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Long-term changes in bryophyte diversity of central European managed forests depending on site environmental features

Cecilia Cacciatori[1] · Janusz Czerepko[2] · Paweł Lech[2]

Abstract

Cryptogamic diversity is a reliable indicator of the state of forest ecosystems. In this study we analysed the variations in both bryophyte species richness overall and number of hemerophobic bryophyte species in Central European managed forests over a 20-year time span, based on data collected in 132 plots scattered across Poland. We tested differences in species richness among five temporal replicates, as well as among site types grouped based on elevation a.s.l., dominant tree species and stand age. The analyses revealed no significant trend in species richness across years. Meanwhile, species richness significantly increased along with elevation a.s.l., especially in broadleaved forests. No significant difference in species number between spruce and pine dominated stands emerged for mature stands, while there was a strong difference for young stands, with spruce forest hosting a much higher number of species. Species richness exhibited a slight, but not significant, increase over time in broadleaved forests, no significant variations in pine dominated stands and significant fluctuations in spruce dominated stands, yet without a significant trend. Out of the tested drivers, dominant tree species exhibited the strongest impact on species community composition. Number of hemerophobic and strongly hemerophobic species did not undergo significant variations across years either. The lack of bryophyte diversity trends highlighted in this study suggests Central European managed forests are in an equilibrium sate, maintained by the opposing effects of climate changes, on one side and of more sustainable forest management and pollutant deposition decline, from the other.

Keywords Anthropogenic disturbance · Cryptogamic diversity · Elevation a.s.l. · Forest type · Hemerophobic species · Stand age

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Introduction

Forests of the temperate belt have undergone profound changes during the last centuries. Management, climate changes and pollutant deposition have deeply altered structure, composition and diversity of these forests (Hannah et al. 1995; Bengtsson et al. 2000; Loustau et al. 2007). In the European continent, the impact of anthropogenic disturbance has been particularly strong, because of the high density of human population and the close proximity of forested areas and inhabited ones. One straightforward way to evaluate the extent of human impact on forest ecosystems is to examine changes in diversity and composition of biological communities. This method is particularly effective when the tested organisms exhibit high responsiveness to anthropogenic disturbance, like cryptogams (Wolf 2005; Werner and Gradstein 2009).

Bryophytes are widely acknowledged to be highly sensitive to environmental changes (Newmaster and Bell 2002; Vanderpoorten and Engels 2002; Rudolphi et al. 2014) and, owing to this property, they are extensively used as indicators of the state of forest ecosystems (Frego 2007; Hofmeister et al. 2015; Mölder et al. 2015; Czerepko et al. 2021). In undisturbed conditions, forest bryoflora is rich and diversified and hosts most rare and endangered bryophyte species, whose survival is strictly linked to the preservation of these conditions (Gustafsson and Hallingback 1988; Cooper-Ellis 1998). That is because forests, by constantly supplying environmental moisture through evapotranspiration and buffering the understory from temperature extremes and water loss thanks to the shading effects of tree canopies, provide stable climatic conditions (Chen et al. 1999; Suggitt et al. 2011; von Arx et al. 2013; Frey et al. 2016), which ensure suitable habitats for poikilohydric organisms such as bryophytes. Canopy Forests also supply a variety of micro-habitats acting as microrefugia for specialized bryophytes, e.g. stumps, logs, cavities/hollows, bark furrows, uplifted root system of uprooted trees.

However, due to anthropogenic disturbance, environmental conditions in forest ecosystems have become less stable, which poses a serious threat to bryophyte diversity (Hodgetts et al. 2019). Climate changes have caused significant increase in tree evapotranspiration rates (Qu and Zhuang, 2019; Teuling et al. 2019) and the decrease in moisture content of forest soils (EEA Report 2017; Pińskwar et al. 2020). Besides, they have also extended the length of dry periods (Kundzewicz and Matczak 2012; Hänsel 2020; IPCC 2021), which threatens the less desiccation tolerant bryophyte species, such as most liverworts. Meanwhile, forest management directly affects forest structure, micro-climate and habitat heterogeneity. Although forest cover in Europe has been constantly increasing since the half of the last century (Kauppi et al. 1992; Houghton 1995), up until recently the mean age of forest stands, as well as their compositional heterogeneity, have been consistently decreasing, old-growth deciduous forests being gradually replaced by even-aged coniferous plantations, coppices or semi-natural forests (Bengtsson et al. 2000; Zerbe 2002; Paquette and Messier 2009; FAO 2011; Forest Europe 2011; West 2014). The systematic removal of large, old trees and of decaying wood determines the loss of micro-habitats for specialized bryophyte species. The paramount importance of variety and distribution of such micro-habitats in driving bryophyte diversity has been extensively described (Ross-Davis and Frego 2002; Shelley et al. 2012; Mills and MacDonlad 2004; NewMaster et al. 2005).

Pollution too contributes to bryophyte diversity decline. Since bryophytes lack a cuticle and stomata, they are more exposed to the effects of nitrogen and sulphur deposition than vascular plants (Longton 1988; Becker-Scarpitta et al. 2017). High levels of N deposition can damage bryophyte species adapted to grow under N poor conditions (Nordin et al.

2005) and facilitates the spread of synanthropic species with highly competitive strategies, which tend to quickly dominate in terms of biomass and ultimately eliminate the more sensitive and less competitive species, thus determining a decrease in bryophyte diversity (Haworth et al. 2007; Roth et al. 2013). Sulphur deposition was also shown to negatively affect sensitive bryophyte species (Farmer et al. 1991, 1992; Lee and Studholme 1992; Makipaa 1995; Sjogren 1995), although its effects are mostly hard to distinguish from those of N deposition.

In view of their sensitivity to disturbance, examination of changes in bryophyte diversity over time may thus provide relevant information about the response of forest ecosystems to anthropogenic pressure. However, not all bryophytes species exhibit high responsiveness to environmental changes. Many of them display a wide tolerance range and occur in different habitats, as well as on different substrates. Others are more demanding in their physiological requirements (Gignac 2001; Proctor et al. 2007) and are thus restricted to habitats characterized by specific micro-environmental conditions. Within this second group, those species unable to live within areas unaffected by anthropogenic disturbance are referred to as hemerophobic (Linkola 1916) or, alternatively, as primeval forest relics (Cieślinski et al. 1996) or woodland indicator species (Müller et al. 2019). Hemerophobic species are mostly associated with undisturbed habitats, shady and moist conditions and specific substrates such as logs in advanced stage of decomposition and large, old trees. These species being restricted in their occurrence to these substrates demonstrates the importance of the latter for organisms otherwise characterized by remarkable dispersal abilities such as bryophytes (Medina et al. 2011; Sundberg 2005, 2013; Szövényi et al. 2012). This is also because bryophytes occurring on the ground have to compete with vascular plants for physical space and access to resources and usually get the worst of it because of their much smaller size (Looman 1964; van Wijik et al. 2003; van der Wal et al. 2005; Walker et al. 2006; Alatalo et al. 2020), so that availability of substrates generally unsuitable for vascular plants (such as tree bark and dead-wood) represents a constraining factor for many bryophyte species, especially for liverworts and tiny mosses.

However, bryophytes also occur in managed forests, provided they can find suitable micro-environmental conditions. Czerepko et al. (2021) found that, while most bryophyte species did not exhibit a significant response to the gradient of forest naturalness expressed by different management regimes and protection time spans, red-listed or primeval forest relics showed a twice higher frequency in undisturbed, close to pristine forest habitats and nature reserves than in managed forests. By analysing patterns of diversity and dynamics of hemerophobic species richness, we may thus obtain a more reliable information about the response and adaptation of forests to anthropogenic disturbance than examining bryophyte diversity overall.

Managed forests make up 95% of the forest area in Europe (Forest Europe 2020), therefore knowledge about the dynamics of bryophyte diversity in these areas is essential to evaluate the state of bryophyte diversity in the European continent. So far, most studies about bryophyte diversity in forest ecosystems have focused on the difference in diversity patterns among areas characterized by different forest types, climate and management regimes, usually comparing two or a few sites (Humphrey et al. 2002; Hofmeister et al. 2015; Müller et al. 2019; Czerepko et al. 2020). Much less is known about temporal changes in forest bryophyte diversity across large areas. Dittrich et al. (2016) examined changes in bryophyte diversity in the German forests since the beginning of the nineteenth century, but their study involved only two temporal replicates and focused just on beech forests. Becker-Scarpitta et al. (2017), instead, followed changes in bryophyte diversity over a thirty-year time span, but with more replicates.

However, these changes were monitored at just one forest site. Lastly, Baumann et al. (2021) monitored changes in ground bryophytes over three decades, but they also focused only on one forest type, i.e. spruce forests. Furthermore, none of these studies examined changes in bryophyte diversity depending on forest site features.

In this study, we aimed at highlighting changes in bryophyte species richness and number of hemerophobic species in forest sites across Poland during a 20-year-lifespan, including five replicates, thus combining both spatial and temporal analyses. Unlike in Dittrich et al. (2016) and Becker-Scarpitta et al. (2017), these study sites encompass different forest types, which were tested separately. Changes in species richness and number of hemerophobic species were analysed for all sites together, as well as for different site clusters based on dominant tree species, stand age and elevation a.s.l. The study was based on data collected between 1998 and 2019 from ICP Forest level II plots.

In particular, we wanted to test the hypotheses that: (1) species richness of bryophytes overall has decreased over time due to increasing dry conditions in Polish forests and the long-term impact of forest management; (2) the highest species richness is to be found at higher elevations, in oldest forests and in broadleaved stands; (3) the number of hemerophobic species decreased over time and this decreased was stronger than the decrease of bryophyte species overall, hemerophobic species being more sensitive to environmental changes than generalists.

Materials and methods

Study site

This study was based on data collected in 132 plots scattered across Poland (Fig. 1), established in the frame of the ICP Forests Monitoring Level II plots and ranging between 11 to 991 m a.s.l. The monitoring network originally included 148 study plots (Fig. 1), but areas where no monitoring was carried out following stand breakdown caused by bark beetle infestation or windstorms were excluded from the study.

The Polish climate is predominantly continental, with an average annual temperature of 8.7 °C in the period 1991–2020 and an average annual precipitation of about 609 mm (Klimat Polski 2021). Precipitation varies greatly from region to region, especially between mountains and lowlands, ranging from over 1300 mm in the Sudetes and Carpathians to about 500 mm in the central part of the country (Wielkopolska, Mazovia) (Kluziński 2021). The forest site types encompassed by the study areas can grouped into oligotrophic (mixed-coniferous—33%, coniferous—26%) and and mesotrophic (deciduous 20%, mixed deciduous 21%). The dominant tree species on the plots was *Pinus sylvestris* (73% of the total surface) followed by by *Picea abies* (8–10%), *Quercus robur* and *Fagus sylvatica*. The mean age of stands at the beginning of monitoring (1998) was 61 years old, ranging between 45 and 96. Most sample plots had a stand age below 80 years, and only the 7% of them was older. All sampled plots were under forest management, selective thinning being carried out every 10–20 years, variations within this range depending on the main tree species, with a percentage of wood volume removed amounting to ca. 6%.
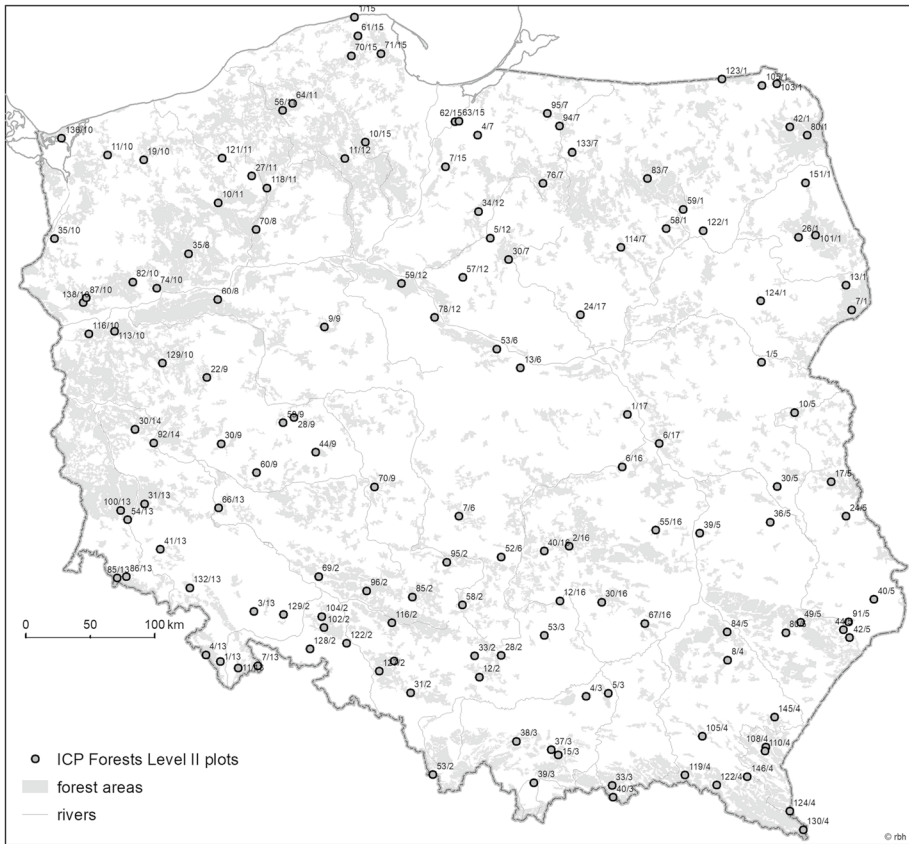
Fig. 1 Distribution of ICP Forests Level II plots in Poland

Sampling design

At each of the 132 monitoring plots, sampling was carried out in a 20×20 m square plot, according to the European protocol for monitoring of forest areas (Stofer et al. 2016). Bryophytes were sampled on living trees up to a height of 2 m, standing and lying dead wood, ground and rocks. Cover relative to the area of the substrate was assigned based on the protocol proposed by Solon and Wawrzoniak (1999), however, to the purposes of this work, only presence absence data were employed, as it is often the case when assemblages growing on different substrates are examined. In fact, since most recorded species occurred in the same plots on different substrates, calculating the mean cover of these species per plot based on covers recorded on different substrates would be methodologically questionable. Sampling was carried out in 1998–1999, 2003, 2008, 2013, 2019.

Out of the whole set of species recorded in the survey, hemerophobic species were identified based on Dierßen (2001) and include both ahemerophobic and oligohemerophobic species. Analyses of changes in species richness were performed both based on the whole community and on the three separate groups identified based on level of hemerophoby: non-hemerophobic (NH), hemerophobic (N) and strongly hemerophobic (SH).

Nomenclature of bryophyte species follows Hodgetts et al. (2020).

Statistical analyses

In order to evaluate the degree of overlap in the sets of species recorded per each year of the survey and thus infer the potential weight of the observer bias, we analysed the trend of the error in measuring the multivariate dispersion of the community with increasing sampling effort by using the Jaccard index. Overall differences in species richness and number of NH, H and SH species across years was tested using Generalized Linear Models (GLM) with a quasi-poisson family error (data being overdispersed). Posthoc multiple comparisons were performed using least-squares means and Holm correction using "emmeans" R package. (Lenth 2022a, b). The variation of bryophyte species richness as a function of elevation and the first-order interaction between stand age (2 levels: M—Mature, Y—Young) and stand type (3 levels: Broadleaved—B, Pine—P, and Spruce—S) was assessed using Generalized Linear Mixed Models (GLMMs) and Poisson error family. Specifically, stand age and stand type were treated as fixed effects while temporal autocorrelation among observations was accounted for using Years as random effect. Model's R2 was computed by means of a standardized generalized variance approach using "r2glmm" R package (Jaeger 2017). Since stands dominated by *Q. robur* and *F.sylvatica* (B) were all over 60 years old, it was not possible to test the interaction between stand ages and dominant tree species within this level which was excluded from this analysis.

The Variation Partitioning approach (Borcard et al. 1992; Økland 2003; Legendre 2008) was used on each group of variables to assess the proportion of compositional variation explained by their unshared and shared effects. Patterns of species compositional variation in samples and their environmental correlates were further explored using a Redundancy Analysis (Legendre and Legendre 2012).

The trend of the error in measuring the multivariate dispersion of the community with increasing sampling effort was obtained by using the SSP R package (Anderson and Santana-Garcon 2015). GLMMs were performed using "lmerTest" and 'lme4″ R packages (Kuznetsova et al. 2017; Bates et al. 2015), while effect plots were obtained using "effects" R package (Fox and Weisberg 2019). Variation Partitioning and RDA was performed using the *vegan* package (Oksanen et al. 2020). All analyses were carried out in the R software 4.1.1 (R Core Team 2021).

Results

Overall, 132 species were recorded, out of which 110 mosses and 22 liverworts (Appendix 1). The total number of species per year ranged between 84 in 1998/1999 and 98 in 2008, while the average number of species per plot ranged between 8 and 9, being the highest in 2008 and the lowest in 2003.

The observations appear relatively robust to the observer bias, no strong deviations in the set of recorded species among different years and in the relative error being observed (Appendix 2).

GLMM exhibited a good explanatory power (R2 = 0.12). No significant variation in species richness across years was highlighted by the model, neither for bryophytes overall, nor for mosses and liverworts separately (Fig. 2). The only significant difference in species richness among years was found between 2003 and 2008 (Table 1).
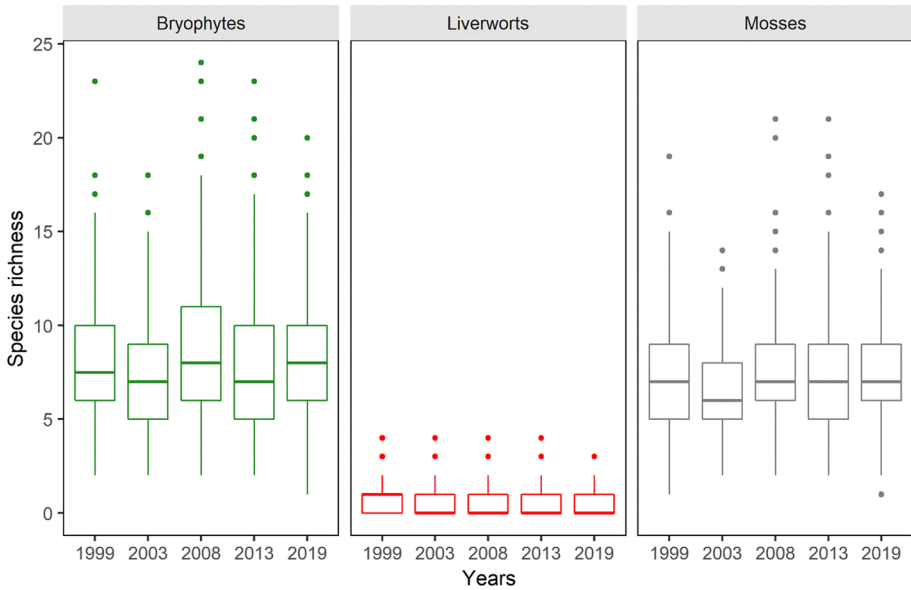
Fig. 2 GLM model showing the differences in species richness among years for bryophytes overall, liverworts and mosses

Table 1 Posthoc test of the GLM model concerning difference among years, calculated using the estimated marginal means (EMMs) and Holm correction

Comparison	Estimate	SE	p-value
Taxa			
Bryophytes—Liverworts	2.518	0.0619	**< .0001**
Bryophytes—Mosses	0.121	0.0247	**< .0001**
Liverworts—Mosses	− 2.397	0.0622	**< .0001**
Years			
1999–2003	0.0909	0.0387	0.1512
1999–2008	− 0.0631	0.0372	0.4503
1999–2013	0.0273	0.0381	1
1999–2019	0.0118	0.0379	1
2003–2008	− 0.1541	0.0382	**0.0006**
2003–2013	− 0.0637	0.0391	0.4503
2003–2019	− 0.0791	0.0389	0.2936
2008–2013	0.0904	0.0376	0.1455
2008–2019	0.0749	0.0374	0.2936
2013–2019	− 0.0155	0.0383	1

"."=marginally significant

Species richness stands exhibited a slight, but not significant, increase in broadleaved forests, no significant variations in pine dominated stands and significant fluctuations in spruce dominated stands, yet without a significant trend (Fig. 3). Since the first years of observations the number of species in broadleaved forest stands increased relative to the number of species in stands dominated by *Pinus* and *Picea*, until it exceeded the number
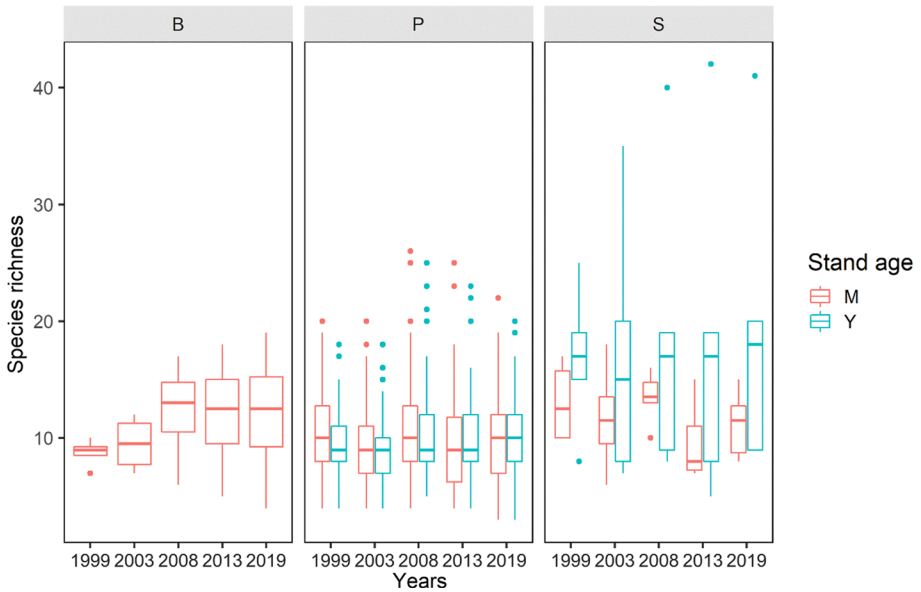
Fig. 3 GLMM model showing the interaction between stand age and dominant tree species controlling for the year. Broadleaved forest stands were excluded from the model since they had no stands younger than 60 years. *B* broadleaved, *P* pine, *S* spruce

of species in *Picea* dominated stands in 2013. Overall, the highest species richness was recorded in stands dominated by *Picea abies*, and the lowest in those dominated by *Pinus sylvestris*.

We observed a positive relationship between bryophyte species richness and elevation (Table 2) which was driven by broadleaved stands (Fig. 4). We also detected a significant interaction between dominant tree species and stand age (Table 2). Surprisingly, no significant difference in species richness between spruce and pine dominated stands emerged for mature stands, while a strong difference was observed for young stands (Table 3). While pine dominated stands the number of species was slightly higher in older than younger stands, in spruce dominated forests it was the opposite, with younger stands exhibiting a significantly higher number of species than old ones (Fig. 5). Fluctuations in the number of species per year were stronger in spruce dominated forests. Without distinction among dominant tree species, the highest number of species was recorded in older forest stands.

Table 2 Summary statistics of the GLMM model

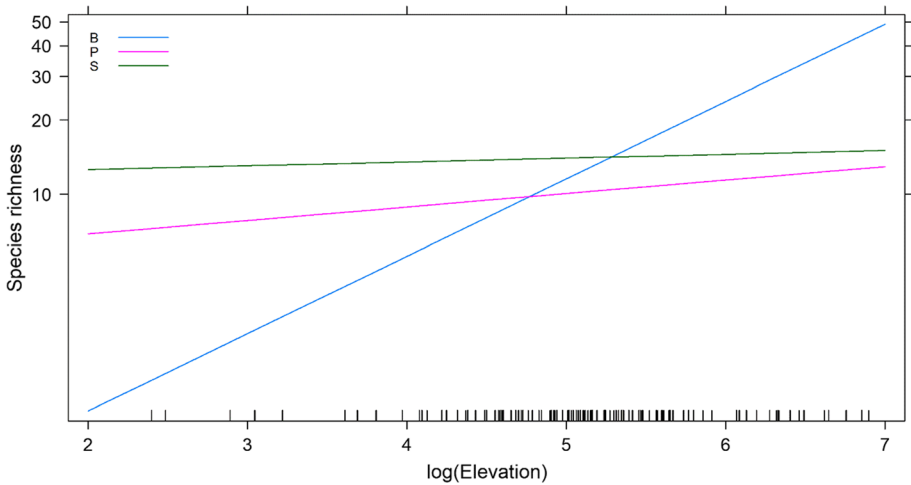|	Estimate	SE	Z value	Pr(>|z|)
(Intercept)	1.72581	0.09471	18.221	<2e−16***
Log_Elevation	0.11478	0.01756	6.537	6.29e−11***
DomSpecies2S	0.03984	0.05847	0.681	0.496
AgeDomFY	0.01893	0.02677	0.707	0.479
DomSpecies 2S:AgeDomFY	0.38801	0.07616	5.095	3.49e−07***

*** indicates p = <0.001

Fig. 4 Relationship between species richness and elevation a.s.l for broadleaved (blue), pine (purple) and spruce (green) forest stands

Table 3 Post-hoc multiple comparison values among the interaction levels of the model

Comparison	Estimate	SE	z-ratio	p-value
P M–S M	− 0.0398	0.0585	− 0.681	1
P M–P Y	− 0.0189	0.0268	− 0.707	1
P M–S Y	− 0.4468	0.0536	− 8.334	<.0001
S M–P Y	0.0209	0.0605	0.346	1
S M–S Y	− 0.4069	0.0711	− 5.722	<.0001
P Y–S Y	− 0.4278	0.0561	− 7.633	<.0001

PM pine mature, *SM* spruce mature, *PY* pine young, *SY* spruce young

Hemerophobic species amounted to 66, while strongly hemerophobic to 13 (Supplementary Materials 2) and neither group showed any significant variation over time (Fig. 6).

Variation Partitioning explained around 10% of the total variation in community composition, both for the overall community and for its sub-groups (NH, H, SH), and showed that the main driver of the community is the dominant tree species, followed by elevation a.s.l. (Fig. 7).

The RDA model explained 23% of the total variation in the community composition (Fig. 8). All axes were significant (Table 4). The main environmental predictor was elevation a.s.l., which correlated with species richness of both SH and NH. Interestingly, the latter two turned out to be strongly correlated with each other.

Discussion

The results of this study show that, contrary to our first hypothesis, bryophyte species richness in central European managed forests has remained quite stable during the last twenty years. This means the environmental changes these forests have undergone during the last
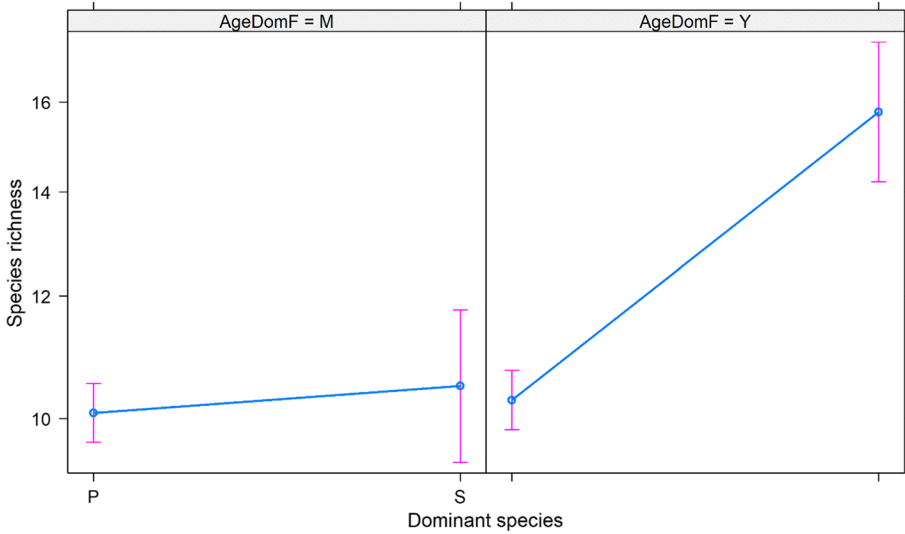
Fig. 5 Interaction between stand age and forest stand type. *P* pine, *S* spruce, *M* mature stands, *Y* young stands
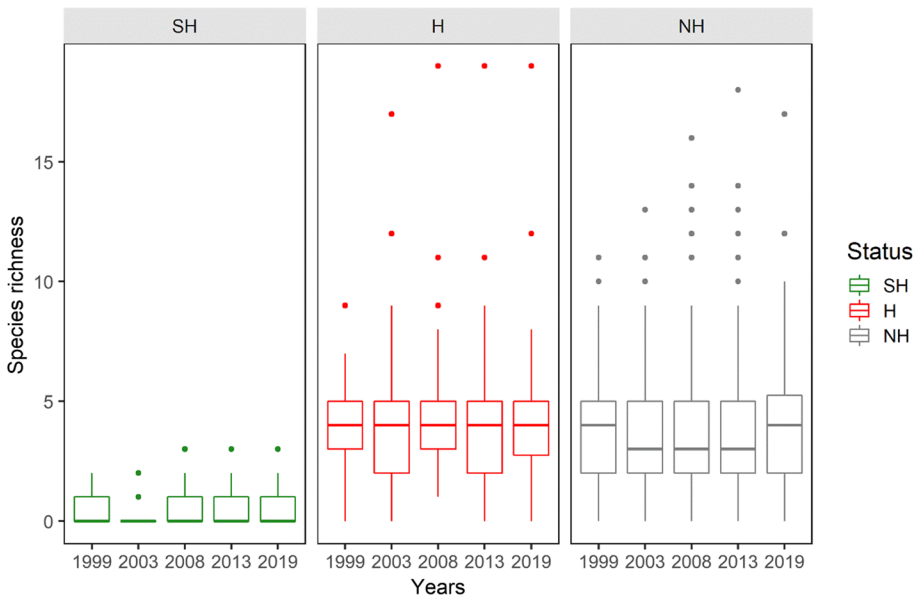

Fig. 6 GLM model showing the variations over time of strongly hemerophobic (SH), hemerophobic (H) and not hemerophobic (NH) species. No significant trend emerged

decades were not such dramatic as to determine significant changes in their bryoflora. The lack of a significant diversity trend is likely to be the result of the opposing effects of climate changes, from one side, and more sustainable forest management and pollutant deposition decline, from the other. In fact, while climate changes are expected to determine a

Fig. 7 Variation Partitioning of: **a** the whole community, **b** non hemerophobic species, **c** strongly hemero-phobic species, **d** hemerophobic species

Fig. 8 RDA of the bryophyte community and the set of biotic and abiotic factors. Continuous variables (elevation a.s.l. and richness of SH, H and NH) are reported in blue, while categorical variables (stand age, dominant tree species) are in green. Species are reported in red

decrease in species richness by affecting metabolic activity, growth and post-desiccation recovery capacity of the less desiccation tolerant species (Gignac 2001, 2011; Proctor 2011; Song et al. 2012; He et al. 2016; Hao and Chu 2021), both the recent advancements in forestry practices towards a more sustainable model and the pollutant deposition decline are likely to bring about an increase in bryophyte diversity, the first by ensuring the reten-tion of increasing amounts of dead-wood and large trees in forests, the second by allowing restoration of suitable physiochemical conditions for the pollution-sensitive species.

Table 4 Axes summary of RDA

	Df	Variance	F	Pr($>$ F)
RDA1	1	0.7437	108.5587	0.001***
RDA2	1	0.2552	37.2454	0.001***
RDA3	1	0.1471	21.4783	0.001***
RDA4	1	0.0839	12.2511	0.001***
RDA5	1	0.0641	9.3518	0.001***
RDA6	1	0.0453	6.6170	0.001***
RDA7	1	0.0228	3.3347	0.001***
RDA8	1	0.0161	2.3492	0.001***
Residuals	651	4.4599		

*** indicates p = < 0.001

Out of these three major anthropogenic drivers of cryptogamic diversity, the impact of climate change on bryophyte diversity is the less straightforward to evaluate. In fact, while studies showed a steady increase in mean and summer temperatures and the lengthening of dry periods due to decrease of precipitation in the summer period and their shift to the winter period (Kundzewicz and Matczak 2012; Ziernicka-Wojtaszek and Kopcinska 2020), Poland is considered to be less vulnerable to adverse climate change impacts than many other countries (Kundzewicz and Matczak 2012). Unlike for temperatures, precipitation patterns do not exhibit a clear trend and are highly variable across the country, so that while some areas of Poland exhibit a moderate decrease of total precipitation frequency and amount, others are experiencing an increase of both, especially in northern Poland (Ziernicka-Wojtaszek and Kopcińska 2020), which ultimately results in a lack of trend at country level. This makes it likely the expected negative impact of climate changes on bryophyte diversity has been so far just moderately strong.

Meanwhile, although managed forests are generally poorer in cryptogams than natural ones and lack the rarest and more threatened species, policy makers and foresters have been paying increasing attention to biodiversity conservation issues. Examples of improvements in forest management, based on research about the more sustainable forestry practices (Miller 1996; Noss 1996; Lindenmayer et al. 2012), are the retention of a minimum amount of dead wood on the forest floor, the reduction in the felling of trees over 100 years-old and the limitation in the use of clear-cuts and their substitution with partial and nested cuts, which lead to an increase in the complexity of the structure of stands, both in terms of age and species (Zasady, Kryteria i Wskaźniki Dobrej Gospodarki Leśnej w Polsce. 2010; Zasady hodowli lasu, 2012; Report on the European Forest Strategy—The Way Forward, 2019). Such practices are expected to have positively affected bryophyte diversity. In fact, according to the species sorting theory, "everything is everywhere, but the environment selects" (Baas-Becking 1934), which was proven to be true for most biological communities (Astorga et al. 2012; Cottenie 2005). Since bryophytes are generally very efficient disperses (Sundberg 2005; Shaw et al. 2011; Szövényi et al. 2012), if the main requirement for their occurrence, i.e. availability of suitable substrates, is ensured, euriecious and also several hemerophobic species may persist and withstand minor disturbance events with little damage. The advancements in forest practices introduced during the last 15–20 years likely played an important role in preventing bryophyte diversity loss, although they were not sufficiently strong to determine an increase of bryophyte diversity. In fact, though more

dead wood is being left to natural decay in Polish managed forests, big logs required by many stenoecious saproxylic species, particularly liverworts, are still missing in these forests, since the latter altogether lack old, big trees, stand age being mostly below 80 years and just in a few cases exceeding 90 years.

The significant decrease of pollutant deposition observed during the last decades (Dirnböck et al. 2018; Vivanco et al. 2018) may have also contributed to the maintenance of bryophyte diversity, counterbalancing the negative effects of climate changes. However, as in the case of forest management practices, the pollution drop was not enough to ultimately determine an increase of bryophyte diversity. Meanwhile, Baumann et al. (2021) ascribed the observed increase in bryophyte species richness and cover in the spruce forests of eastern Germany just to the sharp decline in S deposition. These contrasting conclusions may be accounted for by the difference in the scale of observation. The study by Baumann et al. (2021) examined a limited area of just a few square kilometres, while our study encompassed the whole Poland, and the effects of the S deposition drop are expected to be less obvious at a larger geographical scale, given the increased variability of environmental factors involved in the response of biological communities to changes in disturbance regimes. So, in the end, the net effect of a moderate impact of climate changes, the improvement in forestry practices and a strong pollution decrease, as the three more likely drivers of bryophyte diversity variations, was a lack of trends. The only significant difference in species richness was observed between 2003 and 2008, when it markedly increased after having dropped between 1998/1999 and 2003. Since the observer bias turned out to be quite negligible, we must assume the highlighted increase in species number was determined by some major environmental change, whose effects yet disappeared in a few years. In fact, species richness dropped again between 2008 and 2013, thus returning to a level similar to that of the beginning of the survey.

The lack of significant variations in bryophyte species richness in Polish forests seems at first to supports the results by Dittrich et al. (2016), reporting no trends in overall species richness over a century, and to contrast with those by Becker-Scarpitta et al. (2017), who observed an increase in species richness over a 30-year time span, as well as with those by the above mentioned study by Baumann et al. (2021), also reporting a diversity increase in ground bryophytes. However, in our study we pooled and examined together both coniferous and broadleaved forests, while Dittrich et al. (2016) and Becker-Scarpitta et al. (2017) examined just broadleaved forests and Baumann et al. (2021) just coniferous ones. Maintaining that a reliable comparison of data across different studies should be drawn only when environmental conditions are comparable and considering that in our study a slight, though non-significant, increase in the number of species was found in broadleaved forests, while no significant trend was highlighted for spruce forests, our results are actually closer to those by Becker-Scarpitta et al. (2017) and contrast with both those by Dittrich et al. (2016) and by Baumann et al. (2021). A longer observation period could have clarified whether the slight increase in the number of species observed in broadleaved forests would ultimately generate a significant trend or not. Becker-Scarpitta et al., (2017) could not provide a conclusive explanation to the observed increase in species richness at his study site, except by hinting to a possible recovery from the peak of acid deposition in the 1970s. More favourable trends in species richness in broadleaved than in coniferous forests may be also explained by assuming these forests are more resistant to temperature variations than coniferous forests. Indeed, Schwaab et al. (2020) reported that broad-leaved tree species locally reduce land surface temperatures in summer compared to needle-leaved species, particularly during exceptionally warm periods.

Despite the clear lack of changes in bryophyte species richness highlighted by this study, it is worth remembering that the bryophyte sample analysed in this study, although vast, is still little representative of the overall state of Polish forests, as it is based on randomly chosen sites with a total area corresponding to around 65 ha, whereas the forest area in Poland amounts to 9435 ha, and hosts overall 132 species of bryophytes, representing only 18% of the Polish bryoflora, which amounts to 950 species (Ochyra et al. 2003; Szweykowski 2006).

As for diversity response to environmental drivers, pine dominated forests exhibited, as expected, the lowest species richness, which suggests that, in order to enhance bryophyte diversity in forest ecosystems, these forest types, mostly artificially planted, should be reconverted to broadleaved forests. Comparison of diversity trends in young and mature forest stands was possible only for pine and spruce forests, since broadleaved forests include only mature stands. Here we observed a surprising pattern. While there was no significant difference in the number of bryophyte species between pine and spruce forest stands when mature, a significantly higher number of species occurred in young spruce forests than in young pine forests. This contrasted with our expectations, since we assumed the difference in species richness between pine forests, generally bryophyte poor, and spruce forests, on average much richer, would be driven by the favourable micro-climatic conditions and availability of substrates typical of mature spruce stands, e.g. dead wood. In fact, mature spruce forests are characterized by shaded conditions and a high moisture level; in addition, spruces in Europe are periodically, massively attacked by the spruce bark-beetle and are, on account of their flat and superficial root system, more easily uprooted by strong winds. Because of that, the amount of dead-wood suitable for colonization by bryophytes in mature spruce forests is, where dead wood is not systematically removed, quite high, which favours epixylic bryophytes.

As expected, species richness increased with elevation, which had been already reported by several studies about changes in bryophyte diversity along altitudinal gradients in mountain areas (Zhang et al. 2021; Bruun et al. 2006). In our study the variations in bryophyte species richness were evaluated along an elevational gradient including the whole lowland-upland-mountain range, which provides a more complete picture of the response patterns of bryophyte diversity to altitude than assessments of changes occurring just within the mountain belt. The increase in bryophyte species richness along with altitude is most likely due to the reduced impact of temperature extremes and to the higher moisture retention in forests at higher altitudes. Under this regard, the patterns of bryophyte diversity contrast with the ones of vascular plants, who generally host more species at lower altitudes (Theurillat et al. 2003; Trigas et al. 2013; Gebrehiwot et al. 2019). This difference in the response to increasing elevation is due to the fundamental differences in the physiological requirements of these two plant groups. In fact, while vascular plants are favoured by warmer temperatures, which, besides causing a longer growing season, enhance photosynthetic activity and reproductive output (Rustad et al. 2001; Wu et al. 2011; Peñuelas et al. 2013), bryophytes, due to their poikilohydric nature and their reproductive mechanisms, thrive in moist, cool, shaded conditions (Marschall and Proctor 2004) These requirements characterize especially liverworts and hemerophobic species.

The proportion of variation in the community composition explained by the tested variables turned out to be quite small, which implies bryophyte composition is driven by other environmental factors and/or by stochastic processes. As for the first possibility, local climatic conditions and availability of micro-habitats are the more likely candidates. Forest areas characterized by the same forest type, stand age and elevation, may substantially differ in their climate depending on geographic location, distance from the sea, proximity of mountain relief

and water basins. However, the analysis of the impact of local climatic conditions on biological diversity is usually hindered by the lack of a systematic network of climate monitoring systems and of long-term data. On the contrary, the crucial role of substrate availability for maintaining bryophyte diversity has been highlighted by several authors (Ross-Davis and Frego 2002; Shelley et al. 2012; Mills and MacDonald 2004; NewMaster et al. 2005). The role of stochastic processes in ecology is generally quite tricky to pinpoint. Despite frequently accounting for a large share of variability in community dynamics, stochasticity is not usually regarded as driver of such dynamics (Hart et al. 2017), being rather identified with unexplained variance, noise, or fundamental unpredictability (Shoemaker et al. 2020), namely with that inherent component of natural processes which sets an obstacle to the possibility of explaining natural dynamics and their underlying mechanisms (Boettiger 2018).

Out of the tested environmental factors, dominant tree species turned out to be the major driver of bryophyte community composition, followed by elevation, while stand age had the least influence, which was again in contrast with our hypothesis. Since mean stand age in managed forests is the result of the forest management regime, we may interpret the exiguous influence of stand age on species richness highlighted in this study as a scarce influence of management regimes on species richness. This seems to confirm the report by Müller et al. (2019), who found that species richness of four ecological bryophytes guilds (epigeic, epiphytic, epilxylic, epilithic) was independent of the management regimes and only responded to the availability of different substrates. Though this may at first appear surprising, it can be explained by assuming the managed forests examined by Muller et al. (2019) had a high degree of naturalness and retained all the substrates needed for forest bryophyte species to develop.

Surprisingly, the RDA revealed that plots characterized by a high number of hemerophobic species are independent from those characterized by high number of both strongly hemerophobic and non-hemerophobic, the latter two being correlated between them and with the elevation. The niche convergence of these two ecologically distant groups, marked differing in sensitivity to human disturbance, may be determined by similar requirements in terms of altitude-related environmental and climatic conditions. Meanwhile, it is worth highlighting that the mean number of SH species per plot is extremely low (maximum 2 species per plot), which makes this correlation incidental.

As in the case of overall species richness and again in contrast with our expectations, the number of hemerophobic species did not exhibit changes over time. This means not only generalist, euriecious species remained unaffected by environmental changes during the last 20 years, but also the more stenoecious species, strictly linked to the shaded and moist environment of close-canopy forests, which express the promptest response to environmental changes. This further confirms that Polish forests did not experience significant environmental stress over the last 20 years, since they retained all the more demanding bryophyte species. However, it is worth highlighting that many hemerophobic species do not occur at all in managed forests and are restricted to natural, old-growth forests characterized by high amounts of dead-wood and old trees and/or to areas characterized by the occurrence of disturbances such as windstorms or bark beetle outbreaks, that create new niches for the bryophyte flora associated with uprooted trees (Faliński et al. 1996; Staniaszek-Kik et al. 2021). These strongly disturbed areas were not examined in our study, since all study sites characterized by extensive tree stand breakdown following natural disturbance were excluded from the analyses. Examples of strongly hemerophobic species restricted to the above mentioned habitats are *Dicranum viride, Buxbaumia viridis, Neckera pennata, Anomon viticulosus, Riccardia palmata, Anastrophyllum hellerianum* (Czerepko et al. 2021). Those recorded in the frame of the monitoring of ICP Forest of II level plots are among the less sensitive among these typical

forest species, which means they are able to cope to a certain degree with variations of forest environmental conditions, as long as the integrity of the forest environment overall is not compromised.

Conclusion

This study shows that both overall bryophyte species richness and number of hemerophobic species in Polish forests have not significantly changed during the last two decades. This lack of diversity trends at a time of strong anthropogenic changes may be the result of the general improvement of the state of forest ecosystems over the last decades, preventing a bryophyte diversity loss, and, at the same time, of the limited extent of such improvement, which could not generate a positive diversity trend. Thus, maintaining that bryophyte are reliable indicators of the state of forest ecosystems, we may conclude that Polish forests are in an equilibrium state where the expected negative effects from climate changes are still limited and are being counterbalance by the positive effects of a more responsible forest management and an improvement in air and water quality. Longer monitoring may reveal possible shifts from this momentary equilibrium state.

Appendix 1

List of bryophyte species occuring in the study areas. NH-non hemerophobic; H-hemerophobic; SH-strongly hemerophobic.

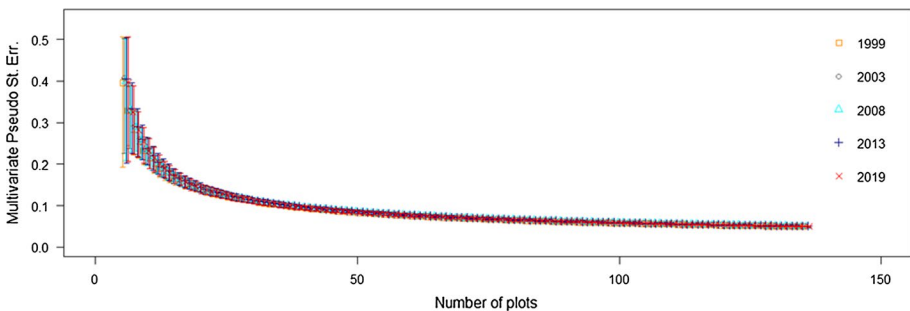| Species	Hemerophoby status
Amblystegium serpens (Hedw.) Schimp	NH
Atrichum undulatum (Hedw.) P.Beauv	NH
Aulacomnium androgynum (Hedw.) Schwägr	H
Aulacomnium palustre (Hedw.) Schwägr	H
Bazzania trilobata (L.) S. Gray	H
Blepharostoma trichophyllum (L.) Dumort	H
Brachytheciastrum velutinum (Hedw.) Ignatov & Huttunen	NH
Brachythecium albicans (Hedw.) Schimp	NH
Brachythecium campestre (Müll. Hal.) Schimp	NH
Brachythecium laetum (Bridel) Schimper	NH
Brachythecium mildaeanum (Schimp.) Schimp	NH
Brachythecium rivulare Schimp	H
Brachythecium rutabulum (Hedw.) Schimp	NH
Brachythecium salebrosum (Hoffm. ex F.Weber et D.Mohr) Schimp	H
Bryum capillare Hedw	NH
Bryum subneodamense Kindb	H
Buxbaumia aphylla Hedw	H
Callicladium haldanianum (Grev.) H.A.Crum	H
Calliergon stramineum (Dicks. ex Brid.) Hedenäs	NH

Species	Hemerophoby status
Calypogeia azurea Stotler & Crotz	NH
Calypogeia integristipula Steph	H
Calypogeia muelleriana (Schiffn.) Müll.Frib	H
Cephalozia bicuspidata (L.) Dumort	NH
Cephaloziella starkei (Sm.) Schiffn	NH
Ceratodon purpuraeus (Hedw.) Brid	NH
Cirriphyllum crassinervium (Taylor ex Wilson) Loeske & M.Fleisch	SH
Cirriphyllum piliferum (Hedw.) Grout	NH
Climacium dendroides (Hedw.) Web. & Mohr	NH
Dicranella cerviculata (Hedwig) Schimp	NH
Dicranella heteromalla (Hedw.) Schimp	NH
Dicranodontium denudatum (Brid.) E.Britton	SH
Dicranoweisia cirrata (Hedw.) Lindb	NH
Dicranum majus Turn	H
Dicranum polysetum Sw	H
Dicranum scoparium Hedw	H
Dicranum spurium Hedw	NH
Dicranum tauricum Sapjegin	NH
Dicranum undulatum Schrad. ex Brid	SH
Diplophyllum albicans (L.) Dumort	NH
Ditrichum heteromallum (Hedwig) E. Britton	NH
Encalypta streptocarpa Hedw	H
Eurhynchium anguistirete (Broth.) T.J. Kop	H
Eurhynchium schleicheri (R. Hedw.) Milde	NH
Eurhynchium striatum (Schreb. ex Hedw.) Schimp	H
Fissidens adianthoides Hedw	H
Fissidens bryoides Hedw	NH
Fissidens osmundoides Hedw	SH
Geocalyx graveolens (Schrad.) Nees	SH
Grimmia pulvinata (Hedw.) Sm	NH
Herzogiella seligeri (Brid.) Z.Iwats	H
Homalia trichomanoides (Hedw.) Schimp	H
Homalothecium sericeum (Hedw.) Bruch, Schimp. & W.Guembel	H
Hylocomium splendens (Hedw.) Schimp	H
Hypnum andoi A.J.E.Sm	NH
Calliergonella lindbergii (Mitt.) Hedenäs	NH
Hypnum cupressiforme Hedw	NH
Hypnum imponens Hedw	NH
Hypnum jutlandicum Holmen & E.Warncke	NH
Hypnum pallescens (Hedw.) P.Beauv	SH
Isothecium alopecuroides (Lam. ex Dubois) Isov	H
Isothecium myosuroides Brid	H
Lepidozia reptans (L.) Dumort	H
Leucobryum glaucum (Hedw.) Ångstr	H

Species	Hemerophoby status
Leucobryum juniperoideum (Brid.) Müll.Hal	NH
Leucodon sciuroides (Hedw.) Schwägr	NH
Lophocolea bidentata (L.) Dumort	NH
Lophocolea heterophylla (Schrad.) Dumort	NH
Lophozia ventricosa (Dicks.) Dumort	H
Metzgeria furcata (L.) Dumort	H
Mnium hornum Hedw	H
Nowellia curvifolia (Dicks.) Mitt	H
Orthodicranum montanum (Hedw.) Loeske	NH
Orthotrichum affine Schrad. ex Brid	NH
Oxyrrhynchium hians (Hedw.) Loeske	NH
Paraleucobryum longifolium (Ehrh. ex Hedw.) Loeske	SH
Pellia epiphylla (L.) Corda	H
Plagiochila asplenioides (L. emend. Taylor) Dumort	H
Plagiochila porelloides (Torrey ex Nees) Lindenb	H
Plagiomnium affine (Blandow ex Funck) T.J.Kop	NH
Plagiomnium cuspidatum (Hedw.) T.J.Kop	H
Plagiomnium rostratum (Schrad.) T.J.Kop	H
Plagiomnium undulatum (Hedw.) T.J. Kop	NH
Plagiothecium cavifolium (Brid.) Z.Iwats	H
Plagiothecium curvifolium Schlieph. ex Limpr	H
Plagiothecium denticulatum (Hedw.) Schimp	H
Plagiothecium laetum Schimp	SH
Plagiothecium nemorale (Mitt.) A.Jaeger	NH
Plagiothecium succulentum (Wilson) Lindb	NH
Plagiothecium undulatum (Hedw.) Schimp	H
Platygyrium repens (Brid.) Schimp	NH
Pleurozium schreberi (Willd. ex Brid.) Mitt	H
Pohlia nutans (Hedw.) Lindb	NH
Polytrichastrum formosum (Hedw.) G. L. Sm	H
Polytrichastrum longisetum (Brid.) G.L.Sm	NH
Polytrichum commune Hedw	H
Polytrichum juniperinum Hedw	NH
Polytrichum piliferum Hedw	NH
Polytrichum strictum Brid	H
Pseudoscleropodium purum (Limpr) M. Fleisch. ex Broth	NH
Pseudotaxyphillum elegans Z. Iwats	H
Pterigynandrum filiforme Hedw	SH
Ptilidium ciliare (L.) Hampe	H
Ptilidium pulcherrimum (Weber) Vain	H
Ptilium crista-castrensis (Hedw.) De Not	NH
Pylaisia polyantha (Hedw.) Schimp	H
Racomitrium heterostichum (Hedw.) Brid	H
Racomitrium sudeticum (Funck) Bruch & Schimp	SH

Species	Hemero-phoby status
Radula complanata (L.) Dumort	SH
Rhizomnium punctatum (Hedw.) T.J. Kop	H
Rhodobryum roseum (Hedw.) Limpr	H
Rhytidiadelphus loreus (Hedw.) Warnst	SH
Rhytidiadelphus squarrosus (Hedw.) Warnst	NH
Rhytidiadelphus subpinnatus (Lindb.) T.J.Kop	H
Rhytidiadelphus triquetrus (Hedw.) Warnst	H
Sanionia uncinata (Hedw.) Loeske	NH
Scapania nemorea (L.) Grolle	H
Sciuro-hypnum oedipodium (Mitt.) Ignatov et Huttunen	NH
Sciuro-hypnum plumosum (Hedw.) Ignatov et Huttunen	H
Sciuro-hypnum reflexum (Starke) Ignatov et Huttunen	H
Sciuro-hypnum starkei (Brid.) Ignatov et Huttunen	H
Sphagnum capillifolium (Ehrh.) Hedw	H
Sphagnum cuspidatum Ehrh. ex Hoffm	H
Sphagnum fallax (Klinggr.) Klinggr	NH
Sphagnum girgensohnii Russow	H
Sphagnum palustre L	H
Tetraphis pellucida Hedw	H
Thuidium philibertii Limpr	H
Thuidium recognitum (Hedw.) Lindb	H
Thuidium tamariscinum (Hedw.) Schimp	H
Ulota bruchii Hornsch	H
Ulota crispa (Hedw.) Brid	H
Ulota phyllantha (Brid.) Sawicki, Plášek & Ochyra	SH

Appendix 2

Trend of the error in measuring the multivariate dispersion of the community as the sampling effort increases calculated by applying Jaccard dissimilarity.

Declarations

Conflict of interest The authors have no relevant financial or non-financial interests to disclose.

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