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## Stand dynamics in natural Scots pine forests as a model for adaptation management?

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**Abstract:** The paper deals with the dynamics of structure, diversity and growth of natural pine stands without direct human impact during the ten-year period in Nature Reserve (NR) Kostelecké bory, Czech Republic. The objective was to determine the main characteristics of the spontaneous development of Scots pine (*Pinus sylvestris* L.) forest stands in relation to their naturalness, ecological stability and adaptation to climate change and air pollution stress.

Horizontal and vertical structure and species diversity of the tree layer, dead wood and natural regeneration of each permanent research plot (PRP) were evaluated ( $n = 6$ ,  $50 \times 50$  m /0.25 ha/, Northern Bohemia, 410–425 m above sea level). The average ring series of PRPs were correlated with the climatic data (precipitation, temperature) according to individual years from the Doksy climatic station, and the air pollution data ( $\text{SO}_2$  in 1988–2015,  $\text{NO}_x$  and AOT40F – ozone exposure in 1992–2015) from Radimovice station.

In 2016, the stand volume increased by 26.0% to  $136 \text{ m}^3 \text{ ha}^{-1}$  ( $108 \text{ m}^3 \text{ ha}^{-1}$  in 2006) and the volume of dead wood increase by 127.2% to  $27 \text{ m}^3 \text{ ha}^{-1}$  ( $12 \text{ m}^3 \text{ ha}^{-1}$  in 2006). The horizontal structure of tree layer and natural regeneration was predominantly aggregated to random. More distinct changes in biodiversity and structural characteristics occurred in the natural regeneration (21.5%) compared to tree layer (2.8%). The precipitation had a significantly higher effect on radial growth compared to temperature. The lack of precipitation in growing season and high temperature in previous autumn and winter were limiting factors for growth. Climatic factors had significant effect on diameter increment in July of the current year ( $P < 0.01$ ) and June of the current and previous year ( $P < 0.05$ ). Radial growth was negatively correlated with  $\text{SO}_2$  concentrations ( $P < 0.01$ ) and ozone exposure ( $P < 0.05$ ).  $\text{NO}_x$  concentrations had low effect on radial growth. The natural stand dynamics had positive effect on biodiversity and functional integrity of natural pine ecosystems.

**Keywords:** *Pinus sylvestris*, forest dynamics, stands structure, air pollution, climatic factors, Central Europe

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## Introduction

Autochthonous Scots pine (*Pinus sylvestris* L.) occurs in the Czech Republic in vegetation zones from the lowlands to the mountains. Its ecotypes are based on populations that survived the last glacial in various isolated refuges (Peřina, 1960). Contemporary autochthonous pine and pine-oak stands are the results of the vegetation development of predominantly the last 10,000 years in the postglacial period (Mikeška & Vacek, 2008). These are azonal communities which gradually evolved from the preboreal and have been preserved only in extreme habitats with the limited competitiveness of other species (Matuszkiewicz et al., 2013). We naturally find these on a large scale in the Czech Republic only on poor and dry sandy soils. In other places, its natural appearance is bound to the relatively smaller extreme locations such as the rock outcrops and the edges of the crystalline and carbonate rocks and the sandstone rock towns (Kučera, 1999; Bohn et al., 2003; Vacek et al., 2017). Among the most important works characterizing these communities in Europe belong Passarge (1963), Lilja and Kuuluvainen (2005), Rouvinen and Kuuluvainen (2005), Gaudio et al. (2011), Matuszkiewicz et al. (2013).

Scots pine is considered to be an undemanding tree with pioneer strategy (Lanier et al., 1986; Zadworny et al., 2016). Apart from the mountain ecotypes, however, it is very demanding on light (De Chantal et al., 2003; Dehlin et al., 2004; Gaudio et al., 2011). At the same time, it is highly tolerant to drought (Picon-Cochard et al., 2006; Sanchez-Gomez et al., 2006). Many of its ecotypes are adapted to the entire range of habitats (Richardson, 2000; Medail, 2001; Ostonen, 2007; Sterck et al., 2012; Reich, 2014; Uria-Diez et al., 2017). Due to this, it is able to survive practically in any environment from waterlogged areas to xerothermic sites (Mikeška & Vacek, 2008; Zadworny et al., 2017).

Pine as important commercial tree species has expanded significantly beyond its natural habitats in Europe in the last few centuries (Zerbe & Brande, 2003; Mirschel et al., 2011). In addition to the increase of forest production, this change in species composition has led to a range of ecological problems, especially in monoculture stands (Kazda & Pichler, 1998; Zaitsev et al., 2014). Recently, there is an evident trend to transform artificial forest into ecosystems with higher degree of naturalness (Zerbe, 2002; Schou et al., 2012; Hlásny et al., 2017) and higher resistance and resilience (Déchéne & Buddle, 2010; Griess et al., 2012; Neuner et al., 2014; Allen et al., 2002; Reynolds et al., 2013; Salamon et al., 2008; Zaistev et al., 2014). In addition, in less productive pine forests, reduction in active management has occurred in recent decades, which may also result

in positive successive changes (Vacek et al., 2017). Since 2006 the monitored stands and the whole Nature Reserve (NR) Kostelecké bory have been left to spontaneous development (Vacek et al., 2012). Practically, however, these stands have not been actively managed since the 1970s.

As such, the forests left to spontaneous development can be an important source of information for understanding natural processes and deriving procedures of close-to-nature silviculture (Burrascano et al., 2011; Petritan et al., 2014; Puettmann et al., 2015; Bílek et al., 2016). Understanding the forest development in response to natural disturbances and changing environmental conditions is very important for the setting of management approaches and measures (Pham et al., 2004; Dobrowolska & Veblen, 2008; Durak & Durak, 2015).

The aim of this paper is to evaluate the structure and development of selected stands of relict pine stands left to spontaneous development in the period from 2006 to 2016. The structure of forest stands can be defined on the basis of a number of parameters (Spies & Franklin, 1991; Poage & Tappeiner, 2005). The structure includes both the vertical and the horizontal components and the species arrangement (Maltamo et al., 2005; Vacek et al., 2017). Since the relict pine stands left to spontaneous development have been scarcely explored from this point of view in Central Europe, we have focused on all the above-mentioned attributes in this paper. The basic scientific questions were as follows:

1. What are the main characteristics of the spontaneous development of natural pine forest under the given conditions?
2. Do these changes lead to higher naturalness and ecological stability of the studied stands?
3. Is the spontaneous development of pine stands on edaphically extreme sites a suitable adaptation measure to the ongoing climate change?

## Materials and Methods

### Study Area

The Kostelecké bory Nature Reserve, with an area of 51.2 hectares, was declared in 2003 and forms rock crests under the hill Kostelec (433 m above sea level). The geological bedrock is formed of the Mesozoic rectangular sandstone of the middle Turon. The most widespread soil type in the area is the arenic Podzol together with the arenic Cambisol on the sandstone slopes. The predominantly sandy soils are minerally poor and low in humus content. Climatically, the NR territory is classified according to Quitt (Quitt, 1971) as a slightly warm area MT9. The average annual temperature is approximately 7.5 °C and

the average annual rainfall is around 650 mm (Tolasz, 2007). The vegetation is formed by acidophilus forest communities. The *Dicrano-Pinetum* forest types (*Pinetum relictum humile saxatile*; Preising et Knapp ex Oberdorfer 1957) are bound to the ridges and rocky edges with a shallow layer of soil, and the cranberry pine-oak forests of *Vaccinio vitis-idaeae-Quercetum roboris* forest type (Oberdorfer 1957) are found marginally on the less exposed habitats. The tree layer of both communities is dominantly formed by pine (Chytrý et al., 2010; AOPK, 2014). The herb layer consists mainly of blueberry, cranberry, and several other acidophytes. Only in extreme locations in the pine stands, a more pronounced moss and lichen layer has developed. Among the most important plant species are the Morrison spurrey (*Spergula morisonii* Boreau) and the chickweed wintergreen (*Trientalis europaea* L.) – (AOPK, 2014).

The permanent research plots (PRP) are situated in altitude 410–425 m above sea level with south-east exposition and mean slope of 5 degrees. The location of PRPs 1–6 50 × 50 m is shown in Fig. 1. According to the forest management plan (2017–2026) the

mean stand age of upper layer is 179 years, respectively 40 years of lower layer. Stand volume is 139 m<sup>3</sup> ha<sup>-1</sup> with 99% share of Scots pine and 1% of Norway spruce (*Picea abies* /L./ Karst.).

## Data Collection

To determine the tree layer structure and natural regeneration, FieldMap technology (IFER-Monitoring and Mapping Solutions Ltd.) was used to establish 6 permanent research plots (PRPs) of 50×50 m (0.25 ha) size in 2006. The same technology was used for repeated measurements of these PRPs in 2016. The positions of all individuals of the tree layer with a diameter at breast height (DBH) ≥ 4 cm were recorded. The height, height of the live crown base, and the crown projection were measured, at least in four directions perpendicular to each other. The diameter of the trees was measured with a metal calliper (accuracy 1 mm) and the heights were measured using a Vertex laser hypsometer (accuracy 0.1 m). From 25 dominant trees on each PRP, the core samples were randomly (RNG Excel) taken with Pressler

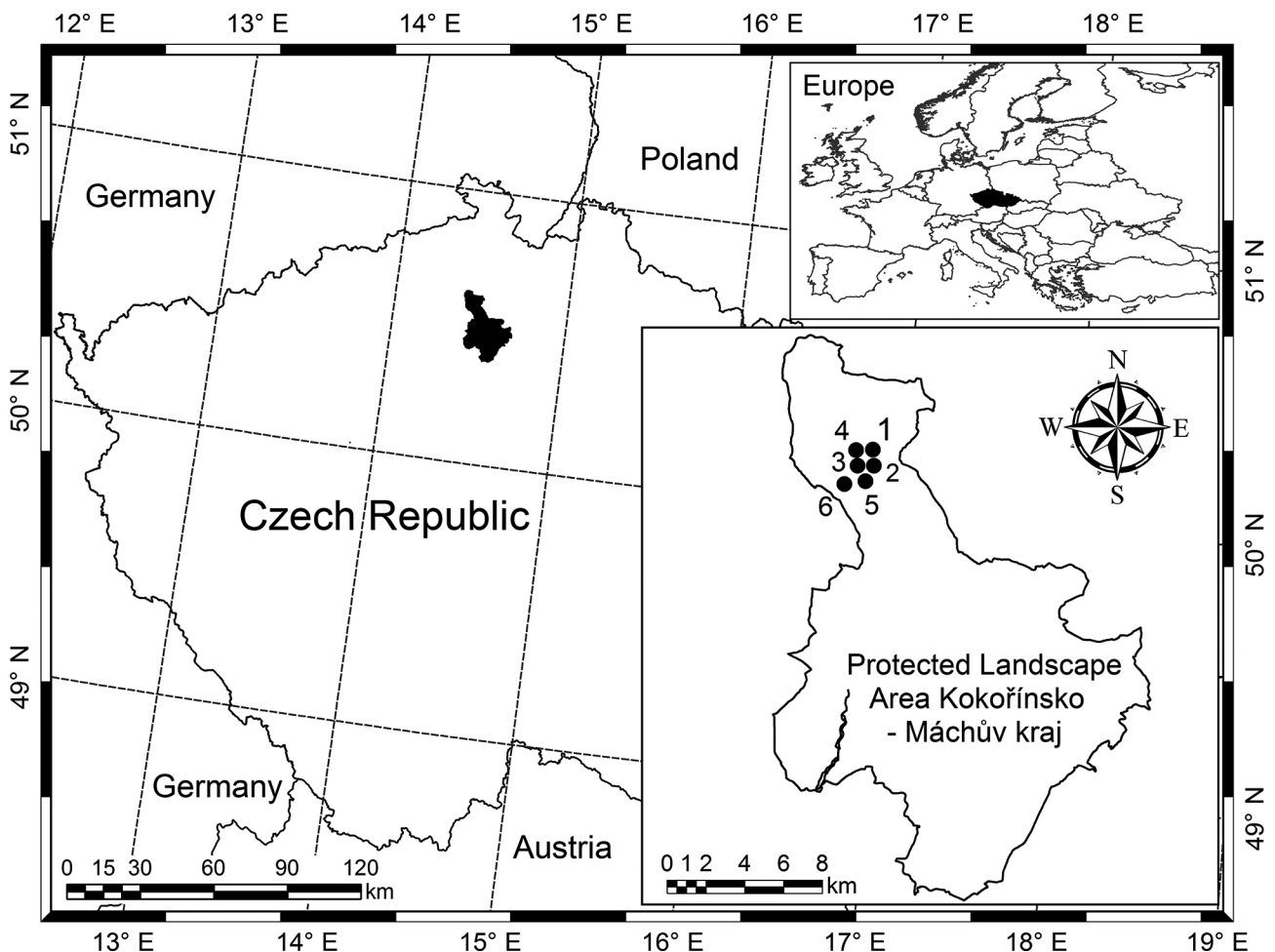


Fig. 1. Location of permanent research plots (PRP) 1–6 with natural pine forest stands in Nature Reserve Kostelecké bory in Protected Landscape Area Kokořínsko – Máchův kraj

auger at DBH perpendicular to the axis of the tree along/against the slope. The annual ring width was measured (accuracy 0.01 mm) using an Olympus binocular magnifying glass on a LINTAB measurement table and registered using the TSAPWin software (www.rinntech.com).

For dead wood, the degrees of decomposition (five-point scale: 1 – undisturbed trunk, 5 – final decay phase; the scale adjusted according to Spetich et al. (2001), its volume and share in the total stand volume were examined. The natural regeneration was measured in 2006 and in 2016 on individual PRPs at 10 × 50 m transects that are representative from the point of regeneration. The following characteristics were measured for the natural regeneration: the position, the height, the height of live crown base and the width of the crown with height gauge rod (1 cm accuracy).

## Data processing

Horizontal and vertical structure and species diversity of the tree layer, dead wood and natural regeneration of each PRP were evaluated. The basic stand characteristics of the tree layer were evaluated using the simulator SIBYLA Triquetra 10 (Fabrika & Pretzsch, TUZVO). The PointPro 2.1 (Zahradnik & Pus, CULS) program was used to calculate the characteristics of the horizontal layout of the individuals on the plot. The test of the significance of deviations from the values expected for the random arrangement of the points was made using Monte Carlo simulations. For the evaluation of biodiversity, the following indices were computed: index of non-randomness (Mountford, 1961), aggregation index (Clark & Evans, 1954), index of cluster size (David & Moore, 1954), indexes of diameter and height differentiation (Füldner, 1995), species richness index (Margalef, 1958), species heterogeneity index (Shanon, 1948), species evenness index (Pielou, 1959), Arten-profile

index and total stand diversity index (Jaehne & Dohrenbusch, 1997) (Table 1). Further, the stand density index (SDI), the crown closure (CC) and crown projection area (CPA) were calculated.

The annual growth ring width series were individually cross-dated (error correction associated with the absence of missing rings) using statistical tests in the PAST application (Knibbe, 2007) and subsequently subjected to visual inspection according to Yamaguchi (Yamaguchi, 1991). If a missing tree ring was found, a tree ring with a width of 0.01 mm was inserted in its place. The individual curves from the PRP were further de-trended in a standard way and the average annual series was created in the ARSTAN program (Laboratory of Tree-Ring Research). The 30-year spline was applied (Grissino-Mayer et al., 1992). Negative significant pointer years were analyzed according to Schweingruber (Schweingruber et al., 1990). For each tree, a significant year was identified as an extremely narrow tree ring, which did not reach 40% of the average tree ring widths from the previous 4 years. The occurrence of the negative year was proven if the strong reduction in growth occurred in at least 20% of the trees in the area. The average ring series of PRPs were correlated with the climatic data (precipitation, temperature) according to individual years from the Doksy station (1948–2016; 284 m a.s.l.), and the air pollution data (SO<sub>2</sub> in 1988–2015, NO<sub>x</sub> and AOT40F – ozone exposure in 1992–2015) from Radimovice station (378 m a.s.l.). DendroClim software (Biondi & Waikul, 2004) was used to model the diameter increment depending on climatic characteristics.

In order to analyze the effect of overall meteorological conditions on the growth, Sielianinov hydrothermal coefficient (*K*) was used (Radzka & Rymuza, 2015). To determine the combined effect of average annual temperature and an annual sum of precipitation on diameter increment of pine, correlation quadratic model was used.

Table 1. Overview of the indexes describing the stand diversity and their common interpretation

Criterion	Quantifiers	Label	Reference	Evaluation
Horizontal structure	Index of non-randomness	$\alpha$ (P&Mi)	Mountford (1961)	mean value $\alpha = 1$ ; aggregation $\alpha > 1$ ; regularity $\alpha < 1$
	Aggregation index	$R$ (C&Ei)	Clark and Evans (1954)	mean value $R = 1$ ; aggregation $R < 1$ ; regularity $R > 1$
	Index of cluster size	CSI (D&Mi)	David and Moore (1954)	mean value $CSI = 0$ ; aggregation $CSI > 0$ ; regularity $CSI < 1$
Vertical diversity	Arten-profile index	$A$ (Pri)	Pretzsch (2006)	range 0–1; balanced vertical structure $A < 0.3$ ; selection forest $A > 0.9$
Structure differentiation	Diameter dif.	$TM_d$ (Fi)	Füldner (1995)	range 0–1; low $TM < 0.3$ ; very high differentiation $TM > 0.7$
	Height dif.	$TM_h$ (Fi)		
Species diversity	Richness	$D$ (Mai)	Margalef (1958)	minimum $D = 0$ , higher $D =$ higher values
	Heterogeneity	$H'$ (Shi)	Shannon (1948)	minimum $H' = 0$ , higher $H' =$ higher values
	Evenness	$E$ (Pii)	Pielou (1975)	range 0–1; minimum $E = 0$ , maximum $E = 1$
Complex diversity	Stand diversity	$B$ (J&Di)	Jaehne and Dohrenbusch (1997)	monotonous structure $B < 4$ ; uneven structure $B = 6–8$ ; very diverse structure $B > 9$

Table 2. Basic stand characteristics of pine forest on individual permanent research plots 1–6 in 2006 and 2016

PRP	Year	Age	dbh	h	v	N	BA	V	HDR	MAI	CC	CPA	SDI
		y	cm	m	m <sup>3</sup>	trees ha <sup>-1</sup>	m <sup>2</sup> ha <sup>-1</sup>	m <sup>3</sup> ha <sup>-1</sup>		m <sup>3</sup> ha <sup>-1</sup> y <sup>-1</sup>	%	ha	
1	2006	195	21.1	11.1	0.230	624	21.8	143	52.6	0.73	77.0	1.47	0.48
	2016	201	22.9	11.9	0.281	624	25.8	176	52.0	0.88	78.1	1.52	0.55
2	2006	201	19.6	10.5	0.205	720	21.6	148	53.6	0.74	78.5	1.54	0.49
	2016	206	21.4	11.2	0.252	724	26.0	183	52.3	0.89	80.2	1.62	0.57
3	2006	183	19.4	12.4	0.221	560	16.5	124	63.9	0.67	72.3	1.29	0.36
	2016	187	21.3	13.3	0.274	560	19.9	153	62.4	0.82	74.2	1.35	0.42
4	2006	172	22.0	12.7	0.295	316	12.0	93	57.7	0.54	57.8	0.86	0.25
	2016	178	23.7	13.5	0.352	324	14.2	114	57.0	0.64	57.9	0.86	0.29
5	2006	154	17.3	8.5	0.134	572	13.4	76	49.1	0.49	66.8	1.10	0.31
	2016	159	18.8	9.3	0.165	608	16.9	100	49.5	0.64	71.3	1.25	0.38
6	2006	163	13.7	7.9	0.074	836	12.2	62	57.7	0.38	68.3	1.15	0.32
	2016	165	14.7	8.4	0.088	996	17.0	88	57.1	0.53	74.1	1.35	0.43

Notes: age – weighted arithmetic mean of ages of the trees forming the particular stand component, dbh – mean quadratic breast height diameter, h – mean height, v – average tree volume, N – number of trees per hectare, BA – basal area, V – stand volume, HDR – slenderness ratio, MAI – mean annual increment, CC – canopy closure, CPA – crown projection area, SDI – stand density index.

In order to determine the response of the stand health status to site conditions, the climatic data (the sum of precipitation and mean temperatures in the current and previous year), air pollution factors (SO<sub>2</sub> concentrations, NO<sub>x</sub> concentration, AOT40F) and radial growth were tested for correlations in the software Statistica 12 (StatSoft). Unconstrained principal component analysis (PCA) in Canoco 5 program (Šmilauer & Lepš, 2014) was used to analyze the relationships among climatic data, SO<sub>2</sub> concentrations, NO<sub>x</sub> concentration, ozone exposure and the ring width. The data were log-transformed, centered and standardized before the analysis. The results of the PCA analysis were visualized in the form of an ordination diagram.

## Results

### Tree Layer Structure and Production

In 2006, the stand density ranged from 316 to 836 trees ha<sup>-1</sup> (for pine it was 224–756 trees ha<sup>-1</sup>) with a stand density index (SDI) of 0.25–0.49 (Table 2). The stand volume was 62–148 m<sup>3</sup> ha<sup>-1</sup>, of which 61–147 m<sup>3</sup> ha<sup>-1</sup> were pines, 8–9 m<sup>3</sup> ha<sup>-1</sup> were spruces (PRP 3–5 only) and the rest was formed by silver birch (*Betula pendula* Roth). The highest stand volume was found on PRP 2, where it reached 148 m<sup>3</sup> ha<sup>-1</sup> and the lowest on PRP 6, 62 m<sup>3</sup> ha<sup>-1</sup>. The highest stand volume of pine was also found on PRP 2 (147 m<sup>3</sup> ha<sup>-1</sup>) and the lowest on PRP 6 (61 m<sup>3</sup> ha<sup>-1</sup>). The stand basal area ranged from 12.0–21.8 m<sup>2</sup> ha<sup>-1</sup> (pine

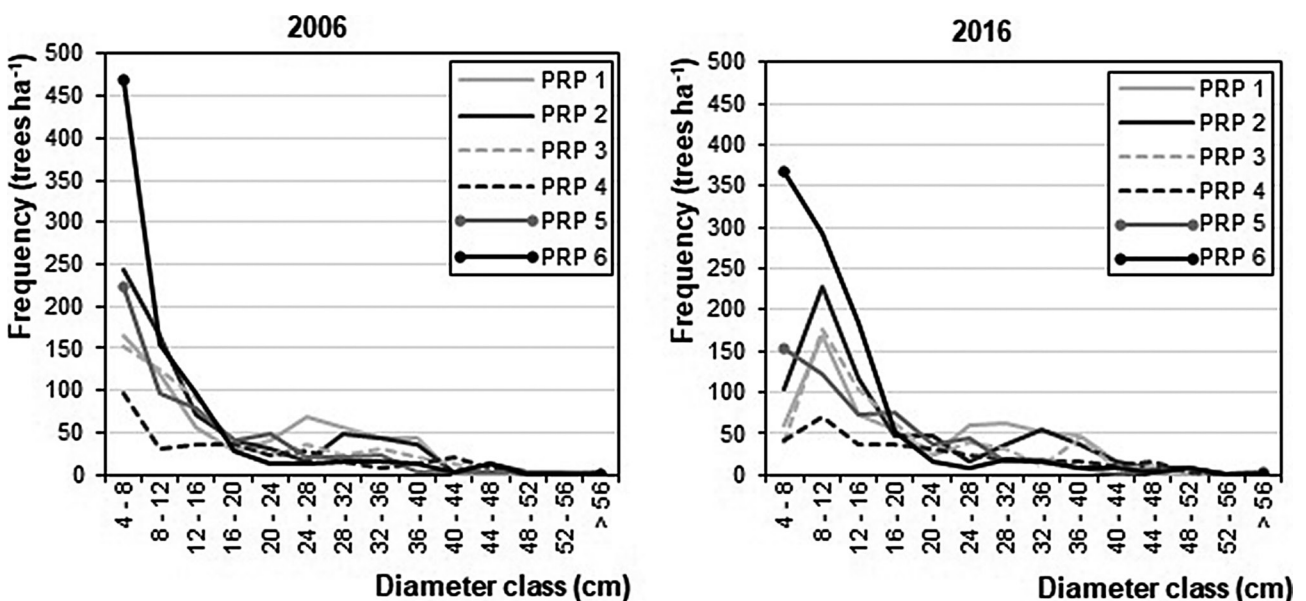


Fig. 2. Histograms of diameter structure of the tree layer on permanent research plots 1–6 Kostelecké bory in 2006 and 2016

9.1–21.4 m<sup>2</sup> ha<sup>-1</sup>) and the mean annual increment was 0.4–0.7 m<sup>3</sup> ha<sup>-1</sup> y<sup>-1</sup> (pine 0.4–0.7 m<sup>3</sup> ha<sup>-1</sup> y<sup>-1</sup>).

In 2016, number of live trees ranged from 324 to 996 trees ha<sup>-1</sup> (pine 224–884 trees ha<sup>-1</sup>) with SDI of 0.29–0.57 (Table 2). The stand volume was 88–183 m<sup>3</sup> ha<sup>-1</sup>, of which 84–182 m<sup>3</sup> ha<sup>-1</sup> were pines, 12–14 m<sup>3</sup> ha<sup>-1</sup> spruces (PRP only 3–5), and the rest was formed by birch. The highest stand volume was found on PRP 2 with 183 m<sup>3</sup> ha<sup>-1</sup> (pine 182 m<sup>3</sup> ha<sup>-1</sup>) and the lowest on PRP 6 with 88 m<sup>3</sup> ha<sup>-1</sup> (84 m<sup>3</sup> ha<sup>-1</sup>). The stand basal area ranged from 14.2 to 26.0 m<sup>2</sup> ha<sup>-1</sup> (pine 10.5–25.7 m<sup>2</sup> ha<sup>-1</sup>) and the mean annual increment was 0.5–0.9 m<sup>3</sup> ha<sup>-1</sup> y<sup>-1</sup> (the pine is 0.4–0.9 m<sup>3</sup> ha<sup>-1</sup> y<sup>-1</sup>). In 2016, the canopy classification ranged from 0.58 to 0.80 in crown closure and from 0.86 to 1.62 in crown area. Comparing year 2006 and 2016, the highest increase was observed in stand volume (+26.0%) and in basal area (+22.9%), while it was the lowest in crown closure (+3.6%), followed by number of trees (+5.7%).

The highest pine trees reached a height of 20–23 m. The highest individuals of admixed spruce on PRPs 3 and 4 reached 20–22 m, but spruce mostly occurred in the middle storey. The birch was predominantly in the middle storey with the highest individuals between 13–15 m. In the course of 10 years, the average height increase of pine and spruce was up to 1.0 m, in case of birch, it was 1.2–1.8 m. In terms of the diameter structure, the diameter class of 4–8 cm prevailed in 2006, only on the PRP 3 prevailed the diameter class of 8–12 cm (Fig. 2). The average DBH of the trees at the PRP was 21.3–23.7 cm, in case of pine, it was 21.6–24.41 cm and the spruce 14.4–17.9 cm.

## Tree Layer Biodiversity

In 2016, the vertical structure according to *A* index was moderately diverse (index values 0.55–0.62)

on PRPs 1–5 and highly varied on PRP 6 (0.72; Table 3). Diameter differentiation  $TM_d$  was predominantly medium (0.29–0.35) and height differentiation  $TM_h$  was low on PRPs 1–4 and 6 (0.22–0.29), only on PRP 5 it was medium (0.33). In terms of species diversity according to *H'* entropy, the species heterogeneity was very low on PRPs 1 and 2 (0.03–0.08), low on PRPs 3, 5 and 6 (0.11–0.23) and PRP 4 had medium biodiversity (0.37). On the basis of species evenness *E*, PRPs 1 and 2 had low diversity (0.10–0.27), PRPs 3, 5 and 6 had medium diversity (0.35–0.47) and PRP 4 was of high biodiversity (0.61). The total complex diversity *B* indicated uneven stand structure (6.34–7.10), only PRP 6 has even stand structure (5.9). The biodiversity of the tree layer changed between 2006 and 2016. Generally, biodiversity increased during the time on PRPs (+2.8%), especially in species heterogeneity *H'* (+5.1%) and height differentiation  $TM_h$  (+3.3%). In total diversity *B*, as the only one, increase was monitored on all PRPs (+1.2%).

The horizontal structure of the tree layer in 2006 and 2016, according to valuated  $\alpha$ , *R* and *CSI* indices, is predominantly random on PRPs (Table 3, Fig. 3). An exception is PRP 2 and 6 with the highest stand density, where the distribution of trees was aggregated. During stand dynamics, the horizontal structure of the tree layer changed only slightly with no apparent trend to clustering or more regular horizontal structure (Table 3).

## Interactions of Radial Growth, Climate Factors and Air Pollution

The average tree ring width in the years 1800–2016 on PRP 1 was 0.65 mm ( $\pm 0.5$  SD), PRP 2 0.77 mm ( $\pm 0.3$  SD), PRP 3 0.68 mm ( $\pm 0.4$  SD), PRP 4 values 0.77 mm ( $\pm 0.3$  SD), PRP 5 values of 0.96

Table 3. Biodiversity indices of pine forest stands on permanent research plots 1–6 in 2006 and 2016

PRP	Year	A	$TM_d$	$TM_h$	<i>H'</i>	<i>E</i>	$\alpha^*$	<i>R</i> <sup>*</sup>	<i>CSI</i> <sup>*</sup>	<i>B</i>
1	2006	0.556	0.291	0.243	0.078	0.253	0.943	1.063	0.058	6.273
	2016	0.573	↗	↗	↗	↗	↗	↗	↘	↗
2	2006	0.566	0.321	0.288	0.026	0.091	1.343 <sup>A</sup>	0.933 <sup>A</sup>	0.372 <sup>A</sup>	6.461
	2016	0.551	↘	↘	↘	↗	↗	↘	↗	↗
3	2006	0.557	0.378	0.293	0.229	0.457	1.337	0.982	0.229	6.382
	2016	0.583	↗	↘	↘	↘	↘	↗	↘	↗
4	2006	0.605	0.337	0.261	0.342	0.601	1.123	1.014	0.056	7.063
	2016	0.624	↗	↗	↗	↗	↘	↗	↗	↗
5	2006	0.613	0.347	0.318	0.203	0.452	1.243	0.938	0.216	6.841
	2016	0.631	↗	↗	↗	↗	↗	↗	↘	↗
6	2006	0.703	0.264	0.203	0.101	0.338	2.502 <sup>A</sup>	0.853 <sup>A</sup>	1.799 <sup>A</sup>	5.798
	2016	0.720	↗	↗	↗	↗	↗	↗	↗	↗

Notes: *A* (Pri) – Arten-profile index,  $TM_d$  (Fi) – diameter differentiation,  $TM_h$  (Fi) – height differentiation, *H'* (Shi) – species heterogeneity, *E* (Pii) – species evenness,  $\alpha$  (P&Mi) – index of non-randomness, *R* (C&Ei) – aggregation index, *CSI* (D&Mi) – index of cluster size, *B* (J&Di) – total stand diversity.

\*statistically significant for horizontal structure (<sup>A</sup> – aggregation, <sup>R</sup> – regularity); changes: ↘ – decrease, ↗ – increase.

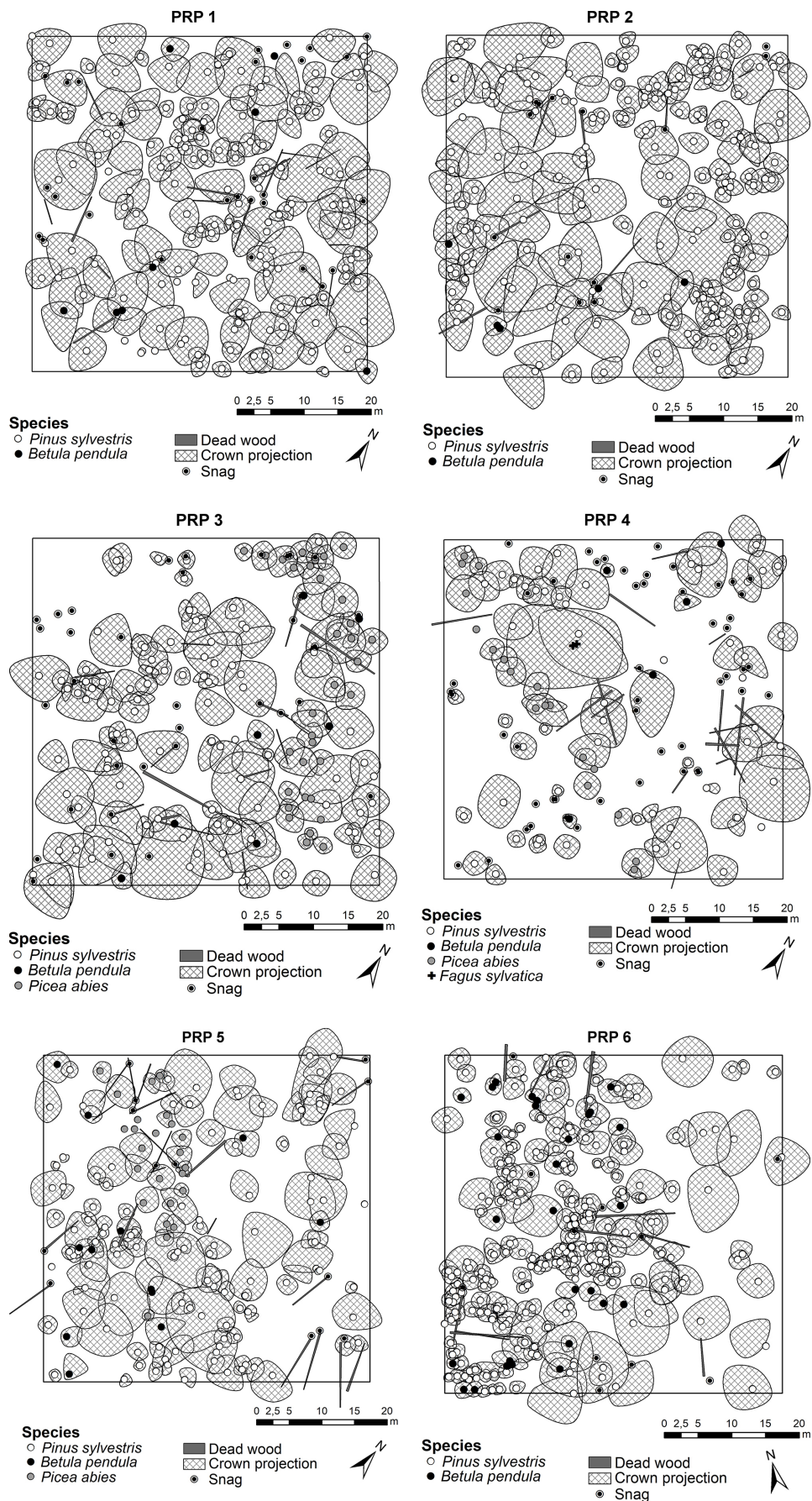


Fig. 3. Horizontal structure of natural pine stands on permanent research plots 1–6 in Kostelecký bory in 2016

mm ( $\pm 0.3$  SD), and PRP 6 values of 0.72 mm ( $\pm 0.4$  SD). Comparison of the average ring-width curves for individual PRPs showed their high reliability of synchronization. From the regional standardized dendrochronology, there is obvious a relatively heterogeneous radial growth in the years 1800–2016 (Fig. 4). The age of the upper layer pine trees was between 237–264 years. The years 1976 were analysed as negative pointer years for low radial growth of pine (January–July precipitation amount 161 mm, mean 340 mm in 1948–2016).

Correlations of diameter increment with the average monthly temperatures and precipitation in 1948–2016 indicated some statistically significant values from software Dendroclim (Fig. 5). There were significant negative correlations of diameter increment with temperature in September of the previous year ( $r = -0.29$ ) and in January of the current year ( $r = -0.23$ ). Conversely, precipitation amount had a predominantly significant positive effect on radial growth, especially in June and July of the previous year ( $r = 0.22$  and  $0.27$ ) and from May to July of the current year ( $r = 0.22$ – $0.34$ ). The negative effect

of the precipitation was observed only in November of the previous year ( $r = -0.22$ , Fig. 5).

The main factor influencing the diameter increment of pine in the study area was identified as the precipitation (Fig. 6). Diameter increment only slightly increased with increasing annual mean temperature, while the considerable increase of growth was observed with increasing annual sum of precipitation. According to hydrothermal index  $K$ , climate (combination of temperature and precipitation) had significant positive impact on radial growth in July of the current year ( $r = 0.37$ ,  $P < 0.01$ ) and June of the current and previous year ( $r = 0.24$ – $0.29$ ,  $P < 0.05$ ).

In addition to climatic factors, air pollution had significant effect on radial growth. Diameter increment was significantly negatively correlated with  $\text{SO}_2$  concentrations (1988–2015), especially in growing season ( $r = -0.56$ ,  $P < 0.001$ ). In terms of month  $\text{SO}_2$  concentrations, there was no significant correlation of radial growth with December, January, and February ( $P > 0.05$ ), while significant negative correlation was observed in all other months with the highest negative effect in July ( $r = -0.58$ ,  $P < 0.001$ ).

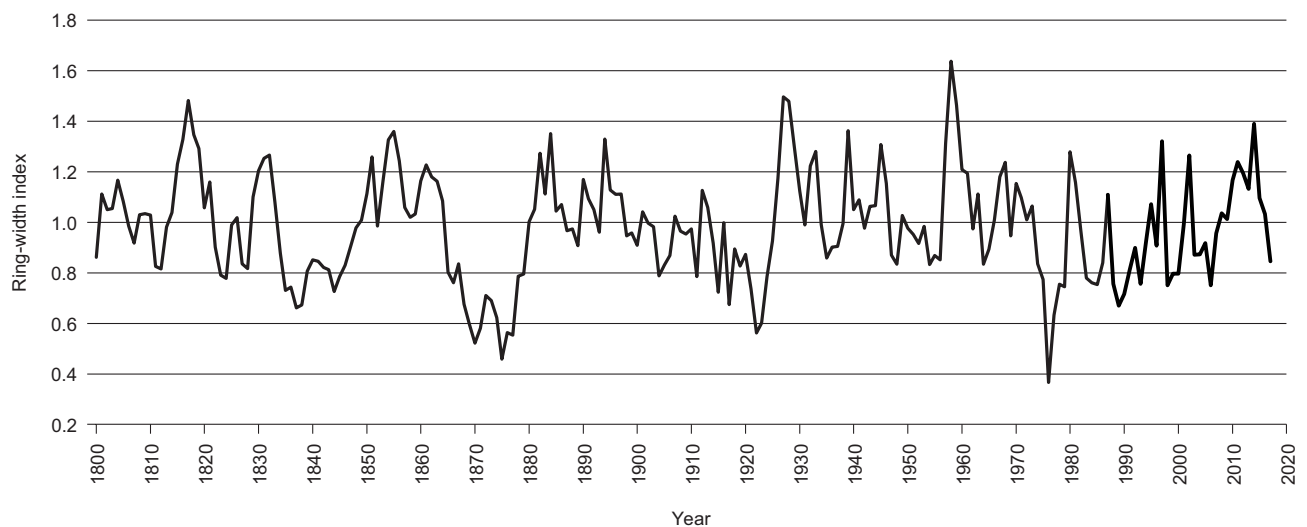


Fig. 4. Standardized average ring width chronology for pine after age detrending in period 1800–2016

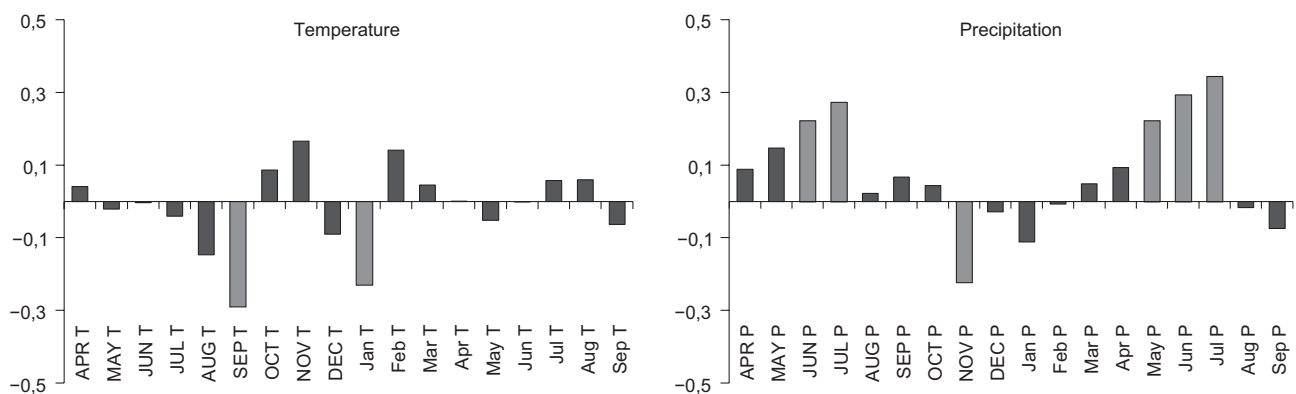


Fig. 5. The values of correlation coefficients of the regional residual index tree ring chronology with the monthly temperatures and precipitation (period 1948–2016) from May of the previous year (capital letter) to September of the current year (small letters). Significant values are displayed by light grey colour ( $\alpha = 0.05$ )



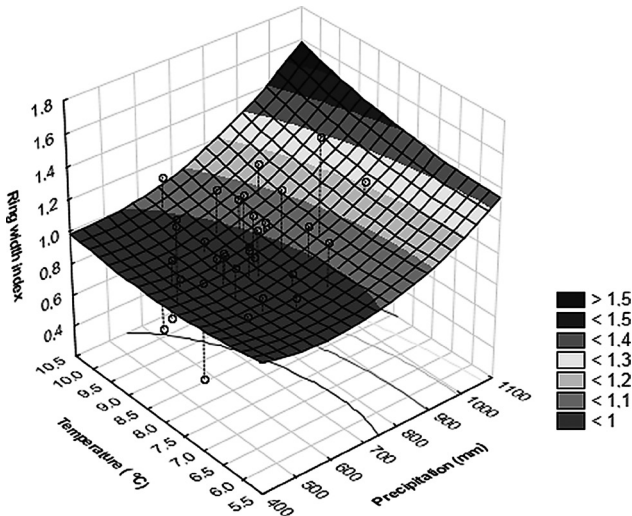


Fig. 6. Response of ring width index of pine to the annual sum of precipitation and annual mean temperature (correlation quadratic model, years 1948–2016)

Similarly radial growth was negatively correlated with ozone exposure (1992–2015), especially in April ( $r = -0.56, P < 0.01$ ) and May ( $r = -0.51, P < 0.01$ ). On the contrary significant  $\text{NO}_x$  effect ( $P > 0.05$ ) on radial growth was not detected. Diameter increment was also significantly ( $P < 0.01$ ) positively correlated with the sum of precipitation in the current and previous growing season and with the sum of precipitation from May to August of both years (1948–2016). No significant effect ( $P > 0.05$ ) of temperature on diameter increment was observed in any time period (Table 4).

Results of the PCA are presented in an ordination diagram in Fig. 7. The first ordination axis explains 23.7% of the variability in the data, the first two axes together 43.4% and the first four axes together 69.9%. The first axis  $x$  represents annual ring width, the sum of precipitation in growing season of the previous year with ozone exposure. The second axis  $y$  represents  $\text{NO}_x$  concentrations with mostly temperature indicators. Radial growth was positively correlated with precipitation in growing season and from May to

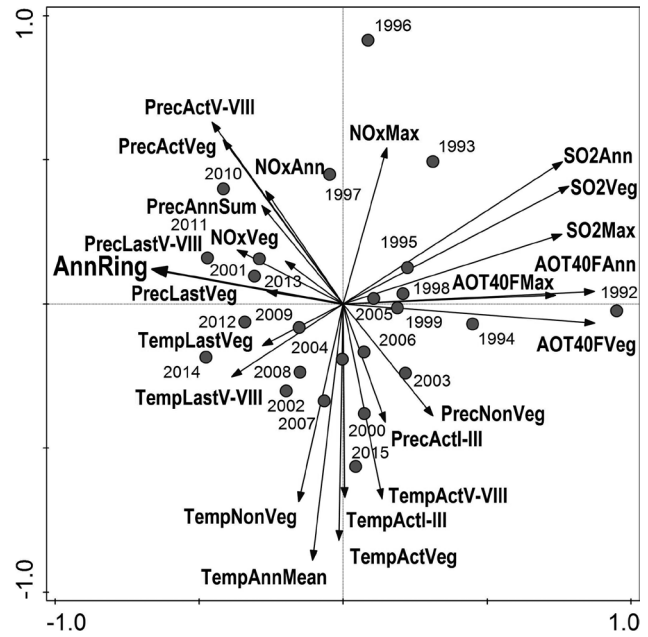


Fig. 7. Ordination diagram showing the results of principal component analysis of the relationships among climatic data (*Temp* – mean temperature, *Prec* – sum of precipitation, *Act* – current year, *Last* – last year, *Veg* – vegetation season, *NonVeg* – non-vegetation season, *Sum* – summary; *I–III, V–VIII months*), air pollutants ( $\text{SO}_2$ *Ann* – mean annual  $\text{SO}_2$  concentrations,  $\text{SO}_2$ *Veg* – mean  $\text{SO}_2$  concentrations in vegetation season,  $\text{SO}_2$ *Max* – maximal annual  $\text{SO}_2$  concentrations;  $\text{NO}_x$  –  $\text{NO}_x$  concentrations, *AOT40F* – ozone exposure) and ring width (*AnnRing* – annual ring width); codes ● indicate years 1992–2015

August of the previous and current year, while these parameters were negatively correlated with  $\text{SO}_2$  concentrations and ozone exposure.  $\text{NO}_x$  concentrations had low effect on radial growth. With respect to time, radial growth during the first third of the investigated period (the 1990s) was related more to strong air pollution ( $\text{SO}_2$  concentrations and ozone exposure), whereas during the second part of the investigated period (2000s, 2010s) it was related more to climatic factors. The lowest contribution of interactions was observed in  $\text{NO}_x$  concentrations in growing season.

Table 4. Correlations between the radial growth increment of pine with climatic data (1948–2016) and air pollution factors ( $\text{SO}_2$  1988–2015; AOT40F,  $\text{NO}_x$  1992–2015); significant correlations are in bold ( $P < 0.05$ ) and underlined ( $P < 0.01$ )

	$\text{SO}_2$ Veg	$\text{SO}_2$ Ann	$\text{SO}_2$ Max	$\text{NO}_x$ Veg	$\text{NO}_x$ Ann	$\text{NO}_x$ Max	AOT40F Veg	AOT40F Ann	AOT40F Max	Temp ActAnn	Temp ActVeg	Temp LastVeg
Increment	<u><b>-0.56</b></u>	<u><b>-0.53</b></u>	<u><b>-0.48</b></u>	-0.10	-0.04	-0.11	-0.42	<u><b>-0.51</b></u>	-0.45	0.05	0.03	-0.07
	Temp ActV-VIII	Temp LastV-VIII	Temp ActI-III	Temp Nonveg	Prec ActSum	Prec ActVeg	Prec LastVeg	Prec ActV-VIII	Prec LastV-VIII	Prec ActI-III	Prec Nonveg	
Increment	0.07	-0.02	0.02	0.04	0.19	<u><b>0.33</b></u>	<u><b>0.41</b></u>	<u><b>0.40</b></u>	<u><b>0.42</b></u>	0.01	0.01	

Notes:  $\text{SO}_2$ *Veg* – mean  $\text{SO}_2$  concentrations in vegetation season,  $\text{SO}_2$ *Ann* – mean annual  $\text{SO}_2$  concentrations,  $\text{SO}_2$ *Max* – maximal annual  $\text{SO}_2$  concentrations,  $\text{NO}_x$  –  $\text{NO}_x$  concentrations, *AOT40F* – ozone exposure, *TempActAnn* – mean annual temperature, *TempActVeg* – mean temperature in the current vegetation season, *TempLastVeg* – mean temperature in the previous vegetation season, *TempActV–VIII* – mean temperature in May–August of the given year, *TempLastV–VIII* – mean temperature in May–August of the previous year, *TempActI–III* – mean temperature in January–March of the given year, *TempNonveg* – mean temperature in the non-vegetation season (from October of the previous year to March of the given year); *Prec* – sum of precipitation.

The dynamics of parameters in the course of 24 years was remarkable especially for the period from 1992 to 1998 as marks of each record are relatively distant from one another whereas marks after the year 1998 were relatively closer together in the diagram.

## Structure and Dynamics of Dead wood

The volume of dead wood ranged in 2016 between 15.8–39.3 m<sup>3</sup> ha<sup>-1</sup> (Table 5). Dead wood volume accounts for 8.0–25.6% of the total wood volume (live and dead trees). The percentage of lying dead wood ranged between 22.0–58.2% (41.9% on average) of the total dead wood volume. Overall, the share of standing dead wood prevailed (58.2%). Dead wood consisted of pine (93.4%), spruce (4.7%) and birch (1.9%). Of the lying dead wood, there were 56.3% in the 4<sup>th</sup> stage of decay, 25.4% in the 3<sup>rd</sup> stage, 11.7% in the stage 5, 5.7% in stage 2 and 0.9% in stage 1 (Table 5).

The proportion of standing dead wood ranged from 41.8–78.0% of the total dead wood volume. Standing dead wood was mainly pine (96.5%) and the rest was spruce. The most volume of dead wood was in the 2<sup>nd</sup>

degree of decomposition (61.8%), in the 3<sup>rd</sup> degree it was 26.0%, in the 1<sup>st</sup> degree 11.6% and in the 4<sup>th</sup> degree 0.6%. The horizontal structure of the standing and lying dead wood was random on all PRPs.

The total volume of dead wood in 2006 was significantly lower in comparison with 2016 (7.2–21.4 m<sup>3</sup> ha<sup>-1</sup>; Table 5). During 10 years, volume of dead wood increased by 127.2%. Dead wood accounted for 3.9–13.2% of the total wood volume (live and dead trees). The share of lying dead wood prevailed slightly (53.7%), while standing dead wood prevailed in 2016 (58.4%). Moreover in 2006, dead wood of birch was not found. Nearly no changes occurred in the proportion of dead wood in the individual stages of decomposition.

## Structure, Dynamics and Game Damage of Natural Regeneration

The number of individuals of natural regeneration ranged from 1,700 (PRP 5) to 10,250 (PRP 2) recruits ha<sup>-1</sup> in 2006 (Table 6). In the course of 10 years, the PRPs 2–6 had seen an increase in the

Table 5. The volume of standing, lying and total dead wood differentiated by the degrees of decomposition on permanent research plots 1–6 in 2006 and 2016

PRP	Year	Degrees of decomposition of dead wood (m <sup>3</sup> ha <sup>-1</sup> )										Total	
		Standing dead wood					Lying dead wood						
		1.	2.	3.	4.	Total	1.	2.	3.	4.	5.		Total
1	2006	2.4	5.2	2.3	0.0	9.9	0.0	0.3	1.0	0.0	0.0	1.3	11.2
	2016	3.1	12.3	6.2	0.0	21.6	0.0	0.1	1.4	4.2	0.4	6.1	27.7
2	2006	0.5	2.3	3.5	0.1	6.4	0.0	0.4	0.4	0.0	0.0	0.8	7.2
	2016	1.7	1.8	8.0	0.0	11.5	0.4	0.1	0.8	3.0	0.0	4.3	15.8
3	2006	0.2	2.8	2.2	0.1	5.3	0.0	2.1	1.4	0.7	0.0	4.2	9.5
	2016	1.2	4.9	4.7	0.6	11.4	0.0	0.4	4.8	6.7	1.4	13.3	24.7
4	2006	6.3	9.0	0.0	0.0	15.3	0.1	1.4	3.7	0.9	0.0	6.1	21.4
	2016	0.6	23.2	1.1	0.0	24.9	0.2	0.0	4.4	7.0	2.8	14.4	39.3
5	2006	2.4	2.9	0.0	0.0	5.3	0.7	3.1	1.3	0.0	0.0	5.1	10.4
	2016	4.4	9.2	0.0	0.0	13.6	0.0	3.3	3.5	5.7	2.0	14.5	28.1
6	2006	0.5	6.2	1.4	0.1	8.2	0.2	0.5	2.8	0.6	0.0	4.1	12.3
	2016	0.0	7.1	4.6	0.0	11.7	0.0	0.0	2.6	12.2	1.5	16.3	28.0

Table 6. Number and share of natural regeneration and mean recruit height differentiated by tree species in 2006 and 2016

PRP	Year	Density								Mean height				Mean	
		<i>Pinus</i>		<i>Picea</i>		<i>Betula</i>		<i>Fagus</i>		Total	<i>Pinus</i>	<i>Picea</i>	<i>Betula</i>		<i>Fagus</i>
		pcs ha <sup>-1</sup>	%	pcs ha <sup>-1</sup>	%	pcs ha <sup>-1</sup>	%	pcs ha <sup>-1</sup>	%	pcs ha <sup>-1</sup>	cm	cm	cm		cm
1	2006	8,250	94.2	250	2.9	250	2.9	–	0.0	8,750	137	14	6	–	129
	2016	7,750	100.0	–	0.0	–	0.0	–	0.0	7,750	280	–	–	–	280
2	2006	9,750	95.2	250	2.4	250	2.4	–	0.0	10,250	89	12	7	–	85
	2016	11,500	97.9	250	2.1	–	0.0	–	0.0	11,750	255	57	–	–	250
3	2006	7,000	70.0	250	2.5	2,250	22.5	500	5.0	10,000	92	16	61	29	80
	2016	9,750	56.5	500	2.9	6,500	37.7	500	2.9	17,250	147	53	122	82	132
4	2006	6,500	72.2	–	0.0	2,500	27.8	–	0.0	9,000	94	–	70	–	87
	2016	9,500	66.7	–	0.0	4,750	33.3	–	0.0	14,250	153	–	142	–	149
5	2006	1,400	82.4	100	5.9	200	11.7	–	0.0	1,700	70	13	12	–	60
	2016	3,900	100.0	–	0.0	–	0.0	–	0.0	3,900	95	–	–	–	95
6	2006	1,300	72.2	100	5.6	300	16.6	100	5.6	1,800	73	10	25	132	65
	2016	2,800	93.3	–	0.0	100	3.3	100	3.3	3,000	109	–	105	240	113

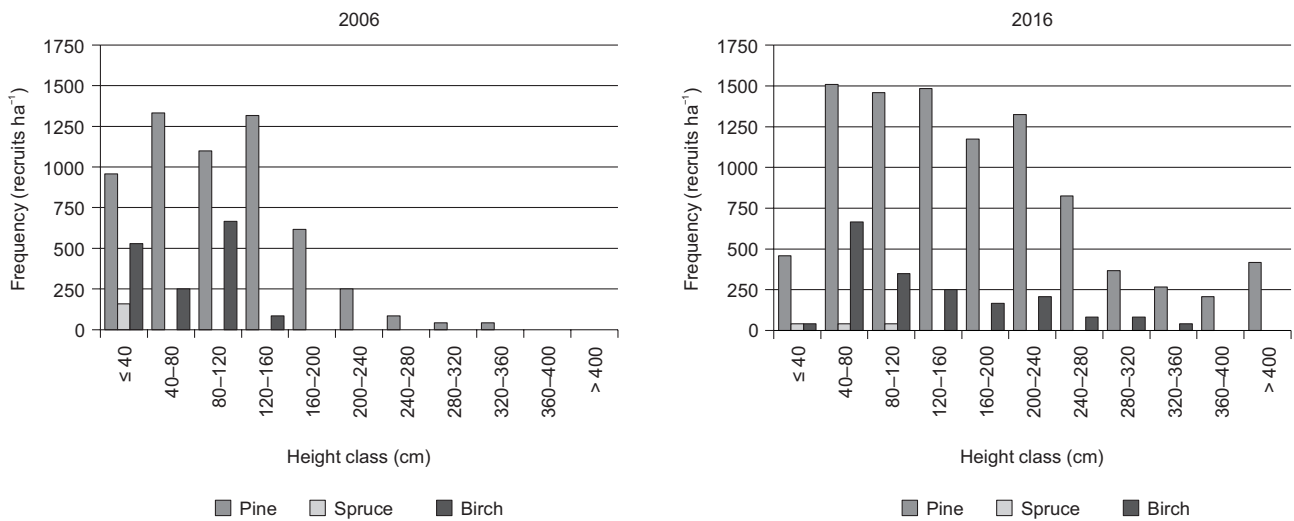


Fig. 8. The average height structure of natural regeneration on permanent research plots differentiated by tree species in 2006 and 2016

number of regeneration individuals, with only PRP 1 slightly decreasing. There occurred a significant shift towards the maturity of natural regeneration on all the PRPs (Fig. 8). In 2016, the number of natural regeneration ranged from 3,000 (PRP 6) to 17,250 (PRP 3) recruits  $\text{ha}^{-1}$  (Table 6). On average, pine represented 78.1%, spruce 1.3%, birch 19.6%, and European beech (*Fagus sylvatica* L.) 1.0% of all regeneration individuals. The average height of the pine regeneration was 95–280 cm, of spruce 53–57 cm, of birch 105–142 cm and of beech 82–240 cm (Table 6).

In 2016, the share of individuals with the terminal shoot damaged by browsing was low (pine 1.6%, spruce 8.7%, birch 0.2%), only in case of beech it was high (36.2%). The most affected were individuals with a height of 20–80 cm. Compared to 2016, the damage was significantly higher in 2006 (pine 12.2%, spruce 19.4%, birch 2.3%, beech 92.5%).

The species richness  $D$  was medium on PRP 3 and low on remaining PRPs. The species heterogeneity

according to the  $H'$  entropy index was low on PRPs 1, 2 and 5 and medium to high on PRPs 3, 4 and 6. The species evenness of regeneration according to the index  $E$  was low on PRPs 1, 2 and 5, medium to high on PRPs 3 and 6 low and very high on PRP 4. On PRPs 2 and 4, the situation was similar in 2016 and 2006. The decrease in biodiversity in the monitored years was observed on PRPs 1, 5 and 6, but it increased significantly only on PRPs 3.

The spatial pattern of the regeneration was significantly aggregated on PRPs except PRP 2 and 4 according to monitored indices in 2016 (Table 7). The clustering of the regeneration individuals according to their distance (spacing) arises also from the Ripley  $L$ -function (Fig. 9). The distinctly clustered natural regeneration pattern was on PRPs 5 and 6, slightly clustered on PRP 3. On PRP 4, the horizontal structure of the regeneration was between the clustered and random spacing. On PRPs 1 and 2, a clustered regeneration was to the distance of 0.5 m and then

Table 7. Biodiversity indices of natural regeneration on permanent research plots 1–6 in 2006 and 2016

PRP	Year	D	$H'$	E	$\alpha^*$	$R^*$	CSI*
1	2006	0.220	0.157	0.143	1.709	0.898 <sup>A</sup>	0.565 <sup>A</sup>
	2016	0.000	0.000	0.000	1.532	0.912	0.330
2	2006	0.217	0.138	0.126	2.348 <sup>A</sup>	0.822 <sup>A</sup>	0.306
	2016	0.107	0.103	0.149	1.668	0.868 <sup>A</sup>	0.253
3	2006	0.312	0.342	0.247	3.307 <sup>A</sup>	0.748 <sup>A</sup>	0.509 <sup>A</sup>
	2016	0.326	0.896	0.646	2.401 <sup>A</sup>	0.780 <sup>A</sup>	0.406 <sup>A</sup>
4	2006	0.110	0.591	0.852	2.703 <sup>A</sup>	0.911	0.409 <sup>A</sup>
	2016	0.109	0.637	0.918	2.907 <sup>A</sup>	0.933	0.285
5	2006	0.269	0.327	0.297	4.056 <sup>A</sup>	0.872 <sup>A</sup>	0.961 <sup>A</sup>
	2016	0.000	0.000	0.000	3.538 <sup>A</sup>	0.871 <sup>A</sup>	0.818 <sup>A</sup>
6	2006	0.271	0.429	0.390	2.664 <sup>A</sup>	0.624 <sup>A</sup>	0.844 <sup>A</sup>
	2016	0.250	0.291	0.265	1.762	0.599 <sup>A</sup>	0.991 <sup>A</sup>

Notes: D (Mai) – species richness,  $H'$  (Shi) – species heterogeneity, E (Pii) – species evenness,  $\alpha$  (P&Mi) – index of non-randomness, R (C&Ei) – aggregation index, CSI (D&Mi) – index of cluster size

\*statistically significant for horizontal structure (<sup>A</sup> – aggregation, <sup>R</sup> – regularity); changes:  $\searrow$  – decrease,  $\nearrow$  – increase.

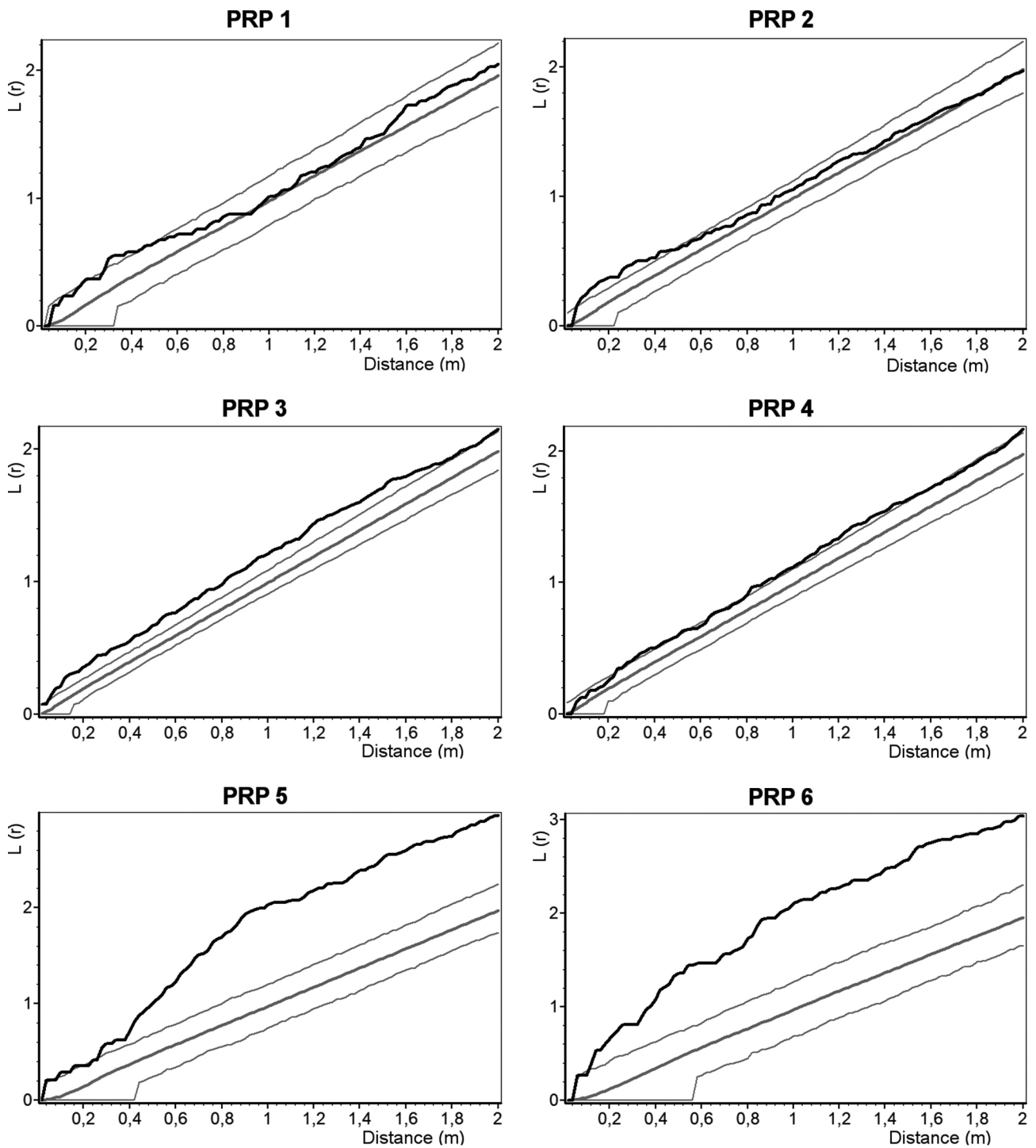


Fig. 9. The spatial pattern of natural regeneration on permanent research plots 1–6 expressed by  $L$ -function in 2016; the black line represents the  $L$ -function for real distances of recruits; the bold grey line represents the mean course for random spatial distribution and the two thinner central curves represent 95% interval of reliability; when the black line of recruits distribution on the plots is under (below) this interval, it indicates a tendency of recruits toward aggregation (regular) distribution

the distribution was random. In 2006 on the PRPs 1–6, there was found clustered distribution of natural regeneration. During the monitored period, on PRPs horizontal structure was more aggregated in 2006 compared to 2016, only on PRP 4 distribution of recruits was more regular.

## Discussion

As part of the ongoing climatic changes (Knoke et al., 2008; Bošela et al., 2016; Dyderski et al., 2018), and in the context of often borderline habitat conditions for the forest existence, natural pine

ecosystems are rightfully receiving more and more attention (Popa et al., 2017; Wang et al., 2017). The structure and growth of pine stands in the Czech Republic were dealt with by Bílek et al. (2016); Vacek et al. (2016) or Sharma et al. (2017). The dynamics of relict pine stands in relation to environmental conditions were dealt with in the Czech Republic by Bílek et al. (2016) and Vacek et al. (2017).

The main characteristics of spontaneous development of natural pine stands in given conditions are high age of individual trees in the upper story, extraordinary regeneration capacity with predominantly clustered spatial distribution of seedlings and saplings, and a significant increase of dead wood during the monitoring period. The summary stand characteristics on PRPs such as tree density, basal area and growing stock have mostly increased over the monitored period and can be regarded as balanced. Generally, we assume that these structural attributes contribute to higher naturalness, heterogeneity and ecological stability of the studied stands, and thus can be considered as a possible mitigation measure to ongoing global climate change. Nevertheless, in the case of the studied areas, and also in comparison with other authors, the variability of the results is generally high. This is due to the interaction of numerous factors such as the growth characteristics of each species, climatic and edaphic habitat conditions, the structure of the stands and the previous management (Forrester, 2014; Bauhus et al., 2017).

According to Forrester et al. (2017), for example, mixed and unmixed stands can vary considerably in the productivity, function, and stability, the extent and direction of these differences being very heterogeneous. In the context of higher structural diversity, correlation with the production of above-ground biomass has been confirmed for the pine stands (Balvanera et al., 2006; Szwagrzyk & Gazda, 2007; Ercanli & Kahriman, 2015). The diameter structure on individual plots remained almost unchanged during the period under review and is markedly left-tailed with the Liocourt curve character. This arrangement is usually the result of the opening of the canopy cover when a relatively rapid onset of natural regeneration takes place (Franklin et al., 2002; Zeibig et al., 2005). The diameter structure in the shape of the Liocourt curve is also referred to as typical for the close to nature stands of other tree species (Král et al., 2010; Sagheb-Talebi et al., 2015). A similar left-tailed distribution as on our plots reported Szmyt and Tarasiuk (2018) from the pine forests in Poland. Their work shows clearly the increase in the thickness of the individuals on the research plots during the 14-year period, which correlates with the decrease of their number.

For the natural regeneration and the tree layer, there is a predominant random to cluster spatial

distribution, while the horizontal structure has changed only slightly with no prevailing trend. A cluster distribution is typical for areas with more extreme habitat conditions (Šerá et al., 2000; Bulušek et al., 2016) and also results from the establishment and growth of natural regeneration in gaps of the parent stand (Bolte et al., 2014). This is the preference of a micro-site with better light conditions. On the contrary, the mortality of individuals in the case of increasing stand density (Getzin et al., 2006; Das et al., 2011), or in the absence of openings in the stand (Haase et al., 1996; Uria-Diez & Pommerening, 2017) contributes to the regularity of the spatial distribution. In connection with this, Szmyt & Tarasiuk (2017) confirm the change in the stand structure during the stand development from random to regular. In the pine stands, a cluster arrangement (Brown et al., 2015; Tuten et al., 2015) and regular arrangement (Li et al., 2012) were confirmed according to various authors.

The tree ring analyses show that the age of the upper layer of the studied stands was in case of pine between 237–264 years. Precipitation had significantly higher effect on radial growth compared to temperature. Especially precipitation in June and July of the previous year and in May–July of the current year influenced radial growth positively. Similarly, the precipitation in May, June and July significantly positively influenced the radial growth of Scots pine trees in the Kuyavian-Pomerania region in Poland, while there was positive effect of the mean monthly temperature for February and March of the current year (Koprowski et al., 2012). Also study from Latvia showed, that the air temperature from the second half of January to the first half of April of the same year has significant effect on radial growth of pine (Zunde et al., 2008). In the relict pine stands in the national nature reserve (NNR) Aadršpach-Teplice Rocks in the Czech Republic, the statistically important correlations of radial growth with the temperature in December of the previous year and in March and August of the current year were recorded. Similarly, significant positive correlations were found with the precipitation amount in July of the previous year and in June of the current year (Vacek et al., 2017). In natural lowlands in eastern Bohemia, radial growth was positively correlated with the temperature in March of the current year and precipitation in November and December of the previous year and February, March and April of the current year (Vacek et al., 2016). Also, other studies from the Mediterranean area (Augustaitis et al., 2007; Oberhuber et al., 2007; Bogino et al., 2009) suggest that drought is a decisive factor for the radial growth of Scots pine. Similarly, in the northeastern lowlands of Brandenburg (Germany), a sufficient amount of precipitation in the autumn of the previous year and summer

precipitation of the current year are very important for foliage formation and radial growth. According to the work of Insinna et al. (2007), the temperature has less influence on growth processes than precipitation. From the regional standardized ring chronology, there is a relatively unstable radial growth between 1800–2017. Years with a low radial increase were in 1922, 1976, and 1998. Especially negative pointer year 1976 was the driest year since 1959 (annual precipitation 492 mm, long-term average 620 mm), the monthly rainfall in June reached only 22 mm (average 69 mm) with high temperatures in the growing season (1.2 °C above the long-term average). Similarly, in 1998, when the very beginning of the growing season was marked by very high temperatures and minimal precipitation (April temperature +2.1 °C and rainfall only 41% of the average).

In accordance with other studies (Vacek et al., 2017; Wilczyński, 2006), radial growth was negatively correlated with SO<sub>2</sub> concentrations and ozone exposure. NO<sub>x</sub> concentrations had low effect on radial growth, while in other studies from natural pine stands in the Czech Republic mean NO<sub>x</sub> concentrations affected the radial growth positively (Vacek et al., 2016). On the other hand, high concentrations of NO<sub>x</sub> and SO<sub>2</sub> in combination with severe climate events can lead to serious defoliation (Vacek et al., 2016) with further degradation of the forest stands.

Dead wood as an important component of natural forest ecosystems (Ódor et al., 2006; Jakoby et al., 2010) occurred in the studied locality in 2016 in the range of 15.8–39.3 m<sup>3</sup> ha<sup>-1</sup>. During the research period, the volume of dead wood increased significantly (by 127.2%) compared to 2006 (7.2–21.4 m<sup>3</sup> ha<sup>-1</sup>). Within natural forest dynamics steep increase of dead wood volumes is mainly related to the degradation phase of the tree layer. Some authors also refer to spatial relationships and mutual competition of trees as important factors in relation to mortality (LeMay et al., 2009; Larson et al., 2015). Significantly higher volume of dead wood in pine primary forests in North America in the range of 37.2–124.1 m<sup>3</sup> ha<sup>-1</sup> are reported by Silver et al. (2013). Uotila et al. (2001) report in the pine primary forests in Finland and Russian Karelia 66.7 m<sup>3</sup> ha<sup>-1</sup>. On the contrary, similar results are presented from the relict pine forests of the NNR of the Ahršpach-Teplice Rocks by Vacek et al. (2017) with an average dead wood stock of 33.1 m<sup>3</sup> ha<sup>-1</sup>. The standing and lying dead wood ratio on studied plots was consistent with the Karjalainen & Kuuluvainen (2002), which presents a substantially identical standing (39%) and lying dead wood (61%) ratio.

Our results also show a significant regeneration capacity of researched pine stands. This is very important from the point of view of natural dynamics since natural regeneration is an important component of

natural forest ecosystems (Petritan et al., 2007; Pardos et al., 2008; Dovčiak & Brown, 2014). The number of natural regeneration individuals ranged from 3,000 to 17,250 recruits ha<sup>-1</sup>. This density is substantially higher in comparison with another relict pine forest in Czech Republic, (Vacek et al., 2017). During the monitored period, a rather significant increase (by 55.0%) in the number of natural regeneration was recorded, with the exception of one PRP, but Martín-Alcón et al. (2015) presents the opposite trend. The works by Štícha et al. (2010) and Prévosto et al. (2012) then present the competition of grass vegetation as a possible negative impact on natural regeneration. Other works present browsing as a negative effect for natural regeneration, especially for the attractive tree species (Ammer, 1996; Čermák et al., 2009). Even though in 2006 the game was damaging also other species, beech has to be judged as the most attractive tree species for ungulates in the studied locality.

## Conclusion

During the monitored years 2006–2016, the changes in the diversity of the relict pine stands were generally low, while significant changes occurred in the development of natural regeneration. Under a reduced pressure of the ungulates, the development of the stand goes to greater spatial diversity and to a larger proportion of admixed trees such as birch, spruce, and beech. We conclude that natural stand dynamics characterised by gap formation and following regeneration process had positive effect on functional integrity of natural pine ecosystems. Under similar conditions, active management of forest stands should aim to achieve these attributes that are specific to natural pine stands. If passive management scenarios are preferred, control methods analysing the regeneration process and vitality of parent trees are needed. With respect to observed changes in the stand structure (success of natural regeneration and related increase in tree species diversity, balanced growing stock and dead wood, vertical and horizontal heterogeneity), spontaneous development on the stand level and in given temporal frame can be judged as suitable adaptation measure to ongoing climate change.

## Author Contributions

S.V., Z.V. and J.R. planned and designed the experiment; Z.V., J.K., D.B. collected stand data, I.H. provided and processed meteorological data; Z.V. and J.K. analysed data; S.V., Z.V., J.B. and L.B. interpreted the results and wrote the paper; all authors reviewed and edited the manuscript.

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## Conflicts of Interest

The authors declare no conflict of interest.

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