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Running title: Vegetation abundance and species diversity on CWD
Epixylic vegetation abundance, diversity and composition vary with coarse woody debris decay class
and substrate species in boreal forest

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Abstract

Although the importance of coarse woody debris (CWD) to understorey species diversity has been recognized, the combined effects of CWD decay and substrate species on abundance and species diversity of epixylic vegetation have received little attention. We sampled a wide range of CWD substrate species and decay classes as well as forest floor in fire-origin boreal forest stands. Percent cover, species richness and evenness of epixylic vegetation differed significantly with both CWD decay class and substrate species. Trends in cover, species richness and evenness differed significantly between non-vascular and vascular taxa. Cover, species richness and species evenness of non-vascular species were higher on CWD, whereas those of vascular plants were higher on the forest floor. Epixylic species composition also varied significantly with stand ages, overstorey compositions, decay classes, substrate species and their interactions. Our findings highlight strong interactive influences of decay class and substrate species on epixylic plant communities, and suggest that conservation of epixylic diversity would require forest managers to maintain a diverse range of CWD decay classes and substrate species. Since stand development and overstorey compositions influence CWD decay classes and substrate species as well as colonization time and environmental conditions in the understorey, our results indicate that managed boreal landscapes should consist of a mosaic of different successional stages and a broad suite of overstorey types to support diverse understorey plant communities.

Keywords: boreal forest; coarse woody debris; decay class; epixylic plants; substrate species

Introduction

Coarse woody debris (CWD) plays a key role in biodiversity and ecosystem functioning as it provides habitat for many plants and animals (Bunnell and Houde 2010; Stokland et al. 2012), and contributes to carbon and nutrient cycles (Harmon et al. 1986; Laiho and Prescott 1999; Ohtsuka et al. 2014). The importance of CWD to maintaining understory species diversity has been emphasized by numerous authors (Andersson and Hytteborn 1991; Crites and Dale 1998; Rambo and Muir 1998; Kruys and Jonsson 1999; Humphrey et al. 2002; Mills and Macdonald 2004; Bunnell et al. 2008; Botting and DeLong 2009; Caruso and Rudolphi 2009; Dittrich et al. 2014; Checko et al. 2015). It is widely recognized that numerous plant species are specialized to a greater or lesser extent on CWD substrates, and such species are termed “epixylic”. The focus of most prior studies of epixylic plants has either been on non-vascular (lichens and bryophytes) or vascular groups occurring on different CWD decay classes. These studies have generally found that species richness and abundance of non-vascular species (lichens and bryophytes) peak in intermediate to later stages of decay, while those of vascular plants continue to increase at advance stages of decay. A few studies have also examined the effect of substrate species of deadwood on patterns of epixylic plant abundance and diversity (McAlister 1997; Rambo 2001; Mills and Macdonald 2004; Nowinska et al. 2009). The simultaneous effects of CWD decay classes and substrate species have recently been examined in terms of understory vegetation species composition (Kumar et al. 2017), but not abundance and species diversity. Species richness and evenness may respond differently to different ecological processes (Stirling and Wilsey 2001; Wilsey and Stirling 2007); however, no studies to our knowledge have explicitly assessed patterns of species evenness in relation to CWD decay. In addition, very few studies

have made a comparison of species abundance and diversity on deadwood substrates to corresponding forest floor substrates (Dittrich et al. 2014; Checko et al. 2015).

Decaying CWD provides a variable substrate at different stages of decomposition and is colonised by a different subset of species as compared with the adjacent forest floor substrates (Lee and Sturges 2001, 2002; Dittrich et al. 2014). Decaying CWD logs are typically colonised by lichens and bryophytes species, which take advantage of lower competition than on the forest floor (Humphrey et al. 2002; Dittrich et al. 2014), whereas the forest floor is mostly dominated by vascular plant species. The structural and chemical properties of CWD change with the decomposition process (Ganjegunte et al. 2004; Butler et al. 2007; Petrillo et al. 2015; Shorohova et al. 2016), until CWD becomes an integral part of the forest floor. These progressive changes in CWD properties over time are likely to be a main driver of the colonization and growth of different non-vascular and vascular species. The early stages of CWD decomposition are dominated by non-vascular (mostly lichen) species, some of which normally grow on living trees as epiphytes, whereas the later stages of decay are characterized by bryophytes and vascular plant species (McCullough 1948; Barkman 1958; Söderström 1988; Jansová and Soldán 2006; Botting and DeLong 2009; Kumar et al. 2017). Eventually, the CWD merges with the forest floor in the final stages of decay; in boreal systems the substrate is occupied by feathermosses and vascular plants that normally grow on the forest floor (Söderström 1988; Andersson and Hytteborn 1991; Kumar et al. 2017). In addition to changes in physical and chemical properties of the CWD with decay (Laiho and Prescott 2004; Butler et al. 2007; Petrillo et al. 2015), the time available for colonization increases (Bartels and Chen 2015). Both the decay process and time elapsed will likely influence abundance and diversity because of dispersal limitation and successional processes.

Patterns in epixylic plant communities may also differ among CWD substrate species because of species-specific differences in physical and chemical traits (pH and texture) of barks (Barkman 1958; Weedon et al. 2009; Mežaka et al. 2012; Pereira et al. 2014; Putna and Mežaka 2014; Shorohova and Kapitsa 2014; Shorohova et al. 2016). For example, the barks of coniferous species are generally drier and more acidic than those of broadleaved tree species (Culbertson 1955; Barkman 1958; Hauck and Javkhlan 2009; Jüriado et al. 2009; Mežaka et al. 2012). Furthermore, broadleaved tree species, particularly fast-growing species such as *Populus* spp. and *Betula* spp. common in boreal forests, generally have higher decomposition rates than coniferous species (Barkman 1958; Weedon et al. 2009; Russell et al. 2014; Shorohova and Kapitsa 2014). As a result, different epixylic plant communities have been observed on broadleaved and coniferous CWD substratum (Palmer 1986; McAlister 1997; Rambo 2001; Mills and Macdonald 2005). Non-vascular species (bryophytes and lichens) can generally tolerate substrates with higher acidity (Hauck and Jurgens 2008; Pereira et al. 2014), whereas most vascular plants establish on substrates that are nutrient-rich and less acidic. Although the species-specificity of non-vascular species associated with CWD species has been recognized (Culbertson 1955; McAlister 1997; Rambo 2001; Spribille et al. 2008; Caruso and Rudolphi 2009; Kumar et al. 2017), the combined effects of CWD decomposition and CWD substrate species on understory vegetation abundance, species richness and evenness remain unclear.

In boreal forests, fire is the major natural disturbance responsible for creation and elimination of dead wood on the forest floor (Arseneault 2001; Karjalainen and Kuuluvainen 2002; Brassard and Chen 2006). However, the importance of other disturbances such as insect outbreak and windthrow in altering stand structure has been also recognized (Chen and Popadiouk 2002; Brassard and Chen 2006; Bergeron et al. 2014). Post-disturbance CWD

101 dynamics usually results in a U-shaped pattern, where the volume of CWD of pre-fire origin
102 decreases logarithmically and the CWD of post-fire origin increases exponentially from
103 increased tree mortality associated with competition, ageing and disturbances such as windthrow
104 and insect outbreaks (Sturtevant et al. 1997; Brassard and Chen 2006; Luo and Chen 2011). In
105 addition to stand development, structure and composition of the overstorey also affect the
106 volume and compositional diversity of CWD (Brassard and Chen 2008), because overstorey
107 structure and composition influences stand productivity (Zhang et al. 2012), tree mortality (Chen
108 and Luo 2015), and CWD decomposition rates (Makinen et al. 2006). The structure and
109 composition of the overstorey varies through forest succession in boreal forests: multiple
110 successional pathways can result in either broadleaf, conifer or mixedwood-dominated stands
111 (Chen and Popadiouk 2002; Taylor and Chen 2011). CWD in broadleaf stands may influence the
112 epixylic plant communities differently than the CWD in conifer-dominated stands as a result of
113 distinct environmental conditions in different stand types (Barbier et al. 2008; Chávez and
114 Macdonald 2012; Bartels and Chen 2013; Huo et al. 2014). Broadleaf stands have higher
115 resource availability in the understorey than conifers (Messier et al. 1998; Hart and Chen 2006;
116 Chávez and Macdonald 2010), and are preferred by species that require resource-rich
117 environments as compared to species that are able to tolerate nutrient-poor conditions in conifer
118 stands. Mixedwood stands on the other hand provide heterogeneous conditions and exhibit
119 greater spatial and temporal variability in understorey resources (Bartemucci et al. 2006;
120 Macdonald and Fenniak 2007). Therefore, stand age along with overstorey species composition
121 may influence CWD volume and diversity as well as the extent of post-disturbance recovery of
122 epixylic plant communities on individual CWD substrata.

123 The purpose of this study was to examine the combined effect of CWD decay classes and
124 substrate species on abundance, species diversity and composition of understory vegetation in
125 the central boreal forest of Canada. To cover a wide range of CWD decay classes and substrate
126 species, we sampled fire-origin boreal forest stands that varied in canopy species composition
127 and stand age. We expected that total vegetation cover would be higher on the later decay classes
128 of the broadleaved substrate species because of higher moisture content at later stages of decay,
129 which would particularly enhance recruitment and growth of feather mosses and vascular plant
130 species at later stages of decay. We hypothesized that both species richness and evenness would
131 be higher on intermediate decay classes of coniferous substrates, because the acidic bark and
132 slower rate of fragmentation in conifers may provide favorable opportunities for establishment
133 and colonization of both non-vascular and vascular species and because some species would out-
134 compete others at late decay stages. By contrast, CWD of broadleaved species might not show
135 such a pattern due to greater bark sloughing and fragmentation. We also expected that epixylic
136 plant community composition would differ with stand age and overstorey composition due to
137 colonization time associated with stand age and environmental conditions as well as physical and
138 chemical properties of CWD substrate species associated with overstorey composition. Finally,
139 we predicted that epixylic plant communities would differ among CWD decay classes and the
140 forest floor, because of increased time available for colonization, and changes in substrate
141 suitability with CWD decay and forest floor development.

142 **Material and Methods**

143 **Study area**

144 Data analyzed are identical to that of a companion study examining species composition on
145 coarse woody debris, with a focus on indicator species of decay class and CWD substrate species
146 (Kumar et al. 2017): additional details on study sites and sampling design are provided in that
147 paper. Sampling was conducted at boreal mixed-wood sites approximately 100 km north of
148 Thunder Bay, Ontario, Canada (49°23'N to 49°36'N, 89°31'W to 89°44'W). Mean annual
149 temperature is 2.5°C and annual precipitation is 712 mm at the closest meteorological station
150 (Thunder Bay, Ontario: (Environment Canada 2015). Canopy trees include jack pine (*Pinus*
151 *banksiana* Lamb.), trembling aspen (*Populus tremuloides* Michx.), white birch (*Betula*
152 *papyrifera* Marsh.), black spruce (*Picea mariana* Mill. B.S.P.), white spruce (*Picea glauca*
153 [Moench] Voss) and balsam fir (*Abies balsamea* L. Mill.). Fire is the main disturbance agent in
154 the region, with an average fire return interval of approximately 100 years (Senici et al. 2010).

155 **Sampling design**

156 We sampled a set of stands representing a replicated chronosequence (with stands of age 34, 98,
157 146, and 210 years since last stand replacing fire) and of diverse overstorey composition
158 (Brassard and Chen 2008). Fire-origin stands in the region can be dominated by conifers,
159 broadleaved trees, or a mixture (Taylor and Chen 2011): in so far as possible we sampled all
160 three overstorey stand types for each age class, with three replicates for each. All combinations
161 of age class and overstorey type were sampled, with the exception of a 146-year-old stand that
162 did not have road access, resulting in a total of 35 sampled stands. All selected stands were

located on mesic sites at flat or mid-slope positions, with no slope exceeding 5%. Soil parent material consisted of well-drained (sandy or silty loam) glacial moraines, >50 cm in thickness.

Data collection

Sampling was conducted in a 400-m² circular plot randomly selected in each stand. Logs ≥ 10 cm in diameter at midpoint within each plot were randomly selected and decay class recorded. We assigned each selected CWD piece (downed woody debris on forest floor only) to one of five decay class categories, following the field manual of BC Ministry of Forests and Range and BC Ministry of Environment (2010). Categorization was based on CWD contact with the ground, wood texture, presence or absence of branches, wood strength, bark intactness, and presence and depth of invading roots. The characteristics of decay class 1 were logs elevated from ground, bark or branches hard and intact, and no invading roots present; those of decay class 2 included logs elevated but slightly sagging, presence of sap rot so that a thumbnail can penetrate, loose bark and soft branches with no invading roots; those of decay class 3 included logs sagging or broken, advanced decay (spongy/large pieces) with trace bark, no branches, and invading roots present in sapwood; those of decay class 4 included logs fully settled on ground, extensive decay (crumbly-mushy), bark and branches absent, and invading roots present in heartwood; and those in decay class 5 included small pieces and soft portions, bark and branches absent, and invading roots present in heartwood. Morphological characteristics as defined by Brassard and Chen (2008) were used to identify CWD to species (as detailed in (Kumar et al. 2017)).

Vegetation surveys were conducted in July and August 2014. We visually estimated the percent cover of each species following the method of Mueller-Dombois and Ellenberg (1974) within a 0.10 x 0.50 m (0.05 m²) quadrat, randomly laid lengthwise on top of the each sampled

CWD log. We also sampled forest floor vegetation by establishing an adjacent plot of the same size at a distance of 1.0 m in a random direction from the CWD vegetation sample. With a few exceptions, all plants were identified to species; we omitted minute liverwort species; *Cladonia coniocraea* (Flörke) and *Cladonia ochrochlora* (Flörke) were recorded as *Cladonia* agg.; and the moss genera *Brachythecium* and *Mnium* were not separated to species. The omission of some minor species could lead to potential bias in our results. However, pooled species constituted only 11.8 % of the total understory vegetation sampled by cover.

Data analyses

Species abundance was evaluated as the sum of individual species percent cover in each quadrat, species richness was treated as the total number of species recorded in each quadrat, and species evenness was expressed as how evenly the species in the community were distributed. Species evenness was calculated following Pielou (1969) as $Evenness = \frac{-\sum p_i \log p_i}{\ln(Richness)}$, where p_i is the proportion of species i percent cover to total vegetation cover. Total vegetation cover was treated as the sum of species-specific cover values on an individual CWD piece. In addition to total understory cover, richness and evenness, we separately analyzed species cover, richness and evenness for non-vascular and vascular groups. The non-vascular species included lichens and bryophytes, whereas vascular plants included herbs, shrubs, trees, ferns, and clubmosses. To test for substrate species and CWD decay class effects on understory cover, species richness and evenness, we used the following general linear mixed effect model:

$$Y_{ijkl} = \mu + D_i + S_j + D \times S_{ij} + \pi_k + \varepsilon_{l(ijk)} \quad (1)$$

205 where Y_{ijkl} is understory plant species cover, richness or evenness (separately analyzed by total,
 206 non-vascular and vascular groups), μ is the overall mean, D_i ($i = 1, 2 \dots 5$) is decay class, S_j ($j = 1,$
 207 $2 \dots 5$) is substrate species, π_k is plot random effect that accounts for spatial autocorrelation
 208 among logs within each sample plot as well as the variation in stand age and overstorey type
 209 related to plot, and $\varepsilon_{l(ijk)}$ ($l = 1, 2 \dots n$) is random sampling error within decay class, substrate
 210 species and plot. We conducted the mixed effect analysis using restricted maximum likelihood
 211 estimation in R with the *lme4* package (Bates et al. 2016; R Development Core Team 2017).
 212 However, vascular plant data did not conform to the assumption of normality based on Shapiro–
 213 Wilk’s test and were skewed to the left. To mitigate the violation to the normality assumption
 214 and to improve coefficient estimates, we bootstrapped the fitted coefficients of linear models by
 215 using "ggplot2" (Wickham 2009). We bootstrapped the 95% confidence intervals and considered
 216 estimates to be significantly different if their confidence intervals did not overlap other’s mean.
 217 For species richness, we specified the residual distribution as Poisson. The significance of the
 218 predictors was tested using F-tests by means of analysis of variance or deviance, and the variance
 219 or deviance explained by each variable in the model was calculated as a percentage of variance
 220 or deviance explained by the variable to that of null model. To explicitly test the effect of stand
 221 age and overstorey composition on understory cover, species richness or evenness, we added
 222 these variables and their two-way interactions (removing non-significant higher order
 223 interactions) in a revised general linear mixed effect model. The results of the revised model are
 224 presented in supplementary information (Table S1).

225 We used permutation multivariate analysis of variance (perMANOVA) to examine the effect
 226 of stand age, overstorey composition, decay class, substrate species, and their interactions on
 227 understory species composition. PerMANOVA is a nonparametric, multivariate analysis that

uses permutation techniques to test for compositional differences between more than one factor (Anderson 2005). We used perMANOVA with Bray-Curtis dissimilarity and 1000 permutations for the composition data. To examine trends in the composition data, we used nonmetric multidimensional scaling (NMDS) (Kruskal 1964), a robust ordination technique for community data that are non-normal or evaluated on discontinuous or ordinal scales (McCune and Grace 2002). The analysis was performed: (a) to examine differences in the species composition on CWD between stand ages and overstorey compositional types, and (b) to examine the differences in species composition between CWD decay classes, CWD substrate species, and forest floor. All statistical analyses were conducted in R3.4.2 (R Development Core Team 2017).

Results

We recorded a total of 68 understory species on CWD and forest floor, including 33 non-vascular species and 35 vascular species. Total epixylic cover differed with decay class ($P < 0.001$; Table 1), and the effect of substrate species was dependent on decay class, indicated by a significant interaction of decay class and substrate species (Table 1). Decay class was the main contributing factor, explaining 47.2% of the variance, while the interaction explained 4.2% of variance. Within decay classes 1 and 2, epixylic vegetation cover did not differ among the five substrate species, while at decay class 3, *Pinus banksiana* and *Populus* substrate species had a higher percent cover than other species (Fig. 1). At decay classes 4 and 5, percent cover was higher on *Populus* spp., *Picea* spp. and *Pinus banksiana* than on *Betula papyrifera* and *Abies balsamea*. Compared with forest floor, *Populus* spp., *Picea* spp. and *Pinus banksiana* at decay classes 4 and 5 had higher percent cover, while all substrate species had lower percent cover on decay classes 1 and 2.

Across all sampling units, percent cover for non-vascular species was on average 33.2% and 4.6% for vascular species. The effects of decay class and substrate species on non-vascular percent cover were similar to those for total percent cover (Table 1, Fig. 1). The percent cover of non-vascular species increased with decay classes, peaked on decay class 4, and decreased thereafter on *Populus* spp., *Pinus banksiana* and *Abies balsamea* substrates, whereas the percent cover on *Betula papyrifera* and *Picea* spp. increased throughout the decay classes. On average, the percent cover was highest on *Populus* spp. The percent cover of vascular plant species varied significantly with decay class but not with substrate species (Table 1). The percent cover of non-vascular species on the forest floor was similar to substrates of decay class 2. Vascular plant species cover was much higher on the forest floor than that on CWD of all decay classes. No vascular plant species were found on decay classes 1 and 2, with the percent cover of vascular plant species increasing from decay class 3 to decay class 5 on all substrate species.

The linear mixed effect model indicated that total species richness differed strongly with decay class and substrate species without a significant interaction (Table 1), but the model violated the normality assumption ($P = 0.005$). Bootstrap analysis showed that total species richness increased continuously with decay class on broadleaved substrates, but peaked at decay class 4 on coniferous substrates (Fig. 2). Non-vascular species richness peaked on decay class 3 or 4 for all substrate species. Vascular plant species richness varied significantly only with decay class ($P < 0.001$; Table 1), and increased from decay class 3 to decay class 5 (Fig. 2). Compared with the forest floor, total species richness on decay classes 1 and 2 was lower, and species richness of non-vascular species was higher in all decay classes except class 1, while species richness of vascular plants was lower on all decay classes. Total species richness on coniferous substrates was higher than that on broadleaved substrates at decay classes 3 and 4, but there was

little difference between two substrate groups in other decay classes (Fig. 2). This pattern was similar for non-vascular species richness (Fig. 2).

Total species evenness differed significantly with decay class and substrate species with a significant interaction between the two factors (Table 1). Decay class was the main contributing factor, explaining 10.2% of the variance, while the interaction explained 13.6% of the variance in species evenness. Due to sparseness of species occurrence, species evenness could not be evaluated on decay class 1. At decay classes 2 and 4, *Pinus banksiana* CWD substrate species, at decay class 3, *Picea* spp., and at decay class 5, *Abies balsamea* CWD substrate species had higher total species evenness than that on other CWD substrate species (Fig. 3). The effect of decay class and substrate species on non-vascular species evenness was similar to that for total species evenness (Table 1, Fig. 3). Vascular plant species evenness increased significantly from decay class 4 to 5. Compared with forest floor, decay classes 2 and 3 had on average similar total species evenness, but decay classes 4 and 5 had lower total species evenness; CWD at decay class 4 had lower, and at class 5 had similar vascular species evenness.

The species composition of epixylic plant communities differed significantly among stand ages, overstorey composition, decay classes and substrate species, with significant interactions among these predictors (Table 2). While main effects of these predictors accounted for majority of the variations in the species composition of epixylic plant communities (as indicated by partial R^2 values), significant interaction terms showed that the compositional responses to one predictor were significantly dependent on the levels of other predictor(s). When patterns of epixylic species composition were visualized using nonmetric multidimensional scaling ordination (Fig. 4a), epixylic communities on CWD in stands of different ages separated well in ordination space, with young stand (34 years old) showing a fair separation from older

stands (210 years old) while intermediate aged stands (98 and 146 years old) were positioned in between. Epixylic species composition on CWD differed between broadleaf and conifer stands, but there was overlap between conifer and mixedwood stands (Fig. 4a). The NMDS ordination also showed clear differentiation of the species composition among CWD decay classes, substrate species and the forest floor (Fig. 4b). Most notably, there is a distinction in species composition according to decay classes: decay class 1 and 2 are grouped apart from later decay classes and there are two distinct groupings of substrates: Conifer species (*Pinus banksiana* and *Picea* spp.) and broadleaf species (*Betula papyrifera* and *Populus* spp.), but with *Abies balsamea* showing species composition common to conifers and broadleaf species. On the other hand, species composition on the adjacent forest floor substrates differed strongly from all CWD substrates, particularly those not well decayed (Fig. 4b).

Discussion

We found that abundance, species richness, and species evenness of epixylic vegetation differed with both decay class and CWD substrate species. Epixylic vegetation abundance, measured as percent cover, increased with decay class from 1 to 5. This finding is consistent with previous studies (Andersson and Hytteborn 1991; Mills and Macdonald 2004; Botting and DeLong 2009; Checko et al. 2015). Likewise, species richness generally increased through the decay process, though a decrease in richness of non-vascular plant species was seen in the later stages of decay. In addition, we found that substrate species strongly influenced understory vegetation patterns, in terms of abundance, species richness and species evenness of total, non-vascular, and vascular species. Moreover, there were significant decay class and substrate species interactions in the analyses, consistent with the conclusion that successional dynamics of epixylic plant communities varies with substrate species. Finally, patterns of epixylic species

composition were also influenced by stand age and overstorey composition as well as their interaction, highlighting the importance of colonization and understorey environments associated with stand age and overstorey composition, respectively.

Non-vascular and vascular plants responded differently to decay class and substrate species. In general, all CWD substrate species show a trend of increased vegetation abundance as CWD decay advances; in particular, feathermosses and vascular plants increase in abundance with the process of CWD decay. The time available for colonization increases (Bartels and Chen 2015), along with changing structure, chemistry and moisture content of the CWD substrate along the decay continuum (Alban and Pastor 1993; Laiho and Prescott 2004; Butler et al. 2007; Petrillo et al. 2015). Thus, the combination of substrate receptivity and an increasing probability of recruitment contribute to increasing abundance of bryophytes, particularly feathermosses and vascular plants in later stages of decay. Although data do not permit an evaluation of the relative importance of these factors, the importance of increasing CWD moisture content and pH is also suggested by the high abundance of understory vegetation found on later decay classes of *Populus* spp., which tends to have higher wood moisture content and pH than other taxa (Culbertson 1955; Alban and Pastor 1993; Putna and Mežaka 2014).

Our findings highlight the importance of both decay class and substrate species as determinants of epixylic plant community richness and evenness. The observed increase in species richness of understory vegetation in higher decay classes is in agreement with the results from previous studies, which have also noted higher species richness in advanced stages of decay (Crites and Dale 1998; Rambo and Muir 1998; Laiho and Prescott 2004; Mills and Macdonald 2004; Bunnell et al. 2008; Botting and DeLong 2009; Caruso and Rudolphi 2009; Dittrich et al. 2014; Checko et al. 2015). However, most of these studies analyzed species richness of

individual groups (either lichens, bryophytes or vascular plants), whereas our study includes overall species diversity for all groups (non-vascular and vascular plants). The increase in species richness with decay reflects continuous colonisation of different species; in addition, heterogeneity in the decay process may also contribute to accumulation of species, as some “holdover” species from prior decay classes persist later in the decay process. High abundance of a few species early in the decay process was associated with low species richness. Early epixylic communities start to dominate with bark sloughing and further decomposition, and finally they are replaced by late epixylic species with humus development in the later stages of decay (McCullough 1948; Barkman 1958; Söderström 1988; Laaka 1995; Rambo and Muir 1998; Rambo 2001; Jansová and Soldán 2006; Botting and DeLong 2009; Kumar et al. 2017). The final stage of succession was characterized by epigeic species, mostly feathermosses and vascular plants that characteristically grow on the forest floor (Söderström 1988; Andersson and Hytteborn 1991; Kumar et al. 2017). The observed decrease in the species evenness at late CWD decay stages is attributable to increasing dominance of specific non-vascular species that varied among substrate species. For example, in a companion study that utilized indicator species analysis on the same data set, we found that decay class 5 logs of *Betula papyrifera* were dominated by Brachytheciaceae and Mniaceae mosses and *Mitella nuda*, logs of *Pinus banksiana* were characterised by *Pleurozium schreberi* and *Cornus canadensis*, logs of *Picea* spp. were characterised by *Dicranum polysetum*, *Ptilium crista-castrensis* and *Gaultheria hispidula*, and logs of *Abies balsamea* were dominated by *Hylocomium splendens* (Kumar et al. 2017).

In addition to effects of decay class, CWD substrate species also affected understory species richness and evenness. Previous studies have noted higher species diversity on broadleaved substrate species than on conifers (McAlister 1997; Rambo 2001; Mills and

Macdonald 2004; Nowinska et al. 2009; Putna and Mežaka 2014; Checko et al. 2015). In contrast, we found on average higher epixylic species richness and evenness on coniferous substrates than broadleaved substrates. More importantly, we found that the effects of substrate species on epixylic species diversity are dependent on decay class and evaluated understory species groups. Species-specific changes in CWD physical and chemical properties may contribute to these differences (Jüriado et al. 2009; Fritz and Heilmann-Clausen 2010; Pereira et al. 2014; Putna and Mežaka 2014; Shorohova and Kapitsa 2014). The coniferous log generally decays slowly and remains stable for many years (Harmon et al. 1986; Harmon 1989; Makinen et al. 2006; Shorohova and Kapitsa 2014), which may provide better opportunities and time for colonisation of lichens and bryophytes, thereby increasing their species diversity. In addition, coniferous bark is generally more acidic (Hauck and Javkhlan 2009; Hauck 2011; Putna and Mežaka 2014) as compared to broadleaved species (Culberson 1955; Kuusinen 1996; McAlister 1997; Mežaka et al. 2008). Among substrate species in the present study, the highest species diversity of epixylic plants was found on *Pinus banksiana*; this may be attributable to its low bark pH and thicker bark (Hauck and Javkhlan 2009). Differences in trends of species richness and evenness between conifers and broadleaf substrates also include a decline in species richness of non-vascular plants from decay class 4 to 5 that is associated with a large increase in the cover of vascular plants (correlation coefficient = -0.55, $P < 0.001$) and a decrease in evenness (correlation coefficient = 0.23, $P = 0.002$), particularly of non-vascular plants. We suggest that this pattern is attributable to the growth of feathermosses and competitive effects of vascular plants at later stages of decay (Kumar et al. 2017).

Sampling in the present study utilized a replicated chronosequence that allowed for the representation of multiple canopy successional pathways in boreal forest (Chen and Popadiouk

2002; Taylor and Chen 2011), allowing analyses that demonstrate distinct epixylic plant communities on CWD decay class and substrate species that depend on stand age and overstorey composition type. Variation in epixylic plant communities with stand age and overstorey composition suggest different successional trajectories for different stands (Fig. 4a). For instance, many lichen species such as *Xanthoria fallax*, *Evernia mesomorpha*, *Cladonia* spp. and mosses such as *Dicranum* spp., *Pleurozium schreberi* were predominant in young stands, whereas the lichen *Usnea subfloridana*, and the moss species *Hylocomium splendens* and *Rhytidiadelphus triquetrus* were found exclusively in older stands. Furthermore, the lichen species *Xanthoria fallax*, *Peltigera canina*, and the mosses *Brachythecium* spp., *Mnium* spp., *Callicladium haldanianum* were found exclusively in broadleaf stands, while *Hypogymnia physodes*, *Cladonia* lichens and *Dicranum* spp., *Pleurozium schreberi* mosses were found predominantly in conifer stands. Moreover, epixylic species composition differed with CWD decay class and substrate species as well as between CWD and forest floor substrates, as found in a companion study (Kumar et al. 2017). Previous studies have also revealed the differences in lichens and bryophytes species composition along the CWD decomposition gradient (Muhle and LeBlanc 1975; Mills and Macdonald 2005; Nascimbene et al. 2008; Botting and DeLong 2009). Differences in understorey plant species composition between conifer and broadleaf substrates have likewise been documented (Barkman 1958; Palmer 1986; McAlister 1997). Differences in moisture, texture and pH levels of the bark of substrate species have been suggested as likely determinants (Culbertson 1955; Hale 1955; McAlister 1997; Mills and Macdonald 2005; Mežaka et al. 2012; Pereira et al. 2014). The beneficial effect of CWD substrates on lichens and bryophytes is in part attributable to reduced competition on deadwood surface relative to the forest floor (Humphrey et al. 2002; Dittrich et al. 2014).

Our results indicate that CWD decay class and substrate species have strong influences on epixylic vegetation abundance, diversity and composition. Furthermore, stands of different ages and overstorey composition types support different epixylic species composition, indicating that shifts in forest age structure and composition can strongly influence the successional dynamics of epixylic plant communities. Management activities strongly affect both forest age structure and composition (Chen et al. 2017), CWD decay class and substrate species (Brassard and Chen 2008), and in turn epixylic vegetation abundance, diversity and composition. For example, short rotation harvesting regimes could result in the loss of epixylic species with affinity for suitable habitat conditions in older stands. On the other hand, epixylic species associated with specific CWD substrate species would go extinct without sufficient presence of the tree species in the overstorey to generate species-specific CWD. Therefore, to minimize impacts to sensitive lichens and bryophytes associated with CWD, it is important to maintain a diverse range of CWD decay classes and substrate species by a diverse range of forest age structure and overstorey composition. These results concur with the previous suggestions that managed boreal landscapes should consist of a mosaic of different successional stages and a broad suite of dominant overstorey species (Boudreault et al. 2002; Brassard and Chen 2008; Bartels and Chen 2015), thereby supplying appropriate amounts of CWD across the full range of decay classes and substrate species, to maintain bryophyte and lichen species habitat in forests.

Conclusion

Our results show that abundance and species richness and evenness of understory vegetation differed with both CWD decay classes and substrate species, and between CWD and the forest floor. The trends in abundance, richness and evenness also differed for non-vascular and vascular plant groups. Abundance of understory vegetation on CWD increased along the decompositional

gradient in all CWD substrate species. These findings indicate that understory species require suitable substrates and an extended period of time to colonize CWD. Epixylic species composition also differed with stand age, overstorey composition, decay class and substrate species, as well as with their interactions. These results highlight that conservation of epixylic diversity and restoration of their ecological functions would require forest managers to maintain a diverse range of CWD decay classes and substrate species in boreal forests. Moreover, distinct epixylic plant communities found in young and older stands and among overstorey composition types further suggest that managed boreal landscapes should consist of a mosaic of different stand ages and a broad suite of dominant overstorey species to support diverse understory plant communities. Future research in this area should focus on further elucidation of species-specific relations between CWD substrate and understory vegetation communities, and on better understanding the underlying mechanisms that determine community patterns.

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References

- Alban, D.H., and Pastor, J. 1993. Decomposition of Aspen, Spruce, and Pine Boles on 2 Sites in Minnesota. *Canadian Journal of Forest Research* **23**(9): 1744-1749. doi: 10.1139/x93-220.
- Anderson, M.J. 2005. *Permutational multivariate analysis of variance*. Department of Statistics, University of Auckland, Auckland, New Zealand.

- 457 Andersson, L.I., and Hytteborn, H. 1991. Bryophytes and decaying wood - a comparison
458 between managed and natural forest. *Holarctic Ecology* **14**(2): 121-130.
- 459 Arseneault, D. 2001. Impact of fire behavior on postfire forest development in a homogeneous
460 boreal landscape. *Canadian Journal of Forest Research* **31**(8): 1367-1374. doi:
461 10.1139/cjfr-31-8-1367.
- 462 Barbier, S., Gosselin, F., and Balandier, P. 2008. Influence of tree species on understory
463 vegetation diversity and mechanisms involved - a critical review for temperate and boreal
464 forests. *Forest Ecology and Management* **254**(1): 1-15. doi:10.1016/j.foreco.2007.09.038.
- 465 Barkman, J.J. 1958. Phytosociology and ecology of cryptogamic epiphytes, including a
466 taxonomic survey and description of their vegetation units in Europe. Van Gorcum &
467 Comp. N.V., Assen, The Netherlands.
- 468 Bartels, S.F., and Chen, H.Y.H. 2013. Interactions between overstorey and understorey
469 vegetation along an overstorey compositional gradient. *Journal of Vegetation Science*
470 **24**(3): 543-552. doi: 10.1111/j.1654-1103.2012.01479.x.
- 471 Bartels, S.F., and Chen, H.Y.H. 2015. Dynamics of epiphytic macrolichen abundance, diversity
472 and composition in boreal forest. *Journal of Applied Ecology* **52**(1): 181-189. doi:
473 10.1111/1365-2664.12360.
- 474 Bartemucci, P., Messier, C., and Canham, C.D. 2006. Overstory influences on light attenuation
475 patterns and understory plant community diversity and composition in southern boreal
476 forests of Quebec. *Canadian Journal of Forest Research* **36**(9): 2065-2079. doi:
477 10.1139/X06-088.

- 478 Bates, D., Bolker, B., Walker, S., Christensen, R.H.B., Singmann, H., Dai, B., and Grothendieck,
479 G. 2016. lme4: Linear mixed-effects models using Eigen and S4. R package version 1.1-
480 10.
- 481 BC Ministry of Forests and Range and BC Ministry of Environment. 2010. Field Manual for
482 Describing Terrestrial Ecosystems. 2nd ed, Research Branch, B.C. Ministry of Forests
483 and Range, Victoria, British Columbia.
- 484 Bergeron, Y., Chen, H.Y.H., Kenkel, N.C., Leduc, A.L., and Macdonald, S.E. 2014. Boreal
485 mixedwood stand dynamics: Ecological processes underlying multiple pathways.
486 Forestry Chronicle **90**(2): 202-213. doi: 10.5558/tfc2014-039.
- 487 Botting, R.S., and DeLong, C. 2009. Macrolichen and bryophyte responses to coarse woody
488 debris characteristics in sub-boreal spruce forest. Forest Ecology and Management **258**:
489 S85-S94. doi: 10.1016/j.foreco.2009.08.036.
- 490 Boudreault, C., Bergeron, Y., Gauthier, S., and Drapeau, P. 2002. Bryophyte and lichen
491 communities in mature to old-growth stands in eastern boreal forests of Canada.
492 Canadian Journal of Forest Research **32**(6): 1080-1093. doi: 10.1139/X02-027.
- 493 Brassard, B.W., and Chen, H.Y.H. 2006. Stand structural dynamics of North American boreal
494 forests. Critical Reviews in Plant Sciences **25**(2): 115-137. doi:
495 10.1080/07352680500348857.
- 496 Brassard, B.W., and Chen, H.Y.H. 2008. Effects of forest type and disturbance on diversity of
497 coarse woody debris in boreal forest. Ecosystems **11**(7): 1078-1090. doi:
498 10.1007/s10021-008-9180-x.
- 499 Bunnell, F.L., and Houde, I. 2010. Down wood and biodiversity - implications to forest
500 practices. Environmental Reviews **18**: 397-421. doi: 10.1139/A10-019.

- 501 Bunnell, F.L., Spribille, T., Houde, I., Goward, T., and Bjork, C. 2008. Lichens on down wood in
502 logged and unlogged forest stands. *Canadian Journal of Forest Research* **38**(5): 1033-
503 1041. doi: 10.1139/X07-206.
- 504 Butler, R., Patty, L., Le Bayon, R.C., Guenat, C., and Schlaepfer, R. 2007. Log decay of *Picea*
505 *abies* in the Swiss Jura Mountains of central Europe. *Forest Ecology and Management*
506 **242**(2-3): 791-799. doi: 10.1016/j.foreco.2007.02.017.
- 507 Caruso, A., and Rudolphi, J. 2009. Influence of substrate age and quality on species diversity of
508 lichens and bryophytes on stumps. *Bryologist* **112**(3): 520-531. doi: 10.1639/0007-2745-
509 112.3.520.
- 510 Chávez, V., and Macdonald, S.E. 2010. The influence of canopy patch mosaics on understory
511 plant community composition in boreal mixedwood forest. *Forest Ecology and*
512 *Management* **259**(6): 1067-1075. doi: 10.1016/j.foreco.2009.12.013.
- 513 Chávez, V., and Macdonald, S.E. 2012. Partitioning vascular understory diversity in mixedwood
514 boreal forests: The importance of mixed canopies for diversity conservation. *Forest*
515 *Ecology and Management* **271**(0): 19-26. doi:
516 <http://dx.doi.org/10.1016/j.foreco.2011.12.038>.
- 517 Checko, E., Jaroszewicz, B., Olejniczak, K., and Kwiatkowska-Falinska, A.J. 2015. The
518 importance of coarse woody debris for vascular plants in temperate mixed deciduous
519 forests. *Canadian Journal of Forest Research* **45**(9): 1154-1163. doi: 10.1139/cjfr-2014-
520 0473.
- 521 Chen, H.Y.H., and Luo, Y. 2015. Net aboveground biomass declines of four major forest types
522 with forest ageing and climate change in western Canada's boreal forests. *Global Change*
523 *Biology*. **21**(10): 3675-3684. doi: 10.1111/gcb.12994.

- 524 Chen, H.Y.H., and Popadiouk, R.V. 2002. Dynamics of North American boreal mixedwoods.
525 Environmental. Reviews **10**(3): 137-166.
- 526 Chen, S., Shahi, C., Chen, H.Y.H., and McLaren, B. 2017. Economic analysis of forest
527 management alternatives: Compositional objectives, rotation ages, and harvest methods
528 in boreal forests. Forest Policy and Economics 85(Part 1): 124-134. doi:
529 <https://doi.org/10.1016/j.forpol.2017.09.006>.
- 530 Crites, S., and Dale, M.R.T. 1998. Diversity and abundance of bryophytes, lichens, and fungi in
531 relation to woody substrate and successional stage in aspen mixedwood boreal forests.
532 Canadian Journal of Botany **76**(4): 641-651.
- 533 Culberson, W.L. 1955. The corticolous communities of lichens and bryophytes in the upland
534 forests of northern Wisconsin. Ecological Monographs: 215-231.
- 535 Dittrich, S., Jacob, M., Bade, C., Leuschner, C., and Hauck, M. 2014. The significance of
536 deadwood for total bryophyte, lichen, and vascular plant diversity in an old-growth
537 spruce forest. Plant Ecology **215**(10): 1123-1137.
- 538 Environment Canada. 2015. Canadian Climate Normals 1981-2010. Available from
539 http://climate.weather.gc.ca/climate_normals/index_e.html [accessed 25.08.15].
- 540 Fritz, O., and Heilmann-Clausen, J. 2010. Rot holes create key microhabitats for epiphytic
541 lichens and bryophytes on beech (*Fagus sylvatica*). Biological Conservation **143**(4):
542 1008-1016. doi: 10.1016/j.biocon.2010.01.016.
- 543 Ganjegunte, G.K., Condron, L.M., Clinton, P.W., Davis, M.R., and Mahieu, N. 2004.
544 Decomposition and nutrient release from radiata pine (*Pinus radiata*) coarse woody
545 debris. Forest Ecology and Management **187**(2-3): 197-211. doi: 10.1016/S0378-
546 1127(03)00332-3.

- 547 Hale, M.E. 1955. Phytosociology of corticolous cryptogams in the upland forests of Southern
548 Wisconsin. *Ecology*: 45-63.
- 549 Harmon, M.E. 1989. Effects of bark fragmentation on plant succession on conifer logs in the
550 *Picea-Tsuga* forests of Olympic-National-Park, Washington. *American Midland*
551 *Naturalist* **121**(1): 112-124. doi: 10.2307/2425662.
- 552 Harmon, M.E., Franklin, J.F., Swanson, F.J., Sollins, P., Gregory, S.V., Lattin, J.D., Anderson,
553 N.H., Cline, S.P., Aumen, N.G., Sedell, J.R., Lienkaemper, G.W., Cromack, K., and
554 Cummins, K.W. 1986. Ecology of coarse woody debris in temperate ecosystems.
555 *Advances in Ecological Research* **15**: 133-302. doi: 10.1016/S0065-2504(08)60121-X.
- 556 Hart, S.A., and Chen, H.Y.H. 2006. Understory vegetation dynamics of North American boreal
557 forests. *Critical Reviews in Plant Sciences* **25**(4): 381-397. doi:
558 10.1080/007352600819286.
- 559 Hauck, M. 2011. Site factors controlling epiphytic lichen abundance in northern coniferous
560 forests. *Flora* **206**(2): 81-90. doi: 10.1016/j.flora.2010.02.001.
- 561 Hauck, M., and Javkhlan, S. 2009. Epiphytic lichen diversity and its dependence on bark
562 chemistry in the northern Mongolian dark taiga. *Flora* **204**(4): 278-288. doi:
563 10.1016/j.flora.2008.03.001.
- 564 Hauck, M., and Jurgens, S.R. 2008. Usnic acid controls the acidity tolerance of lichens.
565 *Environmental Pollution* **156**(1): 115-122. doi: 10.1016/j.envpol.2007.12.033.
- 566 Hill, S.B., Mallik, A.U., and Chen, H.Y.H. 2005. Canopy gap disturbance and succession in
567 trembling aspen dominated boreal forests in northeastern Ontario. *Canadian Journal of*
568 *Forest Research-Revue Canadienne De Recherche Forestiere* **35**(8): 1942-1951. doi:
569 10.1139/X05-126.

- 570 Humphrey, J.W., Davey, S., Peace, A.J., Ferris, R., and Harding, K. 2002. Lichens and
571 bryophyte communities of planted and semi-natural forests in Britain: the influence of
572 site type, stand structure and deadwood. *Biological Conservation* **107**(2): 165-180. doi:
573 10.1016/S0006-3207(02)00057-5.
- 574 Huo, H., Feng, Q., and Su, Y.H. 2014. The influences of canopy species and topographic
575 variables on understory species diversity and composition in coniferous forests. *The*
576 *ScientificWorld Journal* 2014: 252489. doi: 10.1155/2014/252489.
- 577 Jansová, I., and Soldán, Z. 2006. The habitat factors that affect the composition of bryophyte and
578 lichen communities on fallen logs. *Preslia* **78**(1): 67-86.
- 579 Jüriado, I., Liira, J., Paal, J., and Suija, A. 2009. Tree and stand level variables influencing
580 diversity of lichens on temperate broad-leaved trees in boreo-nemoral floodplain forests.
581 *Biodiversity and Conservation* **18**(1): 105-125. doi: 10.1007/s10531-008-9460-y.
- 582 Karjalainen, L., and Kuuluvainen, T. 2002. Amount and diversity of coarse woody debris within
583 a boreal forest landscape dominated by *Pinus sylvestris* in Vienansalo wilderness, eastern
584 Fennoscandia. *Silva Fennica* **36**(1): 147-167. doi: 10.14214/sf.555.
- 585 Kruskal, J.B. 1964. Multidimensional scaling by optimizing goodness of fit to a nonmetric
586 hypothesis. *Psychometrika* **29**(1): 1-27.
- 587 Kruys, N., and Jonsson, B.G. 1999. Fine woody debris is important for species richness on logs
588 in managed boreal spruce forests of northern Sweden. *Canadian Journal of Forest*
589 *Research-Revue Canadienne De Recherche Forestiere* **29**(8): 1295-1299. doi:
590 10.1139/cjfr-29-8-1295.

- 591 Kumar, P., Chen, H.Y.H., Thomas, S.C., and Shahi, C. 2017. Effects of coarse woody debris on
592 plant and lichen species composition in boreal forests. *Journal of Vegetation Science*
593 **28**(2): 389-400. doi: 10.1111/jvs.12485.
- 594 Kuusinen, M. 1996. Epiphyte flora and diversity on basal trunks of six old-growth forest tree
595 species in southern and middle boreal Finland. *Lichenologist* **28**(5): 443-463. doi:
596 10.1006/lich.1996.0043.
- 597 Laaka, S. 1995. Epixylic lichens on conifer logs in four natural forests in Finland. *Graphis*
598 *scripta* **7**(1): 25-31.
- 599 Laiho, R., and Prescott, C.E. 1999. The contribution of coarse woody debris to carbon, nitrogen,
600 and phosphorus cycles in three Rocky Mountain coniferous forests. *Canadian Journal of*
601 *Forest Research-Revue Canadienne De Recherche Forestiere* **29**(10): 1592-1603. doi:
602 10.1139/cjfr-29-10-1592.
- 603 Laiho, R., and Prescott, C.E. 2004. Decay and nutrient dynamics of coarse woody debris in
604 northern coniferous forests: a synthesis. *Canadian Journal of Forest Research-Revue*
605 *Canadienne De Recherche Forestiere* **34**(4): 763-777. doi: 10.1139/X03-241.
- 606 Lee, P., and Sturges, K. 2001. The effects of logs, stumps, and root throws on understory
607 communities within 28-year-old aspen-dominated boreal forests. *Canadian Journal of*
608 *Botany* **79**(8): 905-916.
- 609 Lee, P., and Sturges, K. 2002. Assemblages of vascular plants on logs and stumps within 28-
610 year-old aspen dominated boreal forests. In *Proceedings of the Symposium on the*
611 *Ecology and Management of Dead Wood in Western Forests*. Edited by WF
612 Laudenslayer, Jr., PJ Shea, BE Valentine, CP Weatherspoon, and TE Lisle.(Tech. cords.)
613 USDA For. Serv. Gen. Tech. Rep. PSW-GTR-**181**. pp. 369-380.

- 614 Luo, Y., and Chen, H.Y.H. 2011. Competition, species interaction and ageing control tree
615 mortality in boreal forests. *Journal of Ecology* 99(6): 1470-1480. doi: DOI
616 10.1111/j.1365-2745.2011.01882.x.
- 617 Macdonald, S.E., and Fenniak, T.E. 2007. Understory plant communities of boreal mixedwood
618 forests in western Canada: Natural patterns and response to variable-retention harvesting.
619 *Forest Ecology and Management* **242**(1): 34-48. doi:
620 <http://dx.doi.org/10.1016/j.foreco.2007.01.029>.
- 621 Makinen, H., Hynynen, J., Siitonen, J., and Sievanen, R. 2006. Predicting the decomposition of
622 Scots pine, Norway spruce, and birch stems in Finland. *Ecological applications* : a
623 publication of the Ecological Society of America **16**(5): 1865-1879. doi: 10.1890/1051-
624 0761(2006)016[1865:ptdosp]2.0.co;2.
- 625 McAlister, S. 1997. Cryptogam communities on fallen logs in the Duke forest, North Carolina.
626 *Journal of Vegetation Science* **8**(1): 115-124. doi: Doi 10.2307/3237249.
- 627 McCullough, H.A. 1948. Plant succession on fallen logs in a Virgin Spruce-Fir Forest. *Ecology*
628 **29**(4): 508. doi: 10.2307/1932645.
- 629 McCune, B., and Grace, J.B. 2002. Analysis of ecological communities. MjM Software Design,
630 Gleneden Beach, Oregon.
- 631 Messier, C., Parent, S., and Bergeron, Y. 1998. Effects of overstory and understory vegetation on
632 the understory light environment in mixed boreal forests. *Journal of Vegetation Science*
633 **9**(4): 511-520. doi: 10.2307/3237266.
- 634 Mežaka, A., Brūmelis, G., and Piterāns, A. 2008. The distribution of epiphytic bryophyte and
635 lichen species in relation to phorophyte characters in Latvian natural old-growth broad
636 leaved forests. *Folia Cryptogamica Estonica* **44**: 89-99.

- 637 Mežaka, A., Brūmelis, G., and Piterāns, A. 2012. Tree and stand-scale factors affecting richness
638 and composition of epiphytic bryophytes and lichens in deciduous woodland key habitats.
639 Biodiversity and Conservation **21**(12): 3221-3241.
- 640 Mills, S.E., and Macdonald, S.E. 2004. Predictors of moss and liverwort species diversity of
641 microsites in conifer-dominated boreal forest. Journal of Vegetation Science **15**(2): 189-
642 198. doi: 10.1111/j.1654-1103.2004.tb02254.x.
- 643 Mills, S.E., and Macdonald, S.E. 2005. Factors influencing bryophyte assemblage at different
644 scales in the western Canadian boreal forest. Bryologist **108**(1): 86-100. doi:
645 10.1639/0007-2745(2005)108[86:fibaad]2.0.co;2.
- 646 Mueller-Dombois, D., and Ellenberg, H. 1974. Aims and Methods of Vegetation Ecology. The
647 Blackburn Press, Caldwell, New Jersey.
- 648 Muhle, H., and LeBlanc, F. 1975. Bryophyte and lichen succession on decaying logs-1-analysis
649 along an evaporational gradient in Eastern Canada. Journal of the Hattori Botanical
650 Laboratory(39): p1-33.
- 651 Nascimbene, J., Marini, L., Motta, R., and Nimis, P.L. 2008. Lichen diversity of coarse woody
652 habitats in a *Pinus-Larix* stand in the Italian Alps. The Lichenologist **40**(02): 153-163.
- 653 Nowinska, R., Urbanski, P., and Szewczyk, W. 2009. Species diversity of plants and fungi on
654 logs of fallen trees of different species in oak-hornbeam forests. Roczniki Akademii
655 Rolniczej w Poznaniu. Botanika-Steciana **13**: 109–124.
- 656 Ohtsuka, T., Shizu, Y., Hirota, M., Yashiro, Y., Jia, S.G., Iimura, Y., and Koizumi, H. 2014.
657 Role of coarse woody debris in the carbon cycle of Takayama forest, central Japan.
658 Ecological Research **29**(1): 91-101. doi: 10.1007/s11284-013-1102-5.

- 659 Palmer, M.W. 1986. Pattern in corticolous bryophyte communities of the North-Carolina
660 Piedmont - do mosses see the forest or the trees. *Bryologist* **89**(1): 59-65. doi:
661 10.2307/3243078.
- 662 Pereira, I., Mueller, F., and Moya, M. 2014. Influence of *Nothofagus* bark pH on the lichen and
663 bryophytes richness, Central Chile. *Gayana Botanica* **71**(1): 120-130.
- 664 Petrillo, M., Cherubini, P., Sartori, G., Abiven, S., Ascher, J., Bertoldi, D., Camin, F., Barbero,
665 A., Larcher, R., and Egli, M. 2015. Decomposition of Norway spruce and European larch
666 coarse woody debris (CWD) in relation to different elevation and exposure in an Alpine
667 setting. *Iforest* **9**: 154-164. doi: 10.3832/ifor1591-008.
- 668 Pielou, E.C. 1969. An introduction to mathematical ecology. Wiley Interscience, New York. 286
669 p.
- 670 Putna, S., and Mežaka, A. 2014. Preferences of epiphytic bryophytes for forest stand and
671 substrate in North-East Latvia. *Folia Cryptogamica Estonica* **51**: 75-83.
- 672 R Development Core Team. 2017. R: A language and environment for statistical computing.
673 Version 3.4.0. R Foundation for Statistical Computing, Vienna, Austria.
- 674 Rambo, T.R. 2001. Decaying logs and habitat heterogeneity: Implications for bryophyte
675 diversity in western Oregon forests. *Northwest Science* **75**(3): 270-279.
- 676 Rambo, T.R., and Muir, P.S. 1998. Bryophyte species associations with coarse woody debris and
677 stand ages in Oregon. *Bryologist* **101**(3): 366-376.
- 678 Russell, M.B., Woodall, C.W., Fraver, S., D'Amato, A.W., Domke, G.M., and Skog, K.E. 2014.
679 Residence times and decay rates of downed woody debris biomass/carbon in Eastern US
680 forests. *Ecosystems* **17**(5): 765-777. doi: 10.1007/s10021-014-9757-5.

- 681 Senici, D., Chen, H.Y.H., Bergeron, Y., and Cyr, D. 2010. Spatiotemporal variations of fire
682 frequency in central boreal forest. *Ecosystems* **13**(8): 1227-1238. doi: 10.1007/s10021-
683 010-9383-9.
- 684 Shorohova, E., and Kapitsa, E. 2014. Influence of the substrate and ecosystem attributes on the
685 decomposition rates of coarse woody debris in European boreal forests. *Forest Ecology*
686 *and Management* **315**: 173-184. doi: 10.1016/j.foreco.2013.12.025.
- 687 Shorohova, E., Kapitsa, E., Kazartsev, I., Romashkin, I., Polevoi, A., and Kushnevskaya, H.
688 2016. Tree species traits are the predominant control on the decomposition rate of tree
689 log bark in a mesic old-growth boreal forest. *Forest Ecology and Management* **377**: 36-
690 45. doi: 10.1016/j.foreco.2016.06.036.
- 691 Söderström, L. 1988. Sequence of bryophytes and lichens in relation to substrate variables of
692 decaying coniferous wood in Northern Sweden. *Nordic Journal of Botany* **8**(1): 89-97.
693 doi: DOI 10.1111/j.1756-1051.1988.tb01709.x.
- 694 Spribille, T., Thor, G., Bunnell, F.L., Goward, T., and Björk, C.R. 2008. Lichens on dead wood:
695 species - substrate relationships in the epiphytic lichen floras of the Pacific Northwest
696 and Fennoscandia. *Ecography* **31**(6): 741-750.
- 697 Stirling, G., and Wilsey, B. 2001. Empirical Relationships between Species Richness, Evenness,
698 and Proportional Diversity. *American Naturalist*. **158**(3): 286-299. doi: 10.1086/321317.
- 699 Stokland, J.N., Siitonen, J., and Jonsson, B.G. 2012. Biodiversity in dead wood. Cambridge
700 University Press.
- 701 Sturtevant, B.R., Bissonette, J.A., Long, J.N., and Roberts, D.W. 1997. Coarse woody debris as a
702 function of age, stand structure, and disturbance in boreal Newfoundland. *Ecological*
703 *Applications* **7**(2): 702-712.

- 704 Taylor, A.R., and Chen, H.Y.H. 2011. Multiple successional pathways of boreal forest stands in
705 central Canada. *Ecography* **34**(2): 208-219. doi: 10.1111/j.1600-0587.2010.06455.x.
- 706 Weedon, J.T., Cornwell, W.K., Cornelissen, J.H., Zanne, A.E., Wirth, C., and Coomes, D.A.
707 2009. Global meta - analysis of wood decomposition rates: a role for trait variation
708 among tree species? *Ecology Letters* **12**(1): 45-56.
- 709 Wickham, H. 2009. *ggplot2: Elegant Graphics for Data Analysis*. Springer-Verlag New York.
710 available from <http://ggplot2.org>.
- 711 Wilsey, B., and Stirling, G. 2007. Species richness and evenness respond in a different manner to
712 propagule density in developing prairie microcosm communities. *Plant Ecology* **190**(2):
713 259-273. doi: 10.1007/s11258-006-9206-4.
- 714 Zhang, Y., Chen, H.Y.H., and Reich, P.B. 2012. Forest productivity increases with evenness,
715 species richness and trait variation: a global meta-analysis. *Journal of Ecology* **100**(3):
716 742-749. doi: 10.1111/j.1365-2745.2011.01944.x.
- 717

Table 1. Results of general or generalized linear mixed effects model showing the effects of decay class (*D*) and substrate species (*S*) on understory cover, species richness and species evenness, separately analysed by total, non-vascular and vascular vegetation. Bold fonts indicates statistical significance ($\alpha = 0.05$).

Attribute	Source	df	Total		Non-vascular		Vascular	
			Deviance or variance explained (%)	<i>P</i>	Deviance or variance explained (%)	<i>P</i>	Deviance or variance explained (%)	<i>P</i>
Cover	<i>D</i>	4	47.2	<0.001	34.6	<0.001	48.2	<0.001
	<i>S</i>	4	0.5	0.339	0.5	0.524	0.3	0.918
	<i>D</i> × <i>S</i>	16	4.2	0.003	4.3	0.031	4.5	0.654
Richness	<i>D</i>	4	42.8	<0.001	29.0	<0.001	68.2	<0.001
	<i>S</i>	4	12.6	<0.001	13.0	<0.001	0.5	0.577
	<i>D</i> × <i>S</i>	16	7.1	0.21	7.5	0.137	0.9	0.995
Evenness	<i>D</i>	4	10.2	<0.001	11.4	<0.001	65.3	<0.001
	<i>S</i>	4	3.9	0.009	4.1	0.011	1.0	0.447
	<i>D</i> × <i>S</i>	16	13.6	<0.001	15.8	<0.001	5.1	0.274

Notes: the columns give the degrees of freedom (df), variance or deviance explained and *P* values.

Table 2. Results of permutation multivariate analysis of variance (perMANOVA) testing the effects of stand ages (A), overstorey compositions (C), decay classes (D), substrate species (S) and their interactions on epixylic species composition. Bold fonts indicates statistical significance ($\alpha = 0.05$).

Source	df	SS	F	P	Partial R ²
A	3	8.4	22.4	0.001	0.08
C	2	11.8	47.6	0.001	0.11
D	4	25.4	51.1	0.001	0.23
S	4	5.5	10.9	0.001	0.05
A × D	12	5.8	3.9	0.001	0.05
C × D	8	5.2	5.3	0.001	0.05
A × S	9	2.1	1.9	0.001	0.02
C × S	7	1.3	1.5	0.013	0.01
D × S	14	4.9	2.8	0.001	0.04
A × C × D	18	3.4	1.5	0.002	0.03
A × D × S	11	2.6	1.9	0.001	0.02
C × D × S	6	0.6	0.8	0.855	0.01
Plot	29	10.1	2.8	0.001	0.09
Residual	186	23.1			

Notes: the columns give the degrees of freedom (df), sums of squares (SS), Partial R², F and P values.

Figure captions

Fig. 1. Total, non-vascular and vascular understory vegetation cover (means and bootstrapped 95% confident intervals) in relation to decay class and substrate species. Substrate species are Po- *Populus* spp., Bw- *Betula papyrifera*, Pj- *Pinus banksiana*, Sx- *Picea* spp., Bf- *Abies balsamea* and FF- forest floor.

Fig. 2. Total, non-vascular and vascular understory species richness (means and bootstrapped 95% confident intervals) per 0.05m² quadrat in relation to decay class and substrate species. Substrate species are Po- *Populus* spp., Bw- *Betula papyrifera*, Pj- *Pinus banksiana*, Sx- *Picea* spp., Bf- *Abies balsamea* and FF- forest floor.

Fig. 3. Total, non-vascular and vascular understory species evenness (means and bootstrapped 95% confident intervals) per 0.05m² quadrat in relation to decay class and substrate species. Substrate species are Po- *Populus* spp., Bw- *Betula papyrifera*, Pj- *Pinus banksiana*, Sx- *Picea* spp., Bf- *Abies balsamea* and FF- forest floor.

Fig. 4. Two-dimensional nonmetric multidimensional scaling ordination showing: (a) The differences in the epixylic species composition on CWD between stand ages and overstorey compositional types. Overstorey types are broadleaf (green), conifer (blue) and mixedwood (black) and symbol shapes on legends differentiate stand ages. (b) The differences in epixylic species composition between CWD decay classes, CWD substrate species, and adjacent forest-floor substrates. Substrate species are Po- *Populus* spp. (purple), Bw- *Betula papyrifera* (blue), Pj- *Pinus banksiana* (green), Sx- *Picea* spp. (yellow), Bf- *Abies balsamea* (red) and FF- forest floor (black) and symbol shapes on legends differentiate decay classes. Points nearest each other in ordination space have similar floristic assemblages, whereas those located farther apart are

754 less similar. Vectors (arrows) indicate the significant ($P < 0.05$) joint axis correlation with decay
755 class and substrate species, and length of the vector represents the strength of the correlation.

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757 **FIG. 1**

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759 **FIG. 2**

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761 **FIG. 3**

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763 **FIG. 4**

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766 **Appendix A.** Average percent cover values of nonvascular and vascular understorey vegetation found on each stand age, overstorey
 767 composition, CWD substrate species and decay class in the central boreal forest of Canada. Overstorey compositions are Bro. -
 768 broadleaf, Mix. - Mixedwood, Con. – Conifer, and substrate species are Po- *Populus* spp., Bw- *Betula papyrifera*, Pj- *Pinus*
 769 *banksiana*, Sx- *Picea* spp., Bf- *Abies balsamea* and FF – forest floor.

	Stand ages				Overstorey			Substrate species					Decay classes						
	34	98	146	210	Bro	mix	Con	Po	Bw	Pj	Sx	Bf	1	2	3	4	5	FF	tot. abun
Number of logs	74	89	73	78	92	109	113	97	21	73	32	91	9	50	78	82	95		
Nonvascular species																			
<i>Hypogymnia physodes</i>	0.80	1.20	1.21	1.82	0.90	1.30	1.52	0.57	2.98	1.18	1.75	1.48	1.06	5.36	1.19	0.23	0.05		395
<i>Usnea subfloridana</i>	0.20	0.34	0.45	0.86	0.27	0.56	0.62	0.10	1.21	0.47	0.38	0.81	0.83	2.62	0.22				156
<i>Xanthoria fallax</i>	0.32	0.09	0.05	0.03	0.27	0.05	0.04	0.31		0.11			0.22	0.14	0.13	0.11	0.11		38
<i>Parmelia sulcata</i>	0.14	0.35	0.21		0.15	0.11	0.16	0.22		0.26	0.06	0.02		0.3	0.37				44
<i>Peltigera canina</i>	0.07	0.27	0.19	0.10	0.28	0.04	0.12	0.32		0.07		0.08		0.14	0.22	0.21	0.02		43
<i>Phaeophyscia pusilloides</i>	0.19	0.82	0.48		0.14	0.60	0.12	0.70		0.12		0.15		0.36	0.78	0.12	0.02		91
<i>Evernia mesomorpha</i>	0.43	0.03	0.02		0.11	0.09	0.13	0.10	0.14	0.30			0.33	0.16	0.19	0.11			35
<i>Vulpicida pinastris</i>	0.15	0.11	0.06			0.11	0.08	0.10		0.15				0.34	0.05				21
<i>Leptogium milligranum</i>	0.11	0.06	0.03		0.05	0.03	0.04	0.08		0.07					0.06	0.06	0.03		13
<i>Cladonia coniocraea</i>	1.09	0.55	0.46	0.08	0.33	0.46	0.73	0.31		0.96	0.81	0.42		0.04	1.13	0.74	0.14		164
<i>Cladonia cenotea</i>	0.03	0.06	0.03			0.04	0.03			0.10	0.06				0.04	0.06	0.01		10
<i>Cladonia ochrochlora</i>	0.09					0.06				0.10					0.03	0.06			7
<i>Cladonia agg.</i>	2.62	1.33	1.62	1.06	1.07	1.67	2.30	0.91	0.10	2.86	1.06	2.27		0.62	3.71	2.26	0.37		540
<i>Cladonia chlorophaea</i>	0.07	0.10	0.10		0.04	0.05	0.11	0.04		0.03	0.19	0.10			0.13	0.13			21
<i>Cladonia cervicornis</i>	0.95	0.04	0.03	0.04	0.18	0.19	0.35	0.13		0.81	0.09	0.03			0.50	0.43	0.04	0.01	80
<i>Cladonia rangiferina</i>	0.70	0.09	0.05		0.13	0.11	0.32	0.13		0.55	0.16	0.03			0.22	0.23	0.26	0.04	74
<i>Brachythecium</i> spp.	5.16	9.21	8.02	8.88	18.8	3.94	1.88	17.9	12.2	0.41	0.78	3.40	0.22	2.98	9.82	9.39	7.06	0.02	2365
<i>Mnium</i> spp.	0.12	4.62	3.84	2.49	6.14	1.17	1.18	6.19	1.95	0.07	0.88	1.63		0.10	1.54	4.21	3.71	0.01	825
<i>Dicranum ontariense</i>	4.03	1.02	1.47	0.49	0.60	1.25	3.4	0.10		5.64	1.00	1.33			2.54	4.2	0.35		587
<i>Dicranum fuscescens</i>	0.73	0.07	0.04		0.59		0.05	0.49		0.08		0.07			0.10	0.54	0.08	0.04	60
<i>Dicranum polysetum</i>	2.69	1.88	1.70	0.96	0.89	1.42	2.77	0.65	0.10	2.34	4.03	2.00		0.02	0.31	2.60	3.25	0.38	666
<i>Dicranum flagellare</i>	0.11	0.02	0.01			0.07	0.02	0.08		0.03						0.12			10
<i>Polytrichum commune</i>	0.20	0.07	0.04			0.19				0.21		0.07			0.08		0.16	0.11	54

<i>Polytrichum juniperinum</i>				0.02		0.01			0.05			0.02				0.02	0.05		7
<i>Callicladium haldanianum</i>				0.17		0.29			0.28					0.19	0.09	0.05			27
<i>Orthotrichum speciosum</i>		0.06	0.06			0.11			0.10				0.20						10
<i>Hylocomium splendens</i>		0.26	0.38	1.74	0.45	0.81	0.61	0.19		0.03		1.96				0.54	1.62	0.48	350
<i>Ptilium crista-castrensis</i>	3.15	3.08	2.86	1.27	1.35	1.83	4.17	1.76	0.86	2.78	6.44	1.97			1.06	2.65	5.02	3.31	1815
<i>Pleurozium schreberi</i>	14.0	9.15	8.26	2.62	3.51	7.83	12.4	4.57	0.43	13.5	17.0	6.27		0.06	2.08	9.99	16.5	2.43	3317
<i>Rhytidiadelphus triquetrus</i>		0.17	0.20	1.06	0.22	0.59	0.27	0.18	0.19			1.01		0.08	0.50	0.20	0.57	1.32	526
<i>Sphagnum wulfianum</i>	0.05	0.03	0.02				0.06			0.05		0.03					0.07	0.05	22
<i>Ptilidium pulcherrimum</i>	4.26	1.73	1.53	0.19	1.79	1.91	1.81	1.79	0.62	3.15	0.94	1.42		0.6	3.10	3.22	0.42	0.01	579
<i>Jamesoniella autumnalis</i>	0.07	0.19	0.25	0.05		0.10	0.35			0.16	0.38	0.29		0.14	0.22	0.27	0.04		50
Vascular species																			
<i>Maianthemum canadense</i>	1.07	0.48	0.59	0.63	1.01	0.34	0.82	0.80	0.14	0.81	0.66	0.64				0.3	2.04	3.00	1162
<i>Coptis trifolia</i>		0.08	0.14	0.04	0.01	0.09	0.13	0.02		0.16	0.03	0.12				0.02	0.25	0.31	123
<i>Cornus canadensis</i>	1.88	0.34	0.72	0.76	0.96	0.97	1.07	1.06	0.24	1.45	0.75	0.78				0.56	2.77	5.05	1894
<i>Clintonia borealis</i>		0.20	0.22		0.28		0.08	0.26		0.14						0.10	0.28	4.00	1291
<i>Aralia nudicaulis</i>				0.06			0.05					0.05				0.06		2.72	859
<i>Chamerion angustifolium</i>																		0.08	26
<i>Viola renifolia</i>	0.04					0.03		0.03								0.04		0.32	103
<i>Streptopus roseus</i>			0.07	0.05	0.16			0.11				0.04					0.16	1.41	458
<i>Trientalis borealis</i>	0.26	0.55	0.39	0.59	0.87	0.30	0.13	0.66	0.52	0.14	0.16	0.37				0.51	0.86	0.61	316
<i>Mitella nuda</i>		0.35	0.27	0.72	0.55	0.18	0.26	0.43	0.33			0.56				0.37	0.74	0.94	395
<i>Viola blanda</i>	0.05	0.07	0.07		0.12	0.04		0.11		0.05							0.16	0.68	227
<i>Galium triflorum</i>																		0.07	21
<i>Aster macrophyllus</i>																		1.15	360
<i>Equisetum sylvaticum</i>																		0.18	57
<i>Lycopodium annotinum</i>	0.04	0.10	0.14	0.26		0.13	0.27	0.09		0.10	0.13	0.27				0.05	0.43	0.75	282
<i>Lycopodium obscurum</i>	0.07			0.14	0.17			0.05				0.12					0.17	0.89	295
<i>Lycopodium lucidulum</i>		0.06	0.12		0.15		0.04	0.14			0.16					0.07	0.14	0.22	89
<i>Lycopodium complanatum</i>																		0.07	22
<i>Linnea borealis</i>	1.18	0.40	0.38	0.21	0.13	0.48	0.89	0.26	0.19	1.14	0.47	0.46			0.01	0.73	1.14	0.57	348
<i>Gaultheria hispidula</i>	0.51	1.62	1.23		0.37	0.18	1.62	0.32		1.07	3.69	0.14			0.08	0.57	1.97	0.26	323
<i>Acer spicatum</i>			0.05		0.09			0.08									0.08	1.32	422
<i>Calamagrostis canadensis</i>																		0.04	12
<i>Diervilla lonicera</i>																		1.03	324
<i>Lonicera canadensis</i>																		1.40	441
<i>Vaccinium angustifolium</i>																		0.94	295
<i>Ledum groenlandicum</i>																		0.58	182
<i>Rosa acicularis</i>																		0.48	150

<i>Vaccinium myrtilloides</i>					0.05		0.05			0.05	0.62	199
<i>Rubus pubescens</i>	0.07	0.38	0.21	0.14	0.29	0.21	0.29	0.20		0.48	2.12	712
<i>Ribes triste</i>	0.24				0.20		0.19		0.22		0.06	36
<i>Petasites palmatus</i>											0.07	21
<i>Salix</i> spp.											0.11	36
<i>Picea</i> spp.											0.08	26
<i>Abies balsamea</i>				0.15		0.02	0.09	0.13	0.07	0.06	0.19	72
<i>Danthonia spicata</i>		0.03	0.02				0.03		0.04		0.08	29

770 Notes: tot. abund.: total percent cover values of each species on the present sites

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