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Ecology of epixylic bryophytes in Eurosiberian alder swamps of Latvia

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Abstract

Fallen dead wood is an important structural element in Eurosiberian alder swamp forests that supports diversity of epixylic bryophyte species. The aim of the present study was to assess the bryophyte diversity on logs in relation to abiotic and biotic factors. Four Eurosiberian alder swamp forests stands were studied in three territories of Latvia – Moricsala Nature Reserve, Zvarde Mezi Nature Park and Slitere National Park. In total 102 logs were described. Overall 59 bryophyte species were recorded. The main factor affecting the richness of bryophyte species was decay stage. Composition of bryophyte species gradually changed during succession. Logs that were in the mid decay stage supported the largest number of bryophyte species. The visible perimeter of logs did not affect composition and number of bryophyte species. Differences in bryophyte species composition were found between deciduous and coniferous logs. Some differences in flora of epixylic bryophyte species were recognized between the studied territories.

Key words: decay stage, epixylic bryophytes, Eurosiberian alder swamps, indicator species analysis, logs.

Introduction

Natural Eurosiberian alder swamp forests are wet, fireproof, adapted to water level fluctuations, characterized by mosaic ground vegetation and hummocks (Priedītis 1999; Lārmanis et al. 2000). Decayed logs in different decay stages are an important feature of alder swamp forests (Priedītits 1999; Lārmanis et al. 2000), as they represent a structural element increasing biological diversity (Suško 1998).

The quantity of decayed wood depends on the forest gap creation rate, the decomposition rates of different tree species, and environmental conditions. Dead wood has been removed from forests due to the past forest management in Northern Europe, which has led to a decline in bryophyte species diversity (Andersson, Hytteborn 1991; Bambe 2008). Many bryophyte species depend on decayed wood, and they are often rare as their populations are small, unstable and their dispersal is limited (Ödor, Standovár 2001; Baldwin, Bradfield 2007). The diversity of epixylic bryophyte species is also closely connected with the quantity of logs in the studied territory (Ödor, Standovár 2001; Ödor, Standovár 2002; Pyle, Brown 2002; Ödor et al. 2006), which are often short-term and a patchy substrate for epixylic bryophytes (Bambe 2008).

Bryophytes are one of the first plants that colonize newly formed decay logs and bryophyte composition depends on decay stage and chemical processes in wood (Zielonka, Piatek 2004), tree species (Āboliņa 1968), diameter of decayed log (Bērmanis, Spuņģis 2002), local area (Lindström 2003), moisture content and age of decayed log, presence of bark on log and type of fungus destroying the log (Ödor, Standovár 2001; Ek et al. 2002; Lindström 2003). Humidity is especially important for liverworts, as they are sensitive to microclimatic changes (Hallingbäck, Holmåsen 2000). A large proportion of liverworts grow on decayed logs (Vellak, Paal 1999), and many have a narrow ecological range (Suško 1998).

The aim of the present study was to investigate the distribution of epixylic bryoflora in relation to abiotic factors on decayed wood in Eurosiberian alder swamp forests in different locations of Latvia. We examined the importance of log tree species, decay stage and log visible perimeter for the epixylic bryophytes.

Materials and methods

Study area

The study areas were located in four territories in Latvia – one swamp forest in Moricsala and Zvarde and two in Sliteres Zilo kalnu nogaze (Fig. 1). Moricsalas Island is located in the south - west part of Latvia in Moricsala Nature Reserve, where the climate is relatively moderate.

Zvardes swamp is located in the south-west part of Latvia, in the Zvardes Mezi Nature Park. European alder swamp forests are the most valuable feature of ecological diversity in Zvardes Mezi Nature Park (Celmiņš 2005). Sliteres Zilo Kalnu Nogaze is located in the Slitere National Park. This area contains a wide diversity of natural ecosystems due to

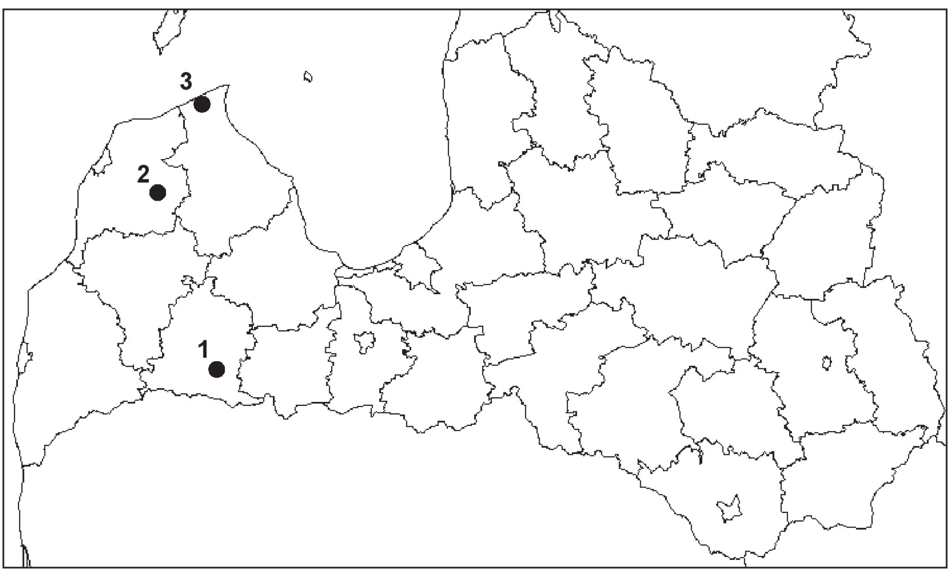

Fig. 1. Map of the Latvia showing the study areas (•). 1, "Zvārdes meži" Nature Park; 2, Moricsala Nature Reserve; 3, "Slīteres Zilo kalnu nogāze", Slitere National Park.

unique geological, geomorphologic, hydrological and climatic conditions (Sāmīte 2007).

Average temperature in January is –4.8 °C and average temperature in July is +16.7 °C. Precipitation in western Latvia is from 650 to 700 mm (Temņikova 1975).

Data sampling

The field work was conducted in Zvarde in October 2005, where 11 decayed logs were described. Investigations in Moricsala were carried out in July 2007. A total of 30 decayed logs were described in Eurosiberian alder swamp forest and 10 in other wet sites in Moricsala. The swamps in Sliteres Zilo Kalnu Nogaze (Z1 and Z2) at the base of the ancient Baltic Sea coast were investigated in July, August and October 2006; in total 51 decayed logs were surveyed. Decayed logs were chosen randomly in each territory.

On each decayed log randomly a maximum of three 1-m-long plots were established. The number of plots was selected depend on the length of the decayed log. Features described were decay stage, length, visible perimeter and species of tree. Logs with visible perimeter less than 0.1 m and length less than 1.5 m were not sampled. All bryophyte species were described in each plot and their projective cover was estimated using the Braun–Blanquet scale (Pakalne, Znotiņa 1992).

Bryophyte species that could not be identified in the field were collected for identification in the laboratory. Species nomenclature follows (Smith 1996; Hallingbäck, Holmåsen 2000; Āboliņa 2002; Ignatovs, Ignatova 2003; Ignatovs, Ignatova 2004; Smith 2004).

Determination of decay stage as a five-part scale followed Pyle and Brown (1998): (1) wood cannot be penetrated with thumbnail, wood is sound, bark is intact, smaller to medium branches are present; (2) thumbnail penetrates in the bark till three centimeters, bark may or may not be attached, wood is sound, bark is decay; (3) thumbnail penetrates till seven centimeters, bark may or may not be attached, wood is somewhat rotten, the biggest trunks and only larger stubs are present; (4) thumbnail penetrates readily, bark is lightly attached, sloughing off or detached, wood texture is soft, decayed log may assume oval shape; (5) all wood texture is squashy and powdered, bark is detached or absent, can be decayed in pieces, wood is indistinguishable from ground.

Each log was assigned one decay stage. If different parts of log were in several decay stages, the predominant stage was chosen.

Study area

Bryophyte community structure and gradients were analyzed with CCA (Canonical Correspondence analysis) and Indicator Species Analysis using the PC-ORD program package (1999 Version 4.17.). CCA species ordination was used to identify major factors that affected variability of composition of bryophyte species. Significant indicator bryophyte species were determined for each decay stage.

The relations of bryophyte species richness with visible perimeter and decay stage were determined by Spearman’s correlation.

The term “signal species” is considered here as including special habitat species, indicator species, and species of microreserve as well as specially protected bryophyte species in the woodland key habitat inventory. Special habitat species are species with a narrow ecological range that need very specific conditions. Indicator species are species with high requirements for a specific environment (Ek et al. 2002).

Results

Bryophyte flora

In total 59 bryophyte species from 29 families were recorded, of which 42 were mosses and 17 liverworts. The most common bryophytes were *Hypnum cupressiforme*, *Brachythecium rutabulum*, *Lophocolea heterophylla*, *Dicranum scoparium*, *Plagiomnium cuspidatum* and *Chiloschyphus pallescens*. In total 13 bryophyte species were found only in one site on one log (Table 1).

In the studied territories one habitat specialist species, *Anastrophyllum hellerianum*, was found in the Zilo Kalnu Nogazes Swamp (Z2). Five bryophyte species were indicator species – *Homalia trichomanoides*, *Jungermannia leiantha*, *Metzgeria furcata*, *Neckera complanata* and *Trichocolea tomentella*.

Comparison between bryophyte species and decay stages of logs

In total 102 decayed logs were described in all territories, representing five tree species (Table 2). Tree species was not determined for 27 decayed logs that were mostly in the fourth and fifth decay stage.

Logs in decay stages 1 and 5 were found in all studied territories, but their number was low. Logs in all decay stages (1, 2, 3, 4, 5) were represented only in the Zilo Kalnu Nogazes Swamp Z1 and Moricsala Island.

Table 1. Occurrence of bryophyte species in studied territories. Number of decayed logs where species were found is shown

Bryophyte species	Zilo kalnu nogaze (Z1)	Zilo kalnu nogaze (Z2)	Zvarde	Moricsala
Amblystegium serpens	-	-	-	1
Anastrophyllum hellerianum	-	7	-	-
Aulacomnium androgynum	-	-	1	-
Blepharostoma trichophyllum	-	-	3	1
Brachythecium rutabulum	28	5	8	29
Brachythecium salebrosum	-	4	-	-
Calliergon cordifolium	2	-	5	1
Calliergonella cuspidata	2	1	4	20
Chiloscyphus pallescens	10	1	4	15
Cirriphyllum piliferum	-	4	-	1
Climacium dendroides	-	2	-	12
Dicranum majus	-	1	-	-
Dicranum montanum	-	4	3	-
Dicranum scoparium	4	16	9	16
Eurhynchium angustirete	-	4	-	-
Eurhynchium hians	1	-	-	-
Eurhynchium striatum	-	1	-	-
Frullania dilatata	-	-	-	1

(continued)

Bryophyte species	**Zilo kalnu nogaze (Z1)**	**Zilo kalnu nogaze (Z2)**	**Zvarde**	**Moricsala**
Herzogiella seligeri	-	12	1	1
Homalia trichomanoides	3	-	-	1
Homalothecium sericeum	-	-	-	3
Hylocomium splendens	3	3	3	2
Hypnum cupressiforme	19	14	9	30
Jungermannia leiantha	-	-	6	-
Lepidozia reptans	-	4	6	2
Leskea polycarpa	-	-	-	1
Leucodon sciuroides	1	1	-	2
Lophocolea heterophylla	20	6	7	14
Lophozia sp.	2	1	-	3
Metzgeria furcata	1	-	-	3
Mnium hornum	1	5	1	10
Neckera complanata	-	3	-	-
Nowellia curvifolia	3	6	3	-
Plagiochila asplenioides	-	2	-	-
Plagiochila porelloides	-	-	1	-
Plagiomnium affine	9	4	3	6
Plagiomnium cuspidatum	10	3	1	17
Plagiomnium ellipticum	-	-	-	9
Plagiomnium medium	-	1	-	-
Plagiomnium undulatum	10	8	4	1
Plagiothecium laetum	-	-	-	2
Platygyrium repens	-	-	-	2
Pleurozium schreberi	3	11	-	2
Polytrichum commune	-	-	2	-
Polytrichum juniperinum	-	-	-	4
Ptilidium pulcherrimum	3	-	3	1
Pylaisia polyantha	-	-	1	-
Radula complanata	7	1	1	3
Rhizomnium punctatum	2	8	4	-
Rhodobryum roseum	1	2	1	-
Rhytidiadelphus triquetrus	4	10	5	1
Riccardia multifida	1	-	-	-
Riccardia palmata	1	15	1	7
Sanionia uncinata	7	5	2	5
Sphagnum girgensohnii	-	1	-	-
Tetraphis pellucida	-	1	3	-
Thuidium tamariscinum	-	10	3	1
Trichocolea tomentella	-	1	-	-
Ulota crispa	9	-	1	3

Table 2. Parameters of studied decaying logs of different tree species

Tree species	Number	Visible perimeter (m)	Length (m)	Decaying stage
Alnus glutinosa	50	0.1 - 0.98	1.5 - 25	1, 2, 3, 4
Betula sp.	14	0.03 - 1.12	2 - 20	2, 3, 4
Picea abies	6	0.15 - 0.8	5 - 19	2, 3, 4
Alnus incana	4	0.34 - 1.26	5 - 10	1, 2, 3
Quercus robur	1	1.11	18	2
Not identified	27	0.15 – 0.85	2 - 20	2, 3, 4, 5

A significant relation between number of bryophyte species and decay stage was not found. The highest bryophyte species richness (mean 7 species per log) was found on logs in decay stages 3 and 4 (Fig. 2).

A total of 14 bryophyte species were significant ($p > 0.05$) indicators of decay stages (Table 3). Nine epiphytic bryophyte species were specific to the first decay stage. In this stage decayed logs still had hard attached bark. Two epixylic bryophyte species were characteristic to the decay stage 4 – *Nowellia curvifolia* and *Riccardia palmata*. In the decay stage 4 bark was not attached and structure of decayed wood was soft. Four indicator species characterized the decay stage 5, of which the two most common were *Calliergonella cuspidata* and *Plagiomnium cuspidatum* (Table 3).

The first axis of the CCA bryophyte species ordination was explained as decay stage (Fig. 3). Logs in the initial decay stage were associated with epiphytic bryophyte species – *Frullania dilatata*, *Metzgeria furcata* and *Radula complanata*. In mid decay stages (mid Axis I) typical bryophyte species were *Lophocolea heterophylla*, *Chiloscyphus pallescens* and *Jungermania leiantha*. In the late decay stages ground bryophytes such as *Climacium dendroides*, *Rhodobryum roseum* and *Dicranum majus* appeared (Fig. 3).

Distribution on tree species

The CCA bryophyte species ordination showed that a unique composition of bryophyte species was found on *Alnus glutinosa* and *Picea abies* logs (Fig. 3). The most common bryophyte species on spruce were *Anastrophyllum hellerianum* and *Pleurozium schreberi* and the highest species richness was also found on these logs (Fig. 3, 4). *Hypnum*

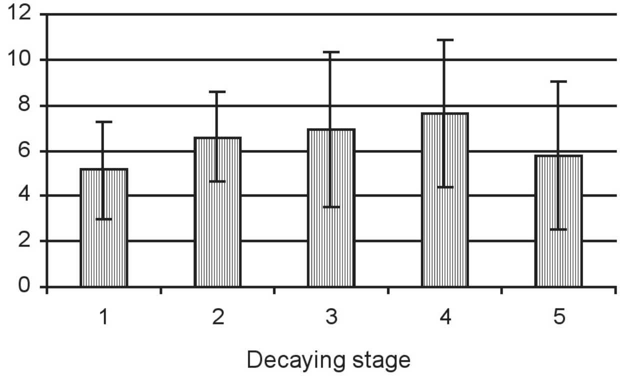

Fig. 2. Average number of bryophyte species per one log in various decay stages.

Table 3. Indicator species of bryophytes in different decay stages. Only significant ($p < 0.05$) indicator species are shown. Bryophyte species are arranged by decay stage. Bryophyte species with larger observed indicator values are more characteristic of the respective decaying stage

Bryophyte species	Decay stage	Observed Indicator Value	P
Hypnum cupressiforme	1	25.6	0.0010
Radula complanata	1	28.3	0.0010
Ulota crispa	1	24.5	0.0010
Homalia trichomanoides	1	7.7	0.0070
Ptilidium pulcherrimum	1	11.0	0.0070
Metzgeria furcata	1	23.1	0.0010
Leucodon sciuroides	1	14.1	0.0010
Homalothecium sericeum	1	20.2	0.0010
Nowellia curvifolia	4	7.9	0.0430
Riccardia palmata	4	10.1	0.0440
Plagiomnium cuspidatum	5	19.5	0.0010
Plagiomnium affine	5	9.8	0.0400
Calliergonella cuspidata	5	27.8	0.0010
Cirriphyllum piliferum	5	5.3	0.0450

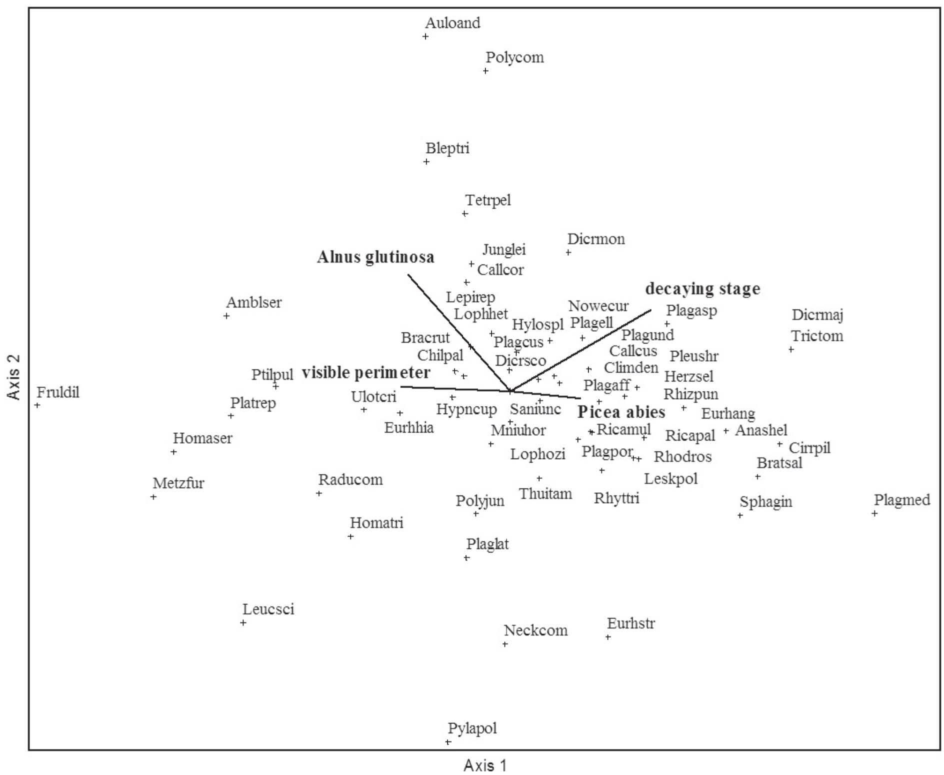

Fig. 3. CCA bryophyte species ordination. Only significant ($p < 0.05$) effects are shown. A longer vector indicates greater correlation.

cupressiforme and *Brachythecium rutabulum* were the most common species on alders (Fig. 3). However, the epixylic bryophyte species were not restricted to any tree species.

In the CCA species ordination visible perimeter was an important factor (p = 0.05) (Fig. 3), but a significant correlation between visible perimeter and species richness was not found.

Distribution in territories

The largest number of bryophyte species was found in the Zilo Kalnu Nogazes Swamp Z2 and the largest mean number of bryophyte species per log was in Zvardes Swamp (Fig. 5). The highest number of signal species was in Zilo Kalnu Nogazes Swamp Z1 and Z2 (Fig. 5). *Dicranum scoparium* was one of the most common bryophyte species in Zilo Kalnu Nogazes Swamp Z2 and in the Zvardes swamp. *Calliergonella cuspidata* was common in Moricsala and *Riccardia palmata* was a widespread species in Zilo Kalnu Nogazes Swamp Z2.

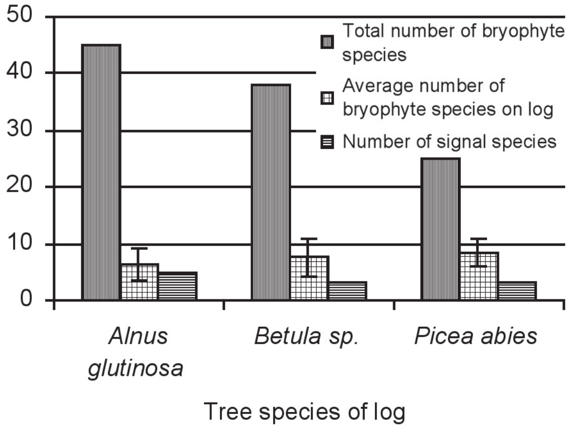

Fig. 4. Occurrence of bryophyte species richness on tree species.

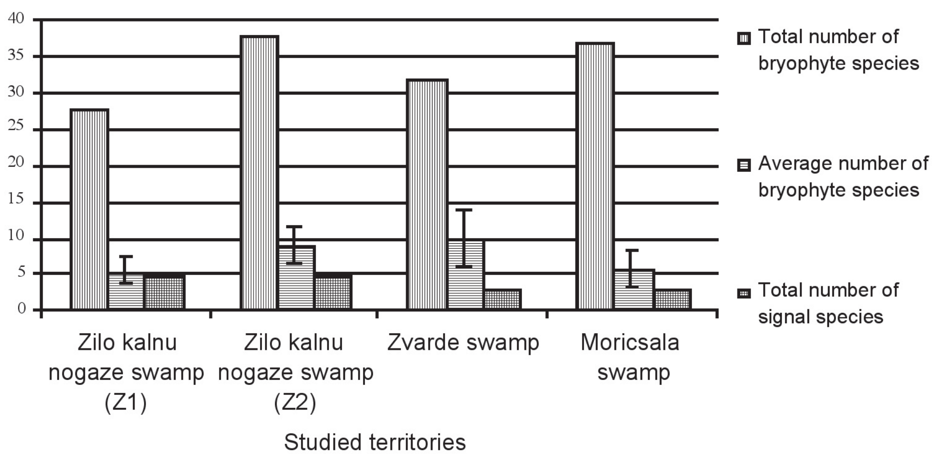

Fig. 5. Bryophyte species richness in relation to territory.

Discussion

In the present study *Hypnum cupressiforme* was found on logs in all decay stages. This, the most common species, has a wide ecological valence and can grow on different substrata (Āboliņa 1968).

Several authors have described decayed logs rich with liverworts (Āboliņa 1968; Vellak, Paal 1999). However in the present study this bryophyte species group represented slightly less than half of all bryophytes and richness was low. A possible explanation may be:

(1) *Picea abies* decayed logs in the studied swamps were not frequent, conifers support rich liverwort diversity (Hallingbäck, Holmåsen 2000; Ódor, Standovár 2002);

(2) liverwort species richness is affected by bark of the decayed log. Epixylic bryophytes grow and develop best when bark has fallen off (Crites, Dale 1998) but in our investigation bark was still attached also in the fourth decay stage.

The decay stage was the main factor affecting bryophyte species composition on decayed logs in Eurosiberian alder swamp forests. The epiphytes growing on living bark are already present on logs in the initial decay stage and remain for a long time until decay stage 4. In the next successional stage epixylic bryophyte species establish in the decay process as bark is lost. Epixylic bryophyte species reach their maximum in decay stage 4. This explains the high number of bryophyte species in the mid decay stages. However epixylic bryophytes are poor competitors and can soon disappear (Andersson, Hytteborn 1991). The decay process continues and ground bryophytes begin to dominate till the wood is not recognizable. Several authors have described this type of succession of bryophyte species on logs (Āboliņa 1979; Crites, Dale 1997; Rambo, Muir 1998; Lindström 2003).

Significant indicator species were not found in decay stages 2 and 3. The composition of bryophyte species also changed little in the decay stages 2 and 3, probably due to intact tree bark.

One problem with our chose field method was that if parts a decayed log were in different decay stages, only the main decay stage was recorded. This has been noted also in other work (Lindström 2003), but distinguishing different parts of logs for establishment of separate sampling plots is problematic.

A relation between decay stage and number of bryophyte species was not found, possibly because logs in I and V decay stage were less frequent. The low amount of logs in decay stage 5 may be related to past forestry management (Stokland 2001) or possibly they were simply missed in the studied territories.

Among the studied factors tree species of log showed an effect on bryophyte species composition and richness. Decay speed depends on tree species of log. Most deciduous trees decay faster than conifers, which do not provide a lasting microenvironment to bryophytes. Deciduous logs are most variable and unstable for bryophyte species (Stokland 2001). Logs of *Picea abies* were observed to be richer with bryophyte species compare with deciduous logs, which is consistent with other studies in Latvia (Bambe 2002; Bambe 2008). The average number of bryophyte species on spruce was nine species, on alder – seven species.

Several authors (Ódor, Standovár 2001; Bērmanis, Spuņģis 2002; Ek et al. 2002; Ódor et al. 2006) have described a relationship between diameter of logs and number of bryophyte species. While it also might be expected that large logs support more space for species, this was not found in our study and in Bambe (2002). In our study no significant correlation between the number of bryophyte species and the visible perimeter was found. Possible explanations may be: (1) biased sampling (few numbers of sampled decayed logs in some perimeter classes); (2) in previous studies, the forest microclimate differed from the studied Eurosiberian alder swamp forest.

The mean number of bryophyte species was not large in Moricsala compared with other studied territories, but there were examined a relative high number of decayed logs. This may be related with the moisture regime. Swamps mostly receive moisture from groundwater (Bušs 1981), but the moisture regime in Moricsala depends on fluctuations of the lake level (Laiviņa, Laiviņš 1980). This might mean greater fluctuation of water level. In summer dry conditions may prevent colonization by many epixylic bryophyte species.

Calliergonella cuspidata was an indicator species in Moricsala of the fifth decay stage. Considering that the largest number of decay logs in decay stage 5 was found in this territory, uneven stratified design likely has caused problem in interpretation, i.e. is this species an indicator of the specific conditions at Moricsala or a typical indicator of the more decayed classes? This problem can be avoided only greatly increasing the number of sampled territories.

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Epiksīlo sūnu ekoloģija Eirosibīrijas melnalkšņu dumbrājos Latvijā

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Kopsavilkums

Atmirusi koksne ir nozīmīgs struktūrelements Eirosibīrijas melnalkšņu staignāju mežos, kas nodrošina epiksīlo sūnu sugu daudzveidību. Pētījuma mērķis bija noskaidrot sūnaugu daudzveidību uz kritalām un abiotiskos, biotiskos faktorus, kas ietekmē sūnu floru. Lai to veiktu, apskatīti četri Eirosibīrijas melnalkšņu dumbrāji trīs Latvijas teritorijās – Moricsalā, Zvārdes mežu dabas parkā un Slīteres Nacionālajā parkā. Pētījumā kopumā aprakstītas 102 kritalas, uz kurām konstatētas 59 sūnu sugas. Par galveno faktoru, kas ietekmē sūnu sugu bagātību uz kritalām, noteikta sadalīšanās pakāpe. Notiekot kritalas trūdēšanas procesam, sūnu sugu sastāvs pamazām nomainās. Vislielākais sūnu sugu skaits vērojams kritalām, kas ir vidēji sadalījušās. Kritalas redzamais apkārtmērs būtiski neietekmēja sūnu sugu sastāvu un skaitu uz kritalām. Sūnu sugu sastāvs atšķīrās starp lapu kokiem un skujkokiem, kā arī nelielas atšķirības epiksīlo sūnu florā konstatētas katrā apskatītajā teritorijā.