CrossMark

Presence of bark influences the succession of cryptogamic wood-inhabiting communities on conifer fallen logs

Helena Kushnevskaya · Ekaterina Shorohova (iD)

Abstract Predictors of cryptogamic wood-inhabiting communities need to be examined to understand the drivers of forest biodiversity. We estimated the influence of bark cover on the wood-inhabiting vegetation on conifer logs in early stages of epixylic succession in mature European boreal and hemi-boreal forests. Abundance of substrate groups with respect to log attributes was estimated with generalized linear and generalized linear mixed models. The structure and composition of epixylic communities was analysed using non-metric multidimensional scaling with subsequent environmental fitting. The abundance of true epixylics was inversely related to bark cover. In the first stage, bark cover did not influence the abundance of epiphytes and epigeous species; positively influenced the abundance of facultative epixylics on spruce logs and negatively influenced it on pine logs. In the second stage, the effect of bark

cover was positive for epiphytes and epigeous species on spruce logs and for facultative epixylics independent of log species identity and negative for epigeous species on pine logs. Generalist species did not depend on bark cover. Total cover of wood-inhabiting vegetation was marginally influenced by bark cover. The effect of bark cover on epixylic vegetation at community level was negligible. In general, bark cover favours the establishment and growth of species with low substrate specificity. This preference may lead to either burial of logs by epigeous bryophytes, or facilitation of succession towards the dominance of ground vegetation.

Keywords Decay · Decomposition · Deadwood · Coarse Woody debris · Bryophytes · Log diameter

H. Kushnevskaya · E. Shorohova
Forest Research Institute of the Karelian Research Centre, Russian Academy of Science, Pushkinskaya str. 11, Petrozavodsk, Russia 185910

H. Kushnevskaya
Saint-Petersburg State University, University Embankment, 7–9, St Petersburg, Russia 199034

E. Shorohova
Saint-Petersburg State Forest Technical University, Institutsky str. 5, Saint Petersburg, Russia 194021

E. Shorohova (✉)
Natural Resources Institute Finland (Luke), Latokartanonkaari 9, FI-00790 Helsinki, Finland
e-mail: shorohova@ES13334.spb.edu

Introduction

Understanding the major drivers of biodiversity is crucial for forest management, restoration and conservation. Wood-inhabiting communities were shown to be biodiversity hot spots in boreal and temperate forests (Ódor et al. 2006; Perhans et al. 2007). Their structure and composition depend on deadwood – a temporary substrate, the availability of which is determined by the successional status of forest ecosystems (Siitonen 2001).

Cryptogamic wood-inhabiting communities and certain plant species groups growing on deadwood are influenced by site moisture and productivity (McCullough 1948; Muhle and LeBlanc 1975; Heilmann-Clausen

⚫ Springer

et al. 2014), forest management (Andersson and Hytteborn 1991 as well as deadwood attributes (McCullough 1948; Andersson and Hytteborn 1991; Söderström 1988; McAlister 1997; Kushnevskaya et al. 2007, Taborská et al. 2015). In conifer-dominated boreal stands, substrate characteristics negligibly influenced by within-stand variation at the mesosite level were shown to be the most important predictors of bryophyte species diversity (Mills and Macdonald 2004). However, the relative importance of factors controlling the establishment and successional dynamics of wood-inhabiting communities in boreal forests remains unclear, partly because of differences in approaches across studies. The most commonly analysed substrate parameters are species identity, log diameter and log position. Results of those analyses are, however, incoherent as behind the observed pattern may be an effect of bark cover, which is seldom studied.

The observed effect of deadwood species identity on wood-inhabiting vegetation (Preikša et al. 2016; Müller et al. 2015) can be partly explained by differences in bark properties between tree species (Culberson 1955; Palmer 1986). Log surface texture is determined by presence and properties of bark (Söderström 1988). Log diameter is one of the most important factors driving vegetation succession on deadwood (Heilmann-Clausen et al. 2014). However, the results of previous studies on the importance of the size of deadwood for cryptogam total species richness are often incoherent (Preikša et al. 2016), which may be partly explained by the possible interrelationship between log diameter and bark cover. Deadwood position regulates the substrate moisture and influences the composition of wood-inhabiting vegetation (Botting and DeLong 2009). However, it can be closely correlated with bark cover (Botting and DeLong 2009).

Bark cover is the least studied deadwood attribute because often it has been 'hidden' in deadwood decay class characteristics (Söderström 1988; Mills and Macdonald 2004; Preikša et al. 2016). However, bark cover is not the best decay class predictor (Shorohova and Shorohov 2001). Bark can either be attached to logs for a long time (Söderström 1988) or slough down quickly or gradually from snags (Muhle and LeBlanc 1975; Ulyshen 2016) or logs (Shorohova et al. 2016). Thus, observed effects of deadwood decay class on wood-inhabiting vegetation do not necessarily reflect bark cover.

Presence of bark on decaying logs may increase the cover of the species that colonize both bark and exposed wood surface (Söderström 1988; McAlister 1997), favour colonization of the species that occur only on bark (Söderström 1988; Rambo and Muir 1998) and indirectly affect the number of moss and liverwort species (Botting and DeLong 2009). Bark fragmentation rate changes colonization rates of wood-inhabiting bryophytes (Harmon 1989). Examining substrate specialization of threatened or indicator epixylic species is important from ecological restoration and nature conservation points of view. The preference of many epixylic species to logs with exposed wood vs. fragmented or complete bark was recorded in some floristic and ecological studies (Söderström 1988; McAlister 1997; Rambo and Muir 1998; Ignatov and Ignatova 2003, 2004; Jansová and Soldán 2006; Kushnevskaya and Potemkin 2014), but not quantitatively estimated. Bark can be attached to logs, bases of living trees and be in fragmented parts included in forest litter and thus be attractive to species with or without substrate specificity.

We estimated the influence of bark cover on cryptogamic wood-inhabiting vegetation on Norway spruce [*Picea abies* (L.) Karst.] and Scots pine (*Pinus sylvestris* L.) logs separately and in association with other deadwood attributes in mature European boreal and hemi-boreal forests located along geographical and habitat gradients. The cover and frequency of individual species, their substrate groups, as well as the structure and composition of whole communities in early stages of epixylic succession were analysed. Based on the literature and expert evaluations, the species were classified as epiphytes, facultative epixylics, true epixylics, epigeous and generalists based on their substrate preferences. The influence of bark cover on total cover of substrate groups was assumed to be stronger compared to that of generally low abundant individual epixylic species. We hypothesized that the joint effect of bark cover, log position, size, decomposition and species identity on the composition of wood-inhabiting vegetation is most pronounced in the first, colonization stage of succession on logs, before the active decay of bark and accumulation of litter on log surface starts, and competition regulates the succession. We hypothesized that bark favours establishment and growth of species with low substrate specificity. Among substrate groups, true epixylics were assumed to be the most sensitive to direct and indirect influence of log bark cover.

Material and methods

Study area and sample plots

The studies were carried out from 1998 to 2010 in a subset of six sites consisting of 16 forest stands located in Russia and Finland (Fig. 1, Table 1). All forest stands were surrounded by a matrix of forested area not less than 10 ha except for site S is southern Finland, which was a part of a fragmented landscape. All forest stands were mature with a mean age of more than 100 years, except for S where mean stand age was 80 years. These stands had naturally regenerated after either clear felling with some uncut patches left, or developed after natural windrow disturbances without any forest management treatments. A and K forest stands were old-growth forests in a Dvina-Pinega watershed (Aakala 2010) and Kenozersky national park (Shorohova and Kapitsa 2015). L, M and P sites were riparian forests protected from felling by Forest Law. S stands were located in the experimental forest surrounded by a fragmented landscape (www.luke. fi/en/natural-resources/attractions/solbole-research-forest). Mean deadwood volume varied from 55 (S) to 145 (K) $m^3 \cdot ha^{-1}$; all decay stages were present.

Sampling and data analysis

Throughout each stand, plots for monitoring wood-inhabiting vegetation were established on randomly selected fallen logs with a DBH (diameter at 1.3 m) of not less than 10 cm. Plots were 50 cm in width with three plots per log located at the distances of 0–1.5 m from the root collar, in the middle and on the top of a log. We used plots of fixed width and varying length, positioned such that each plot covered both the top and sides of a log, so that sampled microsites were relatively homogenous. Width was adjusted to fit the diameter of each log at the point of inventory. The area of inventory covered ca two-thirds of the log surface. We described vegetation on the plots by estimating the projected cover of mosses, liverworts, macrolichens and vascular plants in percentage. Unknown specimens were collected and identified in the lab.
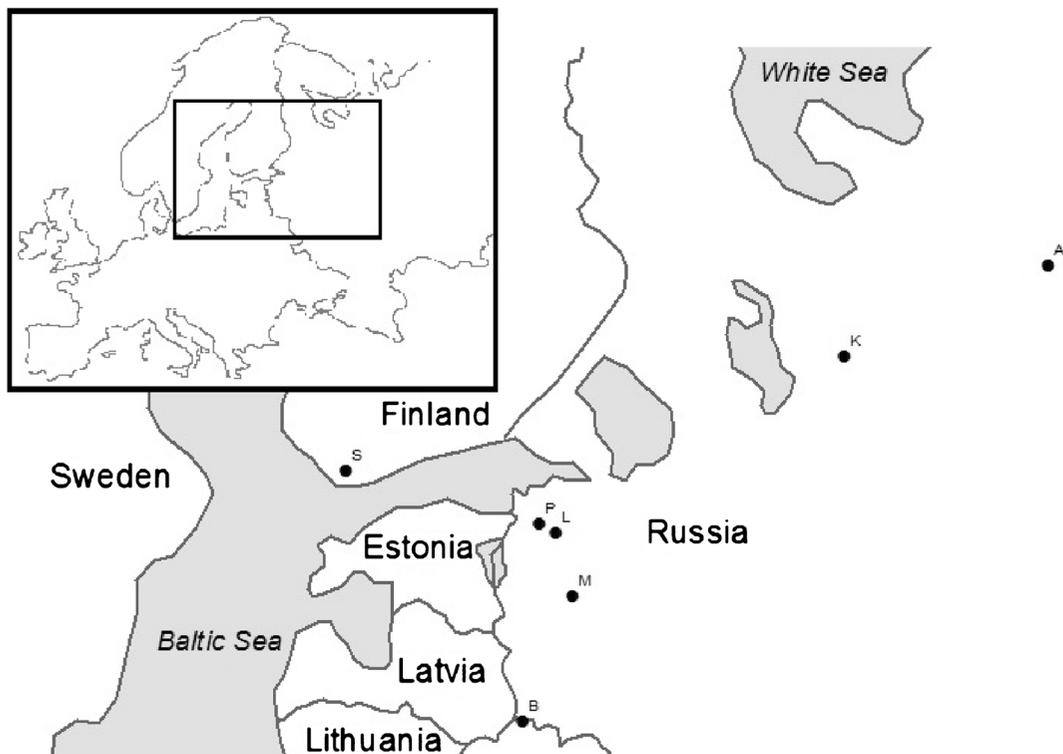
Fig. 1 Location of the study sites

Table 1 Characteristics of the study sites

Site	Latitude and longitude	Altitude [m]	t_{mean} [°C]	$Precip_{mean}$ [mm]	Topography	Bedrock	EUNIS habitat type[1]	Forest type[2]	Number of sample plots
A	62°59' N 44°04' E	170–180	+0.9	516	plain	moraine loamy sand	G3A1	*Piceetum myrtillosum*	17
							G3A4	*Piceetum herboso-sphagnosum*	18
K	61°43' N 37°58' E	180–190	+0.9	613	hills and paludified depressions	moraine mixed loamy sand and sandy clay loam	G3A1	*Piceetum myrtillosum*	16
							G3A1	*Piceetum myrtillosum*	16
							G3D5	*Piceetum myrtilloso-sphagnosum*	15
P	59°15' N 28°50' E	40–50	+4.4	609	edge of river valley	glaciolacustrine loamy sand	G3A2	*Piceetum herboso-oxalidosum*	17
							G3A3	*Piceetum oxalidosum*	16
L	59°06' N 29°19' E	60–70	+4.1	551	edge of river valley	moraine loamy sand	G3A1	*Piceetum myrtillosum*	16
							G3A3	*Piceetum oxalidosum*	16
M	58°07' N 29°10' E	100–110	+3.7	555	edge of river valley	moraine mixed loamy sand and sand	G3A1	*Piceetum herboso-oxalidosum*	18
B	56°04' N 28°20' E	120–130	+4.7	593	eskar hilly plain	moraine mixed loamy sand and sandy clay loam	G3A1	*Pinetum myrtillosum*	16
							G3D5	*Pinetum herboso- sphagnosum*	20
S	60°02' N 23°02' E	40–50	+6.0	661	coastal plain	moraine rubble-loam	G3A1	*Piceetum myrtillosum*	49
							G3A1	*Pinetum myrtillosum*	117
							G3A1	*Pinetum myrtillosum*	41
							G3A3	*Pinetum myrtillosum*	15

[1] http://eunis.eea.europa.eu, [2] Rysin and Savelieva (2002), Aakala (2010), Shorohova and Kapitsa (2015)

We recorded log species identity (spruce or pine), diameter at the plot locations, bark cover (in %), decomposition (depth of knife penetration into the wood, mm), spatial position (expressed as a height above ground, cm), and the stage of epixylic succession. The early first, 'colonization', stage succession was characterized by sparse vegetation cover of bryophytes and lichens. The second stage was characterized by not less than 50–100% cover of mainly species that are not the dominant ground vegetation species (Kushnevskaya et al. 2007; Kushnevskaya 2012). Bark cover can be accurately estimated without disturbing vegetation only if the log was not covered completely by feather mosses. So, only the initial stages of succession were studied (Table 2).

All species were classified into one of five substrate groups according to their general substrate specificity: epiphytic species, facultative epixylics, true epixylics, epigeous species and generalists (See Appendix 1). This classification was based on literature on the ecology of wood-inhabiting communities (Söderström 1988; Andersson and Hytteborn 1991; Ódor and van Hees 2004; Jansová and Soldán 2006) local floristic research (Andersson et al. 2009; Ignatov and Ignatova 2003; Kurbatova 2002; Kushnevskaya and Potemkin 2014; Potemkin and Sofronova 2009) and personal observations. In our study area, the epiphytic species typically occur on living trees above the stem base. The facultative epixylics often establish on deadwood, but can also occur on other substrates, such as tree base or roots, living trees, stones and other moss patches. They can be also called 'early generalists'. The true epixylics occur almost exclusively on deadwood and, the epigeous species are typical of boreal ground vegetation. However, the generalists found on different substrates, such as deadwood, tree base, litter and exposed soil are not typical boreal ground vegetation. For each substrate group the projected covers of species were summed. Summing species by substrate groups helps us to understand how log attributes influence the abundance of wood-inhabiting species, because when individual species are low in abundance they rarely demonstrate a statistically significant reaction to log attributes.

Data distributions for cover and frequency of individual species as well as for cover of substrate groups were tested for normality using a Kolmogorov-Smirnov test. Differences in the abundance of individual species related to log bark cover were analysed using the Kruskal-Wallis non-parametric test. (See Appendix 1 for the results). Bark cover was analysed as a group factor with groups: exposed wood (0–20%), fragmented bark (21–80%) and complete bark cover (81–100%). Grouping was based on our previous field observations and assumptions about the mechanisms of potential influence of bark cover on epixylic vegetation. Bark cover of less than 20% was assumed to be an unstable substrate that does not remain on log long. Fragmented bark was assumed to influence epixylic vegetation through the creation of additional niches such as cracks and small pits filled with litter. Exposed wood and complete bark cover were assumed to diverge as substrates due to differences in their physical and biochemical properties.

The total cover and the cover of substrate groups was first tested with generalized mixed models (GLZMM) separately for the first and second successional stages depending on log attributes as fixed factors and sites as random factors. However, with the GLZMM, random effects were significant only for epiphytes in the first stage. Thus, in further modelling, the total cover and the cover of all substrate groups except epiphytes were analysed using generalized linear models (GZLM) with a Tweedie distribution; the parameter $1.1 < P < 1.6$ was selected individually for each case using the likelihood ratio tests and χ^2 probability. In the second stage, total cover followed a normal distribution. Substrate characteristics such as log bark cover, species identity,

Table 2 Numbers of sample plots

Stage	Species		Diameter [cm]			Bark cover [%]			Position above the ground			Total
	Spruce	Pine	< 15	16–35	> 36	< 20	21–80	> 81	Lying	< 20 cm	> 21 cm	
1	95	120	77	106	29	173	28	14	109	85	21	215
2	115	93	78	109	21	170	19	19	133	60	15	208

diameter, position, decomposition and their paired interrelationships were treated as predictors in GLZM and as fixed effects in GLZMM tested with Wald χ^2 test and Wald F test, respectively. We selected our final models based on the lowest Akaike Information Criterion (AICc) and the highest model weight using backward stepwise selection. The models where bark was and was not included as a predictor with and without interrelationships with other predictors were compared. These analyses were performed in SPSS (SPSS Inc., Chicago IL, version 23.0).

The epixylic vegetation community data for the first and second successional stages was analysed using non-metric multidimensional scaling (NMDS, Vegan package, Oksanen et al. 2013). The square root transformation and Wisconsin double standardization of the species' cover data were applied. Bray-Curtis coefficients were used as measures of dissimilarity.

Environmental variables (log attributes as listed above) were used to interpret the structure of the epixylic vegetation community by the vector fitting procedure. Additionally, geographic and site variables such as latitude, longitude and forest type were included in the modelling. Forest type was classified according to site quality: 1 – oxalidosum and herboso-oxalidosum, 2 – myrtillosum, 3 – myrtilloso-sphagnosum and herboso-sphagnosum (Rysin and Savelieva 2002).

The ordination analyses were carried out for all datasets as well as separately for sites grouped according to fragmentation and forest management history of the landscapes.

Species nomenclature followed Ignatov et al. (2006) for mosses, Konstantinova et al. (2009) with additions from Söderström et al. (2016) for hepatics, and Santesson et al. (2004) for lichens.

Results

First stage (colonization)

The effect of bark cover on the abundance of epiphytes was non-significant (Table 3). Facultative epixylics represented the most abundant substrate group among first colonizers (Appendix 1). For example, *Ptilidium pulcherrimum* occurred on almost all logs. The effect of bark cover on their abundance

was positive on spruce logs and negative on pine logs. Among facultative epixylics, only *Cladonia botrytis* reacted to bark. It avoided exposed wood and established on the logs with partial or complete bark cover (Appendix 1). The cover of true epixylics was always greater on exposed wood than on bark independent of host log species identity (Table 3, 5). Generally found in low abundance, this group was widely scattered in the ordination diagram (Fig. 2). The abundance of generalists did not depend on bark cover (Table 3, 5). The effect of bark cover alone on the abundance of epigeous species was not significant (Table 3). However, *Pleurozium schreberi* and *Rhytidiadelphus triquetrus* occurred more often on logs with fragmented bark (Appendix 1). Logs with well-preserved bark were attractive to *Barbilophozia barbata*; the species that typically prefers litter substrates. This species group was the most compact on the ordination diagram. It was confined mainly to medium sized and large spruce logs in myrtillosum and myrtilloso-sphagnosum forests (Fig. 2).

Total cover of wood-inhabiting vegetation was influenced by log species identity, bark cover and their interrelationship (Table 3, 5). It increased with increasing bark cover and log diameter on spruce logs (Table 3).

The effect of bark cover on the wood-inhabiting cryptogamic communities was significant only in unmanaged forest stands surrounded by a managed forest (Table 6). Log attributes influenced epixylic communities in the sites located in mosaic landscapes under varying forest management regimes and history (sites S, P, L, M and B) and did not influence epixylic communities in the sites located in old-growth forests (sites A, K; Table 6).

Second stage

The number of species dependent on bark cover increased (see Appendix 1). The tendencies in log bark cover preferences changed for epiphytes in the second stage of epixylic succession (Table 4), probably because of decreased abundance of epiphytic species (Appendix 1). Among epiphytic species, only *Parmeliopsis ambigua* preferred exposed wood. Unlike during colonization, the effect of bark cover on the abundance of epiphytes on spruce logs was negative (Table 4, 5). The effect of log attributes on the

Table 3 Results of generalized linear models testing factors affecting the abundance of substrate groups in the colonization stage. For epiphytes, the generalized mixed-effect model with site as a random factor was applied. Significance codes: '***' – 0.001, '**' – 0.01, '*' – 0.05, 'ns' – non-significant. Empty cell-the factor was not included in the final model

	Epiphytes[1]	Facultative epixylics	True epixylics	Generalists	Epigeous sp.	Total cover
Distribution, P	Poisson	Tweedie, 1.2	Tweedie, 1.6	Tweedie, 1.4	Tweedie, 1.4	Tweedie, 1.2
Link function	Log	Log	Log	Log	Log	Log
Full model Wald χ^2	70.0***	92.3***	31.1***	66.0***	47.1***	44.8***
Intercept: estimate (*SE*)	1.858(0.519)	1.480(0.270)	0.702 (0.384)	1.197(0.251)	−0.500(0.3368)	2.704(0.1387)
Log attributes						
Species. Wald χ^2 coefficients: estimate (*SE*)	4,450**	50.0***			13.8***	19.1***
Spruce	−0.587(0.278)	1.907(0.270)			1.002(0.266)	0.467(0.107)
Pine	ns	ns			ns	ns
Position. Wald χ^2 coefficient: estimate (*SE*)	-		5.4** −0.034(0.015)	12.6*** −0.025(0.07)		
Diameter. Wald χ^2 coefficient: estimate (*SE*)	56.0*** −0.106(0.014)		10.4*** 0.051(0.163)		11.7*** 0.042(0.012)	7.3*** 0.016(0.006)
Bark cover. Wald χ^2 coefficient: estimate (*SE*)	–		15.5*** −0.031(0.008)			
Decomposition. Wald χ^2 coefficient: estimate (*SE*)	14.5*** −0.026(0.007)			14.1*** 0.018(0.005)		
Species*Bark. Wald χ^2 coefficients: estimate (*SE*)		21.2***				5.2**
Spruce*Bark		0.009(0.002)				0.130(0.005)
Pine*Bark		−0.011(0.005)				ns
Species*Diameter. Wald χ^2 coefficients: estimate (*SE*)	–	25.6***		39.6***		
Spruce*Diameter		−0.029(0.008)		0.034(0.010)		
Pine*Diameter		0.030(0.009)		−0.009(0.013)		
Species*Position. Wald χ^2 coefficients: estimate (*SE*)		11.0***			11.7***	
Spruce* Position		−0.024(0.007)			ns	
Pine* Position		0.003(0.006)			-0.082(0.023)	
Diameter*Decomp. Wald χ^2 coefficient: estimate (*SE*)				9.7*** 0.001(0.001)		
Diameter*Bark. Wald χ^2 coefficient: estimate (*SE*)						5.9** 0.001(0.0002)
Position*Decomp. Wald χ^2 coefficient: estimate (*SE*)	139.2*** 0.007(0.001)					

[1] GLZMM Wald F for fixed effects are presented

abundance of facultative epixylics was marginal (Table 4, 5). They became more abundant with increasing log decomposition and bark cover independent of log species identity (Table 4). True epixylics increased their abundance (Appendix 1). The strict preference to exposed wood persisted for the whole group and for *Lophocolea heterophylla* and *Cladonia norvegica*. The cover of generalists increased threefold as compared to that in the colonization stage of succession (Appendix 1). As in the first stage, they were more abundant on spruce, than on pine logs, and remain independent of bark cover (Table 4). The preferences for *Brachythecium salebrosum*, *Rhizomnium punctatum*, *Sanionia uncinata* changed from fragmented to total bark cover. *Cladonia chlorophaea* and *Cladonia* sp. were still more abundant on fragmented bark. Epigeous species increased their abundance with increasing bark cover on spruce
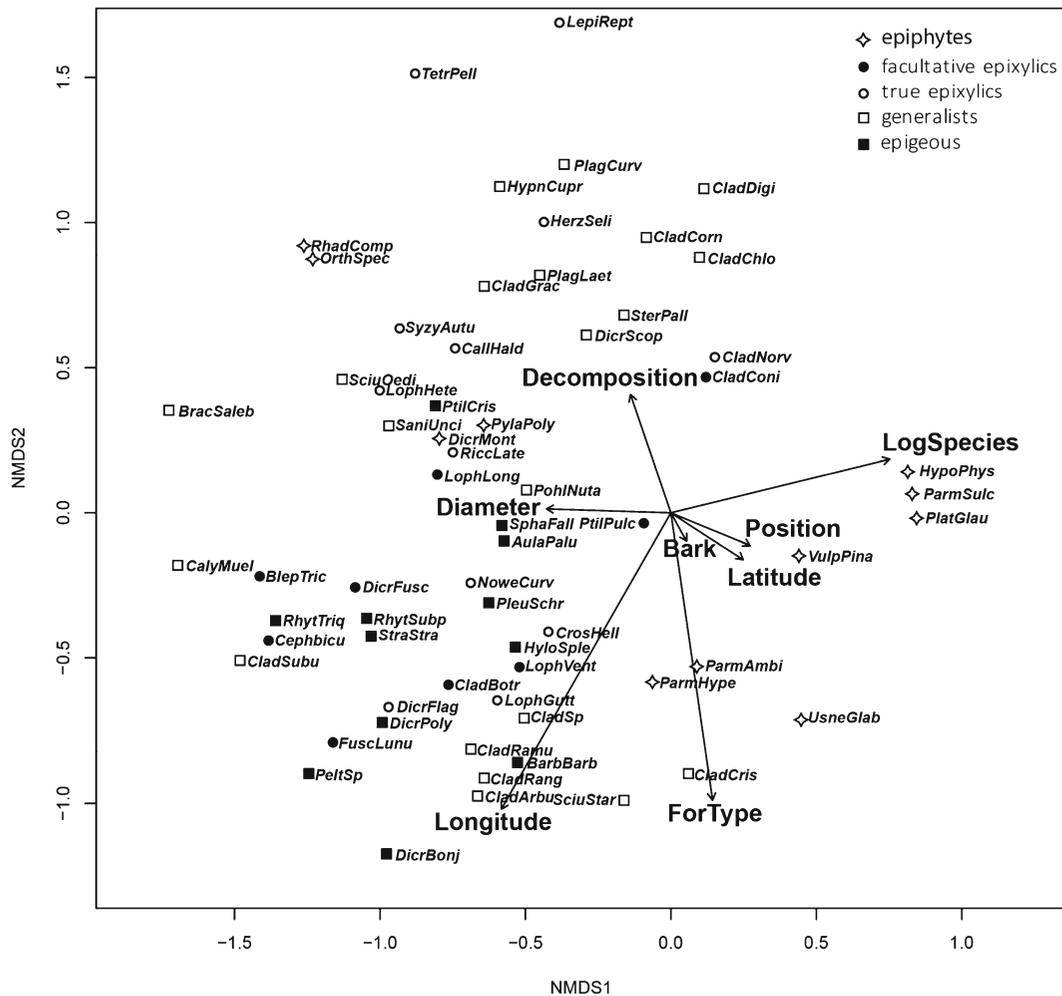
Fig. 2 NMDS ordination of the plots and species in the first stage of epixylic succession (all datasets). The vectors for significant variables – longitude, forest type (ForType: 1 – oxalidosum and herboso-oxalidosum, 2 – myrtillosum, 3 – myrtilloso-sphagnosum and herboso-sphagnosum), log species identity (LogSpecies, 1 – spruce, 2 – pine), diameter, decomposition, latitude and bark cover were fitted to the ordination. For an explanation of the species abbreviations, see Appendix 1

logs and with decreasing bark cover on pine logs (Table 4, 5). Total cover of wood-inhabiting vegetation was marginally influenced by log attributes (Table 4, 5). Bark cover was not among the significant predictors for wood-inhabiting cryptogamic communities (Fig. 3, Table 6).

Discussion

As hypothesized, a rather low number of species demonstrated a reaction to bark cover. This could be interpreted as a true indifference of species to this factor. However, this could also be explained

by the low abundance of many individual species: i.e. the result based on too few occurrences is not statistically significant. The second explanation can be supported by the fact that the abundance of most species was not sensitive to other log attributes either, whereas the abundance of all substrate groups was influenced by bark cover and other log attributes.

The behaviour of different species in relation to bark cover varied. The least number of species was confined to exposed wood. Except for *Parmeliopsis ambigua*, only true epixylics (*Lophocolea heterophylla* and *Cladonia norvegica*) preferred exposed wood. The substrates with fragmented and intact bark cover

Table 4 Results of generalized linear models testing factors affecting the abundance of substrate groups in the second stage of epixylic succession. Significance codes: '***' – 0.001, '**' – 0.01, '*' – 0.05, 'ns' – non-significant. Empty cell: the factor was not included in the final model

	Epiphytes	Facultative epixylics	True epixylics	Generalists	Epigeous sp.	Total cover
Distribution, P	Tweedie, 1.1	Tweedie, 1.4	Tweedie, 1.3	Tweedie, 1.4	Tweedie, 1.2	Gaussian
Link function	Log	Log	Log	Log	Log	Identity
Full model Wald χ^2	65.3***	24.5***	28.4***	28.4***	45.1***	13.3***
Intercept: estimate (SE)	1.827(0.294)	3.258(0.069)	2.146(0.255)	2.53(0.111)	0.971(0.232)	50.746(4.038)
Log attributes						
Species. Wald χ^2 coefficients: estimate (SE)	20.5***		6.5**	18.9***		
Spruce	−1.993(0.440)		0.872(0.343)	0.620(0.143)		
Pine	ns		ns	ns		
Position. Wald χ^2 coefficient: estimate (SE)	8.6*** −0.680(0.023)			10.8*** −0.280(0.008)		
Diameter. Wald χ^2 coefficient: estimate (SE)					28.8*** 0.049(0.009)	13.0*** 0.693(0.193)
Bark cover. Wald χ^2 coefficient: estimate (SE)			9.5*** −0.010(0.003)			
Decomposition. Wald χ^2 coefficient: estimate (SE)		7.7** −0.004(0.001)				
Species*Bark. Wald χ^2 coefficients: estimate (SE)	14.4***				20.4***	
Spruce*Bark	−0.011(0.005)				0.130(0.003)	
Pine*Bark	0.013(0.004)				−0.024(0.012)	
Species*Diameter. Wald χ^2 coefficients: estimate (SE)	14.9***		6.0**			
Spruce*Diameter	0.008(0.013)		−0.012(0.009)			
Pine*Diameter	−0.070(0.018)		0.025(0.012)			
Species*Position. Wald χ^2 coefficients: estimate (SE)			11.1***		9.1**	
Spruce*Position			−0.017(0.008)		−0.017(0.008)	
Pine*Position			0.026(0.010)		0.031(0.015)	
Position*Decomp. Wald χ^2 coefficient: estimate (SE)				12.1*** 0.001(0.0002)		
Diameter*Position. Wald χ^2 coefficient: estimate (SE)	13.1*** 0.004(0.001)					
Bark*Decomp. Wald χ^2 coefficient: estimate (SE)		13.6*** 0.000(0.0001)				
Diameter*Decomp. Wald χ^2 coefficient: estimate (SE)						4.1** −0.002(0.001)

were attractive for species from different substrate groups, mainly generalists and epigeous species. Interestingly, *Lophocolea heterophylla* grew equally well on both exposed wood and bark, which is in agreement with earlier findings (McAlister 1997).

Our hypothesis that the joint effect of bark cover, log position, size, decomposition and species identity on the composition of wood-inhabiting vegetation is most pronounced in the colonization stage of succession on logs was not supported. This effect of log attributes and their interaction varied between groups and factors.

Often, the presence of epiphytic lichens on the logs from recently dead trees is interpreted as a remnant of the epiphytic vegetation of a living tree (Jansová and Soldán 2006). Jansová and Soldán (2006) believe that the growth of epiphytes is

Table 5 Summary of the effects of bark cover and its interactions with log attributes as predictors for the total abundance and the abundance of substrate groups based on the GLZM and GLZMM results. '+' – positive effect, '−' – negative effect. Significant predictors included in the models are highlighted with grey colour

|	Colonization				Mid-succession			
	Bark	Bark* spruce	Bark* pine	Bark* diameter	Bark	Bark* spruce	Bark* pine	Bark* decomposition
Epiphytes						−	+	
True epixylics	−				−			
Facultative epixylics		+	−					+
Epigeous spp.						+	−	
Generalists								
Total cover		+		+				

restricted by bark slough from the log. We observed that epiphytic lichens can establish and grow on logs, including exposed deadwood. Sloughing bark, weakly attached to a log, is not a very attractive substrate for epiphytes. For example, *Parmeliopsis ambigua* is strongly confined to exposed wood. The establishment and spread of this species on exposed wood, after sloughing of bark, is described also by Kharpukhaeva and Mukhortova (2016). They showed that foliose lichens such as *P. ambigua*, *Vulpicida pinastri* and other species excrete substances into decaying wood that inhibit the growth of bacteria and fungi and thus 'conserve' the substrate and influence the vegetation succession on decaying logs.

Facultative epixylics, which represent the most active substrate group in earlier stages of succession, are not very sensitive to the variation in log attributes. In contrast to true epixylics, they do not avoid bark. Some of them even prefer logs with complete bark cover (e.g. *Ptilidium pulcherrimum*).

In agreement with earlier findings (e.g. Jansová and Soldán 2006) and our hypothesis, our results show that during their establishment true epixylics are confined to exposed wood and only marginally influenced by other factors. In the second stage, log position and diameter and their interactions with

log species identity also influence the cover of epixylics. In the study of Andersson et al. (2009) epixylic species were used as indicators of old-growth forests, where 20% of species were true epixylics. Half that proportion of true epixylic species was recorded in this study. The characteristics of true epixylics revealed in this study improve our understanding of their biology. These species require not only high amounts of deadwood, but also special microsites. The ideal substrate for the establishment of this substrate group is a large, partly leaning log without bark. However, in the second stage, their preference for exposed wood is no longer very strong. That shift can be explained by the changes in physical characteristics of bark due to decomposition (Shorohova et al. 2016). The joint effects of log size, species, position and bark cover become more important for true epixylics during the succession process.

In any community, generalists, as opportunistic species, occupy different available non-specific substrates with possibly low competition with other species groups. According to Heilmann-Clausen et al. (2014), opportunistic wood-inhabiting species do not show any specificity to certain factors. According to our study and the study of Jansová and Soldán (2006), *Brachythecium salebrosum* and
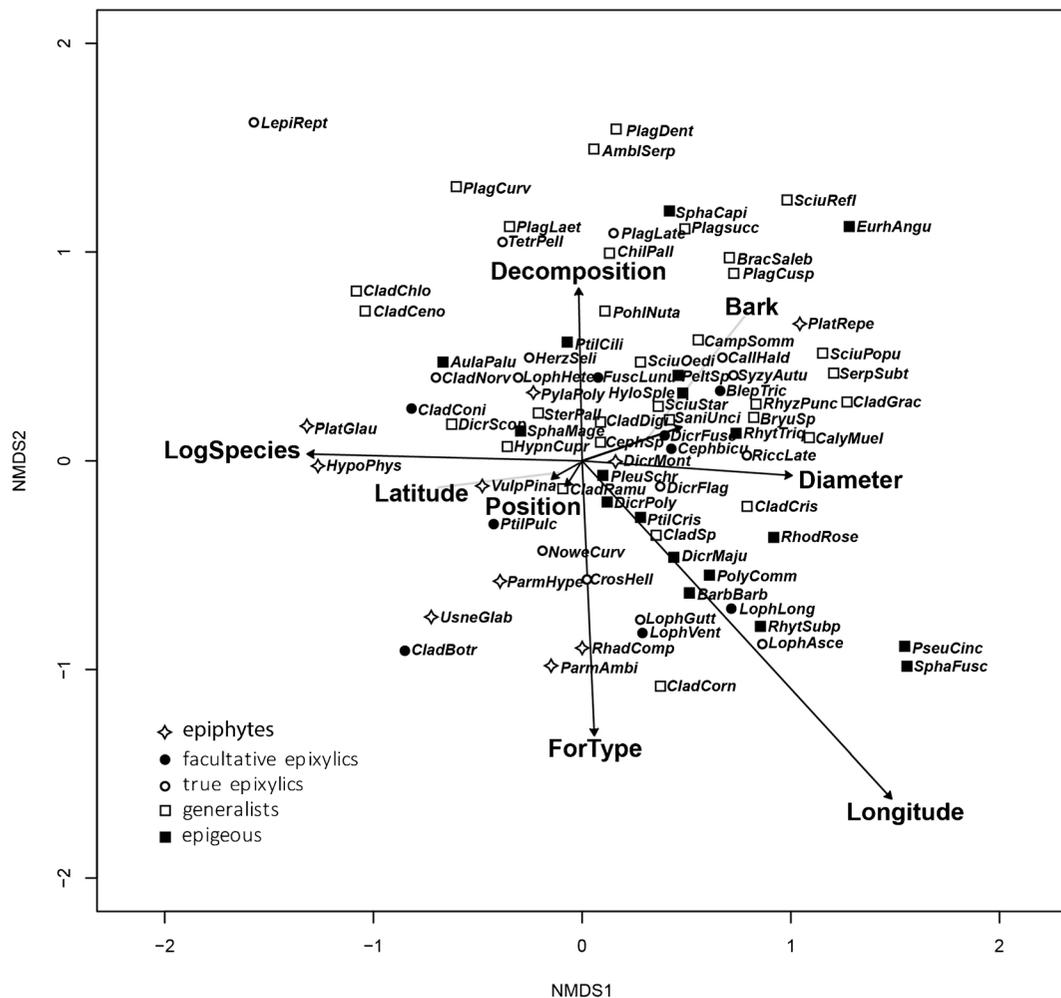
Fig. 3 NMDS ordination of the plots and species in the second stage of epixylic succession (all datasets). The vectors for significant variables – longitude, forest type (ForType: 1 – oxalidosum and herboso-oxalidosum, 2 – myrtillosum, 3 – myrtilloso-sphagnosum and herboso-sphagnosum), log species identity (LogSpecies: 1 – spruce, 2 - pine), diameter, decomposition, latitude and bark cover were fitted to the ordination. For an explanation of the species abbreviations, see Appendix 1

Sanionia uncinata, classified in this study as generalists, prefer growing on bark. In our study, generalist species as a group did not show any response to bark cover. The abundance of such generalist species, as for example *Hypnum cupressiforme*, *Stereodon pallescens* in oxalidosum and herboso-oxalidosum forest types (Fig. 2, 3) suggests the interrelationship between log and site attributes. Fast wood decomposition in rich site conditions (Shorohova and Kapitsa 2014) may lead to a faster epixylic succession.

The spread of generalists facilitates succession towards the state desired for the establishment of ground vegetation. Dynesius et al. (2010) point out

that log contact with the ground increases the covering of downed logs. Bark cover may enhance the effect of this factor by favouring the spread of epigeous species especially on spruce logs.

The total cover of wood-inhabiting vegetation increased during succession, almost independently of log attributes, as all log parts are occupied by different substrate groups.

Our data showed only marginal site-specific effect of bark cover on the wood-inhabiting cryptogamic communities on conifer logs in the first and second stages of epixylic succession (Table 6). Moreover, we revealed differences in log vs site attributes as explanatory variables for wood-inhabiting cryptogamic

Table 6 Coefficient of determination (R^2) and significance (P) of fitted vectors with ordination configurations for species abundance for the whole dataset (Fig. 2, 3) and for grouped sites in the first and second stages of epixylic succession. R^2 values significant at the $P < 0.05$ level is denoted by **bold font**. Significance codes: '***' – 0.001. '**' – 0.01, '*' – 0.05 ', 'na' – no variation in the dataset related to the factor

	All sites, 423 plots	Site S, unmanaged forest stands surrounded by an intensively managed forests in a fragmented landscape, 222 plots	Sites P, L, M, B – unmanaged forest stands surrounded by a managed forest, 119 plots	Sites A and K – old-growth forests, 82 plots
Colonization				
Bark cover [%]	0.006	0.020	**0.245*****	0.036
Log diameter [cm]	**0.049*****	**0.083*****	**0.324*****	0.139
Position [cm]	0.024	0.019	**0.353*****	0.105
Decomposition [mm]	**0.054****	**0.088****	0.069	0.039
Log species identity	**0.163*****	**0.099****	**0.567*****	0.054
Latitude	0.021	na	**0.484*****	**0.401*****
Longitude, landscape	**0.377*****	na	na	**0.401*****
Forest type	**0.237*****	na	**0.407*****	0.007
Mid-succession				
Bark cover [%]	0.019	0.002	0.041	0.008
Log diameter [cm]	**0.082*****	0.036	**0.110****	0.017
Position [cm]	0.003	0.004	< 0.001	0.010
Decomposition [mm]	**0.058****	**0.091****	**0.102****	0.001
Log species identity	**0.143*****	**0.081****	**0.404*****	**0.159*****
Latitude	0.004	na	**0.358*****	**0.306*****
Longitude, landscape	**0.409*****	na	na	**0.267*****
Forest type	**0.139*****	na	**0.359*****	0.059

communities in initial stages of epixylic succession in the landscapes with different forest management history.

Conclusion

The negative effect of bark cover on the abundance of true epixylics, most of which are threatened species, emphasizes the importance of exposed wood for preserving boreal forest biodiversity. Bark cover influences the structure of epixylic cryptogamic communities through interrelating with other log attributes. Bark cover changes log species preferences of epiphytes, facultative epixylics and epigeous species. In the colonization stage, the positive effect of log diameter on the total cover of epixylic cryptogamic vegetation is enhanced by bark cover, especially on spruce logs. However, the effect of bark cover on epixylic vegetation at the community level is negligible. In general, bark cover favours the establishment and growth of species with low substrate specificity. This may lead to either burial of logs by bryophytes (Hagemann et al. 2010) or facilitation of succession towards the dominance of ground vegetation. Our results support the use of bark-scratching as a post-disturbance management and restoration treatment from a biodiversity point of view (Thorn et al. 2016).

Appendix 1

Table 7 Mean abundance (cover) and occurrence (frequency) of species and their substrate groups in the first and second stages of epixylic succession. Epf – epiphyte, f. epx – facultative epixylic, t. epx – true epixylic, gen – generalist, ep – epigeous species. Parameters significantly different for the logs with different bark cover according to the Kruskal-Wallis test at the $P < 0.05$ level are denoted by **bold font**. 1 – species with cover and / or frequency of occurrence significantly higher on the logs with bark cover from 0 to 20%; 2 – species with cover and / or frequency of occurrence significantly higher on the logs with bark cover from 21 to 80%, 3 – species with cover and / or frequency of occurrence significantly higher on the logs with bark cover from 81 to 100%. The species used as indicator of old-growth forests (Andersson et al. 2009) are underlined

Species	Log sp.		Effect of bark cover	Substr. group	First stage		Second stage	
					Frequency	Cover	Frequency	Cover
Amblystegium serpens (Hedw.) Bruch et al.	S[1]	AmblSerp		gen	0	0	0.5	< 0.01
Aulacomnium palustre (Hedw.) Schwägr.	S	AulaPalu		ep	0.5	< 0.01	0.5	< 0.01
Barbilophozia barbata (Schmidel ex Schreb.) Loeske	S	BarbBarb		ep	0.9	< 0.01	1.0	< 0.01
Blepharostoma trichophyllum (L.) Dumort.		BlepTric		f. epx	0.9	< 0.01	5.8	0.16
Brachythecium salebrosum (F. Weber et Dl. Mohr) Giacon		BracSale	↑	gen	0.4	< 0.01	4.8	**0.84**
Bryum sp.	P[2]	BryuSp		ep	0	0	1.0	< 0.01
Callicladium haldanianum (Grev.) H.A. Crum		CallHald		t.epx	0.9	0.02	5.8	0.75
Calypogeia muelleriana (Schiffn.) Müll. Frib.		CalyMuel		gen	0.5	0.07	5.8	0.31
Campylidium sommerfeltii (Myrin) Ochyra		CampSomm		gen	0	0	0.5	< 0.01
Cephalozia sp.		CaphSp		gen	0	0	0.5	< 0.01
Cephalozia bicuspidata (L.) Dumort.		CephBicu		f. epx	0.9	0.03	6.7	0.45
Chiloscyphus pallescens (Ehrh. ex Hoffm.) Dumort.	S	ChilPall		gen	0	0	0.5	< 0.01
Cladonia arbuscula (Wallr.) Flot.	S	CladArbu		gen	0.9	0.01	0	0
Cladonia rangiferina (L.) F. H. Wigg.	S	CladRang	↓	gen	1.9	**0.01**	0	0
Cladonia botrytes (K.G. Hagen) Willd.		CladBotr	↑	f. epx	1.9	**0.05**	0.5	< 0.01
*Cladonia cenotea (*Ach.) Schaer.	P	CladCeno		gen	0	0	1.4	0.01
Cladonia chlorophaea (Florke ex Sommerf.) Spreng.		CladChlo	↑↓	gen	1.4	0.05	3.4	**0.25**
Cladonia coniocraea (Florke) Spreng.		CladConi		f. epx	39.9	2.33	40.0	4.71
Cladonia crispata (Ach.) Flot.	P	ClagCris		gen	0.5	< 0.01	0.5	< 0.01
Cladonia digitata (L.) Hoffm.		CladDigi		gen	0.9	0.08	2.8	0.63
Cladonia gracilis (L.) Willd.	P	ClagGrac		gen	0.5	0.12	0.5	0.02
Cladonia norvegica Tonsberg & Holien		CladNorv	↓	t.epx	3.3	0.26	11.5	**0.83**
Cladonia ramulosa (With.) J.R. Laundon	P	CladRamu		gen	1.7	0.01	2.4	0.07
Cladonia subulata (L.) Weber ex F. H. Wigg.	P	CladSubu		gen	0.5	0.02	0	0
Cladonia cornuta (L.) Hoffm	P	CladCorn		gen	1.4	0.05	0.5	0.05
Cladonia sp.		CladSp	↑	gen	18.3	1.63	22.1	**1.87**
Climacium dendroides (Hedw.) F. Weber et Dl. Mohr.	S	ClimDend		ep	0	0	0.5	< 0.01
<u>*Crossocalyx hellerianus*</u> (Neesex Lindenb.) Meyl.		CrosHell		t.epx	5.2	0.46	7.2	0.49
Dicranum bonjeanii De Not.		DicrBonj		ep	0.9	< 0.01	0	0
<u>*Dicranum flagellare*</u> Hedw.		DicrFlag		t.epx	3.3	0.18	3.4	0.81
Dicranum fuscescens Turner		DicrFusc		f. epx	0.9	0.02	2.9	0.28
Dicranum majus Turner	S	DicrMaju		ep	0	0	0.5	0.01
Dicranum montanum Hedw.		DicrMont		epf	2.8	0.02	11.1	0.22
Dicranum polysetum Sw.		DicrPoly	↑	ep	5.1	0.1	9.6	**0.28**
Dicranum scoparium Hedw.		DicrScop		gen	36.1	1.02	73.1	4.25

Table 7 (continued)

Species	Log sp.		Effect of bark cover	Substr. group	First stage		Second stage	
					Frequency	Cover	Frequency	Cover
Eurhynchium angustirete (Broth.) T.J. Kop.	S	EurhAngu		ep	0	0	0.5	0.01
Fuscocephaloziopsis lunulifolia (Dumort.) Váňa et L. Söderstr.		FuscLunu		f. epx	2.3	0.06	7.7	0.61
Herzogiella seligeri (Brid.) Z. Iwats.		HerzSeli		t. epx	2.8	0.14	10.6	0.30
Hylocomium splendens (Hedw.) Bruch et al.		HyloSple		ep	7.5	0.66	15.4	0.53
Hypnum cupressiforme Hedw.		HypnCupr		gen	5.2	0.08	11.5	1.3
Hypogymnia physodes (L.) Nyl.		HypoPhys		epf	43.2	3.53	15.4	0.74
Lepidozia reptans (L.) Dumort.		LepiRept		f. epx	0.4	0.01	1.9	0.24
Lophocolea heterophylla (Schrad.) Dumort.		LophHete	↓	t.epx	21.6	1.36	44.2	**3.25**
Lophozia ascendens (Warnst.) R.M. Schust.	S	LophAsce		t epx	0	0	0.5	0.02
Lophozia guttulata (Lindb. et Arnell) A. Evans		LophGutt		t.epx	2.8	0.31	7.7	1.67
Lophozia ventricosa (Dicks.) Dumort.		LophVent	↑↓	f. epx	4.7	0.33	8.2	**1.45**
Lophoziopsis longidens (Lindb.) Konstant. et Vilnet		LophLong		f. epx	1.4	0.01	1.4	1.0
Nowellia curvifolia (Dicks.) Mitt.		NoweCurv		t.epx	8.4	1.13	9.1	1.33
Orthotrichum speciosum Nees	S	OrthSpec		epf	0.5	< 0.01	0	0
Parmelia sulcata Taylor	P	ParmSulc		epf	2.3	0.04	0.5	0.01
Parmeliopsis ambigua (Wulfen) Nyl.		ParmAmbi	↓	epf	5.6	0.13	1.4	**0.04**
Parmeliopsis hyperopta (Ach.) Arnold		ParmHype		epf	9.9	0.25	3.8	0.04
Peltigera sp.	S	PeltSp	↑	ep	0.5	**0.01**	1.4	**0.02**
Plagiomnium cuspidatum (Hedw.) T.J. Kop.	S	PlagCusp		gen	0	0	2.4	0.01
Plagiothecium curvifolium Schlieph. ex Limpr.		PlagCurv		gen	0.9	0.09	2.4	0.19
Plagiothecium denticulatum (Hedw.) Bruch et al.	P	PlagDent		gen	0	0	0.5	< 0.01
Plagiothecium laetum Bruch et al.		PlagLaet		gen	7.0	0.24	22.6	1.18
Plagiothecium succulentum (Wilson) Lindb.	S	PlagSucc		gen	0	0	1.0	0.05
Platismatia glauca (L.)W.L. Culb. & C.F. Culb.		PlatGlau		epf	25.4	0.70	10.1	0.33
Platygyrium repens (Brid.) Bruch et al.	S	PlatRepe		epf	0	0	1.0	0.03
Pleurozium schreberi (Brid.) Mitt.		PleuSchr	↑↓	ep	39.9	**1.92**	71.6	**7.65**
Pohlia nutans (Hedw.) Lindb.		PohlNuta		gen	1.9	< 0.01	8.7	0.21
Polytrichum commune Hedw.		PolyComm		ep	0	0	0.5	< 0.01
Pseudobryum cinclidioides (Huebener) T.J. Kop.	S	PseuCinc		ep	0	0	0.5	<0.01
Ptilidium ciliare (L.) Hampe	S	PlilCili		ep	0	0	1.0	<0.01
Ptilidium pulcherrimum (Weber) Hampe		PtilPulc		f. epx	67.6	7.99	77.9	14.97
Ptilium crista-castrensis (Hedw.) De Not.		PtilCris		ep	1.4	0.02	6.2	0.11
Pylaisia polyantha (Hedw.) Bruch et al.	S	PylaPoly		epf	0.9	0.03	3.4	0.07
Radula complanata (L.) Dumort.	S	RaduComp		epf	0.5	< 0.01	0.5	< 0.01
Rhizomnium punctatum (Hedw.) T.J. Kop.	S	RhyzPunc	↑	gen	0	0	2.4	**0.02**
Rhodobryum roseum (Hedw.) Limpr.	S	RhodRoze		ep	0	0	1.0	< 0.01
Rhytidiadelphus subpinnatus (Lindb.) T.J. Kop.	S	RhytSubp		ep	0.5	< 0.01	0.5	< 0.01
Rhytidiadelphus triquetrus (Hedw.) Warnst.	S	RhytTric	↑	ep	0.9	**0.01**	7.2	**0.11**
Riccardia latifrons (Lindb.) Lindb.		RiccLati		t.epx	0.5	< 0.01	3.8	0.09
Sanionia uncinata (Hedw.) Loeske		SaniUnci	↑	gen	14.1	0.75	32.7	**4.0**
Sciuro-hypnum oedipodium (Mitt.) Ignatov & Huttunen		SciuOedi		gen	3.8	0.02	11.1	0.88
Sciuro-hypnum populeum (Hedw.) Ignatov & Huttunen	S	SciuPopu		gen	0	0	0.5	< 0.01

Table 7 (continued)

Species	Log sp.		Effect of bark cover	Substr. group	First stage		Second stage	
					Frequency	Cover	Frequency	Cover
Sciuro-hypnum reflexum (Starke) Ignatov & Huttunen	S	SciuRefl		gen	0	0	1.0	0.7
Sciuro-hypnum starkii (Brid.) Ignatov & Huttunen		SciuStar		gen	1.4	0.01	4.8	0.13
Serpoleskea subtilis (Hedw.) Loeske	S	SerpSubt		gen	0	0	0.5	< 0.01
Sphagnum capillifolium (Ehrh.) Hedw.		SphaCapi		ep	0	0	0.5	< 0.01
Sphagnum fallax H. Klinggr.	S	SphaFall		ep	0.5	< 0.01	0	0
Sphagnum fuscum (Schimp.) H. Klinggr.	S	SphaFusc		ep	0	0	0.5	0.01
Sphagnum magellanicum Brid.		SphaMage		ep	0	0	1.0	0.02
Stereodon pallescens (Hedw.) Mitt.		SterPall		gen	4.7	0.18	7.7	0.69
Straminergon stramineum (Dicks. ex Brid.) Hedenäs	S	StraStra		ep	0.5	< 0.01	0	0
Syzygiella autumnalis (DC.) K. Feldberg, Váňa, Hentschel et Heinrichs	S	SyzyAutu		t.epx	0.9	0.05	2.9	0.11
Tetraphis pellucida Hedw.		TetrPell	↓	t.epx	2.8	0.19	15.9	**1.22**
Usnea glabrata (Ach.) Vain.		UsneGlab		epf	0.9	< 0.01	1.0	< 0.01
Vulpicida pinastri (Scop.) J.-E. Mattsson et M.J. Lai		VulpPina		epf	14.5	0.07	8.2	0.1

[1] Species that occurred only on spruce logs

[2] Species that occurred only on pine logs

References

Aakala T (2010) Coarse woody debris in late-successional *Picea abies* forests in northern Europe: Variability in quantities and models of decay class dynamics. *Forest Ecol Managem* 260: 770–779

Andersson L, Hytteborn H (1991) Bryophytes and decaying wood – a comparison between managed and natural forest. *Holarc Ecol* 2:121–130

Andersson L, Alexeeva M, Kuznetsova E (eds) (2009) *Survey of biologically valuable forests in North-Western European Russia. Vol. 2. Identification manual of species to be used during survey at stand level.* Saint-Petersburg

Botting RS, DeLong C (2009) Macrolichen and bryophyte responses to coarse woody debris characteristics in sub-boreal spruce forest. *Forest Ecol Managem* 258:85–94

Culberson WL (1955) The corticolous communities of lichens and bryophytes in the upland forests of northern Wisconsin. Ecol Monogr 25: 215-231   Sorry, it was a misspelling. Correct name is Culberson

Dynesius M, Gibb H, Hjältén J (2010) Surface covering of downed logs: Drivers of a neglected process in dead wood ecology PLoS ONE 5, 10 e 13237

Hagemann U, Moroni MT, Gleibner J Makeschin F (2010) Accumulation and preservation of dead wood upon burial by bryophytes. *Ecosystems* 13:600–611

Harmon ME (1989) Effects of bark fragmentation on plant succession on conifer logs in the *Picea-Tsuga* forest of Olympic National Park. *Amer Midl Naturalist* 121: 112–124

Heilmann-Clausen J, Aude E, van Dort K, Christensen M, Piltaver A, Veerkamp M, Walleyn R, Siller I, Standovár T, Òdor P. (2014) Communities of wood-inhabiting bryophytes and fungi on dead beech logs in Europe - reflecting substrate quality or shaped by climate and forest conditions? *J Biogeogr* 41:2269–2282

Ignatov M, Afonina O; Ignatova E (2006) Check-list of mosses of East Europe and North Asia. *Arctoa* 15:1–130

Ignatov M and Ignatova E (2003) *Moss flora of the Middle European Russia Vol 1: Sphagnaceae – Hedwigiaceae.* KMK, Moscow [in Russian]

Ignatov M, Ignatova E (2004) *Moss flora of the Middle European Russia Vol 2: Fontinalaceae – Amblistegiaceae.* KMK, Moscow [in Russian]

Jansová I and Soldán Z (2006) The habitat factors that affect the composition of bryophyte and lichen communities on fallen logs. *Preslia* 78:67–86

Kharpukhaeva TM, Mukhortova LV (2016) Dynamics of Interaction between Lichens and Fallen Deadwood in Forest Ecosystems of the Eastern Baikal Region Contemporary Problems of Ecology 9: 125-139

Konstantinova NA, Bakalin VA., Andreeva EN. et al. Checklist of liverworts (Marchantiophyta) of Russia 2009. *Arctoa* 18:1–63

Kurbatova L (2002) Mosses of the Leningrad Province. Dissertation, Komarov' Bot. Inst. [in Russian]

Kushnevskaya H, Mirin D, Shorohova E (2007) Patterns of epixylic vegetation on spruce logs in late-successional boreal forests. *Forest Ecol Managem* 250:25–33

Kushnevskaya E (2012) Epixylic successions in Norway spruce forests in Leningrad region. *Bot Zhurn (Moscow & Leningrad)* 97:917–939 [in Russian]

Kushnevskaya E, Potemkin A (2014) The liverworts of the eastern Leningrad region. *Bot Zhurn (Moscow & Leningrad)* 99:23–34 [in Russian]

McAlister S. (1997) Cryptogam communities on fallen logs in the Duke Forest. North Carolina. *J Veg Sci* 8:115–124

McCullough HA, (1948) Plant successions on fallen logs in a virgin spruce-fir forest. Ecology 29: 508–513

Mills SE, Macdonald SE (2004) Predictors of moss and liverwort species diversity of microsites in conifer-dominated boreal forest. *J Veg Sci* 15:189–198

Muhle H, LeBlanc F (1975) Bryophyte and lichen succession on decaying logs. 1. Analysis along an evaporational gradient in eastern Canada. *J Hattori Bot Lab* 39:1–33

Müller J, Boch S, Blaser S, Fischer M, and Prati D (2015) Effects of forest management on bryophyte communities on deadwood. *Nova Hedwigia* 100:423–438

Ódor P, Heilmann-Clausen J, Christensen M, Aude E, van Dort KW, Piltaver A, Siller I, Veerkamp MT, Walleyn R, Standovár T, van Hees AFM, Kosec J, Matočec N, Kraigher H, Grebenc T (2006) Diversity of dead wood inhabiting fungi and bryophytes in semi-natural beech forests in Europe. *Biol Conservation* 131:58–71

Ódor P, van Hees AFM (2004) Preferences of dead wood inhabiting bryophytes to decay phase, log size and habitat types in Hungarian beech forests. *J Bryol* 26:79–95

Oksanen J, Blanchet GF, Kindt R, Legendre P, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Stevens MH, Wagner H (2013) Vegan: Community Ecology Package. R package version 2.0-10

Palmer MW (1986) Pattern in corticolous bryophyte communities of North Carolina piedmont: Do mosses see the forest or the trees? *Bryologist* 89:59–65

Perhans K, Gustafsson L, Jonsson F, Nordin U, Weibull H (2007) Bryophytes and lichens in different types of forest set-asides in boreal Sweden. *Forest Ecol Managem* 242:374–390

Potemkin AD, Sofronova EV (2009) *Liverworts and hornworts of Russia*. Boton-Spectr, Saint-Petersburg – Yakutsk [in Russian]

Preikša Z, Brazaitis G, Marozas V, Jaroszewicz B (2016) Dead wood quality influences species diversity of rare cryptogams in temperate broadleaved forests. *iForest* 9:276–285

Rambo TR, Muir PS (1998) Bryophyte species associations with coarse woody debris and stand ages in Oregon. *Bryologist* 101:366–376

Rysin L, Savelieva L (2002) *Spruce forests of Russia*. Nauka, Moscow

Santesson R, Moberg R., Nordin A, Tønsberg T, Vitikainen O (2004) *Lichen-forming and lichenicolous fungi of Fennoscandia*. Museum of Evolution, Uppsala University

Shorohova E, Shorohov A (2001) Coarse woody debris dynamics and stores in a boreal virgin spruce forest. *Ecol Bull* 49:129–137

Shorohova E, Kapitsa E (2014) Influence of the substrate and ecosystem attributes on the decomposition rates of coarse woody debris in European boreal forests. *Forest Ecol Managem* 356:273–284

Shorohova E, Kapitsa E (2015) Stand and landscape scale variability in the amount and diversity of coarse woody debris in primeval European boreal forests. *For Ecol Managem* 315:185–190

Siitonen J (2001) Forest management, coarse woody debris and saproxylic organisms: Fennoscandian boreal forests as an example. *Ecol Bull* 49:11–41

Söderström L (1988) Sequence of bryophytes and lichens in relation to substrate variables of decaying coniferous wood in Northern Sweden. *Nordic J Bot* 8:89–97

Shorohova E, Kapitsa E, Kazartsev I, Romashkin I, Polevoi A, Kushnevskaya H (2016) Tree species traits are the predominant control on the decomposition rate of tree log bark in a mesic old-growth boreal forest Forest Ecology and Management 337: 36-45

Söderström L, Hagborg A, von Konrat M, Bartholomew-Began S, Bell D, Briscoe L, Brown E, Cargill DC, Costa DP, Crandall-Stotler BJ, Cooper ED, Dauphin G, Engel JJ, Feldberg K, Glenny D, Gradstein SR, He X, Heinrichs J, Hentschel J, Ilkiu-Borges AL, Katagiri T, Konstantinova NA, Larraín J, Long DG, Nebel M, Pócs T, Felisa Puche F, Reiner-Drehwald E, Renner MAM, Sass-Gyarmati A, Schäfer-Verwimp A, Moragues JGS, Stotler RE, Sukkharak P, Thiers BM, Uribe J, Váňa J, Villarreal JC, Wigginton M, Zhang L, Zhu R-L (2016) World checklist of hornworts and liverworts. *PhytoKeys*. Vol. 59, pp 1–828

Taborská M, Přívětivý T, Vrška T, Ódor P (2015) Bryophytes associated with two tree species and different stages of decay in a natural fir-beech mixed forest in the Czech Republic. *Preslia* 87:387–401

Thorn S, Bässler, C, Bußler H, Lindenmayer D, Schmidt S, Seibold S, Wende B, Müller J (2016) Bark-scratching of storm-felled trees preserves biodiversity at lower economic costs compared to debarking. *Forest Ecol Managem* 364:10–16

Ulyshen MD (2016) Wood decomposition as influenced by invertebrates. *Biol Rev* 91:70–85