

Epixylic diversity in an old-growth boreal forest is influenced by dynamic substrate attributes

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Abstract

Quantifying the factors influencing wood-inhabiting species in boreal forests is crucial for better understanding of their ecology and conservation needs. We estimated the influence of substrate attributes on epixylic diversity on logs of *Picea abies*, *Betula pubescens*, *B. pendula*, *Populus tremula* and *Pinus sylvestris* in a mixed European old-growth boreal forest with high substrate availability and continuity. The number of species of different taxonomic and substrate groups in respect of log attributes was estimated with generalized linear models. The composition of epixylic communities was analysed using non-metric multidimensional scaling with subsequent environmental fitting. Additionally, we calculated species interaction networks of log (tree) species and epixylic plants and lichens. Species richness per log decreased with the increasing height above the ground and increased with the increasing amount of accumulated litter. True epixylics were the most sensitive to a log position above the ground. Aspen and conifer logs harbored the highest richness of rare species of lichens and liverworts. Birch logs hosted mainly species with wide substrate amplitude. The whole epixylic community specialization index decreased in the order lichens, liverworts, mosses, vascular plants. Tree species identity and associated attributes (bark cover, pH, etc.) as well as 'dynamic' attributes (accumulation of litter, wood decomposition and time since tree death) influenced the total species number, their taxonomic diversity, and the composition of epixylic communities. Our results indicate the importance of wood of various age and tree species for the conservation of epixylic diversity in boreal forests.

Keywords: epixylic community, bryophytes, lichens, dead wood, coarse woody debris, decomposition, bark

Introduction

In intensively managed boreal forests, the diversity of epixylic communities is threatened because of the lack of their habitat, and dead wood, especially coarse woody debris (CWD). Better understanding of the relation between epixylic bryophytes and lichens and certain CWD attributes is needed for a sound forest management, ecological restoration, and nature conservation planning (Söderström et al., 1992; Seibold et al., 2015; Sandström et al., 2019). This is especially important in view of the climate change, which is expected to lead to shifts in boreal bryophyte communities towards large, competitive species and to an overall decrease in diversity (Löbel, Schröder, and Snäll, 2021).

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The composition and dynamics of epixylic communities are influenced by many interrelated factors (Söderström, 1988a; Jansova and Soldan, 2006; Botting and DeLong, 2009; Müller et al., 2015; Preikša, Brazaitis, Marozas, and Jaroszewicz, 2016; Żarnowiec, Staniaszek-Kik, and Chmura, 2021). Dead wood species identity influences the occurrence and abundance of epixylic species due to the differences in pH, surface texture and bark properties (Söderström, 1988a,b; Müller et al., 2015; Preikša, Brazaitis, Marozas, and Jaroszewicz, 2016; Kushnevskaya and Shorohova, 2018; Staniaszek-Kik and Żarnowiec, 2018). Among European boreal tree species, spruce logs host maximum epixylic diversity (Söderström, 1988a,b; Andersson and Hytteborn, 1991). In North America, pine and fir commonly show greater epixylic community richness (Kumar, Chen, Thomas, and Shahi, 2018).

Other substrate attributes influencing epixylic species richness and community composition include the dead wood size (Heilmann-Clausen et al., 2014), position, or height above the ground (Botting and DeLong, 2009), accumulation of litter or humus on the log surface (Jansova and Soldan, 2006), as well as decay stage and CWD age, or time since tree death (Caruso and Rudolphi, 2009; Brumelis et al., 2017). Substrate-level factors were shown to be more important than ecosystem-level factors for epixylic species richness (Mills and Macdonald, 2004; Táborská et al., 2017) but not for community composition (Táborská et al., 2017; Kushnevskaya and Shorohova, 2018). The inconclusive results concerning the effects of different substrate attributes on the epixylic communities, e.g., the results on the effects of CWD size (Preikša, Brazaitis, Marozas, and Jaroszewicz, 2016; Kushnevskaya and Shorohova, 2018) and species (Heilmann-Clausen, Aude, and Christensen, 2005; Goia and Gafta, 2018) on epixylic species richness can be explained by the interrelationship between factors of different levels.

In Europe, evidence about epixylic communities has been acquired mainly in intensively managed or semi-natural / natural forests situated as small islands within managed landscapes (Söderström, 1988a,b; Löhmus, Löhmus, and Vellak, 2007), and provides limited knowledge on substrate preferences of rare epixylic species and their role in wood-inhabiting communities. Epixylic communities in old-growth forests with the lack of special connectivity (Löhmus, Löhmus, and Vellak, 2007) and continuity, i.e., with past management, are impoverished in terms of both species richness and composition (Táborská et al., 2017). In boreal forests, several studies have revealed substrate specific and dynamic patterns of epixylic vegetation in North America in the unmanaged forests with high availability and continuity of CWD of different species and good landscape-level connectivity (Crites and Dale, 1998; Mills and Macdonald, 2004; Boudreault et al., 2018; Kumar, Chen, Thomas, and Shahi, 2018). Linking the substrate preferences of individual species and compo-

sition of epixylic cryptogamic communities on decaying logs to the decay stage, time since tree death, tree species, log size and specific substrate attributes may help ranking and quantitatively estimating the role of these factors in epixylic diversity and maintain its continuity for epixylic diversity in European boreal forests.

We examined the influence of substrate attributes on the diversity of epixylic communities on logs of main European boreal tree species: Norway spruce (*Picea abies* Karst.), silver and downy birch (*Betula pubescens* Ehrh. and *B. pendula* Roth.), aspen (*Populus tremula* L.) and Scots pine (*Pinus sylvestris* L.) in a chronosequence of decomposition covering a period up to 66 years after tree death in a mixed old-growth middle boreal forest situated in a large old-growth forest conservation area with good local and landscape scale connectivity. Specifically, we estimated the effects of 1) log (tree) species identity, surface area and diameter, 2) time since tree death, wood softness (degree of decomposition) and the amount of accumulated litter, 3) position (proximity to the ground), as well as 4) cover, area-specific mass, pH and moisture of bark and on the occurrence of wood-inhabiting cryptogamic epixylic species, their taxonomic and substrate groups and the composition of epixylic communities. The taxonomic groups studied included macrolichens, mosses, liverworts and vascular plants. The studied cryptogamic species were classified as epiphytes, facultative epixylics, true epixylics, epigeous and generalists according to their substrate preferences based on the literature and expert evaluations. We examined the relationship between the number of epixylic species used as indicators of old-growth boreal forests and the total number of epixylic species to explore whether specialized species indicate high epixylic richness. We tested the hypotheses that the frequency of occurrence of individual species, species richness of wood-inhabiting bryophytes and macrolichens, and the composition of epixylic communities on decaying logs are log (tree) species-specific and dynamic with maximum bryophyte richness, and especially richness of true epixylics on spruce logs. Aspen and pine logs were assumed to host maximum lichen diversity. Among tested predictors, log species identity and time since tree death were assumed to be the most important for epixylic communities. The number of rare species was assumed to increase with the increase of species number per CWD unit.

Materials and methods

Study area

The study was carried out during the summers of 2015 and 2016 in the middle boreal old-growth forest located in Strict Nature Reserve “Kivach” (after “Kivach” Reserve) in the Republic of Karelia, Russia (62°28'N, 33°95'E). The “Kivach” Reserve was established in 1931 and it is strict-

ly protected (i.e., no forest management is allowed). The protected area occupies 109 km² and over 80 % of the area is covered by semi-natural mainly old-growth forests. The mean annual temperature is +2.4°C, the length of the growing season is 90 days, and the mean annual precipitation is 625 mm (Skorohodova, 2008).

Selected forest stands of ca. 10 ha consisted of Norway spruce (60 %, 90–180 yrs.), silver and downy birch (20 %, 40–90 yrs.), aspen (10 %, 40–80 yrs.) and Scots pine (10 %, 120–220 yrs.). The dominated forest types were *Piceetum oxalidosum* and *Piceetum oxalidoso-myrtillosum* with patches of *P. fontinale* and *P. oxalidoso-myrtillosum* according to the classification of forest ecosystems in the Northwest of Russia (Fedorchuk, Neshataev, and Kuznetsova, 2005). The soils were humic-gley and superficially eluvial gleish sandy-loamy and loamy on varved clays (Fedorets, 2006) and podzolic sandy-loam. The total volume of CWD was 43–52 m³ ha⁻¹. See Shorohova et al. (2016) for more details about CWD composition and diversity.

Sampling

A total of 52 logs representing as broadly as possible within a given tree stand the ranges of tree species, size and decay were selected for the inventory and measured (Table S1). Sixteen spruce logs, 14 pine logs, 8 birch logs and 14 aspen logs from 16 to 80 cm in diameter at breast height (DBH) (DBH, measured at 1.3 m from root collar) were inventoried. The logs formed after the death of trees ranging in age from 60 to a few hundred years old. The mortality modes were either uprooting or stem breakage. The dendrochronological methods of cross-dating, growth release patterns and mechanical scars of neighboring trees were used for the dating of logs, i.e., identifying time since tree death for a period of up to 66 years. In cross-dating, the master chronologies were created from growth rings of living trees. Cross-dating possibly overestimated up to 2 years (Dynesius and Jonsson, 1991) the time since death when the uprooted tree continued to produce tree rings after a fall. In growth release, a possible underestimation of the time since tree death averages 3 years (Dynesius and Jonsson, 1991). The method of dating tree fall scars gives a more precise year of death (Storaunet and Rolstad, 2002).

We recorded the following log attributes: time since tree death, tree species identity, diameter at the 1.3 m from root collar (DBH), bark cover remained on the log (in %), wood softness, or decomposition degree (depth of knife penetration into the wood, mm), spatial position (expressed as a height from the ground, cm), and the amount of accumulated litter, estimated as a litter cover, %.

The lateral surface area of logs was calculated by the formula for a truncated cone's lateral surface area based

on the length and diameters at the stem base, at 1.3 m and the top of all logs.

Several bark samples of approximately 1–3 cm² were taken from each log, measured in two dimensions, and weighed. The moisture of bark in % was calculated based on the field and laboratory mass measurements in the natural and absolutely dry conditions, respectively. The area-specific mass of bark (mass per unit surface area, g cm⁻², later referred as a bark mass) was calculated by dividing the dry mass of a bark sample by the surface area of sample. The pH was measured in distilled water extraction (ratio bark: water = 1 : 25) by potentiometric pH-sensor (Hanna, Germany). The pH-meter was calibrated using the standard buffer solutions. See Romashkin et al. (2018) for more details.

We did a presence / absence survey of epixylic vegetation on all the log microhabitats present, such as branches, side parts, etc. We recorded the presence-absence of all species of bryophytes, vascular plants and macrolichens on each log. In case of any doubt when identifying a specimen in the field, it was collected for later microscopic identification and chemical testing for lichens.

The specimens are deposited to the herbaria at the Institute of the Industrial Ecology Problems of the North of the Kola Science Center of RAS (INEP) and at the Polar-Alpine Botanical Garden-Institute of Kola Science Center of RAS (KPABG).

Data analysis

Based on their general substrate specificity all species were classified as belonging to one of five substrate groups according to their general substrate specificity: epiphytes, facultative epixylics, true epixylics, epigeous species and generalists (Table S2) based on the literature on their ecological traits (Söderström, 1988a,b; Andersson and Hytteborn, 1991; Ódor and van Hees, 2004; Jansova and Soldan, 2006), regional floristic research (Kurbatova, 2002; Ignatov and Ignatova, 2003, 2004; Andersson et al., 2009; Potemkin and Sofronova, 2009) and personal observations. The epiphytic species typically occur on living trees above the stem base. The facultative epixylics often establish on dead wood, but can also occur on other substrates, such as tree bases or roots, living trees, stones and ground moss patches. They can be also called 'early generalists'. The true epixylics occur almost exclusively on dead wood in the studied region. The epigeous species found in the studied region are typical of boreal understory vegetation. The generalists, which are found on different substrates, such as dead wood, tree bases, litter, exposed soil, however, are not typical for boreal understory vegetation. For each substrate group the occurrences of species were summed up. Vascular plants were analyzed as a separate group.

The relationships between epixylic species richness and log attributes were examined with generalized linear models (glm). Gaussian, Poisson and Tweedie distributions with identity and log link functions were applied (Table S3). The effects of 1) log (tree) species identity, surface area and diameter, 2) time since tree death and wood softness (wood decomposition), 3) log position (proximity to ground), as well as 4) cover, area-specific mass, pH and moisture of bark and amount of accumulated litter on the variation in epixylic species number per CWD unit as well as the number of species for substrate groups were estimated with the Wald χ^2 test. The relationships between the above listed independent variables were tested with the Spearman's correlation coefficient. Highly correlated variables (Table S4) were not included in the same model. We selected our final models based on the lowest Akaike Information Criterion (AICc) and the highest model weight using backward stepwise selection. These analyses were performed in SPSS (SPSS Inc., Chicago IL, version 23.0).

The relationship between the number of indicators of old-growth boreal forests (Konechnaya et al., 2009) and total species number was analyzed with glm with negative binomial distribution and log link function. The analysis was performed in R (R Core Team 2017).

The data on the presence/absence of epixylic species on logs was used to analyze the epixylic community composition using the non-metric multidimensional scaling (NMDS, Oksanen et al., 2013). The square root transformation and Wisconsin double standardization of the species' occurrence data were applied. Bray-Curtis coefficients were used as measures of dissimilarity. The Procrustes rotation was used to maximize the spread of log scores along axes. Ordination scores for logs were averaged within log species identity. The environmental variables (substrate attributes) were used to interpret the structure of the epixylic community by the vector fitting procedure. The analysis was performed in R (R Core Team 2017).

In order to assess the degree of relative specialization in relation to log species identity, we calculated the standardized specialization index d' for each lichen and bryophyte species (Blüthgen, Menzel, and Blüthgen, 2006; Müller et al., 2015; Goia and Gafta, 2018). We calculated the normalized specialization index d' (according to Kullback Leibler distance) for each species to log species identity and the two-dimensional Shannon entropy (termed H_2 in order to avoid confusion with the common one-dimensional H), and the frequency-based specialization index (H_2') for the whole epixylic community, following Blüthgen, Menzel, and Blüthgen (2006) with the use of the programme Blüthgen N (<http://rxc.sys-bio.net>). The specialization index d' ranges from 0 (completely generalized) to 1 (completely specialized species) and has the advantage that the abundance of

both plants and lichens, and logs with different species identity are taken into account. In the substrate (log species) specialization indexes d' , the species with frequency of occurrence of less than 1% were removed.

Species nomenclature followed Ignatov, Afonina, and Ignatova (2006) for mosses, Söderström et al. (2016) for liverworts, Nordin et al. (2011) for lichens, and Cherepanov (1995) for vascular plants.

Results

Floristic results and general patterns of species diversity

A total of 115 species was recorded: 17 vascular plants, 34 mosses, 28 liverworts and 36 macrolichens. Of these, 19 species were epigeous, 30 — generalists, 16 — true epixylics, 11 — facultative epixylics, 22 — epiphytes. A few lichen species were not identified to species level.

The indicators of old-growth boreal forests (Konechnaya et al., 2009) were presented by fourteen species including three lichens (*Cladonia norvegica*, *Lepetogium saturninum* and *Nephroma parile*), three mosses (*Eurhynchiastrium pulchellum*, *Hylocomiastrum umbratum* and *Orthotrichum obtusifolium*) seven liverworts (*Crossocalyx hellerianus*, *Lophozia ascendens*, *Neoorthocaulis attenuatus*, *Riccardia latifrons*, *Riccardia palmata*, *Scapania apiculata*, *Syzygiella autumnalis*), and one vascular plant (*Galium triflorum*). Six liverworts (*Cephalozia macounii*, *Lophozia ascendens*, *Scapania apiculata*, *Syzygiella autumnalis* and *Tritomaria exsecta*) and one lichen species (*Lobaria pulmonaria*) are red-listed in the Republic of Karelia (2020).

Species richness per log depended mainly on tree species identity, position, and the amount of accumulated litter (Table 1, Table S3; Fig. 1). Spruce logs hosted the highest total species diversity and the highest diversity of liverworts, whereas the maximum species richness of mosses was recorded on birch logs; that of lichens — on pine logs (Table 1, Table S3, Fig. 2.1). Pine logs were the poorest in terms of species richness of mosses and vascular plants (Fig. 2.1).

Total species number and that of mosses decreased with the increase of substrate height above the ground and increased with the increase of the amount of litter on its surface (Table 1, Table S3, Fig. 1). The number of liverworts decreased with the increase of substrate height above the ground (Table 1, Table S3). The number of lichen species decreased with the increased degree of wood decomposition (Table 1, Table S3). The number of vascular plants in epixylic communities increased with the increase of the amount of litter (Table 1).

Tree species identity, log position, bark specific mass and the amount of accumulated litter influenced the log-level diversity of substrate groups of cryptogamic species

Table 1. Summary of the effects of substrate attributes as predictors for the total abundance and the abundance of substrate groups based on the glm results

Number of species	Species	Decomposition	Bark specific mass	Position	Litter
All species	S+			-	+
Taxonomic groups					
Lichens	P+				
	S- *** B- ** A- *	-			
Liverworts	S+			-	
Mosses	S+*** B+** A+***			-	+
Vascular					+
Substrate groups					
Epiphytes			+		-
Facultative epixylics	S+		-		
True epixylics	S+			-	
Generalists				-	+
Epigeous				-	+

A — aspen, B — birch, P — pine, S — spruce. '+' — positive effect, '-' — negative effect. The number of stars indicate the strength of the effects. Significant predictors included in the models are highlighted with grey colour. See Table S3 for full model details.

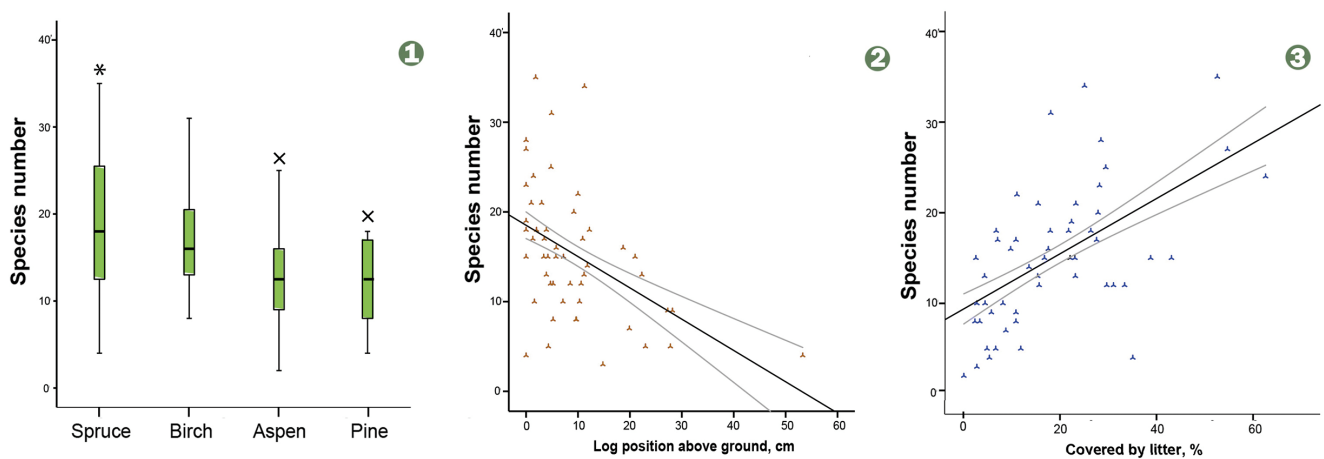


Fig. 1. The change of total species number per log related to tree species identity, log position above the ground and the amount of litter accumulated on the log surface. Estimated glm (generalized linear model) box plots and response curves with SE and original observations are shown. Significant differences between species estimated based on generalized linear models are indicated by stars if positive, and crosses if negative. Illustrations: middle-decomposed logs of different tree species 10–15 years since tree death. Photo: Elena Moshkina.

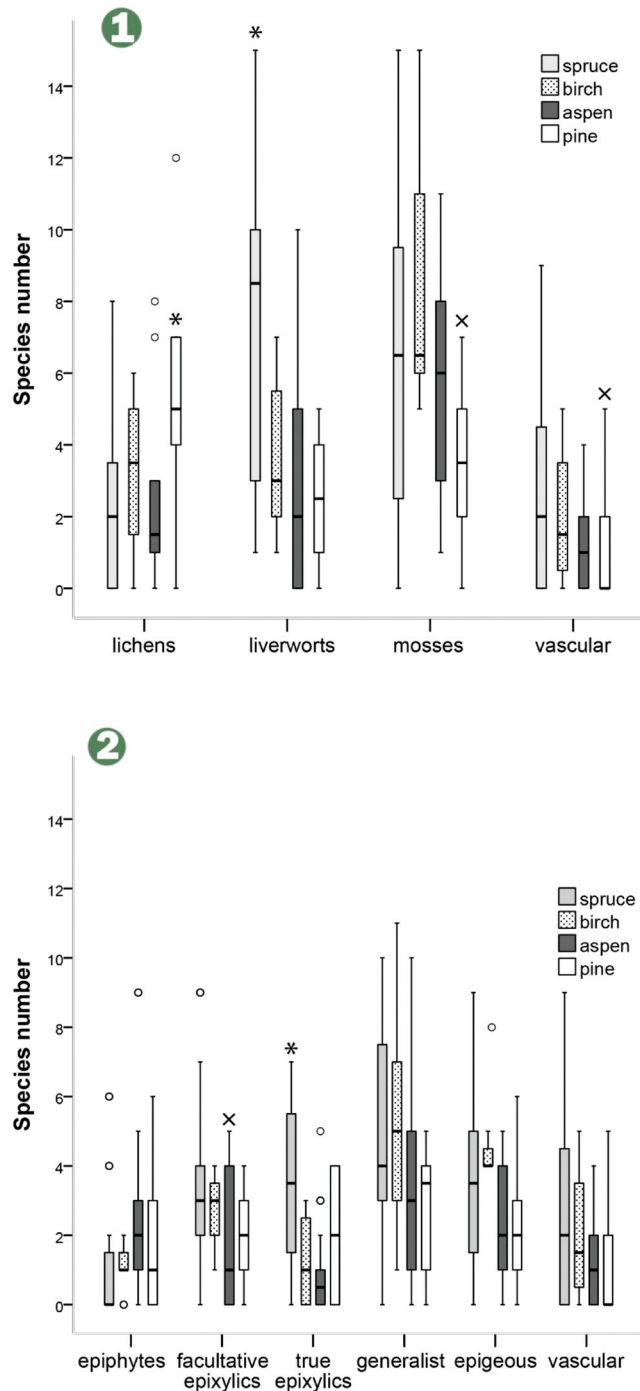


Fig. 2. Boxplots for the number of species per log by 1) taxonomic and 2) substrate groups related to tree species identity. Median values, first and third quartiles, and maximum and minimum values are shown. Significant differences between the stages estimated based on generalized linear models are indicated by stars if positive, and crosses if negative. Outliers are shown by open circles. Only cryptogamic species were analyzed by substrate groups.

in different ways (Table 1, Table S3). The occurrence of true and facultative epixylics increased on spruce logs (Table 1; Table S3; Fig. 2.2). True epixylics were the most sensitive to log position above the ground (Table 1, Table S3). Highly leaning logs were not attractive for true epixylics, generalists and epigeous species. The number

of epigeous and generalist species increased with the amount of litter. Number of epiphytes decreased with the amount of litter (Table 1, Table S3). Bark mass positively influenced the number of epiphytes and negatively influenced the number of facultative epixylics.

Role of different substrate attributes for epixylic communities

Tree species identity was the main factor influencing the composition of epixylic cryptogamic communities (Table S5, Fig. 3.1). This factor also reflected to some extent log diameter, bark cover, or bark fragmentation patterns, and bark pH (Fig. 3.1). Log diameter, bark cover and pH increased in the order: pine < spruce < birch < aspen. The greatest variation was observed for epixylic communities associated with spruce and aspen logs, whereas the least variable were the communities on birch logs (Fig. 3.1).

The second group of factors correlating with each other (Table S3) included time since tree death, amount of litter, wood decomposition and position, or height above ground (Table S5, Fig. 3.1). Among them, litter was the most important for epixylic communities (Table S5). Interestingly, all “dynamic” variables (time since tree death, wood softness, litter amount and bark moisture) pointed in the same direction (Fig. 3.1) which proposes that they explain the species composition in a similar way. Log position pointed in the opposite direction. Early successional species composition shows a lot of variation, caused mainly by tree species identity, whereas the composition of late successional species is much less variable (Fig. 3.2).

Bark moisture and mass correlated with both log species identity and the factors from the second group. Both bark mass and moisture increased in the above listed order of log species and decreased with increasing time since tree death.

Log DBH pointed in the direction of aspen species indicating that the average diameter of the studied aspens was much higher than that of other tree species.

Epiphytic species were scattered in a gradient from the highest height of logs from the ground (‘Position’ vector) and bark mass to the central part of the ordination space (Fig. 3.2). Distribution of epixylic, generalist or epigeous species along the first axis reflected the log-species related variability of substrate (Fig. 3.2). Most epigeous cryptogamic species and vascular plants were related to the highest values of ‘dynamic’ log attributes including bark moisture (Fig. 3.2).

Occurrence of epixylic species by log species

Lichens were the most tree species specific with the maximum occurrence on aspen logs (Fig. 4; Table S2): 10 of 14 species occurred only on aspen logs: *Bac-*

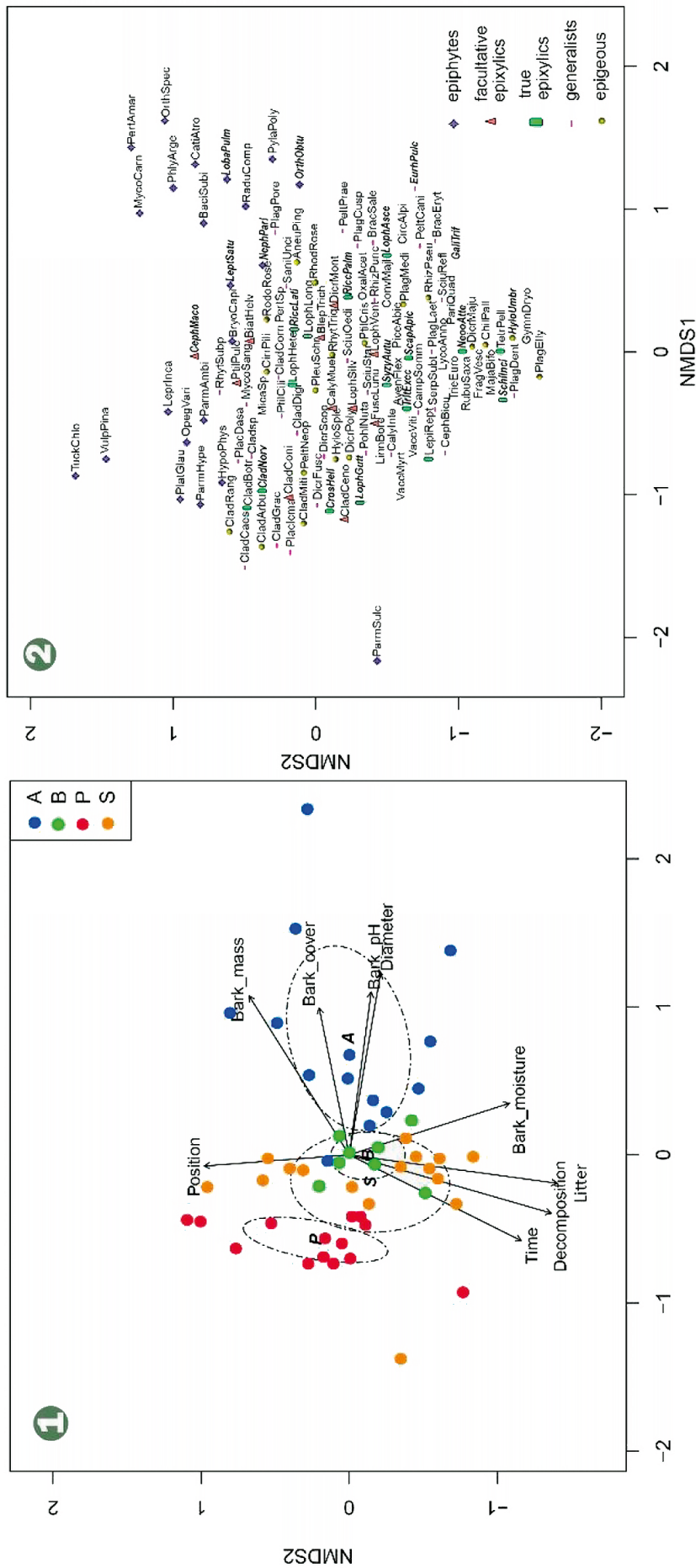


Fig. 3. NMDS ordination of cryptogamic epixylic communities based on the presence/absence of species on fallen logs. 1) Ordination scores for logs along the two dimensions were averaged according to the tree species identity. A — aspen, B — birch, P — pine, S — spruce. Ellipses are SD of the means. Correlation vectors for significant environmental variables (see Table S5) were fitted to the ordination. 2) Species scores and their substrate groups. The indicators of old-growth forests (Konechnaya et al., 2009) and the red-listed species in the Republic of Karelia (2007) are shown in **bold and italics**. See Table S2 for species abbreviations.

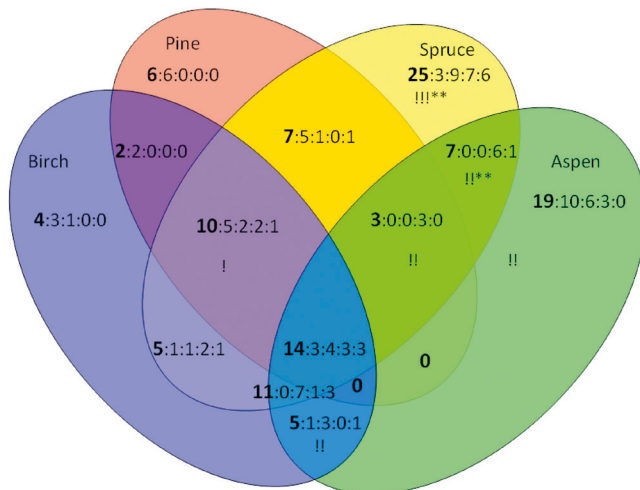


Fig. 4. Vienn diagram showing the number of epixylic species occurring on logs of different tree species. The numbers indicate: total, lichens, liverworts, mosses, vascular plants. ! — the indicators of old-growth forests (Konechnaya et al., 2009). * — species from the The Red DataBook... (2020).

idia subincompta, *Catinaria atropurpurea*, *Leptogium saturninum*, *Lobaria pulmonaria*, *Mycobilimbia carnealbida*, *Peltigera canina*, *Peltigera praetextata*, *Pertusaria amara*, *Phlyctis argena* and *Vulpicida pinastri*. Mosses *Brachythecium erythrorrhizon*, *Brachythecium salebrosum*, *Eurhynchiastrum pulchellum*, *Orthotrichum obtusifolium*, *Orthotrichum speciosum*, *Pylaisia polyantha*, and liverworts *Plagiochila porelloides* and *Radula complanata* were associated with aspen logs as well. Spruce logs hosted the highest number of mosses (9 species of total 25) and liverworts (7 species out of 22) as compared to the logs of other tree species. Lichens *Lepraria incana*, *Opegrapha varia*, *Parmelia sulcata*, mosses *Campylidium sommerfeltii*, *Hylocomiastrum umbratum*, *Plagiomnium ellipticum*, *P. medium*, *Plagiothecium denticulatum*, *Rhytidiadelphus subpinnatus*, *Serpoleskea subtilis*,

Tetraphis pellucida and liverworts *Cephalozia macounii*, *Neorothocaulis attenuatus*, *Schistochilopsis incisa*, *Syzygiella autumnalis*, *Tritomaria exsecta* occurred only on spruce logs. Birch logs hosted mainly species with high substrate amplitude. However, *Biatora helvola*, *Mycoblastus sanguinarius* and *Rhizomnium pseudopunctatum* were found only on birch logs (Fig. 4; Table S2).

The higher was the species number per CWD unit, the less specialized those species were, almost independently of tree species (Table 2). This phenomenon was the most pronounced for mosses and liverworts. The species richness of mosses and liverworts found on the substrate was inversely related to its specialization (Table 2). For example, the largest number of mosses was found on a least specialized substrate — birch logs. The largest number of lichens was found on pine logs, which represented the least specialized substrate.

The whole epixylic community specialization index H_2' was 0.27. This index decreased in the order lichens, liverworts, mosses, vascular plants (Table 2).

The rarest and most threatened species were relatively highly specialized (Table S2). *Cladonia norvegica* occurred on slightly leaning moderately decomposed pine logs. *Leptogium saturninum*, *Nephroma parile* and *Orthotrichum obtusifolium* were associated with aspen logs. *L. saturninum* were found on earlier stages of epixylic succession, whereas *N. parile* and *O. obtusifolium* remained longer in epixylic communities on the logs with preserved bark. *Syzygiella autumnalis*, *Neorothocaulis attenuates* and *Scapania apiculata* preferred spruce logs. The first two species were specialized to the logs with 6–25 years since tree death, whereas the third species preferred well-decomposed logs with the age of 25–40 years.

The number of species indicating forest naturalness increased with the increase of the total species number (Fig. 5).

Table 2. The specialization index (d') related to the total number of species for different taxonomic groups and tree species

		Lichens	Mosses	Liverworts	Vascular plants
Spruce	d'	0.18	0.15	0.21	0.10
	Species #	17	25	22	15
Aspen	d'	0.69	0.22	0.29	0.21
	Species #	14	20	16	8
Birch	d'	0.20	0.14	0.23	0.06
	Species #	15	18	10	9
Pine	d'	0.29	0.38	0.35	0.21
	Species #	21	7	8	5
H_2'		0.33	0.21	0.27	0.14

Discussion

Epixylic diversity at the species and community levels

High epixylic diversity, as well as the occurrence of the regionally red-listed species (The Red DataBook..., 2020) and the old-growth forest indicator species (Konechnaya et al., 2009) are linked with the high diversity and abundance of dead wood (Andersson and Hyttenborn, 1991).

In agreement with our hypothesis, the first group of factors influencing the diversity of epixylic communities represented tree species identity and attributes related to it. This is also in agreement with other studies (McAlister, 1997; Jansova and Soldan, 2006; Mežaka et

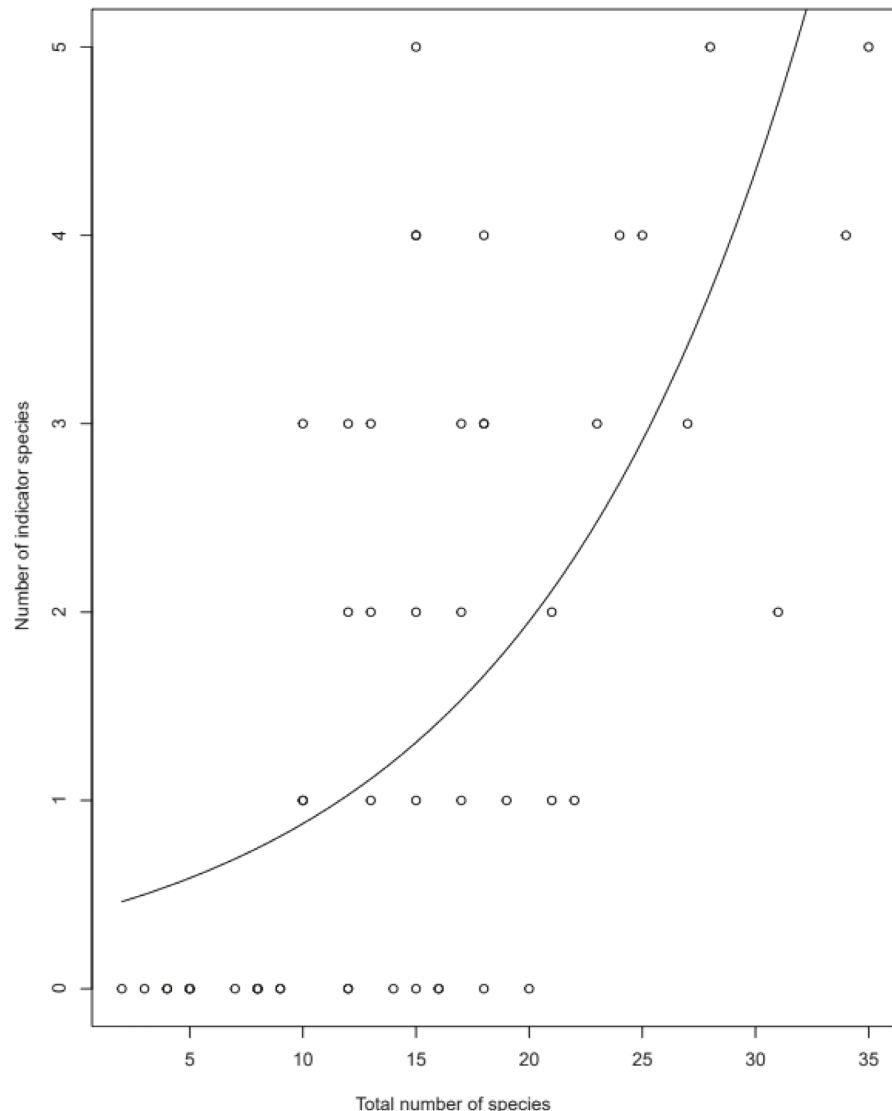


Fig. 5. Relationship between the number of species indicators of virgin and old-growth forests and the total number of species per coarse woody debris (CWD) unit. Estimated glm (generalized linear model, distribution: negative binomial, link function: log) response curves and original observations are shown. All parameters (Intercept = -0.932 (SE = 0.312), z value = -2.989 (SE = 0.003)); coefficient = 0.080 (SE = 0.015), z value = 5.365 (SE < 0.001)) are significant at $p < 0.001$.

al., 2009). Our results from the forest with sufficient substrate diversity and continuity supported the importance of spruce and aspen CWD for threatened epixylic bryophytes revealed in the woodland key habitats in Southern Sweden (Berg et al., 2002).

Our study supported the evidence on the highest species diversity of bryophytes, especially highly specialized liverworts, on spruce CWD compared to other boreal tree species CWD (Söderström, 1988a,b; Andersson and Hytteborn, 1991; Müller et al., 2015). One explanation can be associated with diverse patterns of bark fragmentation creating a variability of microhabitats on spruce logs. Some bark pieces affected by phloem-feeders slough from logs, some — remain attached (Shorohova et al., 2016). Parts with bark are colonized by generalist bryophytes, whereas the side parts of logs without

bark are colonized by true epixylics (Kushnevskaia and Shorohova, 2018), e.g., *Calypogeia muelleriana*, *C. integristipula*, *Fuscocephalozia lunulifolia*, *Riccardia palmata* etc. The high variability of epixylic communities on spruce logs is associated with the long persistence of both early- and late-successional bryophytes along epixylic succession on spruce logs (Söderström, 1989). In our study, spruce logs hosted the highest number of vascular plants compared to the logs of other tree species. Thin, often fragmented, relatively quickly decomposing spruce bark (Shorohova et al., 2016) and accumulated litter on log surface make growth conditions on spruce logs close to those on the ground and consequently favourable to vascular plants.

Among the tree species studied, pine logs are the poorest for bryophytes (this study; Löhmus, Löhmus,

and Vellak, 2007; Müller et al., 2015) and the richest for lichens (this study; Löhmus, Löhmus, and Vellak, 2007). Pine characterized by loose unstable acidic bark hosts specific epiphytic macrolichen (Uliczka and Angelstam, 1999) and species poor epixylic bryophyte assemblages (Löhmus, Löhmus, and Vellak, 2007).

In our study, aspen logs represent the most specific substrate due to its greatest diameter, surface area and bark mass correlated with the greatest moisture (Shorohova et al., 2016) and pH (Romashkin et al., 2018). High substrate specificity of aspen for lichens has been recognized (Uliczka and Angelstam, 1999; Jüriado, Paal, and Liira, 2003). In our study, aspen logs hosted fewer lichen species compared to the logs of other tree species. This result disagrees with earlier studies suggesting high diversity of epiphytic lichens and mosses on aspen trees (Tarasova et al., 2017). Such discrepancy can be explained by rapid changes of physical properties of aspen bark after tree fall (Shorohova et al., 2016) and consequently the change of its attractiveness for lichens. In contrast, pine logs in our study hosted lichens for a longer period. For example, species of *Cladonia* were found during the whole period of epixylic succession. At the same time, rapid changes in substrate make the epixylic communities on aspen logs highly variable as shown in the European boreal forests (this study), as well as in the North American boreal forests (Kumar, Chen, Thomas, and Shahi, 2017).

In our study, birch logs hosted the richest epixylic communities, mainly consisting, however, of species with wide substrate amplitude. Non-specific epiphytic macrolichen flora is generally found on birch trees (Uliczka and Angelstam, 1999). In hemiboreal and temperate forests, the highest number of bryophytes was found on birch logs as compared to that on logs of other tree species (Heilmann-Clausen, Aude, and Christensen, 2005; Löhmus, Löhmus, and Vellak, 2007; Nowinska et al., 2009). Well-preserved smooth birch bark represents a rather nonspecific substrate that almost does not change during log decomposition (Shorohova et al., 2016).

In our study, log size directly explained neither total within log diversity nor the species richness of taxonomic or substrate groups, and explained weakly the variation in species composition. Thus, our results did not confirm a tendency toward an increase of the number of species with the log size reported earlier (Söderström, 1988a; Andersson and Hytteborn, 1991; Ódor and Van Hees, 2004). No distinct effects of size-related variables on wood-inhabiting communities were recognized in some other studies (Heilmann-Clausen, Aude, and Christensen, 2005; Jansova and Soldan, 2006). This may suggest that in old-growth forests with high availability and continuity of dead wood, the size of logs is less important in comparison to managed forests with a lack of dead wood. Heilmann-Clausen, Aude, and Christensen (2005) suggest a relatively humid climate in

the study area, which may make differential effects of the larger water holding capacity of large logs irrelevant, as one possible explanation. This result may also relate to the rather limited variation in tree sizes covered in the study and especially to the lack of trees with a DBH below 20 cm due to tree mortality patterns in a studied forest. Logs with a large diameter are not easily overgrown by ground flora and therefore may host more epixylic species compared to small logs (Söderström, 1988a). All these explanations may also hold true in our study, since the studied sites were rather moist and fertile, and no logs below 16 cm in diameter were studied.

The species richness of liverworts decreased with an increasing log height from the ground. This can be explained by a corresponding decrease of air moisture. Some species, especially true epixylics, have been reported to be drought-sensitive (Söderström, 1988b; Laaka, 1993; Proctor et al., 2007; Táborská, Kovács, Németh, and Ódor, 2020; Kropik et al., 2021). High water availability in deadwood is important for spore germination of epixylic bryophytes (Wiklund and Rydin, 2004). Frisvoll and Prestø (1997) found that most special spruce forest bryophytes grow in humid forest types. Some bryophytes, mainly true epixylics, were not found on leaning logs at all (Söderström, 1989; Botting and DeLong, 2009).

The second group of factors united 'successional' log attributes. Unlike hypothesized, time since tree death was less important for epixylic communities as compared to the degree of wood decomposition, litter amount and log position. Logs of similar age may vary considerably both in their decay stage and in fungal species composition (Ruokolainen et al., 2018) and thus represent different substrates for epixylic species. The role of litter (humus in the authors' terminology) in shaping the composition of cryptogamic communities was detected in temperate old-growth forests (Jansova and Soldan, 2006). Spruce needle deposition enhanced the growth of carpet boreal mosses (Frego and Carleton, 1995). Height from the ground was one of the most important predictors of species richness and composition of macrolichen and bryophyte epixylic communities in mature mesic sub-boreal spruce forests in north central British Columbia (Botting and DeLong, 2009). In our study, the amount of litter and the degree of wood decomposition were inversely related to log position. The accumulation of litter was not correlated with time since tree death and wood decomposition. Probably it is influenced by the location of logs relative to the crowns of living trees, large herb or fern patches and death of early colonized epixylics. Litter accumulation is reduced on leaning logs, and the decomposition rate of leaning logs is less than that of prostrate ones (Shorohova and Kapitsa, 2014). The amount of litter facilitates colonization of logs by epigeous mosses and vascular plants (Jansova and Soldan, 2006), whereas the position above the ground 'keeps' epiphytes in the epixylic community. Thus, the epixylic

succession is facilitated by the accumulation of litter and slowed down by a leaning position of log.

In our study, the epixylic successional patterns were tree-species specific. The interaction effect of decay class and substrate species on epixylic communities was recorded also in European deciduous forests (Heilmann-Clausen, Aude, and Christensen, 2005) and in North-American boreal forests (Kumar, Chen, Thomas, and Shahi, 2017, 2018). The least and moderately decomposed conifer and aspen logs represent ‘ideal’ substrates for epixylic diversity: they host the richest communities and are the most specialized at the same time. At this stage of epixylic succession, epiphytes are still present, but mid- and late-successional bryophytes already colonize the substrate. Successional sequences of species were not pronounced on birch logs. Central position of epixylic communities on birch (*Betula papyrifera*) logs of different decay classes in the ordination space indicating their low successional variability has been reported by Kumar, Chen, Thomas, and Shahi (2017). A possible explanation can be related to probably stable chemical and physical properties of birch bark during log decomposition. Birch bark has poor water permeability and exhibits antifungal and antimicrobial effects (Rastogi, Pandey, and Kumar, 2015). The colonization rate of epiphytic species was fastest on birch trees (Uliczka and Angelstam, 1999).

Epixylic species association with log species

The epixylic species specialization in our old-growth boreal mixed forest was the same as for the whole epixylic bryophyte community specialization in temperate deciduous and coniferous forests (Müller et al., 2015): $H2' = 0.27$. In our study, an increasing specialization of epixylic species by taxonomic groups in the order lichens, liverworts, mosses and vascular plants indicates the highest frequency of vascular plants on spruce logs. Frequency of occurrence and specialization of individual epixylic species are negatively related (this study, Müller et al., 2015).

In our study, the probability of occurrence of species indicators of old-growth forests was higher on logs with higher species richness. This supports the indicator role of those species not only on the level of forest stand, but also on the level of individual logs.

Conclusions and implications for biodiversity conservation

Our study has indicated that the availability of mixed-species CWD in a broad range of decay is important to conserve the full range CWD-dependent lichen and bryophyte species. From the biodiversity conservation perspective, this suggests the need to manage for a mixed tree species composition and a continuous supply of logs within regions with intensive forestry. Prolonged

epixylic succession on leaning logs suggests the importance of creating such logs in restoration of deadwood to maintain the epixylic diversity. Preserving the diversity and continuity of CWD will maintain populations of specialist species thus preventing homogenisation of epixylic communities, and, consequently, global homogenisation (Clavel, Julliard, and Devictor, 2011).

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