Shared affinity of various forest-dwelling taxa point to the continuity of temperate forests

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ABSTRACT

Effective indicators for biodiversity hotspots and refuges of threatened forest species could help with efforts to mitigate the decline of European forest's biodiversity. 'Ancient forest species' (AFS, i.e. a group of forest vascular plant species that rely on forest continuity) were previously noted as possible indicators of biodiversity hotspots. However, different aspects of the forest continuity may be important for different taxa. Using data from two multi-taxa surveys of central European forests, we examined spatial congruence between the richness of AFS and other forest-dwelling groups in stands that differed in various aspects of forest continuity. We provide evidence for a general positive relationship between the richness of AFS and other forest-dwelling taxa (bryophytes, macrofungi, lichens, beetles, moths and some groups of edaphic organisms) in temperate European forests. The ability of AFS to indicate hotspots of forest biodiversity is not seriously affected by forest management even in the case of long-term intensive and specific management practices such as coppicing. Any easily observable characteristics of the forest environment, excepting the richness of AFS, are unlikely to track exactly the complex effects of forest continuity, habitat quality and the delay in the rise and fall of species diversity of forest communities. Some other perennial plant species associated with beech forests are similar to AFS and regularly occupied the refuges of threatened species. The stands with outstanding biodiversity within the area of deciduous temperate forests can be easily revealed via AFS richness and eventually other similar beech-associated species in the case of beech forests. The retention of all small, mutually isolated refuges of endangered species interspersed within large areas of managed forests may be crucial for the mitigation of biodiversity decline in temperate European forests.

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1. Introduction

Habitat degradation is one of the major threats for terrestrial biodiversity in Europe (Dullinger et al., 2013) and worldwide (Newbold et al., 2015). Conversely, habitat continuity promotes local species-richness, particularly, the occurrence of rare species that have slow colonization rates or specific habitat requirements (Jackson and Sax, 2010). However, what counts as habitat continuity may differ according to the taxa considered (Nordén and Appleqvist, 2001). For example, timber harvesting generally disrupts the continuity of forest habitats for fungi and saproxylic beetles (Grove, 2002; Halme et al., 2013), while for vascular plants it does not (Hermy and Verheyen, 2007). The value of forest continuity as an indicator for forest biodiversity has therefore sometimes been questioned, because there is not one widely accepted definition and the uncertainty of what features of forest stands are relevant, and on what temporal and spatial scale (Rolstad and Gjerde, 2002; Webb and Goodenough, 2018).

Yet there is growing evidence that forest continuity encourages species-richness of various groups of forest-dwelling organisms (Fritz et al., 2008; Flensted et al., 2016). Forest continuity seems to have an additional effect to the structural attributes associated with the forest age (overmaturity) as was documented for the diversity of saproxylic beetles (Janssen et al., 2017). For vascular plants, numerous studies convincingly document a restriction of some vascular plant species to forest stands with long continuity, attributable to low colonization ability of these species (e.g. Peterken, 1974; Hermy and Stieperaere, 1981; Flinn and Vellend, 2005; Bergés et al., 2016). Conversely, the presence of particular plant species, the so-called "ancient forest species" (AFS), was suggested as an indicator of forest stands exhibiting continuity in land use (Peterken, 1974) and hence likely forest diversity (Stefańska-Krzaczek et al., 2016).

In a previous study (Hofmeister and Hošek, 2014), we documented that the richness of AFS is strongly correlated with species-richness of macrofungi at the local scale based on the emergence of fruit-bodies. This association would not necessarily be expected between such ecologically-different taxa, suggesting that there might be a shared requirement for forest continuity. If the same relationship can be shown for AFS and other forest-dwelling taxa this would provide a relatively simple way of identifying refuges for forest-dwelling taxa that could be used to promote their protection.

The positive effect of forest continuity on biodiversity may be confounded with the effects of age of the oldest tree strata and substrate availability (Nordén et al., 2014). However, many previously coppiced stands in central Europe have been wooded for many centuries and support exceptionally species-rich assemblages of vascular plants (up to 80 herb layer species per 25 m^2) including AFS (Hofmeister et al., 2013). Because of such intensive coppicing, the age of the oldest tree strata rarely exceeds 100 years and the occurrence of old-forest structures, such as large old trees and dead wood debris, is still very rare. Communities of forest-dwelling taxa associated with habitats rich in old trees and dead-wood substrates are likely to have been impoverished due to forest management (Sverdrup-Thygeson et al., 2014) and the correlation between richness of AFS and macrofungi could be weak.

In this study, we examined (i) whether a relationship exists between the richness of AFS and other forest-dwelling taxa in temperate European forests, (ii) whether some AFS (and which ones) are able to indicate the hot-spots of rare and threatened species of particular forest-dwelling taxa and if so, (ii) whether both hypotheses fail or not in the forest stands with long continuity, but low substrate availability e.g. little dead wood or old trees for many forest-dwelling taxa.

2. Methods

2.1. Study areas

The relationships between spatial distribution of AFS and other forest-dwelling taxa were examined using data from two multi-taxa surveys in central European forests. The two datasets include similar groups of taxa but collected from different types of central European forest stands. The first survey (dataset A) was carried out in representative areas of high forests which predominate in central European forests, whereas the second (dataset B) was focused on small forest fragments in central Bohemia with long-term intensive forest management (coppicing, pasturing etc.) that continued up to the first half of the 20th century.

The first survey (dataset A) was carried out in study areas representing six continuous forest complexes (> 5 km^2 each). These were selected to cover the wide gradients of the geography, geology and elevation (180–935 m a.s.l.) across the Czech Republic (Fig. 1; Table A1). The geological substrates differed among, but not within, study areas. The study areas represent the six prevailing types of high forest stands in central Europe which vary in terms of their tree species composition and forest management practices (details in Table A2). Beech (*Fagus sylvatica*) and oak (*Quercus petraea*) dominate the tree community in unmanaged and managed deciduous forest stands at higher and lower elevations, respectively. Coniferous stands generally consist of monocultures of spruce (*Picea abies*) or pine (*Pinus sylvestris*). The oldest tree strata in managed mature forests averaged approximately 100 years but reached 200 years in deciduous stands. The oldest trees in unmanaged stands are between 150 and 400 years old. The majority of unmanaged forests have been protected since the first half of the 20th century (the oldest since 1838 and the youngest since 1964) (Archive of Nature Conservation Agency of the Czech Republic).

We established between 22 and 48 square plots (2500 m^2 each) in each study area, the number of plots being proportional to the area of the six types of forest stands: the total number of plots was 241 (Tables A1 and A2). Between 2008 and 2011, surveys of vascular plants, bryophytes, beetles, millipedes, terrestrial isopods and birds were carried out in all plots: macrofungal and lichen surveys were limited to a selection of 106 plots due to time constraints (Table A1). Our aim was to capture the species-richness and composition of various taxa corresponding to the same plot area. For sampling procedures of particular taxa see Section 2.2.

The second dataset (dataset B) derives from 23 forest fragments (0.1–255 ha) located in a rural landscape (30 km^2) in central Bohemia (Fig. 1; Table A1). Fragmentation, deforestation and intensive utiliza-
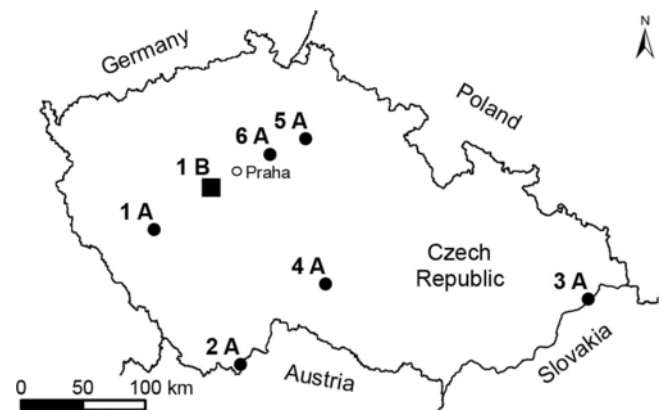

Fig. 1. Location of six and one study sites of datasets A and B, respectively, in the Czech Republic.

tion (coppicing, pasturing) of these forests probably has been going on for several centuries. The altitude of this study area varies from 268 to 497 m a.s.l. and the tree layer is mainly composed of oak, hornbeam (*Carpinus betulus*), with some beech or non-native planted deciduous (*Robinia pseudoacacia*) and coniferous trees (*Pinus nigra*, *P. sylvestris* and *Picea abies*) also present.

We located 227 square plots (225 m^2 each) in the 23 forest fragments, the number of plots in each fragment was in proportional to their size and variability in vegetation and environmental conditions. The plots were positioned randomly, but we checked that each plot could be associated with one of the three types of forest vegetation (deciduous forests, coniferous forest or clearings). The samples of mineral topsoil to a depth of 10 cm were collected in each plot and soil reaction measured in distilled water using a glass combination electrode (soil/water weight ratio = 1:2), because geological substrates vary across this study area. Between 2007 and 2011, vascular plant and bryophyte species composition was surveyed in all plots, ground beetles, moths, millipedes, terrestrial isopods and spiders were surveyed in 54 plots and macrofungi in 45 plots (Tables A1 and A3). The plots selected for the non-vascular plant surveys covered all important environmental gradients (soil reaction, forest fragment size, forest vegetation variability and forest continuity).

2.2. Biodiversity survey

Vascular plants: All vascular plant species in the herb layer (up to 1.3 m above ground) were recorded in each plot in June and July 2009 or 2010 (dataset A) and 2007 (dataset B). Nomenclature of plant species follows Danihelka et al. (2012).

Cryptogams (bryophytes, lichens and macrofungi): All bryophyte and lichen species were recorded during a single visit in either 2009 or 2010 (datasets A and also B for bryophytes). Inventories of macrofungal fruiting bodies were conducted from early spring to late autumn in 2009–2011 (dataset A), 2008 to 2011 (dataset B). Each plot was visited at least nine times during the survey, depending on local field conditions and actual fructification periods. The size of inventoried plots in the small forest fragments (dataset B) was extended from 225 m^2 to ~1000 m^2 to capture a sufficient area for macrofungal survey (Mueller et al., 2004).

Cryptogams were surveyed on all substrates (soil, stones, live trees, and dead wood objects) from the soil surface to 2 m above the ground. The survey of lichens on living trees was limited to five selected trees representing the variability of tree species composition and stem diameter within each of inventoried plots due to difficulties of identifying microlichen species on the bark; other substrates (e.g., dead wood) were examined throughout the plot. Cryptogam species 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. Red-listed species were taken from the current national red lists: Kučera et al. (2012) for bryophytes (including associated Attention List), Liška et al. (2008) for lichens and Holec and Beran (2006) for macrofungi.

Invertebrates (beetles, moths, millipedes, terrestrial isopods and spiders): Invertebrate groups (except moths) were sampled using roofed pitfall traps (ø 9 cm, depth 10 cm, 4% formaldehyde solution). One (dataset A) and five (dataset B) pitfall traps were exposed for one year in each plot and collected monthly. In addition, millipedes and terrestrial isopods were extracted from one (data set A) and five (dataset B) soil samples (area of each 625 cm^2, depth 10 cm) that had been collected in each plot. Extraction was by heat extraction from soil samples using a modified Kempson apparatus (Kempson et al., 1963).

Individuals of 61 beetle families were identified to the species level in pitfall trap samples in dataset A; only ground beetles species (*Carabidae*) were determined in dataset B.

Moths were sampled using one portable battery-run light trap (UV A light bulb, 8 W) located on the ground in the centre of each plot from nightfall to sunrise three or four times (dataset A) and five times (dataset B) from June to September during either one (dataset B) or two (dataset A) years. Moths were collected in the same (moonless) nights in all plots within particular study area. In order to eliminate the differences in sampling effort in dataset A, we selected the two samples with the highest cumulative species richness in each plot. In addition, we removed from the analysis data for 23 plots for which we obtained less than two samples with more than 10 species. Red-listed invertebrate species were classified according to the current national red lists (Farkač et al., 2005).

Birds: The list of all bird species was compiled on the basis of five rounds of point-counting method in each plot from beginning of April to mid-June in 2009 and 2010 (dataset A). All bird species seen and/or heard to the distance of 100 m from the centre of each plot during an interval of 5 min were recorded with exception of transient migrants.

2.3. Species affinity to forests

On the basis of recent literature, vascular plants, bryophytes, moths and spiders were characterized according to their relation with the forest environment and/or human impact. The list of AFS elaborated for central and western Europe by Hermy et al. (1999) was used for check whether plant species are linked with the forest continuity. This list includes 132 plant species, 89 and 67 of which were recorded in dataset A and B, respectively (for details see Tables A4 and A5). Bryophyte classification followed Dierßen (2001) who distinguished species occurring in habitats where human impact is absent (1), weak (2), moderate (3), strong (4) through to very strong (5). Because each species was associated with one, two or three consecutive categories, the mean value for a respective species was used to classify it as hemerophobic (≤2; i.e. human sensitive), hemerophilic (≥3; i.e. human tolerant) or indifferent (between 2 and 3). Five bryophyte species that were not classified by Dierßen (2001) were excluded from respective analysis.

Moth species associated with the forest environment were assessed according to Kadlec et al. (2009); extra species were classified by co-author T. Kadlec. The non-flying species of ground beetles were obtained from Hůrka (1996) and Stanovský and Půlpán (2006), list of references for other beetle families is in Appendix 1. The affinity of spiders with forest was adopted from Buchar and Růžička (2002).

2.4. Forest continuity

Forest continuity was traced back to approximately the second half of 18th century (dataset A) using the maps of the first and second military mappings of Austrian empire or exactly (dataset B) according to historical cadastral maps made in 1840 (map scale 1:2880) archived in Czech Office for Surveying, Mapping and Cadastre in Prague. Historic maps were digitized and compared with current (2006) maps of the Czech Republic (map scale 1:10000) using ArcGIS 9.0.

All plots of the first survey (dataset A) met the assumption of forest continuity since the second half of 18th century, whereas around one fifth of surveyed plots (47) in the second survey (dataset B) were located in parts of forest fragments that originated after 1840 (lack forest continuity).

2.5. Data analysis and modelling

Relationships between both AFS and the remaining herb-layer plant species-richness with the species-richness of other forest-dwelling taxa were evaluated using marginal regression models with heteroscedastic and spatially correlated residuals, using generalized least squares (GLS) (Pinheiro and Bates, 2000; Pinheiro et al., 2017). All models included

species-richness of both AFS and remaining plant species in the herb layer as continuous explanatory variables and other two (dataset A) or four (dataset B) important environmental variables (Table 1). The models allow for heteroscedasticity by allowing for POM (power of the mean) sub-model for the residual variance. This particular form was selected in order to include (and generalize for) second-moment analogue of Poisson or over/under-dispersed-Poisson (corresponding to the unitary, overunitary, subunitary power parameter of the POM model). Spatial autocorrelation was taken into account by including the exponential covariogram, whose parameters were estimated via restricted maximum likelihood as a part of identification of each model (for details see Appendix 2).

We evaluated, in the models, aspects of species composition related to (i) the forest continuity (e.g. number of species associated to the forest environment) and (ii) the contribution of threatened species. The generally low occurrence of red-listed species in the plots did not allow model fits, so the total species-richness was evaluated with increased weight of red-listed species: a weighting factor of 10 was used for species previously thought extinct and critically endangered species, 5 for endangered and vulnerable species and 3 for the remaining categories including the near-threatened species. Data for epiphytic/epixylic lichens and lichens with increased weight of red-listed species were square-root transformed before model analyses.

An association of the plant species with the plots with higher or lower frequency of red-listed species of some group(s) of forest organisms was evaluated using indicator species analysis combining values of positive predictive value (specificity) and sensitivity (fidelity) of the particular plant species (De Cácerés and Jansen, 2015). Both specificity and fidelity values were equalized by different numbers of plots in the categories divided according to the number of red-listed species of respective forest-dwelling taxa. We tested affinity of the plant species to one of three categories of red-listed species frequency (high, medium and low) of respective taxa (Table A6). The indicator value was computed for each plant species with occurrence on more than 5 and 10

plots in case of limited (<100 plots) or large sample size (>100 plots), respectively. The statistical significance of indicator values was assessed by 9999 permutations at P < 0.05.

All computations were performed in R (R Core Team, 2017), using the 'nlme' (Pinheiro et al., 2017) and 'indicspecies' (De Cácerés and Jansen, 2015) packages.

3. Results

3.1. AFS richness

In both datasets, we observed a substantial part of species diversity of the forest-dwelling taxa in central Europe (Fig. 2). Results of generalized least square models (GLS) show consistent positive relationships
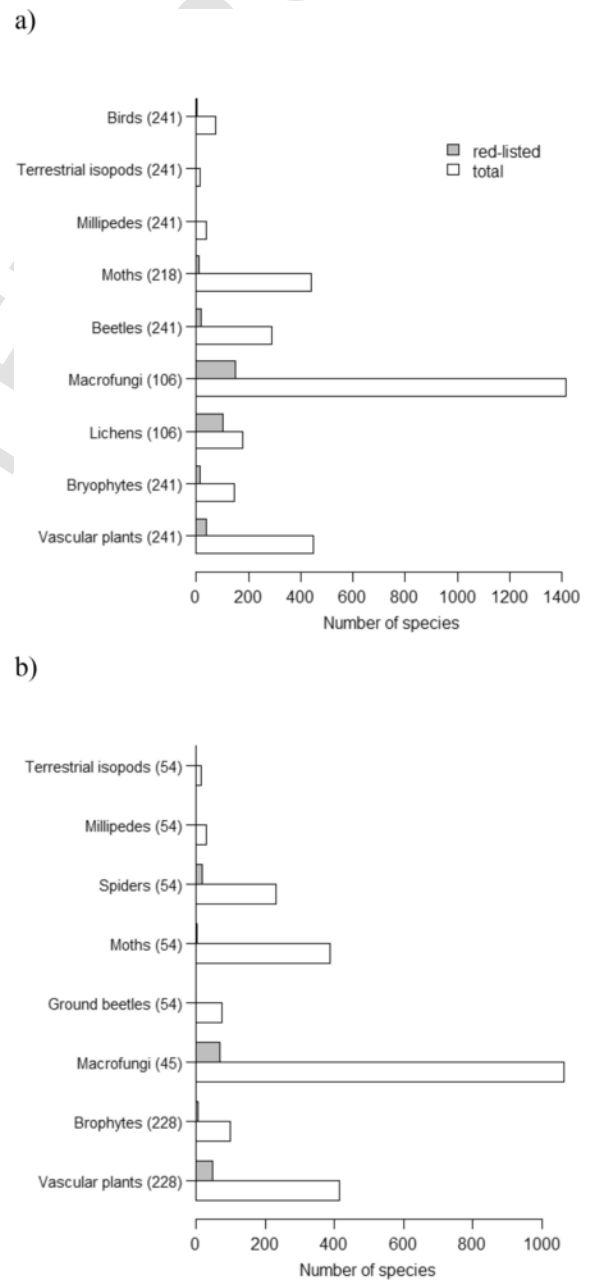
a)

b)

Fig. 2. Total species-richness and the sum of red-listed species (included also near threatened species) for respective taxa in datasets A (a) and B (b). The number of surveyed plots is given in parenthesis.

Table 1
Description of continuous and categorial explanatory variables of the generalized least square (GLS) models of datasets A and B.

Dataset	Continuous variables	Categorial variables (factors)	Levels of categorial variables	
			Count	Description
A	Number of AFS	Study area (region)	6	One of six regions
	Number of all other plant species in the herb layer	Forest stand type	6	Unmanaged forest, Deciduous managed forest (>70 years old),Coniferous managed forest (>70 years old),Young managed forest (11–70 years old),Clearings (2–10 years old), Mosaics of managed stands (e.g. internal ecotones)
B	Number of AFS	Forest continuity	2	Forested in 1840 or not
	Number of all other plant species in the herb layer	Forest fragment size	3	<20 ha, 20–55 ha, 255 ha
		Soil pH	Forest stand type	3	Deciduous forests, Coniferous forests, Shrubs and clearings

between richness of AFS and the majority of other forest-dwelling taxa (Table 2a and b; Fig. 3). This relationship was not only significant for soil-dwelling species, but also for subgroups of epiphytic and/or wood-living species (e.g. epiphytic/epixylic bryophytes and lichens, lignicolous fungi). Richness of plant species excluding AFS was associated with the species-richness of forest-dwelling taxa sometimes positively, but to a lesser extent than AFS (e.g. lichens, subgroup of forest spiders, bryophytes in dataset B), but also negatively (e.g. macrofungi, moths, bryophytes in dataset A). Only total spider species richness showed a reverse picture in that the association with AFS was negative, while the link to other plant species was positive (Table 2b).

All environmental factors included in the models also significantly influenced the species-richness of some forest-dwelling taxa (Table 2a

and b). Models with significant positive effect of AFS explained up to 75% of variability in data, but generally between 30 and 50%. Though the models do not provide a highly accurate prediction of species-richness for particular forest-dwelling taxa, they reliably showed structural and consistent positive relationship between species-richness of AFS and ecologically diverse group of forest-dwelling taxa. Consequently, high richness of AFS pinpoints the species-rich (hotspots) stands for many forest-dwelling taxa (Fig. 3). The relationship between AFS richness and species-richness of some observed taxa was apparent even if we excluded the influence of other environmental factors (Figs. A1a and A1b).

Table 2

Results of generalized least square (GLS) models predicting species-richness of forest-dwelling taxa, species-richness weighted by red-listed species and eventually also number of species of the sub-group of species with affinity to the forest environment on the basis of number of ancient forest species (AFS) and number of remaining plant species in the herb layer. Values of regression coefficients are shown for continuous variable. The results appended by * are significant at $P < 0.05$; ** at $P < 0.01$ and *** at $P < 0.001$.

a) Data A

	Explained variability (%)	AFS	Other plant species	Study area	Forest stand type
Bryophytes	34	0.179***	−0.003***	***	***
Bryophytes × red-listed	34	0.179***	−0.005***	***	***
Hemerophobic bryophytes	41	0.065**	−0.017***	***	***
Epiphytic/epixylic bryophytes	39	0.212***	−0.063***	*	***
Lichens	46	0.137**	0.015*	***	***
Lichens × red-listed	56	0.041***	−0.004**	***	***
Epiphytic/epixylic lichens	56	0.018***	0.008***	***	***
Macrofungi	75	2.118***	−1.013***	***	***
Macrofungi × red-listed	72	2.652***	−1.121***	***	***
Lignicolous macrofungi	73	1.343***	−0.541***	***	***
Mycorrhizal macrofungi	34	0.126	−0.251***	**	***
Beetles	35	0.021	0.094***	***	***
Beetles × red-listed	27	0.024*	0.093***	***	***
Non-flying beetles	45	0.053***	−0.001***	***	**
Moths	38	0.566**	−0.187***	***	**
Moths × red-listed	37	0.574*	−0.201***	***	**
Forest moths	35	0.515*	−0.210***	***	*
Millipedes	29	0.034***	0.009**	***	**
Terrestrial isopods	45	0.021***	0.021	***	***
Birds	26	0.005	0.029	***	***

b) data B

|	Explained variability (%)	AFS	Other plant species	pH	Forest continuity	Forest stand type	Fragment size
Bryophytes	25	0.144***	0.114***	0.628***		**	
Bryophytes × red-listed	25	0.155***	0.120***	0.721***		**	
Hemerophobic bryophytes	18	0.116***	0.021	0.170			
Epiphytic/epixylic bryophytes	23	0.116***	0.027	0.721***			*
Macrofungi	40	4.332***	−0.435	−6.817			**
Macrofungi × red-listed	36	6.226***	−0.395**	−8.376	*		**
Lignicolous macrofungi	21	0.787*	−0.244	0.403			
Mycorrhizal macrofungi	36	1.972**	−0.053*	−7.873**		***	
Ground beetles	13	0.376	−0.101	0.000			*
Non-flying ground beetles	49	0.044*	−0.021**	−0.015	***		
Moths	12	−0.037	−0.220	−1.737		*	
Moths × red-listed	12	0.030	−0.246	−2.042		*	
Forest moths	12	0.045	−0.231	−0.821		*	
Millipedes	49	0.254**	−0.081**	0.920**			*
Terrestrial isopods	13	−0.029	−0.013	−0.004			
Spiders	24	−0.070	0.518***	0.463			
Spiders × red-listed	22	0.024	0.573***	0.584			
Forest spiders	31	0.323**	0.059*	0.553		**	
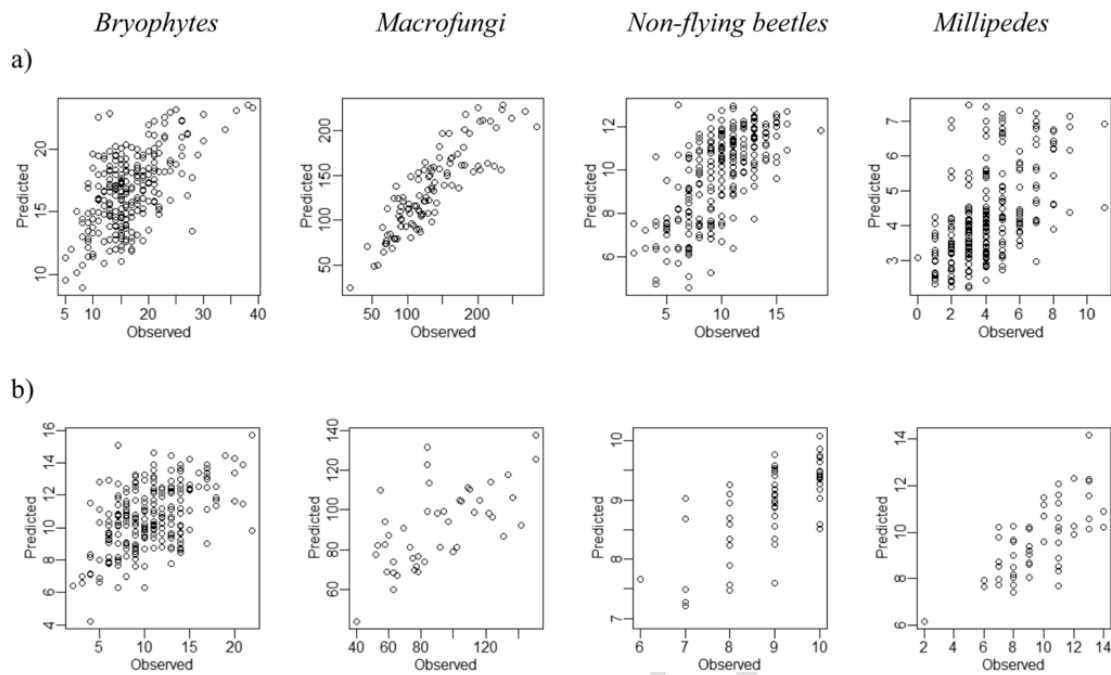
Fig. 3. Relationships between species-richness of particular taxa observed in the plots in the study areas A (a) and B (b), respectively, and species-richness predicted by regression models. All taxa with significant effect of AFS in both study areas are demonstrated.

3.2. AFS composition

The results of indicator analysis showed that the stands with the highest richness of red-listed species of macrofungi were occupied by *Mercurialis perennis* and *Acer platanoides* in both datasets. Other individual plant species were associated with high occurrences of red-listed species, but with differences across the datasets (Table 3) because many of the plants were found only in one set. Many AFS indicated refuges of threatened species for more than one taxonomical group; up to four in the case of *Anemone nemorosa*, *Dentaria bulbifera*, *Gymnocarpium dryopteris* and *Oxalis acetosella*. A strong association with stands rich in threatened species was also shown by some other perennial ground flora species (not AFS) e.g. *Galeobdolon luteum*, *Prenanthes purpurea* and also the trees *Fagus sylvatica* and *Acer pseudoplatanus*. By contrast some other plant species (not AFS, e.g. *Calamagrostis epigejos*, *Galeopsis bifida*, *Carex pilulifera*) were associated with low occurrence of red-listed species.

4. Discussion

4.1. AFS as an integrator of habitat quality in a broader temporal and spatial perspective

The results of models proved clear evidence that the AFS richness consistently indicate local diversity of the most forest-dwelling taxa even if the importance of red-listed species were amplified by weighting. The more a particular (sub)group of forest-dwelling taxa was associated with the forest environment, the closer the relationship with AFS richness was exhibited. The strongest relation to AFS was ascertained for immobile taxa (macrofungi, lichens) the species of which – especially the red-listed ones – have small populations confined to rare substrates (Hofmeister et al., 2016; Dvořák et al., 2017). These specific microhabitats (e.g. later stages of log decay, rough bark on the tree stems) need a long time to develop, a period of several decades or even centuries (Winter and Möller, 2008). Hence, we cannot separate the

particular effects of forest continuity and habitat quality due to the time-dependence of habitat quality.

Sufficient habitat quality is only a prerequisite for, not a guarantee of biodiversity. While quite high diversity of lignicolous or saproxylic species can – at least temporarily – survive in sites where dead wood substrates are declining, colonization of stands in which the volume and heterogeneity of dead wood abruptly increase is generally a slow process depending on the distance to the closest refuges (e.g. Sverdrup-Thygeson et al., 2014). One reason for some of the temporal discrepancy between habitat quality and the species-richness of target communities may therefore lie in the delay of the biodiversity response to the loss or the emergence of key environmental conditions or microhabitats, called an extinction debt or immigration credit, respectively (Vellend et al., 2006; Jackson and Sax, 2010). Any easily observable characteristics of the forest environment are unlikely to track exactly the complex effects of forest continuity, habitat quality and the delay in the rise or fall of local species populations, or the species diversity of forest communities (Lemperiere and Marage, 2010; Hofmeister et al., 2015). However, habitat quality in a broader spatial and temporal context may be integrated and displayed in AFS distribution, and hence, as demonstrated, AFS richness may reliably indicate the diversity of other groups of organisms (and/or their functional subgroups) that rely on the continuity of the forest environment. This relationship is certainly modified by other environmental conditions whose importance is spatially and temporally variable. Therefore, the models that have been demonstrated in this study should be adapted to the most important environmental gradients in the further studies. However, a general positive relationship between richness of AFS and other forest-dwelling taxa is – at least in our study – obvious regardless the role of other environmental factors. Low coincidence between AFS and bird species richness can be explained by high mobility of the birds and low ratio of forest specialist to generalist species in the bird communities (sensu Gregory et al., 2005, 2007).

The fact that AFS are more sensitive to the disruption of the forest continuity than other vascular plants and many other forest-dwelling taxa is mostly caused by their extremely low dispersal (Bossuyt et al., 1999; Brunet, 2007) and/or recruitment (Hérault and Honnay, 2005;

Table 3

List of plant species (AFS in bold) associated with one of three categories of plots according to the number of red-listed species of particular forest-dwelling taxa (high, medium and low). Table included all species with corresponding and significant indication value to more than one taxa sorted in descending order (and then alphabetically). The results of indication analysis indicated by * are significant at $P < 0.05$; ** at $P < 0.01$ and *** at $P < 0.001$. The plant species are appended by their frequency in the plots in which were surveyed respective forest-dwelling taxa: macrofungi and lichens/bryophytes and beetles/moths (dataset A) and macrofungi/bryophytes/moth and spiders (dataset B). The symbol "–" indicates no one record of respective plant species in data, symbol "x" shows that indicator value of the species was not evaluated. The categories according to the number of red-listed species of particular taxa are specified in Table S5.

Plant species	data A						data B				
	Frequency	Macrofungi	Lichens	Bryophytes	Beetles	Moths	Frequency	Macrofungi	Bryophytes	Moths	Spiders
Anemone nemorosa	25/52/49	high	high	high			10/54/10			high	
Dentaria bulbifera	21/49/43	high	high	high	high		≤5/≤10/≤5	x	x	x	x
Gymnocarpium dryopteris	28/63/55	high	high	high		high	–	x	x	x	x
Fagus sylvatica	78/173/149	high	high	high		high	≤5/30/≤5	x		x	x
Oxalis acetosella	76/174/151	high	high	high	high		–	x	x	x	x
Acer platanoides	17/41/38	high	high				21/94/26	high			
Acer pseudoplatanus	62/137/122	high	high		high		13/60/14				
Actaea spicata	13/22/22	high	high		high		≤5/15/≤5	x	x	x	x
Galeobdolon luteum	≤10/28/25	x	x	high	high	high	≤5/≤10/≤5	x	x	x	x
Galeobdolon montanum	23/53/45	high	high			high	–	x	x	x	x
Galium odoratum	35/88/81	high	high		high		31/158/38				
Paris quadrifolia	22/42/37	high	high	high			–	x	x	x	x
Phegopteris connectilis	16/45/32		high	high		high	–	x	x	x	x
Prenanthes purpurea	33/69/57	high		high		high	≤5/≤10/≤5	x	x	x	x
Mercurialis perennis	31/68/62	high	high	medium			20/92/22	high			
Polygonatum verticillatum	21/52/44	high		high	high	low	–	x	x	x	x
Rubus ser. Glandulosi	19/44 / 37	high		high	high	low	–	x	x	x	x
Athyrium filix-femina	56/126/105	high		high			≤5/≤10/≤5	x	x	x	x
Brachypodium pinnatum	≤10/≤10/≤10	x	x	x	x	x	21/96 /23		high		high
Bupleurum falcatum	–	x	x	x	x	x	11/35/13		high		high
Calamagrostis villosa	16/39/29	high	high				–	x	x	x	x
Circaea alpina	13/40/31			high		high	–	x	x	x	x
Circaea × intermedia	16/32/26	high		high			–	x	x	x	x
Chrysosplenium alternifolium	≤10/26/18	x	x	high		high	–	x	x	x	x
Clinopodium vulgare	≤10/≤10/≤10	x	x	x	x	x	10/56/11		high	high	
Cornus mas	–	x	x	x	x	x	12/36/12		high		high
Daphne mezerum	11/24/23	high	high				–	x	x	x	x
Digitalis purpurea	15/35/25		high			high	–	x	x	x	x
Dryopteris carthusiana	73/169/144			high		high	≤5/≤10/≤5	x	x	x	x
Dryopteris dilatata	61/147/130	high		high			≤5/≤10/≤5	x	x	x	x
Geranium robertianum	24/51/47	high	high				14/85/16				
Melica nutans	12/43/41						11/69/14	high	high		
Petasites albus	≤10/22/18	x	x	high	high		–	x	x	x	x
Rhamnus cathartica	≤10/≤10/≤10	x	x	x	x	x	30/115/33		high		high
Sanicula europaea	22/58/53	high			high		≤5/35/7	x			
Securigera varia	≤10/≤10/≤10	x	x	x	x	x	18/67/19		high		high
Stellaria nemorum	15/36/26	high		high			–	x	x	x	x
Viola reichenbachiana	38/87/80	high			high		≤5/19/≤5	x		x	x
Abies alba	30/79/65	high			high	low	–	x	x	x	x
Luzula luzuloides	21/56/50	medium					7/49/8	medium			low
Carex pilulifera	54/134/120	low	low				–	x	x	x	x
Galeopsis bifida	32/76/74		low			low	–	x	x	x	x
Quercus petraea	35/84/83		low	low			35/182/42				
Pinus sylvestris	24/54/51	low			low		≤5/≤10/≤5	x	x	x	x
Calamagrostis epigejos	43/112/101	low		low	low		≤5/19/≤5	x		x	x

Baeten et al., 2009) abilities. The production of a low seed volume combined with a short distance dispersal strategy appears to be an evolutionary adaptation to the relatively stable forest conditions with infrequent and spatially limited disturbances (Honnay et al., 2005). As documented for *Primula elatior*, the number of seeds may be further reduced when the population size decreases (Jacquemyn et al., 2002).

Populations of AFS are considerably suppressed by some kinds of human disturbances, such as past breaks in forest continuity (Flinn and Vellend, 2005) or replacement of semi-natural deciduous tree species by coniferous tree species (Hérault et al., 2005). However, AFS populations are not impaired by some other forest management practices (such as typically coppicing) because they are able to cope with severe but only infrequent disturbance providing that forest environment close to the original can be soon regenerated (Decocq et al., 2004).

We expected that the forest stands coppiced in the past would be occupied by impoverished communities of some forest-dwelling entities due to rarity of structural attributes of old forests. Nevertheless, species-richness of the forest-dwelling taxa corresponded to AFS richness notwithstanding long-lasting effects of the forest fragmentation and management. However, the effects of past forest management may not be equivalent to current interventions because in the past the surrounding landscape almost certainly provided a larger reservoir of forest species for recolonisation than today's rather homogenous, nitrogen-enriched and species-poor landscapes (Verheyen et al., 2012). The spatial distribution of AFS may indeed lag behind drivers of environmental changes (Vellend et al., 2006; Hermy, 2015).

4.2. AFS as an indicator of refuges of threatened species

While most AFS indicated refuges of threatened species of different taxonomical groups, only *Mercurialis perennis* was associated with hotspots of threatened macrofungal species in both datasets. All AFS with the highest indicator potential, – and *Anemone nemorosa* in particular – are extremely sensitive to both fragmentation and deforestation (Brunet et al., 2011) and show very slow colonization rates (Bossuyt et al., 1999).

A strong association with stands rich in threatened species was also shown by some other perennial ground flora and tree species that are all regular parts of long-established beech forests in central Europe (Kučera and Chytrý, 2010). These perennial plants generally have life strategies and dispersal mechanisms similar with AFS. The beech forests represent the previously most widespread (Chytrý, 2012) and least human-influenced forest habitat in central Europe, and so therefore provides refuges for threatened forest-dwelling species (Brunet et al., 2010; Müller et al., 2012). The frequency and area of beech forests has considerably decreased in central Europe during recent centuries, and only a very small part of the remaining area represents old forests (McGrath et al., 2015). The beech-dominated forest refuges still harbour a substantial part of existing regional (or European) diversity of the respective taxa, e.g. fungi (Halme et al., 2013; Dvořák et al., 2017) or saproxylic beetles (Müller et al., 2012). However, the regional (or European) diversity itself might have been reduced and the most sensitive species gone extinct, due to habitat fragmentation and degradation in the past (Grove, 2002).

4.3. AFS richness as an indicator of forest biodiversity

Previous evidence had shown that patterns of species-richness coincided across different taxonomic groups in broader geographical scales, but failed in finer scales of resolution (Reid, 1998; Lewandowski et al., 2010; Sabatini et al., 2016). However, we found that AFS do appear to be a simple and effective tool for approximate evaluation of forest biodiversity at the local scale as well. AFS may therefore be useful as a quick way for the delimitation of biodiversity hotspots and refuges of threatened forest species which deserve protection as nature reserves. The supplementation of a reserve network with the hotspots and refuges is desirable for the maintenance of species diversity of various taxonomical groups in fragmented European forests before the alternation of these hotspots and refuges by ongoing forest management.

Data accessibility

Datasets used in the statistical analyses will be available via Mendeley Data Repository (doi: 10.17632/6rg3p6rgmm.1).

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2019.01.018.

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