

Changes in Altitudinal Vegetation Patterns in Fir Forests of Beskid Niski Mountains Caused by Change in Forest Cover

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Abstract

The species richness pattern exhibits a strong altitudinal dependence which may be altered under the influence of land use-related disturbances. The Beskid Niski Mountains are part of the northern Carpathian Mountains – an area that saw a large-scale relocation of certain ethnic groups after World War II. The subsequent rapid decline in the human population level was the main factor shaping the environment in this area, and contributed to a rapid increase in the forest area, also introducing changes in its functioning. The increase in the forest area was not evenly distributed, showing the largest values at higher locations. The present study is focused on changes in the species richness of the Carpathian fir forests along the altitudinal gradient, in relation to socio-economical transformations. The changes indicated an overall decrease in species richness, especially at higher locations. The main reason for these changes seemed to be forest management-related, causing an increase in the share of blackberry, fern and grass species, as well as the disappearance of species diagnostic of the ancient forests, which led to homogenization of vegetation. The increase in the mountain forest area has proven to be insufficient to secure the species richness of forests.

Keywords: land use change, altitudinal pattern, fir forests, change in forest herbs

Introduction

The factors affecting species richness in mountainous ecosystems operate in accordance with an altitudinal gradient. Relationships between species richness and altitude exhibit two main patterns. The first one assumes a gradual decline in species richness with altitude [1], the other assumes a peak in the species richness at heights located in the middle part of the altitudinal gradient [2, 3]. The main mechanism responsible for the altitudinal changes in species richness is attributed to the altitudinal dependence of productivity. An increase in productivity may cause a

gradual increase in species richness [4], or may result in a decline after reaching a point where productivity exceeds its mean value [5].

Important factors affecting species richness of the Central European mountain forests are disturbances related to human activity, amongst which there is a distinction between those with a direct effect (forest management: felling, fertilization, forest crops; non-forest use of the forest land: cattle grazing, leaf litter and brushwood collection) and an indirect effect (climatic disturbances, climate warming, excess of herbivores, vegetation fragmentation, air pollution). Amongst these, forest management appears to be the main factor. It has had a major influence on the area and species composition of forests since medieval times. Inappropriate forest management in the 19th and in the

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beginning of the 20th century (complete clearing, afforestation discrepant with habitat conditions) lead to a major decrease in forest area and substitution of the large proportion of the deciduous forests with spruce monocultures [6, 7]. After World War II, mountain forests within Polish territory were still suffering major damage despite afforestation and an increase in forest area. Excessive wood acquirement, and the too slow restructurisation of the artificial forest stands, air pollution, harsh climatic conditions and parasitic insect and fungal plagues also contributed to the damages. Beneficial changes in forestry have occurred after the political breakdown in 1989 and 1990. The principles of balanced management, emphasizing the protective and recreational function of the forest. The value of the multi-species forest has been acknowledged for forest clearing and a requirement for immediate afforestation has been introduced [7].

The change in land use is also considered a disturbance and could be exemplified by a marked decline in agricultural area, often involving agricultural area abandonment, following the socio-economic transformations in the second half of the 20th century. In mountainous ecosystems, such phenomenon primarily affects the less accessible and less fertile areas. Agriculturally unused areas are most frequently occupied by the forest (as a result of succession or afforestation). Southeastern Poland (Beskid Niski and Bieszczady Mountains) is a region exhibiting a significant increase in forest area related to the Lemko population relocation carried out after World War II, which was an additional factor facilitating depopulation and abandonment of agricultural areas. It resulted in a substantial increase in forest area, making this type of change the dominant change in land use. In the middle of the 19th century, the average forest cover of Beskid Niski Mts. was 25%, and it did not change significantly until the 1930s. Political resettlement of ethnic groups carried out in 1949-56 resulted in a significant depopulation of human settlements (by 50%) and land abandonment. Abandoned agricultural land was then afforested, increasing the present forest cover to over 50% [8, 9]. The share and the increase of the forest area differed, depending on the altitude and part of Beskid Niski Mts [10, 11]. At the lower locations of the Polish part of Beskid Niski Mts (up to 550 m a.s.l.) it was ca. 25 and increased to over 50%, at higher (over 550 m a.s.l.) it was ca. 35 and increased to ca. 80% [9]. This variation accounts for the uneven rate of the recolonization and human population growth, and a decrease in the importance of agriculture, mainly constrained to the most accessible and valuable areas. The increase in the forest area, facilitating connectivity in a previously fragmented forest, coupled with a decline in non-forest use of the forest land, should be beneficial for the forest ecosystem [12]. On the other hand, a sudden change in land use was a factor introducing a strong disturbance and must have strongly affected the functioning of the existing forest ecosystem. Thus, it should be expected that the greatest transformations in vegetation, that are taking place as a consequence of the change in land use, should manifest themselves at higher locations.

Fir-dominated forests are particularly sensitive to human activity-related disturbances. At the same time, they make up a large proportion (ca. 30%) of the forest area in the Polish Carpathians [13]. The species richness patterns along the altitudinal gradient in the fir forests from the early post-resettlement period (1960s) are known thanks to the detailed phytosociological studies from the Beskid Niski Mts [14-16]. It is interesting how the altitudinal pattern of species richness of the Carpathian fir forest changes, depending on the deepening trend in the change of land use over the past decades. Do the changes that are currently taking place have a beneficial effect on the species richness of the fir forests? The knowledge of the changes in species richness, providing evidence of the naturalness of ancient forest phytocenoses, is particularly important [17].

In the present study, an attempt was made to answer the following questions: Are there any changes in the altitudinal patterns of the species richness of the Carpathian fir forests, occurring due to the change in land use and an increase in forest area? If so, what is their extent and direction? Are there any differences in the species richness pattern changes between the lower and higher locations? Are the current changes in land use and an increase in the forest area sufficient factors protecting the species richness of the Carpathian forests?

Study Area

The study was conducted in fir-dominated production forests in the upper Biała Dunajcowa River basin, northern Carpathians. It covered an area of about 500 km² (49°24'-49°39'N, 20°52'-21°04'E) with the altitude between about 350 m a.s.l. in the north and 997 m a.s.l. in the south. The mean annual air temperature of the area studied varies between 6.9°C in lower locations and 4.4°C in the higher portions of the mountains [18]. Mean annual rainfall is ca. 1000 mm [19]. Dominant soils include typical and acid brown soils [20, 21]. The fir forests represent primarily fertile forests from the order *Fagion sylvaticae* [22].

Experimental Procedures

Relevés of patches with at least 50% fir density in the tree layer were selected from the source materials [14-16]. 134 relevés made in the 1960s and containing additional data on exposure, inclination and elevation were obtained. However, they did not provide exact co-ordinates of the locations, only an approximate description (e.g. mountain name, slope exposition). In 1997-99, after incorporation of the data on locations available, the researchers managed to find and repeat 58 relevés taken across the whole study area at different altitudinal ranges. The 6-point Braun-Blanquet scale [23] was used in order to estimate the quantitative share of the species. The obtained "new relevés" were paired with the "old relevés" and analyzed.

In the analysis of source materials, data on species growing outside the basic patch as well as the taxa of

indefinite species affinity (*Rubus* sp., *Alchemilla* sp.) were omitted. The 12-point cover-abundance scale applied in their preparation was converted into the 6-point Braun-Blanquet scale [23]: r,+/+; 1/1; 2,3/2; 4,5/3; 6,7/4; 8,9,10/5. Analysis regarded vascular plants only. A total of 227 species was obtained (including 34 noted in two or three layers) and used for analysis (183 and 171 species in the 1960s and 1990s, respectively).

In order to obtain an overall picture of the changes, PCA analysis was performed for qualitative and quantitative data, with and without the effect of the species dominating the floor-layer *Rubus hirtus*. Cover-abundance values, according to the Braun-Blanquet scale transformed into the 1-9 scale, were used for calculations [24].

In order to determine changes in the altitudinal patterns of the species richness, a linear correlation of the number of

species and altitude was performed for the relevés from the '60's and '90's. To exclude the effects of the stand composition on the species richness changes, species from the understorey (b) and forest floor layers (c) were analyzed. Assuming that ancient forest species are good indicators of transformations in the forest floor layer, 54 "ancient forest" species [17, 25] were analyzed separately.

In order to detect changes in the occurrence of particular species, 2x2 chi² tables, taking into account Yates's corrections for the observed values of less than 10, were used.

In order to compare the species richness changes depending on the intensity of the growth dynamics of the forest area, on additional analysis was performed for two altitudinal ranges: 350-550 (n=22) and 550-800 m a.s.l. (n=36). In this study, the former range is called "lower locations," and the latter "higher locations."

To test if there were any significant changes in the paired relevés, the Wilcoxon test for paired samples was used.

Names of vascular plants were taken after [26]. *Senecio nemorensis* according to [27].

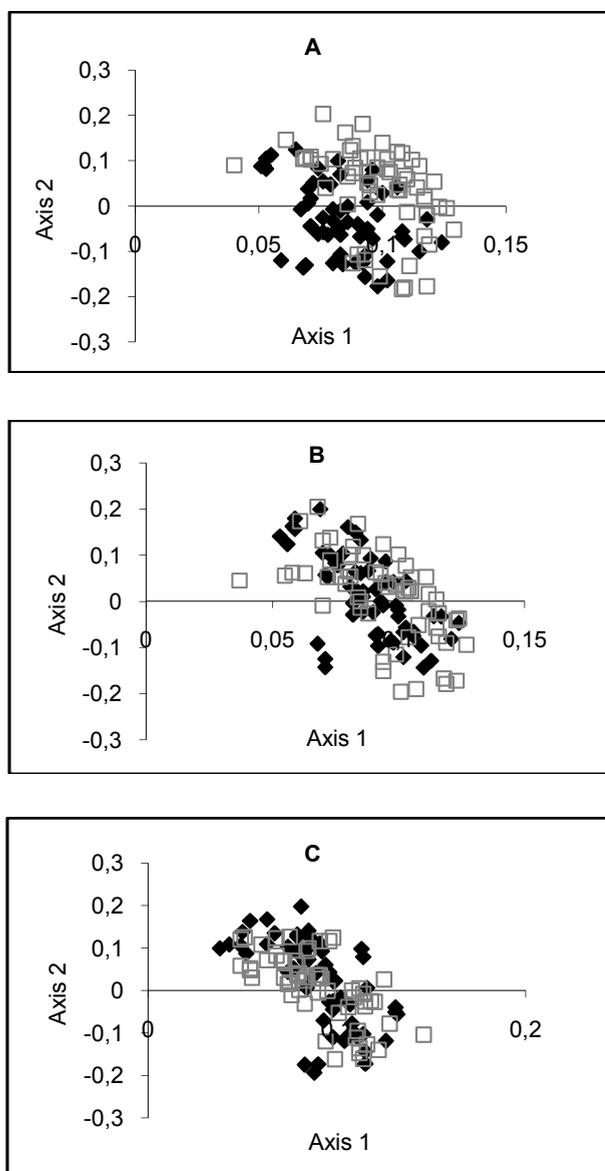


Fig. 1. PCA with 58 relevé pairs. (A) quantitative data, (B) quantitative data without the share of *Rubus hirtus*, (C) qualitative data. Dark markings - relevés from the 1960s, light - relevés from the 1990s.

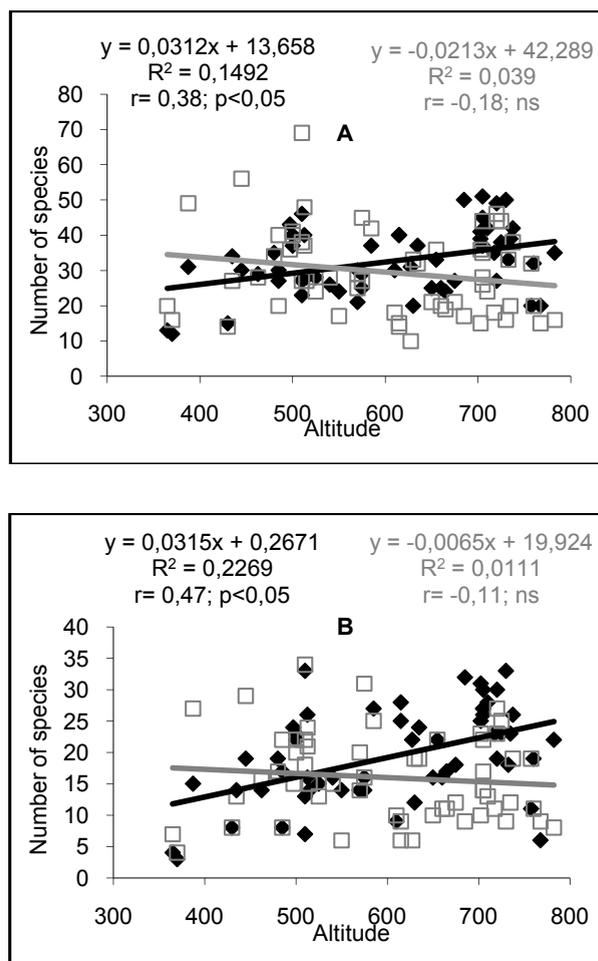


Fig. 2. Correlation of species richness and altitude. (A) all 227 species, (B) 86 ancient forest species. Dark markings - relevés from the 1960s, light - relevés from the 1990s.

Table 1. Wilcoxon test results.

		Valid pairs	T	Z	p-value
W	Number of species	58	603.5	1.77	ns
L		22	82.5	1.15	ns
H		36	137.5	2.91	**
W	Number of ancient species	58	458.5	2.45	*
L		22	91.5	0.50	ns
H		36	105.5	3.28	**
W	<i>Rubus hirtus</i> (abundance)	58	103	5.34	****
L		22	42	2.13	*
H		36	8	4.87	****
	Average altitude of the ancient species appearance	114	1891.5	3.69	***
	Average altitude of species appearance	56	196.5	4.49	****

Significance levels accepted at: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; **** $p < 0.0001$. The analysis was performed for the whole gradient (W) as well as for lower (L) and higher (H) locations, separately.
ns - not significant

Results

Overall Picture of Changes

The average species richness of the fir forests decreased ($\bar{x} = 32.5$; $SD = 91$ and $\bar{x} = 29.5$; $SD = 12.2$ in the '60's and '90's, respectively). However, these changes were not statistically significant. There was a significant decrease in the number of ancient forest species ($\bar{x} = 19.2$; $SD = 7.5$ and $\bar{x} = 16$; $SD = 7$ in the '60's and '90's, respectively) (Table 1). The PCA analysis clearly demonstrated changes in vegetation, which were largely attributed to the changes in the quantitative share of *Rubus hirtus* (Fig. 1). Lower frequency of occurrence was found in 11% of the species and an increased frequency in 7% of species (Table 2). There was no change observed for 187 species. Ancient forest species accounted for over half of the lower-frequency species (58%). 36% of them constituted fast-dispersing anemochorous species, and the slowest dispersing myrmecochorous and barochorous species accounted for 49%. There was a marked decline amongst the remaining species associated with higher thinning sites (*Veronica officinalis*, *Geranium robertianum*, *Fragaria vesca*, *Chamaenerion angustifolium* and *Salix caprea* b).

Ancient forest species represented almost half of the higher-frequency species (44%), amongst which anemochorous species (mainly ferns *Dryopteris dilatata*, *Athyrium filix-femina* and *Gymnocarpium dryopteris*) made up 43%, but myrmecochorous and barochorous species did not occur. Attention was drawn by the higher frequency of deciduous trees in the understorey and seedling layers (*Acer pseudoplatanus* b, c, *Fraxinus excelsior* b, c, *Fagus sylvatica* b, *Sorbus aucuparia* b and *Corylus avellana* b) as well as of *Rubus hirtus* and graminoids more resistant to mechanical damage (*Festuca gigantea*, *Carex pallescens*, *Brachypodium sylvaticum*, *Deschampsia caespitosa*).

Changes in the Altitudinal Pattern of Species Richness

In the '60's, species richness was increasing with altitude (Fig. 2). At the end of the 20th century, no significant relationship between altitude and species richness was found. At the same time, there was a marked decrease in the mean altitude of species occurrence - by 30 m on average ($\bar{x} = 598$ and 570; $SD = 59$ and 54 for all species, $\bar{x} = 595$ and 565; $SD = 76$ and 77 for the ancient forest species in the '60's and '90's, respectively). The intersection of the regression curves on the diagrams of correlation between the number of species and altitude marked the "boundary range" of the altitude (500-550 m) for two opposite trends (Fig. 2). Below the boundary, species richness increased visually, but the changes were not statistically significant. The frequency of 9 species increased, over half of them being easily dispersing tree species (*Acer pseudoplatanus* b, c, *Fraxinus excelsior* b, *Corylus avellana* b) and ferns. The frequency of 9 species, of which 90% were representing ancient forest species, declined.

The number of species on relevés decreased with altitude as compared to the past situation (Table 1, Fig. 2). At higher locations, the frequency of occurrence of 24 species, out of which 79% were ancient forest species, declined significantly. 32% of the ancient forest species consisted of slowly dispersing basidio- and myrmecochorous species. Amongst the lower-frequency species, attention was drawn by the ancient forest species retreating from the higher locations, with a concurrent absence of changes in the lower locations (*Symphytum cordatum*, *Ranunculus lanuginosus*, *Chrysosplenium alternifolium*, *Circaea alpina*, *Dryopteris carthusiana*, *Euphorbia dulcis*, *Paris quadrifolia*). The frequency of 11 species - of which 36% were ancient forest species, mostly represented by ferns and graminoids - increased. In both altitude ranges, the quantitative share of

Table 2. Chi² test results.

Species		Lower locations	Higher locations	Whole gradient
Decrease				
<i>Hieracium murorum</i>	An2	13.8***	23.7****	39.9****
<i>Galium rotundifolium</i>	Ep	12.7***	15.1****	29.8****
<i>Fragaria vesca</i>		ns	27.6****	27.2****
<i>Mycelis muralis</i>	An2	6.3*	20.2****	25.8****
<i>Cardamine impatiens</i>		ns	12.1***	17.6****
<i>Sanicula europaea</i>	Ep	5.1*	6.7**	13.3***
<i>Ajuga reptans</i>	M	ns	14.1***	12.7***
<i>Viola reichenbachiana</i>	M	4.6*	6.1*	12.6***
<i>Cerasus avium c</i>		7.5**	ns	11.3***
<i>Chamaenerion angustifolium</i>		ns	6.9**	11.3***
<i>Carex digitata</i>	M	ns	6.0*	10.1**
<i>Cruciata glabra</i>		6.1*	ns	8.9**
<i>Dentaria glandulosa</i>	B	ns	12.5***	8.3**
<i>Orthilia secunda</i>	An1	ns	ns	7.7**
<i>Salix caprea b</i>		ns	ns	6.6*
<i>Moehringia trinervia</i>	M	ns	12.5****	6.3*
<i>Veronica officinalis</i>		ns	ns	6.0*
<i>Veronica montana</i>	M	ns	7.1**	5.8*
<i>Luzula pilosa</i>	M	5.5*	ns	5.5*
<i>Crepis paludosa</i>		ns	5.7*	5.4*
<i>Actaea spicata</i>	En	ns	5.7*	4.6*
<i>Phyteuma spicatum</i>	An2	ns	4.6*	4.4*
<i>Geranium robertianum</i>			9.9**	4.3*
<i>Lonicera nigra b</i>		ns	ns	4.3*
<i>Solidago virgaurea</i>	An2	4.8*	ns	ns
<i>Circaea alpina</i>	Ep	ns	6.4*	ns
<i>Chrysosplenium alternifolium</i>	Hy	ns	5.7*	ns
<i>Ranunculus lanuginosus</i>	Ep	ns	5.7*	ns
<i>Dryopteris carthusiana</i>	An1	ns	5.0*	ns
<i>Paris quadrifolia</i>	En	ns	4.7*	ns
<i>Symphytum cordatum</i>	unspecified	ns	4.3*	ns
<i>Euphorbia dulcis</i>	M	ns	3.9*	ns
Increase				
<i>Acer pseudoplatanus c</i>		12.7***	16.5****	31.1****
<i>Dryopteris dilatata</i>	An1	13.8***	13.0***	28.1****
<i>Sorbus aucuparia b</i>		ns	16.4****	18.9****
<i>Fagus sylvatica b</i>		ns	20.0****	13.7***

Significance levels accepted at: * p<0.05; ** p<0.01; *** p<0.001; **** P< 0.0001. Dispersal methods given for species diagnostic of the ancient forest: An-anemochorous, Ep-epizoochorous, M-myrmecochorous, B-barochorous, En-endozoochorous, Hy-hydrochorous, Au-autochorous.

ns - not significant

Table 2. Continued

<i>Corylus avellana</i> b	En	7.4**	ns	11.5***
<i>Deschampsia caespitosa</i>		ns	3.9*	7.7**
<i>Fraxinus excelsior</i> c		ns	ns	7.7**
<i>Athyrium filix-femina</i>	An1	ns	7.8**	7.3**
<i>Gymnocarpium dryopteris</i>	An1	7.8**	ns	6.9**
<i>Fraxinus excelsior</i> b		4.8*	ns	6.4*
<i>Festuca gigantea</i>	Ep	ns	3.9*	6.0*
<i>Rubus hirtus</i>		ns	6.6*	5.9*
<i>Carex pallescens</i>		ns	ns	4.4*
<i>Brachypodium sylvaticum</i>	Ep	ns	ns	4.3*
<i>Maianthemum bifolium</i>	En	ns	5.0*	4.3*
<i>Acer pseudoplatanus</i> b		4.8*	ns	4.0*
<i>Caltha palustris</i>		4.8*	ns	ns
<i>Stellaria nemorum</i>	An2	6.3*	ns	ns
<i>Impatiens noli-tangere</i>	Au	8.0**	ns	ns
<i>Fagus sylvatica</i> c		ns	4.6*	ns
<i>Senecio nemorensis</i>		ns	4.5*	ns

Rubus hirtus increased significantly. But the greatest changes, both qualitative and quantitative, were observed at higher locations (Table 1, 2).

Discussion of the Results

An attempt to assess the changes in vegetation was based on a comparison with archival phytosociological relevés. Such an approach is frequently applied for long-term investigations of vegetation dynamics [28]. However, such analysis faces a risk of bias, resulting especially from the subjective estimation of the species cover, omission of some species, selectively chosen patch documentation, absence of the exact locations of the repeated relevés and differences in the relevés areas [29, 30]. The absence of the exact locations of patches from the '60's does not allow for an unequivocal determination of the transformations in particular vegetation patches. The number of the species recorded increases with the plot size. Hence, in the presented comparison one should also take into account the effect of the size of investigated areas (100 and 200 m² in the '60s and '90s, respectively). In spite of this fact (that does not significantly affect the results of the ordination analysis [31]), the analysis of the species showing a decline in frequency of occurrence (disappearance) should be considered to be the most reliable.

In the 1960's-1990's, the altitudinal pattern of species richness changed, and the way and pace of these alterations

were related to changes in land use. In consequence of the resettlement operation, the agricultural and forest landscape was changed into a more uniform forest landscape [11]. The largest changes in species richness were found in the less accessible, higher situated and depopulated areas exhibiting a large increase in forest area. Much smaller changes were found in more accessible and still populated areas with an average increase in forest area growth. Several separate, partially related pathways of the species richness changes were found: a decrease in the mean altitude of species occurrence, a decline in species richness, especially in species diagnostic of the ancient forests, the growing role of blackberry, ferns and graminoids and an increasing share of deciduous tree species.

The ongoing process of afforestation of agricultural land resulted in lowering the lower boundary of the forest [8]. At the same time, the increasing area and connectivity of the forest, as well as an improvement of the species and age structure of the tree stands, contributed to an increase in the diversity of forest habitats. These factors could have favoured the observed lowering of the mean altitude of species occurrence by 30 m.

In spite of the progressing naturalization of the environment, human pressure continues to negatively affect forest species richness, with forest management acting as the main factor shaping it [32]. In the studied forests from the '90s, a decline in species richness can be observed, especially in species diagnostic of the ancient forests. In particular, myrmecochorous and barochorous species are disappearing,

whereas anemochorous species (mainly ferns) are increasing their frequency of occurrence. The observed lack of dependence of the species richness and altitude may be evidence of the progressing homogenisation of vegetation. A similar trend is commonly observed in exploited forest vegetation [33-35]. It leads to a decline in species diversity and homogenization of the vegetation, blurring the differences between habitats [34-36]. The undergoing changes are associated with individual traits of plants related to the rate of their dispersal and tolerance to the changing environment [37]. Slowly dispersing species, mostly representing ancient forest species, proved to be particularly sensitive to changes in environmental conditions [12].

In spite of the constant increase in the forest area, the spatial pattern of the Carpathian forests is less and less compact. The construction of new roads, tourist infrastructure and forest management all contribute to a decrease of the core forest and an increase of patch and perforated forest [38]. The thinned sites which are formed are occupied by large numbers of *Rubus hirtus*, accompanied primarily by ferns [39]. The tolerance to shading of the blackberry allows it to persist long in the forest floor layer. PCA analysis showed that the growing share of this species affects to a large extent changes taking place in the vegetation of the fir forests (Fig. 1). Due to their size, blackberry together with ferns win the fight over access to the resource, displacing smaller forest species and significantly inhibiting their dispersal. Ferns together with graminoids also make up a group whose share increases as a result of intensive deer grazing [34, 40]. Additionally, graminoids, which possess basal meristems, may regenerate shoots damaged by grazing animals or during forest management treatments. Since the '80s, deer populations in the Carpathian forests have been declining [41], and it should be recognized that the main reason for an increase in the abundance of fern and grass species in fir forests is forest management with the partial-cutting system. Plant traits (especially growth form) of blackberries, ferns and graminoids allow them to widely disperse in the conditions altered by forest management, leading to the deepening of homogenization of the vegetation [34].

The increasing share of deciduous tree species can be attributed to at least two processes: an increase in thinned sites associated with forest management and gap formation in the tree stands, which enables colonization by the post-pioneer species – sycamore and ash [42, 43]. The opening of the tree stands providing more access to light also favours beech and rowan restoration [44, 45]. On the other hand, the increased share of deciduous tree species may be a sign of regeneration of pure fir stands or stands with a strong prevalence of silver fir [46]. For example, the share of beech stands in the Forest Experimental Station in Krynica (Beskid Niski Mts) in the years 1966-1998 increased from ca. 8% to 20%. But their previous share (in the '50s) was estimated at 20% [47]. Because deciduous tree species beneficially affect forest phytocenoses, their larger share may also result from the support of their restoration under forest management. The increasing share of the deciduous tree species in coniferous stands indirectly affects

changes in the forest floor layer. In the forest floor, the share of the species preferring more acidified sites is declining in favour of mesotrophic species [48], which may contribute to a decline in species richness.

Conclusions

The study showed changes in the altitudinal patterns of species richness of the Carpathian fir forests, of which extent was increasing with altitude. Overall, there was a decrease in species richness, particularly noticeable at higher locations, despite a large increase in forest area. The main reason for the changes appeared to be related to forest management, causing an increase in the share of blackberry, fern and graminoid species as well as the disappearance of species diagnostic of the ancient forests. It seems that in spite of an increase in forest area, the effect of forest management and other forms of land use would result in homogenization of the vegetation, causing a lack of variation in species richness along the altitudinal gradient. An increase in the mountain forest area is not a sufficient factor for securing the species richness of fir forests. In spite of the continued dominance of fir, the share of deciduous trees will be growing, with a possibly unfavourable effect on species richness.

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