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Original Research Article

Influence of the environmental factors on the species composition of lichen Scots pine forests as a guide to maintain the community (Bory Tucholskie National Park, Poland)

Michał H. Węgrzyn [a, *], Joanna Kołodziejczyk [a], Patrycja Fałowska [a], Piotr Wężyk [b], Karolina Zięba-Kulawik [b], Marta Szostak [b], Agnieszka Turowska [c], Barbara Grzesiak [d], Paulina Wietrzyk-Pełka [a]

[a] *Prof. Z. Czeppe Department of Polar Research and Documentation, Institute of Botany, Faculty of Biology, Jagiellonian University, Gronostajowa 3, PL-30-387, Kraków, Poland*

[b] *Department of Forest Resource Management, Faculty of Forestry, University of Agriculture in Kraków, Al. 29-listopada 46, 31-425, Krakow, Poland*

[c] *Bory Tucholskie National Park, Charzykowy, Długa 33, PL-89-606, Charzykowy, Poland*

[d] *Department of Biology and Parasitology, Medical University of Lodz, Żeligowskiego 7/9, PL-90-752, Lodz, Poland*

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ABSTRACT

Central European lichen Scots pine forests occur in extremely dry and poor sandy areas. This forest type, in terms of phytosociological classification, corresponds to the *Cladonio-Pinetum* association. This community is protected by European Union's legislation (Natura 2000 habitat, code 91T0) and needs active protection to be maintained. The presented study was planned based on the conservation activities performed in 2017, which included thinning of the tree stand in selected areas of the lichen Scots pine forest community in the Bory Tucholskie National Park. Thinning effect was documented by the LiDAR (Light Detection and Ranging) data collected in 2017 before thinning and 2018 after thinning. Next we characterized two different forms of *Cladonio-Pinetum* association (lichen-rich and bryophyte-rich forms) and their relation to local environmental factors. To demonstrate that thinning is beneficial to the lichens we also compared the microclimatic conditions (temperature, humidity and light intensity) in thinned and unthinned areas. Vegetation and organic matter sampling was conducted in 2018 in the 24 sampling plots, each of 100 m^2. Microclimatic measurements was done in 2018–2019 in one sampling plots of the thinned area and one additional control plot in the unthinned area. Sampling plots representing lichen-rich community had significantly lower canopy cover, higher number of lichen species, higher lichen cover and lower bryophyte cover in comparison to bryophyte-rich plots. The results showed that the lower canopy cover creates more favorable conditions for the occurrence of lichens, because of increasing the daily amplitudes of temperature, humidity and light intensity. Reduction of the canopy cover may be the easiest method to maintain the lichen pine forests community with high abundance of lichens in the field layer. This is particularly important in relation to the observed

* Corresponding author.
E-mail addresses: michal.wegrzyn@uj.edu.pl (M.H. Węgrzyn), j.kolodziejczyk@student.uj.edu.pl (J. Kołodziejczyk), patrycja.falowska@student.uj.edu.pl (P. Fałowska), piotr.wezyk@urk.edu.pl (P. Wężyk), karolina.anna.zieba@gmail.com (K. Zięba-Kulawik), marta.szostak@urk.edu.pl (M. Szostak), a.turowska@pnbt.com.pl (A. Turowska), barbara.grzesiak@umed.lodz.pl (B. Grzesiak), paulina.wietrzyk@gmail.com (P. Wietrzyk-Pełka).

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disappearance phenomenon of lichen pine forest in Europe. Due to this tendency, it is particularly important to actively protect these plant communities.
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1. Introduction

Central European lichen Scots pine forests (which belong to communities of *Cladonio-Pinetum* association) represent xerophilous vegetation which occurs in the driest and most nutrient-poor areas, and because of that, they are less productive than other pine forests of mineral soils (Oksanen and Ahti, 1982; Matuszkiewicz et al., 2013). The distribution of this forest type covers Central Europe, in particular, Czech Republic (Husova and Andresova, 1992; Somsák et al., 2004; Mikuska, 2005; Kucera et al., 2006; Dingová Kosuthová et al., 2013; Košuthová et al., 2015), Germany (Rodenkirchen, 1992; Heinken, 1999, 2007; Heinken and Zippel, 1999; Fischer et al., 2009; Hauck, 2009; Dirnböck et al., 2014; Lindner et al., 2014; Reinecke et al., 2014), Lithuania (Solon, 2003) and Poland (Kelly and Connolly, 2000; Solon, 2003; Stefanska-Krzaczek, 2010; Dingová Kosuthová et al., 2013; Węgrzyn and Wietrzyk, 2017; Wężyk et al., 2018). This habitat also occurs in the Netherlands (Emmer and Sevink, 1994), Finland (Oksanen and Ahti, 1982), Norway, Latvia, Estonia (Zobel et al., 1993), and Slovakia (Dingová Kosuthová et al., 2013). Tree stand of *Cladonio-Pinetum* association is built by mostly stunted Scots pine trees with rather low crown density (Dingová Kosuthová et al., 2013). The field layer is characterized by high abundance of fruticose lichens, mainly of the *Cladonia* genus from the *Cladina* section, occasionally the *Cetraria* genus, and also some specific species of bryophytes, but in low abundance (Wegrzyn and Wietrzyk, 2017; Dingová Kosuthová et al., 2013). Until the 1990s, lichen Scots pine forests occurred throughout Europe (Oksanen and Ahti, 1982), present commonly on sandy soils within the valleys of large rivers and postglacial outwash sands (Słowinski et al., 2015). Since the end of the 20th century, the distribution of the habitat significantly decreased its range of occurrence throughout Europe as a result of strong eutrophication processes of substratum (Prietzel, and Kaiser, 2005; Jenssen, 2009; EEA, 2011; Reinecke et al., 2014) and probably due to a gradual increase in carbon sequestration in the forest soils (Niinistö et al., 2004). Currently, well-preserved patches of lichen Scots pine forests occur in the north-west part of Europe especially in Germany and central Poland. The main centres of their occurrence in these countries are: in the Poland – the Tuchola Forest (Dingová Kosuthová et al., 2013; Węgrzyn and Wietrzyk, 2017), the Notecka Wilderness (Węgrzyn and Wietrzyk, 2017) and Lower Silesian Wilderness (Stefanska-Krzaczek et al., 2018); in Germany – The Kaarβer Sandberge natural forest reserve - Lower Saxony (Fischer et al., 2009), the Lower Spreewald region - Brandenburg (Reinecke et al., 2014). The origin of lichen Scots pine forests may be natural or anthropogenic. Current distribution of *Cladonio-Pinetum* association in Europe refers to places with extremely poor and dry conditions associated with a specific substrate formed during the last glacial age (Mangerud et al., 2004; Słowinski et al., 2015), and, by historical land-use practices, such as cattle grazing, litter raking (pine needles, pinecones, small branches), deforestation, and clearfelling (removal of all wood from the forest stand) (Węgrzyn and Wietrzyk, 2017).

Regardless of their origin, Central European lichen Scots pine forests are uncommon and endangered (Ahti and Oksanen, 1990; Prieditis, 2002; Danielewicz et al., 2004). They are protected by UE legislation as the Natura 2000 habitat type code 91T0 (Council Directive, 1992; Kolbek et al., 2010). Most of their localities lie in protected areas localised in Poland (Fig. 1; Sokołowski, 1965; Matuszkiewicz and Matuszkiewicz, 1973; Ermakov and Morozova, 2011; Dingová Kosuthová et al., 2013, Węgrzyn and Masłowska, 2010; Węgrzyn and Wietrzyk, 2017). As lichen Scots pine forests are the only known semi-natural type of forest communities with lichen-rich field layer, they need active protection to be maintained in order to prevent the lichens disappearance (Dingová Košuthová et al., 2013). As suggested by Oksanen and Ahti (1982), Jonsson Cabrajic et al. (2010) and Sandström et al. (2016), mat-forming terrestrial lichens are closely associated with low productive and more open Scots pine forests. In Sweden, in the past, those forest were naturally often subjected to forest fires which contributed to declination of tree canopy as well as shrub and field layers creating favorable conditions for lichen growth (Esseen et al. 1997; Sandström et al. (2016). This as well as above mentioned reasons of lichen Scots pine forest disappearance reflect the crucial role of active protection in maintenance or restoration of those vulnerable habitats.

The presented study was planned based on the conservation activities performed in 2017, which included thinning (selective tree cutting) of standards within the selected areas of the lichen Scots pine forest habitat in the Bory Tucholskie National Park. These activities were the first step in the process of developing effective methods of conservation and/or restoration of lichen Scots pine forests habitat in Europe. The main aim of our study was to: 1) assess the effect of thinning procedure (canopy reduction effect); 2: characterize two forms of *Cladonio-Pinetum* forest (lichen-rich and bryophyte-rich forms) and their relation to local environmental factors; 3) compare the microclimatic conditions (temperature, humidity and light intensity) between thinned and unthinned areas. Two research hypotheses were set: 1) low canopy cover results in lichen-rich field layer and high canopy cover results in field layer dominated by bryophyte species; 2) lower value of total nitrogen in organic layer has a positive effect on terricolous lichens presence. The research was carried out on permanent plots, which in the future will allow to monitor the effectiveness of thinning as a protection method.

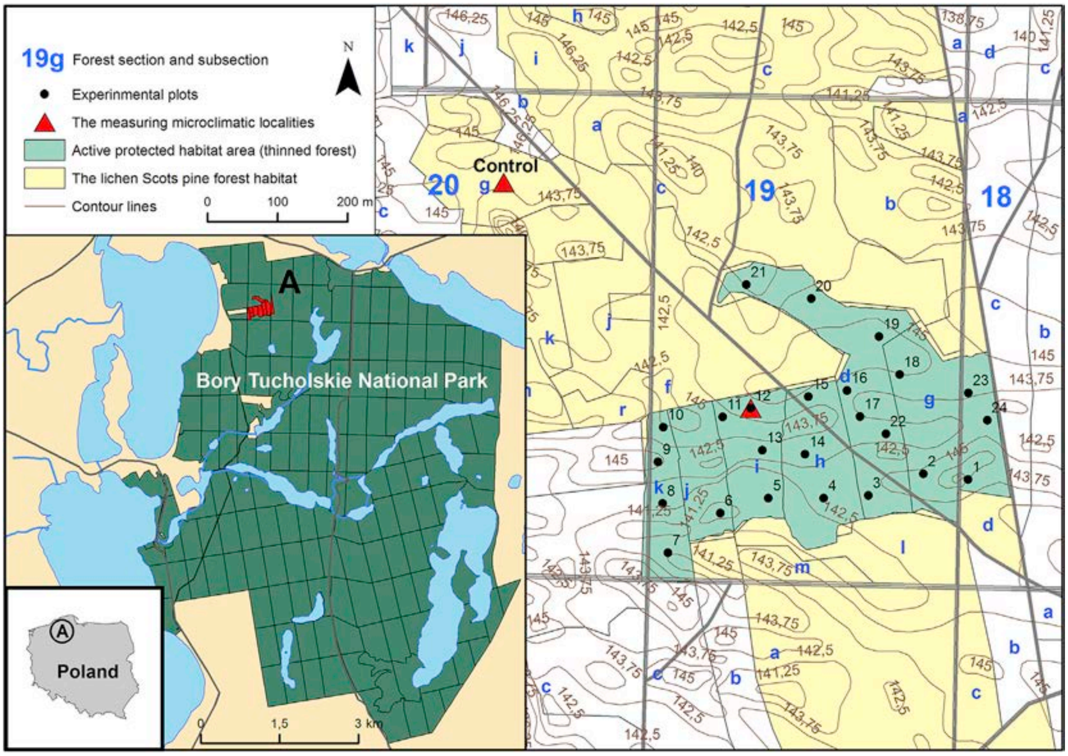

Fig. 1. Map of the lichen pine forest habitat in the Bory Tucholskie National Park (NW Poland). The forestry units are marked by the numbers: 18, 19, 20; the forest subsections are marked by letters: c, g, d, h, i, j, k (individual tree stands); black dots marked 24 sampling plots. Altitude is also presented on the map. Automatic loggers measuring microclimatic parameters: air temperature and humidity as well as light intensity were placed at plot no 12 and the control locality.

2. Materials and methods

2.1. Study area

Tuchola Forest is an area located within the catchment of Brda and Wda rivers, and Tucholska and Charzykowska Plains. It is a complex of mainly Scots pine forests growing on sands deposited on the glacial tills formed during the last glaciation period around 10.700 b2k (Grzelakowska, 1989; Słowiński et al., 2015). The vegetation developing in this area since the beginning of the Holocene underwent numerous secondary transformations related to the global warming and subsequent human activity (Grzelakowska, 1989; Słowiński et al., 2015). In this area the primary forest which evolved after the withdrawal of the last glaciation was mainly represented by deciduous woodlands (Miotk-Szpiganowicz, 1992; Hjelmroos, 1982). The oak and hornbeam forest was the most dominant of these habitats, and the Scots pine forests were scarce and restricted to the most nutrient-poor and sandy areas (Miotk-Szpiganowicz, 1992). The exploitation of primary forests by man has begun in the Neolithic Age about 5000 years ago. These activities have continued through the Middle Ages and have contributed to the impoverishment of the soil substrate. The primitive slash-and-burn cultivation of primary forests started the slow process of substrate sterilization and impoverishment over the large areas of the Tuchola Forest. The top-soil layer was destroyed in due process, and the old deciduous forests were replaced by Scots pine forests (Miotk-Szpiganowicz, 1992). Both the geomorphological processes shaping the substrate (thickness and structure of glacial sand layers, the processes of dunes forming in the Holocene) and non-uniform intensity of human activities had an impact on the distribution of current forest communities in this area. The forest became a place of sourcing not only wood, but also other goods from which the local population benefited leading to the continuous impoverishment of the substrate (Grzelakowska, 1989). Continuous forest-litter raking (pine needles, pinecones, small branches), deforestation and removal of all wood from the forest increasingly hampered the revival and development of forest. Deforested places were transformed into cultivated fields and used for several years. After full impoverishment of these areas, they were converted into pasture for sheep. Ultimately, such places were again afforested. In these localities, the development of lichen Scots pine forest began (Grzelakowska, 1989). Since 1996, when the Bory Tucholskie National Park was created, the stands in individual different age divisions were developing without human disturbances as forest cultivation was significantly reduced, and the influence of the local population was even more limited than before the park was founded.

Currently, the Bory Tucholskie National Park consists of 3908.68 ha woodland habitats, which is 85.18% of its area total. Within these woodland communities *Leucobryo-Pinetum* dominates – 69%; *Cladonio-Pinetum* – 3%; other natural plant communities 3% and phytosociologically indeterminate communities referring to Scots pine forests – 25% (Matuszkiewicz et al., 2012; Węgrzyn and Wietrzyk, 2017).

As a result of the increasing disappearance of lichen Scot's pine forest in the Bory Tucholskie National Park, actions were undertaken to develop modern methods for habitat conservation. In 2017, the area of habitat was selected (Fig. 1) and active conservation measures (including thinning of stands) were carried out in this area. As a result of these activities, around 239 m^3 of Scots pine wood with a trunk diameter greater than 8 cm and about 324 m^3 with a trunk diameter smaller than 8 cm were cut in the designated area.

2.2. LiDAR 3D and remote sensing spectral analyses

Before the thinning in 2017, the ALS (Airborne Laser Scanning) 3D point cloud was collected (mean density approx. 70 pts/sqm; max. density: 208 pts/sqm; type of aircraft: gyrocopter equipped with RIEGL VQ-580 scanner and Digi-CAM-60 RGB camera). The acquired data in test area were used to generate a high resolution DTM (Digital Terrain Model) and to precisely estimate the canopy cover (Cover A_{2017}) and stand structure using the LiDAR metrics. The Digital Surface Model (DSM) was also generated with resolution of 0.5 m GSD and normalised in next step to nDSM product called also CHM (Canopy Height Model). In year 2018, the ULS (Unmanned Laser Scanning) LiDAR airborne campaign (UAV Ricopter with VUX-1 RIEGL scanner on-board + 2 Sony RGB cameras) over the selected forest canopy cover (Cover A_{2018}) was repeated after the tree thinning. The collected 3D LiDAR point clouds allowed to generate a map of canopy cover (range 0–100% of laser beam penetration trough the branches to the ground) which characterised the differences in tree canopy before (Cover A_{2017}) and after stand thinning (Cover A_{2018}).

The TLS (Terrestrial Laser Scanning) point clouds were collected in 2017 prior to stand thinning and in 2018 after thinning. The collected 3D point cloud was used to documenting the structure of sub-canopy space of the stand. We used a FARO FOCUS 3D scanner, which allow to collect points with speed up to 960.000 impulses/sec.

2.3. Sampling plots

Based on preliminary studies (Węgrzyn and Wietrzyk, 2017), we sampled both lichen-rich and bryophyte-rich forms of the lichen Scots pine forest in the thinned area. We chose seven tree stands (forest sections 18 and 19, total area of 12.609 ha, in relatively young tree age 20–54 years, see Table 1 and Fig. 1). In the thinned stands 24 circular sampling plots of 100 m^2 (with a radius of 5.64 m) were designated (Fig. 1). Moreover, one control plot outside the thinned area was selected (forest section 20) and temperature and humidity measurements have been recorded (Table 1, Table 1 supp., Table 2 suppl., Fig. 1).

2.4. Vegetation and organic matter sampling analysis

In April and June of 2018, after thinning was completed, the vegetation data were collected in 24 sampling plots. We estimated percentage cover of shrub layer (Cover B), herb layer (Cover C) and lichen-bryophyte layer (Cover D). Canopy cover (Cover A_{2017}) was calculated on the basis of accessed LiDAR (Light Detection and Ranging) data, which was conducted in August 2017 (see 2.2 section).

All species and their percentage cover in A-D layers were recorded. Percentage frequency and mean cover of each species were calculated for lichen-rich and bryophyte-rich forms (Table 2 supp.). In this table the characteristic species to *Cladonio-Pinetum* association in the phytosociological approach were presented, such as the following lichens: *Cladonia arbuscula, Cl. furcata, Cl. gracilis, Cl. mitis, Cl. rangiferina, Cl. uncialis* (lichens), and the following bryophytes: *Dicranum spurium* and *Ptilidium ciliare* (Matuszkiewicz and Matuszkiewicz, 1973; Barbati et al., 2007; Ahti and Oksanen, 1990,Węgrzyn and Masłowska, 2010).

In April of 2018, in each of the sampling plots, one organic matter sample was gathered from the humus layer. The thickness of this layer as the thickness of organic matter (TOM) was measured by a measuring tape. Collected organic matter samples were analysed in terms of: content of total organic carbon (TOC) and total nitrogen (TN) (determined using a CHN elemental analyser). Also, Carbon to nitrogen ratio (C/N) was calculated. Soil pH (measured potentiometrically in distilled

Table 1
Parameters of forest stands selected for study (see Fig. 1).

Forest stand	Sampling plots (see Fig. 1)	Area [m^2]	Age of stand [years]	Cover A_{2017} (see Fig. 2A)	Cover A_{2018} (see Fig. 2B)
18 c	1, 23, 24	10612.08	53	91.69	80.42
19 d	3, 16, 17, 20, 21, 22	32029.59	38	86.80	66.86
19 g	2, 18	21313.54	44	92.12	70.23
19 h	4, 14, 15	21188.53	24	92.50	69.48
19 i	5, 11, 12, 13	15376.55	20	86.33	70.03
19 j	6	12310.27	54	92.22	70.84
19 k	7, 8, 9, 10	13263.30	39	92.68	72.97

water using a 1:2.5 soil/water ratio with the use of Elmetron CPC-411) and soil electrical conductivity (EC) (measured in water after 24 h with the use of Elmetron CPC-411).

2.5. Microclimatic data analysis

In the thinned area in sampling plot no. 12 and in the unthinned control plot (Fig. 1), two types of loggers were used to measure: 1) light intensity (HOBO MX2202 Underwater Temp/Light, Version Number: 140.59) and 2) air temperature and humidity (HOBO U23-002 Temp/RH, Version Number: 1.10). Loggers recorded microclimate parameters every 3 h, obtaining eight measurements per day from April 2018 to April 2019. All microclimatic data were processed with HOBOware 3.7.14 software. These data were used to investigate changes in microclimatic parameters between thinned and unthinned areas.

2.6. Statistical data analysis

Cluster analysis (UPGMA with the Cosine distance) was used to investigate the similarities between plots in term of species composition. The analysis assigned plots to lichen-rich and bryophyte-rich forms of lichen Scots pine forest. The one-way analysis of variance (ANOVA, $p < 0.05$) was applied to test the significance of differences in cover of A and C layers, species numbers and cover of lichens and bryophytes as well as soil parameters: C/N, TOC, TN, pH, EC, TOM) between lichen-rich and bryophyte-rich forms of lichen Scots pine forest. Difference in canopy cover between 2017 (before thinning – Cover A_{2017}) and 2018 (after thinning Cover A_{2018}) was tested using the ANOVA ($p < 0.05$). Before the analysis the assumptions of normality and variance homogeneity were tested using Lilliefors test and Levene's test, respectively. As microclimatic data did not fulfil ANOVA assumptions, the Wilcoxon test ($p < 0.05$) was applied to investigate the significance of differences between thinned and unthinned areas. We applied the canonical correspondence analysis (CCA) with automatic forward selection procedure of the explanatory variables to relate species composition of C and D layers to available variables: Cover A_{2017}, Cover C, C/N, TOC, TN, pH, EC, TOM. No data transformation was performed and raw data was used for analysis. A Monte Carlo permutation test (999 permutations, $p < 0.05$) was used to assess the statistical significance of relationships between species and used variables (Ter Braak and Smilauer, 2002). Analyses were performed using the Statistica 13 (Statsoft, Tulsa, OK, USA) and CANOCO 4.5 (Ter Braak and Smilauer, 2002).

3. Results

3.1. Comparison of the canopy cover before and after thinning

The ALS/ULS air scanning (Fig. 2), as well as the TLS ground scanning (Fig. 3) before and after thinning treatments enabled to visualize the reduction of canopy cover. In 2017, the stands reached an average value of Cover A_{2017} of 91.1% and after thinning average value of Cover A_{2018} decreased to 71.5% (Table 1; Fig. 5). Whereas for individual experimental plots (each of 100 m^2), the average Cover A_{2017} was 91.1% (Table 2 supp.), however after thinning activities average value of Cover A_{2018} on these plots decreased to 62.2% (see Fig. 4).

The canopy cover in 2017 showed significant difference in comparison to the canopy cover after thinning in 2018 (Fig. 5).

3.2. Species composition and structure of lichen-rich and bryophyte-rich forms of the lichen Scots pine forest

Lichen-rich form of *Cladonio-Pinetum* community was represented by 16 plots, while eight plots belong to the bryophyte-rich form (Table 1 (supp.), Fig. 6). Within the sampling plots 26 terricolous lichen species (24 fruticose lichens and 2 crustose lichens), 7 bryophytes species (6 moss species and 1 liverwort species), and 12 vascular plant species was recorded (Table 2 supp.). The maximum lichen number recorded in plot was 14. Average number of species of lichens per plot in lichen-rich plots was 8, while in bryophyte-rich plots 4. The plots with high species number of the terricolous lichen (11–14) were located in the middle of the studied fragment of *Cladonio-Pinetum* community (plots 13, 14, 22, Fig. 1). Within each plot, only *Cladonia mitis* was noted obtaining an average cover in the D layer of 21% for lichen-rich plots and 4% for bryophyte-rich plots. In 21 plots *Cl. gracilis* (cover 20.8% for lichen-rich plots and 3% for bryophytes-rich plots) and *Cl. rangiferina* (6.9% for lichen-rich plots and 1.2% for bryophytes-rich plots) were found. In the 18 plots *Cl. uncialis* was recorded (4.5% for lichen-rich plots and 0.8% for bryophytes-rich plots) (Table 2 supp.).

Sampling plots representing lichen-rich community had significantly lower tree cover (Cover A_{2017}), higher lichens species number, higher lichen cover and lower bryophyte cover in comparison to bryophyte-rich plots (Table 2. Fig. 7).

These lichen taxa had a very high cover in lichen-rich plots, which decreased in the plots representing bryophyte-rich community (Table 2 supp.).

According to the CCA, four variables significantly influenced species distribution: TOM, Cover A_{2017}, TN and pH. The presence of *Pleurozium schreberi*, *Dicranum polysetum* and *Hypnum cupressiforme* was associated with increasing TOM (Fig. 8). The appearance of terricolous lichens (*Cladonia gracilis, Cl. mitis, Cl. zophii, Cl. deformis* and *Cetraria acuelata)* was connected with lower tree cover (Cover A_{2017}) and lower soil pH (Fig. 8). Increase of total nitrogen content in organic matter positively affected the occurrence of vascular plant species such as *Deschampsia flexuosa*, *Luzula palescens* and *Vaccinium myrtillus*

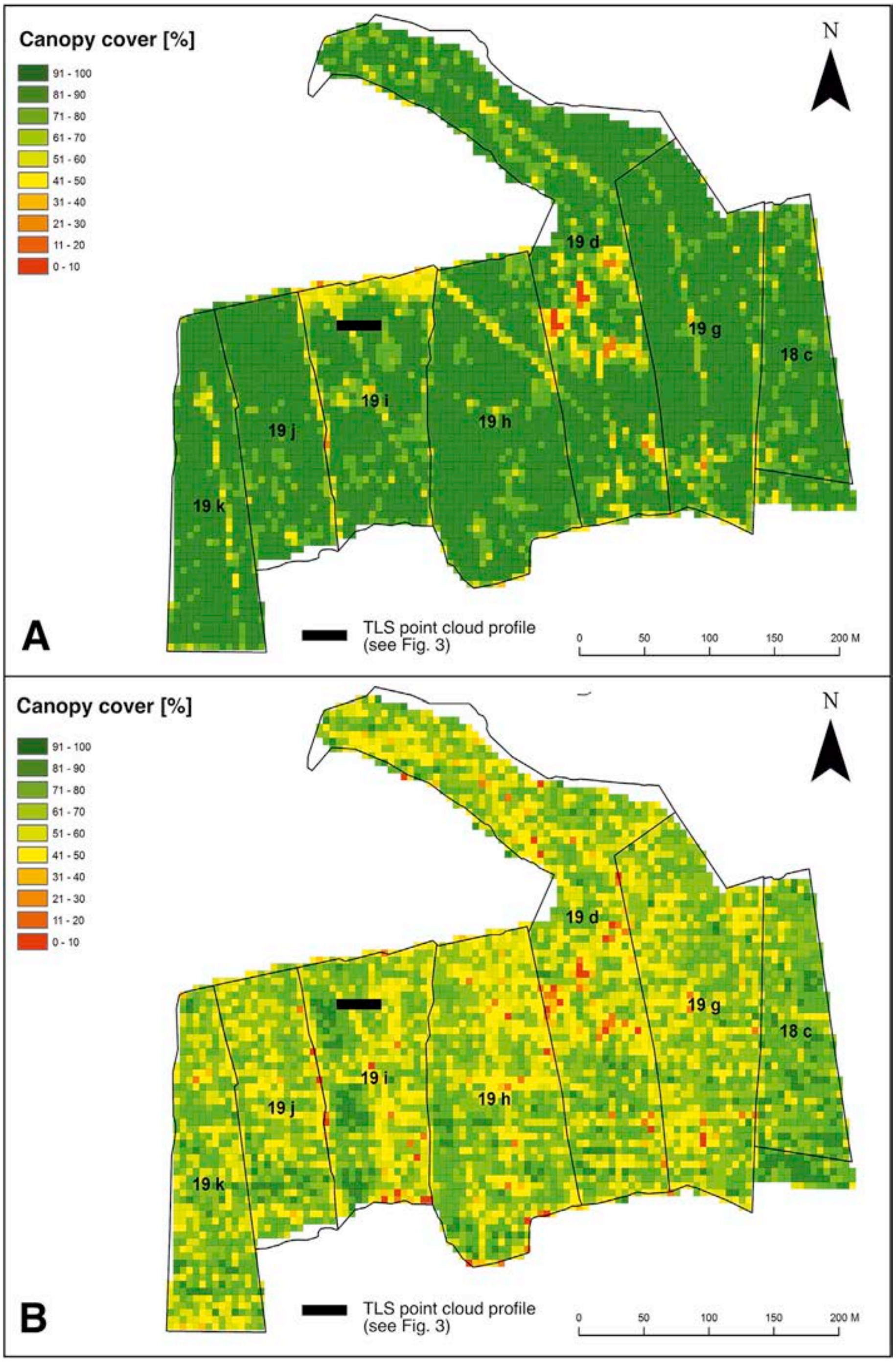

Fig. 2. The canopy cover (percentage; 0–100%): **A** – before (CoverA $_{2017}$) and **B** – after light thinning of the tree stand (CoverA $_{2018}$) based on analysis of ALS (2017) and ULS (2018) point clouds. Also, TLS point cloud profile was marked.

(Fig. 8). The Monte Carlo permutation test (Table 5) showed that both the first axis and all canonical axes taken together were statistically significant ($F = 2.64$, $p = 0.02$ and $F = 1.79$, $p = 0.001$, respectively).

3.3. Microclimatic conditions in thinned and unthinned areas

Air temperature, air humidity and light intensity differed significantly between thinned and unthinned areas (Table 3). Also, when analysing the data in terms of time of measurement conducted, almost all of them differed significantly (Table 4.,

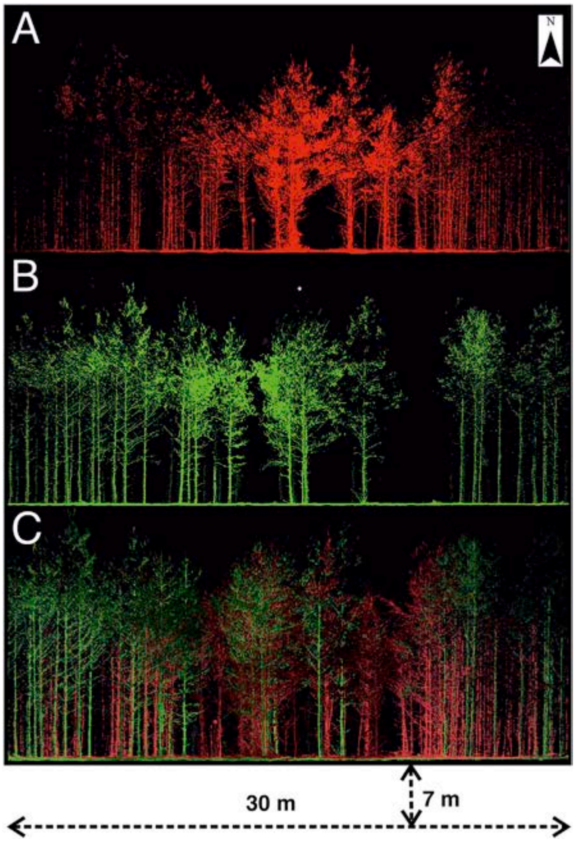

Fig. 3. Visualization of vertical structure of 19i forest subsection based on the TLS FARO FOCUS 3D point cloud (A – 2017 before thinning; B – 2018 after thinning; C – two-point clouds merged together).

Fig. 9). Based on average daytime temperature, humidity and light intensity measurements, higher amplitudes of these microclimatic factors were recorded in the thinned area (Table 4, Fig. 10).

4. Discussion

4.1. Variability of lichen Scots pine forests shaped by environmental factors

Within the analysed plots, 26 lichen species and 7 bryophyte species were recorded (Table 2 supp.). Two of these bryophytes, *Ptilidium cilliare* and *Dicranum spurium*, are associated with the lichen Scots pine forest community (Matuszkiewicz and Matuszkiewicz, 1973). This confirmed high species richness despite the slow disappearance of this habitat observed in local and regional scale (Stefanska-Krzaczek et al., 2018). *Pleurozium schreberi*, *Dicranum polysetum*, *D. scoparium* and *Hypnum cupressiforme* are the most expansive bryophyte species which have the ability to displace the terricolous lichen in the lichen Scots pine forest habitat (Schmalholz and Hylander, 2009).

The division of sampling plots into lichen-rich and bryophyte-rich forms of lichen Scots pine forest community (Fig. 6) corresponded to the successive stages of the habitat studied (Ahti and Oksanen, 1990; Reinecke et al., 2011). The phenomenon of the disappearance of lichen field layer and the spread of bryophytes in Central Europe has been repeatedly suggested by Matuszkiewicz (2007), Reinecke et al. (2011), Fischer et al. (2009, 2015), Stefanska-Krzaczek et al. (2018). Potential causes of this phenomenon were also given, including natural (autogenic successional processes) and anthropogenic (allogenic-N atmospheric deposition) changes of substrate (Reinecke et al., 2014; Fischer et al., 2015), increase in soil moisture (Sulyma and Coxson, 2001; Dingová Košuthová et al., 2013) and reduction of light availability (Botting and Fredeen, 2006; Boudreault et al., 2013; Haughian and Burton, 2015). Our research showed that only Cover A_{2017} significantly differed between lichen-rich and bryophyte-rich forms (Table 2, Fig. 7). Other factors directly connected with soil fertility, such as: Cover C, pH, EC, TOC, TN, C/N, and TOM, did not differed significantly between studied forms (Table 2, Fig. 7). However, as shown in the CCA analysis these variables affected species composition influencing each other probably in a synergistic way. Stefan;ska-Krzaczek et al. (2018) indicated that the canopy cover does not affect lichens displacement by bryophytes. This is connected with the fact that the habitat of the lichen Scots pine forest in most cases are commercial forests, which are regularly thinned – thanks to that the

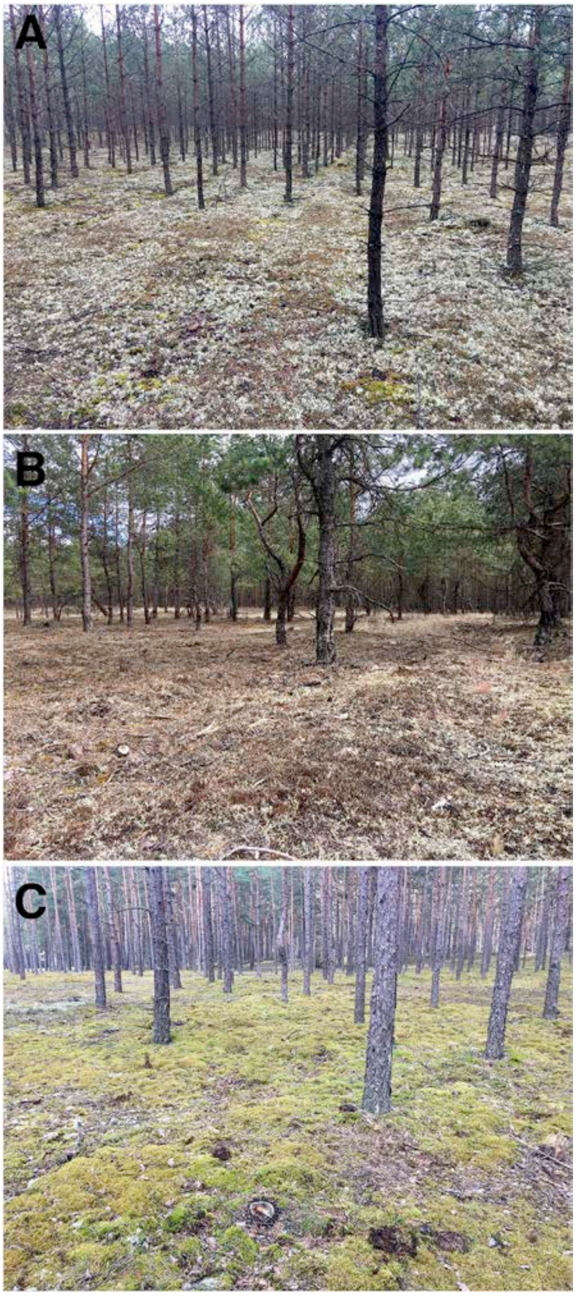

Fig. 4. Photos of lichen-rich community type in: A – 12 plot, B – 22 plot and bryophytes-rich community type in C – 23 plot.

availability of light increases during stand growth (Aussenac, 2000; Stefanska-Krzaczek et al., 2018). Obtained results from sampling plots referred to the stands in the age range from 20 to 54 years (Table 1), in whose thinning of the tree stands was not carried out due to the law protection of Bory Tucholskie National Park area. High light intensity positively effects the presence of individuals of *Cladonia* genus which are photophilic organisms (Friedmann and Gabun, 1967; Bültmann and Daniëls, 2009; Boudreault et al., 2013). In contrast, bryophytes that displaced lichen, definitely prefer shady habitat (Valanne, 1984; Marschall and Proctor, 2004). The results of our analyses confirmed the first hypothesis assuming that the increase of the tree canopy affects the disappearance of lichens in the field layer and resulted in disappearance of lichen pine forest community.

The thinning carried out in 2017 in the area of study, at the analysed sampling plots resulted in a reduction of Cover A_{2017} that was at an average level of 62.2% (Cover A_{2018}, Table 2 supp., Figs. 2 and 3). Stefańska-Krzaczek (2012, 2016) suggested that

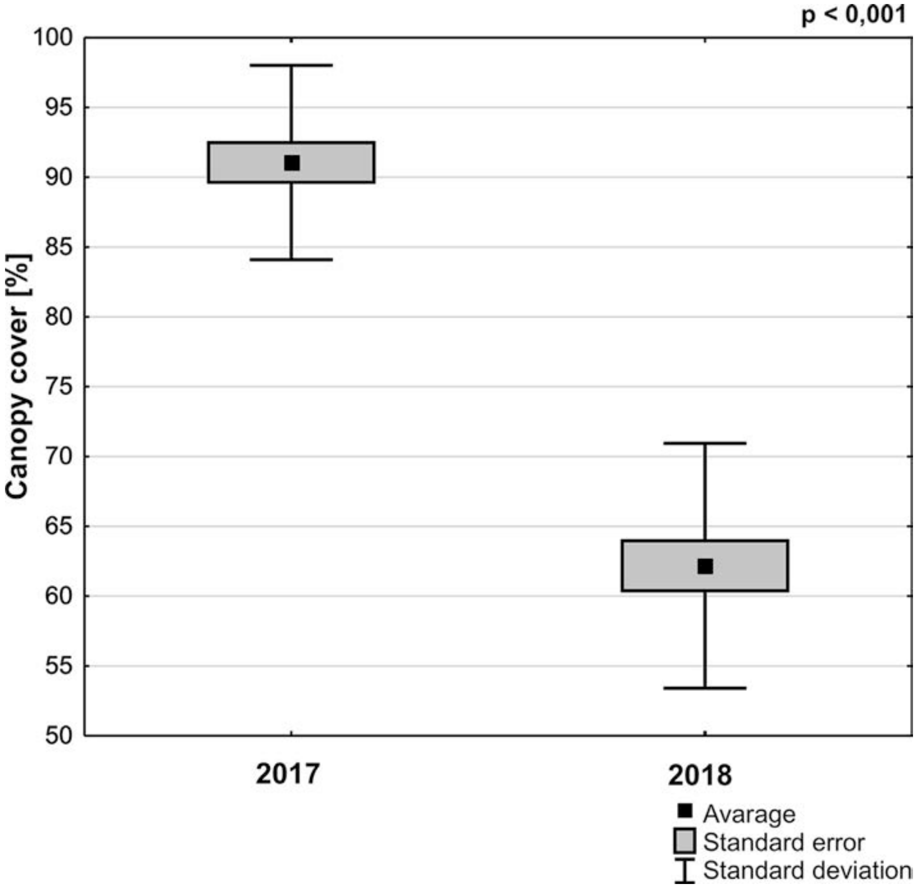

Fig. 5. Average ± SD of the canopy cover in 2017 (CoverA $_{2017}$) and in 2018 (CoverA $_{2018}$). The difference between the parameters was tested using ANOVA ($p < 0.05$) and the result is presented in the top right corner.

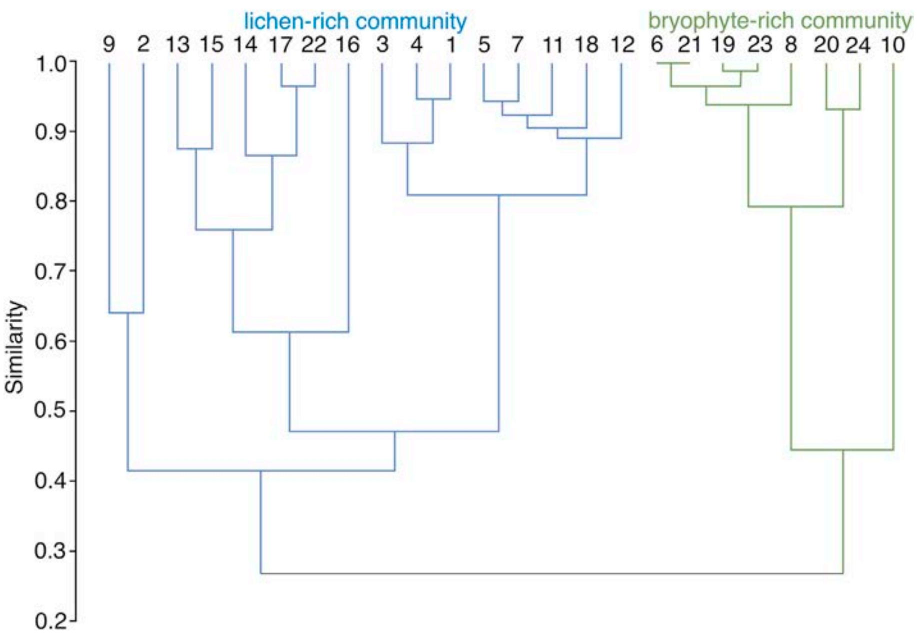

Fig. 6. Dendrogram classifying the 24 plots into two groups: lichen-rich community and bryophytes group community. For species characteristic of plots see Table 2 (supp.).

Table 2
The result of ANOVA test ($p < 0.05$) showing variables analysed in the lichen-rich and bryophyte-rich forms of *Cladonio-Pinetum* – values significantly different are marked in bold. For means see Fig. 7. Abbreviations of variables: Cover A_{2017} – canopy cover in 2017, Cover C_{2018} – herb layer in 2018, pH – soil pH, EC – soil electrical conductivity, TOC – total organic carbon, TN – total nitrogen, C/N – carbon to nitrogen ratio, TOM – thickness of organic matter.

Variables	df	F	p
Cover A_{2017}	**22**	**43630**	**0.001**
Cover C	22	0.41	0.529
pH	22	41640	0.296
EC	22	0.418	0.524
TOC	22	0.243	0.626
TN	22	0.182	0.673
C/N	22	0.25	0.62
TOM	22	31079	0.105
Species number of bryophytes	22	0.222	0.642
Species number of lichens	**22**	**5.395**	**0.029**
Cover of bryophytes	**22**	**14.65**	**0.0009**
Cover of lichens	**22**	**19.38**	**0.0002**

a large tree cover affects the field layer species by reducing the light intensity, which was clearly visible in young tree stands in which the tree canopy closes quickly. However, our results showed that it also affects the temperature and humidity of the habitat (Tables 3 and 4 and Figs. 9 and 10). An analysis of the temperature and humidity (Table 4 and Fig. 9) revealed that their extremes are much more noticeable in an area with lower canopy cover. Mornings at thinned localities were colder and more humid, however, the temperature and humidity rapidly increased till noon, and reached higher values in comparison to those recorded at the control localities. Also, the decrease in temperature and humidity in the afternoon occurred more rapidly in a thinned areas (Table 4 and Fig. 9). Different climatic conditions throughout the day in areas with lower tree cover may limit the development of vascular plants due to more severe temperature and humidity regime (Van Cleve et al., 1983; Bonan and Shugart, 1989). From the other hand, lichens, in particular, species from *Cladonia* genus are perfectly adapted to high daily air temperature amplitudes and prolonged periods of drought, therefore they are classified as xerofrigid organisms (Friedmann and Gabun, 1967; Bültmann and Daniëls, 2009). Light intensity measurements showed significantly higher values at thinned areas, which has a positive effect on lichen species by limiting the expansion of bryophytes (Heinken, 1999, 2007).

4.2. Impact of environmental factors on changes occurring in the habitat

According to CCA analysis (Table 5, Fig. 8), the following factors influenced distribution of lichens, bryophytes and vascular plants species in the lichen pine forest: TOM, Cover A, TN, and pH. The field layer of bryophytes-rich form was related to increasing TOM (Fig. 8). While the appearance of terricolous lichen species was connected with lower Cover A_{2017} and lower substrate pH (Fig. 8). High value of TN content in organic matter was positively connected with the occurrence of the following vascular plant species: *Deschampsia flexuosa*, *Luzula pallescens* and *Vaccinium myrtillus* (Fig. 8), which confirms the truthfulness of the second hypothesis that lower value of total nitrogen in organic layer has a positive effect on terricolous lichens presence. Oligotrophic lichen-rich pine forests are mostly organic matter layer-poor degenerative stages, originating in litter raking, which formed in areas after nutrient depletion (Heinken, 2007; EEA, 2011; Aggenbach et al., 2017). The abandonment of litter-raking practices causes increase in the organic matter layer and the lichen pine forest habitats formed in poor anthropogenic areas are beginning to disappear, transforming into bryophyte-rich communities of the mesotrophic forest type (Ellenberg and Leuschner, 2010). As the amount of organic matter increases, the pH decreases, and the processes of organic matter decomposition increase TN content in the substrate. Increase of this factor also intensifies the disappearance of lichen species (van Dobben et al., 1999, 2017; Prietzel and Kaiser, 2005; Dirnböck et al., 2014). Nevertheless, we are still unable to determine the participation of autogenic-recovery processes of habitats and atmosphere allogenic-N deposition in the nitrogen input. This is because the cessation of raking litter coincided with the onset of an increase in air pollution (Dzwonko and Gawronski, 2002). However, comparing vegetation succession sequences from *Cladonio-Pinetum* association to the *Leucobryo-Pinetum* association, and further to the *Deschampsia-Pinus* association (Heinken, 1999, 2007), with more recent research (Reinecke et al., 2014), it turned out that current changes in species composition are different. This may indicate that the observed changes in species composition cannot be easily attributed to only autogenic successional processes (Reinecke et al., 2014). Thus, the allogenic-N atmospheric deposition, is large enough to maintain the lichen pine forest communities at current or better condition will be extremely difficult. The same situation is regarding to gradual increase in carbon sequestration in the forest soils as a response to rising atmospheric CO2 in the result of climate changes, where the determination of importance for this process requires further study (Niinistö et al., 2004).

4.3. Importance of thinning process as the valuable method of active protection of lichen pine forest community

The presented results are documentation for the implemented active protection in the area of lichen pine forest community in the Bory Tucholskie National Park. Preparations of thinning process in selected stands of this habitat gave the opportunity to collect data that was used in presented paper and can will be used to assess the further changes of the

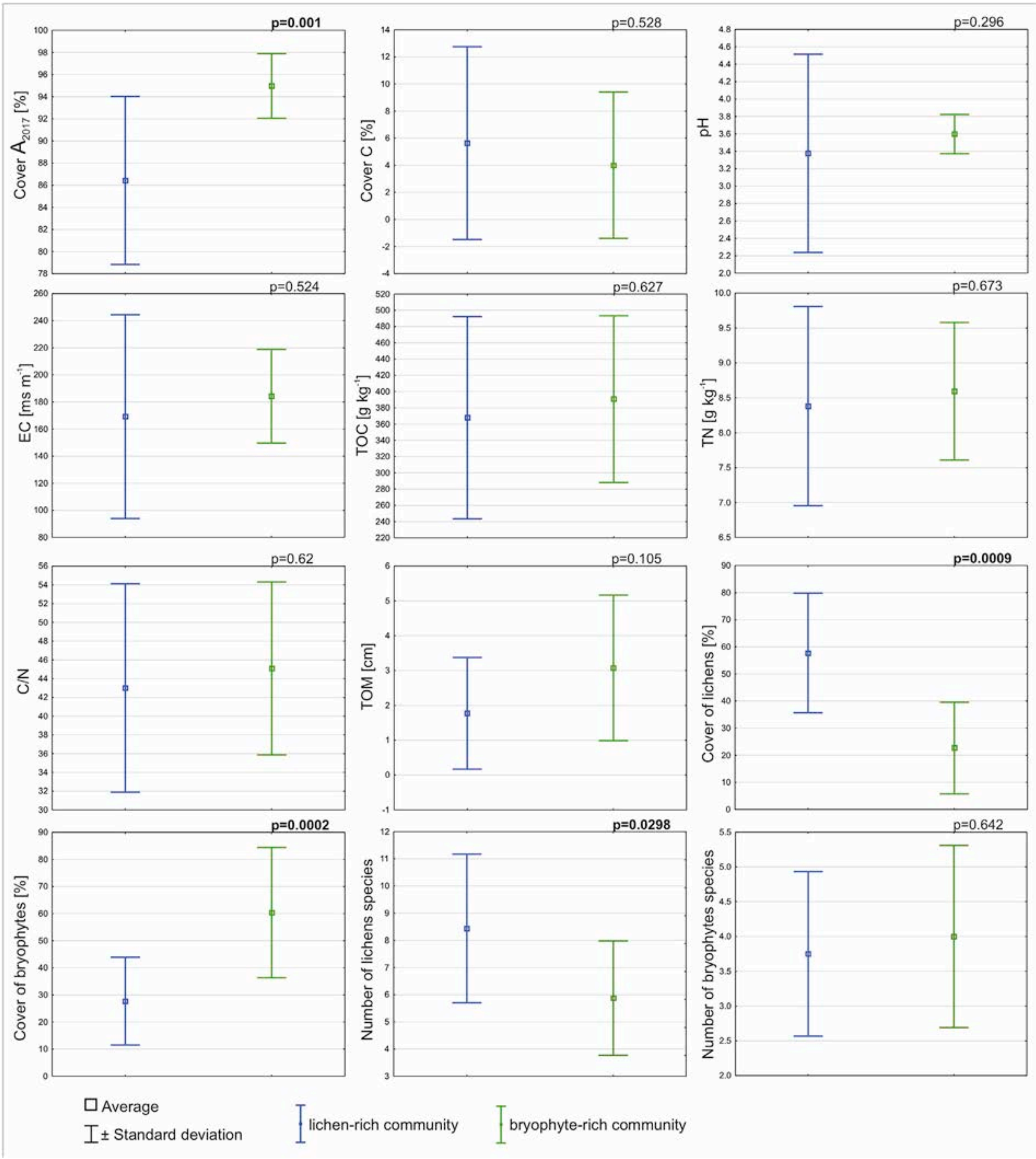

Fig. 7. Average ± SD of studied variables including community form (lichen-rich and bryophytes-rich). The results of ANOVA ($p < 0.05$) are presented graphically.

endangered habitat in the future. Until now, no such detailed research on the differences between lichen-rich and bryophyte rich community types and lichen field layer active protection has been performed.

The proposed simple method of forest stand thinning seems to be the most effective form of protection of lichen pine forest community. Its effectiveness has been confirmed in long-term observations carried out in Finland (Miina et al., 2020). The results of our research showed that the decreasing of percentage of tree canopy cover, allowed to provide favorable habitat conditions for lichens, and at the same time effectively limited the unwanted and expansive bryophytes species.

In our research, we also indicated the importance of soil fertility for the occurrence of lichen field layer, which is also demonstrated in the latest study conducted in the forests of Finland (Miina et al., 2020). However, it is necessary to consider

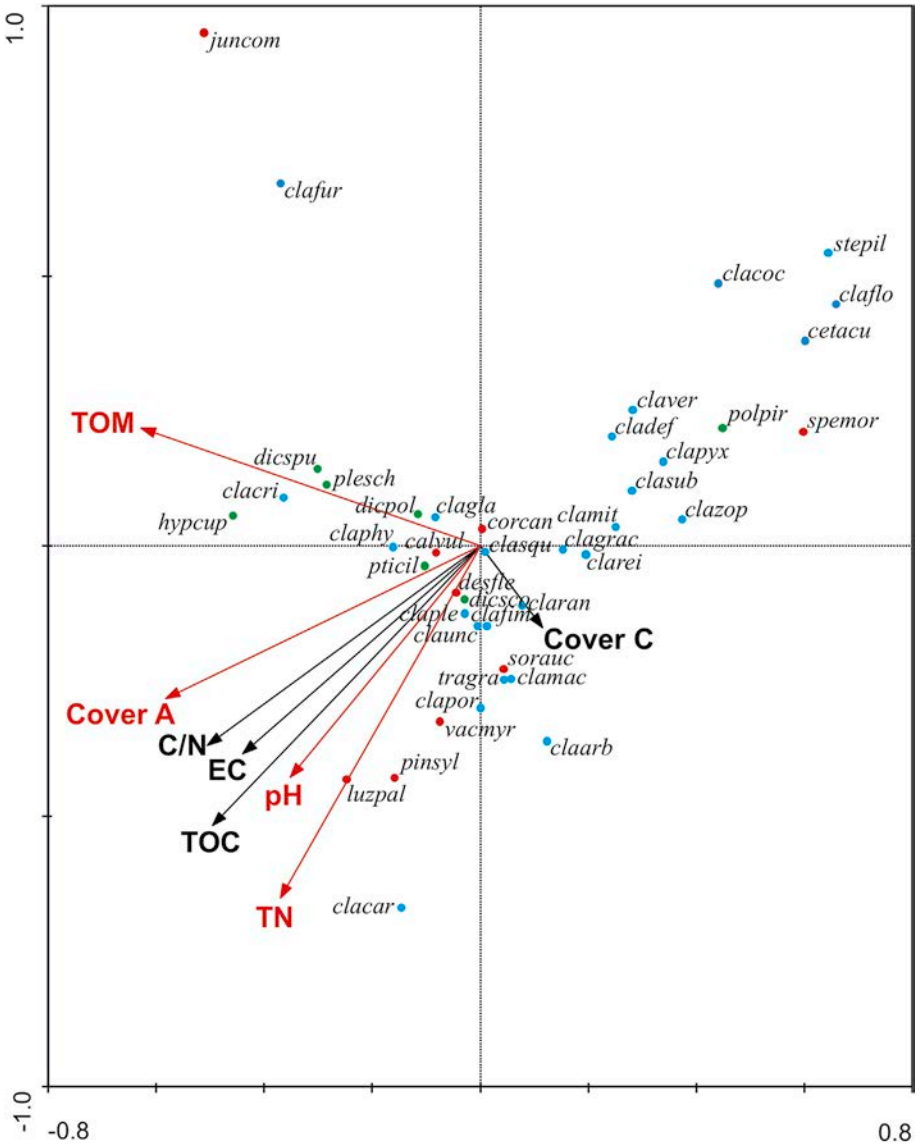

Fig. 8. CCA biplot with species and environmental variables. The variance explained by the first canonical axis is 29.7%, by second axis is14%, whereas tested variables explained 7,23% of variability in species composition (eigenvalue of first canonical axis – 0.314; eigenvalue of second canonical axis – 0.149). Significant variables identified in forward selection procedure are marked by red colour (Table 5). Abbreviations of variables: Cover A – cover of tree layer in 2017, TOM – thickness of organic matter, pH – soil pH, EC – soil electrical conductivity, TOC – total organic carbon, TN – total nitrogen, C/N – carbon to nitrogen ratio. Abbreviations of species names: vascular plants (red dots) - calvul – *Calluna vulgaris*, corcan – *Corynephorus canescens*, desfle – *Deschampsia flexuosa*, juncom – *Juniperus communis*, luzpal – *Luzula pallescens*, pinsyl – *Pinus sylvestris*, sorauc – *Sorbus aucuparia*, spemor – *Spergula morisonii*, vacmyr – *Vaccinium myrtillus*,; bryophytes (green dots) - dicpol – *Dicranum polysetum*, dicsco – *D. scoparium*, dicspu – *D. spurium*, hypcup – *Hypnum cupressiforme*, plesch – *Pleurozium schreberi*, polpir – *Polytrichum piliferum*, pticil – *Ptilidium ciliare*.; lichens (blue dots) - cetacu – *Cetraria acuelata*, claarb – *Cladonia arbuscula*, calcar – *Cl. cariosa*, clacoc – *Cl. coccifera*, clacri – *Cl. crispata*, cladef – *Cl. deformis*, claflo – *Cl. floerkeana*, clafim – *Cl. fimbriata*, clafur – *Cl. furcata*, clagla – *Cl. glauca*, clagrac – *Cl. gracilis*, clamac – *Cl. macilenta*, clamit – *Cl. mitis*, claphy – *Cl. phyllophora*, clapyx – *Cl. pyxidate*, claple – *Cl. pleurota*, clapor – *Cl. portentosa*, claran – *Cl. rangiferina*, clarei – *Cl. rei*, clasqu – *Cl. squamosa*, clasub – *Cl. subulata*, claunc – *Cl. uncialis*, claver – *Cl. verticillata*, clazop – *Cl. zopfi*, stepil – *Stereocaulon pileatum*, tragra – *Trapeliopsis granulosa*. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Table 3
The result of Wilcoxon test ($p < 0.05$) showing differences in air temperature, air humidity, light intensity between thinned and unthinned areas.

Microclimatic parameter	Z	p-value
Air temperature	3.117094	0.001826
Air humidity	14.21972	0.000000
Light intensity	33.99620	0.000000

Table 4
The result of Wilcoxon test ($p < 0.05$) showing differences in air temperature, air humidity, light intensity between time of measurement between thinned and unthinned areas. For means see Fig. 9.

Wilcoxon	Hour of measurement	Z	p-value
Air temperature	00:00	11.81295	p < 0.001
	03:00	12.77818	p < 0.001
	06:00	7.730325	p < 0.001
	09:00	1.550115	0.121114
	12:00	12.06704	p < 0.001
	15:00	16.10427	p < 0.001
	18:00	5.063517	p < 0.001
	21:00	11.73963	p < 0.001
Air humidity	00:00	12.96823	p < 0.001
	03:00	13.06187	p < 0.001
	06:00	12.11075	p < 0.001
	09:00	1.879651	0.060156
	12:00	6.563568	p < 0.001
	15:00	5.735730	p < 0.001
	18:00	4.604194	p < 0.001
	21:00	11.88877	p < 0.001
Light intensity	06:00	13.15316	p < 0.001
	09:00	13.50434	p < 0.001
	12:00	12.14344	p < 0.001
	15:00	18.52921	p < 0.001
	18:00	15.36471	p < 0.001
	21:00	10.09998	p < 0.001

Table 5
Results of forward selection and Monte Carlo permutation tests from CCA (Fig. 10). Environmental variables are listed by the order of their inclusion in the model (lambda A). Significant variables are in bold ($p < 0.05$). Abbreviation for variables: TOM – thickness of organic matter, Cover A_{2017} – canopy cover in 2017, TN – total nitrogen, pH – soil pH, C/N – carbon to nitrogen ratio, TOC – total organic carbon, EC – soil electrical conductivity, Cover C – cover of vascular plant layer.

Variable	Lambda1	LambdaA	P	F
TOM	**0.20**	**0.20**	**0.001**	**2.50**
Cover A_{2017}	**0.18**	**0.19**	**0.003**	**2.50**
TN	**0.15**	**0.12**	**0.028**	**1.67**
pH	**0.14**	**0.12**	**0.047**	**1.64**
C/N	0.14	0.11	0.054	1.66
TOC	0.15	0.08	0.314	1.11
EC	0.14	0.07	0.336	1.12
Cover C	0.06	0.06	0.516	0.93

whether supplementing the active protection of the habitat by using methods for reduction soil fertility, e.g. raking the mulch and removing the bryophyte layer, will bring rapid effects of regrowth of the terricolous lichens layer.

The project implementation is long-term. The designated sampling plots will be continuously studied in terms of changes resulting from performed active protection in the upcoming years. Thanks to that the effectiveness of the proposed methods will be detailed evaluated in practice after several years elapsed after implementation of thinning.

5. Conclusion

Our research conducted in the Bory Tucholskie National Park provides information on environmental factors that shape the lichen Scot's pine forest community. Our results show the negative impact of increasing TOM, TN and Cover A_{2017} (the latter one leads to changes in microclimatic conditions) on lichen field layer. Due to the fact that mat-forming terrestrial lichens are closely associated with low productive areas with easy access to light, they are not able to compete with bryophytes in habitats with high TOM and TN contents in soil as well as high tree canopy. The increase of sunlight reduces the development of bryophytes and thus reduces the growth of biomass in the field layer and inhibits the development of an organic matter layer. It also indirectly affects the TOM which for creating conditions appropriate to lichen growth should reach the value of less than 2 cm. Reduction of the canopy cover to the level of 60% may be the easiest method to maintain lichen pine forests with high abundance of lichens in field layer. This is particularly important in relation to the observed disappearance of lichen pine forest habitats in Europe. Due to this tendency, it is particularly important to actively protect the lichen pine forest communities, especially in designated sites protected by law. This will allow to preserve species diversity, observe of the community changes, and improve the applied methods of habitat protection.

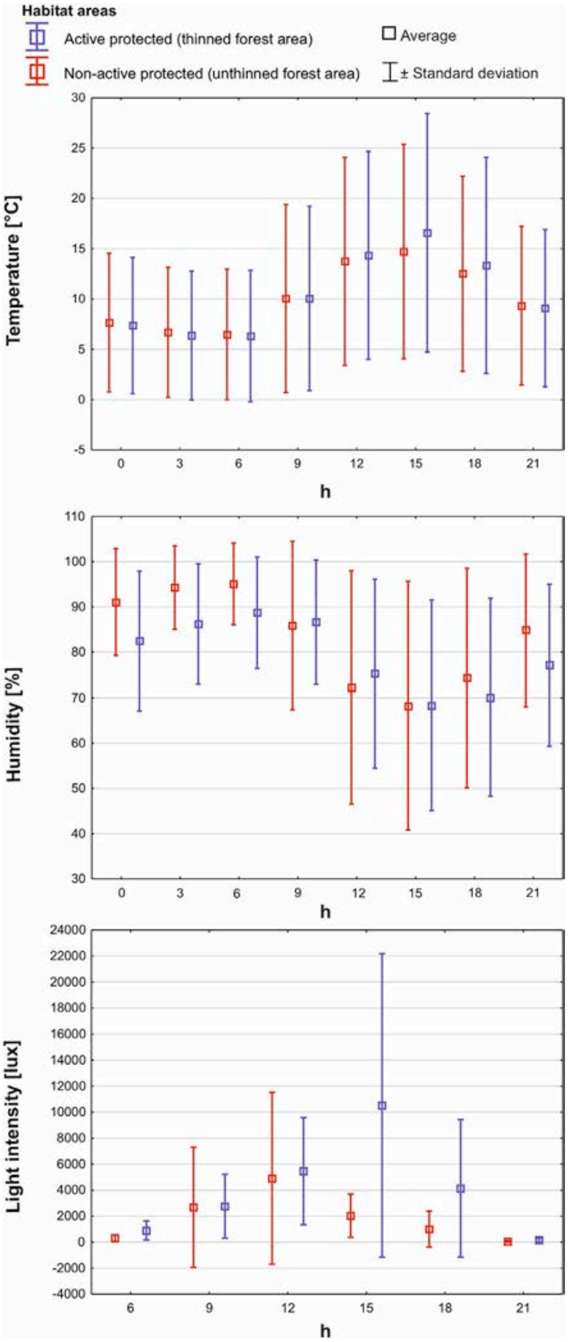

Fig. 9. Average ± SD of air temperature, air humidity and light intensity in relation to measuring hours, between thinned (19i forest subsection) and unthinned (20g forest subsection) areas using the Wilcoxon test for $p < 0.05$.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

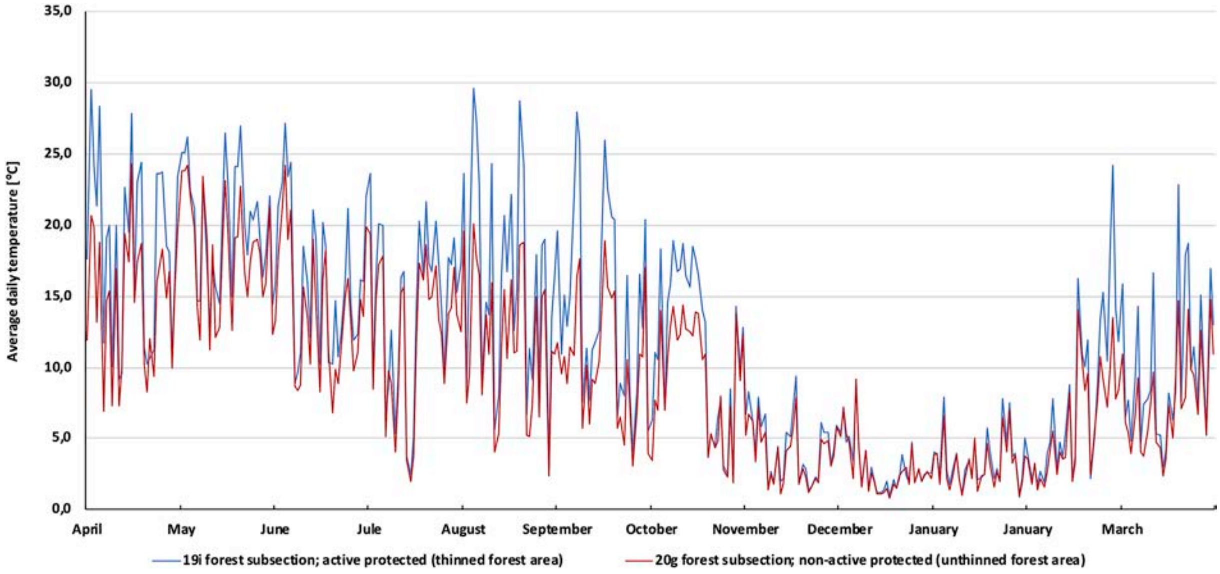

Fig. 10. Average daily temperatures measured at two localities: in the thinned (19i forest subsection) and unthinned (20g forest subsection) areas.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.gecco.2020.e01017.

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