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Biodiversity of bryophytes growing on the faeces of ungulates – a case study from north-eastern Poland

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Abstract – Seventeen moss species developed on 262 samples of faeces of 5 ungulate species, collected on Biebrza Marshes and in Białowieża Forest. Over half of them have not been previously reported for Białowieża Forest and over 30% for both sites. The most common species in the field were not found in the samples. Only *Ceratodon purpureus* (Hedw.) Brid. and *Leptobryum pyriforme* (Hedw.) Wilson grew on each type of faeces. Moss species growing on most of the faeces types were of neutral or calcicole habitats, while those present on the faeces of only one animal species were of weakly calcifuge to neutral habitats. Our study demonstrated that the dung of ungulates allows for the development of moss species with preferences for neutral and alkaline soils and bare ground habitats. It can be concluded that the presence of large herbivores, especially tarpan (*Equus gmelini* Ant.), elk (*Alces alces* L.) and European bison (*Bison bonasus* L.), and their faeces in the landscape contributes to the biodiversity of bryophyte flora.

Białowieża Forest / Biebrza Marshes / endozoochory / dung / herbivores / moss

Résumé – On a constaté la présence de 17 espèces de mousses dans 262 échantillons d'excréments de 5 espèces d'ongulés, prélevés dans les marécages de Biebrza et dans la forêt de Białowieża. Plus de la moitié des mousses notées n'avait jamais été citée de la forêt de Białowieża et plus de 30 % n'étaient connues dans aucun des deux sites. Les espèces les plus communes dans ces régions n'ont pas été trouvées sur les excréments. Seuls *Ceradoton purpureus* Hedw. et *Leptobryum pyriforme* (Hedw.) Wilson sont présents sur les excréments de chaque espèce animale. Les mousses se développant sur la majorité de types d'excréments préfèrent des habitats neutres ou calcicoles, tandis que celles présentes sur les excréments d'une seule espèce préfèrent les habitats faiblement calcifuges à neutres. Nos recherches démontrent que les excréments des ongulés favorisent l'expansion des mousses

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préférant les sols neutres et alcalins et les habitats sans couvert végétal. Nos résultats suggèrent que la présence dans la nature de grands herbivores et notamment du tarpan (*Equus gmelini* Ant.), de l'élan (*Alces alces* L.) et du bison (*Bison bonasus* L.) et de leurs excréments a des effets positifs sur le maintien de la diversité des espèces de mousses.

Forêt de Białowieża / Marécages de Biebrza / endozoochorie / bouses / herbivores / mousses

INTRODUCTION

Bryophytes are a group of organisms that have colonized practically all habitats. They cover tree trunks and soil in forests, are found in meadows and moors, colonize rocks, stones and sand, and are even present in fresh water bodies. Anemochory is the major mechanism of bryophyte dispersal. Spores, because of their small dimensions, are easily driven and transported by wind (Vanderpoorten & Goffinet, 2009). The spores of many bryophyte species can be transported in air over distances of thousands of kilometres (Bremer, 1980).

Zoochory is one of the basic mechanisms for the dispersal of vascular plants (Howe & Smallwood, 1982; Eycott *et al.*, 2007). A relatively high number of papers on endozoochory have been published recently on the role of birds (e.g. Czarnecka & Kitowski, 2008), rabbits (e.g. Malo *et al.*, 1995; Pakeman *et al.*, 1999), sheep (e.g. Wessels & Schwabe, 2008), and other large herbivores (e.g. Eycott *et al.*, 2007) in plant dispersal. All these studies document development of the vascular plants on animal faeces. Studies on the role of large herbivores in plant dispersal in Białowieża Forest demonstrated that on dung of the European bison can develop as many as 178 vascular plant species (Jaroszewicz *et al.*, 2009) and that some individuals of the dispersed species are able to produce the next generation of propagules in new habitats (Jaroszewicz *et al.*, 2008).

Zoochory in bryophytes is mostly known from the moss family Splachnaceae, with coprophilous species such as *Splachnum ampullaceaum* Hedw., *Splachnum sphaericum* Hedw. and *Tetraplodon angustatus* (Hedw.) Bruch & Schimp., in which dispersal is mediated by flies (Bates, 2009; Vanderpoorten & Goffinet, 2009). At present, there is some evidence for the existence of zoochory in more bryophytes, and their numbers are constantly increasing. This mainly concerns epizoochory, *i.e.* transportation on animal bodies, for example by forest birds (Davison, 1976; Ignatov & Ignatova, 2001), roe deer (Heinken *et al.*, 2001), arthropods, mice and frogs (Ignatov & Ignatova, 2001). Although vertebrate herbivores have never been observed to graze heavily on mosses, except those in Arctic regions, accidental ingestion may also occur (Vanderpoorten & Goffinet, 2009). In this way viable fragments can be dispersed over long distances via passage through the digestive tracts of some species of birds and flying foxes (Proctor, 1961; Parsons *et al.*, 2007). However, there are only single reports regarding this type of dispersal of bryophytes by ungulates. For example Bråthen *et al.* (2007), in their study on the role of reindeer in the endozoochoric dispersal of vascular plants in Norway, recorded the presence of viable fragments of 16 bryophyte species in dung samples.

In this study we ask: (1) Which ecological group of bryophyte may potentially develop on faeces of large herbivores? (2) Faeces of which animals may have the largest significance as substrate for development of bryophytes? (3) Is there any potential for endozoochoric dispersal of the spores of bryophytes by large herbivores?

MATERIALS AND METHODS

The study was conducted on sites lying at a distance of over 100 km from each other: Biebrza Marshes (53°40'51"N, 23°05'52"E) and Białowieża Forest (52°42'04"N, 23°52'10"E). The Biebrza Marshes cover the valley of the Biebrza river, together with aquatic communities, marshes, moors, rushes and forest communities. Unfortunately, the bryoflora of this area is poorly known, and only scanty information was published by Bloch (1974), Bloch *et al.* (1979) and Pałczyński (1988). The latter, in his monograph, stated that the most common bryophytes recorded in this study area include: *Bryum pseudotriquetrum* (Hedw.) Gaertn., B.Mey. & Scherb, *Calliergonella cuspidata* (Hedw.) Loeske, *Calliergon giganteum* (Schimp.) Kindb., *Drepanocladus aduncus* (Hedw.) Warnst., *Hamatocaulis vernicosus* (Mitt.) Hedenäs, *Limprichtia cossonii* (Schimp.) L.E.Anderson, H.A.Crum & W.R.Buck, *Aulacomnium palustre* (Hedw.) Schwägr., *Plagiomnium elatum* (Bruch *et* Schimp.) T.J.Kop. and *Plagiomnium cuspidatum* (Hedw.) T.J.Kop.

Białowieża Forest is spatially dominated by forest communities formed on mineral soils. There are also forests formed on boggy soils, and non-forest communities: open wet meadows, fields, and forest edge and aquatic communities (Sokołowski, 2004). The bryoflora of Białowieża Forest is better known, but the overwhelming majority of papers concern the bryoflora of forest communities (e.g. Klama, 1995, 2002; Żarnowiec, 1995). Thus, the available data about bryophytes of non-forest habitats are sparse (for example Bloch *et al.*, 1979; Karczmarz & Sokołowski, 1981; Melosik, 2006). The diversity of cryptogamous plants in Białowieża Forest was studied in the framework of the Crypto project at the end of the 1980s and the beginning of the 1990s. According to the results of this project, the most common bryophytes in Białowieża Forest are: *Hypnum cupressiforme* Hedw., *Orthodicranum montanum* (Hedw.) Loeske, *Pohlia nutans* (Hedw.) Lindb., *Tetraphis pellucida* Hedw., *Herzogiella seligeri* (Brid.) Z.Iwats., *Dicranum scoparium* Hedw., *Polytrichastrum formosum* (Hedw.) G.L.Sm. and *Plagiothecium laetum* Schimp. (Faliński & Mułenko, 1997). It is worth noting that in the Crypto project faeces were taken into consideration as one of the substrata (as excrement) but no moss (Żarnowiec, 1995) or liverwort (Klama, 1995) species were noted on them.

About 50 km^2 of both Biebrza Marshes and Białowieża Forest were investigated in search of fresh animal faeces. Samples were collected over 1 year: between September 2008 and August 2009. The faeces of each herbivore species were collected in a separate container (1000 cm^3), until it was filled completely. A container filled with the faeces of a particular species was considered one sample. In total 262 samples of animal faeces were collected: 28 from elk (*Alces alces* L.), 66 from tarpan horse (*Equus gmelini* Ant.; only from the semi-free breeding centre of Biebrza National Park), 12 from roe deer (*Capreolus capreolus* L.), 82 from red deer (*Cervus elaphus* L.) and 74 from European bison (*Bison bonasus* L.; only from Białowieża Forest). Faeces were dissolved in distilled water and mixed with sterilized sand in a proportion of three units of sand to one unit of faeces. The sieved sand was sterilized in a laboratory dryer for 48 hours at a temperature of 110°C. Samples mixed with sand were placed in $30 \times 40 \times 10$ cm containers and kept for the two following years in an unheated greenhouse. When necessary, samples were watered with demineralised water to maintain constant soil humidity. A control sample with sterilized sand kept constantly humid was placed in the greenhouse, along with 46 samples of soil taken from coniferous forest for studying soil seed banks.

Bryophytes for identification were collected mainly after a sporophyte was formed. The nomenclature for mosses follows Ochyra *et al.* (2003). Characteristic habitat requirements for mosses were analyzed based on information from the following works: Szafran (1959, 1961), Smith (2004), Meinunger & Schröder (2007 a, b). Ecological numbers and living-form follow Ellenberg *et al*. (1992). The liverwort *Marchantia polymorpha* L., which grew on dung samples as well as on other samples kept in the greenhouse, was excluded from further analyses.

Floristic similarity of moss, between dung samples obtained from studied animal species, was analysed using cluster analysis, with the Raup-Crick coefficient as the measure of similarity (Raup & Crick, 1979). This gives the probability that two sets of species share fewer species than expected under a null model (Vellend, 2004). We used this as most of the other indices are sensitive to the number of species in compared data sets, which was the case in our work. The species richness of plants growing on the faeces of different animal species was compared by sample-based rarefaction, allowing for the comparison of taxonomical diversity in samples of different sizes. All statistical analyses were carried out using PAST 1.86b software (Hammer *et al*., 2001).

RESULTS

Seventeen moss species were recorded on 262 samples of animal faeces, but only 35 samples contained any mosses. It is worth noting, that among bryophytes there were no coprophilous species of the Splachnaceae family, although the type of habitat allows to expect them. However, in the north-eastern part of Poland only one species, *Splachnum ampullaceaum* occurs very rarely (Szmajda *et al*., 1990). Nowadays, it is considered as threatened in Poland (Żarnowiec *et al.*, 2004). The highest rates of samples (over 30%) with mosses were recorded for roe deer and elk (Tab. 1). Most of the recorded moss species were present on the samples of more than one dung type. Only a few species grew on the dung of just one animal species: three species exclusively on tarpan horse faeces, two on elk faeces, and one on the faeces of each: roe deer and bison. There were no species found exclusively on the faeces of red deer. The mosses growing on the samples of many animal faeces were those with high ($6<R<7$) Ellenberg indicators for acidity (neutral-calcicole to weakly calcicole). The moss species with low R between 3 and 5 (weakly calcifuge to neutral) were those present in the dung of only one animal species. The only exception was *Amblystegium juratzkanum* Schimp., recorded from almost all dung types but with R=4 (Tab. 2). The rest of the analysed Ellenberg indicators: for light (L) and for moisture (F) did not show any specific differences between the dung samples (Tab. 2).

The most diverse flora of bryophytes was recorded on the faeces of the tarpan horse (12 species), elk (11 species) and bison (9 species) (Tab. 1). Cumulative species richness curves (Fig. 1), at the number of samples which allows comparison of all dung samples, showed that moss flora of elk and roe deer feaces had the highest species richness . The shape of the curves suggests that the number of moss species detected on the dung of these two species is close to complete, while in the case of the others a considerable number of species may not have been detected in the study.

Twelve out of the 17 recorded moss species belonged to plants of non-forest habitats, including nine with a preference towards anthropogenic and

Table 1. Alphabetically ordered moss species recorded on dung samples of elk (*Alces alces*), tarpan horse (*Equus gmellini*), red deer (*Cervus elaphus*), European bison (*Bison bonasus*) and roe deer (*Capreolus capreolus*) collected in Białowieża Forest and Biebrza Marshes (NE Poland); the numbers by animal name indicates the number of samples with moss/total number of samples.

Moss species	*Elk 9/28*	*Tarpan 10/66*	*Red deer 2/82*	*Bison 10/74*	*Roe deer 4/12*
Amblystegium juratzkanum	♦	♦	♦	♦	
Barbula unguiculata	♦	♦	♦	♦	
Brachythecium albicans	♦				
Brachythecium rutabulum	♦	♦		♦	♦
Bryum argenteum	♦	♦		♦	
Bryum caespiticium				♦	
Bryum klinggraeffii		♦			
Bryum pseudotriquetrum	♦	♦			♦
Ceratodon purpureus	♦	♦	♦	♦	♦
Climacium dendroides		♦			
Funaria hygrometrica	♦	♦		♦	♦
Leptobryum pyriforme	♦	♦	♦	♦	♦
Physcomitrium pyriforme		♦		♦	
Plagiomnium cuspidatum	♦		♦		♦
Rhytidiadelphus squarrosus	♦				
Sciuro-hypnum oedipodium					♦
Tortula truncata		♦			

ruderal habitats and substrates. Five of them had never been previously recorded, either from Białowieża Forest or from Biebrza Marshes (Tab. 2). Most of the forest mosses: *Brachythecium albicans* (Hedw.) Schimp., *Climacium dendroides* (Hedw.) F.Weber & D.Mohr, *Rhytidiadelphus squarrosus* (Hedw.) Warnst and *Sciuro-hypnum oedipodium* (Mitt.) A.Jaeger were present on the faeces of only one animal species. The only exception was *Plagiomnium cuspidatum*, which grew on the dung samples of all *Cervids*.

Only *Ceratodon purpureus* (Hedw.) Brid. and *Leptobryum pyriforme* (Hedw.) Wilson, common and cosmopolitan species having no preference for habitats or substrates, grew on every type of faeces. However the latter species had not been previously recorded, either for Białowieża Forest or for Biebrza Marshes (Tab. 2). *Amblystegium juratzkanum*, *Barbula unguiculata* Hedw., *Brachythecium rutabulum* (Hedw.) Schimp. and *Funaria hygrometrica* Hedw. were also common on the dung samples (present on the dung of 4 animal species). The last species, widely distributed and cosmopolitan, had never been previously recorded for either of the studied sites. The floristic similarity of samples, measured by the Raup-Crick coefficient, divided samples into two branches: tarpan horse (Biebrza Marshes) and European bison (Białowieża Forest) versus three *Cervid* species (Fig. 2), with the only exception being for red deer samples from Białowieża Forest, which were clustered together with those of bison and tarpan. The division of samples according to the taxonomy of animals suggests that the species composition of mosses growing on animal faeces is influenced by chemical and physical properties of substrates.

Table 2. Ecological characteristics of mosses recorded on ungulate dung samples collected in Białowieża Forest and Biebrza Marshes (NE Poland), including life forms of Raunkiaer (L.F.: C – chamaephyte; E – epiphyte; H – hemicryptophyte; T – therophyte) and Ellenberg indicators for acidity (R: 3 – weakly calcifuge, 4 – neutral to calcifuge, 5 – pH neutral, 6 – neutral-calcicole, 7 – weakly calcicole, x – not indicated), moisture (F: 2 – xerophilous, 4 – weakly hygrophilous, 5 – hygrophilous, 6 – strongly hygrophilous, 7 – aquatic to markedly hygrophilous, x – not indicated) and light (L: 3 – weakly shade-loving, 4 – neutral-shade-loving, 5 – light neutral, 7 – weakly photophilous, 8 – photophilous, 9 – strongly photophilous, x – not indicated) *(continued)*

Species	*Substratum*	*Habitat*	*Białowieża Forest*	*Biebrza Marshes*	*Geographical distribution*	*L.F.*	*R*	*F*	*L*
Amblystegium juratzkanum Schimp.[1]	Rotten wood, bark of trees, rocks, stones, wet litter and soil	Wetlands, deciduous forest	Not recorded	Recorded in some phytosociological releves (H. Bartoszuk unpubl.)	Holarctic species; frequent in Poland	C (E)	4	6	5
Barbula unguiculata Hedw.	Bare soil, rocks, walls	Meadows, ruderal habitats, roadsides, paths, arable fields	Not recorded	Forest habitats (H. Bartoszuk unpubl.)	Holarctic species; common in Poland	C	7	2	7
Brachythecium albicans (Hedw.) Schimp.	Mineral soil, walls	Dry and sandy habitats, young coniferous forests, ruderal places	Numerous forest compartments (Herbarium of the Forest Research Institute in Białowieża); *Carici elongatae-Querceum* (Sokołowski 1994)	Recorded in some phytosociological releves (H. Bartoszuk unpubl.)	Holarctic species; common in Poland	C	x	2	9
Brachythecium rutabulum (Hedw.) Schimp.	Soil, stones, bark of trees, litter, rotten wood	Forests and meadows, ruderal places, arable fields	Numerous forest compartments (Herbarium of the Forest Research Institute in Białowieża); forest habitats (Faliński and Mułenko 1997); *Carici elongatae-Alnetum; Vaccinio myrtilli-Piceetum; Calamagrostio arundinaceae-Piceetum; Tilio-Carpinetum; Circaeo- Alnetum* (Sokołowski 1994);	Recorded in some phytosociological releves (H. Bartoszuk unpubl.)	Sub-cosmopolitan species; common in Poland	C (E)	x	4	5
Bryum argenteum Hedw.	Walls, rocks, soil, nitrogen-rich substratem	Grasslands, ruderal habitats, arable fields	Not recorded	Not recorded	Cosmopolitan species; common in Poland	C	6	x	7
Bryum caespiticium Hedw.	Sandy soils, rocks, walls	Grasslands, ruderal places	Not recorded	Recorded in some phytosociological releves (H. Bartoszuk unpubl.)	Sub-cosmopolitan species; common in Poland	C	6	5	8
Bryum klinggraeffii Schimp.	Wet mineral soil	Arable fields, grasslands, ruderal places	Not recorded	Not recorded	Holarctic species; frequent in Poland	C	x	7	8
Bryum pseudotriquetrum (Hedw.) Gaertn., B.Mey. et Scherb	Peat, wet soil	Edges of peatbogs and water courses, wet meadows, fens	Forest habitats (Faliński and Mułenko 1997)	Recorded in some phytosociological releves (H. Bartoszuk unpubl.)	Bipolar species; common in Poland	C	7	7	7

Ceratodon purpureus (Hedw.) Brid.	Soil, rocks, walls, tree trunks, rotten wood	Meadows, grasslands, mesic coniferous forests, bogs, anthropogenic habitats, burnt areas	Forest habitats (Faliński and Mułenko 1997; herbarium of the Forest Research Institute in Białowieża),	Recorded in some phytosociological releves (H. Bartoszuk unpubl.)	Cosmopolitan species; common in Poland	C (E)	x	2	8
Climacium dendroides (Hedw.) F.Weber *et* D.Mohr	Soil, peat	Meadow, grasslands, riverine forest, springs, peatbog	Numerous records in forest habitats (Faliński and Mułenko 1997); Carici elongatae-Alnetum; Dryopteridi thelypteris-Betulum pubescentis; Tilio-Carpinetum; Circaeo- Alnetum; Ficario-Ulmetum (Sokołowski 1994)	Very common and present in most habitats (Jasnowski 1952)	Holarctic species; common in Poland	C	5	6	7
Funaria hygrometrica Hedw.	Soil, nitrogen-rich sites, burnt sites, walls	Ruderal places, arable-fields	Rare (Faliński and Mułenko 1997)	Not recorded	Cosmopolitan species; common in Poland	T	6	6	8
Leptobryum pyriforme (Hedw.) Wilson	Soil, peat	Water banks, peat bogs, ruderal places	Not recorded	Not recorded	Cosmopolitan species; common in Poland	C, T	7	6	x
Physcomitrium pyriforme (Hedw.) Bruch. *et* Schimp	Wet soil	Meadows, edges of peatbogs, pond and ditch embarkments	Not recorded	Not recorded	Holarctic species; frequent in Poland	T	6	7	8
Plagiomnium cuspidatum (Hedw.) T.J.Kop	Soil, litter, tree trunks, rocks, walls	Deciduous forests, meadows, anthropogenic habitats	Numerous records (Faliński and Mułenko 1997; herbarium of the Forest Research Institute in Białowieża)	Recorded in some phytosociological releves (H. Bartoszuk unpubl.)	Holarctic species; common in Poland	H	7	5	4
Rhytidiadelphus squarrosus (Hedw.) Warnst	Soil, peat	Mesic coniferous and mixed forests, meadows, grasslands, forest edges, lawns	Not recorded	Recorded in some phytosociological releves (H. Bartoszuk unpubl.)	Holarctic species; common in Poland	C	5	6	7
Sciuro-hypnum oedipodium (Mitt.) A.Jaeger	Rotten wood, litter wood	Mesic coniferous forests	Numerous forest compartments (Herbarium of the Forest Research Institute in Białowieża);	Not recorded	Holarctic species; frequent in Poland	E, C	3	6	3
Tortula truncata (Hedw.) Mitt.	Bare soil	Arable fields, meadows	Not recorded	Not recorded	Holarcic species; frequent in Poland	T	5	7	7

[1]In many floras (for example Hill *et al*., 2006) this species name is treated as a synonym of *Amblystegium serpens* (Hedw.) Schimp.

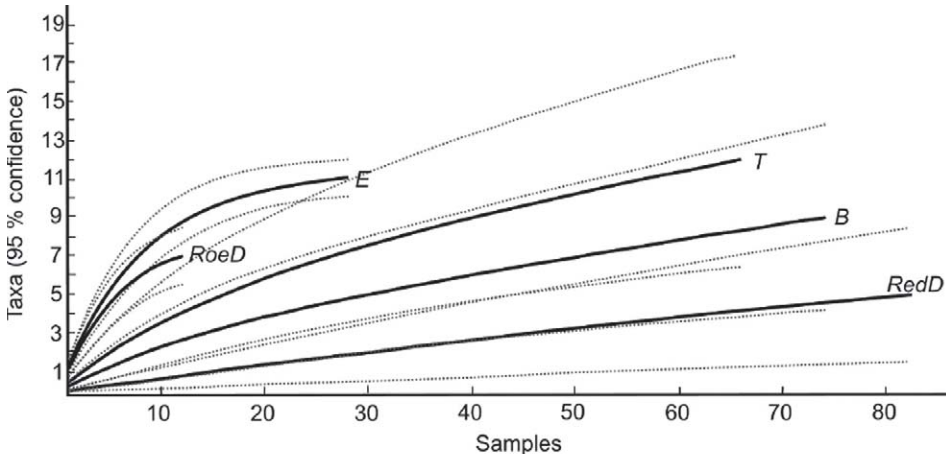

Fig. 1. Cumulative species richness curves of mosses recorded on samples of the dung of elk *Alces alces* (E), red deer *Cervus elaphus* (Red D), roe deer *Capreolus capreolus* (Roe D), bison *Bison bonasus* (B) and tarpan horse *Equus gmelini* (T) obtained by means of sample rarefaction analysis. Dashed lines show 95% of data confidence.

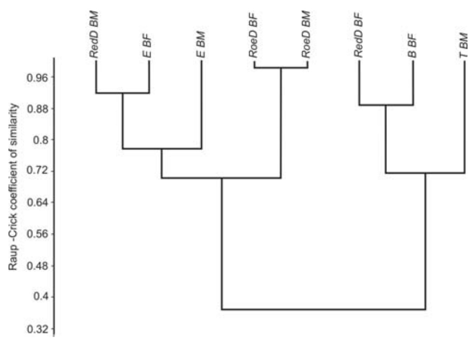

Fig. 2. Dendrogram of (dis)similarities between bryofloras recorded on dung samples of elk *Alces alces* (E), red deer *Cervus elaphus* (RedD), roe deer *Capreolus Capreolus* (RoeD), European bison *Bison bonasus* (B) and tarpan horse *Equus gmelini* (T) from Białowieża Forest (BF) and Biebrza Marshes (BM), produced by cluster analysis with the use of the Raup-Crick distance as the similarity measure.

DISCUSSION

The results obtained in this study demonstrated that the faeces of ungulates, or soil with a high admixture of dung, are suitable micro-habitats for development of bryophytes. Species with the ecological optimum of disturbed, neutral to alkaline, bare ground habitats, find conditions facilitating their growth there. As many as 30% of species had not been reported earlier from either of the studied sites, and a further 30% had been recorded from one of the sites only. This suggests airborne rather than endozoochoric origin of spores or gemmae of the following species recorded on dung samples: *Amblystegium juratzkanum*, *Barbula unguiculata*, *Brachythecium rutabulum*, *Bryum argenteum*, *Bryum* *caespiticium*, *Bryum klinggraeffii* Schimp., *Ceratodon purpureus*, *Funaria hygrometrica*, *Leptobryum pyriforme* and *Physcomitrium pyriforme*. However, in our opinion, if spores or gemmae of bryophytes had an anemochoric origin, then these species would have high frequency on both types of substrata: dung samples and samples not containing any animal faeces, similarly to *M. polymorpha* (for this reason excluded from analyses).

Lack of records of common cosmopolitan species in the studied areas can be explained by the small size of most of the considered bryophytes, which makes them difficult to detect in field conditions. In our opinion the rarity and short spatial and chronological persistence of micro-habitats (faeces, bare ground) allowing their development influence the detectability of the species in question.

The origin of bryophyte spores germinated on samples is debatable. Several herbivores graze bryophytes but it is also possible that their spores were deposited on vascular plants and then swallowed with their biomass by animals. Hence, large herbivores can also potentially disperse spores via endozoochory. Several species of spore plants are known to be grazed by reindeer. Bråthen *et al.* (2007) reported 16 bryophyte taxa from reindeer faeces samples. However, they were not able to prove whether spores had survived passage through the digestive tract of reindeer, or whether spores were merely on the surface of the faeces upon collection.

In our study the small number of samples containing mosses, and the distinct floristic differences between samples obtained from different animal species suggest that the dung samples included moss spores upon collection. If the bryophytes recorded in samples had originated from a local spore source (e.g. from the greenhouse interior), then a higher share of samples would have included them and this share was low and ranged between 0.33 for roe deer and 0.02 for red deer. We expect that the floristic differences between animal species would not be significant if spores were of airborne origin. It must also be stressed that the most common moss species for Białowieża Forest (Faliński & Mułenko, 1997; Sokołowski, 1993, 2004), where the greenhouse experiment was carried out, were not recorded from samples. Although the greenhouse was located at a distance of approximately 1 km from the forest edge. Beyond any doubt bryophyte species common in a particular area are the predominant group of anemochorically dispersed spores in terms of their quality and quantity. Absence of these species in the samples from a particular area shows that anemochory does not assure their successful establishment. In our opinion this proves that endozoochory should be taken into consideration as potential dispersal mechanisms for moss spores.

The moss flora developed on *Cervids*' faeces differed from those of tarpan and bison. This can be explained by differences in digestive physiology between *Cervids*, bison (also ruminant but of cattle type) and tarpan (caudal fermenter; Hume, 2002). Type of digestion could influence the species composition of mosses growing on dung samples via different rates of survival of spores passing through the digestive tracts of animals, as well as via faeces properties: suitability of their surface for the sticking of spores and chemical properties of dung influencing germination of spores.

It can be hypothesised that the spores of mosses belonging to floras of calcifuge soils can not germinate on samples containing faeces because this is an alkaline substrate. However, no mosses germinated on the samples not containing faeces. One must also take into consideration the possibility that freshly deposited faeces may act as a specific "fly-paper" for spores, facilitating a good substrate for their germination and development after mixing with sand. Thus conclusive proof for the endozoochoric origin of bryophytes found in faeces samples of studied animals can be obtained in future studies only on material collected directly from the intestines and grown under sterile conditions.

Our study demonstrated that micro-habitats created by faeces allow for the development of moss species with preferences for neutral/alkaline and bare ground habitats. There are some evidences that not all bryophytes recorded on the samples were of airborne origin. Thus, it can be concluded that the presence of large herbivores, especially tarpan, elk and bison, and their faeces in the landscape, contributes to the biodiversity of bryophyte flora.

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