Journal of Forest Science, 66, 2020 (12): 501–510 *Original Paper*

https://doi.org/10.17221/139/2020-JFS

The long-term dynamics of the old-growth structure in the National Nature Reserve Badínsky prales

Ladislav Šumichrast, Jaroslav Vencurik, Ján Pittner, Stanislav Kucbel*

Department of Silviculture, Faculty of Forestry, Technical University in Zvolen, Zvolen, Slovakia

**Corresponding author: ladislav.sumichrast@tuzvo.sk*

Citation: Šumichrast L., Vencurik J., Pittner J., Kucbel S. (2020): The long-term dynamics of the old-growth structure in the National Nature Reserve Badínsky prales. J. For. Sci., 66: 501–510.

Abstract: The main goal of this paper was to evaluate structure dynamics in the fir-beech, old-growth forest Badínsky prales. Measurements were taken on four permanent research plots (0.5 ha each) between 1970 and 2018, typically in ten-year intervals. In order to assess long-term structure dynamics, this study used basic stand characteristics and selected structural indices – the relative density (*RD*), coefficient of homogeneity (*H*), and structural complexity index (*SCI*). Species composition was quantified by the relative importance value (*RIV*), and a detrended correspondence analysis was carried out for the visualisation of long-term changes. The long-term mean of the stand volume reached 634 ± 99 $m^3 \cdot ha^{-1}$, and the mean of the basal area was 36.6 ± 4.0 $m^2 \cdot ha^{-1}$. Calculated values of the coefficient of homogeneity (1.46–2.54) were similar to values in other old-growth forests with a comparable tree species composition. An increasing trend in beech *RIV* values was observed; on the other hand, fir *RIV* values fell by approximately 20%–25%. In 2018, maximal values of the basal area, stand volume and relative density were recorded. These high values may indicate better growth conditions due to climate change, as well as fewer disturbance events in the last few decades.

Keywords: old-growth forests; structural dynamics; structural indices; *Fagus sylvatica*; *Abies alba*

In past decades, the investigation of forests with no or minimal human intervention has been of great importance for researchers. Intact forest ecosystems are important in terms of biodiversity, habitat for wildlife, and the numerous social and environmental values they provide (Wirth et al. 2009; Watson et al. 2018). These forest ecosystems also serve as the critical sources of knowledge for the formulation of principles for close-to-nature silviculture (Bauhus et al. 2009; Schütz et al. 2016). In the near future, as climate change and its impact on disturbance regimes (Seidl et al. 2017) put the sustainable supply of ecosystem services under pressure, the study of primeval forests may become even more important (Millar, Stephenson 2015; Thom, Seidl 2016).

The beginning of more intensive research on structure and dynamics in European primeval forests dates back to the middle of the 20th century. Leibundgut (1959) described the development of primeval forests using several developmental phases. Subsequently, Korpeľ (1989) proposed a simplified model of the forest developmental cycle consisting of three basic stages: growth, optimum, and breakdown. Recently, researchers have been interested in the studying the driving forces behind cy-

---

Supported by the Slovak Research and Development Agency, Project APVV-18-0195, and by the Slovak Grant Agency for Science, Project VEGA 1/0021/18, Project IPA 10/2020.

clic structural changes in primeval forests, with research focused on disturbance events and regimes (Kucbel et al. 2010; Feldmann et al. 2018).

The traditional approach to description of primeval forest structure has been based on quantification of simple stand characteristics, usually the stem number, basal area, and stand volume (Korpeľ 1989). Nevertheless, stand structure is a far more complex issue; according to Del Río et al. (2016), the most important attributes include the stand density, species composition, horizontal tree distribution pattern, vertical tree distribution pattern, mean tree size distributions, and age composition. Description of old-growth structures, and especially the possibility of their comparison, can be improved by the application of structural indices that involve more of these attributes (Jaehne, Dohrenbusch 1997; McElhinny et al. 2005). The main aim of this study was to evaluate the structural dynamics of the NNR Badínsky prales over the past 50 years. In particular, we were interested in (*i*) long-term variability of basic stand characteristics, (*ii*) long-term changes in structural diversity, and (*iii*) species composition.

MATERIAL AND METHODS

The research object of this study was the old-growth forest of the National Nature Reserve (NNR) Badínsky prales, located in the Kremnické vrchy mountains (48.6836°N, 19.0515°E). Forest stands in the reserve are dominated by European beech (*Fagus sylvatica* L.) and silver fir (*Abies alba* Mill.); other tree species present include sycamore maple (*Acer pseudoplatanus* L.), wych elm (*Ulmus montana* With.), and European ash (*Fraxinus excelsior* L.). The reserve, a protected area of 30.03 ha, is situated on the northern and north-eastern slopes at an elevation of 700–850 m a.s.l. The mean annual temperature reaches 5.3–5.8 °C, and mean annual precipitation ranges from 800 to 1 100 mm (Korpeľ 1989). The bedrock is formed by andesite conglomerates covered by lava flows of pyroxenic andesite with breccias. The most frequent soil types are cambisols; less common are andosols and fluvisols (Bublinec, Pichler 2001). From a phytocoenological view, the main forest communities in the NNR Badínsky prales are *Fagetum typicum* (70%) and *Abieto-Fagetum* (20%). The rest of the area belongs to *Fraxineto-Alnetum* and *Fageto-Aceretum* (Križová 2000). In 1947, part of the reserve (6.1 ha) was affected by a severe windstorm, causing a large-scale disturbance (Jaloviar et al. 2017).

In 1970, four 0.5-ha permanent research plots (PRP) of rectangular shape were established in order to represent different developmental stages. At the time of establishment, PRP 1 represented the advanced breakdown stage, PRP 2 the initial breakdown stage, PRP 3 the initial growing-up stage, and PRP 4 the advanced optimum stage (Korpeľ 1989). Since 1970, measurements have been carried out typically at ten-year intervals (Saniga 2012). On the entire plot, the basic dendrometric attributes were registered for all living trees with diameter at breast height (DBH) > 8 cm, with the more detailed measurements on a 10 m wide transect (for a description of measurement protocol, see Korpeľ 1989). In 2018, the exact positions of all living stems were recorded for the first time on the entirety of all four plots.

In the first step of the analysis, we quantified basic stand characteristics (stem number – *N*, basal area – *G*, stand volume – *V*) for each PRP and measurement year. Stem volumes were calculated using the two-parameter (DBH, height) volume equations of Petráš and Pajtík (1991). We applied the function by Prodan (1951) to fit the stand height curve. Tree heights required for model fitting were obtained from the historical measurements database of the Department of Silviculture, Faculty of Forestry, Technical University in Zvolen. In addition to the basic stand attributes, we characterised the structure of the old-growth forest using selected structural indices. Instead of the more commonly applied stand density index (*SDI*) by Reineke (1933), the stand density was quantified by the relative density index (*RD*) by Ducey and Knapp (2010), which was designed to be applicable in uneven-aged mixed stands. Their study used wood specific gravity to put in proportion tree species with different growth features. The values of *RD* range from 0 to 1, with the upper limit (1) representing the maximal stand density, Equation (1):

$$RD = \sum_i (0.00015 + 0.00218 SG_i) \left(\frac{DBH_i}{25}\right)^{1.6} \qquad (1)$$

where:

SG_i – refers to the specific gravity;

DBH – indicates the diameter at breast height.

To quantify the DBH structure, we used the coefficient of homogeneity (*H*) developed by Camino (1976). *H* represents the relationship between the stem number and its volume in diameter classes. The theoretical range of values varies from 1 to infinity, where lower values represent more heterogenous structure and vice versa. In selection forests *H* usually reaches a value between 1.3–2.8, and in the homogenous stands tended by thinning from bellow reaches 4.0–10.0, Equation (2):

$$H = \frac{\sum_{i=1}^{n-1} SN\%_i}{\sum_{i=1}^{n-1} SN\%_i - SV\%_i} \tag{2}$$

where:

SN% – the cumulative relative frequency of the stem number;

SV% – the cumulative relative frequency of the stand volume;

n – the number of diameter classes.

Another index applied to evaluate the stand structure was the structural complexity index (*SCI*) by Zenner and Hibbs (2000), which also takes horizontal tree distribution into account. Input values are the positions of trees (*x*, *y* coordinates) and values of the selected dendrometric variable (*z*, usually DBH or height). The minimal value (1) indicates the most homogeneous structure, i.e. all trees have the same DBH value. In our analysis, this index could only be applied in 2018 due to the absence of stem position data in previous measurements, Equation (3):

$$SCI = \frac{\sum_{i=1}^{N} \frac{1}{2}|a_i b_i|}{A_T} \tag{3}$$

where:

N – the number of triangles in the model;

a_i – coordinates of the vector AB (x_{ib}-x_{ia}, y_{ib}-y_{ia}, z_{ib}-z_{ia});

b_i – coordinates of the vector AC (x_{ic}-x_{ia}, y_{ic}-y_{ia}, z_{ic}-z_{ia});

A_T – the sum of the projected areas.

The tree species composition was evaluated using the relative importance value (*RIV*) by Cottam and Curtis (1956), which represents the arithmetic mean of species dominance (the basal area of one species as a percentage of the total basal area), relative density (the stem number of one species as a percentage of the total stem number), and relative frequency (the number of occurrences of one species as a percentage of total number of occurrences). We used only the relative dominance and relative density, because we did not have spatial data from measurements before 2018.

To explore long-term changes in the tree species composition on each PRP, we carried out a detrended correspondence analysis (*DCA*). This is an indirect gradient analysis delineating trends in species composition within investigated sites. *DCA* is a modification of correspondence analysis (*CA*), and was developed to forego 'the arch effect' (Hill, Gauch 1980). *RIV* was selected as the input variable, and the analysis was performed using the package 'vegan' in R 3.6.2. (R Core Team 2019).

RESULTS

During the observation period, stem density (*N*) in individual plots ranged from 112 to 640 ha^{-1} (Table 1). The overall mean reached 314 ha^{-1} with the coefficient of variation (*CV*) at 39%. We registered significant differences in the long-term stem number variability between individual PRPs, which ranged from relatively stable structures in PRPs 1 and 2 (*CV* below 10%) to structures with distinctively higher variation in stand density in PRPs 3 and 4 (27% and 70%, respectively). The basal area (*G*) ranged between 29.4 and 43.6 $\text{m}^2\cdot\text{ha}^{-1}$, with an overall mean of 36.6 $\text{m}^2\cdot\text{ha}^{-1}$ and the lowest variability of the basic stand characteristics (overall *CV* 11%, with within-plot values 8%–13%). The overall mean of growing stock (*V*) reached 634 $\text{m}^3\cdot\text{ha}^{-1}$, ranging from 459 to 831 $\text{m}^3\cdot\text{ha}^{-1}$, with variability similar to that of the basal area. The relative density (*RD*) varied between 0.60 and 0.96, with an overall mean of 0.81. Only 25% cases were less than 0.75, indicating a relatively high density during the investigated period. The homogeneity coefficient (*H*) reached an overall mean of 2.11, varying from 1.46 to 2.54. Values of *H* were relatively stable ($CV < 6\%$), with the exception of PRP 4 (*CV* 20%). In the long term, higher *H* values and thus lower heterogeneity were characteristic of PRPs 2 and 3.

In the structure dynamics of individual PRPs, certain common trends were visible (Table 1). We observed increases of *RD*, *G*, and *V* that began in 1996 at the latest, and much earlier in the cases of PRP 1 and 2 (1977 and 1986, respectively). Regarding the stem density, the situation was much more variable. While the stem numbers were relatively stable in PRPs 1 and 2, they showed a decreasing trend in PRP 3, and a steep increase in PRP 4 during the last two decades as a result of canopy mortality and subsequent regeneration. When analysing the association between diameter differentiation quantified by *H* and basic stand characteristics, we found no significant relationships, i.e. differentiated structures occurred at relatively wide distributions of *N*, *G* and *V*. The strongest, although not

Table 1. Temporal changes of basic stand variables and selected structural indices in all permanent research plots (PRP) during the investigated period 1970–2018.

Year/plot	Variables			Indices		
	N (N·ha^{-1})	G (m^2·ha^{-1})	V (m^3·ha^{-1})	RD	H	SCI
PRP 1						
1970	369	38.6	630	0.83	1.70	n.a.
1977	288	31.6	540	0.71	1.67	n.a.
1986	300	35.3	634	0.81	1.82	n.a.
1996	288	35.6	663	0.81	1.62	n.a.
2007	298	40.7	777	0.90	1.67	n.a.
2018	319	**43.6***	**831***	**0.96***	1.83	11.25
Average ± SD	311 ± 28	37.6 ± 3.9	679 ± 97	0.84 ± 0.08	1.72 ± 0.08	
PRP 2						
1970	340	37.3	582	0.82	2.52	n.a.
1977	289	41.0	680	0.87	2.37	n.a.
1986	240	34.6	595	0.77	2.49	n.a.
1996	262	35.7	624	0.81	2.38	n.a.
2007	275	37.9	683	0.86	2.22	n.a.
2018	288	42.8	788	**0.96***	2.11	8.88
Average ± SD	282 ± 31	38.2 ± 2.9	659 ± 69	0.85 ± 0.06	2.35 ± 0.14	
PRP 3						
1970	**640***	42.4	594	0.93	2.24	n.a.
1977	478	33.2	465	0.77	2.25	n.a.
1986	431	31.7	459×	0.77	2.52	n.a.
1996	369	30.0	459×	0.71	2.28	n.a.
2007	280	33.2	542	0.74	2.42	n.a.
2018	361	39.5	649	0.91	**2.54***	8.00
Average ± SD	427 ± 114	35.0 ± 4.4	528 ± 74	0.81 ± 0.08	2.38 ± 0.12	
PRP 4						
1970	172	37.2	670	0.79	2.44	n.a.
1977	133	37.8	719	0.79	2.43	n.a.
1986	112×	32.9	631	0.67	2.32	n.a.
1996	114	29.4×	570	0.60×	1.88	n.a.
2007	325	34.7	666	0.74	1.57	n.a.
2018	567	41.4	774	0.92	1.46×	8.32
Average ± SD	237 ± 164	35.5 ± 3.8	672 ± 64	0.75 ± 0.10	2.01 ± 0.40	

N – stem density; G – basal area; V – growing stock; RD – relative density; H – homogeneity coefficient; SCI – structural complexity index; SD – standard deviation; the overall highest (*) and the lowest values (×) of separate attributes are highlighted with bold numbers; n.a. – data not available

significant, correlation ($R = -0.381$, $P = 0.065$) was observed in the cases of H and V, indicating the tendency of increasing structure differentiation with increasing stand volume. In 2018, the values of SCI confirmed the highest structure differentiation in PRP 1, while, surprisingly, a relatively low value was observed in structurally heterogenous PRP 4.

In the PRP 1 and PRP 2, the diameter structure has not changed substantially over the course of the observation period (Figure 1). The diameter structure of PRP 3 shows a decline in lower diameter classes, while the opposite trend can be seen in PRP 4. The tree species composition of all PRPs changed significantly during the investigated period (Table 2).

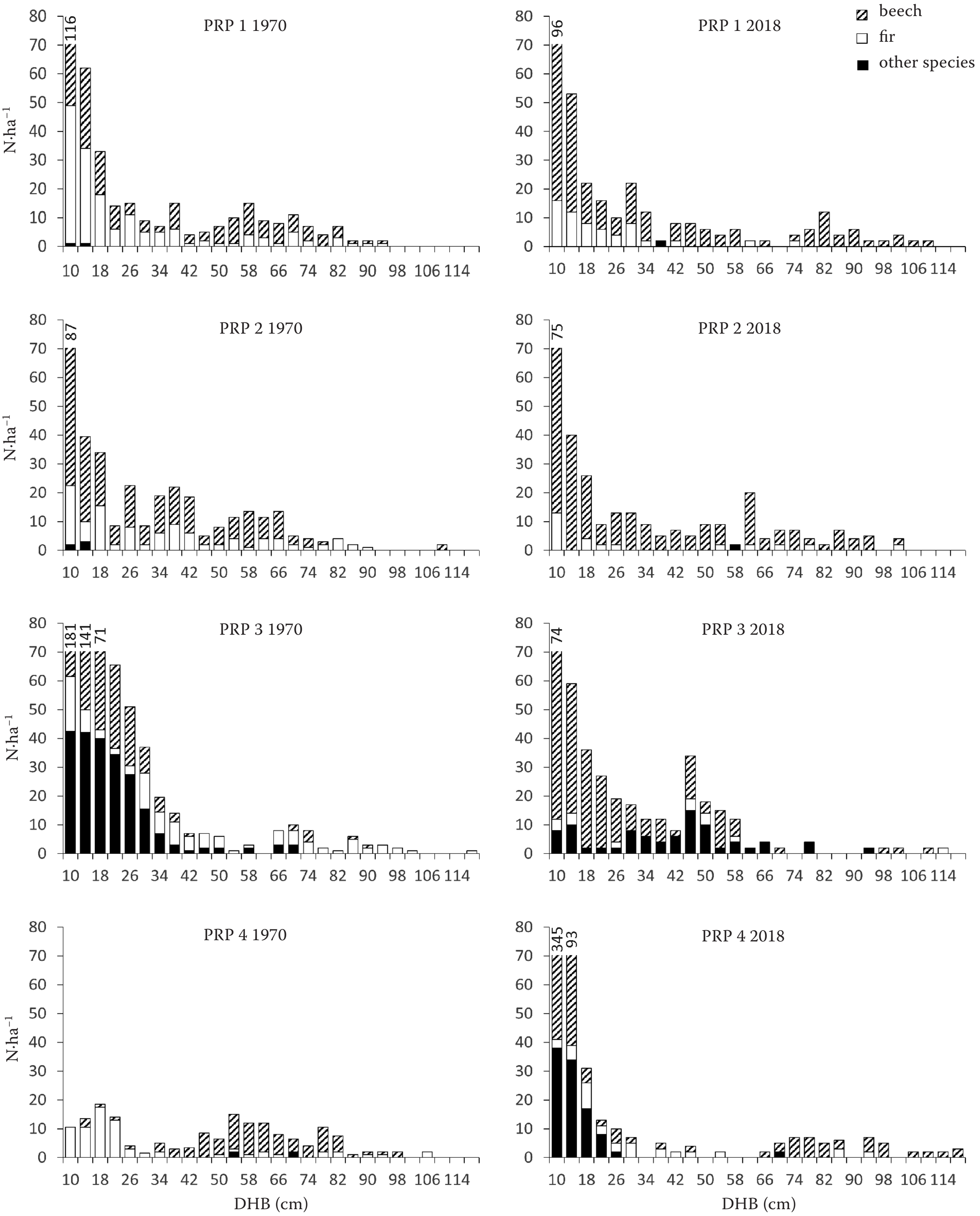

Figure 1. The diameter distribution on each permanent research plot in the first and last measurement year (a number above the column indicates the maximal value)

In general, we observed a long-term growth trend of beech proportions, mostly at the expense of decreasing fir (Figure 2). Between 1970 and 2018, the proportion of fir in individual PRPs decreased by 20–25%. This decreasing trend corresponded with the nearly equal increase in beech proportion, with

https://doi.org/10.17221/139/2020-JFS

Table 2. The relative importance value (*RIV*) in the first and last measurement year in all permanent research plots (PRP)

Year	*RIV*				
	FaSi	AcPs	UlMo	FrEx	AbAl
PRP 1					
1970	60.8	0	0.3	0	38.9
2018	85.5	0	0.6	0	13.9
PRP 2					
1970	66.1	0.8	0	0	33.1
2018	88.9	0.9	0	0	10.2
PRP 3					
1970	36.3	12.6	15.3	1.2	34.6
2018	59.3	19.6	6.8	2.7	11.6
PRP 4					
1970	66.7	1.0	1.4	0	30.9
2018	77.6	7.5	3.6	0.8	10.5

FaSi – *Fagus sylvatica*; AcPs – *Acer pseudoplatanus*; FrEx – *Fraxinus excelsior*; UlMo – *Ulmus montana*; AbAl – *Abies alba*

the exception of PRP 4. In PRP 4, the declining fir was replaced not only by beech (+11%) but also by other broadleaved species (maple, elm, and ash, together +12%). In PRP 3, unlike the other plots, we registered special dynamics within the other broadleaved species, with the significant decrease of elm and corresponding increase of ash and especially maple population proportions.

DISCUSSION

The long-term variability of basic stand characteristics (*N*, *G*, *V*) in the investigated old-growth forest Badínsky prales showed features in common with other old-growth beech-dominated and mixed forests of the Carpathians – Havešová (Saniga et al. 2018), Dobroč (Filípek 2019), Stužica (Saniga et al. 2019) and Sinca (Petritan et al. 2015) – and the Dinaric Alps – Pecka (Nagel et al. 2006). The coefficient of variation for basal area in Badín (11%) was near the reported range of 12–13%, and a similar situation was registered for stand volume with a *CV*

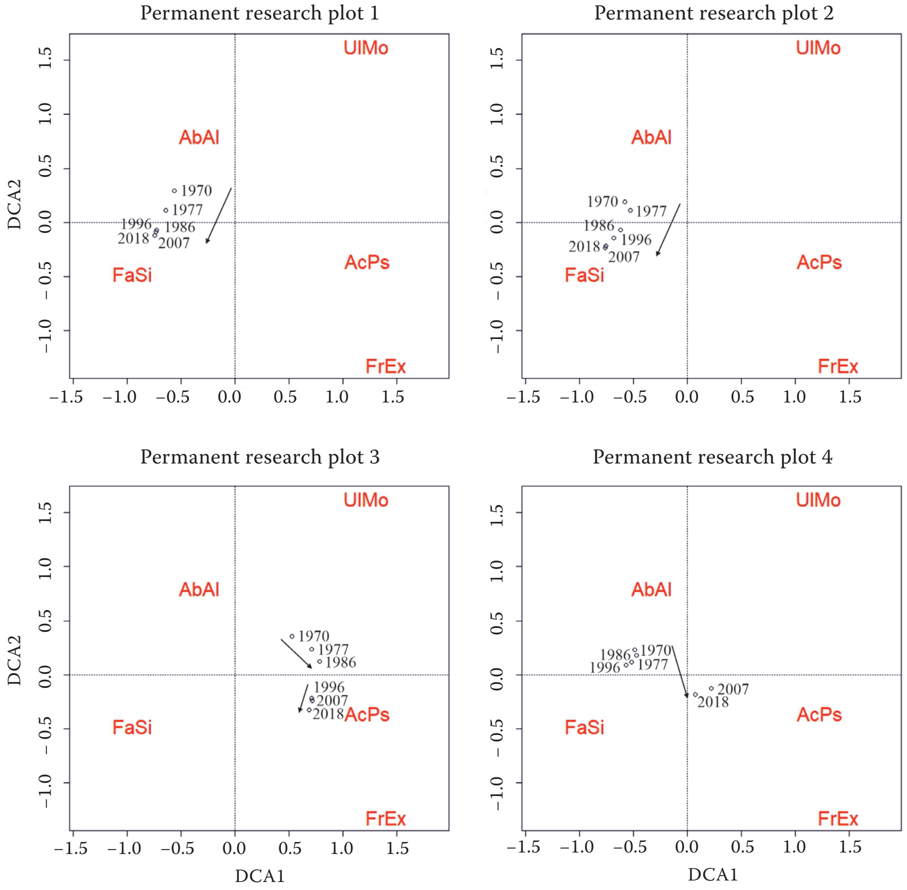

Figure 2. *DCA* biplots showing long-term changes in tree species diversity (FaSi – *Fagus sylvatica*; AcPs – *Acer pseudoplatanus*; FrEx – *Fraxinus excelsior*; UlMo – *Ulmus montana*; AbAl – *Abies alba*)

of 16%, falling in the reported range of 13–16%. As expected, the most variable stand attribute was the stem number, with the *CV* in Badín (39%) nearly two-fold higher in comparison to other old-growth forests (18–24%). Here, the increased variability was heavily affected by the significant emergence and development of natural regeneration following a disturbance event.

The level of structural differentiation in surveyed plots was quantified by two indices – the coefficient of homogeneity *H* and the structural complexity index *SCI*. The values of *H* did not exceed 2.54, thus varying in the range typical for selection forest structures (1.3–2.8). The similarly high degree of diameter differentiation, with $H < 2.8$, has been confirmed also in other beech-dominated, old-growth forests (Havešová, Stužica) of the Western Carpathians (Saniga et al. 2018, 2019). On the other hand, the increasing admixture of conifers (fir, spruce) in the old-growth forest seems to extend the variation of *H* towards the less heterogenous structures, as observed in old-growth forest Dobroč (1.47–3.62, Filípek 2019). The values of *SCI*, which exceeded in all plots the threshold of 8, confirmed the assessment of structure differentiation made by the *H* index, with the exception of PRP 4. In PRP 4, the highest degree of diameter differentiation detected by *H* did not correspond with the lower structural complexity quantified by $SCI = 8.32$. The most likely reason for this discrepancy seems to be the spatial arrangement of understory stems, which is not included in the computation of *H*. In this case, the understory stems are concentrated in structurally and relatively homogenous clusters. The *SCI* is responsive to such features, resulting in lower values of structural complexity.

In order to evaluate the stand density of investigated mixed and multi-aged forests, we tried to test a novel index, the relative density (*RD*). The most widely used variables for density quantification are the stand density index (*SDI*) by Reineke (1933) and its modification, the additive stand density index (*ASDI*) by Long and Daniel (1990). *SDI* was initially developed for even-aged monocultures. *ASDI* already allowed for calculation of the density in uneven-aged stands, but not in mixed stands. Application of *ASDI* in stands containing tree species with different crown characteristics is questionable, as we are unable to compare results from plots with different tree species composition. To resolve this issue, we applied *RD* (Ducey, Knapp 2010), which considers stand mixtures by incorporating wood-specific gravity into the calculation. The dynamics of *RD* are identical to those of the basal area ($R = 0.94$) and stand volume ($R = 0.82$), confirming its suitability for quantification of stand density and indicating it as a better option than *ASDI* for uneven-aged mixed stands.

In terms of species composition characterised by *RIV*, we observed an expansion of beech (and partly of other broadleaved species) and a corresponding decrease of fir. With the exption of PRP 4, the most significant fir decline was noted between 1970 and 1986. In this period, decreases of 23% (PRP 1), 17% (PRP 2), and 19% (PRP 3) in *RIV* were recorded. From 1986 to 2018, fir *RIV* values decreased only by 2%–7% per decade; in the last 10 years, a slight increase (ca. 1%) has even been observed. The decline in fir could be related to the fir dieback caused by immissions during the period of the 1960s to 1980s (Elling et al. 2009). Another factor to consider is past human influence on species composition. In his earlier papers, Korpeľ (1958, 1968) wrote about traces of charcoal production recorded in the Badínsky prales, using beech as the preferred tree species. Therefore, we can assume that the human-induced reduction of beech may have contributed to the artificially elevated proportion of fir in the upper layer in the distant past. Another important factor to consider is ungulate over-browsing. Browsing damage and its negative impact on regeneration processes have been reported since the first research activities in the Badínsky prales 70 years ago, but has accelerated significantly during the last decade (Korpeľ 1958, Saniga et al. 2012). Silver fir decline is not limited to the Badínsky prales, and has also been recorded in several other European primeval forests. The main cause has been cited as anthropogenic impact (air pollution and human-induced high deer density) on the coexistence of beech and silver fir (Diaci et al. 2011).

Evaluating the overall dynamics of the structural characteristics, we observed a general trend of increasing basal area, stand volume, and relative density in all four PRPs during the last 25 years. In 2018, nearly all of these variables reached their maximum in each plot. Studying the disturbance regime in the Badínsky prales, Kucbel et al. (2010) detected the highest frequency of gaps with natural regeneration between 20 and 25 year old, which was interpreted as the result of a higher disturbance frequency in the 1980s. In general, they observed significant

https://doi.org/10.17221/139/2020-JFS

fluctuations in gap frequencies in regards to gap age, a result similar to those reported by Nagel and Diaci (2006), Firm et al. (2009), and Feldmann et al. (2018). The significantly lower frequency of younger gaps originated in the last 20–30 years (Kucbel et al. 2010) would seem to indicate a lower number of disturbance events and conditions favourable for the accumulation of biomass in recent decades. The increase of stand biomass was likely also affected by the enhanced growth conditions consequent to recent climate change. Increasing temperatures may result in a longer growing season (Prislan et al. 2019), but also pose an increasing drought risk (Seidl et al. 2017). Nevertheless, in the case of areas with sufficient water availability, higher temperatures were confirmed to lead to increasing production (Linder et al. 2010; Dulamsuren et al. 2016; Prislan et al. 2019). Another factor that certainly contributed to the observed biomass accumulation was the tree species composition with the natural absence of Norway spruce and therefore spared from the current Norway spruce dieback and subsequent biomass loss. An interesting observation is that despite the continuously increasing basal area, stand volume, and relative density, the diameter structure remains relatively heterogeneous.

Nevertheless, broader generalisation of these results to the old-growth forests of the fir-beech altitudinal zone of the Carpathians should be undertaken with caution, as they might to a certain extent be affected by the subjective selection of sample plots representing particular developmental stages. Subjective and unrepresentative selection may lead to overestimation or underestimation of stand characteristics (Holeksa et al. 2009; Král et al. 2010; Peck et al. 2015), and this may also be affected by site quality or the subliminal old-growth stereotype (Peck et al. 2015). However, the primary importance of research plots in the Badínsky prales lies in the ability to follow and analyse the dynamics of old-growth structures in the long term, spanning nearly five decades.

CONCLUSION

The evaluation of structural characteristics in four permanent research plots in this mixed fir-beech old-growth forest, revealed that the stands maintained the heterogenous structure over the majority of the observation period. The coefficient of homogeneity indicated a diameter structure comparable to other highly heterogeneous stands. We detected substantial changes in tree species composition. Our results showed a significant silver fir decline, mainly between 1970 and 1986. Beech proportion increased proportionally, with the exception of one permanent research plot where other broadleaved species proportion also grew. The silver fir decline could be partly the result of earlier human influence, however, anthropogenic impact through immissions and human-induced high deer density is a more likely significant cause.

Over the last few decades, we observed considerable growth in the stand volume, basal area, and relative density, all of which reached their maximal values in 2018. These high values can be attributed to the absence of disturbance events, together with the impact of enhanced growth conditions due to climate change. To identify the implications of structural changes for natural regeneration and future development, more rigorous investigation will be needed.

REFERENCES

Bauhus J., Puettmann K., Messier C. (2009): Silviculture for old-growth attributes. Forest Ecology and Management, 258: 525–537.

Bublinec E., Pichler V. (2001): Slovenské pralesy: Slovak primeval forests diversity and conservation: diverzita a ochrana. Zvolen, Ústav ekológie lesa SAV: 200.

Camino R.D. (1976): Zur Bestimmung der Bestandeshomogenität, Allgemeine Forst- und Jagdzeitung, 147: 54–58.

Cottam G., Curtis J.T. (1956): The use of distance measurements in phytosociological sampling. Ecology, 37: 451–460.

Del Río M., Pretzsch H., Alberdi I., Bielak K., Bravo F., Brunner A., Condés S., Ducey M.J., Fonseca T., Von Lüpke N., Pach M., Peric S., Perov T., Souidi Z., Spathelf P., Sterba H., Tijardovic M., Tomé M., Vallet P., Bravo-Oviedo A. (2016): Characterization of structure, dynamics, and productivity of mixed-species stands: review and perspectives. European Journal of Forest Research, 135: 23–49.

Diaci J., Rozenbergar D., Anic I., Mikac S., Saniga M., Kucbel S., Visnjic C., Ballian D. (2011): Structural dynamics and synchronous silver fir decline in mixed old-growth mountain forests in Eastern and Southeastern Europe. Forestry, 84: 479–491.

Ducey M.J., Knapp R.A. (2010): A stand density index for complex mixed species forests in the north-eastern United States. Forest Ecology and Management, 260: 1613–1622.

Dulamsuren C., Hauck M., Kopp G., Ruff M., Leuschner C. (2016): European beech responds to climate change with growth decline at lower, and growth decrease at higher elevations in the center of its distribution range (SW Germany). Trees, 31: 673–686.

Elling W., Dittmar C., Pfaffelmoser K., Rötzer T. (2009): Dendroecological assessment of the complex causes of decline and recovery of the growth of silver fir (*Abies alba* Mill.) in Southern Germany. Forest Ecology and Management, 257: 1175–1187.

Feldmann E., Drössler l., Hauck M., Kucbel S., Pichler V., Leuschner Ch. (2018): Canopy gap dynamics and tree understory release in a virgin beech forest, Slovakian Carpathians. Forest Ecology and Management, 415–416: 38–46.

Filípek M. (2019): Štrukturálna diverzita a jej dynamika vo vybraných prírodných lesoch Slovenska. [Ph.D. Thesis.] Zvolen, Technical University in Zvolen, Faculty of Forestry. (in Slovak)

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

Hill M.O., Gauch H.G. (1980): Detrended correspondence analysis: an improved ordination technique. Vegetation, 42: 47–58.

Holeksa J., Saniga M., Szwagrzyk J., Czerniak M., Staszyńska K., Kapusta P. (2009): A giant tree stand in the West Carpathians – an exception or a relic of formerly widespread mountain European forests? Forest Ecology and Management, 257: 1577–1585.

Jaehne S., Dohrenbusch A. (1997): Ein Verfahren zur Beurteilung der Bestandesdiversität. Forstwissenschaftliches Centralblatt, 116: 333–345.

Jaloviar P., Saniga M., Kucbel S., Pittner J., Vencurik J., Dovciak M. (2017): Seven decades of change in a European old-growth forest following a stand-replacing wind disturbance: A long-term case study. Forest Ecology and Management, 399: 197–205.

Korpeľ Š. (1958): Príspevok k štúdiu pralesov na Slovensku na príklade Badínskeho pralesa. Lesnícky časopis, 4(6): 349–385. (in Slovak)

Korpeľ Š. (1968): Badínsky prales. Československá ochrana prírody, 6: 311–315. (in Slovak)

Korpeľ Š. (1989): Pralesy Slovenska. Bratislava, Veda: 328. (in Slovak)

Král K., Janík D., Vrška T., Adam D., Hort L., Unar P., Šamonil P. (2010): Local variability of stand structural features in beech dominated natural forests of Central Europe: implications for sampling. Forest Ecology and Management, 260: 2196–2203.

Križová E. (2000): Lesné spoločenstvá NPR Badínsky prales. Chránené územia Slovenska: štvrťročný odborno-metodický a informačný časopis štátnej ochrany prírody, 46: 36–37. (in Slovak)

Kucbel S., Jaloviar P., Saniga M., Vencurik J., Klimaš V. (2010): Canopy gaps in an old-growth fir-beech forest remnant of Western Carpathians. European Journal of Forest Research, 129: 249–259.

Leibundgut H. (1959): Über Zweck und Methodik der Struktur und Zuwachsanalyse von Urwäldern. Schweizerische Zeitschrift für Forstwesen, 110: 111–124.

Linder M., Maroschek M., Netherer S., Kremer A., Barbati A., Garcia-Gonzalo J., Seidl R., Delzon S., Corona P., Kolström P., Lexer M.J., Marchetti M. (2010): Climate change impacts, adaptive capacity, and vulnerability of European forest ecosystems. Forest Ecology and Management, 259: 698–709.

Long J.N., Daniel T.W. (1990): Assessment of growing stock in uneven-aged stands. Western Journal of Applied Forestry, 5: 93–96.

McElhinny C., Gibbons P., Brack C., Bauhus J. (2005): Forest and woodland stand structural complexity: Its definition and measurement. Forest Ecology and Management, 218: 1–24.

Millar C.I., Stephenson N.L. (2015): Temperate forest health in an era of emerging megadisturbance. Science, 349: 823–826.

Nagel T.A., Diaci J. (2006): Intermediate wind disturbance in an old-growth beech-fir forest in southeastern Slovenia. Canadian Journal of Forest Research, 36: 629–638.

Nagel T.A., Svoboda M., Diaci J. (2006): Regeneration patterns after intermediate wind disturbance in an old-growth Fagus-Abies forest in southeastern Slovenia. Forest Ecology and Management, 226: 268–278.

Peck J.E., Commarmot B., Hobi M.L., Zenner E.K. (2015): Should reference conditions be drawn from a single 10 ha plot? Assessing representativeness in a 10,000 ha old-growth European beech forest. Restoration Ecology, 23: 927–935.

Petráš R., Pajtík J. (1991): Sústava československých objemových tabuliek drevín. Lesnícky časopis, 37: 49–56. (in Slovak)

Petritan I.C., Commarmot B., Hobi M.L., Petritan A.M., Bigler C., Abrudan I.V., Rigling A. (2015): Structural patterns of beech and silver fir suggest stability resilience of the virgin forest Sinca in the Southern Carpathians, Romania. Forest Ecology and Management, 356: 184–195.

Prislan P., Gričar J., Čufar K., de Louis M. Merela M., Rossi S. (2019): Growing season and radial growth predicted for Fagus sylvatica under climate change. Climatic Change, 153: 181–197.

Prodan M. (1951): Messung der Waldbestände. Frankfurt am Main, J. D. Sauerländer's Verlag: 260.

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

Saniga M., Kucbel S., Jaloviar P., Vencurik J. (2012): Štruktúra, vývoj, textúra, disturbančný režim a produkčné procesy Badínskeho pralesa. Zvolen, Technická univerzita vo Zvolene: 60. (in Slovak)

Saniga M., Pittner J., Kucbel S., Filípek M., Jaloviar P., Sedmáková D., Vencurik J. (2019): Dynamické zmeny štruktúry, regeneračné procesy a zmena objemu mŕtveho dreva v rámci vývojového cyklu bukového pralesa NPR Stužica (časová štúdia). Zvolen. Technická univerzita vo Zvolene: 61. (in Slovak)

Saniga M., Pittner J., Kucbel S., Jaloviar P., Sedmáková D., Vencurik J. (2018): Štruktúra, produkcia bio- a nekromasy a regeneračné procesy bukových pralesov NPR Havešová a Kyjov (časová štúdia). Zvolen, Technická univerzita vo Zvolene: 54. (in Slovak)

Schütz J.P., Saniga M., Diaci J., Vrška T. (2016): Comparing close-to-nature silviculture with processes in pristine forests: lessons from Central Europe. Annals of Forest Science, 73: 911–921.

Seidl R., Thom D., Kautz M., Martin-Benito D., Peltoniemi M., Vacchiano G., Wild J., Ascoli D., Petr M., Honkaniemi J., Lexer M.J., Trotsiuk V., Mairota P., Svoboda M., Fabrika M., Nagel T.A., Reyer C.P.O. (2017): Forest disturbances under climate change. Nature Climate Change, 7: 395–402.

Thom D., Seidl R. (2016): Natural disturbance impacts on ecosystem services and biodiversity in temperate and boreal forests. Biological Reviews, 91: 760–781.

Watson J.E.M., Evans T., Venter O., Williams B., Tulloch A., Stewart C., Thompson I., Ray J.C., Murray K., Salazar A., McAlpine C., Potapov, P., Walston J., Robinson J.G., Painter M., Wilkie D., Filardi C., Laurance W.F., Houghton R.A., Maxwell S., Grantham H., Samper C., Wang S., Laestadius L., Runting R.K., Silva-Chávez G.A., Ervin J., Lindenmayer D. (2018): The exceptional value of intact forest ecosystems. Nature Ecology & Evolution, 2: 599–610.

Wirth C., Gleixner G., Heimann M. (2009): Old-Growth Forests: Function, Fate and Value – an Overview. In: Wirth C., Gleixner G., Heimann M. (eds.): Old-Growth Forests. Ecological Studies (Analysis and Synthesis), Vol. 207. Springer, Berlin, Heidelberg: 3–10.

Zenner E.K., Hibbs D.E. (2000): A new method for modelling the heterogeneity of forest structure. Forest Ecology and Management, 129: 75–87.

Received: Setember 3, 2020
Accepted: November 2, 2020