–355.
- Dröbler, L., Lüpke, B., 2005. Canopy gaps in two virgin beech forest reserves in Slovakia. *Journal of Forest Science*, 51, 446–457.
- Dröbler, L., Meyer, P., 2006. Waldentwicklungsphasen in zwei Buchen-Urwaldreservaten in der Slowakei. *Forstarchiv*, 77, 155–161.
- von Gadow, K., Zhang, C. Y., Wehenkel, C., Pommerening, A., Corral-Rivas, J., Korol, M., Myklush, S., Hui, G. Y., Kiviste, A., Zhao, X. H., 2012. Forest Structure and Diversity. In T. Pukkala, von Gadow, K. (Eds.), *Continuous Cover Forestry, Managing Forest, Ecosystems 23* (2nd ed., pp. 29–83). Springer, Dordrecht.
- Glatthorn, J., Feldmann, E., Pichler, V., Hauck, M., Leuschner, C., 2018. Biomass stock and productivity of primeval and production beech forests: greater canopy structural diversity promotes productivity. *Ecosystems*, 21(4), 704–722.
- Hobi, M. L., Commarmot, B., Bugmann, H., 2015a. Pattern and process in the largest primeval beech forest of Europe (Ukrainian Carpathians). *Journal of Vegetation Science*, 26(2), 323–336.
- Kenderes, K., Král, K., Vrška, T., Standovar, T., 2009. Natural Gap Dynamics in a European Mixed Beech-Spruce-Fir Old-Growth Forest. *Ecoscience*, 16(1), 39–47.
- Korpel, Š., 1995. Die Urwälder der Westkarpaten. Gustav Fischer Verlag, Stuttgart.
- Král, K., Daněk, P., Janík, D., Krůček, M., Vrška, T., 2018. How cyclical and predictable are Central European temperate forest dynamics in terms of development phases? *Journal of Vegetation Science*, 29(1), 84–97.
- Leibundgut, H., 1993. Europäische Urwälder - Wegweiser zur naturnahen Waldwirtschaft. Paul Haupt.
- Leuschner, C., Ellenberg, H., 2017. Ecology of Central European Forests. *Vegetation Ecology of Central Europe*, Vol. I., Springer Nature, Cham.
- Nagel, T. A., Svoboda, M., 2008. Gap disturbance regime in an old-growth Fagus–Abies forest in the Dinaric Mountains, Bosnia-Herzegovina. *Canadian Journal of Forest Research*, 38, 2728–2737.
- Nagel, T. A., Svoboda, M., Rugani, T., Diaci, J., 2010. Gap regeneration and replacement patterns in an old-growth Fagus–Abies forest of Bosnia–Herzegovina. *Plant Ecology*, 208(2), 307–318.
- Nagel, T. A., Svoboda, M., Kobal, M., 2014. Disturbance, life history traits, and dynamics in an old-growth forest landscape of southeastern Europe. *Ecological Applications*, 24 (4), 663–679.
- Oliver, C.D., Larson, B.C., 1996. *Forest Stand Dynamics*. Wiley, New York.
- Parviainen, J., 2005. Virgin and natural forests in the temperate zone of Europe. *Forest, Snow and Landscape Research*, 79(1/2), 9–18.

- Pretzsch, H., Biber, P., 2005. A re-evaluation of Reineke's rule and stand density index. *Forest science*, 51(4), 304-320.
- Reineke, L. H., 1933. Perfecting a stand-density index for even-aged forests. *Journal of Agricultural Research*, 46, 627-638.
- Remmert, 1991
- Remmert, H., 1991. The mosaic-cycle concept of ecosystems—an overview, in: Remmert, H. (Ed.), *The mosaic-cycle concept of ecosystems*, Springer, Berlin, Heidelberg, pp. 1–21.
- Röhrig, E., Lüpke, B., Bartsch, N., 2006. *Waldbau auf ökologischer Grundlage*. Ulmer, Stuttgart.
- Rozenbergar, D., Mikac, S., Anić, I., Diaci, J., 2007. Gap regeneration patterns in relationship to light heterogeneity in two old-growth beech–fir forest reserves in South East Europe. *Forestry*, 80(4), 431–443.
- Rozenbergar, D., Diaci, J., 2014. Architecture of *Fagus sylvatica* regeneration improves over time in mixed old-growth and managed forests. *Forest ecology and management*, 318, 334-340.
- Schall, P., Gossner, M. M., Heinrichs, S., Fischer, M., Boch, S., Prati, D., Jung, K., Baumgartner, V., Blaser, S., Böhm, S., Buscot, F., Daniel, R., Goldmann, K., Kaiser, K., Kahl, T., Lange, M., Müller, J., Overmann, J., Renner, S. C., Schulze, E. D., Sikorski, J., Tschapka, M., Türke, M., Weisser, W. W., Wemheuer, B., Wubet, T., Ammer, C., 2018. The impact of even-aged and uneven-aged forest management on regional biodiversity of multiple taxa in European beech forests. *Journal of Applied Ecology*, 55(1), 267-278.
- Seidel, D., Fleck, S., Leuschner, C., & Hammett, T. (2011). Review of ground-based methods to measure the distribution of biomass in forest canopies. *Annals of Forest Science*, 68(2), 225-244.
- Seymour, R. S., White, A. S., deMaydenadier, P. G., 2002. Natural disturbance regimes in northeastern North America - evaluating silvicultural systems using natural scales and frequencies. *Forest Ecology and Management*, 155(1), 357–367.
- Splechtna, B. E., Gratzner, G., 2005. Natural disturbances in Central European forests: approaches and preliminary results from Rothwald, Austria. *Forest, Snow and Landscape Research*, 79, 57–67.
- Tilman, D., 1982. *Resource competition and community structure*. Princeton University Press, Princeton. 296 pp.
- Trotsiuk, V., Hobi, M.L., Commarmot, B., 2012. Age structure and disturbance dynamics of the relic virgin beech forest Uholka (Ukrainian Carpathians). *Forest Ecology and Management*, 265, 181–190.
- Veen, P., Fanta, J., Raev, I., Biriş, I. A., de Smidt, J., Maes, B., 2010. Virgin forests in Romania and Bulgaria: results of two national inventory projects and their implications for protection. *Biodiversity and Conservation*, 19(6), 1805–1819.
- Wagner, S., 1999. *Ökologische Untersuchungen zur Initialphase der Naturverjüngung in Eschen-Buchen-Mischbeständen*. Schriften aus der Forstlichen Fakultät der Universität Göttingen und der Niedersächsischen Forstlichen Versuchsanstalt, 129.
- Watt, A. S., 1947. Pattern and Process in the Plant Community. *Journal of Ecology*, 35, 1–22.
- Whitmore, T. C. (1989). Canopy gaps and the two major groups of forest trees. *Ecology*, 70(3), 536-538.



## Curriculum vitae

**Eike Feldmann**, born on 23.09.1979 in Hannover

- 2013 - dato:** Ph.D. study at the department of Plant Ecology and Ecosystem Research, Albrecht-von-Haller Institute for Plant Sciences, Georg-August University, Göttingen, Germany
- 2008 - dato:** Freelancing activities, mainly data collection with focus on stand structure and structural dynamics in strict forest reserves
- 2005 - 2008:** M.Sc. study at the Faculty of Forest Sciences and Forest Ecology, Georg-August-University, Göttingen, Germany;  
Titel of master thesis: Vergleich der Entwicklung von Naturverjüngung nach Windwurf im Naturwald und im Wirtschaftswald  
(Comparison of regeneration development following severe windthrow in a strict forest reserve and a managed forest)
- 2001 - 2005:** B.Sc. study at the Faculty of Forest Sciences and Forest Ecology, Georg-August-University, Göttingen, Germany;  
Titel of bachelor thesis: Urwälder Europas im internationalen Vergleich  
(Virgin forests of Europe)
- 2000 - 2001:** Civil service in a workshop for disabled people
- 2000:** Abitur at the Carl-Friedrich-Gauss-Schule, Hemmingen, Germany

## Erklärung

Hiermit erkläre ich an Eides statt, dass ich die vorliegende Dissertation mit dem Titel

„Forest Structure and Structural Dynamics of Virgin Beech Forests in Slovakia“

selbstständig verfasst habe. Es wurden keine anderen als die angegebenen Quellen und Hilfsmittel benutzt sowie alle wörtlich oder sinngemäß übernommenen Stellen in der Arbeit als solche und durch Angabe der Quelle gekennzeichnet. Dies gilt auch für Zeichnungen, Skizzen, bildliche Darstellungen sowie für Quellen aus dem Internet.

Hannover, 15.10.2018

Eike Feldmann

