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ORIGINAL PAPER

Large beech (*Fagus sylvatica*) trees as 'lifeboats' for lichen diversity in central European forests

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Abstract The forest management practices used in central Europe in the last several centuries have led to loss of lichen diversity that may be largely attributed to a loss of substrate variability and quantity. In an attempt to obtain information enabling us to mitigate this process, we surveyed affinity of lichen species to the substrates they currently occupy in six forest areas in the Czech Republic, located between 200 and 1000 m a.s.l. Tree bases and stems represented the most important substrate for lichen species, and especially so for threatened (i.e. red-listed) species. Lichen species richness per individual tree generally increased with stem diameter, especially for beech. Stems and tree bases of large-diameter beeches provide habitats that have enabled the survival of a crucial component of the red-listed lichen species in central Europe, far outweighing other tree species. The deciduous tree species that are commonly considered as favourable for lichen diversity (e.g. maples, ash, elms) were inhabited by only a few other lichen species additional to those associated with beech. This may be due to the low frequency of these tree species in most managed forests, and also some forest reserves, at the present time. Similarly, low incidence of dead wood in managed forests has likely limited its contribution to the lichen diversity, despite the high potential for lichen diversity associated with such substrates. It is

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thus apparent that bark of large-diameter live beech trees comprises a keystone habitat element in the provision of lichen diversity in central European forests.

Keywords Dead wood · Forest management · Red-listed species · Tree species

Introduction

Beech (*Fagus sylvatica*) dominated forest has been the prevalent type of vegetation in central Europe since the second half of the last post-glacial period, with the exception of land at elevations over 1000 m a.s.l. (Margi 2008; Chytrý 2012). These forests have generally been enriched by many other deciduous tree species (e.g. *Acer platanoides*, *A. pseudoplatanus*, *Fraxinus excelsior*, *Ulmus glabra*), silver fir (*Abies alba*) and at higher altitudes also by Norway spruce (*Picea abies*) (Pott 2000; Chytrý 2012). Although the expansion of beech-dominated forests was contemporaneous with human activity since its initial phase, it seems that the pattern of beech dominated forests in central Europe has been primarily shaped by natural processes (Tinner and Lotter 2006; Margi 2008). However, almost the entire current area of these forests has been patch fragmented and—at least temporarily—deforested during the most recent several centuries of forest exploitation in Europe (Jones 1945). Introduction of even-aged (mainly coniferous) plantations in the last two centuries has led to tree age structure simplification, disappearance of old and decaying trees and dominance of coniferous monocultures at the expense of tree species-rich deciduous and mixed forests (Bengtsson et al. 2000). Accordingly, all these processes have altered or completely degraded considerable areas of habitat suitable for forest dwelling taxa, including lichens (Hauck et al. 2013; Nascimbene et al. 2013).

The factors determining lichen species richness and composition in temperate forests have been repeatedly explored and described (e.g. Nascimbene et al. 2007, 2013; Fritz et al. 2008a; Moning and Müller 2009). High lichen diversity has been particularly associated with those deciduous tree species having less acidic bark surfaces, as for example stems of ash (*Fraxinus excelsior*), maples (*Acer* spp.) and elms (*Ulmus* spp.) (Thor et al. 2010; Mežaka et al. 2012) or stems of old beech with rot holes (Fritz and Heilmann-Clausen 2010). An association of large old trees with high lichen diversity has been often emphasized (Fritz et al. 2008b; Ranius et al. 2008; Dymytrova et al. 2014), but also sometimes questioned (Schei et al. 2013). Generally, lichen species richness is associated with high tree structural and compositional heterogeneity, and particularly the presence of dead trees, because some lichen species show strong preference for deadwood substrates (Ellis 2012; Nascimbene et al. 2013). Presence of exposed stone (such as pebbles, boulders and outcrops) on the forest floor allows for saxicolous lichen species, the diversity of which is again influenced by forest management (Boch et al. 2013b).

In northern Europe, some management measures have been even examined with a view to mitigating the negative effects of forest management on lichen diversity (e.g. retention forestry) (Rosenvald and Lõhmus 2008; Perhans et al. 2009; Ranius et al. 2014). If the effort to maintain lichen diversity in central European forests is to be successful, forest management must necessarily incorporate some measures that effectively support lichen diversity (Hauck et al. 2013). However, in central Europe we do not have suitable data on lichen species distribution and their substrate associations in either the small remnants of old unmanaged forests or the much larger areas of managed forests that surround them.

Therefore, we do not know exactly where or how current lichen diversity could be effectively supported.

In an attempt to obtain the missing information, we surveyed lichen diversity in the most widespread types of both unmanaged and managed forests (including various temporal stages such as clearings and young forests) in six large forest complexes in the Czech Republic that covered a gradient of environmental conditions in central Europe between 200 and 1000 m a.s.l. The distribution of threatened (red-listed) lichen species was evaluated in relation to the occupied substrates. We aimed to find and demonstrate the most important substrates for current lichen diversity which should be supported by management measures.

Methods

Study areas and study plots

Each of the six forested areas (SA1-SA6) consisted of a continuous forest patch with an area of 1.4–10.0 km^2. They were distributed across the Czech Republic with the intention to cover environmental variability (e.g. geology, phytogeographical regions, climate) and include important types of central European forest stands, with the exception of lowland floodplains and montane forests above 1000 m a.s.l. (Table 1; Fig. 1). Inside each study area, we established 20 (SA1–SA4) or 13 (SA5 and SA6) square sampling plots, each of 2500 m^2, categorized according to the forest age and forest management (Table 1; Appendix 1 in ESM): (a) nature reserves without regular forest management (referred to here as unmanaged forest), (b) mature managed stands of deciduous, coniferous and eventually mixed tree species, (c) immature managed forests from 11 to 69 years old, (d) stands that were clear-cut between 2 and 10 years ago (clearings) and (e) heterogeneous unclassifiable managed stands (including mosaics of different forest types, internal ecotones etc.). The size of sampling plots was chosen to reliably cover the tree layer structural

Table 1 Description of study areas and number of sampling plots in different types of forest stands to examine lichen diversity across the Czech Republic: A unmanaged forest, B mature deciduous forests (>70 years old), C mature coniferous forests (>70 years old), D immature managed forests from 11 to 69 years old, E clearings, F other heterogeneous forest stands

Study area	Size (km^2)	Altitude range (m a.s.l.)	Mean temperature (°C)	Mean precipitation (mm year^{-1})	Number of sampling plots in particular types of forest stands					
					A	B	C	D	E	F
1	6.75	436–585	6–7	600–650	4	4	4	2	2	4
2	9.95	732–935	4–5	700–800	4	4	4	2	2	4
3	4.60	635–880	4–5	1000–1200	4	4	4	2	2	4
4	7.39	590–730	5–6	600–650	4	4	4	2	2	4
5	10.00	250–280	7–8	550–600	0	3	3	2	2	3
6	1.36	180–210	7–8	550–600	3	3	3	1	0	3

Data of mean temperature and precipitation (from 1961 to 2000) were taken from Tolasz (2007)

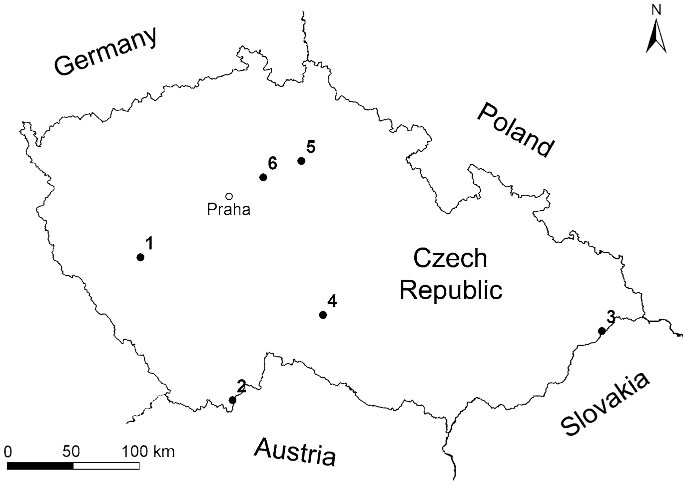

Fig. 1 Location of the six forest study sites to examine lichen diversity in the Czech Republic

and compositional variability in all forest management types including the most diverse in unmanaged beech-dominated forests. Distance among sampling plots of a certain forest management within the respective study area varied from 92 m to 5019 m (Appendix 2 in ESM).

Beech (*Fagus sylvatica*) is the dominant tree species in unmanaged forest stands, with exception of those at the lowest elevations, which are dominated by oak (*Quercus petraea*). Spruce (*Picea abies*) and silver fir (*Abies alba*) are also present in the beech-dominated unmanaged forests, both increasing at higher elevations. Beech and oak dominate the tree community in deciduous managed forests at higher and lower elevations, respectively. Spruce and pine (*Pinus sylvestris*) are dominant species of coniferous stands. Other deciduous tree species, such as *Acer platanoides*, *A. pseudoplatanus*, *Fraxinus excelsior*, *Tilia cordata*, *T. platyphyllos* and *Ulmus glabra*, occur rarely in both unmanaged and managed forests. The age of mature managed forests was around 100 years, but reached up to 180 years in deciduous stands. The age of currently unmanaged forests ranges between 150 and 400 years; most have been protected since the first half of the twentieth century (the oldest since 1838 and the youngest since 1964). However, protection does not necessarily mean immediate exclusion of all management interventions, so that some large tree or fallen logs were likely removed even after several decades of protection.

Lichen survey

In each of 106 sampling plots, we surveyed lichen species on all substrates (soil, stones, living trees, and dead wood) from the soil surface to 2 m above ground. We examined all substrates within the plots comprehensively except for living trees, where we sampled five stems per plot. Stems were selected to be representative of the species and diameter class composition of the tree population within each plot. Observations were made from two zones defined on each sampled stem: 'tree base', from ground level to 50 cm above ground level, and 'stem', from 50 to 200 cm above ground level. All trees (live and standing dead) were classified into two groups according to diameter (<40 and ≥40 cm) measured at breast height (1.3 m).

Samples that could not be determined in the field were collected and identified in the laboratory and eventually referred to the relevant specialist for identification if needed. The voucher specimens are housed in herbaria PRA, PRC and the private herbarium of J. Malíček. Species nomenclature and conservation status were taken from the Checklist and Red List of lichens of the Czech Republic (Liška et al. 2008). Conservation status of the species not included in Checklist and Red List of lichens of the Czech Republic were classified as 'data deficient'. The substrate was specified for each lichen record according to the list of 32 primary substrates, which were subsequently grouped into the 12 categories (Fig. 2).

Data analysis

A relationship between lichen species richness and stem-diameter of particular tree species was assessed by Pearson's correlation at a significance level of $P < 0.05$. Species accumulation curves were built for determination of total lichen species pools associated with the particular tree species (sensu Gotelli and Colwell 2001). We used the randomisation curves computed with 100,000 permutations of the data that show the mean lichen species number with conditional standard deviation (standard deviation for all trees = 0).

Indicator values of lichen species were computed for both tree species and forest stand types according to the procedure designed by De Cácerés and Legendre (2009) according to the equation:

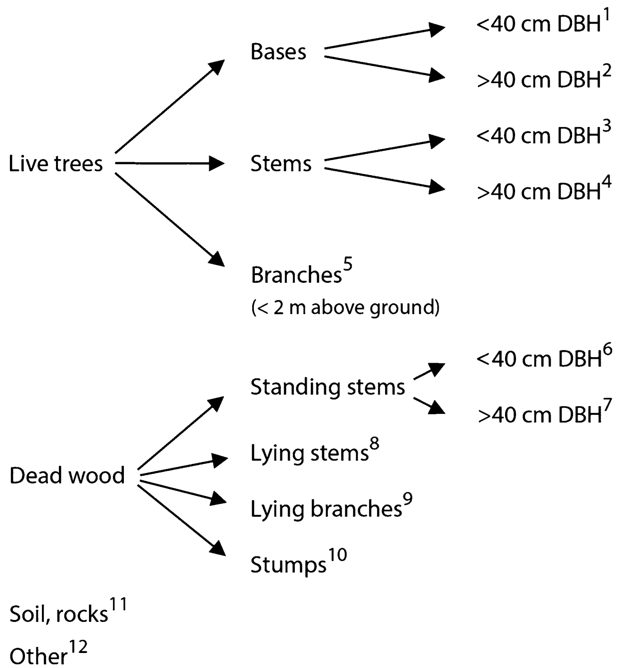

Fig. 2 List of 12 substrate categories on which lichens were recorded in six representative forest sites across the Czech Republic

$$\sqrt{\mathrm{IndVal}_{\mathrm{pa}}^{\mathrm{g}}} = \sqrt{\mathrm{A}_{\mathrm{pa}}^{\mathrm{g}} \times \mathrm{B}_{\mathrm{pa}}} = \sqrt{\frac{n_{\mathrm{p}}/N_{\mathrm{p}}}{\sum_{k=1}^{K} n_k/N_k} \times \frac{n_{\mathrm{p}}}{N_{\mathrm{p}}}}$$

where $\mathrm{A}_{\mathrm{pa}}^{\mathrm{g}}$ is the positive predictive value, B_{pa} is the sensitivity of the species, N is the total number of sites, N_{p} is the number of sites belonging to the target site group, n is the number of occurrences of the species among all sites, n_{p} is the number of occurrences of the species within the target site group, K is the number of site groups, N_k is the number of sites belonging to the kth site group and n_k is the number of occurrences of the species in the kth site group.

The indicator value is combined from two components: positive predictive value (specifity) and sensitivity of the species (fidelity). Specifity is the number of occurrences of particular lichen species within sampling plots (or trees) belonging to the target forest stand type (or tree species), divided by the number of occurrences of that lichen species across all sites. Fidelity is expressed as the relative frequency of particular lichen species in sampling plots (or trees) belonging to the target forest stand type (or tree species). The procedure equalized both specifity and fidelity values of different numbers of sampling plots and tree species individuals, respectively. Statistical significance of indicator values was assessed by 999 permutations at $P < 0.05$.

Differences in species richness and environmental conditions among forest stand types were assessed by one-way analysis of variance (ANOVA) followed by Tukey HSD test to denote different means at $P < 0.05$. Additionally, we counted correlations between dissimilarities in mutual distances and lichen species composition among sampling plots

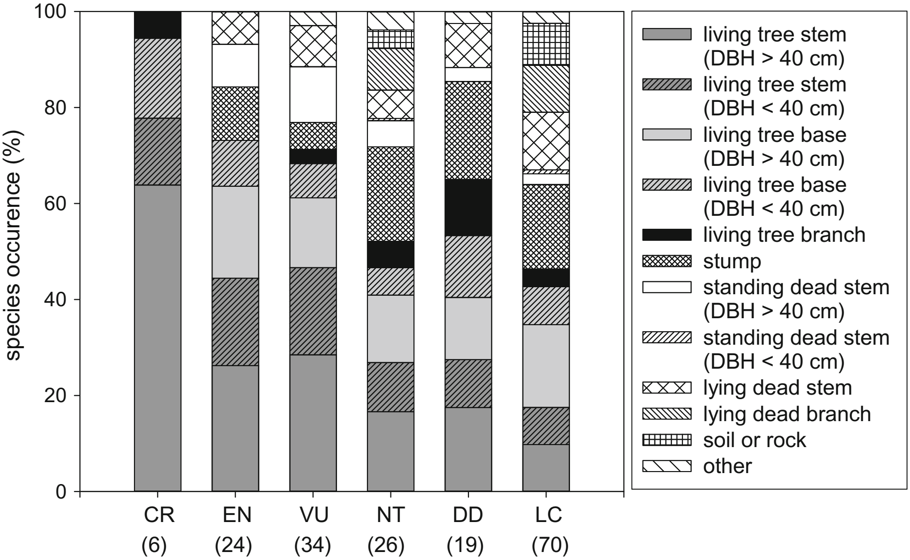

Fig. 3 Affinity of the lichen species of respective Red List categories to the substrates in six representative forest sites of the Czech Republic. Abbreviations of Red List categories (Liška et al. 2008): *CR* critically endangered species, *EN* endangered species, *VU* vulnerable species, *NT* near-threatened species, *DD* species with data deficient and unclassified in Red List, *LC* species of least concern. *DBH* means diameter at breast height. *Numbers* of lichen species in the Red List categories are indicated beneath respective category in *parenthesis*

within each study area to detect eventual distance-based effects on patterning of lichen species composition. We used a Mantel test based on Pearson's correlation, in which significance was evaluated by 9999 permutations at $P < 0.05$. Differences in lichen species composition were assessed by Jaccard dissimilarity index. All computations were performed in R (R Development Core Team 2014), using the "vegan" (Oksanen et al. 2012) and "indicspecies" packages (De Cáceres and Jansen 2015).

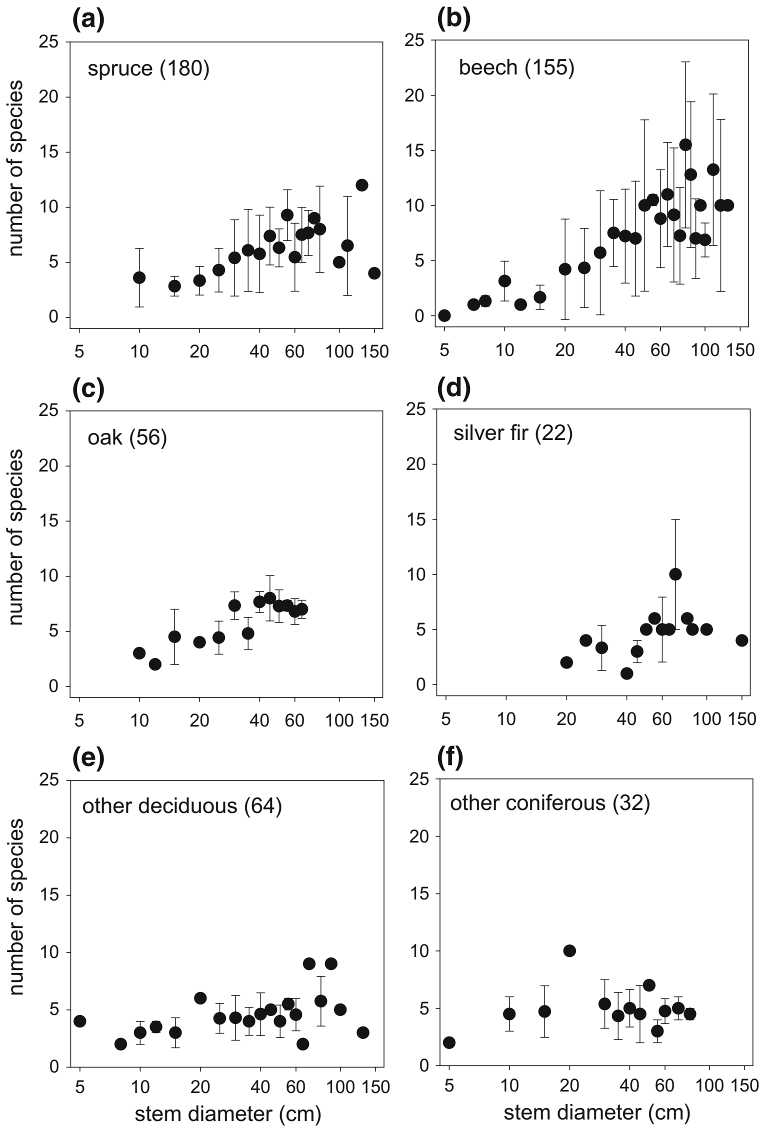

Fig. 4 Relationship between tree stem diameter (log-transformed) and mean lichen species richness per tree individual (±s.d.) in the respective stem diameter classes in six representative forest sites across the Czech Republic. *Number* of surveyed stems of respective tree species is indicated in *parenthesis*

The importance of the substrates for lichen species occurrence was expressed as the proportion of the respective species assemblage recorded on particular substrates. The contribution of each lichen species was equal regardless of differences in species frequency, which was either ascribed to one or proportionally divided among more substrates, according to the occupation frequency of respective species.

Results

In total, we found 179 lichen species, of which 136 (76 %) occupied living trees (up to a height of 2 m), 34 (19 %) standing dead stems, 60 (34 %) lying dead wood, 66 (37 %) stumps, 17 (9 %) soil and rocks and 14 (8 %) other substrates (Appendix 3 in ESM). More than one third of total lichen diversity was recorded exclusively on the surfaces of live trees (65), whereas smaller numbers of lichen species were associated strictly with dead wood substrates (35 species) and only six species were associated with the remaining substrates. Moreover, the importance of bases and stems of living trees as substrates for lichen species increased according to their conservation status. The higher category of Red List we evaluated, the greater proportion of lichen species were recorded on the bark (tree bases and stems) of the living trees (Fig. 3). The threatened species occurred more frequently on the trees with stem diameters greater than 40 cm (Fig. 3). Lichen species richness per tree individual increased with stem diameter for deciduous tree species: beech (Pearson's correlation, $r = 0.424$, $P < 0.001$), oak ($r = 0.519$, $P < 0.001$), all other deciduous species together ($r = 0.306$, $P = 0.014$), but also spruce ($r = 0.349$, $P < 0.001$) (Fig. 4).

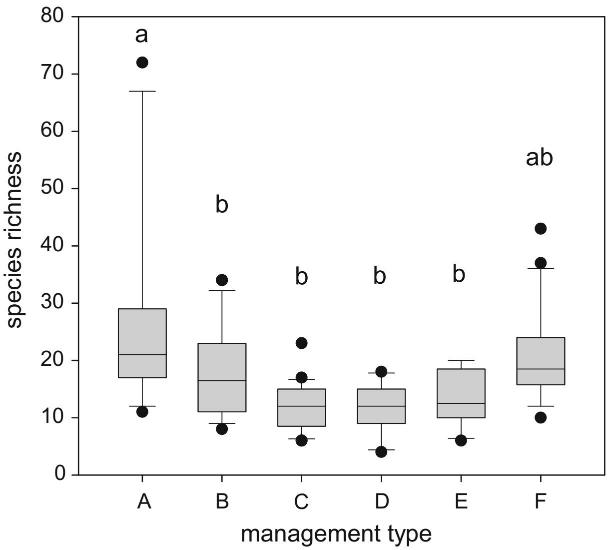

Fig. 5 Lichen species richness in plots in a given type of forest stand across six representative forest sites in the Czech Republic: *A* unmanaged forest, *B* mature deciduous forests (>70 years old), *C* mature coniferous forests (>70 years old), *D* immature managed forests from 11 to 69 years old, *E* clearings, *F* other heterogeneous forest stands. *Median*, *lower*, and *upper* quartiles, and deciles and outliers of species richness are depicted. *Different letters* indicate differences in species richness (ANOVA followed by Tukey HSD test; $P < 0.05$)

Unmanaged forests had the greatest species richness compared to all other stands in managed forests (Fig. 5). Differences in lichen species composition were not significantly correlated with mutual distances among sampling plots in any of the six study areas (Mantel test, $P > 0.05$).

Beech showed the greatest lichen species richness per live tree individual with the maximum reaching 33 species and also the greatest contribution to the total lichen species pool (Fig. 6). Live beeches were one of the most important substrates for red-listed species because they were occupied by 69 % of all critically endangered, endangered and vulnerable lichen species found in this study. Twelve of these lichen species (e.g. *Biatora chrysantha*, *Lopadium disciforme*) were found on two or more beeches, but they were not recorded from other tree species (Table 2). If we summed all species recorded exclusively on the particular tree species, dead wood or soil, stones and other ground substrates, the major role of live beech was again revealed (Fig. 7). Although several lichen species showed high specifity to beech, they occupied only a minor subset of observed beeches (i.e. they lack fidelity) (Table 2). The most frequent lichens associated with beech were *Graphis scripta*, *Ropalospora viridis* and *Pyrenula nitida* (Table 2); *Graphis scripta* represented the most abundant red-listed species in studied forests.

The coniferous trees hosted usually ubiquitous acidophilic lichens and only a few less frequent boreal-montane or poorly known species (e.g. *Fellhanera gyrophorica*, *Lecanora sarcopidoides*, *Lecidea leprarioides*) were observed exclusively on spruces. Some other lichens had high specifity either to oaks (e.g. *Chaenotheca chrysocephala*) or maple, including some threatened species (Table 2), but many of them were recorded only once or twice. The most widespread lichens regardless of substrate were *Lepraria* spp. (mostly *L. finkii*), *Micarea prasina* agg. (mainly *M. micrococca*), *Cladonia coniocraea*, *Coenogonium pineti*, *Hypogymnia physodes*, and *Lecanora conizaeoides*. In coniferous forests, *Hypocenomyce scalaris* was another very common lichen, *Porina aenea* predominated in deciduous (mainly beech) woodlands, and *Lecanora expallens* was a characteristic species of oak stands.

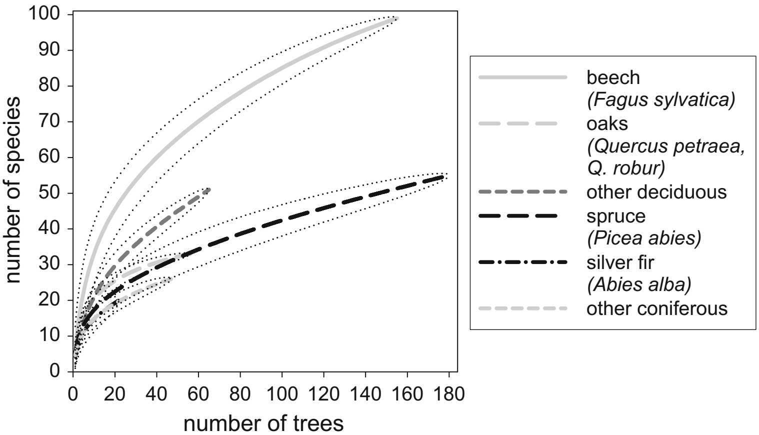

Fig. 6 Random species accumulation curves (based on 100,000 permutations) and their standard deviations of lichen species associated with either particular tree species or groups of other less frequent deciduous and coniferous tree species in six representative forest sites across the Czech Republic

Table 2 List of lichen species associated to the live stems of respective tree species, the number of occupied individuals of respective tree species, and specifity, fidelity and indicators value for given tree species in six representative forest sites across the Czech Republic

Tree species	Lichen species	Red List	Number of trees	Specifity	Fidelity	Indicator values
Beech	*Graphis scripta*	VU	50	1.000	0.323	0.568
(155)	*Ropalospora viridis*	LC	30	0.972	0.194	0.434
	Pyrenula nitida	EN	33	0.744	0.213	0.398
	Agonimia repleta	DD	20	1.000	0.129	0.359
	Mycoblastus fucatus	LC	34	0.584	0.219	0.358
	Buellia griseovirens	LC	16	1.000	0.103	0.321
	Lecanora pulicaris	LC	23	0.622	0.148	0.304
	Parmelia saxatilis agg.	LC	14	1.000	0.090	0.301
	Parmeliopsis ambigua	LC	24	0.566	0.155	0.296
	Biatora chrysantha	VU	12	1.000	0.077	0.278
	Lopadium disciforme	EN	9	1.000	0.058	0.241
	Pertusaria leioplaca	VU	12	0.582	0.077	0.212
	Biatora efflorescens	VU	10	0.644	0.065	0.204
	Pertusaria amara	NT	11	0.561	0.071	0.200
	Lecanora thysanophora	DD	6	1.000	0.039	0.197
	Arthonia radiata	VU	9	0.511	0.058	0.172
	Fellhaneropsis vezdae	VU	4	1.000	0.026	0.161
	Ochrolechia androgyna	VU	5	0.745	0.032	0.155
	Dictyocatenulata alba	DD	3	1.000	0.019	0.139
	Lecanora albella	EN	3	1.000	0.019	0.139
	Pertusaria coronata	VU	3	1.000	0.019	0.139
	Phaeophyscia endophoenicea	EN	3	1.000	0.019	0.139
	Trapelia corticola	EN	3	0.778	0.019	0.123
	Bacidina phacodes	EN	2	1.000	0.013	0.114
	Biatora helvola	EN	2	1.000	0.013	0.114
	Buellia disciformis	VU	2	1.000	0.013	0.114
	Buellia erubescens	CR	2	1.000	0.013	0.114
	Calicium salicinum	VU	2	1.000	0.013	0.114
	Peltigera praetextata	NT	2	1.000	0.013	0.114
	Pertusaria coccodes	VU	2	1.000	0.013	0.114
	Pertusaria pertusa	EN	2	1.000	0.013	0.114
	Arthonia leucopellaea	EN	2	0.700	0.013	0.095
	Micarea prasina s.str.	LC	2	0.700	0.013	0.095
Larch (19)	*Usnea scabrata*	CR	2	0.864	0.105	0.302
Norway maple	*Arthonia excipienda*	DD	1	1.000	0.333	0.577*
(3)	*Opegrapha vermicellifera*	VU	1	1.000	0.333	0.577*
	Bacidia rubella	VU	1	0.963	0.333	0.566*
	Gyalecta flotowii	CR	1	0.963	0.333	0.566*
	Opegrapha varia	NT	1	0.945	0.333	0.561*
Oaks	*Chaenotheca chrysocephala*	NT	9	0.967	0.161	0.394
(56)	*Chaenotheca ferruginea*	LC	23	0.334	0.411	0.370

Table 2 continued

Tree species	Lichen species	Red List	Number of trees	Specifity	Fidelity	Indicator values
	Chaenotheca stemonea	VU	9	0.659	0.161	0.325
	Parmelia sulcata	LC	4	1.000	0.071	0.267
	Chaenotheca trichialis	NT	4	0.928	0.071	0.257
	Scoliosporum schadeanum	VU	4	0.787	0.071	0.237
Spruce	*Hypocenomyce caradocensis*	LC	42	0.592	0.232	0.371
(180)	*Cladonia norvegica*	VU	7	0.857	0.039	0.182
	Cladonia cenotea	LC	3	1.000	0.017	0.129
	Micarea peliocarpa	LC	3	1.000	0.017	0.129
	Lecanactis abietina	EN	3	0.720	0.017	0.109

The indicator values indicated by * are significant at $P < 0.05$. The total number of individuals of respective tree species is associated with name of tree species in parenthesis. Species with either one record or specifity <0.5 were excluded from the table except lichens with significant indicator value. Tree species with only one record were not evaluated. Red-list categories (Liška et al. 2008): *CR* critically endangered species, *EN* endangered, *VU* vulnerable, *NT* near threatened, *DD* data deficient and unclassified in Red List, *LC* species of least concern

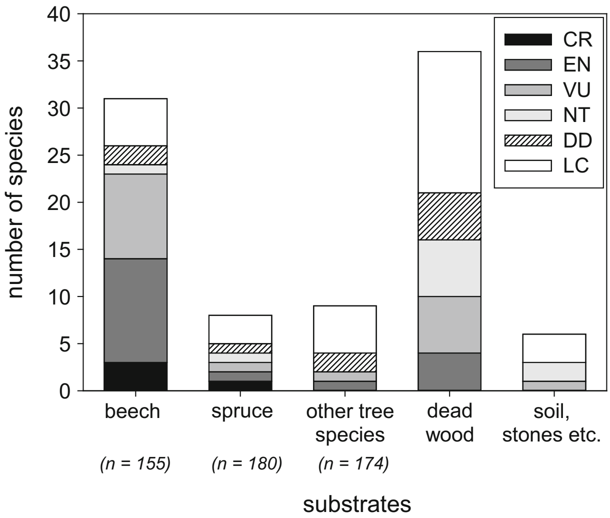

Fig. 7 Subsets of lichen species assemblages associated exclusively to living trees of beech, spruce and other tree species, and dead wood, soil, stones and other ground substrates in six representative forest sites across the Czech Republic. Red-listed status of the species (sensu Liška et al. 2008) is indicated: *CR* critically endangered species, *EN* endangered, *VU* vulnerable, *NT* near threatened, *DD* data deficient and unclassified in Red List, *LC* species of least concern. The *total numbers* of surveyed trees (*n*) are indicated beneath respective category in *parenthesis*

The contribution of dead wood substrates to the total lichen diversity was less than that of living trees (Figs. 3, 6). However, the greater fraction of critically endangered, endangered and vulnerable lichen species on standing dead firs and beeches (7 of 14 and 10

Table 3 List of lichen species associated with respective type or two types of forest stand, the number of occupied sampling plots of the respective stand type(s), and specifity, fidelity and indicators value for given forest stand type(s) in six representative forest sites across the Czech Republic

Forest stand type	Lichen species	Red List	Number of occupied sampling plots	Specifity	Fidelity	Indicator values
A	*Opegrapha niveoatra*	NT	9	0.839	0.473	0.630***
A	*Anisomeridium polypori*	LC	12	0.558	0.631	0.594**
A	*Thelotrema lepadinum*	EN	7	0.890	0.368	0.573***
A	*Chaenotheca xyloxena*	VU	8	0.755	0.421	0.564***
A	*Biatora veteranorum*	EN	6	1.000	0.315	0.562***
A	*Lecanora thysanophora*	DD	5	1.000	0.263	0.513***
A	*Agonimia repleta*	DD	8	0.606	0.421	0.506**
A	*Phlyctis argena*	LC	7	0.618	0.368	0.477**
A	*Pertusaria amara*	NT	5	0.852	0.263	0.474**
A	*Arthonia vinosa*	VU	4	1.000	0.210	0.459**
A	*Fellhaneropsis vezdae*	VU	4	1.000	0.210	0.459**
A	*Lopadium disciforme*	EN	4	1.000	0.210	0.459**
A	*Ochrolechia androgyna*	VU	4	1.000	0.210	0.459**
A	*Parmelia saxatilis* agg.	LC	5	0.743	0.263	0.442**
A	*Chaenotheca chrysocephala*	NT	5	0.658	0.263	0.416*
A	*Micarea prasina* s.str.	LC	5	0.658	0.263	0.416*
A	*Trapelia corticola*	EN	4	0.822	0.210	0.416*
A	*Lecanactis abietina*	EN	3	1.000	0.157	0.397*
A	*Arthonia leucopellaea*	EN	3	1.000	0.157	0.397*
A	*Bacidia rubella*	VU	3	1.000	0.157	0.397*
A	*Dictyocatenulata alba*	DD	3	1.000	0.157	0.397*
A	*Opegrapha varia*	NT	3	1.000	0.157	0.397*
A	*Biatora efflorescens*	VU	4	0.698	0.210	0.383*
A	*Biatora chrysantha*	VU	4	0.698	0.210	0.383*
A	*Bacidina phacodes*	EN	2	1.000	0.105	0.324*
A	*Gyalecta flotowii*	CR	2	1.000	0.105	0.324*
A	*Chaenotheca brachypoda*	VU	2	1.000	0.105	0.324*
A	*Chaenotheca furfuracea*	LC	2	1.000	0.105	0.324*
A	*Chaenotheca chlorella*	EN	2	1.000	0.105	0.324*
D	*Micarea viridileprosa*	NT	4	0.787	0.363	0.535***
E	*Placynthiella oligotropha*	LC	4	0.814	0.400	0.571***
E	*Trapeliopsis flexuosa*	LC	5	0.492	0.500	0.496**
E	*Lecanora saligna*	LC	2	0.687	0.200	0.371*
A + B	*Pyrenula nitida*	EN	17	0.824	0.414	0.585**
A + B	*Arthonia spadicea*	NT	17	0.822	0.414	0.584***
A + E	*Bacidia subincompta*	VU	7	1.000	0.241	0.491***
A + F	*Buellia griseovirens*	LC	8	0.897	0.195	0.419*
B + F	*Arthonia radiata*	VU	9	0.886	0.204	0.426*
C + F	*Hypocenomyce caradocensis*	LC	16	0.793	0.363	0.537**

Table 3 continued

Forest stand type	Lichen species	Red List	Number of occupied sampling plots	Specifity	Fidelity	Indicator values
D + F	*Micarea misella*	LC	15	0.656	0.468	0.555*

A unmanaged forest, *B* mature deciduous forests (>70 years old), *C* mature coniferous forests (>70 years old), *D* immature managed forests from 11 to 69 years old, *E* clearings, *F* other heterogeneous forest stands. The indicator values indicated by * are significant at $P < 0.05$; ** at $P < 0.01$ and *** at $P < 0.001$. Red List categories (Liška et al. 2008): *CR* critically endangered species, *EN* endangered, *VU* vulnerable, *NT* near threatened, *DD* data deficient and unclassified in Red List, *LC* species of least concern

of 21 species, respectively) is noteworthy. Many rare lichens were concentrated on large logs as well. Moreover, these results may not reliably show the importance of dead wood substrates because of the low frequency or even complete lack of these forest components in central European forests. Stumps, which were by far the most common type of dead wood object in managed forests, hosted a substantial fraction of lichen species of less conservation concern as well as a very small fraction of threatened species (Figs. 3, 7). The same evidence was found for lichen diversity on soil, stones and other forest floor substrates (Figs. 3, 7).

The frequency of rare and red-listed lichens was greatest in unmanaged forest reserves, in accordance with far greater occurrence of both large living trees and large standing and lying woody debris (Table 3). According to the analysis of indicator values, 29 lichen species were determined as indicators of unmanaged forest stands (Table 3). The best indicators (lichens with the highest specifity and fidelity) of unmanaged forests were *Opegrapha niveoatra*, *Thelotrema lepadinum*, *Biatora veteranorum* and *Lecanora thysanophora*. However, the species indicators of unmanaged forests included also some widespread and ubiquitous taxa (e.g. *Anisomeridium polypori*, *Parmelia saxatilis*, *Pertusaria amara, Phlyctis argena*). Lichen species composition was uniform and showed little species-specificity in all other forest stand types in comparison with the unmanaged forests. The stems of large trees were also generally species rich in the managed forests (if they were present), but the number of red-listed lichen species associated with these trees rarely matched that of unmanaged forests.

Discussion

Similarly to our study, species-rich lichen communities have been recently found in the oldest beech-dominated forests in Bavaria, Germany (Moning and Müller 2009) and southern Sweden (Fritz et al. 2008a; Fritz and Brunet 2010), while rather species-poor lichen communities were found on beech in north-eastern Germany (Friedel et al. 2006) and Hungary (Nascimbene et al. 2012; Ódor et al. 2013). A regional difference was revealed when beech-dominated forests were compared in three areas in Germany (Boch et al. 2013b). Extraordinarily species-rich lichen communities are associated with beech in the largest old-growth beech forest reserve in Europe in the Ukrainian Carpathians (Dymytrova et al. 2014). As with all lichen communities in general, epiphytic lichen communities associated with beech became impoverished in central Europe due to long lasting negative effects of acid deposition and unfavourable forest management (Hauck et al. 2013). The effects of acid deposition on maintaining bark surface acidity can be still important despite substantial declines in sulphur emission in recent decades (Vestreng et al.

2007). Therefore, the importance of tree species with less acidic bark for survival of lichen diversity has been emphasized (Thor et al. 2010; Mežaka et al. 2012). Regional differences in lichen diversity are further attributed to differences in climate characteristics (e.g. precipitation and humidity) (Marini et al. 2011) or acid deposition (Svoboda et al. 2010).

In our study, no other tree species matched the lichen diversity recorded on beech. Tree species such as maples (*Acer platanoides*, *A. pseudoplatanus*), limes (*Tilia cordata, T. platyphyllos*), elms (*Ulmus glabra, U. minor*) and ash (*Fraxinus excelsior*) did not exceed the lichen species richness of adjacent beeches. Distribution of these admixtured deciduous tree species is scarce across central European forests. Only a few individuals of these tree species were found within a limited area of unmanaged forests as well as over wide areas of managed forests. Occurrence of infrequent tree species may not meet optimal habitat conditions regarding the canopy closure, humidity and other factor important for lichen diversity. For trees meeting suitable environmental conditions, the establishment of a species-rich lichen assemblage depends on successful dispersal of lichen propagules from surrounding populations (Scheidegger and Werth 2009; Sverdrup-Thygeson et al. 2014). All these factors may seriously affect population viability and maintenance of the lichen species associated with scarcely distributed tree species. As a result, lichen diversity associated with the admixtured deciduous trees in the forests of the Czech Republic was not as high as expected. Some rare taxa—'niche specialists' (e.g. *Bacidia rosella*, *Sclerophora pallida*) that were not encountered on beech were recorded on one single old maple (*Acer platanoides*) growing outside of sampling plots included in this study (Malíček and Palice 2013). On the other hand, beech also appeared to be the most important tree species for lichen diversity in large old-growth forest in the Ukrainian Carpathians with greater admixture of *Acer platanoides* and *A. pseudoplatanus* (Dymytrova et al. 2014). The greatest species richness in this old-growth forest was recorded on beech stems, with figures exceeding 30 lichen species per tree (which is comparable with results from our study). Accordingly, the majority of rare lichen species were restricted to old beeches in this old-growth forest (Dymytrova et al. 2014).

Dispersal limitation may not constrain lichen diversity only on deciduous tree species with a sparse distribution as we mentioned above, but also on beech as the most abundant deciduous tree species. A likely explanation is that even beech frequency considerably decreased in central European forests during recent centuries. Beech-dominated stands probably represent a dominant type of 'natural' vegetation from the lowlands to 1000 m a.s.l. (Bolte et al. 2007; Chytrý 2012). Instead, they occupy less than 8 % of the present forested area in the Czech Republic (Vašíček 2007), of which only a negligible part is represented by mature and old-growth stands. The continuity of these fragmented and isolated mature stands has been impaired by forest management with the exception of some small areas in unmanaged forest reserves. The preference for large old beech by red-listed lichens as well as the lichen diversity as a whole may arise from formation of age-related microhabitats (e.g. rough bark, rot holes etc.) and longer periods of time available for colonization (Ranius et al. 2008; Ellis 2012). For instance, bark pH is less acidic below rot holes in beech due to exudates from the rotting wood and these microhabitats are favourable for many epiphytic lichens of conservation concern (Fritz and Heilmann-Clausen 2010). The unique role of beech as a lichen substrate is largely due to the variability of bark surface characteristics from acidic and smooth in young and middle aged trees, to less acidic and rough with many suitable microhabitats in old trees. This range can even be covered by a single beech tree (Fritz and Heilmann-Clausen 2010).

Old large trees would be commonly colonized by lichens not only at the base and lower part of stem, but also higher in the canopy. Age-related substrates expand higher to the tree canopy in old trees as well as containing suitable microclimate conditions in old forest stands (Fritz 2009; Boch et al. 2013a). Moreover, branches in the canopy are less shaded than the stems and bases of trees and light availability may also be a contributing factor in lichen diversity (Dymytrova et al. 2014). Therefore, we suppose that we might have recorded higher values of lichen diversity on the old beeches if we had also surveyed the bark surfaces above 2 m. Accordingly, the superiority of old large beeches for lichen diversity would had been even more impressive (see Boch et al. 2013a). On the other hand, lichen indicators of unmanaged forests include some widespread and ubiquitous species that we rarely found beneath dense tree canopies in managed forests (up to 2 m above the soil surface), but which could be commonly present in less shaded conditions. Moreover, some extremely small taxa could be easily overlooked when growing in small quantities in suboptimal conditions (e.g. *Anisomeridium polypori*). Hence, the strength and reliability of indicator species shall be further tested in future studies.

Microhabitats suitable for rare lichen species are surfaces of damaged, slowly-dying and recently dead trees of large stem diameter. Unfortunately, such trees are preferably removed from stands in managed forests. On the other hand, substrates left in clear-cut and young replanted stands—such as stumps, bare soil and stones—may serve as niches for common lichen species, but only exceptionally for lichens of higher red-list categories (Fig. 3). The negative effect of plantation forestry has been already documented (Humphrey et al. 2002; Rosenvald and Lõhmus 2008), but not much reflected by changes in forest management practices. The implementation of such management measures such as retention of patches occupied by old large trees in forest harvesting procedure does have a positive effect (Rosenvald and Lõhmus 2008; Gustafsson et al. 2012); however, the size of retention patches as they have been typically made (up to 0.5 ha) is likely to be too small for preservation of sensitive lichen species (Perhans et al. 2009). Suitable size of retention patches as well as the form of retention forestry practices is still little explored and probably differs in relation to the tree species composition, forest history and forest fragmentation in a broader landscape context (Lindenmayer et al. 2012). It can be assumed that even a generously applied retention forestry approach may not assure preservation of the most sensitive lichen species, which may require strict protection with a complete absence of timber harvesting (Baker and Read 2011; Lindenmayer et al. 2012).

Centuries of forest management and decades of acid deposition have adversely affected lichen diversity in the whole central Europe, however the patterns of these effects are neither spatially nor temporally uniform (Svoboda et al. 2010). In our study, the greatest species richness and the highest contribution of red-listed species was found in study area 2, which was characterized by a relatively low acid deposition and relatively short history of regular forest management (probably not exceeding three centuries). Moreover, study area 2 includes the largest area of unmanaged forests (100 ha) with the longest period of protection (since 1838). A detailed description of lichen diversity in study area 2 has been already carried out in a separate study (Malíček and Palice 2013). In contrast, lichen diversity is generally low in traditionally inhabited landscape of central Bohemia (study areas 5 and 6) in which extensive disruption of forest continuity began at least a millennium ago (Pokorný 2005). Consequently, oaks as dominant tree species of human inhabited lowland landscape in central Europe may host lower lichen diversity than their potential, as suggested by the results of previous studies in other regions (Ranius et al. 2008; Ódor et al. 2013). For the same reason, the superiority of beech as a tree species for lichen diversity may be partly attributable to the fact that beech has dominated in those forest stands that have been least affected by forest management and atmospheric pollution.

Within the area of extant forest in central Europe, these large-stemmed beeches appear to play a unique and crucial role in supporting lichen diversity, in terms of both extent and variability of substrate, and sometimes even outside the forest reserves. Therefore, future efforts should focus on providing conditions for the increasing the presence of critical substrates (such as deadwood, including snags and logs, and large stems of subdominant deciduous tree species) in managed forests, but also prevent the decline of abundance of large old beeches resulting from harvesting of the oldest managed forest stands. Hence, we argue that the retention of all small, mutually isolated and lichen-rich refuges of old beech-dominated forests within large areas of managed forests is strongly justified, regardless of whether they previously belonged to managed forests or not.

Conclusions

We have outlined the crucial role of large-diameter beech trees for maintaining lichen diversity in extant central European forests. However, the contribution of other potentially important substrates associated with some other deciduous trees (e.g. maples, elms, ash), as well as standing and lying dead trees may be underestimated due to the rarity of these components in most managed forests. In attempting to maintain (and enhance) the lichen diversity in central European forests, we strongly recommend: (a) complete cessation of forest management in the most valuable fragments of old beech-dominated managed forests, and (b) substitution of traditional clear-felling interventions by nature-based forestry to assure a continual presence of old large-diameter live, dying and dead trees. These old trees should be both dispersed individually and aggregated into old-forest patches across the entire area of managed forests in order to effectively maintain lichen diversity.

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References

Baker SC, Read SM (2011) Variable retention silviculture in Tasmania's wet forests; ecological rationale, adaptive management and synthesis of biodiversity benefits. Aust For 74:218–232

Bengtsson J, Nilsson SG, Franc A, Menozzi P (2000) Biodiversity, disturbances, ecosystem function and management of European forests. For Ecol Manag 132:39–50

Boch S, Müller J, Prati D, Blaser S, Fischer M (2013a) Up in the tree—the overlooked richness of bryophytes and lichens in tree crowns. PLoS ONE 8:e84913

Boch S, Prati D, Hessenmöller D, Schulze E-D, Fischer M (2013b) Richness of lichen species, especially of threatened ones, is promoted by management methods furthering stand continuity. PLoS ONE 8:e55461

Bolte A, Czajkowski T, Kompa T (2007) The north-eastern distribution range of European beech—a review. Forestry 80:413–429

Chytrý M (2012) Vegetation of the Czech Republic: diversity, ecology, history and dynamics. Preslia 84:427–504

De Cácerés M, Jansen F (2015) Relationship between species and groups of sites. R package 'indicspecies,' version 1.7.4

De Cácerés M, Legendre P (2009) Association between species and groups of sites: indices and statistical inference. Ecology 90:3566–3574

Dymytrova L, Nadyeina O, Hobi ML, Scheidegger C (2014) Topographic and forest-stand variables determining epiphytic lichen diversity in the primeval beech forest in the Ukrainian Carpathians. Biodivers Conserv 23:1367–1394

Ellis CJ (2012) Lichen epiphyte diversity: a species, community and trait-based review. Perspect Plant Ecol 14:131–152

Friedel A, von Oheimb G, Dengler J, Härdtle W (2006) Species diversity and species composition of epiphytic bryophytes and lichens—a comparison of managed and unmanaged forests in NE Germany. Feddes Repert 117:172–185

Fritz Ö (2009) Vertical distribution of epiphytic bryophytes and lichens emphasizes the importance of old beeches in conservation. Biodivers Conserv 18:289–304

Fritz Ö, Brunet J (2010) Epiphytic bryophytes and lichens in Swedish beech forests—effects of forest history and habitat quality. Ecol Bull 53:95–107

Fritz Ö, Heilmann-Clausen J (2010) Rot holes create key microhabitats for epiphytic lichens and bryophytes on beech (*Fagus sylvatica*). Biol Conserv 143:1008–1016

Fritz Ö, Gustafsson L, Larsson K (2008a) Does forest continuity matter in conservation? A study of epiphytic lichens and bryophytes in beech forests of southern Sweden. Biol Conserv 141:655–668

Fritz Ö, Niklasson M, Churski M (2008b) Tree age is a key factor for the conservation of epiphytic lichens and bryophytes in beech forests. Appl Veg Sci 12:93–106

Gotelli NJ, Colwell RK (2001) Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. Ecol Lett 4:379–391

Gustafsson L, Baker SC, Bauhus J, Beese WJ, Brodie A, Kouki J, Lindenmayer DB, Lõhmus A, Pastur GM, Messier C, Neyland M, Palik B, Sverdrup-Thygeson A, Volney WJA, Wayne A, Franklin JF (2012) Retention forestry to maintain multifunctional forests: a world perspective. Bioscience 62:633–645

Hauck M, de Bruyn U, Leuschner C (2013) Dramatic diversity losses in epiphytic lichens in temperate broad-leaved forests during the last 150 years. Biol Conserv 157:136–145

Humphrey JW, Davey S, Peace AJ, Ferris R, Harding K (2002) Lichens and bryophyte communities of planted and semi-natural forests in Britain: the influence of site type, stand structure and deadwood. Biol Conserv 107:165–180

Jones EW (1945) The structure and reproduction of the virgin forests of the north temperate zone. New Phytol 44:130–148

Lindenmayer DB, Franklin JF, Lõhmus A, Baker SC, Bauhus J, Beese W, Brodie A, Kiehl B, Kouki J, Martínez Pastur G, Messier C, Neyland M, Palik B, Sverdrup-Thygeson A, Volney J, Wayne A, Gustafsson L (2012) A major shift to the retention approach for forestry can help resolve some global forest sustainability issues. Conserv Lett 5:421–431

Liška J, Palice Z, Slavíková Š (2008) Checklist and Red List of lichens of the Czech Republic. Preslia 80:151–182

Malíček J, Palice Z (2013) Lichens of the virgin forest reserve Žofínský prales (Czech Republic) and surrounding woodlands. Herzogia 26:253–292

Margi D (2008) Patterns of post-glacial spread and the extent of glacial refugia of European beech (*Fagus sylvatica*). J Biogeogr 35:450–463

Marini L, Nascimbene J, Nimis PL (2011) Large-scale patterns of epiphytic lichen species richness: photobiont-dependent response to climate and forest structure. Sci Total Environ 409:4381–4386

Mežaka A, Brūmelis G, Piterāns A (2012) Tree and stand-scale factors affecting richness and composition of epiphytic bryophytes and lichens in deciduous woodland key habitats. Biodivers Conserv 21:3221–3241

Moning C, Müller J (2009) Critical forest age thresholds for the diversity of lichens, molluscs and birds in beech (*Fagus sylvatica* L.) dominated forests. Ecol Indic 9:922–932

Nascimbene J, Marini L, Nimis PL (2007) Influence of forest management on epiphytic lichens in a temperate beech forest of northern Italy. For Ecol Manag 247:43–47

Nascimbene J, Marini L, Ódor P (2012) Drivers of lichen species richness at multiple spatial scales in temperate forests. Plant Ecol Divers 5:355–363

Nascimbene J, Dainese M, Sitzia T (2013) Contrasting responses of epiphytic and dead wood-dwelling lichen diversity to forest management abandonment in silver fir mature woodlands. For Ecol Manag 289:325–332

Ódor P, Király I, Tinya F, Bortington F, Nascimbene J (2013) Patterns and drivers of species composition of epiphytic bryophytes and lichens in managed temperate forests. For Ecol Manag 306:256–265

Oksanen J, Blanchet FG, Kindt R, Legendre P, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Stevens MHH, Wagner H (2012) Community ecology package. Package 'vegan,' version 2.0–5

Perhans K, Appelgren L, Jonsson F, Nordin U, Söderström B, Gustafsson L (2009) Retention patches as potential refugia for bryophytes and lichens in managed forest landscapes. Biol Conserv 142:1125–1133

Pokorný P (2005) Role of man in the development of Holocene vegetation in Central Bohemia. Preslia 77:113–128

Pott R (2000) Palaeoclimate and vegetation—long-term vegetation dynamics in central Europe with particular reference to beech. Phytocoenologia 30:285–333

R Development Core Team (2014) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria, http://www.r-project.org/Accessed, Jun 2014

Ranius T, Eliasson P, Johansson P (2008) Large-scale occurrence patterns of red-listed lichens and fungi on old oaks are influenced both by current and historical habitat density. Biodivers Conserv 17:2371–2381

Ranius T, Caruso A, Jonsell M, Juutinen A, Thor G, Rudolphi J (2014) Dead wood creation to compensate for habitat loss from intensive forestry. Biol Conserv 169:277–284

Rosenvald R, Lõhmus A (2008) For what, when, and where is green-tree retention better than clear-cutting? A review of the bidoiversity aspects. For Ecol Manag 255:1–15

Schei FH, Blom HH, Gjerde I, Grytnes J-A, Heegaard E, Sætersdal M (2013) Conservation of epiphytes: single large or several small host trees. Biol Conserv 168:144–151

Scheidegger C, Werth S (2009) Conservation strategies for lichens: insight from population biology. Fungal Biol Rev 23:55–66

Sverdrup-Thygeson A, Gustafsson L, Kouki J (2014) Spatial and temporal scales relevant for conservation of dead-wood associated species: current status and perspectives. Biodivers Conserv 23:513–535

Svoboda D, Peksa O, Veselá J (2010) Epiphytic lichen diversity in central European oak forests: assessment of the effects of natural environmental factors and human influences. Environ Pollut 158:812–819

Thor G, Johansson P, Jönsson MT (2010) Lichen diversity and red-listed species relationships with tree species and diameter in wooded meadows. Biodivers Conserv 19:2307–2328

Tinner W, Lotter AF (2006) Holocene expansions of *Fagus silvatica* and *Abies alba* in Central Europe: Where are we after eight decades of debate? Quaternary Sci Rev 25:526–549

Tolasz R (ed) (2007) Climate atlas of Czechia. Czech Hydrometerorological Institute, Prague

Vašíček J (ed) (2007) National Forest Inventory in the Czech Republic 2001–2004. Forest Management Institute, Brandýs nad Labem

Vestreng V, Myhre G, Fagerli H, Reis S, Tarrasón L (2007) Twenty-five years of continuous sulphur dioxide emission reduction in Europe. Atmos Chem Phys 7:3663–3681