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Influence of pH, nitrogen and sulphur deposition on species composition of lowland and montane coniferous communities in the Tatrzański and Słowiński National Parks, Poland

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Nitrogen and sulphur deposition is considered as a negative factor for biodiversity, usually leading to changes in species composition and structure of plant communities, and ultimately to the impoverishment of biodiversity. In this study we investigated the variation over time (2001, 2006, 2011) in species composition and structure of the understory vegetation at varying levels of sulphur and nitrogen deposition in two conifer plantations (>100 year-old) growing in different climate areas of Poland (Scots pine at the Słowiński National Park, northern seaside; Norway spruce at the Tatrzański National Park, southern mountains). The structure of the floor vegetation at both sites changed markedly during the studied decade, as clearly confirmed by principal component analysis. Among the environmental variables analyzed (NH_4^+, NO_3^-, SO_4^{2-}, pH in the throughfall and in soil solution sampled at two different depths), only nitrates were non-significantly correlated with PC axes. The results confirmed the negative effects of the concentration of both elements on undergrowth and tree recruitment in the coastal stand (*Empetro nigri-Pinetum*). On the other hand, in the mountain stand (*Abieti-Piceetum*) we observed an increase over time of nitrophilous species typical of the beech forest, which represent the natural vegetation of this area, suggesting a gradual natural restoration of the native vegetation in the long run.

Keywords: Nitrogen Deposition, Sulphur Deposition, Climatic Changes, Coniferous Communities, Biodiversity

Introduction

Most European forests have lost their primary character. Exploitation of tree stands, both deciduous on fertile soils and coniferous on poor soils, began with the intensive development of agriculture and the industrial revolution which took place at the beginning of the 19th century. Although the poor soils that support the growth of coniferous trees were less valuable for agricultural production, they provided precious raw material and fuel needed in industry. Past management reduced the proportion of natural broad-leaved forests from 66% to 33% of the forested area in Central Europe (Kenk & Guehne 2001). Later, deforested areas were mostly planted using fast growing conifers (mainly Norway spruce and Scots pine), regardless of whether their soil requirements corresponded to the potential habitat. The results of this more than 100-year-old process of planting Scots pine trees in the lowlands and Norway spruce in the mountains are extensive, even-aged, monospecific stands very sensitive to snow and wind damage (Kenk & Guehne 2001), pollutants (NO_x and SO_2), or outbreaks of pests and fungal infections (Vogt et al. 1994, Orzel & Socha 2000, Karolewski et al. 2005). Currently, such plantations are subject to an extensive dieback across all Central Europe and to adverse changes in the habitat, especially these located on fertile deciduous forest sites.

Progress in the field of environmental protection helped to reduce the inflow of pollutants, but their concentration in the soil, along with the impact of climatic factors, still have an effect on the plant composition of forest communities. In Poland, the dieback of conifer forests in vast mountain areas had all features of ecological disaster and led to the hydrogeological instability in the drainage basins of the main Polish rivers (Mazurski 1986, Stachurski et al. 1994, Holeksa 1998, Bytnerowicz et al. 1999, Jadczyk 2009). Currently, the restoration of forests with tree species consistent with the local potential vegetation has become a pressing need in many degraded areas. Recreating the natural structure and desirable species composition in degraded forests is referred to as rehabilitation, which may be based on natural succession and/or anthropogenic methods like planting, partial overstory removal, etc. (Kenk & Guehne 2001, Stanturf et al. 2014). Rehabilitation of degraded forests can be realized by transformation or conversion (Stanturf 2005). The first approach consists in the anthropogenic restoration of the more desirable forest structure while maintaining its continuity (O'Hara & Ramage 2013); the latter is based on natural or artificial regeneration of the forest after the removal of damaged trees (Hansen & Spiecker 2005).

The deposition of nitrogen and sulphur has a great relevance for the functioning of the whole forest ecosystem at various levels. Overrun of critical loads affects soil processes (nitrification, mineralisation, a-

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cidification and decomposition of organic matter), individual trees (photosynthesis, drought tolerance, regeneration, susceptibility to pest and pathogens) and biodiversity (lichens, fungi, bryophytes, herbs and fauna). In soils poor in nitrogen its input can stimulate the growth of roots and stems, whereas in other types of soil it may clearly inhibit it. The increased N deposition may change the nutrition of trees by increasing the N concentration in leaves and/or decreasing the uptake of other nutrients, like Mg, K or P by trees and herbs (Bobbink & Hettelingh 2011). It may also reduce the microbial biomass of the ecosystem (Treseder 2008). Many observations showed an increase in the abundance of nitrophilous species in forests as N deposition increases (Bobbink & Hettelingh 2011). Herb species in deciduous forests respond to N deposition by, among others, higher growth rates of some nitrophilous species (Falkengren-Grerup & Diekmann 2003), but in oligotrophic pine forests dominated by bryophytes, lichens, and heather, the undergrowth dramatically changes and is replaced by common grasses (mostly *Deschampsia flexuosa* and *Festuca ovina*), thus significantly decreasing the understory diversity of these forests (Bobbink & Hettelingh 2011). It is generally accepted that the impact of pollutants like nitrogen and sulphur oxides on vegetation is negative, leading to habitat nitrification and to the decrease of soil pH; this entails the simplification of species composition in plant communities and have a negative impact on biodiversity (Hülber et al. 2008, Bobbink et al. 2010, Dirnböck et al. 2014).

The aim of this study was to assess the direction of changes in species composition and structure of forest floor at varying levels of sulphur and nitrogen deposition in two protected coniferous forests growing in different climate areas in Poland. Our objective was to disentangle the role of former land-use, habitat characteristics and the potential plant cover on the composition and structure of the plant community.

Materials and methods

Study sites

Słowiński National Park

The area is located on fixed dunes with gentle slopes (about 10°) and SW aspect in the Baltic coast at an altitude of 5 m a.s.l. The tree stand is composed of 110-year-old Scots pine trees planted in the phytocoenosis *Empetro nigri-Pinetum* (Libb. et Siss. 1939 n.n.) Wojt. 1964, which is a typical habitat for pine. The main diagnostic species, *Empetrum nigrum,* and the combination of species characteristic of this association were present from the beginning of the survey.

Tatrzański National Park

The area is located in the lower montane zone at 1140 m a.s.l. on a 40° slope with N aspect. The tree stand is an approximately 140-year-old Norway spruce monoculture that was planted in the habitat of a fertile beech wood (*Dentario glandulosae-Fagetum* W. Mat 1964 ex Guzikowa et Kornas 1969), which later evolved into *Abieti-Piceetum montanum* Szaf., Pawl. et Kulcz. 1923 em. J. Mat. 1978. The beech did not appear in the understory until recently, but species of the class *Querco-Fagetea* have been present since the beginning of the study, as expected based on the potential vegetation of this habitat (Matuszkiewicz et al. 1995).

Data collection

The survey was conducted in two permanent plots (0.25 ha) established in 2001, according to the Programme Coordinating Centres (1994), which are representative of the old spruce monocultures in the mountains (Tatrzański NP) and in the coastal pine forest (Słowiński NP). The observations were carried out in three years (2001, 2006 and 2011). The factors investigated in the study included species composition, vegetation cover, throughfall, soil solution and climatic parameters.

Each plot was subdivided in one hundred squares of area 25 m^2 (subplots) and surveyed to estimate the coverage of each vascular plant species in all layers. The assessment was made for each species according to the following scale: 1%, 5%, 10%, 20% up to 100%. This enabled detecting even small changes in the coverage of particular species.

The habitat preferences of the species in relation to soil pH (F) and the nitrogen concentration (N) were assessed based on the environmental indices of Ellenberg et al. (2001). The names of syntaxa and syntaxonomic characteristics of the species were determined according to the "Guide to the determination of plant associations of Poland" (Matuszkiewicz 2002).

To assess the load of nitrogen and sulphur reaching the forest soil, the concentration of these elements was estimated from the throughfall and not from the open field. Such an approach was adopted in other similar experiments (Hülber et al. 2008, Stevens et al. 2011, Dirnböck et al. 2014). Throughfall was collected every month using ten five-litre polyethylene bottles per plot with 14.5 cm diameter funnels, which were replaced with 21 cm diameter polyethylene snow sleeve collectors in the winter time. The soil solution was collected using six ceramic cup lysimeters installed at the depth of 25 and 50 cm and sampled once a month in the spring and summer. Mixed samples of throughfall collected every month and mixed soil solution samples were taken for analyses. The ion chromatographic method was used to determine SO_4^{2-} and NO_3^- concentrations in water (Dionex DX100®, Ion-Pac AS4A column). The concentration of NH_4^+ in water samples was determined using the Nessler method.

To calculate the annual loads of sulphur and nitrogen for each particular year the monthly concentrations of SO_4^{2-}, NO_3^- and NH_4^+ were multiplied by the amount of throughfall and the obtained values were summed up.

Data analysis

All statistical analyses were performed using the packages "stats" (R Core Team 2016) and "vegan" (Oksanen et al. 2016) in the R environment. In order to investigate the trends in vegetation changes, unconstrained unimodal Detrended Correspondence Analysis (DCA) was used. Since the lengths of axes were relatively short in this ordination, linear Principal Components Analysis (PCA) was conducted instead of DCA for both study plots (Jongman et al. 1987). The significance of changes in vegetation among particular years was assessed using the "envfit" function implemented in the "vegan" package. The differences among centroids of sample scores of subplots along the first two PCA axes were tested by 999 permutations. Vegetation of a specific year was considered as a single group of vegetation data in PCA ordination. The particular years were treated as factors (2001, 2006, 2011). The value of centroids, statistics of the R^2 values (goodness-of-fit) and p-value were obtained using the function "enfit".

The "envfit" function of the package "vegan" was also applied to explore the relationships between the distribution of points (representing the subplots in the PCA ordination space) and the soil variables (nitrogen, ammonia, sulphates and pH). The impact of these variables on vegetation was assessed by plotting the direction of variation of each variable in the PCA biplots. The significance of the influence of these factors was tested by 999 permutations.

The same permutational test based on vector fitting was used to examine the impact of the soil variables (nitrogen, ammonia, sulphates and pH) on vegetation during the study. Differences in the frequency of selected species among study years were analysed using the log-likehood test (G-test). The frequency of each species in each plot was calculated as the proportion of subplots where each species occurs. Since the obtained data deviated from the normal distribution, non-parametric tests were used. The significance of changes in species cover among the sampling years was tested using the Friedman's rank test followed by the Conover's test for pairwise comparisons or the Wilcoxon's paired test in the case the species was absent in the first years of the study (Sokal & Rohlf 1995).

Meteorological data (average monthly temperatures and monthly precipitation) were collected for the period of 1951-2011 and analysed for particular decades in order to identify possible trends of climate changes in both areas.

Results

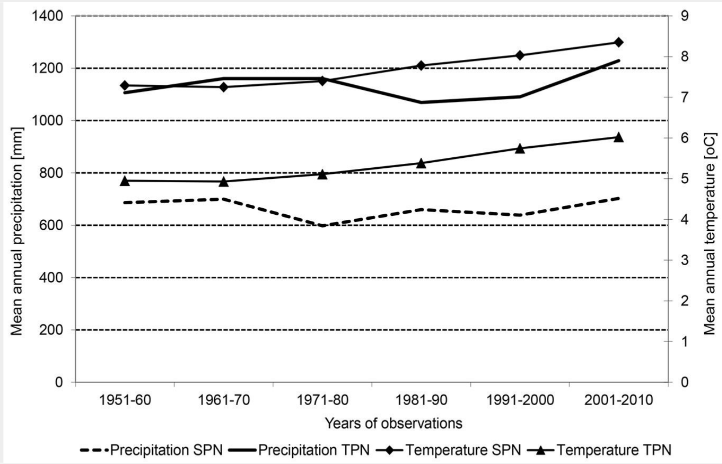

Fig. 1 - Mean annual precipitation and temperature in decades during the period of 60 years in two analysed areas. (SPN): Słowiński National Park; (TPN): Tatrzański National Park.

Słowiński NP

The forest stand in the Słowiński NP is formed by Scots pine planted in the habitat of coastal pine woodland, *Empetro nigri-Pinetum*, about 110 years ago. There was no bush layer in the plot. The species composition of the floor vegetation and especially the presence of species characterising this association – *Empetrum nigrum* – still indicate that the natural plant composition was present at the beginning of the survey. Despite the changes in the abundance and frequency of individual species in the understory, 13 species of vascular plants and 3 species of bryophytes were recorded over the ten years of observations. The undergrowth was primarily composed of species preferring acidic soils poor in nitrogen (index F = 1-2; index N = 1-3 – Tab. 1).

The most noticeable changes in species composition through time (2001 to 2011) at the Słowiński NP site were: (i) the progressive disappearance of *Pinus sylvestris* seedlings in the herb layer; (ii) the replacement of *Quercus robur* with *Q. petraea* in the understory; (iii) the increasing share (6% to 10%) of beech seedlings; and (iv) the significant decrease in the characteristic species *Empetrum nigrum* (17% to 4% – Tab. 1).

An increase in the average annual temperature of 1 °C has been recorded in the analysed area since the 1960s, while the average precipitation has remained at the same level (Fig. 1).

The input of total nitrogen into the forest soil in 2006 estimated by throughfall analysis increased to over 13 kg ha^{-1} (Fig. 2a), while it declined to a lower level in 2011. A similar pattern was observed for the sulphur load, which was somewhat lower than the nitrogen load in each investigated year and ranged from 9.2-12.6 kg ha^{-1} (Fig. 2a).

During the study period a decrease in the concentration of N and S in soil solutions from both shallow and deep layers was observed. The most pronounced decrease in concentrations was found for N-NH_4^+. These decreasing values are reflected by the increase of pH values in the soil solution from both layers (Fig. 3a).

Tatrzański NP

The Tatrzański site is a 140 year-old monoculture of Norway spruce planted in the habitat of beech forest. The ratio of the number of species representing the class *Vaccinio-Piceetea* to the species of *Querco-Fagetea*, changed from 7:6 to 7:11 and 7:10 in 2001, 2006 and 2011, respectively. Beech occurred as a single seedling only in one observation season (Tab. 2).

The death of a number of spruces in the central part of the plot significantly altered the light conditions in the forest floor, and likely affected the composition and structure of the herb layer. Indeed, we recorded an increase in the percentage of species having higher light requirements (index L = 7), such as *Gentiana asclepiadea, Rubus idaeus*, and *Veratrum lobelianum*. Among the most acidophilic species (index R = 2) only the frequency of *Vaccinium myrtillus* remained constant. Species requiring soils with higher pH (index R = 7-8), such as *Gentiana asclepiadea* and *Galeobdolon luteum,* significantly increased their share over

Tab. 1 - Changes in floor vegetation of *Empetro nigri-Pinetum* phytocoenosis at the Słowiński National Park (5 m a.s.l.; pine monoculture approx. 110 years old, planted in pine forest habitat). (index R=1-3): species characteristic of acidic soils; (index N=1-3): species of soils poor in nitrogen; (V-P): class of coniferous forests - *Vaccinio-Piceetea*; (Q-F): class of deciduous forests - *Querco-Fagetea*; (A): tree layer; (C): herb layer; (D): moss layer. Asterisks near the value in the frequency columns indicate that this differs significantly from the remaining values after G-test, whereas asterisks in the cover data columns indicate significant differences after Friedman's or paired Wilcoxon's tests (*: p<0.05; **: p<0.01; ***: p<0.001). Different letters near the value in the same row indicate significant differences (p<0.05) after Conover's test.

Class	Species / Layer	Frequency [%]			Cover [%] (Range / Mode)		
		2001	2006	2011	2001	2006	2011
V-P	*Pinus sylvestris* / A	99	99	100	20-80/50	10-70/60	10-70/50
V-P	*Pinus sylvestris* / C	5	1	-	1/1	10/10	-
V-P	*Vaccinium myrtillus* $^{R=2,N=3}$	100	100	100	10-90/60 ^{b}	20-90/70 ^{a}	5-80/50 ^{b} ***
V-P	*Vaccinium vitis-idaea* $^{R=2,N=1}$	100	100	98	1-30/20 ^{a}	5-20/10 ^{b}	1-20/5 ^{c} ***
-	*Deschampsia flexuosa* $^{R=2,N=3}$	98	100	100	1-40/20 ^{b}	10-70/20 ^{a}	5-50/10 ^{c} ***
V-P	*Melampyrum pratense* $^{R=3,N=2}$	98	100	100	1-30/20 ^{b}	10-90/20 ^{a}	1-30/10 ^{b} ***
-	*Quercus robur*	38	17	23	5-10/5	5-10/10	1-10/10
-	*Calluna vulgaris* $^{R=1,N=1}$	23	18	23	1-30/10	5-30/10	5-20/20
V-P	*Empetrum nigrum* $^{N=2}$	17 **	6	4	1-20/1 ^{a}	5-20/5 ^{b}	5-10/5 ^{b} ***
-	*Quercus petraea*	14	18	20	1-10/10	5-10/10	1-10/10
V-P	*Picea abies*	12	9	12	1-30/5	5-30/20	10-40/10
Q-F	*Fagus sylvatica*	6	4	10	1-30/30 ^{b}	10-30/30 ^{b}	1-40/30 ^{a} **
-	*Betula pendula*	4	3	-	1-10/5	10/10	-
-	*Sorbus aucuparia*	1	1	2	5/5	10/10	1-10/10
V-P	*Luzula sylvatica*	-	-	1	-	-	5/5
V-P	*Dicranum scoparium* / D	100	100	100	100	100	100
-	*Dicranella heteromalla*						
V-P	*Hylocomium splendens*						

Tab. 2 - Changes in floor vegetation of coniferous phytocoenosis (*Abieti-Piceetum*) at the Tatrzański National Park (1140 m a.s.l.; spruce monoculture approx. 140 years old, planted in the habitat of fertile beech forest *Dentario glandulosae-Fagetum*). (Index N=7-8): species of soils rich in nitrogen; (index N = 1-3): species of soils poor in nitrogen; (index R = 7-8): species of alkaline soils; (index R = 1-3): species of acidic soils; (V-P): class of coniferous forests - *Vaccinio-Piceetea*; (Q-F): class of deciduous forests - *Querco-Fagetea*; (M-A): class of subalpine and montane tall-herbs - *Mulgedio-Aconitetea*; (A): tree layer; (C): herb layer; (D): moss layer. Asterisks near the value in the frequency columns indicate that this differs significantly from the remaining values after G-test, whereas asterisks in the cover data columns indicate significant differences after Friedman's or paired Wilcoxon's tests (*: p<0.05; **: p<0.01; ***: p<0.001). Different letters near the value in the same row indicate significant differences (p<0.05) after Conover's test.

Class	Species / Layer	Frequency [%]			Cover [%] (Range / Mode)		
		2001	2006	2011	2001	2006	2011
V-P	*Picea abies* / A	100	100	95	5-90 / 70	5-90 / 60	5-80 / 50
V-P	*Picea abies* / C	3	-	-	1	-	-
-	*Oxalis acetosella*	100	100	100	20-90 / 40	20-80 / 30	20-90 / 50
-	*Athyrium filix-femina*	99	100	98	10-70 / 30	10-60 / 30	10-70 / 30
V-P	*Dryopteris dilatata* $^{N=7}$	98	99	100	10-60 / 30	10-50 / 30	5-60 / 20
Q-F	*Prenanthes purpurea*	92 **	98	100	5-50 / 20 ^{c}	10-40 / 20 ^{b}	5-60 / 30 ^{a} ***
-	*Rubus idaeus*	66	78	77	5-50 / 10	5-50 / 10	5-50 / 20
V-P	*Luzula sylvatica*	43	40	43	1-20 / 10	1-10 / 10	5-70 / 10
-	*Sorbus aucuparia*	37	42	41	1-10 / 10	1-10 / 10	5-30 / 10
Q-F	*Dryopteris filix-mas*	25	26	47 **	5-20 / 10 ^{b}	5-20 / 10 ^{b}	5-40 / 20 ^{a} ***
V-P	*Homogyne alpina* $^{N=2}$	20	19	28 **	1-20 / 5	5-10 / 10	1-10 / 20 *
-	*Petasites albus*	16	15	18	1-20 / 10	5-20 / 10	5-20 / 10
-	*Sambucus racemosa* $^{N=8}$	16	21	28	5-20 / 10 ^{b}	5-20 / 10 ^{b}	10-50 / 20 ^{a} ***
-	*Gentiana asclepiadea* $^{N=2,R=7}$	14	15	41	1-10 / 10 ^{b}	5-10 / 10 ^{b}	5-30 / 10 ^{a} ***
Q-F	*Stellaria nemorum*$^{N=7}$	14	18	52 **	1-10 / 10	1-10 / 10	5-20 / 5 ***
Q-F	*Galeobdolon luteum*	12	17	27 *	1-10 / 5	5-10/5	5-20 / 10 ***
M-A	*Polygonatum verticillatum*	8	9	9	1-10 / 10	5-10 / 10	5-10 / 10
M-A	*Doronicum austriacum* $^{R=7,N=7}$	8	12	11	5-10 / 5	1-10 / 5	1-20 / 10
V-P	*Vaccinium myrtillus* $^{R=2,N=3}$	8	8	7	5-10 / 10	5-10 / 5	5-10 / 10
-	*Cardamine trifolia* $^{R=8,N=7}$	6	7	8	5-10 / 5 ^{b}	5-10 ^{b}	5-20 / 10 ^{a} *
-	*Mycelis muralis*	4	4	6	10 / 10	5-10 / 10	5-10 / 10
V-P	*Calamagrostis villosa* $^{R=2,N=2}$	4	1	2	1-10 / 5	5	5-10
M-A	*Calamagrostis arundinacea.*	3	3	6	1-5 / 1 ^{b}	1-5 / 5 ^{b}	5-20 / 10 ^{a}
M-A	*Senecio nemorensis*	3	4	5	5 / 5	1-5 / 5	5-10 / 10
Q-F	*Luzula luzuloides* $^{R=3}$	2	4	5	1 / 1	1-5 / 1	5-10 / 5
Q-F	*Lonicera xylosteum* $^{R=7}$	2	3	7	10-20 / 20 ^{b}	10-20 / 10 ^{b}	5-30 / 20 ^{a} **
-	*Hieracium murorum*	2	2	4	5-10	10 / 10	1-10 / 10
-	*Carex pilulifera* $^{R=3,N=3}$	1	1	-	1 / 1	1 / 1	-
M-A	*Streptopus amplexifolius*	1	1	4	5 / 5	5 / 5	5-10 / 10
-	*Soldanella carpatica*	1	2	4	10 / 10	5-10	5-10 / 5
M-A	*Veratrum lobelianum*	1	-	1	5 / 5	-	20
Q-F	*Fagus sylvatica*	-	1	-	-	1 / 1	-
-	*Gymnocarpium dryopteris*	-	2	3	-	1-10	5-10 / 5
-	*Phegopteris connectilis*	-	12	38	-	1-10 / 10	1-20 / 5
Q-F	*Actaea spicata*$^{N=7}$	-	6	4 *	-	1-10 / 5	5-10 / 10
Q-F	*Phyteuma spicatum*	-	1	3	-	5 / 5	5-10 / 10
M-A	*Adenostyles alliariae* $^{N=8}$	-	2	15 ***	-	5-10	10-80 / 60 ***
Q-F	*Acer pseudoplatanus* $^{N=7}$	-	4	4 *	-	10 / 10	10-30 / 10
Q-F	*Dentaria glandulosa* $^{R=7,N=7}$	-	1	3	-	5	1-10 / 10
V-P	*Plagiothecium undulatum* / D	100	100	90	10-100	10-90	10-80
-	*Polytrichum attenuatum*						

time (Tab. 2). Others, like *Cardamine trifolia* and *Lonicera xylosteum*, also increased their frequency, albeit to a lesser extent. Among the species that do not tolerate a higher content of nitrogen in soil (index N = 2) only *Gentiana asclepiadea* and *Homogyne alpina* significantly increased their share in the undergrowth. Other species of the same group, such as *Vaccinium myrtillus,* remained stable, whereas *Calamagrostis villosa* reduced slightly its share. Moreover, species that tolerate a higher nitrogen content in soil (index N = 7-8), such as *Sambucus racemosa, Stellaria nemorum, Cardamine trifolia* and *Adenostyles alliariae* significantly increased their share in the phytocoenosis. In the entire studied period an increase in the number of vascular plant species from 30 to 37 was observed (Tab. 2).

A remarkable change in the undergrowth composition occurred in 2011, likely related with an increase of the soil pH (Fig. 3b). The subplots from 2011 were the most diverse in terms of species composition, while subplots from 2001 and 2006 were much closer to each other.

Sulphur and ammonia were significantly correlated and their content was higher in subplots from 2001 and 2006. As mentioned above, the significant change in the light conditions in the plot, a marked increase in precipitation (after decreasing for 20 years) and the increase in the average annual temperature of 1 °C also could have significantly affected the present structure of floor vegetation at the Tatrzański NP site (Fig. 1).

Changes in the input of nitrogen and sulphur were slightly different in this plot compared with the Słowiński NP site. Total nitrogen concentration in the throughfall did not vary in 2001 and 2006, and slightly declined from 16 to 15 kg ha^{-1} in 2011. Over the whole investigated period the annual

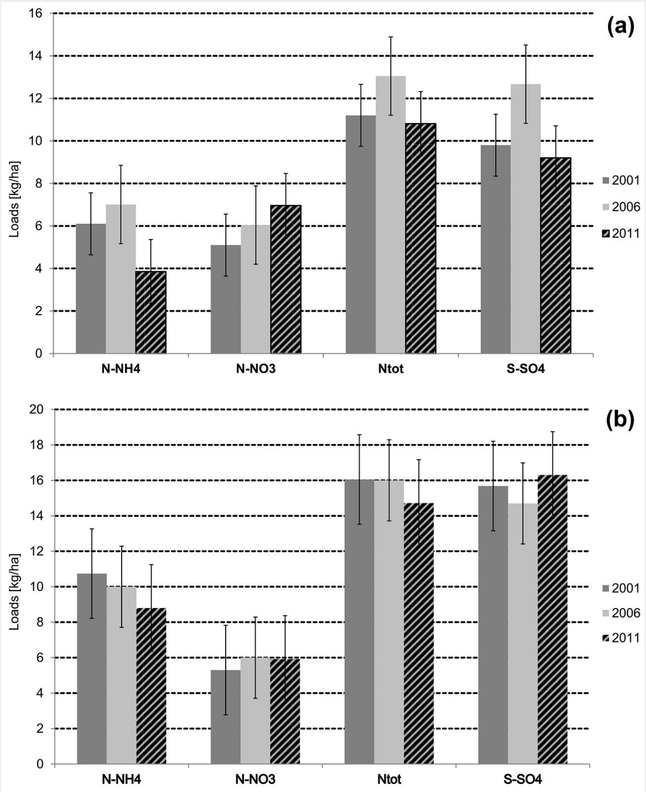

Fig. 2 - Comparison of annual nitrogen and sulphur loads in the throughfall in the Słowiński National Park (a) and in the Tatrzański National Park (b), in 2001-2011.

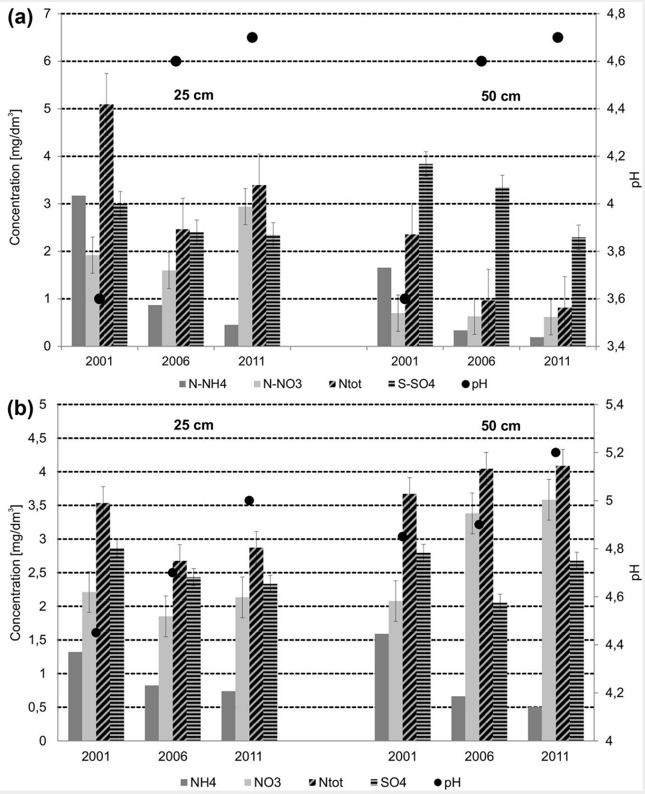

Fig. 3 - Concentrations of N and S compounds and pH values in the soil solution at two depths in the Słowiński National Park (a) and in the Tatrzański National Park (b), in 2001-2011.

loads of the total nitrogen and sulphur in the Tatrzański NP site were at a similar level and ranged from 15 to 16 kg ha^{-1} and from 15 to 16.5 kg ha^{-1}, respectively (Fig. 2b).

In the analysed period, N concentration in the soil solution decreased in the shallow layer and increased in the deeper layer, while S concentration decreased in both layers. The most pronounced decrease in concentrations was observed for N-NH$_4^+$. In the soil solution of both layers a systematic increase in the pH value from 2001 to 2011 was recorded (Fig. 3b).

Relationship between environmental factors and species composition

The structure of the floor vegetation at both sites changed markedly during the studied decade (Fig. 4). Indeed, the distance between subplots in Tatrzański NP from 2001 and those from 2011 as well as

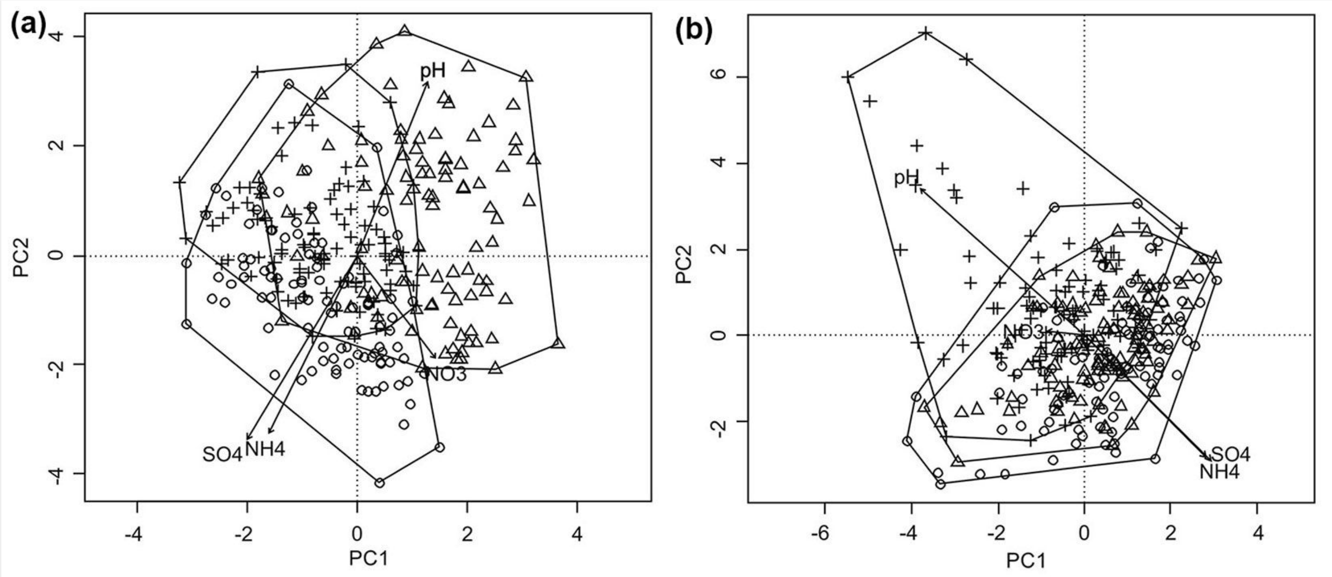

Fig. 4 - Ordination diagram of subplots (100 squares) along the first two axes of Principal Components Analysis (PCA) based on species cover on permanent plots in (a) the Słowiński National Park and (b) in the Tatrzański National Park, over the period 2001-2011. (circles): 2001; (triangles): 2006; (crosses): 2011.

Tab. 3 - Results of vector fitting of time as a factor (2001, 2006, 2011) and environmental variables in Principal Components Analysis of vegetation in the studied plots. (ns): non significant.

Site	Variable	PC1	PC2	R^2	Prob.
Tatrzański NP	NH_4^+	0.7048	-0.70934	0.1569	0.001
	NO_3^-	-0.9959	0.09024	0.0071	ns
	SO_4^{2-}	0.7095	-0.70473	0.1681	0.001
	pH	-0.7428	0.66951	0.2574	0.001
	year	-0.7392	0.67349	0.2485	0.001
Słowiński NP	NH_4^+	-0.44113	-0.89744	0.1898	0.001
	NO_3^-	0.60251	-0.79811	0.0811	0.001
	SO_4^{2-}	-0.51134	-0.85938	0.2211	0.001
	pH	0.37709	0.92618	0.1676	0.001
	year	0.01124	0.99994	0.1022	0.001

subplots in Słowiński NP from 2006 is well reflected by their separation along the first axis of PCA.

The higher contents of ammonia and sulphates were significantly associated with the ordination of subplots from 2001, while subplots from 2006 in case of the Słowiński NP and 2011 in the Tatrzański NP were characterised by a significantly higher pH (Fig. 3a, Fig. 3b). The significance of changes among the years is reported in Tab. 3. Among the variables tested (NH_4^+, NO_3^-, SO_4^{2-}, pH, year), only nitrates were non-significantly correlated with the obtained ordination (Fig. 3a, Fig. 4a, Tab. 3).

The subplots from the Słowiński NP in 2001 were characterised by a higher content of NH_4^+ and SO_4^{2-}. A greater influence of pH on the structure of the floor vegetation was observed in 2006, whereas ammonia changed across the years (Fig. 4a). In the Tatrzański NP the situation was different and the greatest impact of pH was noted in 2011, whereas vegetation changes seems to be associated to the higher content of ammonia and sulphates in 2001 and 2006 (Fig. 4a).

Discussion

The choice of assessing nitrogen and sulphur deposition by throughfall analysis may seem disputable due to the differences between the content of individual elements in throughfall and the precipitation collected in the open field. At low N deposition, the loads of $N\text{-}NO_3$ and $N\text{-}NH_4$ were found to be lower in throughfall than in the open field due to nitrogen uptake from the canopy (Ferretti et al. 2014). However, the throughfall N deposition is generally higher than the open field N deposition, because the former also includes the dry deposition of particles on tree canopies (Berger et al. 2008, Staszewski & Kubiesa 2008, Ferretti et al. 2014). Such regularity was also found in a dozen spruce stands in southern Poland (Staszewski 2004). Therefore, in order to determine the real input of nitrogen to the forest floor the throughfall analysis was chosen in this study.

In the last few decades, climate change and the deposition of air pollutants have significantly affected the structure of vegetation all over the globe. Generally, the observed effects of these changes have been considered as negative, in terms of simplification of the plant community structure, decrease in biodiversity, reduction in the distribution ranges of plants or changes the habitat of stenotypic species, which are the most sensitive to any environmental changes due to their low adaptive potential (Jefferies & Perkins 1977, Roelofs 1983, Aerts et al. 1992, Lee & Studholme 1992, Kiehl et al. 1997, Nielsen et al. 2000, Aerts et al. 2001).

In our study the aforementioned effects of climate change and deposition of air pollutants were more complex and differed between the two examined areas. At the Słowiński NP site we recorded the disappearance of species characterising the coastal coniferous forest *Empetro nigri-Pinetum*, while other species preferring fertile habitats appeared during the investigated decade (2001-2011). Such change in the typical composition of this plant community has been reported for many areas in Europe (Bobbink et al. 2010, Dirnböck et al. 2014) and could be due to the interplay among several factors. Research on the Danish coastal dune heaths showed a linear increase in the share of *Empetrum nigrum* increasing the concentration of nitrogen in the soil (Nielsen et al. 2000), although other studies did not reveal such a dependence (Tybirk et al. 2000). Furthermore, a decrease through time in the frequency of *Quercus robur* (a species with a continental distribution range), and at the same time an increase in the share of *Q. petraea* (a species with an Atlantic distribution range) were observed in the undergrowth at the Słowiński NP site. Although the observation period was too short to draw far-reaching conclusions, the possibility exists that a slight increase in global warming may foster species typical of warmer climates and disadvantage those more adapted to colder climates. Therefore, we can conclude that the combined effect of climate change and the deposition of air pollutants at the Słowiński NP have a negative effect on local biodiversity.

The results of the studies carried out in the mountain plot of the Tatrzański National Park were different. Across all Western Carpathians a dramatic reduction of the vitality of Norway spruce plantations in fertile habitats at lower altitudes occurred, and restoration activities aimed at the establishment of the native vegetation are taking place in many areas. Although the situation is similar to that in the Tatra Mts. (southern Poland), deforestation at Tatrzański did not occur as it was taken under protection as a national park. Here, the impoverishment of the habitat through the long-term planting of Norway spruce resulted in the natural elimination of many undestory species typical of the beech forest (*Dentario glandulosae-Fagetum*), which constitute the potential vegetation in this area. In this case, the nitrogen enrichment of the habitat due to atmospheric deposition may favour the return of nitrophilous species that are typical of the fertile deciduous forests. This is clearly indicated by the changes in the undergrowth that we observed in this study, and in this context the effect of N deposition on local biodiversity would be positive. Indeed, the appearance of *Acer pseudoplatanus* and species of the class of subalpine tall herb (*Mulgedio-Aconitetea*) suggest the incipient conversion of this phytocoenosis into the rich habitat Natura 2000 code 9140 (Central European subalpine and mountain beech forests of sycamore), which is supported by the topography (steeply inclined slope). Nonetheless, the presence of beech seedlings in the undergrowth has been observed only sporadically in the study area, and this could hamper the natural restoration of the native beech forest. Any support for the phytocoenosis (*e.g.*, beech planting), could enhance the biodiversity of this area and restore the potential vegetation which is consistent with the natural habitat.

Conclusions

The variation over time of soil acidity (pH) seems to have the greatest impact on species composition and structure of the forest floor at both sites. However, a significant increase in the share of extreme nitrophilous species was also observed over the analysed period. Not all species considered as bioindicators (*e.g.*, *Vaccinium myrtillus* or *Calluna vulgaris*) showed a clear relationship with the analysed environmental parameters. However, all the diagnostic species for a given phytocoenosis or for higher syntaxonomic units showed the most significant variation.

In the case of the Scots pine stand (Słowiński NP), the floristic changes recorded over 10 years suggest the gradual disappearance of the main diagnostic species for this plant community (*Empetro nigri-Pinetum*). Contrastingly, in the case of the Norway spruce stand (Tatrzański NP) planted in the habitat of the fertile beech wood (*Dentario glandulosae-Fagetum*), the floristic changes recorded suggest the occurrence of a gradual restoration in the long term of the native vegetation of the area (beech forest).

Further studies are needed in order to better elucidate the impact of changes in soil pH or the deposition of nitrogen and sulphur on the understory vegetation, in the light of the history of land-use and the potential vegetation of the habitat.

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