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Hot-spots of epiphytic and epixylic lichens in fragmented temperate forests are underpinned by microhabitat heterogeneity and spatiotemporal habitat continuity

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ABSTRACT

Habitat loss, fragmentation and degradation are major causes of the ongoing decline of epiphytic and epixylic lichen species in temperate forests throughout Europe. We investigated how extant species richness and composition of epiphytic and epixylic lichen communities in ten hot-spots of lichen diversity in the Czech Republic reflected the occurrence and properties of potentially suitable microhabitats and habitats. At each hot-spot, we surveyed a pair of 1-ha square plots, one in (over-)mature managed and the second in unmanaged forest. In total, we recorded 513 epiphytic and epixylic lichen species which represent a substantial part of lichen biota in Central Europe. Species richness and composition of lichen communities were explained by microhabitat heterogeneity, and also by the area of near-natural forest habitats (habitat extent) at the landscape scale. In addition, lichen species richness and number of red-listed species were explained by a categorial variable distinguishing mature managed and unmanaged plots, used as a proxy of temporal continuity of natural succession. This finding illustrates that temporal continuity of natural succession in unmanaged forests likely had an extra stimulus for lichen communities that may not be reflected by observed aspects of forest habitats. Hence, we confirmed indispensable positive effects of (micro)habitat heterogeneity, and spatial and temporal continuity for preserved hot-spots of lichen diversity in Central Europe. Due to generally slow colonization-extinction dynamics of epiphytic and epixylic lichens we call for strengthening microhabitat heterogeneity, and the spatial and temporal continuity of European temperate forests at the landscape scale.

1. Introduction

Long-term fragmentation and habitat loss of temperate forests in Central Europe, changes in their tree species composition, age and stand structure due to forest management and overall human land-use are among the most important threats for forest biodiversity (Haddad et al., 2015; Mikoláš et al., 2023). However, we still lack sufficient information to determine the critical characteristics of forest habitats for populations of threatened species at the local (in relation to age, tree composition and structure) and landscape (minimum area/share of a particular habitat type or forest in the landscape) scales (Hofmeister et al., 2015; Rybicki et al., 2020; Thorn et al., 2020). Consequently, we cannot set up sufficient and effective requirements for forest management and/or habitat protection at both scales to ensure a halt of biodiversity loss in Europe (Dullinger et al., 2013; Johnson, 2013). The vast majority of forests in Central Europe have been managed for extensive time periods; therefore, the possibility of regaining natural characteristics and forest biodiversity after being left to spontaneous natural successional processes is sometimes questioned or considered very long-term (over several centuries) (Paillet et al., 2015; Van Meerbeek et al., 2019).

Epiphytic and epixylic lichens represent taxa generally sensitive to anthropogenic influences of the environment (Ellis, 2012; Nascimbene

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et al., 2013). As slow-growing and long-living organisms, they appear to be useful indicators of habitat quality across wide spatial and temporal scales (Ellis, 2015; Hauck et al., 2013). Epiphytic and epixylic lichens are often associated with microhabitats that arise on old and dead trees (Fritz and Heilmann-Clausen, 2010; Hofmeister et al., 2016; Kozák et al., 2023) and many threatened species are extremely sensitive to the loss of habitat continuity – in both the spatial and temporal sense (Fritz et al., 2008; Johansson et al., 2013a). As such, microhabitat heterogeneity and frequency are sometimes utilised as predictors of species diversity in forests instead of the results of regular survey of any particular taxa (Asbeck et al., 2021; Paillet et al., 2018).

More than one third of the lichen species in the Czech Republic are categorized as threatened according to the Checklist and Red List of lichens of the Czech Republic (Liška et al., 2008). Epiphytic and epixylic lichen species contribute substantially to the threatened lichen species list (Liška et al., 2008), notwithstanding that forest habitats still cover 34 % of the area of the Czech Republic. Therefore, we need to understand the requirements of epiphytic and epixylic lichen species of forest habitats in relation to microhabitat frequency and heterogeneity, and habitat extent and temporal continuity at various scales.

In an attempt to fulfil this proposed aim, we carried out a survey of epiphytic and epixylic species occurrence in ten hotspots of lichen diversity in the Czech Republic that cover a gradient of near-natural forest vegetation of temperate forests in Central Europe. In this study, we hypothesized that lichen species diversity in the hotspots is supported by continuity of (semi-)natural forest habitats in the spatial (i.e., habitat extent in the vicinity of the plots) and temporal sense (i.e., time elapsed since abandonment of regular forest management). We expected that even a short-term absence (lasting several decades) of forest management improves the conditions of forest habitats for lichen diversity that can be observed by changes in variability and frequency of microhabitats. Based on the results from the hotspots in unmanaged temperate forests and adjacent (over)mature managed forests, we attempt to investigate effects of microhabitat frequency and variability, and habitat extent and continuity for completeness of epiphytic and epixylic lichen communities. Particularly, we tried to answer the following questions: (i) can we show a positive effect of microhabitat frequency and variability on species richness of epiphytic and epixylic lichens and the presence of threatened species?, (ii) can we determine the effect of the area of near-natural forest habitats at the landscape scale on lichen diversity at the local scale?, (iii) can we document an additional positive effect of forest management abandonment on lichen diversity that is not mediated (and observable) by forest structure (e.g., frequency and/or variability of microhabitats)?

2. Materials and methods

2.1. Study plots

Based on recent information (e.g. Hofmeister et al., 2016; Man et al., 2022; Vondrák et al., 2022) about the occurrence of natural forest habitats and lichens in the Czech Republic, we selected ten hot-spots of epiphytic and epixylic lichen diversity in various forest habitats to cover the most widespread types of natural forests in Central Europe. The forest types spanned an elevational gradient from lowland oak-dominated forests, followed by beech-dominated and ravine forests to mountain spruce-dominated forests (Table S1). The hot-spots are considered localities with apparently higher species richness of epiphytic and epixylic lichens and occurrences of rare species in the Czech Republic.

At each locality, a pair of 1-ha square plots was established in representative natural forest habitats, of which one plot was under regular management (located in mature managed forest), while the second had been without forest management for at least several decades (located in nature reservations or core zones of national parks). These paired plots were selected in the study to address — and distinguish between — the effects of forest structure and temporal continuity of natural succession from the abandonment of regular forest management. Based on forestry evidence, we can estimate the age of the oldest tree strata to be between 150 and 300 years in the unmanaged plots and mostly between 100 and 140 years in the managed plots. The prevalent management approach in the past was clearcutting, therefore the extant forest vegetation in the managed plots represents mostly natural regeneration after clearcut, however in some plots this was supplemented by planting. Currently, the (over-)mature managed forests in our study are at, or beyond, the age when they are usually (clear-)cut. The logging is quite likely in the near future in these forests as well, although the necessity of their protection for supporting biodiversity of the adjacent area-limited unmanaged forest reservations is also under debate. Distances between paired plots averaged 1709 m, and ranged between 570 and 4340 m. The distribution of the plots within the Czech Republic is shown in Fig. 1, and their description is in Tables S1 – S3.

In each of the plots, we carried out a detailed inventory of the forest structure, heterogeneity and frequency of microhabitats and species occurrence of epiphytic and epixylic lichens.

2.2. Inventory of heterogeneity and frequency of microhabitats

In each plot, we inventoried all objects of forest structure (i.e., living and dead trees, standing deadwood as well as logs) with a diameter >10 cm. The frequency of objects was surveyed in three diameter classes (10 to 39 cm, 40 to 80 cm, and >80 cm). Microhabitats significant for lichen occurrence were counted simultaneously for each class and object type up to a height of 2 m from the forest ground. The catalogue of the microhabitats was adopted from Kraus et al. (2016) and Larrieu et al. (2018) with the addition of some microhabitats specific for rare epiphytic lichens, e.g., parts of stems protected from rain as potential microhabitat for ombrophobic lichens (species of the genera *Chaenotheca* and *Sclerophora*). On the other hand, we removed some other microhabitats from the previous lists not relevant for lichens. An overview of the types of microhabitats is given in Table S4.

2.3. Lichen survey

The inventory of the species composition of epiphytic and epixylic lichen communities was carried out in all plots by three lichenologist experts from the author's team: Zdeněk Palice, Jaroslav Šoun and Jan Vondrák. All potentially important substrates were examined over the entire 1 ha plot, particularly the stems of living and standing dead trees up to 2 m above the surface and logs. This survey enabled us to provide (i) a meaningful comparison of lichen species richness and composition between different forest habitats due to inclusion of small-scale habitat heterogeneity, (ii) species lists that are reasonably close to complete, (iii) appropriate sampling effort to obtain reliable results (Vondrák et al., 2018).

Identification of well-known lichens was done directly in the field. Less well-known lichens were identified on the basis of microscopic features or the content of specific lichen substances (using TLC — thin layer chromatography). DNA barcodes (ITS or mtSSU) were also obtained from several samples to confirm or determine identity. The collected lichens were deposited in the herbarium of the PRA (Botanical Institute of the CAS).

In addition to the total number of lichens in the plot, we further evaluated the number of red-listed species, i.e., the number of threatened species that are included in one of the following categories of the Red List of Lichens of the Czech Republic (Liška et al., 2008): RE — extinct, CR — critically endangered, EN — endangered, VU — vulnerable. In addition, lichen-allied or lichen-like fungi, traditionally studied by lichenologists were recorded. These fungi were not categorized and indicated as "-" (Table S5).

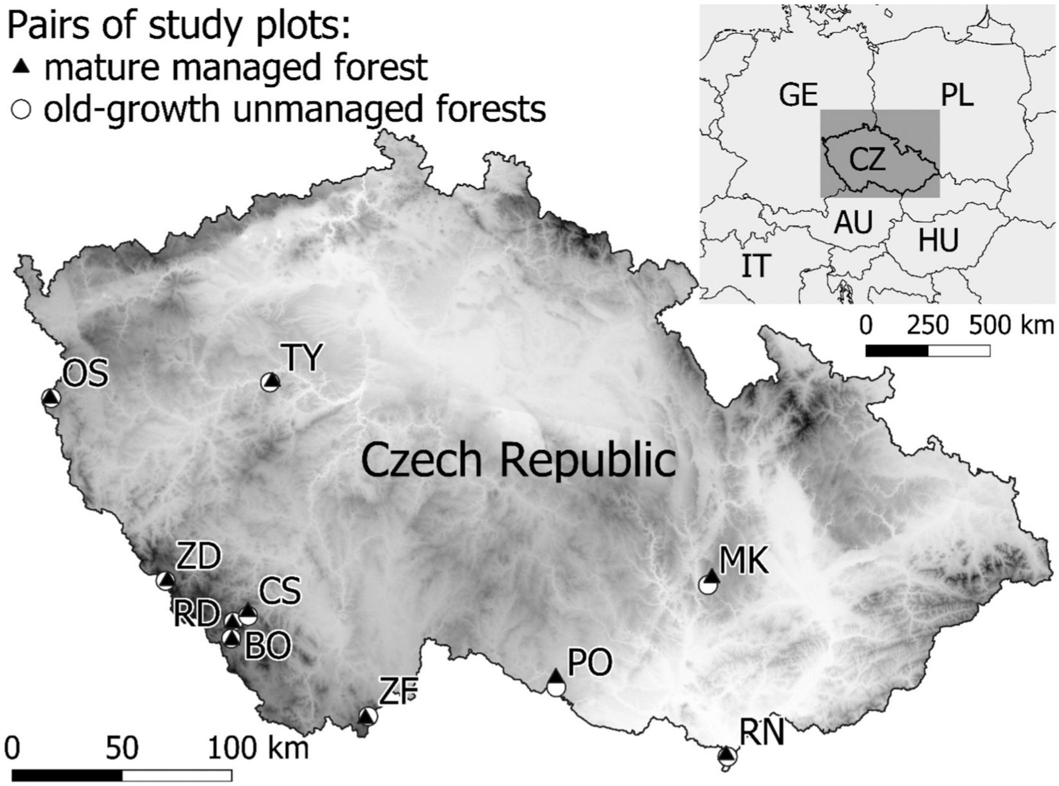

Fig. 1. Location of pairs of study plots in ten hot-spots of epiphytic and epixylic lichen species diversity in the Czech Republic. Elevation gradient of the Czech Republic (100–1600 m a.s.l.) is indicated on white-black scale. Each hot-spot is indicated by abbreviation. Description of the plots is in Table S1.

2.4. *Data analyses*

2.4.1. *Stand conditions and forest structure*

Differences in environmental conditions and structural attributes of forest habitats between unmanaged and managed forests were evaluated using Wilcoxon signed rank test in R (R Core Team, 2023).

2.4.2. *Species richness (α-diversity)*

Species diversity at the plot level was modelled with generalized least squares (GLS) models allowing for variance changing with a power of the mean (heteroscedasticity) in the “nlme” package (Pinheiro et al., 2022) in R (R Core Team, 2023) in order to emulate Poisson-like behaviour. A basic model was built for the total number of epiphytic and epixylic lichen species per plot. The set of potential explanatory variables included elevation (as a fundamental driver of lichen communities), number of microhabitat types per plot (as a measure of microhabitat heterogeneity) and number of living and dead trees with microhabitat occurrence and diameter $\geq$ 40 cm (as a measure of microhabitat frequency and stand maturity). Additionally, the effect of habitat extent was evaluated in the initial model, which included the area of near-natural forest habitats within a radius 100 m from the plot centre. We used relative area of habitat extent instead of absolute values that are dependent on circle radius. Area of near-natural forest habitats was adopted via QGIS from two data layers and evaluated in two alternative models: a) CORINE Land Cover 2018 and b) NATURA 2000 mapping provided by the Nature Conservation Agency of the Czech Republic. Broad-leaved forests (code 311), mixed forests (code 313) and transitional woodland-shrub (code 324) were the assessed near-natural forest habitats using CORINE. Coniferous forests (code 312) were included in the plots above 1000 m a.s.l. in elevation where these forests represent natural forest vegetation (Chytrý, 2012). Using NATURA 2000, we added the area of all natural forest habitats (Chytrý et al., 2010). We ran a set of models in which we subsequently substituted the variable of the area of near-natural forest habitats with increasing radius around the plots. The upper limit of this radius differed between input layers: the largest radius for CORINE Land Cover had 25 km while NATURA 2000 ended at radius 1 km because some sites were adjacent to the state border, and we had no data for neighbouring countries. We checked significance of the variables and compared relative effect sizes of the habitat extent variable and Akaike Information Criterion (AIC) of the models.

The temporal effect of the spontaneous development of forest habitats after abandonment of regular forest management was generally evaluated by division of managed and unmanaged (protected) forest habitats into two categories, and these were inserted into the model as a factor. We used this general simple approach despite knowing the year of declaration of nature protection for unmanaged forests (Table S2). However, these dates hardly represent the real time of abandonment of forest management that could have been stopped much earlier, or, for the reservations protected since the first half of the 20th century, it could have continued in a mild form (e.g., the individual removal of deadwood) for decades after the declaration of protection. Similarly, in all the plots in managed forests, the intervention has not been carried out for at least one, but often several, decades. Therefore, a feasible expression of natural continuity is the general separation of managed and unmanaged stands, with an absence of clear-cutting in the latter in the past 150 years at least and with certainty of having several decades longer continuity of spontaneous development without any management intervention at each locality.

Potential autocorrelation of the GLS models was eliminated by incorporating an exponential covariogram. Model parameters were estimated through restricted maximum likelihood (REML) estimation. The same set of GLS models was also built for number of red-listed species as response variable. In addition, we computed the GLS models with standardized coefficients of all continuous explanatory variables.

2.4.3. Species composition (β-diversity)

Evaluation of the similarity of epiphytic and epixylic lichen species composition between plots (β-diversity) was performed by calculating Sørensen indices of dissimilarity of communities using the "betapart" package (Baselga et al., 2015). To assess the degree of dissimilarity in microhabitat representation between plots, the same procedure was applied to the dataset of microhabitat types found in each plot.

A partial Mantel test was carried out to recognize congruence between dissimilarities in the composition of microhabitat types and lichen communities in the plots, taking into account the geographic distances between the plots. Significance of the Mantel statistic was assessed with the Monte Carlo procedure with 9999 permutations using the "vegan" package (Oksanen et al., 2012).

2.4.4. Species pool (γ-diversity)

To evaluate the overall epiphytic and epixylic lichen diversity of plots in managed and unmanaged stands (γ-diversity), species accumulation curves were generated using the "vegan" package (Oksanen et al., 2012).

3. Results

3.1. Microhabitat heterogeneity and frequency, and size of near-natural forest habitats

Structural features of the forest plots differed only moderately between mature managed and unmanaged plots (Table S1). Heterogeneity of microhabitats was slightly higher in unmanaged (mean = 15, SD = 2) than in managed forests (12 ± 2), out of a total of 19 microhabitat types. While each microhabitat type occurred in at least two plots in unmanaged forests, two microhabitat types were absent in mature managed forests (moist microsites and lianas). Conversely, the frequency of microhabitats was higher in mature managed forests, in which we recorded an average of 130 living and dead trees with diameter ≥ 40 cm with at least one microhabitat, while 122 of such trees were recorded in unmanaged plots. The contribution of near-natural forest habitats was on average 10 percentage points higher in the vicinity of unmanaged than managed plots up to the radius of 2.5 km from the plot centre (Table S3).

3.2. Lichen species diversity

The number of epiphytic and epixylic lichen species recorded in the plots was always higher in the unmanaged (mean = 143, SD = 20) than the paired mature managed plot (95 ± 20), ranging from 54 to 174 species per plot (Fig. S1). The number of red-listed species in unmanaged forests (44 ± 9) exceeded more than twice the records from mature managed forests (20 ± 8).

The GLS models revealed a strong positive effect of microhabitat heterogeneity on both lichen species richness and the number of red-listed species, while microhabitat frequency had no or even a negative effect (Table 1). Regarding the spatial continuity of near-natural forest habitats, we documented a positive effect of these habitat extents in the vicinity of the plots for lichen species richness and, less convincingly, for the richness of red-listed species. For lichen species richness, the effect was strongest when we evaluated an area with a radius of 1 km around the plot (i.e., >300 ha) (Table S6). Therefore, we can conclude that both microhabitat heterogeneity and the surrounding habitat extent convincingly supported lichen species richness. The results of the GLS models with standardized continuous explanatory variables show that values of the coefficients do not differ considerably (Table S7 and S8). In addition, a significant part of the variability of lichen species richness and number of red-listed species in the plots was further explained in the models by the affiliation of the plot to mature managed or unmanaged forests, as a proxy of temporal continuity of natural succession after forest management abandonment (Fig. 2).

Species composition of lichen communities varied among plots considerably and the main component of dissimilarity represented spatial turnover. However, if we look at the paired plots, lichen communities in mature managed forests were partially nested to communities in unmanaged forests (Fig. S2). Dissimilarity in species composition among plots corresponded with dissimilarities in composition of microhabitat types (Fig. 3).

In ten 1-ha large plots in unmanaged forests, we recorded 482 epiphytic and epixylic lichen species while only 323 species in the mature managed forests (Fig. 4; Table S5). In total, these 513 species represent a substantial part of epiphytic and epixylic lichen biota in Central Europe. Regarding species pools of threatened species, we found 185 and 112 red-listed species in unmanaged and mature managed forests, respectively. More than a third of the species (191) were strictly associated with unmanaged forests while only 32 species were recorded only in mature managed forests. Hence, the lichen communities in managed forests represent rather a subset of those in unmanaged forests.

4. Discussion

4.1. Microhabitat heterogeneity as indices of habitat quality

Based on an exhaustive survey of ten hot-spots covering a substantial part of the epiphytic and epixylic lichen species pool in Central Europe, we provide support that species richness and composition of these

Table 1

Results of final GLS models predicting species richness and number of red-listed species in the study plots on the basis of the set of explainable variables. Regression coefficients, confidence intervals and significance levels are given for explanatory variables. The symbol *** indicates significance at the level $p < 0.001$, ** $p < 0.01$ and * $p < 0.05$. Two data sources used for areas of near-natural forest habitats brought significant effect on species richness (CORINE Land Cover and NATURA 2000 forest habitats). Selection of the final models is presented in Table S6.

	Species richness				Number of red-listed species			
	(CORINE)		(NATURA 2000)		(CORINE)		(NATURA 2000)	
	Regression coefficient	Confidence intervals (Lower; upper)	Regression coefficient	Confidence intervals (Lower; upper)	Regression coefficient	Confidence intervals (Lower; upper)	Regression coefficient	Confidence intervals (Lower; upper)
Elevation	0.0273	−0.0146; 0.0692	0.0215	−0.0212; 0.0642	0.0069	−0.0087; 0.0225	0.0055	−0.0105; 0.0215
Microhabitat frequency	−0.1254*	−0.3425; 0.0917	−0.1579*	−0.3868; 0.0710	−0.0410**	−0.1052; 0.0232	−0.0473**	−0.1170; 0.0224
Microhabitat heterogeneity	3.5210***	−1.6073; 8.6493	3.2994***	−1.9692; 8.5680	1.4316***	−0.1893; 3.0525	1.3107***	−0.3564; 2.9778
Near-natural forest habitats in area with radius of 1 km	0.3058*	−0.0017; 0.6133	0.3398*	−0.0741; 0.7537	0.0909*	−0.0094; 0.1912	0.0892	−0.0499; 0.2283
Managed/unmanaged stand (as factor)	36.7927**	17.9761; 55.6092	37.4087**	18.0862; 56.7311	20.9564***	15.1599; 26.7529	21.2643***	15.3537; 27.1748

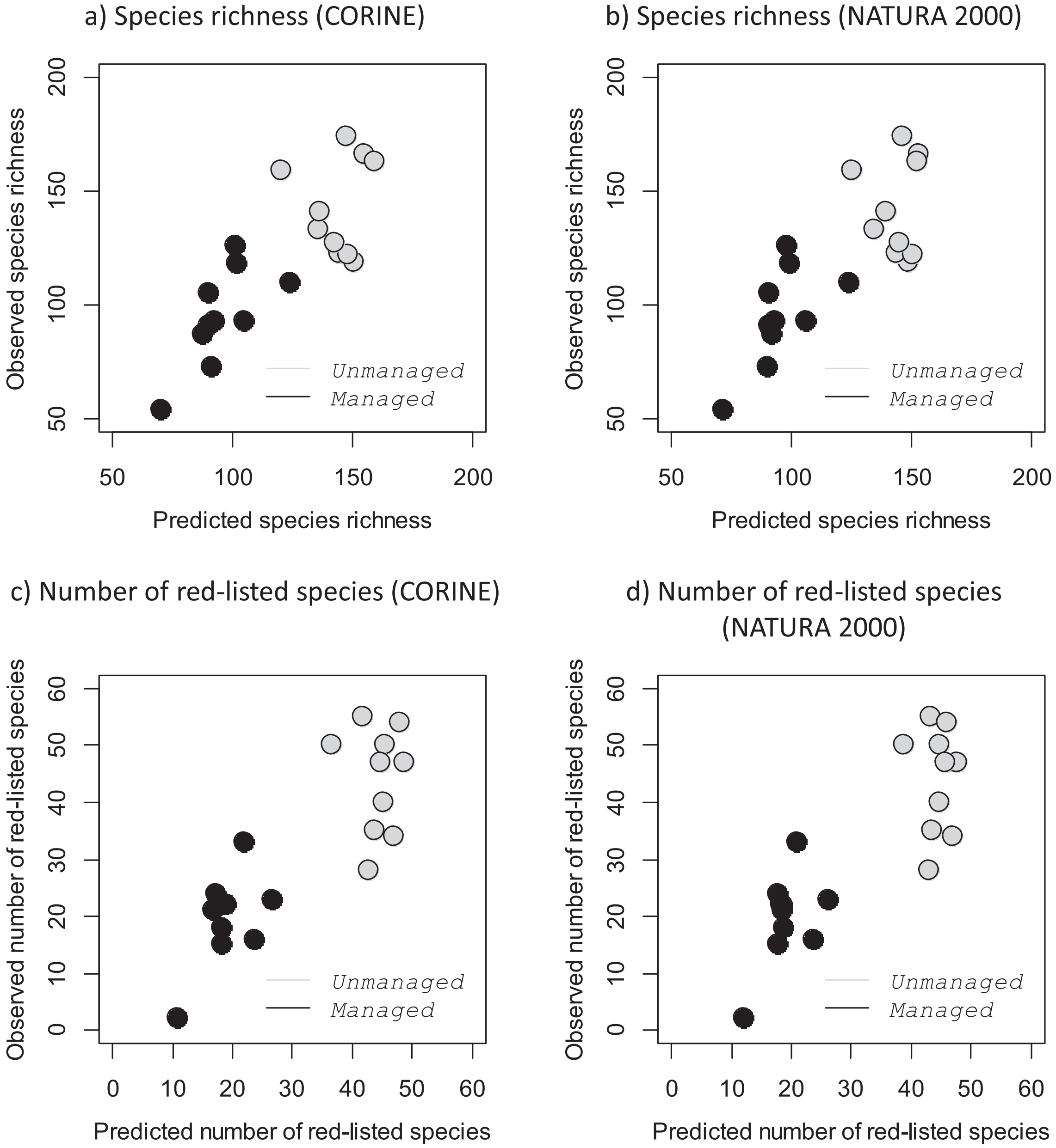

Fig. 2. Relationships between lichen species richness (a and b) and number of red-listed species (c and d) observed in the study plots and predicted by the GLS models. In models (a) and (c), CORINE Land Cover was used for the determination of the area of near-natural forest habitats, the layer NATURA 2000 habitats was used in models (b and d). Complete results of the models are in Table 1.

communities in fragmented temperate forests strongly correlate with microhabitat heterogeneity at the local scale. It is important to note that we found a negative effect of microhabitat frequency on species richness. Hence, the simple frequency of microhabitats may not bring any support for lichen communities while moderate – and in the forest quite inconspicuous — differences in microhabitat heterogeneity may deeply influence both species richness and composition of lichen communities. The importance of specific (micro)structures for epiphytic and epixylic lichen species, and especially those threatened, has been already documented in boreal and temperate forests (Fritz and Heilmann-Clausen, 2010; Johansson et al., 2012; Ranius et al., 2008). A novel finding of our study is the demonstration of a close correspondence between variability in compositions of microhabitats and lichen species communities at the regional scale. In other words, spatial turnover of microhabitat types goes hand in hand with changes in lichen species composition. This fact provides further support that microhabitat heterogeneity is a prerequisite for lichen species diversity at the regional scale.

Lichen species diversity is also related to some other structural features of forest habitats, e.g., the occurrence of large and old trees (Hofmeister et al., 2016; Johansson et al., 2013b). All these structures are derived from forest (tree) age, and their occurrence generally increases with stand maturity (Kozák et al., 2023; Ranius et al., 2008). In our study, we surveyed only mature managed and unmanaged forests and, therefore, most of these structural attributes, such as the presence of old trees with fissured bark, were quite similar throughout the plots. This shortening of the gradient of many potentially important forest structural attributes enabled us to isolate the effect of microhabitat heterogeneity.

Due to focusing the research on mature managed and old unmanaged forests, the potential positive effect of microhabitat frequency for lichen communities might be reversed. In our study, the number of mature

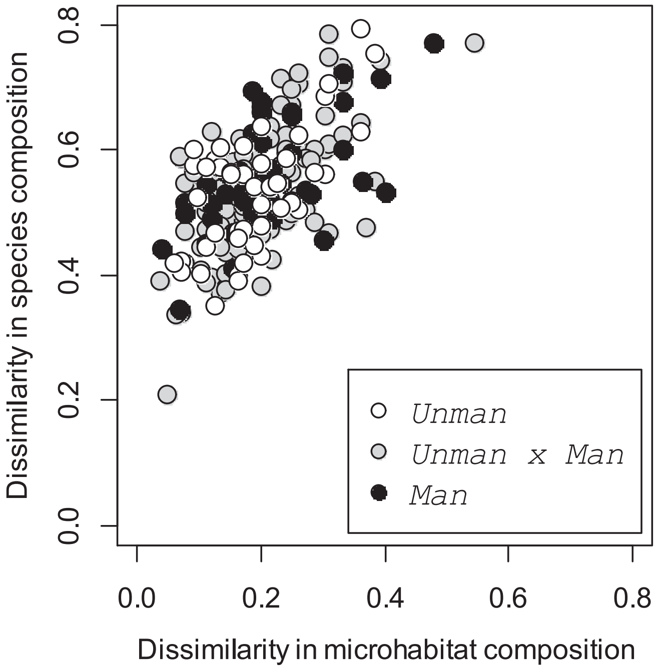

Fig. 3. Relationship between dissimilarity in composition of microhabitat types and dissimilarity in lichen species composition in the study plots; dissimilarity is expressed by Sørensen dissimilarity indexes between each pair of the plots (Mantel statistic $r = 0.5784$, $p < 0.001$).

trees tended to be higher in mature managed forests than in naturally more open unmanaged forests. As tree age increases, so does the probability that at least one microhabitat appears (Ranius et al., 2008). Consequently, the frequency (density) of the trees with microhabitat(s) in mature managed forests mostly exceeded their number in unmanaged forests in our study. Similar frequency of microhabitats in managed and unmanaged forests has been previously documented in other temperate forests (Larrieu et al., 2014). Due to the high number of young trees in the plots, and especially those with rather lower lichen species richness (Table S2), the negative effect of microhabitat frequency on lichen species richness would not be reduced even if we included them into the models. However, if we surveyed managed forests along the entire gradient of their age structure, the microhabitat frequency would be probably considerably higher in unmanaged forests (Hofmeister et al., 2015, 2016).

4.2. Area of near-natural forest habitats as indices of habitat extent

We showed that lichen species richness and number of red-listed species were affected by the area of near-natural forest habitats in the surrounding landscape as was previously documented in other regions of European temperate forests by Paltto et al. (2006) and Nascimbene et al. (2012). Based on our results, an appropriate scale for the protection of extant lichen diversity should optimally have a radius of about 1 km, which means an area exceeding 300 ha. The area of near-natural forests represented >50 % of this area around more than half of the plots in both managed and unmanaged forests. The near-natural forests rich in old living and dead trees with the area larger than several tens of hectares are very scarce in the Central European landscape except for within national parks. However, national parks protect only some types of forest vegetation (e.g. mountain spruce forests, lowland oak-dominated forests) while the other types (e.g. beech forests) are protected in small and mutually isolated forest reservations with areas of a few tens of hectares. Lichen species closely associated with specific microhabitats have little chance of sustaining viable populations, as specific microhabitats may simply disappear for a certain period from area-limited habitats (Johansson et al., 2012; Roberge et al., 2011). Low dispersal rate of lichens likely further exacerbates the negative effect of small and mutually isolated suitable habitats on lichen populations (Ellis, 2012). Low dispersal rate may even determine colonization of new habitats rather than the structural attributes of those habitats (Sillett et al., 2000). On the contrary, the generally low dispersal ability of lichen species has been sometimes questioned and lichens are considered to be organisms capable of – at least occasional – long-distance dispersal (Gjerde et al., 2015).

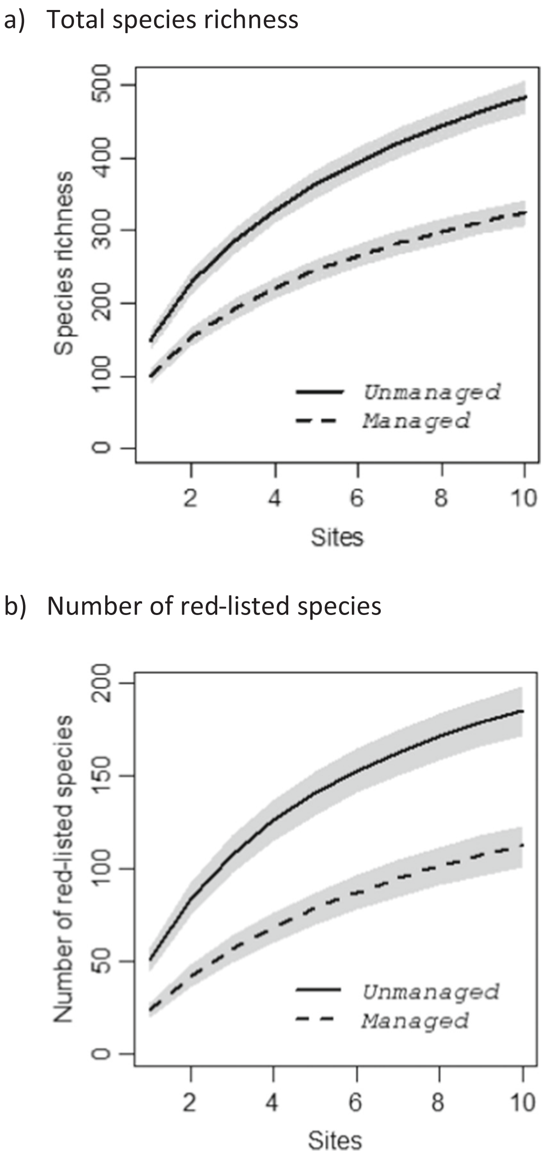

Fig. 4. Species accumulation curves for total species richness (a) and number of red-listed species (b).

Notwithstanding lichen dispersal ability, we have enough data demonstrating that species-rich communities of epiphytic and epixylic lichens with threatened species are spatially limited to relatively small hot-spots in Central Europe (Malíček et al., 2019; Malíček and Palice, 2013; Vondrák et al., 2022). A major part of the Central European landscape is occupied by a small subset of generalist epiphytic lichen species (Hauck et al., 2013; Hofmeister et al., 2015, 2016). In this study, we convincingly documented that even (over-)mature near-natural managed forests hosted only parts of species pools of nearby unmanaged forests, even if the area of near-natural forest habitats were larger around the plots of mature managed forests than unmanaged forests in forest reservations. This result does not diminish the importance of the extent of near-natural forests in surrounding landscape, but merely points to the uppermost importance of microhabitat heterogeneity and temporal continuity at the local scale.

Some localities of mature near-natural forest habitats in the Czech Republic, where forest structure and microhabitat heterogeneity might be potentially important for lichen biota, are still species poor, likely due to lingering influence of past acid deposition (Hauck et al., 2013; Hofmeister et al., 2016; Malíček et al., 2019). This fact can partly explain the concentration of the study plots (hot-spots) in the southern portion of the Czech Republic, where historic deposition loads were generally lower (Oulehle et al., 2016).

4.3. Temporal continuity of spontaneous forest succession

Lichen species richness and number of red-listed species were consistently higher in unmanaged than managed forests, even if we take into account differences in microhabitat heterogeneity at the local scale and the area of near-natural forest habitats (habitat extent) that surrounded them. We used the categorisation of managed and unmanaged forests as a proxy for the length of natural succession after the abandonment of regular forest management, i.e., temporal continuity of "natural" forest habitats. Although we should acknowledge that this categorisation is only an approximate and qualitative approach, nothing more precise is available. It would be illusory trying to determine the time elapsed since the last management intervention, especially since we selected plots in (over-)mature managed forests where the last intervention likely happened decades ago. Similarly, we cannot determine the time of forest management abandonment even in forest reserves. Although we know the exact year of the formal announcement of their protection (from 1838 to 1992), in some cases, and always in the case of reservations established in the 1990s, there had been several decades without any management intervention before the protection was declared. On the contrary, certain management interventions (e.g., individual deadwood removal) were regularly carried out in many forest reservations established in the first half of 20th century long after their protection was declared. Overall, the simple distinction of managed and unmanaged stands can be used as a proxy of temporal continuity since the unmanaged forests have not been clear-cut at least in the past 150 years and with certainty, they had several decades longer continuity of spontaneous development than the managed forests at each locality. The results of the models strongly suggest that even simply expressed temporal continuity of natural succession likely provides an extra stimulus for lichen communities that may not be reflected by some measurable aspects of forest structure, at least those considered in our study. The continuity of the forest habitats can be closely linked with the age of particular trees that should be closely coincided. The oldest trees likely provide the highest heterogeneity of forest microhabitats and (micro) habitat conditions, including higher pH of the bark (Fritz and Heilmann-Clausen, 2010). Hence, the effect of habitat continuity can be – at least partially — explained by extraordinary properties inherent to the oldest trees that are lacking in the mature managed forests.

At the level of forest habitats, habitat continuity is more or less related to habitat maturity — which both supports lichen species diversity — but these effects should not be confused (Janssen et al., 2019; Nordén et al., 2014). In our study, we reduced the influence of different habitat maturity between managed and unmanaged forests through the selection of the oldest managed forests in the vicinity of forest reservations, where age was mostly not far from the age of the forests in the reservations. In fragmented temperate European forests, both habitat maturity and habitat continuity are the prerequisites for establishment of habitat conditions that would be suitable for the widest range of forest-dwelling taxa, including epiphytic and epixylic lichens (Flensted et al., 2016; Hofmeister et al., 2019; Janssen et al., 2017). The positive effect of forest continuity on lichen diversity may be confounded with the effect of some other structural features (e.g., deadwood volume) and/or characteristics derived from forest structure (e.g., canopy closure) that have not been measured and evaluated in this study (Nascimbene et al., 2013). However, these properties of forest habitats are inevitably connected with forest continuity and, at least partially, are the result of continuity (spontaneous forest development).

When assessing lichen diversity in relation to habitat conditions, like in this study, we should also consider some uncertainty due to the time lag between extinction and recolonization of populations in the respective habitat (Öckinger and Nilsson, 2010; Watts et al., 2020). In this respect, our results can be interpreted in two ways. On the one hand, the still high species richness and the contribution of threatened species in the unmanaged forests may exceed the environmental capacity of the habitat, thus providing an overly optimistic view of the status of the lichen community. This description would indicate that the lichen community live in extinction debt (Jackson and Sax, 2010). On the other hand, we may also think that conditions in mature managed and still species-poor forests may already be suitable for many other species, including rare ones, and if we protect these habitats from management interventions, they will be colonized in the (near) future (Watts et al., 2020). The latter explanation gives further support for the effect of temporal continuity on lichen species richness observed in our study.

5. Conclusions and implication for conservation

The results of this study confirmed the crucial importance of microhabitat heterogeneity, and spatial and temporal habitat continuity for lichen species maintenance in fragmented temperate European forests. We further documented that species-rich lichen communities, including rare species, still survive in the spatially restricted hot-spots and capture a substantial part of the lichen biota of temperate forests. However, the current size of the hot-spots may not guarantee continual maintenance of suitable conditions and substrates for specific lichens and the survival of lichen populations in the coming decades. Effective measures that support these species are required to address all relevant aspects of habitats: their quality (microhabitat heterogeneity), and spatial and temporal continuity. Specifically, this means a cessation of forest management in mature managed forests in the landscapes surrounding lichen hot-spots, but even better, in the entire Central European landscape. In this sense, the implementation of the 2030 Biodiversity Strategy that calls for strict protection of 10 % of the territory appears to be an effective step towards lichen conservation. Currently, only about 1.5 % of the territory of the Czech Republic is strictly protected, but at the same time it has a relatively high area of over-mature managed forests (~3 % of the area of the Czech Republic), that are partially neither protected nor economically attractive (Anonymous, 2022). It is the protection of these over-mature managed forests that could be key measure towards effective conservation of lichens in the Czech Republic and Central Europe as a whole.

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CRediT authorship contribution statement

Jeňýk Hofmeister: Writing – review & editing, Writing – original draft, Methodology, Formal analysis, Data curation, Conceptualization. **Václav Pouska:** Writing – review & editing, Methodology, Investigation, Data curation. **Zdeněk Palice:** Writing – review & editing, Investigation, Data curation. **Jaroslav Šoun:** Writing – review & editing, Investigation, Data curation. **Rhinnanon Gloor:** Writing – review & editing. **Marek Brabec:** Writing – review & editing, Formal analysis. **Jan Vondrák:** Writing – review & editing, Methodology, Investigation, Data curation, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

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