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ORIGINAL PAPER

Does quarter of century of protection differentiate protected from managed mixed fir stands in Polish lowland?

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ABSTRACT

In Central Europe, there is no forest ecosystem that is exempt from human influence. Nevertheless, in many European regions it is very important to protect late successional forests, as they play an essential role in maintaining biodiversity, ecological function and providing ecosystem services. The objective of this study is to investigate the effects of forest management, or lack of management intervention, on forest structure and natural regeneration at similar stages of stand development. It is also important to know whether the forest structure in protected areas changes towards a higher degree of 'naturalness'. The study was conducted in the Janów Forests in southeastern Poland in three types of mixed stands. In each stand type, 40 sample plots were established (20 in protected stands and 20 in managed stands). All seedlings and saplings were classified into two categories based on their light requirements. Our study shows that the diverse structure of mixed fir stands can be achieved by passive or low-intensity management that supports natural forest regeneration. DBH structure and species composition of stands did not differ between managed and protected stands. Our studies indicate that in managed mixed fir stands, passive management limited to low intensity salvage cutting promotes the creation of differentiated spatial structure and species composition, similar to protected stands of the same type. To increase the proportion of complex mixed fir stands, the rotation age should be increased. Single tree selection cuttings can help maintain such complex stand structures.

KEY WORDS

Abies alba, deadwood, management, mixed forests, protection, stand structure

Introduction

In Central Europe, there is no forest ecosystem that is exempt from human influence (Bilek *et al.*, 2011). Only few of them can be called semi-natural forests (Sabatini *et al.*, 2018). The same situation is observed in Poland, where semi-natural forests are very rare. It is known that even the semi-natural forests are difficult to restore to primeval forests, and the development of natural disturbance dynamics and typical structure formation takes decades (Sabatini *et al.*, 2018).

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However, it is very important to protect late-successional forests in many European regions, as they play an essential role in terms of biodiversity conservation, ecological function and ecosystem service provision. There is a lack of systematic research to quantify the dynamics of semi-natural protected forests in Europe, to assess whether forests are sufficiently protected or to understand what determines their changes. Moreover, the area of protected forests in Europe is likely to increase (Sitzia *et al.*, 2012). Protected mature forests have the potential to develop into old-growth forests. Nature reserve will inherit a structure created by past management that should be preserved as a starting point for the future forest structure (Bilek *et al.*, 2011). Forest reserves have been established in Europe in the last decades aiming to increase the share of old forests in the landscape. On the other hand, earlier studies shown that management legacies can persist for decades to centuries after management ceases (Thom *et al.*, 2018). The establishment of new protected areas therefore raises questions about their future development, in particular whether formerly managed forests are actually capable of returning to old-growth conditions under changing environment, how long such a process might take, and how the old-growth forests of the future might differ in composition, structure, and function from today's old forests. To date, little research has been done on these questions, particularly in Europe (Vandekerkhove *et al.*, 2009; Paillet *et al.*, 2015; Burrascano *et al.*, 2018).

Forest stand structure including the architectural and functional elements constitutes the forest (Fournier *et al.*, 2003; Wan *et al.*, 2019) and plays an important role in the ecosystem processes (Nakashizuka, 2001). It includes both the spatial and non-spatial structure of the forest. Forest structure comprises various components such as tree density, deadwood and regeneration (Holeksa *et al.*, 2007; Kulakowski *et al.*, 2017). Stand density determines growth (Forrester, 2019) and size distribution quantifies stand structure (Fien *et al.*, 2019). The diversity measures and forest summary characteristics of selected stands can help to monitor the influence of both natural processes and silviculture (Motz *et al.*, 2010). Stand structural elements should include summary forest characteristics, spatial tree patterns, different size classes of trees. In addition, tree mortality, tree growth, and regeneration are important factors in forest ecosystem development (Zanini *et al.*, 2006). Deadwood is a crucial feature of a natural forest (Kunttu *et al.*, 2015; Keren and Diaci, 2018) and its species diversity (Hekkala *et al.*, 2016), and can be used to compare natural and managed stands. Deadwood is an important habitat because it facilitates the growth of tree seedlings (Zielonka and Niklasson, 2001) and protects against browsing (Hagge *et al.*, 2019). It is also important for many taxa obligatory connected with deadwood (Doerfler *et al.*, 2018). Birds also profit from standing deadwood stems (Kroll *et al.*, 2017). Deadwood removing also has consequences for the regeneration (Svoboda *et al.*, 2010).

Although the extensive research on forest structure has been done (Sitzia *et al.*, 2012; Brzeziecki *et al.*, 2018; Szmyt and Tarasiuk, 2018; Baran *et al.*, 2020), knowledge of how forest management and protection affect silver fir forests growing in lowlands is insufficient. Most studies have been conducted in the mountain forests composed of European beech *Fagus sylvatica* L., Norway spruce *Picea abies* (L.) Karst, and silver fir *Abies alba* Mill.(Bartkowicz and Paluch, 2019). In addition, most studies focusing on changes in lowland forests are from northwestern Europe (Belgium, England). Information on more continental parts of Europe is largely missing (Hédl *et al.*, 2010).

So far, well-preserved old-growth stands that have been protected for at least 50 years have been compared with mostly younger stands that are managed in a simplified manner. However in some of managed stands, the rotation period is such that natural processes (*i.e.*, tree death) associated with tree aging and biotic disturbances (fungi, pests) can develop. It is interesting to compare the structure of old managed and protected stands. The objective of the study is to investigate the effects of management or lack of interventions on forest structure and natural regeneration of light-demanding and shade-tolerant tree species at similar stages of stand development. We hypothesized that structural diversity is higher in protected forests than in managed stands. It is also important to know whether the forest structure of natural reserves is changing towards a higher degree of 'naturalness'. We addressed the following questions:

(i) Does protection promote differences in species composition between managed and protected mixed fir forests?
(ii) Is the amount of deadwood similar in protected and managed mixed fir forests?
(iii) Does discontinuation of management change the species composition of natural regeneration in protected mixed fir forests?

Material and Methods

STUDY AREA. The study was carried out in the Janów Forests in the southeastern Poland. The area of the Janów Lubelski Forest District is 31,566 ha. The mean temperature is in July (18.5-19.0°C), and the lowest in February (–4.5°C). The average annual temperature is 7.1°C and the total annual precipitation is 700 mm. The growing season lasts 210-220 days (Lorenc, 2005). The Janów Lubelski Forest District is dominated by coniferous and mixed forests. In the landscape of pine forests there are also fragments of fir and mixed deciduous forests.

Silver fir grows as an admixture in mixed stands, which we divided into 3 types: 1) pine-fir stands (PF) growing on soils with a water table deeper than 1 m below the surface, and 2) pine--alder-fir stands (PAF) and 3) beech-alder-fir stands (BAF) growing on moist sites with a water table below 1 m to the soil surface. The study was conducted in managed and protected stands (duration of protection ranged from 21 to 34 years). Sample plots representing protected stands were established in nature reserves where management activities have been limited only to sanitary cuttings in all reserves or selection cuttings aimed to promote silver fir regeneration (Szklarnia reserve).

The Szklarnia reserve established in 1989, covers an area of 278.14 ha. The study plots were established in pine-alder-fir (PAF) type in 2017. We selected 3 stands with age 69-149 years, growing on Dystric Gleysol soils. The next reserve – Lasy Janowskie – covers an area of 2676.87 ha and was established in 1984. In 2018, data was collected in 4 mixed stands consisting mainly of pine and fir (pine-fir type (PF). The age of the stands varied from 67 to 130 years. They grew on Endocalcaric Cambisols soils. The Łęka reserve was established in 1998 and covers an area of 376.9 ha. In the Łęka reserve we established sample plots in 3 beech-alder-fir (BAF) stands aged 98-163 years, growing on Dystric-Gleysols soils. The data was collected in 2019.

We selected managed stands based on species composition and age comparable to protected stands. Sample plots were located in 11 managed stands where only salvage cuttings of low intensity were done without initiating natural fir regeneration. Ages of managed stands ranged from 50-170, 49-138, and 56-148, respectively for PAF, PF, and BAF stands. They grew on Dystric gleysols and Dystric Brunic Arenosols. Data on species composition and tree age were taken from the forest district survey.

DATA COLLECTION. The data was collected on randomly selected 120 circular plots. In each type of mixed fir stands (PF, PAF and BAF) 40 sample plots were established (20 in protected and 20 in managed stands). Each sample plot consisted of three concentric circles with different radii and area. Seedlings (h≤0.5 m) were measured in 10 m^2 nested plots (radii 1.78 m). Saplings (height

>0.5 m and diameter at breast height (DBH)<7 cm) were measured in 100 m^2 nested plots (radii 5.64 m). All trees with DBH≥7 cm were measured in 500 m^2 plots (radii 12.62 m). Polar coordinates (azimuth and distance from the sampling plot centre) were measured for all trees with DBH≥7 cm.

We measured coarse woody debris (diameter >10.0 cm) on 500 m^2 plots. The volume of dead trees was calculated using following formulas:

For lying dead trees (eqn. 1):

$$V = (B_0 + B_1) \cdot l \cdot (0.5) \tag{1}$$

where:

B_0 – area of thinner end,
B_1 – area of thicker end,
l – length of trees.

For stumps (eqn. 2):

$$V = \pi r^2 \cdot h \tag{2}$$

where:

h – height of a stump,
r – middle radius of a stump.

For standing dead as well as also broken trees (eqn. 3):

$$v = d_2/1000 \cdot [1 + 0.03 \cdot (h - 30)] \tag{3}$$

where:

v [m^3] – tree volume of dead trees,
d [cm] – diameter at breast height (1.3 m),
h [m] – tree height.

We have divided all seedlings and saplings into two categories based on light requirements of tree species (Niinemets and Valladares, 2006). The light-demanding category included the following trees: birch, oak, rowan, ash, alder, aspen, pine, hazel, and spindle. Shade-tolerant trees were: beech, hornbeam, lime, maple, fir, spruce, elm and buckthorn.

STATISTICAL ANALYSES. Tree diameters distributions and stands composition.

The distributions of trees diameters in different stands were compared with Kolmogorov--Smirnov test (two sample K-S test). The differences in the species composition between the reserved and managed stands were assessed using the Robič Index of Dissimilarity (RID) (Bončina and Robič, 1998; Bončina e*t al.*, 2017). This index allows to compare the species composition in two stands. In each stand, composition must be expressed as a relative prevalence index (*e.g.* share of particular tree species in the basal area of tree stand). The RID index is calculated as the quotient of the Euclidean distance D and the maximum Euclidean distance Dmax between the species composition of the analysed stands. It takes values from 0 to 100, where 0 means identical species composition and 100 completely different species composition (not having even one common species). Detailed formulas necessary to calculate the RID value can are presented below:

$$RID = \frac{100 \cdot D}{D_{\max}}$$

$$D = \sqrt{\sum_i (Y_i - X_i)^2}$$

$$D_{\max} = \sqrt{\sum_i X_i^2 + Y_i^2}$$

where:

i – the number of tree species (or groups of tree species) (i=1,..., n),
Y_i – the reference proportion of tree species i in the total abundance,
X_i – the current proportion of tree species i in the total abundance.

Structural analyzes were carried out on 4 groups of trees, including:

1. all trees (ALL) with DBH≥7 cm,
2. large trees (BIG) with DBH≥35 cm,
3. medium trees (MEDIUM) with DBH 12-34.99 cm,
4. small trees (SMALL) with DBH 7-11.99 cm.

Deadwood volume comparisons. To check which of two predictors, namely forest status (protected, managed) and forest type (PF, BAF, PAF) had influence on observed volume of different kinds of deadwood on sampling plots the robust rank-based ANOVA was used. The analyses were performed using the raov procedure from the Rfit package (Kloke and McKean, 2012) in the R computing environment due to strong right skewed distribution of original data, which could not be successfully transformed to meet the assumptions of classical parametric ANOVA.

Spatial tree distribution. To test the differences in the type of tree distribution in the studied stand categories and protection type algorithm developed by Ramón *et al.* (2016) was used. This algorithm is an extension of the nonparametric one-way ANOVA-like method by Diggle *et al.* (1991) to the two-factor variant. The main goal of this analysis is not the identification of the type of tree distribution (*e.g.* clustered, random, regular) but the falsification of the null hypothesis that particular factor differentiate observed patterns in statistically important manner *e.g.* patterns observed in managed or protected stands differ. It could happen that both types they are clustered but differ in statistically important manner because of different spatial scale of clustering. The second tested hypothesis was that observed pattern was the same in different forest types. Applied methodic allow also test the presence of interactions between factors, *e.g.* it could happen trees are that in majority of analyzed forest type in managed forest trees are more regularly placed than in protected but in one forest type the situation is opposite. The used algorithm at the beginning calculates for each circular sample area the estimator of Ripley's K(r) which represents replications of selected analyzed factor. In the second step the algorithm generates the averaged values of the K function estimator for each level and combination of analyzed factor levels. In the third step algorithm calculates statistics analogous to the sum of squared deviations between the variants (BTSS) like in the classical ANOVA (Ramón *et al.*, 2016). Analyzes were performed using replicatedpp2w library (Ramón *et al.*, 2016) in R environment.

Results

Stand species composition and diameter structure. The species composition of the studied stands was very diverse (14 tree species were found). The dominant tree species was fir, especially in PF forests (Table 1). The other main tree species were pine, alder and beech, but their share in the total number of trees was less than 27%. Spruce, oak, and hornbeam were present in all types of stands, but with a share of less than 10%. The total number of trees ranged from 546 to 847 pieces per ha. The volume of the studied stands was highest in PF protected forests (Table 2) and lowest in BAF protected stands. The proportion of fir in the total stand volume

Table 1.
The share of tree species [%] in the total number of trees in the forest stands of different categories

Stand type	Protection status	Trees density [pcs./ha]	Fir	Pine	Alder	Beech	Spruce	Aspen	Birch	Elm	Hagberry	Hazel	Hornbeam	Oak	Rowan	Sycamore
PF	protected	651	73.27	14.44	1.08	0.46	8.60	–	–	–	–	0.15	0.77	0.46	0.77	–
PF	managed	599	76.13	6.84	0.17	3.34	7.01	–	1	–	0.17	–	4.51	0.83	–	–
PAF	protected	546	50.18	5.86	13.00	0.18	21.98	0.73	5.68	0.92	–	–	0.18	1.1	0.18	–
PAF	managed	560	48.21	8.04	26.96	0.36	12.14	–	2.32	–	–	–	0.36	1.43	0.18	–
BAF	protected	847	51.24	0.59	9.56	11.92	10.15	0.71	4.37	–	–	–	9.68	1.53	–	0.24
BAF	managed	654	43.58	1.07	20.95	5.50	16.82	–	4.43	–	–	0.31	5.20	1.07	0.46	0.61

Table 2.
The share of tree species [%] in the total volume of the forest stands of different categories

Stand type	Protection status	Trees density [pcs./ha]	Fir	Pine	Alder	Beech	Spruce	Aspen	Birch	Elm	Hagberry	Hazel	Hornbeam	Oak	Rowan	Sycamore
PF	managed	316.73	52.83	32.98	0.29	2.80	5.20	0	0.90	0	0	0	3.04	1.96	0	0
PF	protected	496.32	67.21	78.48	2.60	0.10	7.93	0	0	0	0	0	0.20	0.12	0.06	0
PAF	managed	355.85	43.26	34.35	25.74	0.01	7.19	0	0.99	0	0	0	0.23	0.59	0	0
PAF	protected	288.97	38.69	22.44	13.67	0.03	9.24	2.14	3.69	0.66	0	0	0.24	0.45	0	0
BAF	managed	297.96	40.18	3.59	27.92	4.73	9.31	0	2.48	0	0	0.01	2.42	3.11	0.06	0.26
BAF	protected	284.13	33.34	5.52	19.94	16.66	3.87	1.32	3.88	0	0	0.01	2.50	2.57	0	0.10

was lower than in the total number of trees (42.75% on average). The proportion of beech and spruce was less than 10% (except in BAF stands).

The values of Robić dissimilarity index presented (Table 3) suggest that species composition of managed and protected stand was rather similar in all analyzed tree size classes. The RID values for all trees (DBH≥7 cm) showed the similarity of species composition for all studied stands, especially for PAF stands, where the lowest RID index was observed (13.48). The highest compatibility of species composition between managed and protected stands was observed for medium and small trees in PF (9.67 and 9.72, respectively) and for large trees in PAF stands (9.51) what was rather close to theoretical minimum (0). The RID index for medium trees in PAF stands was almost four times higher (38.92) but still far from theoretical maximum (100). We found increasing similarity in species composition for trees of smaller size classes in protected and managed PF stands. In the case of PAF stands, the trend was reversed.

The DBH distribution of all and large trees in protected PF stands was significantly different from that in managed stands (K-S test; $p=0.0350$ and $p=0.0026$, respectively) (Table 3). However, differences between the small and medium tree categories were not significant ($p>0.05$). The number of smallest trees was significantly lower in managed stands than in protected stands (K-S test; $p=0.0237$). However, the DBH distribution of all trees showed significant differences between managed and protected stands (K-S test; $p=0.0001$). The process of continuous regeneration was observed in both protected and managed stands (Fig. 1). The species composition of the studied stands was very diverse (14 tree species were found). The dominant tree species was fir, especially in PF forests (Table 1). The other main tree species were pine, alder and beech, but their share in the total number of trees was less than 27%. Spruce, oak, and hornbeam were present in all types of stands, but with a share of less than 10%. The total number of trees ranged from 546 to 847 stems per ha. The volume of the studied stands was highest in PF protected forests (Table 2) and lowest in BAF protected stands. The proportion of fir in the total stand volume was lower than in the total number of trees (42.75% on average). The proportion of beech and spruce was less than 10% (except in BAF stands).

Deadwood. Summary statistics of deadwood volume at the sample plots are presented in Table 4. The average total deadwood volume was significantly higher in reserves than in managed stands (Robust ANOVA; $p<0.001$). No significant differences were found among the habitat types/stands studied. Total volume of deadwood was highest in protected PF stands. However, the lowest total volume of deadwood was found in managed PAF stands. The volume of standing dead trees

Table 3.

Comparison of species composition and DBH structure of different tree size categories between managed and protected stands based on the Robič Index of Dissimilarity (RID) and Kolmogorov-Smirnov tests ($p<0.05$ means significant differences), respectively

Stand type	DBH≥7 cm	DBH≥35 cm	DBH: 12-35 cm	DBH: 7-12 cm
		Robič Index of Dissimilarity (RID)		
PF	19.00	16.86	9.67	6.72
PAF	13.48	9.51	38.92	29.98
BAF	18.80	24.25	20.60	30.92
		Kolmogorov-Smirnov test		
PF	**0.0320**	**0.0026**	0.3796	0.0528
PAF	0.1753	0.3386	0.8311	**0.0237**
BAF	**<0.0001**	0.0771	0.6158	0.2040

Note: significant differences were bolded

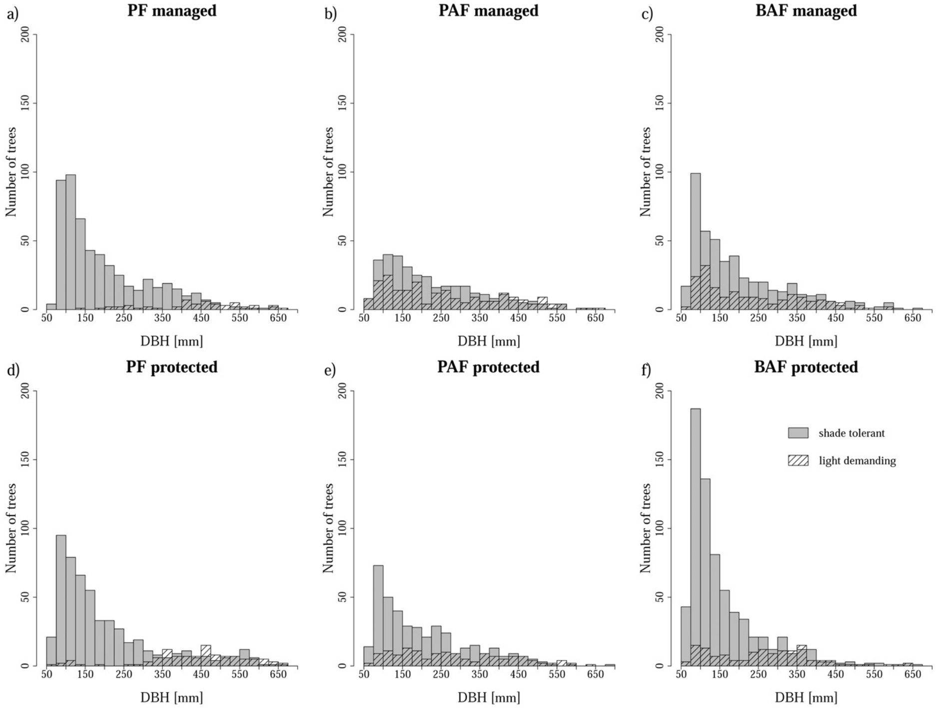

Fig. 1.
Histograms of distribution of light demanding and shade tolerant trees in managed and protected stands

Table 4.
Summary statistics of the deadwood volume observed on sampling plots

Category of deadwood	Forest status	Type	Min volume [m^3/ha]	Median volume [m^3/ha]	Mean volume [m^3/ha]	Max volume [m^3/ha]
Total deadwood	managed	PF	0.13	28.66	40.06	179.24
		PAF	3.31	17.03	25.89	91.22
		BAF	4.60	17.06	37.77	217.41
	protected	PF	2.59	36.91	63.17	276.83
		PAF	7.99	39.17	46.12	138.86
		BAF	7.88	47.28	54.58	126.28
Standing deadwood	managed	PF	0.00	0,00	6.30	45.36
		PAF	0.00	0.00	2.42	24.47
		BAF	0.00	1.97	14.56	77.69
	protected	PF	0.00	3.39	10.68	36.05
		PAF	0.00	0.90	12.11	61.99
		BAF	0.00	6.78	23.43	121.19
Lying deadwood	managed	PF	0.00	14.19	27.54	151.38
		PAF	0.00	7.20	16.79	88.89
		BAF	0.00	5.92	17.63	156.49
	protected	PF	1.24	24.11	47.36	271.86
		PAF	4.09	26.36	29.99	82.23
		BAF	1.99	23.44	27.41	70.77

was significantly different with respect to stand composition (Robust ANOVA; p=0.011) and type of protection (managed vs. protected; Robust ANOVA; p=0.006). The highest volume of dead standing trees was found in protected BAF stands. In managed BAF stands, the volume of dead standing trees was high and even higher than in other managed and protected stands. Most of the dead wood consisted of lying trees (Table 4). The type of protection influenced the amount of lying deadwood (Table 5). Protected stands had significantly more lying deadwood than managed stands (Robust ANOVA; p<0.001). The highest volume of lying trees was observed in protected PF stands, and the lowest in managed PAF stands.

SPATIAL TREE DISTRIBUTION. For the spatial patterns formed by all trees the statistically important difference was observed between forest types but was not observed between different level of protection status (Table 6). The L(r) estimators representing patterns created by trunk positions of trees in different forest stands are presented on Figure 2a. The run of L(r) estimator for PAF forest type is placed distinctly above global average value (solid line) and all its values are above 0. The runs of both estimators for BAF and PF forest types are placed distinctly below solid line and majority of their values are less than 0. Such outcome suggest that trees in PAF forest type have bigger tendency to form groups but in BAF or PF forest types trees are distributed differently in more random or even regular manner. The runs of L(r) estimators representing different protection status ware shown on Figure 2b. Both of them are rather similar and wave around the global average value (depicted with solid line).

NATURAL REGENERATION. Total seedling density depended on forest type (Robust ANOVA; p=0.001). Protection had no effect on seedlings (Robust ANOVA; p>0.05). The interaction of forest type and protection was significant (p=0.0316). The significantly lower seedling density was observed in BAF managed and protected forests, while the highest density was found in PAF managed forests (Fig. 3). Light-demanding seedling density did not depend on forest type

Table 5.

The robust rank-based ANOVA analysis outcome for different deadwood types on sampling plots

Deadwood category	Predictor	DF	RD	Mean RD	F	*p*-value
Total deadwood	type	2	2.401	1.200	0.144	0.866
	forests status	1	127.865	127.865	15.350	**<0.001**
	type:forests status	2	0.799	0.399	0.048	0.953
Lying deadwood	type	2	2.401	1.200	0.144	0.866
	forests status	1	127.865	127.865	15.350	**<0.001**
	type:forests status	2	0.799	0.399	0.048	0.953
Standing deadwood	type	2	23.211	11.606	4.698	**0.011**
	forests status	1	19.594	19.594	7.932	**0.006**
	type:forests status	2	6.665	3.333	1.349	0.264

Note: significant differences were bolded

Table 6.

Results of the non-parametric analysis of the replicated all trees point patterns. BTSS: sum of squared differences. p-value estimated after 1000 samples with replacement (bootstrap) of the residual functions. To calculate the BTSS, L(r) functions estimated from r=0.05 to r=6 m, at intervals of 0.1 m was used

Factor	BTSS	p
Forest type	0.20-0.64	**<0.001**
Protection status	2732.208	**0.9340**
Type – Protection status	0.000	**0.4995**

Note: significant differences were bolded

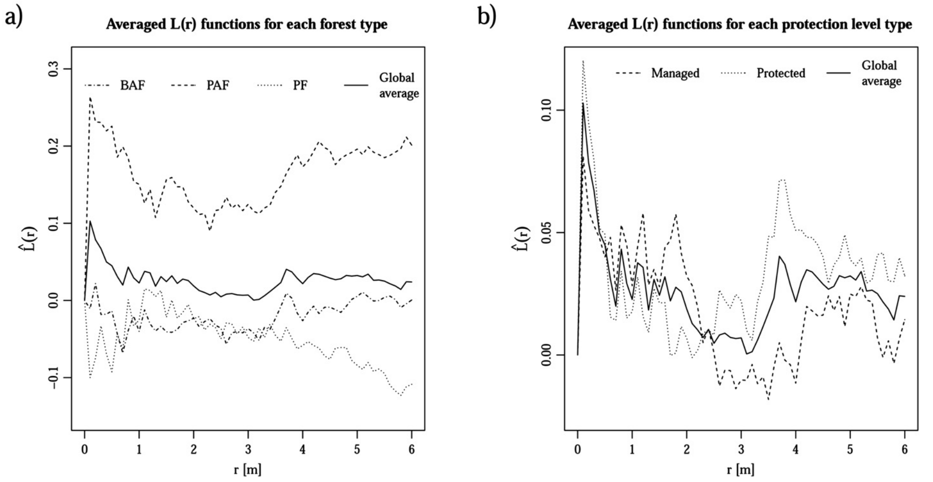

Fig. 2.

Averaged values of L(r) functions ($L(r)=\sqrt{K(r)/\pi}-r$) estimated for the distributions of all tress present on sampling The left panel (a) presents the L-functions for different forest types and the right panel (b) – different forest status

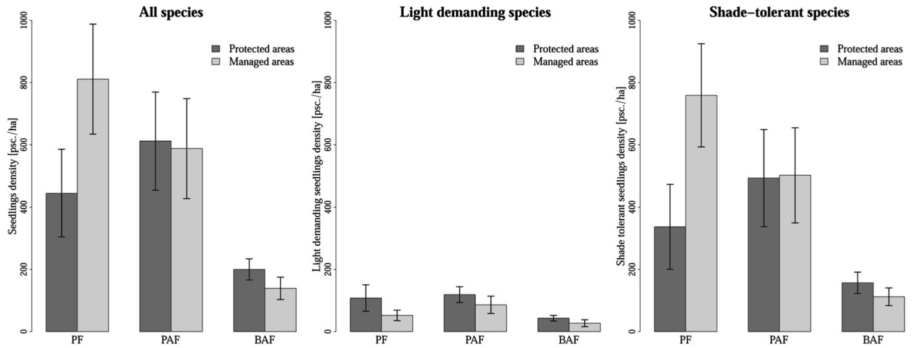

Fig. 3.

Density of seedlings (ind./ha) in studied stands according to stand type and protection

and protection (Robust ANOVA; $p>0.05$), although seedling density was higher in protected stands than in managed stands. The opposite situation was found in shade tolerant species – both tested variables affected their density. The highest density was found in PF managed forests, while BAF stands had the lowest density of seedlings.

The total sapling density depended only on forest type (Robust ANOVA; $p<0.001$). The highest density was found in PAF forests (both managed and protected stands). For light-demanding saplings their density was influenced by forest type and protection (Robust ANOVA; $p=0.000$ and $p=0.011$, respectively). The sapling density of light-demanding trees was significantly higher in protected forests (Fig. 4). The best conditions for light-demanding saplings were found in PAF forests of both protection categories. The only variable that influenced the density of shade-tolerant saplings was forest type (Robust ANOVA; $p=0.0105$). The highest density of shade-tolerant saplings was observed in PAF stands.

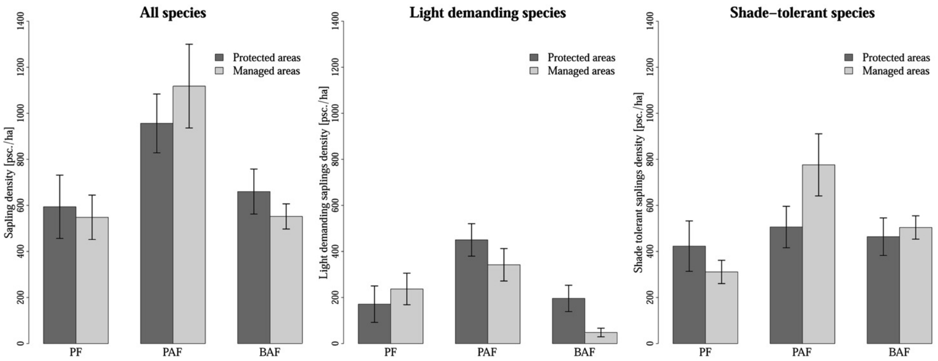

Fig. 4.

Density of saplings (ind./ha) in the studied stands according to stand type and protection

Discussion

STAND STRUCTURE. We focused on differences in stand structure in ageing, protected, or managed mixed silver fir stands. We observed some changes in forest structure, species composition, and proportion of deadwood as a result of past stand development shaped by natural or anthropogenic disturbance events. The most important characteristic of stands we studied (managed and protected) is their diverse species composition, which is the result of spontaneous development processes. If management remains moderate (Dieler *et al.*, 2017) species composition and structure change only slightly between protected and managed forests. The differences between managed and protected stands could be blurred when semi-natural approach is applied. Many protected forests in Central Europe tend to become more homogeneous for at least a few decades without disturbances which create substantial structural heterogeneity (Dieler *et al.*, 2017; Brzeziecki *et al.*, 2020). The mixed fir stands we studied preserve diverse structure even more than many mountain fir dominated stands (Bončina, 2000; Dobrowolska *et al.*, 2017).

Lack of differences between protected and managed stands let to hope that the accuracy can be find in mixed fir stands in other locations.

DEADWOOD. The amount of deadwood in natural forests depends mainly on the forest type, the type of disturbances and management (Lombardi *et al.*, 2008). The average deadwood volume in the studied stands ranged from 34.60 to 54.63 $m^3 \cdot ha^{-1}$ in managed and reserve stands, respectively. Böhl and Brändli (2007) stated that at least 20-40 $m^3 \cdot ha^{-1}$ of deadwood should be present in European forests. However, the amount of deadwood ranges from 5.6 to 33.1 $m^3 \cdot ha^{-1}$, with an average value of 15.8 $m^3 \cdot ha^{-1}$ in European forests, with 9.9 $m^3 \cdot ha^{-1}$ for Poland (Puletti *et al.*, 2019). The deadwood volume in both categories of protection in studied stands was much higher than in the European and Polish forests (Bujoczek *et al.*, 2021). We found that deadwood volume was significantly lower in managed stands. Our result supports the statement that deadwood in managed stands is generally present in rather small amounts compared to natural forests (Vítková *et al.*, 2018). Only 2-30% of deadwood in protected forests normally occurs in managed stands (Jonsson, 2000). The amount of deadwood in protected and managed mixed fir stands was 13-19% and 7-13%, respectively. However, significant amounts of deadwood may also remain in managed forests (Bretz Guby and Dobbertin, 1996). The high amount of deadwood in managed forests is the result of low-intensity forest management. Standing deadwood of larger dimensions is considered particularly important for ecological accounting. In the stands studied, especially in BAF-protected stands, the proportion of standing dead trees was also high because of the death of ash (BAF-managed and reserved stands) and spruce (other stands). A high proportion of deadwood, especially standing dead trees, was observed in mixed beech-dominated forests (Böhl and Brändli, 2007).

Spatial tree distribution. Our spatial analysis is limited to a small spatial scale due to the size of the sample plot (12.62 m radius). The spatial arrangement of trees observed at this scale is mainly the result of interference between canopy trees or by one-sided influences of certain canopy trees on seedlings and saplings below. However, other factors such as site conditions in the stands under study or management practices used may also influence the spatial arrangement of trees. Spatial analysis suggests that management interventions did not influence the spatial arrangement of trees. Salvage cutting in managed stands (*e.g.*, reduced amount of standing deadwood) did not influence tree distribution pattern differently than less intensive interventions in forest reserves applied to promote fir regeneration (Dobrowolska *et al.*, 2020). On the other hand, stand type appeared to have an influence on the point pattern formed by all trees (Fig. 2).The absence of differences in the spatial pattern between managed and protected stands could be attributed to the specific development phase of the studied stands. Both categories of the studied stands (managed and protected) were managed in the past. The quarter century of protection did not make protected stands different because the commercial stands were not intensively managed (no thinning or regeneration cutting). It is likely that the processes of tree mortality and tree recruitment were similar in both stand categories, meaning that extending the rotation age could create a similar structure to a protected stand. All of these similarities may change dramatically if regeneration cutting is initiated in managed stands.

Natural regeneration. Stand variables, mostly stand density and mean stand diameter or forest type, are often the most important predictors of tree regeneration (Käber *et al.*, 2021). Regeneration patterns may be changed by silvicultural systems and the ecological requirements of tree species (Klopčič *et al.*, 2015; Käber *et al.*, 2021). In our study we concentrated on forest status (species composition), management/protection, and light demands of tree species. Stand type influenced the density of shade-tolerant seedlings and light-demanding and shade-tolerant saplings. Only the density of light-demanding seedlings did not depend on stand species composition. Klopčič *et al.* (2015) also found that stand species composition is an important factor in regeneration and recruitment of both light-demanding and shade-tolerant tree species. The impact of stand species composition can be related to regeneration patterns. Light-demanding trees are usually abundant during the establishment phase, while shade-tolerant trees have moderate and periodic establishment, and their survival rate is usually higher (Kimmins, 2004). However, the density of light-demanding seedlings was very low, less than 120 individuals ha^{-1} compared to shade-tolerant seedlings (150-800 individuals ha^{-1}). Initial regeneration density may be less dependent on light (Hasenauer and Kindermann, 2006) and more reliant on factors such as seed availability and presence of competing understory vegetation. If shade-tolerant species established at a site, they usually outcompete early-successional species because they have higher growth-rate and survivorship in low light conditions (Niinemets and Valladares, 2006). However, even within the same survival strategy, the survival rate of species regeneration may differ due to external factors such as forest management. In general, protection had no effect on the total number of seedlings and saplings. We found only a significant effect of protection on the density of shade-tolerant seedlings (in PF stands) and light-demanding saplings (in BAF stands). In PF stands, conditions were better for shade-tolerant trees in managed stands. However, saplings of light-demanding trees were more numerous in BAF-protected stands. Ongoing natural processes, such as ash and spruce dieback, improve light conditions for light-demanding saplings. Although shade-tolerant seedlings, mainly firs, can grow under the canopy of pines (Bartkowicz and Paluch, 2019) and fir for many years (Bončina *et al.*, 2017) passive management can improve the conditions for their establishment and initial growth.

We did not notice any relationship between the density of regeneration and deadwood in managed and protected stands.

Conclusions

Our research indicates that in managed mixed fir stands, passive management limited to low-intensity cutting promotes the creation of differentiated spatial structure and species composition comparable to that of protection. To increase the proportion of complex mixed fir stands, the establishment of reserves is not the only way to achieve the goal. The same effect can be achieved by increasing the age of fir rotation in such stands. The application of single tree selection cuttings in the mixed stands with increased rotation age can help maintain such complex stand structures in the future. The greatest differences between managed and protected stands were found in the amount of deadwood. Protected stands had more deadwood, especially dead standing trees. The total amount of seedlings and saplings was also not affected by protection. Some important differences were found in shade-tolerant seedlings and light-demanding saplings. Stand type was much more important for regeneration than protection. Overall, our results indicate that tree regeneration depends primarily on stand characteristics such as species composition and shade tolerance of individual species in the overstory. Our results suggest that mixed fir stands may play an important role in the Central European lowlands. The mixed fir stands and their (spatial and non-spatial) structures are ideal examples of semi-natural forests that have developed after low-severity disturbance of natural or anthropogenic origin. Such stands with smaller gaps and an intermediate overstory densities clearly favor fir (Stancioiu and O'Hara, 2006; Dănescu *et al.*, 2018).

Authors' contribution

D.D. – conceptualization, methodology, investigation, supervision, writing-original draft; B.P. – investigation, writing-review and editing; L.B. – formal analysis, writing-review and editing.

Conflicts of interest

Authors declare no conflicts of interests.

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STRESZCZENIE

Czy ćwierćwiecze ochrony różnicuje mieszane drzewostany jodłowe podlegające ochronie od drzewostanów gospodarczych na niżu w Polsce

Chociaż przeprowadzono szeroko zakrojone badania struktury lasów (Baran i in. 2020), wiedza o tym, jak gospodarka leśna i ochrona lasów wpływają na lasy jodłowe rosnące na nizinach, jest niewystarczająca. Większość badań koncentrujących się na zmianach w lasach nizinnych pochodzi z północno-zachodniej Europy (Belgia, Anglia). Brakuje informacji na temat bardziej kontynentalnych jej części (Hédl i in. 2010). Celem badania było określenie wpływu gospodarki leśnej lub braku interwencji na strukturę lasu i naturalne odnowienie gatunków drzew światłożądnych i cienioznośnych na podobnych etapach rozwoju drzewostanu. Badania przeprowadzono w Lasach Janowskich w południowo-wschodniej Polsce. Jodła pospolita rośnie jako domieszka w drzewostanach mieszanych, które podzielono na 3 typy: 1) drzewostany sosnowo-jodłowe (PF) rosnące na glebach o zwierciadle wody głębiej niż 1 m pod powierzchnią oraz 2) drzewostany sosnowo-olszowe (PAF) i 3) drzewostany bukowo-olszowe (BAF) rosnące na siedliskach wilgotnych o zwierciadle wody bliżej niż 1 m od powierzchni gleby. Badania przeprowadzono w drzewostanach gospodarczych i chronionych (okres ochrony wynosił od 21 do 34 lat). Dane zebrano na losowo wybranych 120 powierzchniach kołowych. W każdym typie drzewostanów jodłowych założono 40 powierzchni próbnych (20 w drzewostanach chronionych i 20 w drzewostanach gospodarczych). Każda powierzchnia próbna składała się z 3 koncentrycznych okręgów o różnych promieniach

i powierzchniach. Wszystkie naloty i podrosty podzielono na 2 kategorie w oparciu o wymagania świetlne.

Skład gatunkowy badanych drzewostanów był bardzo zróżnicowany: stwierdzono 14 gatunków drzew. Dominującym gatunkiem była jodła, zwłaszcza w lasach PF (tab. 1). Pozostałe główne gatunki drzew to sosna, olsza i buk, ale ich udział w ogólnej liczbie drzew nie przekraczał 27%. Miąższość badanych drzewostanów była najwyższa w lasach chronionych PF (tab. 2), a najniższa w drzewostanach chronionych BAF.

Wartości RID dla wszystkich drzew (DBH≥7 cm) wykazały podobieństwo składu gatunkowego dla wszystkich badanych drzewostanów, zwłaszcza dla drzewostanów PAF, gdzie zaobserwowano najniższy wskaźnik RID (tab. 3). Średnia całkowita objętość martwego drewna była istotnie wyższa w rezerwatach niż w drzewostanach gospodarczych (tab. 4). Rodzaj ochrony miał wpływ na ilość leżącego martwego drewna (tab. 5). W przypadku wzorów przestrzennych tworzonych przez wszystkie drzewa zaobserwowano statystycznie istotną różnicę między typami lasu, ale nie zaobserwowano jej między różnymi poziomami statusu ochrony (tab. 6). Estymatory L(r) reprezentujące wzorce tworzone przez pozycje pni drzew w różnych drzewostanach przedstawiono na ryc. 2a. Przebiegi estymatorów L(r) reprezentujących różne statusy ochrony pokazano na ryc. 2b. Oba są raczej podobne i falują wokół globalnej wartości średniej (przedstawionej linią ciągłą).

Liczebność nalotu zależała od typu lasu. Istotnie niższą liczebność nalotu zaobserwowano w lasach gospodarczych i chronionych BAF, podczas gdy najwyższe zagęszczenie stwierdzono w lasach gospodarczych PAF (ryc. 3).

Badania pokazały, że zróżnicowaną strukturę mieszanych drzewostanów jodłowych można osiągnąć poprzez bierne lub mało intensywne gospodarowanie wspierające naturalne odnowienie. Struktura pierśnic i skład gatunkowy nie różniły się między drzewostanami gospodarczymi i chronionymi (z wyjątkiem pewnych różnic w drzewostanach PF i BAF). Opisane badania wskazują, że w zagospodarowanych drzewostanach jodłowych gospodarka ograniczona do cięć o niskiej intensywności sprzyja tworzeniu zróżnicowanej struktury przestrzennej i składu gatunkowego porównywalnego z drzewostanami chronionymi. Tworzenie rezerwatów nie jest jedynym sposobem zwiększenia udziału mieszanych drzewostanów jodłowych o złożonej strukturze. Ten sam efekt można osiągnąć, zwiększając wiek rębności jodły w takich drzewostanach. Zastosowanie cięć selekcyjnych w drzewostanach mieszanych o zwiększonym wieku rębności może pomóc w utrzymaniu takich drzewostanów w przyszłości. Największe różnice pomiędzy drzewostanami zagospodarowanymi i chronionymi stwierdzono w zakresie ilości martwego drewna. Drzewostany chronione cechowała większa ilość martwego drewna, zwłaszcza martwych drzew stojących. Ochrona nie miała również wpływu na liczebność nalotu i podrostu. Istotne różnice stwierdzono w przypadku cienioznośnych nalotów i światłożądnych podrostów. Typ drzewostanu miał większe znaczenie dla odnowienia niż ochrona. Ogólnie rzecz biorąc, wyniki wskazują, że odnowienie zależy przede wszystkim od cech drzewostanu, takich jak skład gatunkowy i tolerancja na zacienienie poszczególnych gatunków w drzewostanie. Mieszane drzewostany jodłowe mogą odgrywać ważną rolę na nizinach środkowoeuropejskich. Są one idealnymi przykładami lasów półnaturalnych, które powstały po zaburzeniach w małej skali pochodzenia naturalnego lub antropogenicznego. Drzewostany z małymi lukami i umiarkowanym zwarciem wyraźnie faworyzują jodłę (Stancioiu i O'Hara 2006; Dănescu i in. 2018).