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Bryophytes and decaying wood in *Hepatica* site-type boreo-nemoral *Pinus sylvestris* forests in Southern Estonia

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ABSTRACT

The aim of the study was to establish the amount of decaying wood (logs and stumps) in various groups of *Hepatica* site-type pine forests of different age and management intensity and to analyse the composition of bryophytes in dependence of these factors. The average volume of CWD in old unmanaged forests was 47.5 m^3/ha, which is rather well comparable with respective estimations from Fennoscandia. Reduced human impact contributes positively to the amount of CWD. Diversity of log diameter classes and decay stages is larger in old forests. Altogether 73 bryophyte species were recorded, 65 species on logs and 55 on stumps. Species richness on stumps was higher in managed forests than in unmanaged ones. At the same time, the species having high indicator value for man-cut stumps are very common species in boreal forests and grow on other substrata as well. Species composition and ecological conditions differed between stumps and logs. Logs are more humid microhabitats than stumps, therefore the occurrence of hepatics is more frequent on them. According to species composition on decaying wood the old unmanaged forests distinguished from others. As the differences of substratum characteristics were notable between old and young forests, the stand age described a considerable part of species variance on logs.

1. Introduction

Many species in forest ecosystems depend on decaying wood as a substratum, especially insects, fungi and bryophytes (Jonsson et al., 2005). Decaying wood is a temporary substratum, which changes during the decaying process until it finally disappears. This means that species can grow on logs or stumps only for a finite period of time and then have to disperse to another log or stump to maintain its population (Söderström, 1988b).

Characteristics of decaying wood (wood texture, moisture content, pH, diameter of fallen trees (logs) and stumps, etc.) vary in age, size and decay stage. Depending on the features of decaying wood, species having different life strategy and demands for substratum features, e.g. facultative epiphytes, early epixylics, late epixylics, ground flora species can grow on it (Söderström, 1988a). Large amount of decaying wood is especially characteristic of old natural forests (Qian et al., 1999; Christensen et al., 2005) as in those forests more logs are added continuously as a result of various disturbances. In old natural forests falling and decaying of logs are mostly in balance. Numerous studies show that bryophyte species richness and composition are dependent on stand age (Frisvoll and Presto, 1997; Söderström, 1988b; Jonsson and Esseen, 1990; Lesica et al., 1991). In the course of management large fallen logs are transported out of the forest and that reduces the amount of decaying wood considerably (Andersson and Hytteborn, 1991). In that way, human activities have an adverse impact to species richness and composition of forest bryophytes (Lesica et al., 1991; Söderström, 1988a,b; Andersson and Hytteborn, 1991; Trass et al., 1999; Vellak and Paal, 1999); and it is hepatics that are first of all negatively influenced (Söderström, 1988b; Vellak and Paal, 1999) as they are essentially associated with decaying wood in old forests (Lesica et al., 1991; Meier and Paal, in press).

One of the common direct results of human activities in forests is the appearance and increasing number of stumps. Similarly to logs they gradually moulder and serve as substratum for various bryophytes according to their decay stage. Quite little attention has been paid to differences of bryophytes on decaying logs and stumps. Still Andersson and Hytteborn (1991) have briefly discussed this problem; their results, however, do not demonstrate any good difference between logs and stumps as wood substratum for bryophytes.

As *Hepatica* site-type boreo-nemoral forests grow on fresh fertile soils and are productive, they have been mostly intensively

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managed. In spite of this, results of our earlier study (Meier et al., 2005) showed that the richness of bryophyte species was higher in forests of *Hepatica* site-type, having better productivity than in less productive alvar forests though these generally have smaller human impact (Liira et al., 2007). In our previous study (Meier and Paal, in press) the decaying wood appeared to be the species richest substratum by cryptogams and it had quite a unique bryophyte species composition in alvar forests. In the current paper we focus in more detail on decaying wood and bryophytes on this substratum in *Hepatica* site-type forests.

The aims of the present study were:

(1) to describe the characteristics of decaying wood in *Hepatica* site-type forests of different management and age classes;
(2) to compare the composition of bryophytes growing on logs and stumps in these forests;
(3) to evaluate the effects of forests age and management on bryophyte species composition.

2. Material and methods

2.1. Study area and experiment design

The fieldwork was carried out in the summers of 2004–2006 in southern Estonia, in Otepää Nature Park and in Karula National Park (between 57°40′54″ and 58°06′50″ N and 26°21′44″ and 34′19″ E; Fig. 1). Studied stands represent *Hepatica* site-type boreo-nemoral forests (*sensu* Paal, 1997). Forests of this site-type are considered as degraded remnants of boreo-nemoral mixed spruce forests from a warmer Atlantic climatic period (Laasimer, 1965), they grow on the deep Rendzinas, Cambisols and Luvisols of moraine-rich areas, particularly on hillocks distributed throughout the Baltic region (Lõhmus, 2004).

In studied forests the dominant species in the tree layer was *Pinus sylvestris*, while in the second tree layer *Picea abies* prevailed. Forests of three age classes were selected: (1) young forests with age of 40–55 years, (2) mature forests with age of 65–70 years and (3) old forests with age of more than 120 years. All stands were divided into two classes according to the management index (see Section 2.3). All in all 25 stands were studied: five old unmanaged forests, seven old managed forests, six mature managed forests, three young unmanaged forests and four young managed forests.

2.2. Sampling

For data collection circular sample plots with a radius of 25 m were used. If necessary, for remaining within the same community,

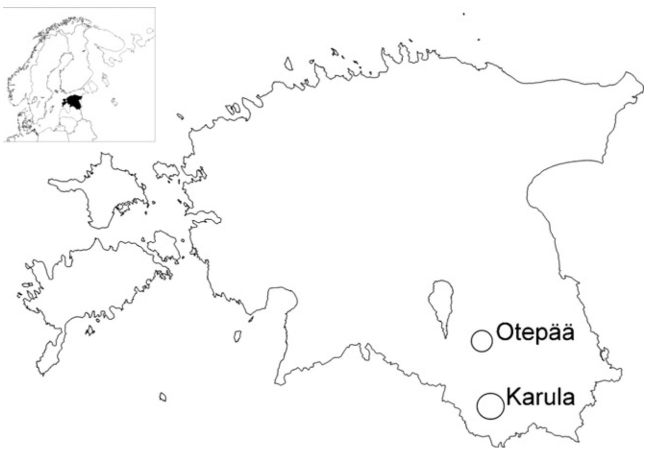

Fig. 1. Location of the study areas.

the shape of sample plots was changed a little, maintaining the surface area about 1950 m^2.

For logs taller than 1 m and having diameter ≥10 cm the following characteristics were recorded: length, diameters at both ends and decay stage. Average diameters were divided into four classes: 10–19 cm, 20–29 cm, 30–39 and ≥40 cm. Decay stages were estimated according to Renvall (1995) and Sippolaa et al. (2005) as: (1) recently died, wood hard, bark and phloem fresh, knife penetrates only a few millimetres into the wood, (2) wood hard, most of the bark is still staying but no fresh phloem present, knife penetrates 1–2 cm into the wood, (3) wood partly decayed from the surface or in the centre (depending on tree species), large pieces of bark are usually loosened or detached (conifers), knife penetrates 3–5 cm into the wood, (4) most of wood is throughout soft, usually without bark (conifers), the entire blade of the knife penetrates easily into the wood, (5) wood very soft, disintegrates when lifted, log surface covered by ground-layer mosses and lichens. Measurements were done with logs having a diameter of ≥10 cm and ≥20 cm around the sample plots central point within concentric circles with a radius of 10 m and 25 m respectively. Term ‘coarse woody debris’ (CWD) was used for logs with a diameter of ≥10 cm.

In the current study tree remains not higher than 0.4 m were considered stumps. They were classified as natural and man-cut, and their diameter and decay stage were measured. Stumps with a diameter of ≥10 cm were taken into consideration on areas with a radius of 10 m and stumps with a diameter of ≥40 cm on areas with a radius of 25 m.

Bryophyte species were registered separately on logs and stumps. Species abundance was evaluated by rank values from one to six according to the Braun–Blanquet’ scale (Kreeb, 1983). The specimens that were not identified in the field were collected for further laboratory investigation. Nomenclature of species follows Ingerpuu and Vellak (1998).

2.3. Data treatments

The volume of a log was calculated according to the volume of the frustum of a cone:

$$V = \frac{\pi h}{12}(D_2^2 + D_1^2 + D_2 D_1), \tag{1}$$

where h is length of the trunk and D_2 and D_1 are the larger and smaller diameters of the trunk. The surface potentially covered with bryophytes was considered as 2/3 of the mantel area (S) of each log:

$$S = \frac{\pi l}{2}(D_2 + D_1), \tag{2}$$

where l is the length of the trunk (Andersson and Hytteborn, 1991). The logs surface area values in different diameter classes and decay stages were used further for calculation of the Shannon diversity index (McCune and Mefford, 1999). Respective indices in case of stumps were calculated according to stumps number *per* 0.1 ha. Volumes were calculated for the purpose of comparing the results with other studies and the available substratum area to associate this with species data.

To express human impact on stands, management intensity index (MI) was used (Liira et al., 2007). At each study site, visible signs of anthropogenic activities (e.g. cut stumps, forest tracks, trampling, ditches, trash, etc.) were recorded. Each indicator of anthropogenic activities got a score 1 or 2 that describes the proportional effect. The management intensity index is the sum of scores of indicators of anthropogenic disturbances, weighed by the distance class. The observation of any indicator within a radius of 0–25 m around the sample plot centre doubled the scores effect compared to the score effect within a radius of 25–60 m. The management intensity index is equal to zero if none of the anthropogenic activity indicators were present within a radius of 60 m. The maximum value of the MI-index for forestland fraction can reach the value of 30 in the case of a forest clear-cut area with soil damage, trash pollution, intersecting ditches and road, and surrounded by neighbouring arable fields or buildings.

According to the value of management index all studied forests were divided into two classes: MI < 4 – unmanaged stands and MI $\geq$ 4 – managed stands. Because of great importance of cutting activities for this study we verified that all unmanaged stands were without regular cuttings as typical management of Estonian forests means thinnings at 20-year intervals (Kaar, 1986). We also inspected critically the management effects in the forests with MI $\geq$ 4. After some changes we got two final groups of forest: eight unmanaged and seventeen managed stands.

All bryophyte species were divided into four groups: (1) epixylics – occurring on dead wood as their main substratum, (2) epiphytes – growing mainly on the stems of living trees, (3) epigeics – species normally cover the forest ground, and (4) generalists – occur on a large number of different exposed substrata. With this grouping we followed Andersson and Hytteborn (1991); if some species in the cited paper were lacking, ecological checklists presented by Dierβen (2001) and Ulvinen et al. (2002) were used.

Habitat lightness, moisture and acidity were evaluated by means of calibration (Jongman et al., 1995), based on the ecological indicator values of bryophyte species (Düll, 1991) and weighted averaging algorithm.

2.4. Data analysis

To test age, management and age-management interaction effects on the dead wood characteristics the general linear model analysis (GLM) was applied. For analysing age-management interaction the mature and young forests were merged into one age class, the second age class constituted the old stands. To compare characteristics of decaying wood between three age classes (young, mature and old forests) the one-way ANOVA was exploited. Pairwise multiple comparisons were performed with Tukey's HSD test (StatSoft Inc., 2001).

The variation in species composition in stands of different age and management intensity, as well as on two decaying substrata was analysed using ordination techniques (ter Braak and Šmilauer, 2002). First the length of the species variation gradient was estimated by detrended correspondence analysis (DCA). As the gradient length appeared to be relatively short (<2SD), subsequently principal component analysis (PCA), a method based on a linear relationship between species abundances and ordination axes was used. Species which occurred less than three times were removed from analysis.

Redundancy analysis (RDA) (ter Braak and Šmilauer, 2002), which is appropriate for short gradients (<2SD), was employed in order to examine relationships between species composition and the environmental variables. To establish forest age and management pure effects on vegetation data, two separate partial RDA analyses were carried out where one of the variables was treated as covariable. Then the RDA analysis was repeated without covariable and the variance decomposition of considered effects was evaluated. Significance of all canonical axes (trace) was evaluated by the Monte Carlo permutation test (499 permutations).

The multi-response permutation procedures (MRPP-test; McCune and Mefford, 1999) were used to test bryophyte compositional differences between logs and stumps, as well as between forests of different age and management groups: older–younger, unmanaged–managed stands and between five groups of forest stands: old unmanaged (Ou), old managed (Om), mature managed (Mm), young unmanaged (Yu) and young managed (Ym).

The indicator values for grouping of the species in forests of different age and management classes, natural and man-cut stumps, logs and stumps were calculated by the Dufrêne and Legendre (1997) method included into program package PC-ORD (McCune and Mefford, 1999). The statistical significance of the obtained indicator values were evaluated by the Monte Carlo permutation test.

3. Results

3.1. Decaying wood in forests of different age and management classes

Volume of down CWD varied in different study sites from 0.7 m^3/ha in a young managed forest to 87.6 m^3/ha in an unmanaged young forest. The average volume of CWD was the highest in old unmanaged forests (47.5 m^3/ha) and the lowest in young managed forests (5.9 m^3/ha). There was more variation in logs diameter in old forests than in young ones (Fig. 2). Management had significant effect on volume of all down CWD, while age effect appeared in case of large logs ($d \geq 20$ cm) (Table 1). Amount of down CWD was higher in unmanaged stands than managed forests and the older forests had more fallen logs than young or mature forests.

The available substratum area of logs differed in unmanaged and managed forests: the unmanaged forests had more logs than managed stands considering all decay stages and diameter classes together or separately, but the effect was statistically relevant in the case of decay stages 3 and 5, and two smaller diameter classes (Table 1). The amount of logs in old forests was higher than in young and mature stands in case of $d \geq 20$ cm (together and diameter classes separately) and lower for logs with diameter 10–19 cm (Fig. 3). Age effect on logs appeared statistically reliable in case of logs with diameters 10–19, 30–39 and $\geq$40 cm (Table 1). One-way ANOVAs showed that diversity of diameter classes and decay stages differed significantly between three age classes ($F = 14.1$, $p < 0.001$ and $F = 5.2$, $p = 0.012$, respectively, Fig. 4).

The number of stumps was influenced only by management ($p < 0.05$), effects of age and age-management interaction appeared to be insignificant. Man-cut stumps were found only in managed stands, number of natural stumps was higher in unmanaged forests though this difference was not statistically significant (Table 1). The managed forests had more stumps than unmanaged stands also by all decay stages and diameter classes

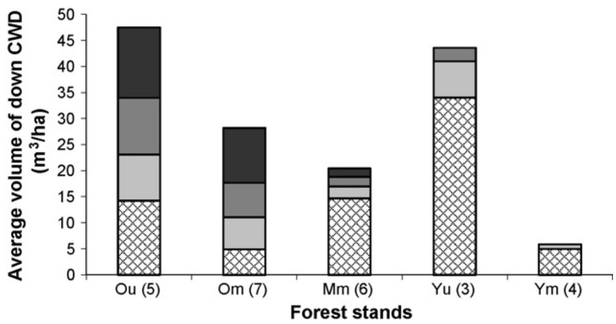

Fig. 2. Average volume of logs and their diametrical structure in different forest groups. Forest groups: Ou, old unmanaged; Om, old managed; Mm, mature managed; Yu, young unmanaged and Ym, young managed. Notations of four diameter classes (cm) are shown on figure. Numbers in brackets indicate sample size.

Table 1
Effects of forests management and age on the dead wood characteristics according to the general linear model analysis (GLM); in table the *F*-criterion values are presented.

Dead wood characteristics	Factor effect			
	Age	*M*	Age × *M*	Intercept
Volume (m^3/ha)				
Down CWD	0.8	6.4*	0.3	49.3***
Large logs ($d \geq 20$ cm)	9.0**	1.2	0.1	23.5***
SA of logs (m^2/0.1 ha)				
CWD	0.6	9.3**	0.8	54.4***
Decay stage 1	0.6	1.3	0.1	27.0***
Decay stage 2	2.3	<0.1	0.1	11.0**
Decay stage 3	0.1	7.8*	<0.1	31.9***
Decay stage 4	1.4	3.1	1.6	19.4***
Decay stage 5	0.9	8.0**	3.1	17.4***
D = 10.19 cm	4.8*	6.6*	1.2	29.9***
D = 20.29 cm	2.6	6.0*	0.9	49.2***
D = 30.39 cm	20.0***	3.7	0.9	45.2***
$D \geq 40$ cm	5.1*	0.3	0.5	6.0*
Diversity of diameter classes	19.5***	0.2	0.2	92.6***
Diversity of decay stages	4.0†	0.7	0.2	173.5***
Stumps (number/0.1 ha)				
Number of stumps	1.2	7.7*	0.5	59.3***
Number of cut stumps	0.1	11.7**	0.1	11.7**
Number of natural stumps	0.5	3.0	<0.1	18.6***
Decay stage 1	0.2	2.7	<0.1	6.4*
Decay stage 2	0.9	5.3*	<0.1	15.8***
Decay stage 3	<0.1	2.3	0.2	9.7**
Decay stage 4	0.3	2.0	<0.1	17.1***
Decay stage 5	1.0	1.4	0.4	23.0***
D = 10.19 cm	2.2	2.6	<0.1	33.2***
D = 20.29 cm	1.4	5.3*	0.3	16.7***
D = 30.39 cm	0.3	4.1†	0.1	7.8*
$D \geq 40$ cm	1.8	6.6*	2.0	15.3***
Diversity of diameter classes	1.1	5.3*	0.7	101.6***
Diversity of decay stages	0.9	2.1	0.5	90.8***

Two age classes were used (mature and young forests were merged). Notations: M, management; SA, available substratum area.
* $p < 0.05$.
** $p < 0.01$.
*** $p < 0.001$.
† $p < 0.06$.

separately, but the management effect was statistically relevant in case of decay stage 2 and diameter classes 20–29 and ≥40 cm (Table 1). The most frequent were stumps of decay stage 5. Management had effect to the diversity of stump diameter classes ($p < 0.05$).

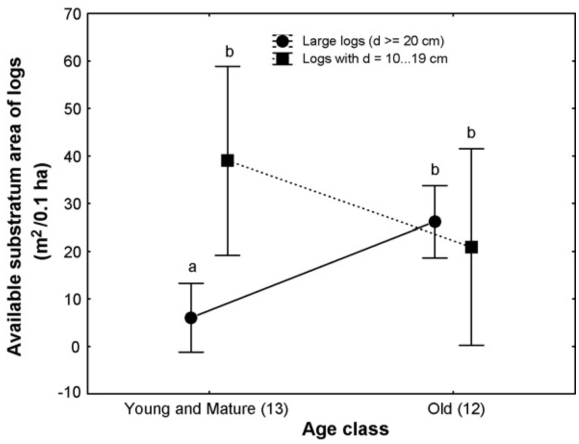

Fig. 3. Average (±95% confidence intervals) available substratum area of logs in relation to age class. Letters a and b indicate homogeneity groups according to the Tukey's HSD test. Numbers in brackets indicate sample size.

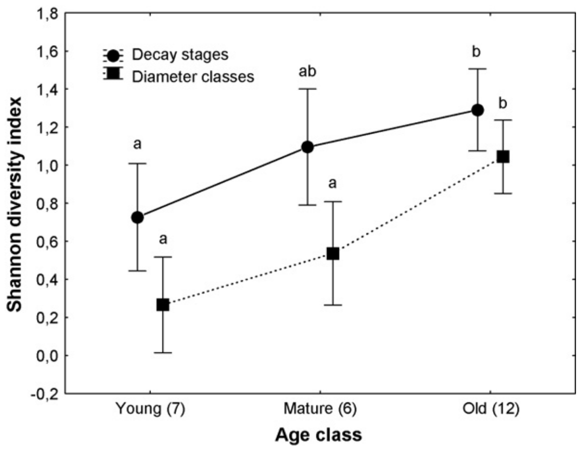

Fig. 4. Average (±95% confidence intervals) diversity of logs diameter classes (10–19 cm, 20–29 cm, 30–39 cm, ≥40 cm) and decay stages (1–5). Shannon index is calculated according to potential surface area (m^2/0.1 ha) inhabited by cryptogams. Letters a and b indicate homogeneity groups according to the Tukey's HSD test. Numbers in brackets indicate sample size.

3.2. Species diversity and composition on logs and stumps

All in all 73 bryophyte species (inc. 17 hepatics) were recorded; among them 15 species occurred with frequency more than 75%, e.g. *Hylocomium splendens*, *Lophocolea heterophylla*, *Dicranum scoparium*, *Brachythecium oedipodium*, *Herzogiella seligeri* and *Sanionia uncinata* (Appendix A). The average number of species on decaying wood per sample plot was 26 (on logs 22 species and on stumps 17 species). The highest species number per community was 33 species and the lowest number 17 species.

Total number of species recorded on logs was 65 (inc. 16 hepatics) and on stumps 55 (inc. 10 hepatics). The largest part of species on both substrata belongs to generalists (Fig. 5), about a quarter of all species are epigeic ground flora species and approximately one fifth constitute epixylic species preferring decaying wood as a primary substratum. The proportion of epiphytes on logs was slightly higher than on stumps. The most frequent species on logs were *H. splendens* (total frequency of occurrence 100%), *L. heterophylla* (100%), *D. scoparium* (96%), *B. oedipodium* (92%), *Hypnum cupressiforme* (92%) and *S. uncinata* (92%). On stumps *D. scoparium* (100%), *L. heterophylla* (96%), *Plagiothecium laetum* (92%), *H. seligeri* (88%), *Plagiomnium affine* (84%) and *Pleurozium schreberi* (84%) were common. According to the MRPP test, species composition on logs and stumps is significantly ($p < 0.001$) different. 18 species were recorded only on logs (e.g. *Orthotrichum speciosum* in 13 stands, *Climacium dendroides* in five stands and *Calypogeia suecica* in four stands) and six species only on stumps (e.g. *Fissidens adianthoides* in two stands). From species registered exclusively on logs the largest part (about one third) are epiphytes, while among species found only on

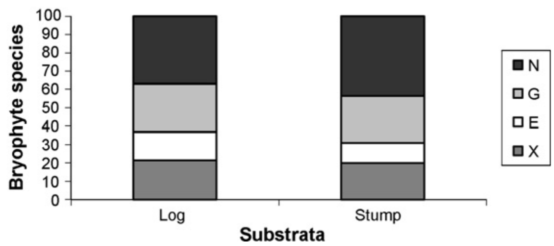

Fig. 5. Bryophyte species richness on logs and stumps according to the ecological groups. X, epixylics; E, epiphytes; G, epigeics; N, generalists.

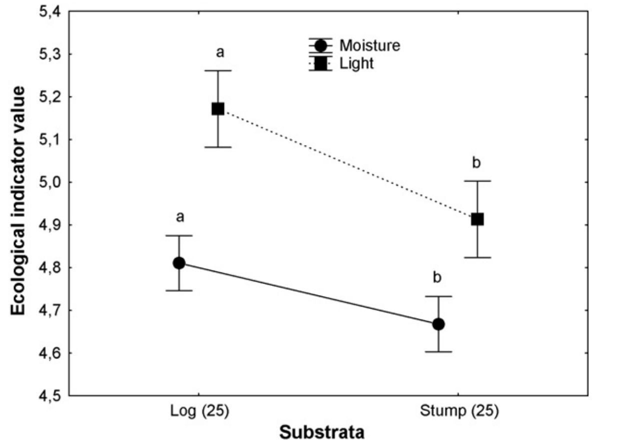

Fig. 6. Average (±95% confidence intervals) ecological indicator values of moisture and light (Düll, 1991) for logs and stumps. Letters a and b indicate homogeneity groups according to the Tukey's HSD test. Numbers in brackets indicate sample size.

stumps half are represented by generalists. The majority of hepatic species (14) grew on logs more frequently than on stumps.

Species of logs having significant grouping indicator value ($p < 0.05$) were the following: *H. splendens*, *H. cupressiforme*, *L. heterophylla*, *Nowellia curvifolia*, *O. speciosum*, *Ptilidium pulcherrimum*, *Ptilium crista-castrensis*, *Rhytidiadelphus triquetrus* and *S. uncinata*. In case of stumps three species, *Dicranum montanum*, *P. laetum* and *Tetraphis pellucida*, had a reliable indicator value. According to the MRPP test, significant ($p = 0.001$) difference was discovered between species composition on man-cut and naturally formed stumps. Species of man-cut stumps with significant indicator value were: *B. oedipodium*, *Brachythecium rutabulum*, *Dicranum polysetum*, *H. splendens*, *P. affine* and *Plagiomnium cuspidatum*. There was no bryophyte species for natural stumps having a reliable grouping indicator value. According to the species ecological indicator values it appeared in addition that the logs are more humid and light microhabitats for bryophytes than stumps (Fig. 6).

The stumps and logs are also rather clearly separated on the ordination plot (Fig. 7), where the first axis characterises 21.8% of total variance and the second axis 15.8%. Some samples from logs of younger and managed forests are intermixed with samples from stumps but samples from stumps among samples of logs are from old forests. The species position along the first ordination axis is mainly in accordance with their pH indicator values: on the axis negative end species having respective indicator value 1–3 (e.g. *P. pulcherrimum*, *L. heterophylla*, *S. uncinata*, *N. curvifolia* and *P. schreberi*) are located, while for the species on the axis positive end (e.g. *Rhodobryum roseum*, *Cirriphyllum piliferum*, *Brachythecium velutinum*, *Bryum caespiticium* and *Plagiochila asplenioides*) indicator values of 6–7 are characteristic. Position of species by the second ordination axis can be interpreted in terms of moisture gradient: the corresponding ecological indicator values of species decrease from the positive end of the axis towards negative end.

3.3. Species content in forests of different management and age groups

Age and management did not have any significant effect on bryophyte species richness on logs, but management had positive effect on species richness on stumps ($p < 0.05$).

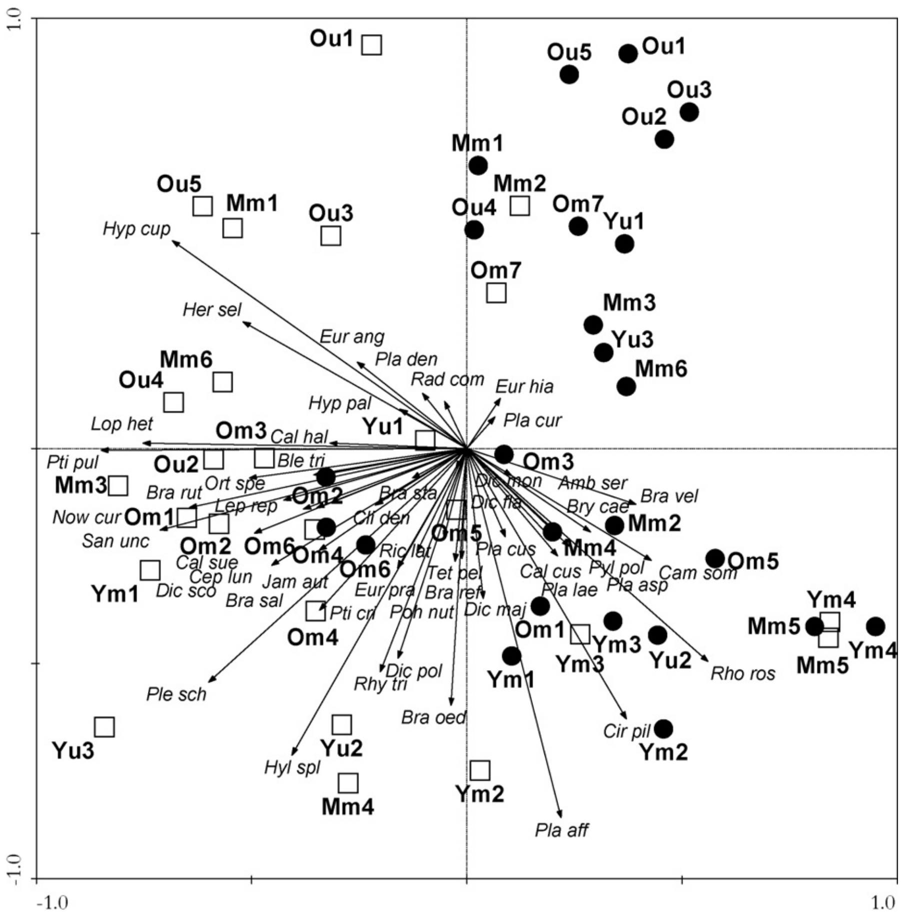

Fig. 7. PCA of species growing on logs (squares) and stumps (filled circles). Forest groups: Ou, old unmanaged; Om, old managed; Mm, mature managed; Yu, young unmanaged and Ym, young managed. For full names of species see Appendix A.

Species growing on logs did not differ much in unmanaged and managed forests (MRPP-test, $p = 0.196$) neither between three age classes ($p = 0.248$) but between all five considered groups of forests, the difference appeared to be nearly significant ($p = 0.081$). *H. seligeri* and *Plagiothecium curvifolium* had a statistically significant ($p < 0.05$) indicator value for old unmanaged forests. For young unmanaged forests *Jamesoniella autumnalis* and *Riccardia latifrons*, and for young managed forests *B. oedipodium* have a reliable grouping indicator value. According to log species data, old unmanaged stands are all located in the same quarter on the ordination plot (Fig. 7). 13.5% of species variance was explained by forest age and management by RDA analysis; significance level of all canonical axes was $p = 0.028$. The partial RDA tests confirmed forest age significant effect (7.8% of total variance, $p = 0.032$) on bryophyte vegetation.

Species composition on stumps differed significantly between unmanaged and managed forests (MRPP-test, $p < 0.001$). Difference by three forests age classes was marginally insignificant ($p = 0.083$) but significant between two forest age classes ($p = 0.021$) and between the all five groups of forests ($p < 0.001$). Species with significant grouping indicator value in managed stands were *B. oedipodium*, *D. montanum*, *H. splendens*, *P. schreberi*, *P. affine* and *P. cuspidatum*. *H. seligeri* and *Lepidozia reptans* appeared to be characteristic for old forests and *B. oedipodium* and *P. affine* for young forests. By bryophyte species ecological indicator values of pH, lightness and moisture we did not discover any reliable difference between the forests of considered age and management classes.

According to stump species data, old unmanaged stands are rather clearly separated from others on the ordination plot (Fig. 7). 21.3% of species variance was explained by age and management by RDA analysis (significance of all canonical axes $p = 0.002$). The partial RDA tests showed significant management (12.2% of total variance, $p = 0.002$) and age (8.7% of total variance, $p = 0.008$) pure effects on the bryophyte vegetation.

4. Discussion

4.1. Decaying wood in forests of different age and management classes

The volumes of dead wood in forests ascertained in the current study are rather well comparable with respective estimations from Fennoscandia. For example, the average volume of down CWD in old unmanaged forests was 47.5 m^3/ha according to our analyses, which approximately equals an average of 50 m^3/ha for three old protected areas dominated by *P. sylvestris* in northern Sweden (Linder et al., 1997), to an average of 48.7 m^3/ha for protected old-growth forests in eastern Finland (Rouvinen et al., 2005), and to an average of 42.6 m^3/ha from natural *P. sylvestris* forests in eastern Fennoscandia (Karjalainen and Kuuluvainen, 2002). However, in *Pseudotsuga menziesii* stands of age 80–199 years in western Oregon and Washington the average volume of decaying logs was 148 m^3/ha (Spies et al., 1988).

In Estonian old-growth natural forests the amount of dead wood was about eight times higher than in young managed forests. This result is also rather similar to the respective values in forests of Fennoscandia (Siitonen, 2001; cf. Jonsson et al., 2005). Volumes of dead wood in managed forests start to increase noticeably in stands more than 60 years of age (Ranius et al., 2003). At the same time, the amount of down CWD did not differ significantly in forests of compared age classes. In addition to several studies confirming good positive relationship between forest age and dead wood amount (cf. Jonsson et al., 2005; Christensen et al., 2005) there are also results which disagree with these facts (Spies et al., 1988; Boudreault et al., 2002; Rubino and McCarthy, 2003). The amount of CWD depends also on tree species content of stands and habitat conditions (Spies et al., 1988; Fridman and Walheim, 2000; Nilsson et al., 2003; Rubino and McCarthy, 2003). However, increase in stand age contributed positively to the amount of large logs ($d \geq 20$ cm). Söderström (1988a), Samuelsson et al. (1994) and Humphrey et al. (2002) have emphasized the importance of large logs for bryophytes, especially for rare species. These logs decay slowly and are thus available as substratum for a longer time than smaller logs. Negative influence of management on the amount of CWD verified in the current study is in a good concordance with the results of earlier studies (e.g. Jonsson and Jonsell, 1999; Krankina et al., 2002; Kohv and Liira, 2005; Köster et al., 2005). The amount of decaying wood has been considered one of the main factors distinguishing managed and unmanaged forests (Cooper-Ellis, 1998).

In addition to the amount of logs, the diversity of log decay stages and diameter classes are of great importance for bryophytes (Söderström, 1988a; Ódor and Standovár, 2001). Diversity of logs seems to be more influenced by forest age than management rate; Söderström (1988b), e.g. did not find difference between natural and managed stands in diversity of diameter classes. Crites and Dale (1998) have demonstrated greater diversity of substrata (different decay stages and diameter classes) in old stands compared with young and mature stands as in the current study. However, considerably low amount of logs in decay stages 5 and 3, as well as logs with diameter 10–29 cm in managed forests can be caused by regular thinning what makes distribution of logs uneven; logs with some diameter classes are rare in managed forests simply because trees are cut before they succumb to senescence or natural disturbance (Jonsson et al., 2005).

4.2. Species diversity and composition on logs and stumps

Bryophyte species richness on decaying wood appeared to be rather high in the studied forests. Though we do not have yet generalized data about the number of bryophytes inherent for Estonian forests of different site types or on various substrata, the average bryophyte species number on decaying wood in a sample plot (26 species) found in the current study is very similar to the respective number established on sample plots of the same size for *Hepatica* site type pine forests in western Estonia (28 species). In alvar *Calamagrostis* site type pine forests growing on periodically dry moderately thick (up to 30 cm) Rendzic Leptosols this number was considerably lower—19 species (Meier et al., 2005, detailed data unpublished). The total number of bryophyte species registered by us on decaying wood (73) is about half of the number of bryophyte species characteristic for Swedish coniferous forests (122) and Finnish forests in total (144) (Hallingbäck, 1996; Ulvinen et al., 2002). On decaying wood in a natural *P. abies* and a managed *P. sylvestris* forest in Sweden, Andersson and Hytteborn (1991) recorded 54 species of bryophytes. Fourteen epixylic bryophyte sepecies found in the current study is nearly half of the 35 Finnish forests bryophyte species occurring mainly on dead wood (Ulvinen et al., 2002). The number of bryophyte species facultatively utilising logs and stumps is much larger than the number of species actually depending on decaying wood. For instance, Laaka (1993) found a total of 99 bryophyte species growing on decaying wood in old spruce-dominated forests in different parts of Finland (cf. Siitonen, 2001).

Our results demonstrated rather clearly the difference in bryophyte species composition on logs and stumps. That proceeds from the ecological conditions peculiar to these microhabitats: logs lying on ground are more saturated with moisture than stumps and this is one of the main factors determining the bryophyte species assemblages on both substrata (McCullough, 1948; Jansová and Soldán, 2006). The humid microhabitats are favourable first of all to the hepatics (Söderström, 1988b; Rambo and Muir, 1998; Jansová and Soldán, 2006), therefore they were considerably more frequent on logs than on stumps. Hepatics grow usually on steep slopes on the sides of logs to avoid the humus layer, which accumulates easier on the flat upper parts of logs. Hepatics might thus also escape competition with faster expanding pleurocarpous mosses that usually occupy the upper parts of logs (Jansová and Soldán, 2006).

The higher ecological indicator value of lightness for logs than for stumps seems a bit confusing. This result accrued from the fact that several bryophytes actually growing on logs are remnants of the original epiphytic bryophyte assemblages on living trees (Rambo and Muir, 1998). Epiphytic species mainly associated with logs (e.g. *O. speciosum*, *P. pulcherrimum*) or found by us only on logs (other *Orthotrichum* species) have high light indicator value (7–8) (Düll, 1991). But usually the *Orthotrichum* species grow higher on tree stems and larger branches (Dierβen, 2001), where light conditions are better than in microhabitats closer to ground. In addition to that, several ground flora species (e.g. *R. triquetrus*, *H. splendens*) also having high light indicator value (6–7; Düll, 1991) were more frequent on logs than on stumps. In that way the scoring indicator value of light conditions can be misleadingly high for logs. At the same time, *P. laetum* and *T. pellucida* recorded by us on stumps, prefer ordinarily shadow places (light indicator value 3–4; Düll, 1991). *P. laetum* is especially common on bases of *P. abies*.

Bryophyte species identified by their grouping indicator value as bounded to logs, have various ecological behaviour (Andersson and Hytteborn, 1991). Among them epixylic specialists (e.g. *L. heterophylla*, *N. curvifolia*), epiphytes (*O. speciosum*, *P. pulcherrimum*), competitive epigeics (*H. splendens*, *P. crista-castrensis*, *R. triquetrus*) and opportunistic generalists (*H. cupressiforme*) are represented. Species content changes during the decaying process, being favoured by facultative epiphytes in early decay stages and by ground flora species in late decay period. Therefore variation in decay stages gives an opportunity of growing to species having different life strategy. Abundance of logs of various diameter classes is also important for bryophyte species diversity, because, e.g. late epixylics use mostly only large logs, which will not become quickly overgrown by strong competitors from the forest floor bryophytes (Söderström, 1988a; Rambo and Muir, 1998).

T. pellucida, being characteristic for stumps in the current study was found by Söderström (1988b) on the stumps as the only member of the late epixylic group (*sensu* Söderström, 1988a). This species can grow on different substrata but has perianth/sporophytes much more frequently on stumps than on logs or other substrata; stumps are, therefore, important substratum for persistence, other substrata may be regarded as suboptimal (Söderström, 1993). Nevertheless, this species is usually represented in natural stands (e.g. Andersson and Hytteborn, 1991; Vellak and Paal, 1999; Jansová and Soldán, 2006), being in some cases even remarkably more frequent there than in managed stands (Økland et al., 2003).

Number of species found only on a particular substratum was higher on logs than on stumps. Andersson and Hytteborn (1991) have achieved similar results when data for managed and natural forests were treated together.

4.3. Species content in forests of different management and age groups

Age is an important factor for evolving species composition on decaying wood. In young stands there has not been enough time for developing suitable microhabitats and establishing many potential bryophyte species. Therefore, species composition of deadwood-dependent organisms varies markedly through the process of wood decay and particular species prefer decaying wood of different decay stages and diameter classes (Söderström, 1988a; Kushnevskaya et al., 2007) which are more diverse in old forests. Species compositional differences between older and younger stands have been established earlier for different types of forests (e.g. Crites and Dale, 1998; Boudreault et al., 2002). Several bryophyte species depend on large logs, for instance more than 50% of the wood-dependent species in Sweden occur primarily on logs having diameter >20 cm and about 15% of the species are confined to dead wood with diameter >40 cm (Jonsson et al., 2005).

A more numerous and diverse substratum of stumps in managed stands than in unmanaged forests increases the number of species growing there. From this follows that regular thinning will favour bryophyte species richness on stumps. Nevertheless the characteristic species of man-cut stumps (e.g. *B. oedipodium*, *D. polysetum*, *H. splendens* and *P. affine*) are very common species in boreal forests on several substrata and thereby the total bryophyte species richness often may not increase in these communities after loggings.

H. seligeri having a significant indicator value for logs in old unmanaged stands is considered as characteristic species for old-growth natural deciduous forests in Sweden (Gustafsson et al., 1992); it is also the most frequent species in old natural beech forests in the Czech Republic (Jansová and Soldán, 2006).

Species richness and composition on logs did not differ noticeably in unmanaged and managed forests in spite of an observably larger amount of available substratum area in unmanaged forests. In our previous study in alvar forests, the management effect on species composition (all substrata together) did not appear clearly either (Meier and Paal, in press). Anyway, according to the results of the current study, stump species compositional differences between management and age classes were notable. As species composition on logs and stumps differed most between five groups of forests (old unmanaged, old managed, mature managed, young unmanaged and young managed), the combined age and management effect appeared to be essential, especially for distinguishing old unmanaged stands from others. Continuous occurrence of suitable microhabitats over time is important for wood-dependent species and this is more inherent for old natural stands than for young and managed ones (Jonsson et al., 2005).

5. Conclusions

The main characteristic of substrata, which was favoured by stand age, was diversity of log diameter classes. Management had negative effect to the amount of logs. However, number of stumps and bryophytes growing on them was higher in managed forests than in unmanaged ones. At the same time, the species having high indicator value for man-cut stumps are very common species in boreal forests and grow on other substrata as well. Species composition and ecological conditions differed between stumps and logs. That proceeds from the ecological conditions: logs are more humid microhabitats than stumps and suit better for growth of several hepatics. In spite of much more available surface area in unmanaged forests, the species richness and composition on logs did not differ remarkably between managed and unmanaged forests. As the differences of substratum characteristics were notable between old and young forests, the stand age described a considerable part of species variance.

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Appendix A

Occurrence of bryophyte species. The figures in table show in how many stands the species was recorded. Ecological groups: X, epixylics; E, epiphytes; G, epigeics; N, generalists. Forest groups: Ou, old unmanaged; Om, old managed; Mm, mature managed; Yu, young unmanaged and Ym, young managed. L, log; S, stump; abbr., abbreviations; Freq., frequency of occurrence.

Species (abbr.)	Ecological group	Log						Stump					
		Ou; n = 5	Om; n = 7	Mm; n = 6	Yu; n = 3	Ym; n = 4	Freq.%	Ou; n = 5	Om; n = 7	Mm; n = 6	Yu; n = 3	Ym; n = 4	Freq.%
Amblystegium serpens (*Amb ser*)	N	3	2	2	–	1	32	–	1	2	–	1	16
A. subtile	E	–	–	–	–	–	0	–	–	–	1	–	4
A. varium	E	1	–	–	–	–	4	–	–	–	–	–	0
Atrichum undulatum	G	–	1	–	1	–	8	–	–	–	–	–	0
Blepharostoma trichophyllum (*Ble tri*)	X	2	1	2	1	–	24	–	–	1	1	–	8
Brachythecium oedipodium (*Bra oed*)	N	4	7	5	3	4	92	1	6	6	3	4	80
B. reflexum (*Bra ref*)	N	1	2	1	–	1	20	–	–	1	–	3	16
B. rutabulum (*Bra rut*)	N	4	3	2	2	2	52	–	4	3	–	1	32
B. salebrosum (*Bra sal*)	N	2	3	3	1	2	44	–	3	2	1	2	32
B. starkei (*Bra sta*)	N	1	2	–	1	1	20	–	1	1	1	1	16
B. velutinum (*Bra vel*)	X	4	3	3	1	1	48	1	3	3	1	2	40
Bryum argenteum	N	–	–	–	–	–	0	–	–	1	–	–	4
B. caespiticium (*Bry cae*)	N	–	–	1	–	–	4	–	1	1	–	–	8
B. flaccidum	E	–	1	1	–	–	8	–	–	–	–	–	0
Callicladium haldanianum (*Cal hal*)	N	1	1	1	2	–	20	1	–	–	–	–	4
Calliergonella cuspidata (*Cal cus*)	G	–	1	1	–	1	12	–	1	–	–	–	4
Calypogeia muelleriana	N	–	–	–	1	–	4	–	–	–	–	–	0
C. suecica (*Cal sue*)	X	1	–	2	1	–	16	–	–	–	–	–	0
Campylium sommerfeltii (*Cam som*)	X	1	1	1	–	1	16	–	1	1	–	1	12
Cephalozia bicuspidata	X	–	–	1	1	–	8	–	–	–	–	–	0
C. lunulifolia (*Cep lun*)	X	1	–	–	1	1	12	–	–	–	–	–	0
Cephaloziella rubella	N	–	–	–	–	–	0	1	1	–	–	–	8
Ceratodon purpureus	N	–	–	–	–	–	0	–	1	–	–	–	4
Cirriphyllum piliferum (*Cir pil*)	N	–	5	3	3	3	56	–	2	3	1	2	32
Climacium dendroides (*Cli den*)	G	–	1	3	1	–	20	–	–	–	–	–	0
Dicranum flagellare (*Dic fla*)	X	–	–	1	–	–	4	–	1	–	–	1	8
D. majus (*Dic maj*)	G	–	1	1	–	1	12	–	–	–	–	2	8
D. montanum (*Dic mon*)	E	4	4	4	2	2	64	3	6	5	2	4	80
D. polysetum (*Dic pol*)	G	1	5	1	2	4	52	–	3	2	–	2	28
D. scoparium (*Dic sco*)	N	5	7	6	3	3	96	5	7	6	3	4	100
Eurhynchium angustirete (*Eur ang*)	G	3	5	3	–	1	48	1	2	4	–	1	32
E. hians (*Eur hia*)	G	2	–	–	–	–	8	–	1	–	–	–	4
E. praelongum (*Eur pra*)	N	–	–	–	1	2	12	–	–	–	1	1	8
Fissidens adianthoides	G	–	–	–	–	–	0	–	–	1	–	1	8
Geocalyx graveolens	N	–	–	–	1	–	4	–	–	–	–	–	0
Herzogiella seligeri (*Her sel*)	X	5	5	5	2	3	80	5	7	4	3	3	88
Hylocomium splendens (*Hyl spl*)	G	5	7	6	3	4	100	1	7	4	1	4	68
Hypnum cupressiforme (*Hyp cup*)	N	5	7	5	3	3	92	5	5	5	2	3	80
H. pallescens (*Hyp pal*)	N	4	3	1	1	–	36	–	3	2	–	1	24
Jamesoniella autumnalis (*Jam aut*)	X	–	–	1	2	1	16	–	–	–	1	–	4
Lepidozia reptans (*Lep rep*)	X	2	3	2	2	1	40	1	4	1	–	–	24
Lophocolea heterophylla (*Lop het*)	X	5	7	6	3	4	100	5	7	6	3	3	96
Neckera pennata	E	–	–	–	–	–	0	–	1	–	–	–	4
Nowellia curvifolia (*Now cur*)	X	4	3	4	2	1	56	–	2	–	–	–	8
Orthotrichum affine	E	1	–	1	–	–	8	–	–	–	–	–	0
O. obtusifolium	E	–	–	1	–	–	4	–	–	–	–	–	0
O. speciosum (*Ort spe*)	E	2	5	5	1	–	52	–	–	–	–	–	0
Pellia endiviifolia	G	–	–	1	–	–	4	–	–	–	–	–	0
Plagiochila asplenioides (*Pla asp*)	G	–	–	1	–	1	8	–	–	1	–	1	8
P. porelloides	N	–	–	–	–	1	4	–	–	–	–	–	0
Plagiomnium affine (*Pla aff*)	G	2	7	5	2	4	80	2	7	5	3	4	84
P. cuspidatum (*Pla cus*)	N	5	3	4	2	2	64	–	3	5	1	2	44
P. elatum	G	–	–	–	1	–	4	–	–	–	–	–	0
Plagiothecium curvifolium (*Pla cur*)	N	4	–	1	1	1	28	2	5	2	2	–	44
P. denticulatum (*Pla den*)	N	1	1	–	–	1	12	1	–	–	–	–	4
P. laetum (*Pla lae*)	N	3	4	3	2	3	60	4	7	5	3	4	92
P. nemorale	N	–	1	–	–	–	4	–	–	–	–	–	0
Platygyrium repens	E	1	–	–	–	–	4	–	–	–	–	–	0
Pleurozium schreberi (*Ple sch*)	G	4	7	5	3	3	88	2	7	5	3	4	84
Pohlia nutans (*Poh nut*)	N	–	1	–	–	2	12	–	2	–	1	1	16
Polytrichum longisetum	G	–	–	–	–	–	0	–	–	1	–	–	4
Pseudoleskeella nervosa	N	–	1	–	–	–	4	–	1	–	–	–	4
Ptilidium pulcherrimum (*Pti pul*)	E	5	6	5	3	3	88	3	6	3	3	1	64
Ptilium crista-castrensis (*Pti cri*)	G	2	2	2	3	2	44	–	–	2	–	–	8
Pylaisia polyantha (*Pyl pol*)	E	–	1	2	–	1	16	–	–	1	–	–	4
Radula complanata (*Rad com*)	E	1	1	1	–	–	12	–	–	–	1	–	4
Rhodobryum roseum (*Rho ros*)	G	–	1	2	2	3	32	–	1	2	1	3	28
Rhytidiadelphus squarrosus	G	–	1	–	–	–	4	–	–	–	–	–	0
R. triquetrus (*Rhy tri*)	G	2	6	4	3	4	76	–	7	1	2	3	52

Appendix A (*Continued*)

Species (abbr.)	Ecological group	Log						Stump					
		Ou; n = 5	Om; n = 7	Mm; n = 6	Yu; n = 3	Ym; n = 4	Freq.%	Ou; n = 5	Om; n = 7	Mm; n = 6	Yu; n = 3	Ym; n = 4	Freq.%
Riccardia latifrons (*Ric lat*)	X	–	–	–	2	–	8	–	–	1	2	–	12
Sanionia uncinata (*San unc*)	N	4	7	6	3	3	92	–	4	4	1	1	40
Tetraphis pellucida (*Tet pel*)	X	3	1	3	2	1	40	2	7	4	2	3	72
Thuidium spp.	N	–	–	–	–	–	0	–	–	–	1	–	4

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