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Value of old forest attributes related to cryptogam species richness in temperate forests: A quantitative assessment

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ABSTRACT

Changes in temperate forest ecosystems resulting from a long history of forest exploitation may severely impact current cryptogam diversity. We documented the distribution of cryptogams in representative forest types between 200 and 1000 m a.s.l. in central Europe, in managed and unmanaged stands. This survey included one-time inventories of lichens and bryophytes, 2 years of regular monitoring of macrofungi, and a detailed description of forest structure (live trees and dead woody debris) in 96 sampling plots (2500 m^2 each) in six study areas in the Czech Republic. On this basis, we attempted to identify the quantitative limits of forest structural attributes that affect cryptogam diversity along a gradient of forest management practices in central Europe. In total, we recorded 1387, 173 and 103 species of macrofungi, lichens and bryophytes, respectively, of which 149, 99 and 4 were red-listed species. Species richness was correlated among observed taxa at the plot scale, and rare and red-listed species made higher contributions in species-rich communities. Cryptogam species richness showed both common and taxa-specific patterns in relation to forest structure, tree species composition, age of the oldest tree strata and elevation. We found a positive influence of the largest-diameter tree classes (stem diameter >80 cm) on the species richness of all cryptogam taxa, whereas the contribution of dead wood to the fit of a linear mixed effect model was minimal. Nevertheless, the magnitude of total and red-listed species richness was remarkably high in plots in which at least one large tree or woody object occurred compared to plots lacking these attributes. The effect of large dead wood debris (diameter >80 cm and unit volume >1 m^3) was not replaced by total dead wood volume, even though it was relatively high (>40 m^3 ha^{-1}). Hence, both large live trees and woody debris compartments are probably important for the species

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richness of cryptogam communities. However, the spatial pattern of cryptogam communities at a given time point (i.e., the time of our survey) was associated with the spatial and temporal heterogeneity of live tree structures, but less with that of dead wood substrates. Large tree and woody debris characterize forests that have been unmanaged for at least several decades and occasionally occur in the oldest of moderately managed forests. The importance of these cryptogam refuges in managed forests should not be underestimated because their continuing disappearance will probably result in the impoverishment of cryptogam richness at regional scales.

1. Introduction

The on-going debate concerning the loss of cryptogam diversity resulting from exploitation of temperate forests has produced a few conclusions that can provide a basis for effective changes in forest management practices (Brockerhoff et al., 2008; Brunet and Fritz, 2010). Although clear negative effects of some management practices (e.g., clear-cutting) on cryptogam diversity have been demonstrated (e.g., Rosenvald and Lõhmus, 2008; Rudolphi et al., 2014), many foresters still ignore this evidence, arguing that large areas of temporarily unaffected, managed forests remain that provide a stable habitat for cryptogams. In central Europe, which has a long history of forest management, the discussion is further complicated by past modifications of forest ecosystems and biodiversity (Grove, 2002; Vrška et al., 2009). Thus, there is often poor evidence for, and differences in perception regarding, what is or what could be "natural" in this region (Lindenmayer and Laurance, 2012).

Despite such uncertainty, heterogeneity of forest structure in terms of tree species composition, age structure, and size distribution of live trees and dead wood has been identified as the most important stand-level factor affecting cryptogam diversity (Ódor et al., 2006; Ellis, 2012; Halme et al., 2013; Sverdrup-Thygeson et al., 2014). In particular, the effects of forest age, large old trees, and dead wood on cryptogam diversity have been repeatedly emphasized (e.g., Fritz et al., 2008; Ranius et al., 2008; Lindenmayer et al., 2012b). However, little evidence is available as to which old forests are sufficiently old, what quantitative attributes make trees sufficiently large and old, and what size of dead wood objects is the most suitable for cryptogams.

In this study, we attempted to identify the distribution of cryptogam diversity (macrofungi, lichens, and bryophytes) and forest structural attributes that may be important for cryptogams in the most widespread forest types in the Czech Republic, in relation to environmental conditions and intensity of forest management. These forests represent prevailing conditions over a wide area of central Europe within altitudes from 200 to 1000 m a.s.l. Our main objective was to identify the quantitative limits of forest structural attributes that affect cryptogam diversity along a gradient of forest management practices in central Europe. We hypothesized that cryptogam diversity is related to forest structure at the stand scale and that suitable structures form the basis for the metapopulation structure of cryptogams in European forests (Löbel et al., 2006; Halme et al., 2013). Such studies are needed to develop recommendations for future forest management and for implementing these practices.

2. Materials and methods

2.1. Study areas

We selected six study areas (SA1–SA6) in the Czech Republic that included spatially important types of central European forest stands, with the exception of lowland floodplains and montane forests above 1000 m a.s.l. (Table 1 and Fig. 1). Each study area consisted of a continuous forest patch (1.4–10.0 km^2) that included stands representing spatiotemporal variability in tree species composition and forest management approach, i.e., nature reserves without regular forest management (referred to here as unmanaged forest); mature managed stands of deciduous, coniferous and eventually mixed tree species; immature managed forests aged 11–69 years; and heterogeneous unclassifiable managed stands (including internal ecotones).

Beech (*Fagus sylvatica*), spruce (*Picea abies*), and fir (*Abies alba*), the respective frequencies of which increase with elevation, were the dominant tree species in unmanaged forest stands, except for those at the lowest elevations, which were dominated by oak (*Quercus petraea*). Accordingly, beech and oak dominated the tree community in deciduous managed forest stands at higher and lower elevations, respectively. Coniferous stands generally consisted of monocultures of spruce or pine (*Pinus sylvestris*). The age of mature managed forests averaged approximately 100 years, but reached 160 years in deciduous stands. However, small remnants of old managed forest have survived for more than 200 years. Unmanaged forests were between 150 and 400 years old; most have been protected since the first half of the 20th century (the oldest since 1838 and the youngest since 1964).

2.2. Forest inventory

We established between one and four 2500-m^2 sampling plots in each forest management type within each study area. Eighteen plots were established in study area (SA)1 to SA4, and 11 and 13 plots were established in SA5 and SA6, respectively ($n = 96$ sampling plots) (Table 1; for details, see Table S1, Supporting information). A forest inventory was conducted in each plot between 2009 and 2011. We measured the stem diameter of each tree at 1.3 m above the ground, excluding those with diameter <5 cm. The diameter and length of each dead wood object (standing and lying stems, branches, stumps and other materials) with diameter >5 cm

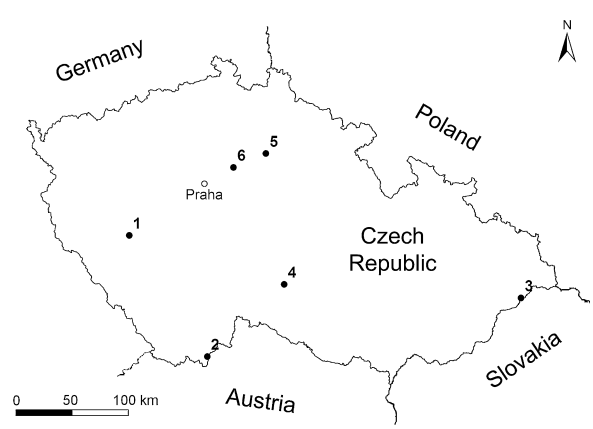

Fig. 1. Location of the six study areas.

Table 1
Description of study areas (SA) and distribution of sampling plots in unmanaged and managed forests. Data for mean temperature and precipitation (from 1961 to 2000) were taken from Tolasz (2007).

SA	Area (km^2)	Altitude (m a.s.l.)	Mean temperature (°C)	Mean precipitation (mm $year^{-1}$)	Number of sampling plots	
					Unmanaged forests	Managed forests
1	6.75	436–585	6–7	600–650	4	14
2	9.95	732–935	4–5	700–800	4	14
3	4.60	635–880	4–5	1000–1200	4	14
4	7.39	590–730	5–6	600–650	4	14
5	10.00	250–280	7–8	550–600	0	11
6	1.36	180–210	7–8	550–600	3	10

were recorded to calculate their respective volumes. The volume of individual pieces of dead wood was calculated using geometric approximations or values of wood volume tables (Lesprojekt, 1952). The volume of irregularly shaped objects was estimated using approximate measurements.

2.3. Sampling of macrofungi, lichens, and bryophytes

We surveyed the species composition of macrofungi, lichens, and bryophytes in the 96 sampling plots. Two-year inventories of macrofungal fruiting bodies (with a minimum of five visits each year) were conducted from early spring 2009 or 2010 to late autumn 2010 or 2011. A list of lichen and bryophyte species was compiled during a single visit in either 2009 or 2010.

All cryptogams were surveyed on all substrates (soil, stones, live trees, and dead wood objects) from the soil surface to 2 m above the ground throughout each plot. The only exception was the survey of lichens on live trees, which was limited to five selected trees representing the variability of tree species composition and stem diameter within each plot; other substrates (e.g., dead wood and stones) were examined exhaustively. Red-listed species were determined according to the current national red lists: Holec and Beran (2006) for macrofungi, Liška et al. (2008) for lichens and Kučera et al. (2012) for bryophytes. Fungi, lichens, and bryophytes that could not be readily identified in the field were sampled, dried, and identified by microscopy and/or chromatography, or by specialists in the respective genera.

2.4. Data analysis

The species richness of macrofungi, lichens, and bryophytes was analyzed separately using linear mixed effect models (LME) (Laird and Ware, 1982; Pinheiro and Bates, 2000). In these models, we sequentially increased the set of explanatory variables that were potentially important for cryptogam diversity and compared the model Akaike information criterion (AIC) values considering the principle of parsimony. The full set of explanatory variables obtained in the final model consisted of elevation, tree species composition, age of the oldest tree strata, sum of stem basal areas of all measured live trees, and volume of dead wood. Age effect was evaluated in the models as a parametric term having linear and quadratic term. Tree species composition was assigned to one of four classes according to the species that occupied >75% of the basal area in the plot: (i) beech-dominated forests, (ii) mixed deciduous species, (iii) mixture of deciduous and coniferous species, and (iv) monocultures or mixed coniferous species. The sums of the stem basal areas of living trees and volume of dead wood (excluding stumps) were divided into 18 categories according to the diameter of individual objects (details in Table S2 and S3, Supporting Information). The influence of the total stand basal area of live trees and total volume of dead wood on cryptogam species richness was size-dependent in the sense that the regression coefficient depended on the diameter of a particular tree or item of woody debris. Hence, the contribution of a given stand basal area or volume to species richness differed depending on the size of individual trees or pieces of dead wood. The functional form of the size dependence was not assumed a priori, but rather was inferred flexibly (non-parametrically) from the data. This enabled testing of the effect of size dependence. Size dependency (diameter of live stems and dead wood objects) was specified analogously to the parsimonious Almon parameterization (Almon, 1962; Johnston, 1984) to suppress collinearity. Therefore, the coefficients corresponding to the weights of individual stem diameter or dead wood diameter classes were forced to lie on a flexible B-spline curve (details in Appendix S1, Supporting Information). Two size-varying coefficients were used in all models: (a) a coefficient for the total stem basal area of live trees in 18 stem diameter classes, and (b) a coefficient for total dead wood volume in 18 object diameter classes. The parameters of each of the spline-basis functions were estimated from the data, together with other parameters of the LME. To address the spatial correlation among adjacent sampling plots, we allowed for spatial correlation in the residuals by using an exponential covariogram, the parameters of which were estimated via restricted maximum likelihood (REML) as part of the model identification.

The type of forest stand was not used as an explanatory variable in our models because our goal was to generate statistical models using data from first principles; we used data on the availability of growth substrates (live and dead wood) rather than prior classification of forest stands, which indirectly influences the substrate quantity. In addition to investigating direct influences, this approach is valuable in circumventing the effect of spatial and temporal variation in forest practices.

We first tested the total species richness of macrofungi, lichens, and bryophytes as response variables. Weighted species-richness models were also created, in which the presence of red-listed species in plots was weighted by a factor of 10 for extinct, critically endangered, and endangered macrofungi and lichens, and by 5 for the remaining red-list categories. For bryophytes, the group of red-listed species was extended by species included in the associated Attention List (Kučera et al., 2012). When we tested the numbers of red-listed species alone, the models failed because the response variables had zero or close to zero values in a large proportion of the sampling plots. Finally, we examined the species richness of lignicolous macrofungi only. All model analyses were based on data from 96 plots ranging in age from 14 to 315 years. Differences in the species richness of macrofungi, lichens, and bryophytes between plots with and without large diameter trees and dead wood, respectively, were assessed using non-parametric Kruskal–Wallis tests at the $P < 0.05$ significance level, adjusted according to Hochberg (1988). Additional simple correlations were performed using the Pearson correlation coefficient (R) at $P < 0.05$. All computations were performed in R (R Development Core Team, 2013), using the 'nlme' (Pinheiro et al., 2013) and 'agricolae' (de Mendiburu, 2014) packages.

3. Results

3.1. Live trees and dead wood

The 96 surveyed sampling plots contained 15,599 living trees and shrubs (24 species), 292 standing dead stems, 9882 lying dead stems and branches, 8195 stumps, and 3926 pieces of dead wood left by logging operations. The total volume of dead woody debris ranged from 1.6 to 352 m^3 ha^{-1}. Relatively fewer plots had live trees and dead woody objects in the large-diameter classes (Tables S2 and S3, Supporting Information). All plots with dead woody objects with diameter and unit volume higher than 80 cm and 1 m^3, respectively, also had live trees with a diameter larger than 80 cm (11 sampling plots). However, there were 15 plots with large live trees (diameter >80 cm) but without large dead woody objects. Most plots with large trees (diameter >80 cm) were located in unmanaged forest reservations (54%), and this relationship was even stronger for large dead wood objects (diameter >80 cm and unit volume >1 m^3; 91%).

3.2. Species richness of cryptogams

We recorded 1387, 173, and 103 species of macrofungi, lichens, and bryophytes, respectively, in the 96 plots, of which 149, 99, and 4 were red-listed species. We found an average of 140, 18, and 17 species of macrofungi, lichens, and bryophytes per plot, respectively. The minimum (and maximum) numbers of macrofungal, lichen, and bryophyte species observed in individual plots were 65 (284), 4 (72), and 7 (38), respectively. At the plot scale, cryptogam species richness was significantly correlated between taxa groups: macrofungi vs. lichens ($R = 0.519$; $P < 0.001$), macrofungi vs. bryophytes ($R = 0.523$; $P < 0.001$) and lichens vs. bryophytes ($R = 0.485$; $P < 0.001$).

Unmanaged plots generally had higher species richness of cryptogam communities than in managed plots, and the lowest was found in mature coniferous forests. Uncommon, rare, and red-listed species mostly occurred in species-rich communities, while the opposite was true for widespread generalist species. As a result, the ratio of rare to common species (occupying <10 and >30 sampling plots, respectively) increased with species richness of macrofungi ($R = 0.608$; $P < 0.001$), lichens ($R = 0.630$; $P < 0.001$) and bryophytes ($R = 0.926$; $P < 0.001$). The contribution of lignicolous macrofungal species to the total macrofungal species richness in the sampling plot ranged from 15 to 64%, with an average of 38%.

3.3. Species richness vs. live tree diameter and dead wood volume

The generated linear mixed effect models showed mostly universal, but some taxa group-specific, patterns of cryptogam species richness in relation to the explanatory variables (Table 2). Regarding forest structure, cryptogam species richness was affected by tree diameter classes (Table 2; Fig. 2). A strong positive effect of the largest- and smallest-diameter tree classes (>80 and <20 cm, respectively) for living trees was found for macrofungi, especially for lignicolous fungi, and a moderate but still positive effect of the largest-diameter classes was observed for bryophytes providing that the weight of red-listed species was increased. When the analysis was weighted by red-listed species, an effect of large trees with a diameter >110 cm on lichen species richness was observed (Fig. 2). If we neglect other significant explanation variables incorporated in the models, then the mean cryptogam and red-listed cryptogam species richness was significantly higher in sampling plots with large-diameter trees (>80 cm) than that in other plots (Table 3).

The AIC of the initially built model for macrofungal species richness did not decrease after addition of total dead wood volume or 18 diameter class parameters with class-varying coefficients.

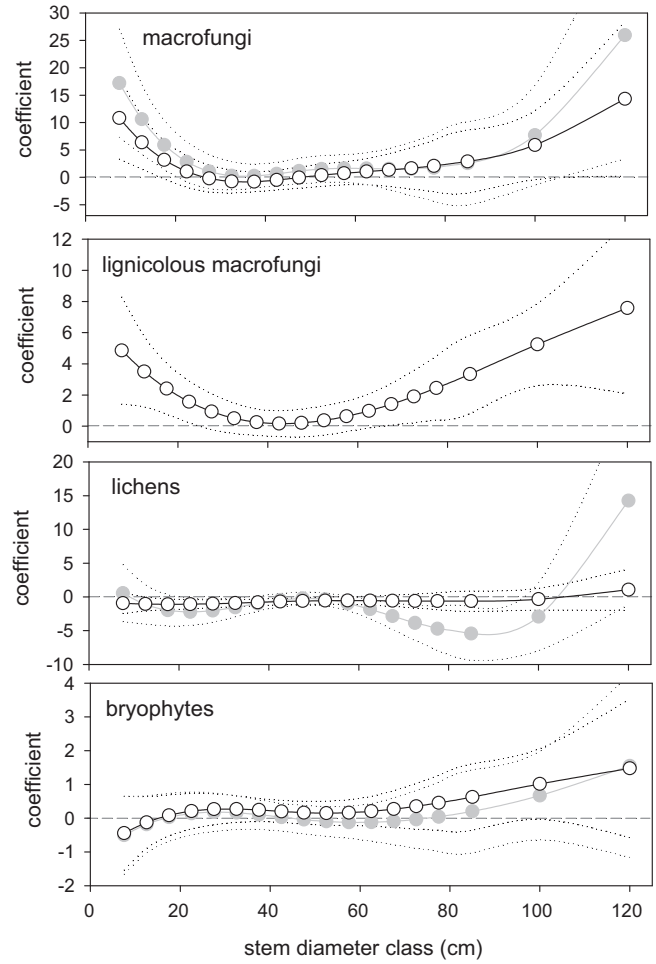

Fig. 2. Regression curves with 95% point-wise constructed confidence intervals for cryptogam species richness (black lines and open circles) and cryptogam species richness weighted by red-listed species (gray lines and gray circles) vs. the sum of the stem basal area for each stem diameter class of living trees. Circles indicate the median values of the class-varying coefficient for the total stem basal areas of living trees for each of 18 stem diameter classes. The estimated curves show how the contribution of total stem basal area to species richness changes with stem diameter.

Nearly half of the 15 sampling plots with very high macrofungal species richness (>200 species) also had the absolutely highest dead wood volumes, ranging from 47 to 82 m^3 (without stumps), whereas four of the other plots had a dead wood volume of less than 5 m^3 (without stumps). Nevertheless, the use of dead wood as an explanation variable clearly improved the model for species richness of lignicolous fungi (Table 2; Fig. 3). A positive effect on species richness of lignicolous fungi was observed for finer (diameter <20 cm) and intermediate (40–80 cm) woody debris, whereas the effect of large woody debris appeared to be insignificant (Fig. 3). Despite lack of a significant effect in the model, cryptogam species richness was higher in the sampling plots with large dead wood objects, as in plots with large-diameter living trees (Table 3). There was no evidence that the effect of large-diameter logs or snags on richness could be attributed to a large volume of dead wood, as only a mean level of species richness of lichens (19 ± 9) and bryophytes (18 ± 8) and slightly above-mean species richness of macrofungi (177 ± 43) occurred in plots with large volumes of dead wood (11–42 m^3 without stumps), but without large woody debris.

3.4. Other factors relevant to cryptogam species richness

As expected, cryptogam species richness was positively correlated with age of the forest overstory (Table 2). Cryptogam species

Table 2
Results of linear mixed effects models (LME) predicting species richness of cryptogams and species richness weighted by red-listed species. In the models, the set of explanatory variables potentially important for cryptogam diversity was sequentially increased, and the model Akaike information criterion (AIC) was thus evaluated. Differences in the AIC (ΔAIC) and significance level (*P*) of added terms are given; ΔAIC is the difference in the AIC of a particular model with an added term compared to the AIC of the initial model without the term.

Explanation variables	Step		Species richness			Modified species richness			Number of lignicolous macrofungi
			Macrofungi	Lichens	Bryophytes	Macrofungi	Lichens	Bryophytes	
None	1	AIC	986.45	700.87	582.90	1095.15	1015.50	619.51	900.32
Elevation + Tree species composition	2	ΔAIC	−40.68***	−32.74***	−11.77***	−69.87***	−70.53***	−9.29***	−74.17***
Age (linear + quadratic)	3	ΔAIC	−7.47**	−31.05***	−7.78**	−17.97***	−57.15***	−12.75***	−4.87*
Stand basal area in stem-diameter 18 classes	4	ΔAIC	−18.61***	−6.37**	1.45n.s.	−24.24***	−36.20***	−1.72*	−31.63***
Dead wood volume in 18 diameter classes	5	ΔAIC	3.49n.s.	−2.00*	−2.32*	4.16n.s.	17.82n.s.	6.56n.s.	−19.9***

n.s., not significant.
* Significant level at $P < 0.05$.
** Significant level at $P < 0.01$.
*** Significant level at $P < 0.001$.

richness clearly increased with elevation, and species richness of macrofungi and lichens was further influenced by tree species composition. Species-rich communities of macrofungi and lichens were generally associated with either beech or mixed stands, whereas species-poor communities were associated with pure coniferous stands.

4. Discussion

4.1. Live trees and cryptogam diversity

We obtained clear evidence that the species richness of cryptogam communities in central European forests was higher in stands with the presence of large old trees, ideally in combination with abundant tree rejuvenation, such as that occurring in natural forests after the downfall of old trees in the canopy layer (resulting from natural death or external disturbance) as described, e.g., by Peterken (1996). The vital role played by large, old, slowly dying trees in supporting biodiversity has been revealed recently (Ranius et al., 2008; Winter and Möller, 2008), even at the global scale (Lindenmayer et al., 2012b). In this study, cryptogam species richness was high in stands where stem diameter exceeded 80 cm, even when only one or a few large trees were present in a given forest habitat. Such trees are quite common in unmanaged forests (74% of plots in unmanaged forests in this study) and only occasionally present in moderately managed forests stands (18% of plots in managed forests in this study).

We confirmed the positive and negative effects of mixed deciduous tree species and spruce monocultures, respectively, on cryptogam species richness as previously reported (Vanderpoorten et al., 2004; Mežaka et al., 2012). Species-poor cryptogam communities were also found in oak-dominated forests at lower elevations, consistent with the observations by Heilmann-Clausen et al. (2005) for macrofungi, but contrasts with the report of Ódor et al. (2013) for lichens and bryophytes. Annual precipitation generally increases with elevation (Tolasz, 2007), which likely favors cryptogam communities at higher elevations, and some other environmental factors vary with elevation as well (e.g., geology). Moreover, the paucity of cryptogam species observed in oak-dominated lowland forests in our study may reflect the influence of several millennia of forest exploitation and fragmentation in the lowland region (Pokorný, 2005) more than an effect of the tree species currently present. Forests in the central European lowlands have been utilized and fragmented since the first half of the Holocene and extensively since the High Middle Ages. The historic duration and spatial extent of anthropogenic pressure decreases with elevation; permanently managed forests have dominated higher-elevation areas for a few centuries at most (Kaplan et al., 2009; Chytrý, 2012). Differences in the history of forest exploitation should be considered when searching for explanations for the generally low species richness of cryptogam communities in the present lowland forests.

4.2. Dead wood and cryptogam diversity

Similarly to live trees, but even more notably, there were relatively few plots with large-diameter dead wood objects (Table 3). The spatial pattern of large dead wood objects (logs and snags)

Table 3
Mean cryptogam species richness (±SD) in sampling plots that either included or did not include at least one live tree or dead woody object with a given stem diameter or object diameter and unit volume, respectively. The numbers of plots in each category are indicated in italics in parentheses. Significant differences between plots with and without trees with a stem diameter >80 cm and plots with or without dead woody objects with a diameter >80 cm and unit volume >1 m^3 are indicated by asterisks.

	Trees with diameter (cm)		Dead woody objects with diameter (cm) and unit volume (m^3)	
	<80 only (*70*)	>80 (*26*)	<80 only (*85*)	>80 (>1 m^3) (*11*)
Macrofungi				
Species richness	122 ± 35	188 ± 48***	130 ± 41	215 ± 35***
Number of red-listed species	4 ± 3	13 ± 9***	5 ± 4	19 ± 9***
Lichens				
Species richness	16 ± 7	26 ± 16***	16 ± 8	31 ± 20***
Number of red-listed species	2 ± 3	10 ± 12***	3 ± 4	13 ± 14***
Bryophytes				
Species richness	16 ± 4	20 ± 7**	17 ± 5	24 ± 3***
Number of red-listed species	0.0 ± 0.2	0.1 ± 0.3	0.0 ± 0.2	0.2 ± 0.4*

* $P < 0.05$
** $P < 0.01$
*** $P < 0.001$.

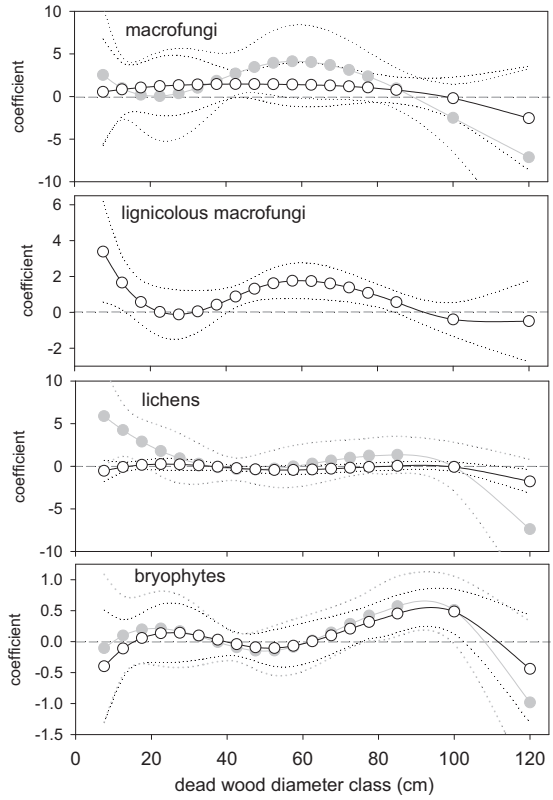

Fig. 3. Regression curves with 95% point-wise constructed confidence intervals for cryptogam species richness (black lines and open circles) and cryptogam species richness weighted by red-listed species (gray lines and gray circles) vs. dead wood volume in diameter classes. Circles indicate median values of the class-varying coefficient for total stem circumference of live trees in each stem-diameter class.

corresponded with that of large live trees; large woody debris occurred only in a subset of plots occupied by large trees. This finding may explain why dead wood as a variable was redundant in most models built to explain cryptogam species richness and particularly why there was a lack of positive effect of large-diameter dead wood in these models. Moreover, both the appearance and disappearance of large dead wood objects are more variable in time than those of large live trees, which may result in less equilibrium between the actual species richness of cryptogam communities and dead wood availability at the particular time of the survey (Christensen et al., 2004; Jönsson et al., 2008).

The comparison of cryptogam species richness in plots with and without large logs or snags suggested that they were essential structures with positive effects on cryptogam species richness (Table 3). This result is consistent with previous findings that emphasized the importance of both coarse and fine woody debris (Nordén et al., 2004; Küffer et al., 2008) because large woody debris is generally accompanied by finer material. However, we documented that even relatively high total volumes of dead wood cannot guarantee high cryptogam diversity unless there is sufficient size variability in the woody debris, including large objects in particular.

The suitability of dead wood as a substrate for particular cryptogam species changes with the degree of decomposition (Heilmann-Clausen and Christensen, 2003) and differs among tree species (Heilmann-Clausen et al., 2005); we did not evaluate these effects separately. However, the variability of decay generally increases with the quantity of dead wood and is likely to be less important to species richness than the size of the woody debris (Küffer et al., 2008; Nordén et al., 2013). In our study, major differences in the species composition of dead wood corresponded to differences in the composition of live trees.

4.3. Forest age and cryptogam diversity

The increased cryptogam species richness with increasing forest age provided further evidence for the vital importance of old forests to cryptogam diversity, in agreement with previous evidence (Fritz et al., 2008). Forest age is associated with the time available for colonization but also contributes to the formation of forest structure and dead wood heterogeneity. These three attributes have synchronous effects on cryptogam diversity and it can be difficult to separate their individual influences. The concept of forest continuity, referring to the continuous presence of forest, is also relevant (Nordén and Appleqvist, 2001), although different aspects of forest continuity may be important for different taxa. Continuity of forest land use (including clear-cut and intensive utilization) appears to be sufficient for the survival of several forest plant species (Graae and Sunde, 2000), whereas most cryptogams also require continuity of forest cover (clear-cutting in this case disrupts continuity) or even continuity of a dead wood supply (Westphal et al., 2004; but see Hofmeister et al., 2014).

4.4. Cryptogram diversity in the metapopulation context

As a result of previous management interventions conducted in limited areas of these presently unmanaged stands, suitable microhabitats may have disappeared along with their associated cryptogam species (Löbel et al., 2006; Halme et al., 2013). Species loss can continue long after the cessation of management operations as a result of extinction debt: the smaller the area of unmanaged stands and the longer the distance to the nearest refuge, the less likely species are to survive (Nordén et al., 2013). Regional metapopulation patterns also influence the probability of recolonization of cryptogam species that previously disappeared from the local species pool when the appropriate substrates are re-established (Ranius et al., 2008). Therefore, the low cryptogam species richness in some recently unmanaged and substrate-rich habitats in our study may reflect a delay in colonization from nearby refuges.

Alternatively, we questioned whether the presence of unmanaged forests closer to old and moderately managed forests could explain the remarkable diversity of red-listed macrofungi found in some of the latter habitats. One explanation is that unmanaged forests may provide a lasting source of cryptogam species for surrounding managed forests that allows only transient survival of these species (Malíček and Palice, 2013). A more likely explanation is based on the notion that neither small remnants of old managed forests nor limited areas of unmanaged forest can fulfill the habitat requirements of all potential cryptogam species (Lindenmayer and Laurance, 2012). This perspective is supported by our finding that cryptogam communities (particularly macrofungi) in the oldest managed forests did not consist of only a subset of the species observed in nearby unmanaged forests. We assume that the managed stands have the potential to expand the environmental conditions, microhabitats, and substrates covered by limited areas of unmanaged forests, which may help to maintain higher regional cryptogam diversity. Hence, the continuing disappearance of species-rich managed stands caused by logging will lead to impoverishment of cryptogam diversity not only at the local scale but also at the regional scale. Even maintenance of existing remnants of both unmanaged and managed old forests cannot prevent future reductions in species diversity as a result of extinction debt (Ranius et al., 2008).

4.5. Implications for conservation

We consider that heterogeneity of forest structure and dead woody substrates, such as that observed in unmanaged forests, is a necessary condition for the maintenance of cryptogam diversity. However, this habitat heterogeneity would probably encompass a larger area than is presently occupied by unmanaged forests in central Europe. Therefore, remnants of old forests adjacent to unmanaged forest areas should be protected (not logged) and expanded, and attributes of old-growth forests should be encouraged. Regeneration of cryptogam diversity will be less effective in large areas of managed forests that do not include remnants of old forests because of the long distances to the nearest cryptogam refuges (Nordén et al., 2013). Regardless, the characteristics of old growth (e.g., old trees with diameter >80 cm and large woody debris with diameter >80 cm and volume >1 m^3) should be encouraged or provided in managed forests in an effort to reduce the spatial isolation between refuges of rare cryptogams. Retention forestry is an appropriate approach for achieving inclusion of old growth attributes in managed forests in which significant forest structures are retained during logging operations (Lindenmayer et al., 2012a). Adoption of this approach as a regular management practice is desirable as an alternative to traditional management practices based on clear cutting or recurrent selection harvesting, which systematically remove all large old trees and dead trees from forest stands. We caution against complacency, even if the principles of retention forestry are broadly implemented, because the requirements of highly sensitive species may remain unmet (Perhans et al., 2009; Löbel et al., 2012). Hence, an effective network of sufficiently large unmanaged forest stands probably represents an essential foundation for the protection of cryptogam diversity.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ecolind.2015.05.015

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