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Biodiversity dynamics of differently managed lowland forests left to spontaneous development in Central Europe

Biodiversitätsdynamik unterschiedlich bewirtschafteter Tieflandwälder in Mitteleuropa, die der natürlichen Entwicklung überlassen wurden

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Keywords: Stand structure, Coppice, High forest, Mixed forest, Protected landscape area, Conservation

Schlüsselbegriffe: Bestandesstruktur, Niederwald, Hochwald, Mischwald, Landschaftsschutzgebiet, Naturschutz

Abstract

European coppice forests covered a large area in historical times and almost 90 % of them were gradually transformed to different forest types during the last century. Recently forest managers across Europe have out more emphasis on increasing biodiversity, which has now a key priority of forest management. The objective of this study was to evaluate the diversity, structure and production of lowland forests left to spontaneous development with different historical management since the 1950s. Our study region were calciphilic beech forests, hornbeam-oak forests and stony colluvial forests in the Český kras Protected Landscape Area, Czech Republic. The study period extends over a period of 15 years from 2002 to 2017 and the management systems under consideration were coppice, coppice with standards and high forest. Our main focus was on changes in species composition, structural and total stand

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diversity separated between tree layer and natural regeneration. The results indicate that during 15 years only small changes in the biodiversity of the tree layer occurred, while natural regeneration exhibited a significant increase in biodiversity. Specifically, in the tree layer the height differentiation, species richness and timber production increased and in natural regeneration the species heterogeneity and density increased during the study period. Comparing the natural regeneration with the tree layer, we observed a significant increase of maple species (*Acer* sp.) and European ash (*Fraxinus excelsior* L.), while the share of sessile oak (*Quercus petraea* [Matt.] Liebl.) significantly decreased. The forest stands managed as coppice or coppice with standards had distinctive dynamics and significantly higher biodiversity than similar forests that has been converted into high forests.

Zusammenfassung

Niederwälder haben früher in Europa ein großes Gebiet bedeckt und etwa 90 % wurden im letzten Jahrhundert allmählich in andere Bewirtschaftungsformen wie Hochwald oder Mittelwald umgewandelt. In letzter Zeit hat das Waldmanagement der Erhöhung der Biodiversität mehr Bedeutung gegeben und Biodiversität ist nun eine wichtige Zielsetzung in der Waldbewirtschaftung. Das Ziel dieser Studie war es die Diversität, Struktur und Produktivität von Tieflandwäldern zu quantifizieren, die seit den 50er Jahren der natürlichen Entwicklung überlassen wurden. Unser Untersuchungsgebiet sind kalziphilen Buchenwäldern, Hainbuchen-Eichenwäldern und Schuttwäldern im Landschaftsschutzgebiet Český kras in der Tschechischen Republik. Unser Untersuchungszeitraum erstreckt sich über 15 Jahre von 2002 bis 2017 und die untersuchten Bewirtschaftungsformen sind Niederwald, Mittelwald und Hochwald. Unser Fokus lag auf Veränderungen in der Artenzusammensetzung und der strukturellen Diversität der Baumschicht und der natürlichen Verjüngung. Wir konnten zeigen, dass es nach 15 Jahren nur zu minimalen Veränderungen in der Biodiversität der Baumschicht gekommen ist, während die Biodiversität der natürlichen Verjüngung bedeutend angestiegen ist. Es haben sich insbesondere die Höhendifferenzierung, Artenvielfalt und Holzproduktion in der Baumschicht erhöht, während in der natürlichen Verjüngung die Artenheterogenität und die Bestandesdichte größer wurde. Vergleicht man die Baumschicht mit der Verjüngung war eine Zunahme an Ahornarten (*Acer* sp.) und der Gemeinen Esche (*Fraxinus excelsior* L.) zu beobachten. Im Gegensatz dazu ist der Anteil der Traubeneiche (*Quercus petraea* [Matt.] Liebl.) im Untersuchungszeitraum gesunken. Die Waldbestände, bis zu den 50er Jahren des 20. Jahrhunderts als Niederwald oder Mittelwald bewirtschaftet, haben eine andere Dynamik und eine deutlich höhere Biodiversität als vergleichbare Wälder, die seitdem in Hochwälder umgewandelt worden waren.

1. Introduction

Since the early 90s of the 20th century major efforts were made to maintain and to increase biodiversity and the interest in mixed forests has been increasing as well (Ngo Bieng et al. 2013). This is *inter alia* caused by the currently important topic of climate change and driven by the question on how forest ecosystems will adapt to potential environmental changes (Bengtsson et al. 2000; Lenoir et al. 2008; Milad et al. 2011). Compared to mono-specific forests, mixed forests appear to be more stable in terms of their reaction to abiotic influences (Ngo Bieng et al. 2013; Petritan et al. 2014; Králíček et al. 2017) as well as to biotic threats like damage for instance caused by insects (Jactel & Brockerhoff 2007). At the same time mixed forests were reported to be better utilize nutrients and water resources (Kelty 2006). Biodiversity is one of the six main criteria of sustainable forestry in Europe and supporting biodiversity is one of the main objectives of the International Convention on Biological Diversity of MCPFE (2003) and related international strategies (Bengtsson et al. 2000; Barbier et al. 2009).

In forests the species composition and the codominant and dominant tree density are important factors for biodiversity and these factors also directly influence the resource availability for the ground vegetation (Vacek et al. 1999; Mölder et al. 2008; Vild et al. 2013; Bílek et al. 2014) and disturbance regimes (Hunter 1999; Lorz et al. 2010; Vacek et al. 2017a). Biodiversity is also influenced by forest type (Bengtsson et al. 2000; Van Calster et al. 2008; Vacek et al. 2016) and applied forest management system and socio-economic conditions (Bílek et al. 2011; Vild et al. 2013; Sjölund & Jump 2015; Chudomelová et al. 2017).

Historically, to ensure fast regeneration of forest stands at lowland and hilly regions the re-sprouting ability of many broadleaved tree species such as *Quercus*, *Carpinus*, *Tilia* and *Corylus* has been utilized (Bruckman et al. 2011; Lassauce et al. 2012; Suchomel et al. 2012) and this management type is called coppice. These coppice forests were historically very intensively exploited and subject to frequent disturbance using a rotation period of about 30 to 40 years (Van Calster et al. 2008). Coppicing was caused by intensive demand for fuelwood (also including the roots), collecting leaf litter as fodder and bedding for livestock and occasionally also subject to deforestation by slash and burn clearing for agricultural purposes (Nožička 1957; Konvička et al. 2008). Pronounced patchiness of microsites (Van Calster et al. 2007) from shaded locations to open grown canopies combined with low nutrient availability are typical for this very intensive management form. These characteristics support the occurrence of light-demanding oligotrophic species in the ground layer (Birks 2005; Ciancio et al. 2006; Konvička et al. 2008; Plue et al. 2013; Vild et al. 2013). At the same time coppice forests allow the survival of shade-tolerant species (Van Calster et al. 2007; Hédl et al. 2010) and in general appear to exhibit higher biodiversity (Van Calster et al. 2008; Milad et al. 2011; Plue et al. 2013; Petritan et al. 2014; Müllerová et al. 2015).

The coppice system as an intensive method of forest management in Europe was gradually abandoned from the second half of the 18th century to the mid-20th century (Bruckman et al. 2011; McGrath et al. 2015; Sjölund & Jump 2015). Across Europe, this method was originally used on 25 million hectares over a long period, while currently it is used on merely 2.9 mio. ha (Sjölund & Jump 2015). Coppicing persisted in lowlands and hilly areas due to its ability to cope with negative effects of drought on the tree regeneration (Lassauce et al. 2012; Plue et al. 2013; Vild et al. 2013). Changing management by conversion into high forest by a reduction in the shoot number and/or planting (Müllerová et al. 2015) or extending the rotation period and subsequent abandonment of coppice management (Lassauce et al. 2012) resulted in a gradual increase in canopy closure (Van Calster et al. 2007; Müllerová et al. 2015). Consequently, this caused a reduction of light-demanding species (Müllerová et al. 2014) and a decrease in species diversity (Janík et al. 2008; Plue et al. 2013; Müllerová et al. 2015), particularly in forests dominated by European beech (*Fagus sylvatica* L.) (Mölder et al. 2008; Plue et al. 2013). Abondment of coppicing decreased also the occurrence of competitive and stress-tolerant species (Van Calster et al. 2007) and increased the occurrence of typical forest species (Brunet et al. 2011).

In turn greater attention should be paid to valuable lowland forests frequently managed as coppice forests compared to the extensively described structure and dynamics of mountain forests (Ammer 1996; Král et al. 2015; Bulušek et al. 2016; Vacek et al. 2016; Slanař et al. 2017; Vacek et al. 2017b). Areas left to spontaneous development enable us to study the natural processes of forest dynamics after the termination of management activities (Vacek 2003; Vandekerkhove et al. 2005; Petritan et al. 2012; Arefjev 2017). For this purpose long-term research plots are very valuable as they allow monitoring changes in forest ecosystems (Bakker et al. 1996; Vacek et al. 2017). Knowledge of the forest structure and dynamics of these stands could be used in the management of cultivated forests that are comparable in terms of site and stand conditions (cf. Korpeľ 1995; Vrška et al. 2009; Veen et al. 2010; Bölöni et al. 2017).

The mission of this study was to evaluate the biodiversity of lowland forest stands left to spontaneous development since the 1950s, considering stands continuously managed by coppicing and stands transformed into coppice with standards or high forest. The specific objectives were to explore (1) differences in tree diversity (structural, species) between high forest, coppice with standards and coppice forest; (2) changes in production, structure and diversity of forest stands between tree layer and natural regeneration, considering damage caused by game, and (3) relationship between forest type, tree layer structure and natural regeneration diversity.

2. Material and Methods

2.1. Study area

Karlštejn National Nature Reserve (NNR) was selected as study region and is situated in the Český kras Protected Landscape Area (PLA) in Czech Republic (Fig. 1). It is an old settlement territory in a climatically favourable area in the oak to oak-beech forest altitudinal zone exhibiting hornbeam-oak forests (*Quercetum Carpini*), stony colluvial forests (*Aceri-Carpinetum*) and calciphilic beech forests (*Cephalanthero-Fagion*) (Janík et al. 2008). Until the middle of the 20th century the forests of Karlštejn locality were managed as coppices with standards with a low share of the mature trees in the overstorey, high intensity of felling in coppice forest and cattle grazing. The Karlštejn NNR was declared in 1955 on an area of 1 547 ha to protect a wide range of biotopes (including oak-hornbeam and beech forests) and a rich variety of fauna unique on limestone bedrock, exposed rocks and variety of relief types.

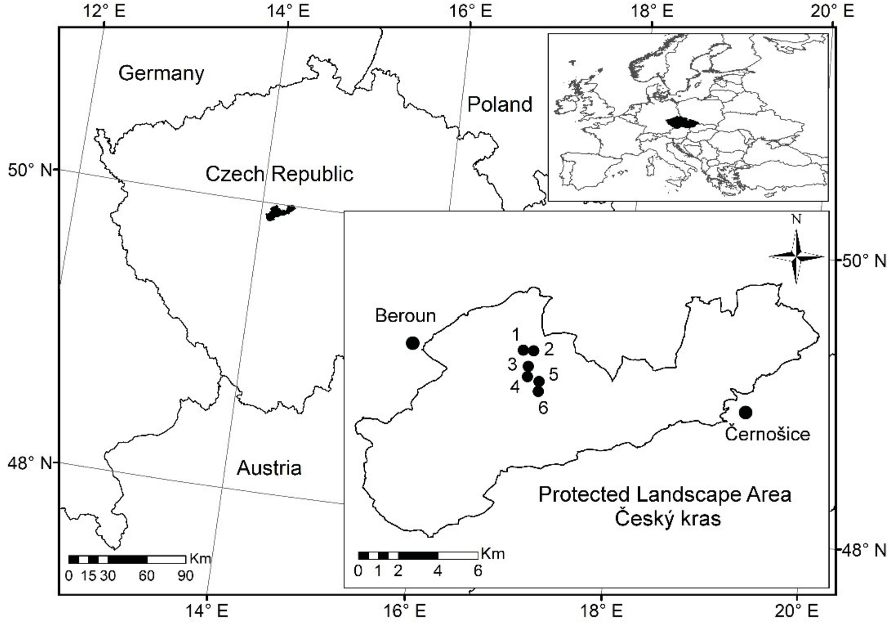


Figure 1: Localization of permanent research plots 1–6 in Karlštejn National Nature Reserve (the map was made in ArcGIS Program Copyright 1995-2010 ESRI).

Abbildung 1: Lage der permanenten Beobachtungsflächen 1–6 im Nationalen Naturschutzgebiet Karlštejn (Karte wurde im ArcGIS-Programm Copyright 1995-2010 ESRI erstellt).

Maximum altitude of the study area is 433 m a.s.l., while annual average temperature ranges between 8 and 9 °C and annual precipitation sum is 564 mm (Tolasz et al. 2007). The bedrock is mainly composed of grey or red limestones. Rendzinas, Luvisols and Cambisols are prevailing; Lithosols are scarce (Němeček et al. 2001). Dominant forests alliances are *Tilio-Acerion*, *Melampyro nemorosi-Carpinetum* and *Cephalanthero-Fagetum* (Knollová & Chytrý 2004; Kubíková 2007; Janík et al. 2008).

The prevailing part of forest stands in the area of interest was established as coppice forests presumably in the medieval age. Six permanent research plots (PRP 1, 2 – high forest, PRP 3, 4 – coppice with standards, PRP 5, 6 – coppice forest) were selected in the Doutnáč forest locality, that has a total size of 67.64 ha. On PRP 1-2 the forest stands have been converted to high forest since the 1950s. The stands of PRP 3-4 have been converted to coppice with standards since the 1950s; on PRP 5-6 the stands were left as a coppice with prolonged period. The entire Doutnáč locality was left to spontaneous development and forest management activities were completely terminated in 2004, yet forest management was extensive before this time. The last officially executed management practice was carried out in 1986 aimed to support trees with high quality originated from seeds and to remove sprouts on PRP 1-4 and support high-quality stump sprouts on PRP 5-6. Previous silvicultural thinning was conducted in the years 1978 and 1972. Tab. 1 summarizes the basic characteristics of the analyzed PRPs.

Table 1: Summary information of permanent research plots (PRP). Stand characteristics represent year 2017 and we show all species contributing > 5% by stand volume.

Tabelle 1: Zusammenfassung der verwendeten Dauerbeobachtungsflächen. Die gezeigten Bestandeskennwerte (Baumartenanteil) repräsentieren das Jahr 2017 und wir zeigen alle Baumarten > 5 % des Bestandesvolumens.

PRP	**Location**	**Altitude** (m)	**Aspect**	**Slope** (°)	**Plant associations**	**Soil type**	**Forest manage-ment**	**Age** (y)	**Stand volume** (m^3 ha^{-1})	**Tree species**	**%**
1	N 49°57‘45“ E 14°09‘17“	413	NE	6	*Cephalanthero-Fagetum*	Rendzina Cambisol	High forest	96	525	*Fagus s.*	94
										Larix d.	6
2	N 49°57‘44“ E 14°09‘21“	415	NE	8	*Cephalanthero-Fagetum*	Rendzina Cambisol	High forest	94	590	*Fagus s.*	97
3	N 49°57‘32“ E 14°09‘11“	430	NE	2	*Melampyro nemorosi-Carpinetum*	Modal Rendosol	Coppice with standard	97	246	*Tilia* c.	32
										Quercus p.	30
										Carpinus b.	11
										Fagus s.	11
										Fraxinus e.	8
4	N 49°57‘34“ E 14°09‘13“	425	NE	3	*Melampyro nemorosi-Carpinetum*	Modal Rendosol	Coppice with standard	106	305	*Tilia* c.	31
										Quercus p.	27
										Fagus s.	26
										Carpinus b.	8
										Fraxinus e.	5
5	N 49°57‘23“ E 14°09‘15“	418	SE	19	*Aceri-Carpinetum*	Rendosol melanic	Coppice forest	81	233	*Quercus* p.	46
										Tilia c.	36
										Fraxinus e.	8
										Carpinus b.	6
6	N 49°57‘20“ E 14°09‘15“	412	SE	16	*Aceri-Carpinetum*	Rendosol melanic	Coppice forest	81	200	*Quercus* p.	47
										Tilia c.	35
										Carpinus b.	10
										Fraxinus e.	5

2.2. Data collection

To determine the tree layer structure six PRPs of 50×50 m (0.25 ha) were established in 2002. The measurement was repeated in 2017 using the Field-Map technology (IFER 2017). The positions (coordinates) of all trees exceeding a breast height diameter (DBH) ≥ 4 cm were localized. DBH of the tree layer were measured with a calliper (accuracy 1 mm) and tree heights and heights of the crown base were measured with a Vertex laser hypsometer (accuracy 0.1 m). The four crown radii were measured perpendicular to each other through the centroid of the crown by the Field-Map technology. The first azimuth was defined as the direction from the subject tree to the centre of the measurement plot (Sharma et al. 2016).

In 2002 natural regeneration (height ≥ 10 cm and DBH < 4 cm) was measured on the whole area of PRP 1, 3 and 5 and in 2017 on transects of 10×50 m. Transects representative from the aspect of regeneration character were chosen in the middle of PRP according to average stand and habitat conditions. The parameters measured for natural regeneration were position, height, obviously alive crown height, crown width and terminal shoot browsing.

2.3. Data analysis

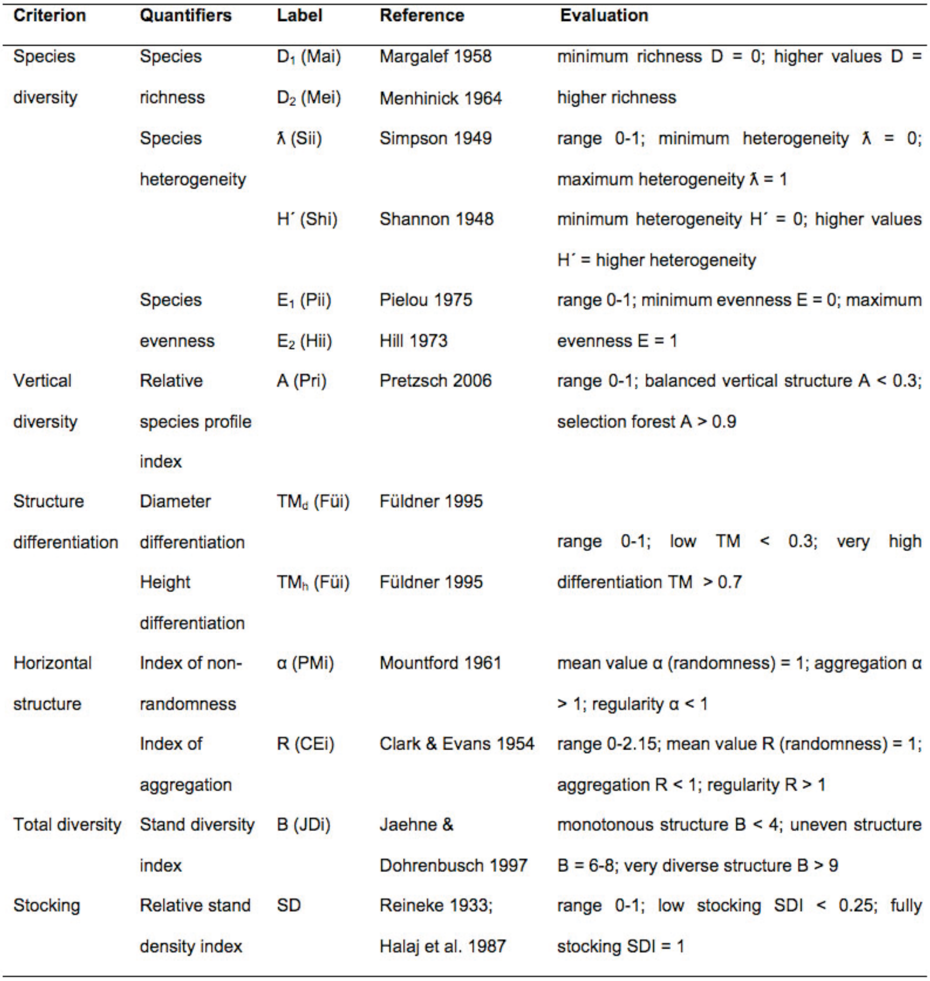
Stand characteristics (production, stocking, canopy, species and vertical diversity) of the tree layer were evaluated by the SIBYLA 5.1. software (Fabrika & Ďurský 2005). The relative stand density index (SD), the crown closure (Crookston & Stage 1999) and the crown projection area (CPA) were observed for each plot. The CPA was automatically derived from measured crown radii by the Field-Map software and visualized by the function "smoothing crowns" (IFER 2017). The maximum SDI value was derived from the model of yield tables (Halaj et al. 1987). The layout maps were made in the ArcGIS 10.0 software (ESRI 2010).

Species diversity was analysed in the framework of species richness (Margalef 1958; Menhinick 1964), species heterogeneity (Shannon 1948; Simpson 1949) and species evenness (Hill 1973; Pielou 1975). The structural diversity assessment included the calculations of diameter and height differentiation index (Füldner 1995), relative species profile index (based on three tree layers; Pretzsch 2006) and stand diversity index (Jaehne & Dohrenbusch 1997). The stand diversity index is based on the composition of tree species, vertical structure, distribution of stems and structural characteristics of crowns. The spatial distribution (horizontal structure) of trees on PRP was determined according to the index of non-randomness (Mountford 1961) and aggregation index (Clark & Evans 1954) and calculated using the PointPro 2.2. software (Zahradník & Puš 2010). The significance of deviations from expected values for the random point layout was tested using Monte Carlo simulations (testing of differences between randomly generated points and actual observed data). The criteria of analysed diversity and structural indices are shown in Table 2, equations are described in the Appendix

1 (formulas 1-14) and detailed description was published by Pretzsch (2009).

Table 2: Overview of calculated diversity and structural indices.

Tabelle 2: Überblick über die berechnete Diversitäts- und Struktur-Indices.



Criterion	**Quantifiers**	**Label**	**Reference**	**Evaluation**
Species diversity	Species richness	D_1 (Mai) D_2 (Mei)	Margalef 1958 Menhinick 1964	minimum richness D = 0; higher values D = higher richness
	Species heterogeneity	ƛ (Sii)	Simpson 1949	range 0-1; minimum heterogeneity ƛ = 0; maximum heterogeneity ƛ = 1
		H´ (Shi)	Shannon 1948	minimum heterogeneity H´ = 0; higher values H´ = higher heterogeneity
	Species evenness	E_1 (Pii) E_2 (Hii)	Pielou 1975 Hill 1973	range 0-1; minimum evenness E = 0; maximum evenness E = 1
Vertical diversity	Relative species profile index	A (Pri)	Pretzsch 2006	range 0-1; balanced vertical structure A < 0.3; selection forest A > 0.9
Structure differentiation	Diameter differentiation	TM_d (Füi)	Füldner 1995	range 0-1; low TM < 0.3; very high differentiation TM > 0.7
	Height differentiation	TM_h (Füi)	Füldner 1995	
Horizontal structure	Index of non-randomness	α (PMi)	Mountford 1961	mean value α (randomness) = 1; aggregation α > 1; regularity α < 1
	Index of aggregation	R (CEi)	Clark & Evans 1954	range 0-2.15; mean value R (randomness) = 1; aggregation R < 1; regularity R > 1
Total diversity	Stand diversity index	B (JDi)	Jaehne & Dohrenbusch 1997	monotonous structure B < 4; uneven structure B = 6-8; very diverse structure B > 9
Stocking	Relative stand density index	SD	Reineke 1933; Halaj et al. 1987	range 0-1; low stocking SDI < 0.25; fully stocking SDI = 1

Statistical analyses were processed in the R software (R Core Team 2017). Multidimensional ANOVA (or simple ANOVA in the case of testing differences in one parameter) was used for testing of differences between multidimensional characteristics of particular plots. Unconstrained principal component analysis (PCA) in the CANOCO 5.03 program (Šmilauer & Lepš 2014) was used (centred and standardized data) to analyse relationships between stand parameters, stand biodiversity (structure and species), regeneration density, regeneration biodiversity and similarity of PRP (1-6) during the time (2002, 2017).

3. Results

3.1. Tree layer structure and development

The numbers of living trees in the tree layer ranged between 368 and 2160 trees ha^{-1} and also the differences in stand structure between the three studied forest types were large (Tab. 3). The high forest stands had one tree layer, while the coppice with standards hat two to three layers and coppice had three layers. The relative stand density (SDI / SDI$_{max}$) exhibited a range of 0.54 to 0.97. The average basal area varied between the studied forest types by about 25 %. The highest stand volume of 525 and 590 m^3 ha^{-1} were observed in the stands converted to high forest. The lowest stand volume (200 m^3 ha^{-1} and 246 m^3 ha^{-1}) was measured on the plots managed as coppice in the past.

The proportions of tree species contributing substantially to the stand volume differed on the particular plots. In high forest European beech represented with 92-96 % most of the stand volume (Tab. 1). In coppice with standards the stand mixture was richer and the stand volume was composed of 31 % small-leaved linden (*Tilia cordata* Mill.) and 26-30 % sessile oak (*Quercus petraea* [Matt.] Liebl.), while the contribution of beech and European hornbeam (*Carpinus betulus* L.) was more variable (10-26 % and 9-14 %, respectively). The coppice stands also was a mixture of broadleaves, with oak contributing with 44 % the largest share, followed by linden (34-37 %) and hornbeam (8-12 %).

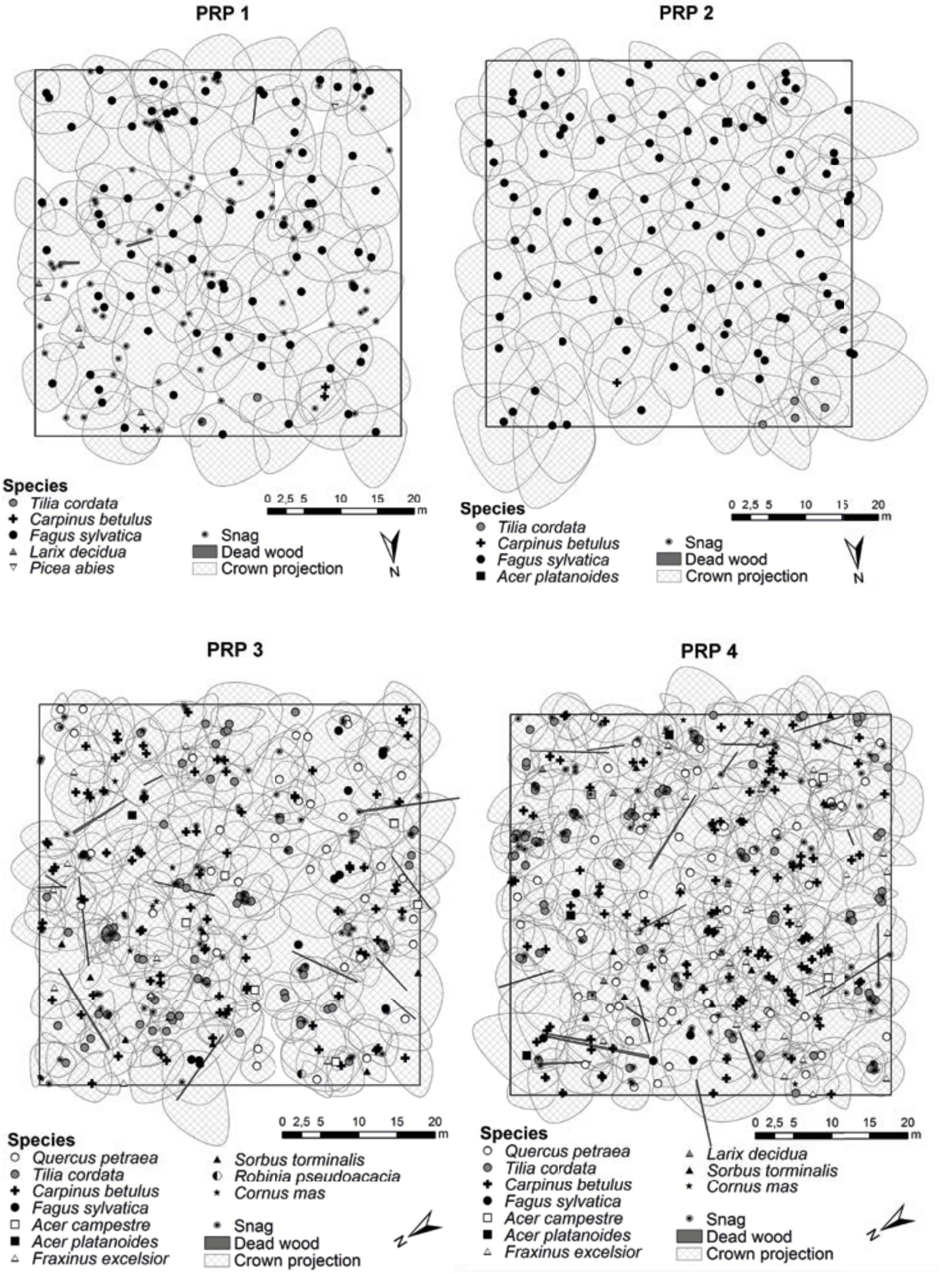
Table 3: Average stand characteristics of the six permanent research plots in 2002 and 2017.

Tabelle 3: Mittlere Bestandeskennwerte der sechs Dauerversuchsflächen in den Jahren 2002 und 2017.

PRP	**Year**	**Age** (y)	**Diameter** (cm)	**Height** (m)	**Number of trees** (trees ha^{-1})	**Basal area** (m^2 ha^{-1})	**Stand volume** (m^3 ha^{-1})	**Crown closure** (%)	**Crown projection area** (ha ha^{-1})	**Relative stand density**
1	2002	85	33.1	27.4	360	31.0	431	90.6	2.38	0.54
	2017	99	35.5	27.9	368	36.5	525	94.8	2.95	0.61
2	2002	82	32.0	26.7	428	34.4	481	93.0	2.72	0.60
	2017	96	34.4	27.0	440	40.9	590	96.7	3.39	0.70
3	2002	86	17.4	14.2	1132	27.0	191	97.3	3.57	0.60
	2017	99	18.6	14.2	1228	33.2	246	98.1	4.76	0.73
4	2002	95	20.7	15.3	848	28.6	244	95.0	3.02	0.58
	2017	108	21.5	15.1	936	34.1	305	97.1	3.91	0.69
5	2002	71	14.1	11.6	1992	31.0	165	97.3	4.44	0.78
	2017	83	15.6	11.7	2160	41.2	233	98.0	5.73	0.97
6	2002	71	13.9	11.6	1748	26.4	140	96.4	3.70	0.67
	2017	83	15.5	11.7	1888	35.6	200	97.0	4.84	0.86

Within the 15 years of the study period, the number of trees in the canopy increased by 5-8 % along with an increase in relative stand density. Average basal area showed a moderate increase from 26.4-34.4 m^2 ha^{-1} (2002) up to 33.2-41.2 m^2 ha^{-1} (2017). The stand volume also increased by about 20-25 % (Tab. 3).

Figure 2 illustrates the horizontal structure of tree layer on PRP 1-6 in 2017. Stem number in the tree layer and the relation of DBH to tree height on the particular PRP are shown in Figures 3 and 4, respectively.


PRP 1
Species
Tilia cordata
Carpinus betulus
Fagus sylvatica
Larix decidua
Picea abies
Snag
Dead wood
Crown projection
0 2,5 5 10 15 20 m
N
PRP 2
Species
Tilia cordata
Carpinus betulus
Fagus sylvatica
Acer platanoides
Snag
Dead wood
Crown projection
0 2,5 5 10 15 20 m
N
PRP 3
Species
Quercus petraea
Tilia cordata
Carpinus betulus
Fagus sylvatica
Acer campestre
Acer platanoides
Fraxinus excelsior
Sorbus torminalis
Robinia pseudoacacia
Cornus mas
Snag
Dead wood
Crown projection
0 2,5 5 10 15 20 m
N
PRP 4
Species
Quercus petraea
Tilia cordata
Carpinus betulus
Fagus sylvatica
Acer campestre
Acer platanoides
Fraxinus excelsior
Larix decidua
Sorbus torminalis
Cornus mas
Snag
Dead wood
Crown projection
0 2,5 5 10 15 20 m
N

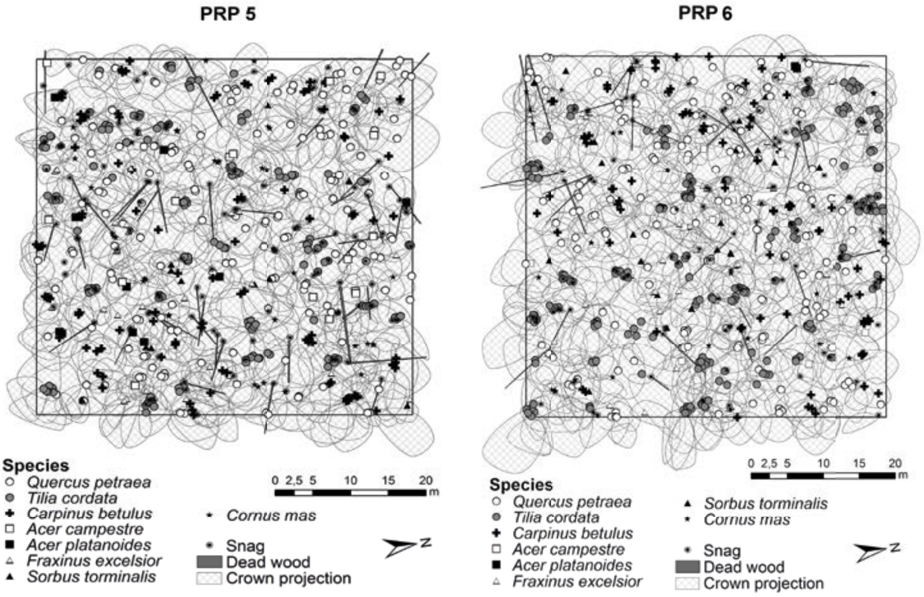


Figure 2: Horizontal structure of the permanent research plots in Karlštejn National Nature Reserve, Český kras Protected Landscape Area in 2017.

Abbildung 2: Horizontale Struktur der Dauerbeobachtungsflächen im Nationalen Naturschutzgebiet Karlštejn, Český kras – Landschaftsschutzgebiet 2017.

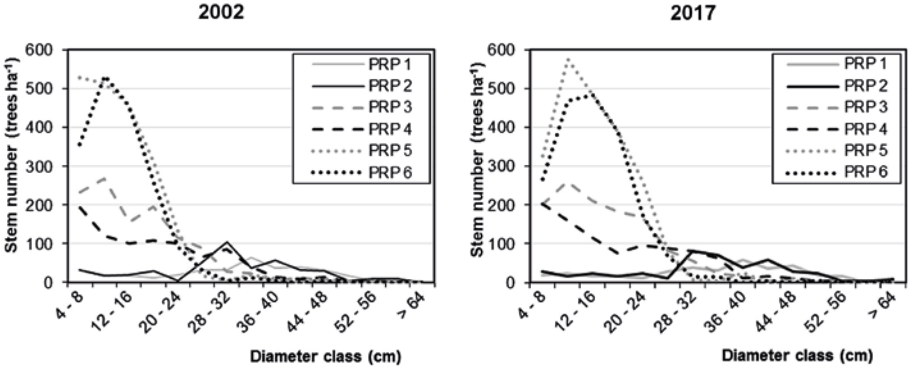


Figure 3: Stem number distribution by diameter classes of the tree layer on the permanent research plots in 2002 and 2017.

Abbildung 3: Stammzahlverteilung der Dauerbeobachtungsflächen in den Jahren 2002 und 2017.

The distribution of diameter classes showed another distinct difference between the forest types. In high forest, the lowest number of trees belongs to small diameter classes while this number is obviously the highest in coppice forest, and in coppice with standards the values are rather close to coppice forest with even higher variability (Fig. 3).

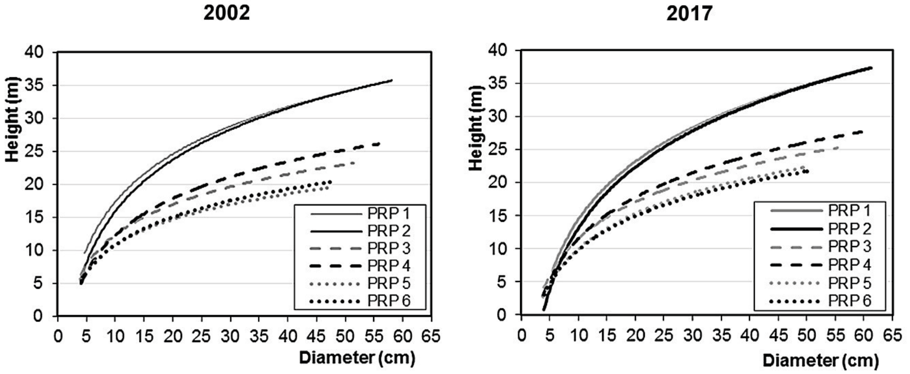


Figure 4: The relationship between breast height diameter and tree height on the permanent research plots in 2002 and 2017.

Abbildung 4: Die Bestandeshöhenkurven auf den Untersuchungsflächen in den Jahren 2002 und 2017.

3.2. Biodiversity in the tree layer

The biodiversity of tree layer on PRP 1-6 is documented in Tab. 4. The species richness evaluated by D_1 and D_2 indices and the species diversity of tree layer according to λ indices and H' were intermediate in high forest (PRP 1-2) and high or very high in both coppice types. The species evenness of tree layer according to E_1 index shows low biodiversity in high forest and high biodiversity on the other plots. The species evenness of tree layer according to E_2 index shows the medium biodiversity of tree layer in high forest and high biodiversity on the other plots. Comparing the species diversity of tree layer across all indices in both years, forest types showed significant differences (MANOVA, $F_{(2,9)} = 12.26$, $p<0.001$).

*Table 4: Indices describing the diversity of tree layer on permanent research plots in 2002 and 2017. Statistically significant value for horizontal structure are displayed by * (α=0.05).*

Tabelle 4: Indexe, die Diversität der Baumschicht auf den Beobachungsflächen in den Jahren 2002 und 2017 beschreiben. Statistisch signifikante Werte sind mit * (*α*=0.05) gezeichnet.

				Species				Vertical	Differentiation		Horizontal		Total
PRP	**Year**	**richness**		**heterogeneity**		**evenness**		**diversity**	**diameter**	**height**	**structure**		**diversity**
		D_1	D_2	λ	H´	E_1	E_2	A	TM_d	TM_h	α	R	B
1	2002	0.510	0.211	0.205	0.463	0.334	0.438	0.189	0.439	0.243	0.931	1.126	6.711
	2017	0.676	0.259	0.218	0.510	0.317	0.419	0.199	0.430	0.277	0.962	1.134	6.781
2	2002	0.495	0.193	0.158	0.360	0.260	0.432	0.228	0.409	0.265	0.843*	1.151*	6.545
	2017	0.493	0.191	0.154	0.353	0.254	0.429	0.246	0.383	0.273	0.778*	1.127	6.729
3	2002	1.138	0.267	0.751	1.606	0.731	0.759	0.697	0.374	0.256	1.145	0.974	10.467
	2017	1.263	0.284	0.753	1.628	0.707	0.743	0.683	0.383	0.309	1.172	0.891*	10.310
4	2002	1.186	0.309	0.742	1.583	0.720	0.743	0.655	0.411	0.305	1.051	0.949*	9.905
	2017	1.308	0.321	0.755	1.665	0.723	0.718	0.657	0.423	0.353	1.114	0.893*	10.496
5	2002	0.790	0.157	0.714	1.436	0.738	0.780	0.669	0.330	0.239	1.438*	0.713*	9.389
	2017	0.906	0.168	0.744	1.582	0.761	0.754	0.686	0.321	0.282	1.388*	0.717*	9.228
6	2002	0.938	0.191	0.740	1.530	0.736	0.785	0.629	0.316	0.227	1.336*	0.728*	9.540
	2017	1.050	0.199	0.776	1.692	0.770	0.781	0.654	0.314	0.271	1.357*	0.727*	9.391

The horizontal structure in high forest (PRP 1) is random to regular according to *α* and *R* indices. In coppice with standards the horizontal structure is aggregated according to both indices, significantly in the understorey. As expected, coppice forest has significantly aggregated structure. The vertical structure is quite variable on the particular PRP (A = 0.189-0.697), it varies from low (on plots of high forest) to relatively differentiated spatial diversity, which is composed of 2-3 storeys on PRP 3-6. The *TM* index of height and diameter differentiation indicates the stands with mostly medium structural differentiation with low variability of these characteristics within a specific type of forest.

From the aspect of stand diversity index *B*, the stands have a very diverse structure on plots PRP 3 and 4 (B = 9.905-10.496) and PRP 5 and 6 (B = 9.228-9.540) of coppice with standards and coppice forest, respectively, and in high forest (B = 6.711-6.781) the values indicate the relatively uneven structure.

The diversity changes in the course of 15 years were only moderate. The species diversity of the tree layer according to λ indices and *H´* increased similarly like D_1 and D_2 indices. The species evenness of tree layer according to E_1 index moderately decreased on plots with beech dominance (PRP 1-2) and on PRP 3 and moderately increased on the other plots, while the species evenness of tree layer according to E_2 index slightly decreased on all PRPs. Comparing PRPs over the time, species diversity of the tree layer on all plots generally increased.

Also changes in horizontal structure that occurred in the course of 15 years were only small and vertical variability increased moderately on all plots except for PRP 3. While height differentiation moderately increased in the course of 15 years, diameter differentiation increased only in coppice with standards. The stand diversity moderately increased in the study years on the plots of high forest and on PRP 3.

Comparing the structural diversity (*A*, *TMd*, *TMh*) of tree layer across all indices in both years, forest types showed significant differences ($F_{(2,\ 9)} = 24.28$, $p<0.001$). For stand diversity index (*B*) in the course of 15 years, no significant changes were observed ($F_{(2,\ 3)} = 0.789$, $p = 0.53$).

3.3. Structure and development of natural regeneration

The horizontal structure of tree natural regeneration (recruits) on all PRPs is aggregated. Regeneration differs significantly in number within the particular types of forest in the range of 368-34,768 ind ha^{-1} (density increasing with lower canopy closure). The onset of natural regeneration is obviously slower in coppice with standards, and at the present time only 1 % of recruits overtop the height of the average herb layer, i.e. 30 cm. The lowest number of individuals in the regeneration is in coppice forest and less than 1 % are taller than 30 cm.

The density of natural regeneration significantly changed in the period 2002-2017. The number of recruits increased from 264 ind ha^{-1} up to 34,768 ind ha^{-1} (Tab. 5). In 2002 regeneration on all plots only exceptionally (ca. 8 %) overtopped the herb layer height. The numbers of recruits were in the range of 264-18,216 ind ha^{-1}, the number being sufficient only in high forest with dominant beech (82 %). After 15 years the height and the number increased especially in high forest: 53 % of recruits overtopped the herb layer and were taller than 30 cm. Dominant beech accounted for 75 % and Norway maple (*Acer platanoides* L.) proportion increased to 12 %.

The influence of hoofed game on the condition of natural regeneration is negative. In total the terminal shoot browsing was observed in 88 % of individuals in high forest, 75 % in coppice with standards and 63 % in coppice forest. Losses are related with the height of recruits; at a height above 50 cm the recruits have already avoided such damage and only about 50 % of them are browsed. Damage is also related with the tree species: the lowest number of damaged individuals being hornbeam (7 %), followed by small-leaved linden (28 %) and beech (31 %). The 50-84 % of other interspersed tree species had severely damaged terminal shoots (especially Norway maple) and in a taller height category 100% of common hazel (*Corylus avellana* L.) and 47-57 %

of maple, hornbeam and common hawthorn (*Crataegus monogyna* Jacq.) terminal shoots were damaged.

Table 5: Tree species composition of tree layer and natural regeneration (density and percentage representation) on the permanent research plots in 2002 and 2017. Mark "+" indicates density < 0.5 %.

Tabelle 5: Baumartenzusammensetzung in der Baumschicht und der natürlichen Verjüngung (Anzahl und prozentuale Darstellung) auf den Beobachtungsflächen in den Jahren 2002 und 2017. Zeichen "+" steht für Bestandesdichte < 0.5.

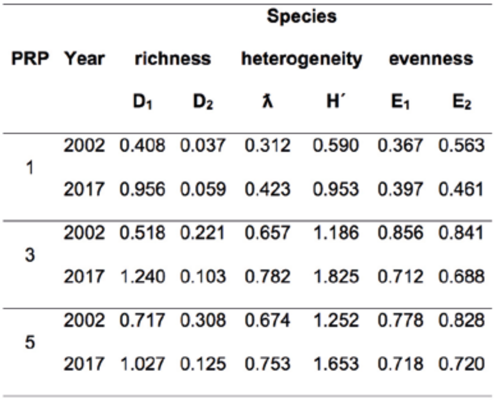
PRP	Level	Year	Sum	*Fagus sylv.*	*Quercus petraea*	*Tilia cord.*	*Carpinus bet.*	*Acer plat.*	*Acer camp.*	*Acer pseud.*	*Fraxinus exc.*	*Corylus avel.*	*Cornus sang.*	*Crataegus monog.*
			(ha^{-1})	(%)										
1	Trees	2002	360	89	0	2	3	0	0	0	0	0	0	0
		2017	368	88	0	2	3	0	0	0	0	0	1	0
	Reg.	2002	18216	82	0	+	0	5	0	13	+	0	0	0
		2017	34768	75	0	1	1	13	4	6	0	1	0	1
3	Trees	2002	1 132	2	18	24	38	1	1	0	12	0	0	0
		2017	1 228	2	16	28	36	1	1	0	11	0	1	0
	Reg.	2002	328	10	0	0	0	10	38	0	42	0	0	0
		2017	15944	5	11	0	7	15	15	1	39	1	4	2
5	Trees	2002	1 992	0	31	40	13	1	1	0	10	0	0	0
		2017	2 160	0	28	38	14	1	2	0	8	0	4	0
	Reg.	2002	264	0	3	0	3	18	42	0	34	0	0	0
		2017	6 380	0	9	0	3	7	20	1	41	0	15	4

3.4. Biodiversity of natural regeneration

In 2002 the species richness of natural regeneration evaluated by D_1 index was intermediate on the prevailing part of plots (D_1 = 0.408-0.518) and high only in the coppice forest (D_1 = 0.717) similarly like for the tree layer (Tab. 6). Over the 15 years it considerably increased to a high level on all PRPs. The value of D_2 index for natural regeneration was low in high forest and coppice with standards (D_2 = 0.037-0.221), and medium in coppice forests (D_2 = 0.308) and decreased substantially within 15 years to the values much lower in comparison with the tree layer. The species diversity of natural regeneration according to λ index was medium in coppice forests (λ = 0.674) and low in high forest (λ = 0.308), even though it was higher by 30-60 % in comparison with the tree layer and it increased during the 15 years to the medium or high level (λ = 0.423-0.782). The *H´* index of natural regeneration was high in all plots ($H' = 0.590$-1.252) and increased considerably in time, with values comparable to the values of the tree layer (except for high forest). The species evenness (E_1 and E_2) was medium for natural regeneration in high forest ($E = 0.367$-0.563) and high in the other two types of forest ($E = 0.778$-0.856) although it decreased by 10-15 % on all plots in 15 years. For species richness (D_1 and D_2 indices) in the course of 15 years, no differences were observed between the indices ($F_{(2,\ 3)} = 0.9$, $p = 0.52$), similarly like in species heterogeneity ($F_{(2,\ 3)} = 1.5$, $p = 0.31$) and species evenness ($F_{(2,\ 3)} = 1.6$, $p = 0.29$).

Table 6: Overview of calculated diversity and structural indices.

Tabelle 6: Überblick über die berechnete Diversitäts- und Struktur-Indices.



PRP	Year	Species richness		Species heterogeneity		Species evenness	
		D_1	D_2	λ	H'	E_1	E_2
1	2002	0.408	0.037	0.312	0.590	0.367	0.563
	2017	0.956	0.059	0.423	0.953	0.397	0.461
3	2002	0.518	0.221	0.657	1.186	0.856	0.841
	2017	1.240	0.103	0.782	1.825	0.712	0.688
5	2002	0.717	0.308	0.674	1.252	0.778	0.828
	2017	1.027	0.125	0.753	1.653	0.718	0.720

3.5. Relationships between stand parameters, stand biodiversity and natural regeneration

The interrelations between stand parameters and characteristics of regeneration are presented as PCA ordination diagram in Figure 5. The first ordination axis represents height, dbh, density and spatial pattern of the tree layer. The second ordination axis represents time, stand diameter differentiation and stand species richness (D_2). The first ordination axis explains 61 % and all the four axes together explain 97 % of the variation in the data. Stand volume, height and dbh of the tree layer were negatively correlated with relative species profile index and stand overall diversity. Differences between plots are visible: coppice forest (PRP 5, 6 and partially PRP 3, 4) occupied the left part of the diagram showing higher stand density, species heterogeneity, species evenness and stand overall diversity, while higher stand volume and more regular spatial pattern were characteristic of high forest (PRP 1 and 2). The cluster spatial pattern of regeneration was increasing with regeneration density, but concurrently decreasing with density and spatial pattern of the tree layer. Stand regeneration species evenness (E_1) was positively correlated with stand species evenness as the regeneration species heterogeneity (*H'*) was positively correlated with stand species heterogeneity and stand canopy. These parameters were independent of time. Regeneration density in the course of time was increasing with height differentiation, mean age and species richness of the tree layer, while regeneration species richness was decreasing in time. The dynamics of parameters in the course of time was remarkable especially on PRP 3-6 (demonstrated by distant marks) whereas closer marks for PRP 1 and 2 show the stability of parameters.

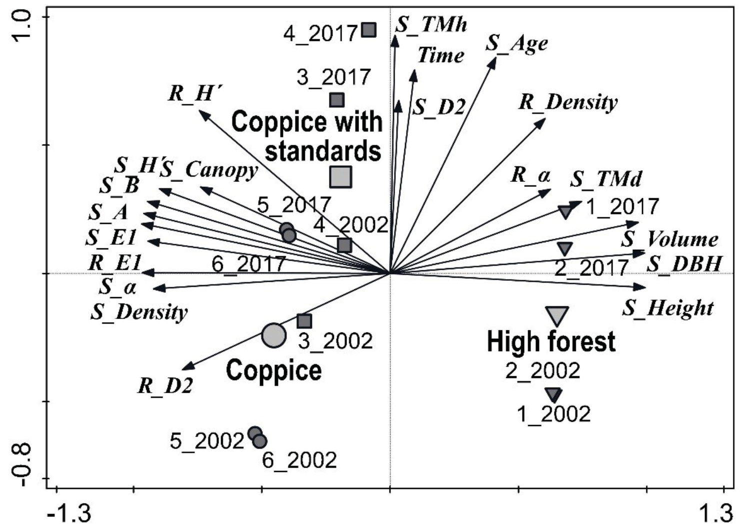


Figure 5: Ordination diagram showing relationships between stand (S_+) parameters (Age – mean stand age, Canopy – crown projection area, DBH – mean diameter at breast height, Height, Volume), stand species diversity (D2 – species richness, H' – species heterogeneity, E1 – species evenness), stand structural diversity (A – relative species profile index, TMd – diameter differentiation, TMh – height differentiation, α – index of non-randomness, B – total diversity), regeneration (R_+) density, regeneration species diversity and time (year of measurement); Codes indicate ● coppice, ■ coppice with standards and ▼ high forest with the plot number and the year of measurement (2002, 2017).

Abbildung 5: Ordinationsdiagramm der Beziehungen zwischen (S_+) Bestandesparametern (*Age* – mittleres Alter des Waldbestandes, *Canopy* – Kronenprojektion, *DBH* – Durchmesser, *Height* – Höhe, *Volume* – Volumen), Artendiversität (*D2* – Artenreichtum, *H* – Artenheterogenität, *E1* – Artengleichmäßigkeit) strukturelle Diversität (*A* – Artenprofilindex, *TMd* – Durchmesserdifferenzierung, *TMh* – Höhendifferenzierung, *α* – non-randomness Index, *B* – Gesamtdiversität), Verjüngung (*R_*+) Dichte, Artendiversität und Zeit (Jahr der Messung); ● Niederwald, ■ Mittelwald und ▼ Hochwald mit Anzahl der Versuchsflächen und dem Jahr der Messung (2002, 2017).

4. Discussion

Forest conversion and eventually also abandonment of forestry activities have a very strong influence (in the framework of Europe) on the character of forests (Gondard 2001; Bürgi and Russell 2001; Van Calster et al. 2008). In the study area of Karlštejn NNR, the abandonment of coppicing and small-plot management of even-aged stands have led to an increase of canopy, in places even to the full canopy closure and to the gradual disappearance of patches of sunlit microsites (Kubíková 2007). Also, the species composition change resulted in an increase of the European hornbeam and field maple (*Acer campestre* L.) proportion. The results indicate that the management history in the above-mentioned forest stands has been recognizable until now, and the plots with different history are significantly different, especially in the number of trees, stocking, stand height and volume.

The stand volume was substantially influenced by the species composition and type of forest. Reaching over 530 $m^3 ha^{-1}$ it was highest in high forest with beech, which is close to the lower boundary of values cited for near-natural oak-beech stands, 630-874 $m^3 ha^{-1}$ (Suchomel et al. 2012; Petritan et al. 2014), and above the total stand volume for productive lowland broadleaved forests – 240 $m^3 ha^{-1}$ (Petritan et al. 2014). The stand volume in both coppice types was lower by 48-71 % compared to high forest, this difference being based on the level of the average volume and basal area of tree. On the other hand, the number of trees was higher by 164 % in coppice with standards and by 394 % in coppice forest than in high forest.

The canopy stabilization at as much as 91-98 % on all plots is interesting, although the canopy increase after abandonment of a coppice system can be expected (Van Calster et al. 2008; Mölder et al. 2008; Plue et al. 2013). The species composition is the factor contributing to the structure and dynamics of forest stand especially in the combination of shade-tolerant and light-demanding tree species, which was obvious on the plots with different forest type. The loss of species diversity in broadleaved forests after conversions was already observed in some studies (Von Oheimb & Brunet 2007; Bartha et al. 2008; Hédl et al. 2010). Our results suggest a difference in biodiversity caused by the differing past management method (Rooney et al. 2004; Van Calster et al. 2008). The species richness index documents low diversity in high forest plots and high diversity in both coppice variants, and the species diversity and evenness of tree layer have similar trends. Diameter differentiation increases with time.

The trend of decreasing biodiversity in the conversion of coppice forests was demonstrated not only in lowland hornbeam-oak stands in Bohemia (Müllerová et al. 2015) but also in oak forests in Denmark (Strandberg et al. 2005) and in Italy (Ciancio et al. 2006). However, at the same time the spreading of European ash (*Fraxinus excelsior* L.), field maple, small-leaved linden, European hornbeam or potentially European beech has been documented. This process was described at the same study location (Hofmeister et al. 2004) and also elsewhere (Lameire et al. 2000; Von Oheimb and

Brunet 2007). We thus can confirm the hypothesis of differences in changes of diversity between herb-rich beech forests (*Asperulo-Fagetum*) and oak-hornbeam forests, since both intraspecific and interspecific competition has a crucial influence on the dynamics of mixed forests (Ngo Bieng et al. 2013; Fichtner et al. 2013; Del Río et al. 2014). The plots show positive correlations between the richness of upper storeys and the richness of undergrowth similarly like in other studies (Barbier et al. 2008; Mölder et al. 2008; Van Calster et al. 2008).

The spatial structure of the tree layer is usually random (Petritan et al. 2014) in the natural distribution, while the aggregated structure is generally more recognizable at lower storeys and may be influenced not only by management, but also by the availability of water and light (Milad et al. 2011; Plue et al. 2013; Petritan et al. 2014; Del Río et al. 2014). On the study plots the regular horizontal structure is prevailing in high forest, like e.g. in beech forests in Slovenia (Rugani et al. 2013) and aggregated structure was documented on the coppice and coppice with standards plots, consistently with the description of near-natural mixed oak-beech forests (Petritan et al. 2014). Similarly, significant aggregated structure (R = 0.709) was observed in coppice forests in Austria (Sterba & Zingg 2006) in comparison with our study (R = 0.721). Height and diameter differentiations mostly indicate medium differentiation and low variability within the specific type of forest. The vertical structure is quite variable on the study plots even though it clearly shows a difference between high forest (low variability) and both coppice variants forming a multilevel forest stand which is usual in this form (Hédl et al. 2010; Müllerová et al. 2015). The stand diversity suggests similar findings – pronounced structure on the plots of the original coppice types of forests and relatively less rich structure on the plots of the originally high forest, which is consistent with the results of Rooney et al. (2004).

Our study documents that in the short period (15 years) after spontaneous development only few significant changes in the stand diversity of the tree layer occurred. As for the height differentiation, a moderate increase was observed in overall diversity, mainly in high forest. In the last 15 years species richness and heterogeneity have increased moderately while species evenness has moderately decreased due to disappearance of light-requiring species on the study plots, but it is still a too short period to confirm this result. The site shifts to more natural forests and their dynamics may benefit from a decrease in anthropogenic disturbances and support of self-regulation (Fichtner et al. 2013).

The natural regeneration was suppressed for a long time and its expansion started in the last decades showing a pronounced increase both in the number of individuals and height. The numbers of recruits increased from tens of individuals to tens of thousands per hectare, apparently thanks to richer mast years, but due to the short time period only 20 % of them overtopped the herb layer and resisted the game pressure that was probably a limiting factor in the last decades (Strandberg et al. 2005; Hédl et al. 2010; Vild et al. 2013; Vacek et al. 2014).

In mixed beech-oak forests the tree layer is of crucial importance as the main light-limiting and competition forming factor, thus the aggregated spatial structure of natural regeneration is usually assumed (Hofmeister et al. 2014; Petritan et al. 2014; Müllerová et al. 2015), just like in our case. The beech regeneration takes advantage of shady conditions and thus it clearly prevailed (75 %) in beech high forest on the study plots. Natural regeneration of beech prefers microsites under oak crowns compared to beech crowns (Fichtner et al. 2013), while this trend appeared not only on the high forest plots but also on coppice plots, with a higher proportion of beech regeneration in comparison with the beech proportion in the tree layer. The lower numbers of recruits in coppice forest than in coppice with standards correlate with the higher value of the stand density index (Barbier et al. 2009). The growth of natural regeneration in both coppice forests is slower (only 1-10 % of recruits overtop the herb layer) and the numbers of recruits are distinctly lower than in high forest, although the number of tree species and species diversity are much higher.

The species structure of oak-hornbeam forests converted from coppice forest usually changes in time, when the proportion of ash and maple increases and the proportion of hornbeam and linden changes (Hofmeister et al. 2014; Müllerová et al. 2015). An increase in the ash proportion was pronounced in our study (ash regeneration accounted for about 40 %) and there was also a slight (about 10 %) increase of the Norway maple proportion. The representation of linden can oscillate with the tree species dynamics after the forest type conversion (Müllerová et al. 2015), although stability in some stands was also reported (Milad et al. 2011). The linden representation was quite low on our plots and as its proportion in the tree layer is substantially higher than in natural regeneration, the loss is probably caused by game damage and limited by light availability. Results of oak dynamics may differ (Bruckman et al. 2011) and oak regeneration in our conditions was present only on the plots of coppice with standards and coppice forest. Field maple natural regeneration decreased by half, mainly due to a slower increase in the total numbers of recruits rather than due to higher mortality or damage by game. Maple attractivity in relation to browsing losses was documented also in other studies (Konôpka & Pajtík 2015; Vacek et al. 2018). In our condition, higher biodiversity of coppice forest and coppice with standards was formed also by the admixture of such species as cornelian cherry, hawthorn and scarcely also hazel.

In the study period, the species richness of regeneration (D_1 index) increased significantly from a medium to a high level contrary to a drop in D_2 index which was caused by a large increase in the number of recruits (up to 49 times) in disproportion with an increase in the number of new species. The species diversity of natural regeneration increased to a medium or a high level and there was a decrease in species evenness. Substantially greater changes in the biodiversity of the tree species were observed e.g. in Milovice (Hédl et al. 2010), which is common for the juvenile phases of stand development (Beneš et al. 2006).

Dynamic processes in forests in the study localities are similar to those in other long-term anthropically influenced European localities in the areas with low forest cover (Bürgi & Russell 2001). In these areas, forests have been substantially exploited as a limited resource since the Middle Ages (Müllerová et al. 2014) while thermophilic and hornbeam-oak forests were managed for a long time by traditional methods of coppice forest that maintain the open stand canopy (Birks 2005). After conversions, there was a crucial change in canopy, possibilities of regeneration and species diversity especially in natural regeneration (Plue et al. 2013), which often causes a conflict with the species protection of plants and animals (Konvička et al. 2008).

5. Conclusion

There are several possible causes of the observed differences and changes in the biodiversity between hornbeam-oak forests and calciphilic beech forests in Karlštejn NNR. The change in silvicultural practices from coppice forest to high forest and the distinct reduction in active management since 1955 are likely among the main causes. The management history in the past had a strong influence on the current state and diversity of forest types, since the plots with different history were significantly different, in particular the stem number, stocking, stand height and volume. High forests reached 2.7 times higher stand volume and 4.7 times lower number of trees compared to coppice forests. On the other hand, the coppice forest has clearly higher species, structural and total diversity compared to coppice with standards and high forest. Within the study period (2002-2017) the diversity of the tree layer showed only minimum changes, while changes in natural regeneration diversity were more pronounced. During the 15 years of this study, the regeneration density increased by 204 % with the highest expansion of maple species. Natural regeneration also exhibited positive changes regarding species, age and spatial structure, although the growth of attractive tree species were limited by game damage.

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References

Ammer, C. 1996. Impact of ungulates on structure and dynamics of natural regeneration of mixed mountain forests in the Bavarian Alps. Forest Ecology and Management 88: 43–53.

Arefjev, Y.F. 2017. Spontaneous Development of Forests of the Central Russian Upland is Desirable. American Journal of BioScience 5(6): 89-103.

Bakker, J.P., Olff, H., Willems, J.H. & Zobel, M. 1996. Why do we need permanent plots in the study of long-term vegetation dynamics? Journal of Vegetation Science 7: 147–156.

Barbier, S., Gosselin, F. & Balandier, P. 2008. Influence of tree species on understory vegetation diversity and mechanisms involved – a critical review for temperate and boreal forests. Forest Ecology and Management 254: 1–15.

Barbier, S., Chevalier, R., Loussot, P., Bergès, L. & Gosselin, F. 2009. Improving biodiversity indicators of sustainable forest management: Tree genus abundance rather than tree genus richness and dominance for understory vegetation in French lowland oak hornbeam forests. Forest Ecology and Management 258: 176–186.

Bartha, S., Merolli, A., Campetella, G. & Canullo, R. 2008. Changes of vascular plant diversity along a chronosequence of beech coppice stands, central Apennines, Italy. Plant Biosystems 142: 572–583.

Beneš, J., Čížek, O., Dovala, J. & Konvička, M. (2006) Intensive game keeping, coppicing and butterflies: The story of Milovicky Wood, Czech Republic. Forest Ecology and Management 237: 353–365.

Bengtsson, J., Nilsson, S.G., Franc, A. & Menozzi, P. 2000. Biodiversity, disturbances, ecosystem function and management of European forests. Forest Ecology and Management 132: 39-50.

Bílek, L., Remeš, J. & Zahradník, D. 2011. Managed vs. unmanaged. Structure of beech forest stands (*Fagus sylvatica* L.) after 50 years of development, Central Bohemia. Forest Systems 20(1): 122-138.

Bílek, L., Remeš, J., Podrázský, 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.

Birks, H.J.B. 2005. Mind the gap: how open were European primeval forests? Trends in Ecology and Evolution 20(4): 154–156.

Bölöni, J., Ódor, P., Ádám, R., Keeton, W.S. & Aszalós, R. 2017. Quantity and dynamics of dead wood in managed and unmanaged dry-mesic oak forests i n the Hungarian Carpathian. Forest Ecology and Management 399: 120-131.

Bruckman, V.J., Yan, S., Hochbichler, E. & Glatzel, G. 2011. Carbon pools and temporal dynamics along a rotation period in Quercus dominated high forest and coppice with standards stands. Forest Ecology and Management 262(9): 1853-1862.

Brunet, J., Valtinat, K., Mayr, M.L., Felton, A., Lindbladh, M. & Bruun, H.H. 2011. Understory succession in post-agricultural oak forests: Habitat fragmentation affects forest specialists and generalists differently. Forest Ecology and Management 262(9): 1863-1871.

Bulušek, D., Vacek, Z., Vacek, S., Král, J., Bílek, L. & Králíček, I. 2016. Spatial pattern of relict beech (*Fagus sylvatica* L.) forests in the Sudetes of the Czech Republic and Poland. Journal of Forest Science 62(7): 293-305.

Bürgi, M. & Russell, E.W.B. 2001. Integrative methods to study landscape changes. Land Use Policy 18: 9–16.

Chudomelová, M., Hédl, R., Zouhar, V. & Szabó, P. 2017. Open oakwoods facing modern threats: Will they survive the next fifty years? Biological Conservation 210: 163–173.

Ciancio, O., Corona, P., Lamonaca, A., Portoghesi, L. & Travaglini, D. 2006. Conversion of clearcut beech coppices into high forests with continuous cover: A case study in central Italy. Forest Ecology and Management 224(3): 235-240.

Clark, P.J. & Evans, F.C. 1954. Distance to nearest neighbour as a measure of spatial relationship in populations. Ecology 35: 445–453.

Crookston, N.L. & Stage, A.R. 1999. Percent canopy cover and stand structure statistics from the Forest Vegetation Simulator. Gen. Tech. Rep. RMRS-GTR-24. Ogden, UT. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 11 p.

del Río, M., Condés, S. & Pretzsch, H. 2014. Analyzing size-symmetric vs. size-asymmetric and intra- vs. inter-specific competition in beech (*Fagus sylvatica* L.) mixed stands. Forest Ecology and Management 325: 90–98.

Environmental Systems Research Institute, Inc. (ESRI) 2010. ArcGIS 10, ArcMap Tutorial. Redlands, United States of America.

Fabrika, M., & Ďurský, J. 2005. Algorithms and software solution of thinning models for SIBYLA growth simulator. Journal of Forest Science 51(10): 431-445.

Fichtner, A., Sturm, K., Rickert, C., von Oheimb, G. & Härdtle, W. 2013. Crown size-growth relationships of European beech (*Fagus sylvatica* L.) are driven by the interplay of disturbance intensity and inter-specific competition. Forest Ecology and Management 302: 178-184.

Füldner, K. 1995. Strukturbeschreibung in Mischbeständen [Structure description in mixed stands]. Forstarchiv 66: 235–606 (In German).

Gondard, H., Romane, F., Grandjanny, M., Li, J. & Aronson, J. 2001. Plant species diversity changes in abandonment chestnut (*Castanea sativa*) groves in southern France. Biodiversity and Conservation 10: 189–207.

Halaj et al. 1987. Rastové tabuľky hlavných drevín ČSSR [Yield tables of the main tree species of Czechoslovakia]. Príroda Bratislava, 361 p. (In Slovak).

Hédl, R., Kopecký, M. & Komárek, J. 2010. Half a century of succession in a temperate oakwood: from species-rich community to mesic forest. Diversity and Distributions 16: 267–276.

Hill, M.O. 1973. Diversity and evencess: A unifying notation and is consequenses. Ecology 54: 427–432.

Hofmeister, J., Mihaljevič, M. & Hošek, J. 2004. The spread of ash (Fraxinus excelsior) in some European oak forests: aneffect of nitrogen deposition or successional change? Forest Ecology and Management 203: 35–47.

Hofmeister, J., Hošek, J., Brabec, M., Dvořák, D., Beran, M., Deckerová, H., Burel, J., Kříž, M., Borovička, J., Běťák, J. & Vašutová, M. (2014). Richness of ancient forest plant species indicates suitable habitats for macrofungi. Biodiversity and Conservation 23(8): 2015-2031.

Hunter, M.L. 1999. Maintaining biodiversity in forest ecosystems. Cambridge University Press, Cambridge, United Kingdom, 325 p.

Institute of Forest Ecosystem Research - Monitoring and Mapping Solutions, Ltd. (IFER) 2017. Field-Map Software and Hardware Catalogue. Jilove u Prahy, Czech Republic, 51 p.

Jactel, H. & Brockerhoff, E.G. 2007. Tree diversity reduces herbivory by forest insects. Ecology Letters 10: 835–848.

Jaehne, S.C. & Dohrenbusch, A. 1997. Ein Verfahren zur Beurteilung der Bestandesdiversität [A method for assessing stand diversity]. Forstwissenschaftliches Centralblatt 116: 333-345 (In German).

Janík, D., Šamonil, P., Vrška, T., Adam, D., Unar, P., Hort, L. & Král, K. 2008. Doutnáč - monitoring lokality ponechané samovolnému vývoji [Doutnáč - monitoring sites left to spontaneous development]. Folia Forestalia Bohemica 9, Kostelec n. Č. L., Lesnická práce, Czech Republic, 60 p. (In Czech).

Kelty, M.J. 2006. The role of species mixtures in plantation forestry. Forest Ecology and Management 233: 195–204.

Knollová, I. & Chytrý, M. 2004. Oak-hornbeam forests of the Czech Republic: geographical and ecological approaches to vegetation classification. Preslia 76: 291–311.

Konôpka, B., & Pajtík, J. 2015. Why was browsing by red deer more frequent but represented less consumed mass in young maple than in ash trees?!. Journal of Forest Science 61(10): 431-438.

Konvička, M., Novák, J., Beneš, J., Fric, Z., Bradley, J., Keil, P., Hrček, J., Chobot, K. & Marhoul, P. 2008. The last population of the Woodland Brown butterfly (Lopinga achine) in the Czech Republic: habitat use, demography and site management. Journal of Insect Conservation 12: 549–561.

Korpeľ, Š. 1995. Die Urwälder der Westkarpaten [Primeval forests of the Western Carpathians]. Stuttgart, Jena, Gustav Fischer Verlag, 310 p. (In German).

Král, J., Vacek, S., Vacek, Z., Putalová, T., Bulušek, D. & Štefančík, I. 2015. Structure, development and health status of spruce forests affected by air pollution in the western Krkonoše Mts. in 1979–2014. Forestry Journal 61(3): 175-187.

Králíček, I., Vacek, Z., Vacek, S., Remeš, J., Bulušek, D., Král, J., Štefančík, I. & Putalová, T. 2017. Dynamics and structure of mountain autochthonous spruce-beech forests: impact of hilltop phenomenon, air pollutants and climate. Dendrobiology 77: 121–139.

Kubíková, J. 2007. Kopec Doutnáč v NPR Karlštejn, modelové území geobotanických studií [Hill Doutnáč in the NPR Karlštejn, model area of geobotanic studies]. Bohemia centralis 298: 287–320 (In Czech).

Kucbel, S., Saniga, M., Jaloviar, P. & Vencurik, J. 2012. Stand structure and temporal variability in old-growth beech-dominated forests of the north-western Carpathians: A 40-years perspective. Forest Ecology and Management 264: 125–133.

Lameire, S., Hermy, M. & Honnay, O. 2000. Two decades of change in the ground vegetation of a mixed deciduous forest in an agricultural landscape. Journal of Vegetation Science 11: 695–704.

Lassauce, A., Anselle, P., Lieutier, F. & Bouget, C. 2012. Coppice-with-standards with an overmature coppice component enhance saproxylic beetle biodiversity: A case study in French deciduous forests. Forest Ecology and Management 266: 273-285.

Lenoir, J., Gégout, J.C., Marquet, P.A., de Ruffray, P. & Brisse, H. 2008. A significant upward shift in plant species optimum elevation during the 20th century. Science 320: 1768–1771.

Lorz, C., Fürst, C., Galic, Z., Matijasic, D., Podrázský, V., Potocic, N., Simoncic, P., Strauch, M., Vacik, H. & Makeschin, F. 2010. GIS-based probability assessment of natural hazards in forested landscapes of central and south-eastern Europe. Environmental Management 46(6): 920-930.

Margalef, R. 1958. Information theory in ecology. General Systematics 3: 36–71.

McGrath, M.J., Luyssaert, S., Meyfroidt, P., Kaplan, J.O., Bürgi, M., Chen, Y., Erb, K., Gimmi, U., McInerney, D., Naudts, K., Otto, J., Pasztor, F., Ryder, J., Schelhaas, M.-J. & Valade, A. 2015. Reconstructing European forest management from 1600 to 2010. Biogeosciences, European Geosciences Union 12(14): 4291-4316.

MCPFE 2003. Improved pan-European indicators for sustainable forest management as adopted by the MCPFE Expert Level Meeting. In: Ministerial Conference on the Protection of Forests in Europe, Liaison Unit Vienna, Vienna, Austria, 6 p.

Menhinick, C.F. 1964. A comparison of some species-individuals diversity indices applied to samples of field insects. Ecology 45: 859–861.

Milad, M., Schaich, H., Bürgi, M. & Konold, W. 2011. Climate change and nature conservation in Central European forests: A review of consequences, concepts and challenges. Forest Ecology and Management 261(4): 829-843.

Mölder, A., Bernhardt-Römermann, M. & Schmidt, W. 2008. Herb-layer diversity in deciduous forests: raised by tree richness or beaten by beech? Forest Ecology and Management 256: 272–281.

Mountford, M.D. 1961. On E. C. Pielou's index of non-randomness. Journal of Ecology 49: 271–275.

Müllerova, J., Szabó, P. & Hédl, R. 2014. The rise and fall of traditional forest management in southern Moravia: A history of the past 700 years. Forest Ecology and Management 331: 104–115.

Müllerova, J., Hédl, R. & Szabó, P. 2015. Coppice abandonment and its implications for species diversity in forest vegetation. Forest Ecology and Management 343: 88–100.

Němeček, J., Macků, J., Vokoun, J., Vavříček, D. & Novák, P. 2001. Taxonomický klasifikační systém půd České republiky [Taxonomic classification system of soils of the Czech Republic]. ČZU, Praha, Czech Republic, 78 p. (In Czech).

Ngo Bieng, M.A., Perot, T., de Coligny, F. & Goreaud, F. 2013. Spatial pattern of trees influences Forest Ecology and Management species productivity in a mature oak–pine mixed forest. European Journal of Forest Research 132: 841–850.

Nožička, J. 1957. Přehled vývoje našich lesů [Overview of our forests development]. SZN, Praha, Czech Republic, 459 p. (In Czech).

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, I.C., Marzano, R., Petritan, A.M. & Lingua, E. 2014. Overstory succession in a mixed *Quercus petraea–Fagus sylvatica* old growth forest revealed through the spatial pattern of competition and mortality. Forest Ecology and Management 326(15): 9-17.

Pielou, E.C. 1975. Ecological diversity. New York: Wiley, USA, 165 p.

Plue, J., Van Gils, B., De Schrijver, A., Peppler-Lisbach, C., Verheyen, K. & Hermy, M. 2013. Forest herb layer response to long-term light deficit along a forest developmental series. Acta Oecologica 53: 63-72.

Pretzsch, H. 2006. Wissen nutzbar machen für das Management von Waldökosystemen. Allgemeine Forstzeitschrift/Der Wald 61:1158–1159.

Pretzsch, H. 2009. Forest dynamics, growth and yield. Springer Heidelberg: Berlin, pp. 223-290.

R Core Team 2017. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Reineke, L.H. 1933. Perfecting a stand-density index for even-aged forests. Journal of Agricultural Research 46: 627–638.

Rugani, T., Diaci, J. & Hladnik, D. 2013. Gap Dynamics and Structure of Two Old-Growth Beech Forest Remnants in Slovenia. PloS One 8: e52641.

Shannon, C.E. 1948. A mathematical theory of communications. Bell System Technical Journal 27: 379–423.

Sharma, R.P., Vacek, Z. & Vacek, S. 2016. Individual tree crown width models for Norway spruce and European beech in Czech Republic. Forest Ecology and Management 366: 208-220.

Simpson, H. 1949. Measurement of diversity. Nature 163: 688.

Slanař, J., Vacek, Z., Vacek, S., Bulušek, D., Cukor, J., Štefančík, I., Bílek, L. & Král, J. 2017. Long-term transformation of submontane spruce-beech forests in the Jizerské hory Mts.: dynamics of natural regeneration. Central European Forestry Journal 63(4): 213-225.

Sterba, H., & Zingg, A. 2006. Abstandsabhängige und abstandsunabhängige Bestandesstrukturbeschreibung. Allgemeine Forst-und Jagdzeitung 177(8/9): 169-176.

Sjölund, M.J. & Jump, A.S. 2015. Coppice management of forests impacts spatial genetic structure but not genetic diversity in European beech (*Fagus sylvatica* L.). Forest Ecology and Management 336: 65-71.

Suchomel, C., Pyttel, P., Becker, G. & Bauhus, J. 2012. Biomass equations for sessile oak (*Quercus petraea* (Matt.) Liebl.) and hornbeam (*Carpinus betulus* L.) in aged coppiced forests in southwest Germany. Biomass and Bioenergy 46: 722-730.

Šmilauer, P., & Lepš, J. 2014. Multivariate analysis of ecological data using CANOCO 5. Cambridge university press, United Kingdom, 361 p.

Rudel, T.K., Perez-Lugo, M. & Zichal, H. 2000. When Fields Revert to Forest: Development and Spontaneous Reforestation in Post-War Puerto Rico, The Professional Geographer 52(3): 386-397.

Tolasz, R., Míková, T., Valeriánová, T. & Voženílek, V. (eds.) 2007. Climate atlas of Czech. Czech Hydrometeorological Institute and Palacký University, Olomouc, Czech Republic, 255 p.

Vacek, S. 2003. Minimum area of forest left to spontaneous development in protected areas. Journal of Forest Science 49(8): 349–358.

Vacek, S., Bastl, M. & Lepš, J. 1999. Vegetation changes in forests of the Krkonoše Mts over a period of air pollution stress (1980–1995). Plant Ecology 143: 1–11.

Vacek, S., Vacek, Z., Bílek, L., Simon, J., Remeš, J., Hůnová, I., Král, J., Putalová, T. & Mikeska, M. 2016. Structure, regeneration and growth of Scots pine (*Pinus sylvestris* L.) stands with respect to changing climate and environmental pollution. Silva Fennica 50(4): id 1564.

Vacek, S., Černý, T., Vacek, Z., Podrázský, V., Mikeska, M. & Králíček, I. 2017a. Long-term changes in vegetation and site conditions in beech and spruce forests of lower mountain ranges of Central Europe. Forest Ecology and Management 398: 75–90.

Vacek, S., Vacek, Z., Kalousková, I., Cukor, J., Bílek, L., Moser, W. K., Bulušek, D., Podrázský, V. & Řeháček, D. (2018). Sycamore maple (*Acer pseudoplatanus* L.) stands on former agricultural land in the Sudetes-evaluation of ecological value and production potential. Dendrobiology 79: 61-76.

Vacek, Z., Vacek, S., Bílek, L., Král, J., Remeš, J., Bulušek, D. & Králíček, I. 2014. Ungulate Impact on Natural Regeneration in Spruce-Beech-Fir Stands in Černý důl Nature Reserve in the Orlické Hory Mountains, Case Study from Central Sudetes. Forests 5: 2929–2946.

Vacek, Z., Vacek, S., Podrázský, V., Král, J., Bulušek, D., Putalová, T., Baláš, M., Kalousková, I. & Schwarz, O. 2016. Structural diversity and production of alder stands on former agricultural land at high altitudes. Dendrobiology 75: 31-44.

Vacek, Z., Vacek, S., Bulušek, D., Podrázský, V., Remeš, J., Král, J. & Putalová, T. 2017b. Effect of fungal pathogens and climatic factors on production, biodiversity and health status of ash mountain forests. Dendrobiology 77: 161-175.

Van Calster, H., Baeten, L., De Schrijver, A., De Keersmaeker, L., Rogister, J.E., Verheyen, K. & Hermy, M. 2007. Management driven changes (1967–2005) in soil acidity and the understorey plant community following conversion of a coppice-with-standards forest. Forest Ecology and Management 241(1–3): 258-271.

Van Calster, H., Baeten, L., Verheyen, K., De Keersmaeker, L., Dekeyser, S., Rogister, J.E. & Hermy, M. 2008. Diverging effects of overstorey conversion scenarios on the understorey vegetation in a former coppice-with-standards forest. Forest Ecology and Management 256(4): 519-528.

Vandekerkhove, K., Keersmaeker, L.D., Baeté, H. & Walleyn R. 2005. Spontaneous re-establishment of natural structure and related biodiversity in a previously managed beech forest in Belgium after 20 years of non intervention. Forest Snow and Landscape Research 79(1):145-156.

Veen, P., Fanta, J., Raev, I., Biriş, I.A., Smidt, J.D. & 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.

Vild, O., Roleček, J., Hédl, R., Kopecký, M. & Utínek, D. 2013. Experimental restoration of coppice-with-standards: Response of understorey vegetation from the conservation perspective. Forest Ecology and Management 310: 234–241.

von Oheimb, G. & Brunet, J. 2007. Dalby Söderskog revisited: long-term vegetation changes in a south Swedish deciduous forest. Acta Oecologica 31: 229–242.

Vrška, T., Adam, D., Hort, L., Kolář, T. & Janík, D. 2009. European beech (*Fagus sylvatica* L.) and silver fir (Abies alba Mill.) rotation in the Carpathians - a developmental cycle or a linear trend induced by man? Forest Ecology and Management 258:347–356.

Zahradník, D. & Puš, V. 2010. Program PointPro, Version 2.2. Czech University of Life Sciences Prague, Faculty of Forestry and Wood Sciences, Prague.

Appendix

Formulas (1-14) for calculation of diversity and structural indices.

Formeln (1-14) zur Berechnung von Diversitäts- und Struktur-Indices.

Species richness index (Margalef 1958):

$$D_1 = \frac{m-1}{\ln{(N)}} \tag{1}$$

where m = number of tree species, N = number of trees per hectare.

Species richness index (Menhinick 1964):

$$D_2 = \frac{m}{\sqrt{N}} \tag{2}$$

where m = number of tree species, N = number of trees per hectare.

Species heterogeneity index (Simpson 1949):

$$\lambda = 1 - \sum_{i=1}^{m} w_i^2 \tag{3}$$

where m = number of tree species, w_i = basal area proportions of individual tree species.

Species heterogeneity index (Shannon 1948):

$$H' = \frac{-\sum_{i=1}^{m}[w_i . \ln{(w_i)}]}{\ln{(10)}} \tag{4}$$

where m = number of tree species, w_i = basal area proportions of individual tree species.

Species evenness index (Pielou 1975):

$$E_1 = \frac{H'.\ln(10)}{\ln(m)} \tag{5}$$

where H´= Species heterogeneity index according to Shannon (1948) – Eq. 4, m = number of tree species.

Species evenness index (Hill 1973):

$$E_2 = \frac{\frac{1}{1-\lambda}-1}{e^{H'.\ln(10)}-1} \tag{6}$$

where λ = Species heterogeneity index according to Simpson (1949) – Eq. 3, H´= Species heterogeneity index according to Shannon (1948) – Eq. 4.

Relative species profile index (Pretzsch 2006):

$$A = \frac{-\sum_{i=1}^{m}\sum_{j=1}^{3}[p_{ij}.\ln(p_{ij})]}{\ln(3.m)} \tag{7}$$

where m = number of tree species, p_{ij} = proportion of basal area of trees of i^th^ tree species in j^th^ stand layer.

Diameter differentiation index (Füldner 1995):

$$TM_d = \frac{1}{n}.\sum_{i=1}^{n}(1 - rd_{ij}) \tag{8}$$

where rd = ratio between the larger and the smaller diameter of the nearest neighbor tree pair, n = number of neighbor trees.

Height differentiation index (Füldner 1995):

$$TM_h = \frac{1}{n} \cdot \sum_{i=1}^{n} (1 - rh_{ij}) \tag{9}$$

where rh = ratio between the larger and the smaller height of the nearest neighbor tree pair, n = number of neighbor trees.

Index of non-randomness (Mountford 1961):

$$\propto = \frac{1}{n} \pi \left(\frac{N}{P}\right) \sum_{i=1}^{n} \omega'_i \tag{10}$$

where n = number of sample points, N = number of trees in the plot, P = plot area, ω'_1 = quadratic distance from sample point to the nearest tree.

Index of aggregation (Clark & Evans 1954):

$$R = \frac{\frac{1}{N} \cdot \sum_{i=1}^{N} r_i}{0.5 \sqrt{\frac{P}{N}} + 0.0514 . \frac{u}{N} + 0.041 . \left(\frac{u}{N}\right)^{\frac{3}{2}}} \tag{11}$$

where r_i = distances between two nearest neighbors, N = number of trees in the plot, P = plot area, u = the perimeter of plot.

Total diversity index (Jaehne & Dohrenbusch 1997):

$$B = \left\{4[\log(m) . (1.5 - Z_{max} - Z_{min})] + 3\left(1 - \frac{h_{min}}{h_{max}}\right) + \left(1 - \frac{r_{min}}{r_{max}}\right) + [1 - \log(HCB_{\min})] + \left(1 - \frac{CD_{min}}{CD_{max}}\right)\right\} \tag{12}$$

where m = number of tree species, Z_{max} = maximum tree species proportion, Z_{min} = minimum tree species proportion, h_{min} = minimum tree height in the stand, h_{max} = maximum tree height in the stand, r_{min} = minimum tree spacing, r_{max} = maximum tree spacing, HCB_{min} = minimum height to crown base, CD_{min} = minimum crown diameter, CD_{max} = maximum crown diameter.

Stand density index (Reineke 1933):

$$SDI = N.\left(\frac{25}{dbh_g}\right)^{-1.605} \tag{13}$$

where dbh_g = quadratic mean diameter, N = the number of trees per hectare.

Relative stand density index:

$$SD = \frac{SDI}{SDI_{max}} \tag{14}$$

where the SDI_{max} = maximum stand density index represents the maximum tree number per hectare at full density derived from the model of yield tables (Halaj et al.1987).