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Historical charcoal burning and coppicing suppressed beech and increased forest vegetation heterogeneity

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Abstract

Questions: Long-term legacies of historical human activities in temperate forests are increasingly recognised as an important driver of vegetation diversity and composition. To uncover centuries-old legacies, novel approaches are, however, needed. Here, we combine anthracology of historical charcoal kilns and long-term vegetation resurveys. We asked whether the historical coppicing oriented on charcoal production affected tree-species composition and how the forest understorey vegetation changed after the coppicing was abandoned.

Location: Temperate broadleaved forests in the Slovak Karst National Park, central Europe.

Methods: To explore the historical forest structure and long-term changes in tree composition, we sampled charcoal remains from 28 historical kilns, identified the burnt tree taxa and estimated the original diameter of the burnt wood. To analyse the vegetation changes over the last four decades, we resurveyed plant composition of 60 quasi-permanent plots established in 1975.

Results: Historical charcoal burning was associated with coppicing, which decreased *Fagus sylvatica* dominance and favoured *Quercus* spp. in the tree layer. Several decades after the abandonment of coppicing, we observed the decline of *Quercus* spp. and spread of shade-casting tree species with nutrient-rich litter. This probably triggered the identified demise of light-demanding species, the spread of nitrophytes and taxonomic homogenisation of the forest understorey.

Conclusions: The shift from historical coppicing to current high-forest management was likely a main driver of the observed taxonomic homogenisation and decline of light-demanding plants, as in other European lowland forests. Long-term data from charcoal kilns showed, however, that closed-canopy forests dominated by beech were historically more common and observed changes in vegetation thus represent a natural process. Findings also suggest that coppicing taking place over centuries enhanced diversity of forest understorey vegetation. Our novel approach combining a vegetation resurvey and charcoal kiln anthracology thus uncovered otherwise hidden links between current biological processes and the historical human legacies, with consequent important implications for nature protection and management.

KEYWORDS

anthracology, biotic homogenisation, charcoal burning, charcoal kiln, coppicing, forestREplot, historical ecology, historical forest management, human legacies, land-use change, vegetation resurvey

1 | INTRODUCTION

The biodiversity of temperate forests is changing due to ongoing environmental and land-use changes. In European lowland forests, abandonment of traditional forest management during the 19th and 20th centuries caused significant diversity loss and compositional turnover in forest vegetation (Keith *et al*., 2009; Kopecký *et al*., 2013; Perring *et al*., 2018). Most of these changes have been documented by resurveying of historical vegetation plots (Verheyen *et al*., 2017). Vegetation resurveys can reach only a few decades into the past but observed vegetation changes can reflect processes from further back (Bernhardt-Römermann *et al*., 2015). Therefore, to elucidate forest changes over longer timescales, other methods like paleoecology, dendrochronology and archaeology must be applied (Szabó and Hédl, 2011; Feiss *et al*., 2017). A combination of different methods can provide novel insights and often reveal the significant role of historical human management (e.g. Samojlik *et al*., 2013a; Pini *et al*., 2017).

Analyses of soil charcoal are increasingly used as an effective method to allow detailed and spatially explicit reconstruction of forest history (Touflan *et al*., 2010; Robin *et al*., 2013; Adámek *et al*., 2015). Charcoal remains from former charcoal kilns provide information at fine spatial scales, capturing local woody-species composition and revealing the history of landscape management (Ludemann, 2003; Deforce and Haneca, 2015; Knapp *et al*., 2015; Dupin *et al*., 2017). The wood used for charcoal burning came from the immediate vicinity of kilns and, with some exceptions (Deforce *et al*., 2013; Samojlik *et al*., 2013b), it was used unselectively and thus accurately reflects tree-species composition of a site (Ludemann *et al*., 2004; Knapp *et al*., 2015; Ludemann *et al*., 2017).

In this study, we combine the resurvey of historical vegetation plots with analyses of charcoal kiln remains to investigate the impact of historical changes in forest management on the vegetation dynamics of temperate forests situated in the Slovak Karst National Park (southeastern Slovakia) included, since 1977, in the UNESCO's "Man and the Biosphere Programme" due to its high biodiversity values and karst phenomenon. Due to the specific forest-use history that combined coppicing with charcoal production and rich legacy of historical vegetation plots, this region provides a unique opportunity to apply a combination of these methods. For centuries, the forests in the Slovak Karst supplied wood charcoal for the iron industry but, from the end of the 19th century, the demand for charcoal rapidly declined (Lasák, 1987; Bergl and Lasák, 1988). Whether and how this affected forests, their tree-species composition and structure, is quite unknown. Historically, many forests in the Slovak Karst were coppiced or managed as coppice-with-standards. This management was also very likely associated with charcoal burning and continued until the 1950s. Abandoned coppices were transformed to high forests during the latter half of the 20th century. Whether these substantial changes in forest management affected vegetation diversity and composition in this biologically valuable region is, however, unknown.

To investigate the legacies of historical charcoal burning and to link them to long-term vegetation changes, we combined anthracological analysis of historical charcoal kilns with vegetation resurveying of quasi-permanent plots. Specifically, we: (i) used anthracology to reconstruct tree-species composition during the period of charcoal production and compared it to the tree-species composition from resurveyed vegetation plots; (ii) investigated forest stand structure during charcoal burning; and (iii) explored whether the plant communities exhibited taxonomic homogenisation and compositional shifts during the last four decades due to the forest succession after the abandonment of coppicing. Answering these questions are important not only because there is a lack of evidence of recent vegetation changes from this biologically unique region, but also because our approach, which combines methods and evidence reflecting different time periods, could bring new insights on human legacies in forests.

2 | METHODS

2.1 | The Slovak Karst and its history

Located in the southeast of Slovakia, the Slovak Karst is in one of the most well-developed karst regions in central Europe, overlapping the border between Slovakia and Hungary. The investigated forests are situated mostly on the Koniarska and Silická plateaus, with elevations ranging from 270 m up to 700 m a.s.l. The bedrock is mainly formed by limestones and dolomites of the Middle and Upper Triassic on which the most frequent soils are Eutric and Chromic Cambisols on the plateaus and (Chromi-) Rendzic Leptosols on the slopes. On plateaus (at 600 m a.s.l.), the mean annual temperature is around 7°C and the mean annual precipitation reaches around 750 mm (Čermák, 1994).

Forests are mainly dominated by *Quercus* spp. (*Quercus petraea* agg., *Quercus cerris*) or, depending on site conditions, *Fagus sylvatica*. The lower tree layers are often dominated by *Carpinus betulus*. On the steep slopes or more rocky sites *Acer platanoides*, *Fraxinus excelsior*, and *Tilia* spp. are admixed. In general, the woody-species diversity is rather high and other trees like *Acer campestre*, *Sorbus torminalis* or *Prunus avium* frequently accompany the dominants. Forest vegetation is variable from supramediterranean thermophilous types on steep, south-exposed plateau edges to mesophilous submontane beech-dominated stands on the highest hilly positions of the plateaus. Calcareous bedrock, environmental heterogeneity with a biogeographical position between the Carpathian mountains and the Pannonian Basin, as well as no glaciation during the Pleistocene epoch enhance the overall biodiversity of the local biota (Mráz and Ronikier, 2016; Večeřa *et al*., 2019).

The history of forest use was closely associated with the iron industry and was at its peak during the 19th century when immense amounts of charcoal were needed to smelt iron ore. According to the historical sources, iron had been produced in the area since the Iron Age, but production markedly increased after the 17th century (Lasák, 1987; Bergl and Lasák, 1988; Nagy, 2008). At the end of the 18th century, there were 24 so-called "Slovak furnaces" consuming altogether around 24,000 m^3 of wood per year. At the beginning of the 19th century, these old-type furnaces were replaced by blast furnaces and local iron-works were producing one-third of the iron in the whole Kingdom of Hungary. Until 1885, all blast furnaces in Slovakia were using charcoal (Petrík and Mihok, 2007). The change to coke fuel was rather slow and, during the first quarter of the 20th century, all iron industry in the region declined.

There is a lack of information about how forests in this region were managed during charcoal burning but, according to typical forest management practices of that time and the current state of forests, coppicing is very likely. Moreover, such management continued even after the abandonment of charcoal production (Appendix S3). During the second half of the 20th century across Slovakia all coppiced stands gradually transformed into high forests. This was also the case in the Slovak Karst, where the transformation was most intensive between the 1960s and 1980s. Currently, coppicing is no longer practised in the area.

2.2 | Charcoal kilns: density, taxon identification and wood diameter

In the field, we identified charcoal hearth remains based on the following criteria: (a) the circular or slightly ellipsoidal shape of a platform; ad (b) the presence of a charcoal layer on the soil surface or a significant admixture of charcoal in the topsoil. Each identified kiln was located using GPS. The mean distance from each charcoal kiln platform to the nearest two others was 115.3 m (min. 14.3, max 465.4 m) which implies an approximate density of 75 platforms per 1 km^2.

To reconstruct historical tree-species composition and forest stand structure, we sampled 28 of the 113 identified charcoal platforms that were nearby the vegetation plots. From each charcoal platform, we took approx. 1 litre of soil sampled from five soil trenches distributed over the platform's surface and extracted from the entire thickness of the charcoal layer. Five subsamples were then mixed to secure homogeneity and to reduce the impact of the fragmentation of single wood particles. In the laboratory, we separated charred wood particles from the mineral soil fraction with flotation and wet sieving on 1-mm mesh (Carcaillet and Thinon, 1996). Remaining rootlets and other unburnt organic debris was removed by hand picking under a stereomicroscope.

From each sampled kiln, we taxonomically identified at least 50 charcoals observing transversal, tangential and radial sections under an incident light microscope. Their determination was based on distinct anatomical features, which were compared to published atlases (Schweingruber, 1990; Benkova and Schweingruber, 2004) and personal reference collections.

We attempted to estimate dimensions of the exploited wood by measuring the size distribution of charcoal remains (Ludemann, 2008). This enabled us to link anthracological data to wood used for charcoal production and to speculate on forest structure and, therefore, prevailing form of forest management (coppice vs. high forest) in the surroundings of each historical kiln site. This was carried out during the taxonomic identification by measuring the maximum diameter of each charcoal fragment (maxD, $n = 1{,}361$). We adopted a diameter stencil method (Nelle and Ludemann, 2002; Nelle, 2003), but the protocol was modified by the use of image analysis to estimate more rigorously the bending of growth rings. First, we captured a digital image of charcoal's transversal section under a low-magnification stereomicroscope. Then, we computed the best-fitting circle of 30 test points located along one of the outermost tree rings present in the charcoal fragment. The image processing and diameter calculations were done with the aid of ImageJ (Schneider *et al*., 2012). To ensure data quality, we omitted charcoal pieces with a wave-like form of tree rings and fragments that did not display a transversal wood section to a sufficient extent (ca > 2 cm^2).

To allow a relative comparison of the size-class distribution of burnt wood between each kiln site, we employed the formula proposed by Nelle and Ludeman (2002). A mean diameter (meanD) value was calculated based on all measured charcoal fragments present in a particular charcoal assemblage. To explore the relationship between mD and proportion of different tree species in charcoal spectra we used generalised additive models fitted with the *mgcv* R package (Woods, 2011). Moreover, by comparison of the mD-value with known size-class distributions of experimental charcoal burning (Ludemann, 2008), we were able to make inferences about the woods used for charcoal production.

2.3 | Vegetation survey and resurvey

To explore the vegetation changes during the last four decades, we resampled 60 semi-permanent plots originally established within the national forest vegetation survey in 1975 (Randuška *et al*., 1986). In each 500-m^2 plot, experienced forest ecologists identified all vascular plant species and estimated their cover using Zlatník's scale (Zlatník, 1978). To capture the stand structure, they recorded tree and shrub species separately in seven vertical layers defined according to their relative height. Additionally, various site characteristics were recorded according to the standardised methodology of the survey. The plot position was indicated on a detailed topographic map (1:10,000 scale) and a tree in the middle of the plot was specifically marked (Appendix S2).

In 2013 and 2015, using the information about plot co-ordinates extracted from the historical survey maps, a description of plot topography and tree-species composition, we relocated approximately 50 plots and 10 plots exactly (the original mark on the central tree was found). The relocation should therefore be sufficient in terms of error resulting from approximate plot relocation (Kopecký and Macek, 2015; Verheyen *et al*., 2018). We recorded the vegetation on all relocated plots using the original sampling protocol.

2.4 | Data analyses — changes in tree species composition

To explore long-term changes in tree-species composition, we first matched each sampled charcoal platform to the nearest vegetation plot. The mean distance between sampled platforms and resurveyed vegetation plots was 142.3 m (min. 13.7, max. 328.6 m). Then, we compared relative proportions of tree species between the 28 sampled charcoal platforms and 28 pairs of baseline and resurvey vegetation records from the nearest vegetation plots. Due to the uncertainties in charcoal identification of some taxa (e.g. *Acer* spp.) and because charcoal spectra were dominated by few species, we distinguished four tree-species groups of different taxonomical levels to link charcoal and vegetation records: (i) *Carpinus betulus*; (ii) *Fagus sylvatica*; (iii) *Quercus* spp. (*Quercus petraea* agg. and *Q. cerris*); and (iv) others (mainly *Acer platanoides*, *A. pseudoplatanus*, *Tilia* spp. and *Fraxinus excelsior*). The proportion of tree species from vegetation records was calculated only with cover estimates from tree and shrub layers (i.e., height above 1.3 m, therefore excluding tree regeneration which varies interannually due, for example, to mast years).

To test whether tree-species composition changed significantly through time, we used permutation-based MANOVA (Anderson, 2001) calculated on a mBray–Curtis dissimilarity matrix and tested with 999 permutations restricted within temporally connected samples. Because significant result from PERMANOVA can reflect both changes in species composition and heterogeneity (Anderson, 2001), we also compared changes in compositional heterogeneity through the test of multi-variate homogeneity of group dispersions (Anderson, 2006) using 999 permutations restricted within temporally connected samples.

2.5 | Data analyses — changes in understorey vegetation

First, we standardised species taxonomy between the surveys according to Marhold and Hindák (1998) and, to further reduce possible observer bias, we merged several taxa with potentially problematic determination during field survey (Appendix S1). Cover estimates of these merged taxa were combined in Juice 7.0 (Tichý, 2002) following the formula described in Fischer (2015).

To visually compare vegetation patterns between the surveys of all 60 vegetation plots, we used Non-metric Multi-Dimensional Scaling (NMDS) ordination based on the dissimilarity matrix calculated with the Simpson dissimilarity index. We used this index because it is not sensitive to richness differences and thus represents a robust measure of species turnover between surveys (Baselga, 2010). We ran global NMDS with weak treatment of ties with many random starts to reduce the possibility of finding a sub-optimal solution using the *metaMDS* function from the vegan R package (Oksanen *et al*., 2018). The convergent two-dimensional configuration with the lowest stress was centred and rotated by PCA to maximise variance along the first ordination axis. To show overall changes in compositional heterogeneity between surveys, we calculated standard deviation ellipses around multi-variate medians of the plots from each survey using an *ordiellipse* function based on the 0.95 standard deviation of plot co-ordinates in NMDS space. Finally, we projected vectors showing increasing proportion of *Fagus*, *Quercus* spp. and *Carpinus* in the tree layer into NMDS space passively using the *envfit* function from the vegan R package.

To explore whether vegetation changes after the abandonment of historical management resulted in vegetation homogenisation, we compared plot dispersion around multi-variate centroids between the baseline and the resurvey (Anderson *et al*., 2006). As a measure of the multi-variate centroid, we used the multi-variate median instead of the less robust mean. To calculate the statistical significance of the difference between the baseline and the resurvey, we used the test of multi-variate homogeneity of group dispersions (Anderson, 2006) based on 999 permutations restricted within temporally paired samples.

To identify species that have significantly decreased or increased in frequency between the surveys (loser and winner species), we tested whether the proportion of plots occupied by each species changed over time. For the test, we used 999 permutations and adjusted the resulting p-values using Šidák's correction for multiple testing (De Cáceres and Legendre, 2009).

To test whether changes in species occurrence between the surveys were related to species' ecological requirements, we used permutation trees implemented with the *ctree* function in the *party* R package (Hothorn *et al*., 2006). As information about species' ecological requirements, we used Ellenberg Indicator Values (EIV, Ellenberg *et al*., 1992). In contrast to problematic community-weighted means of EIV (Zelený and Schaffers, 2012), our approach treats each species individually and uses a permutation test to explore whether species' ecological requirements are able to discriminate between declining and increasing species (Kopecký *et al*., 2013). This approach thus avoids problems associated with community-weighted means, accounts for non-linear hierarchical relationships among variables, properly treats species' EIV as ordinal data, and deals with species that have a not-specified EIV for some environmental gradients (Figure 1).

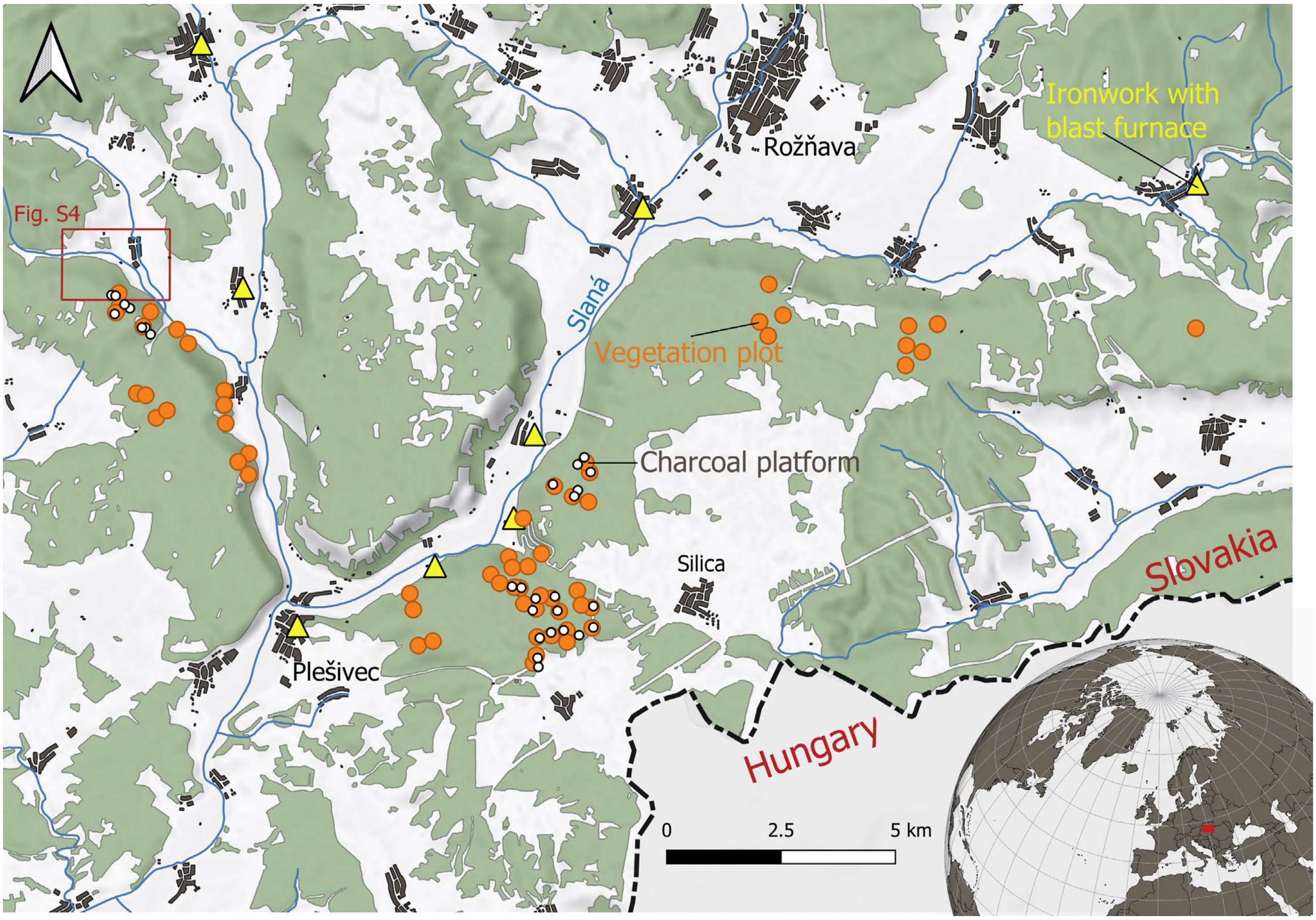

FIGURE 1 Map of the study area showing the position of ironworks with blast furnaces in operation during the 19th century, resurveyed vegetation plots and sampled charcoal platforms (only part of the area was inspected for charcoal platforms). Green shading indicates forests and the red rectangle is the area shown in Figure S4

3 | RESULTS

3.1 | Changes in tree-species composition

The charcoal spectra were dominated by *Fagus sylvatica*, while *Carpinus betulus* was the most dominant tree species in the baseline vegetation survey as well as in the resurvey (Figure 2). The proportion of *Quercus* spp. was similar in charcoal kilns and the baseline survey but decreased in the resurvey. By contrast, the other tree species, mainly *Acer platanoides*, *Tilia* spp. and *Fraxinus excelsior* increased between the vegetation surveys.

Tree-species composition significantly changed through time (PERMANOVA: $F = 4.95$, $p = 0.001$) and these changes were not accompanied by changes in compositional heterogeneity (PERMDISP: $F = 0.34$, $p = 0.74$).

The maximal diameter found in charcoal assemblages was 47.6 cm and the minimum was only 0.6 cm. The mean for the whole dataset was 7.1 cm. This indicates that most forests used for historical charcoal burning had a rather short rotation period and were most likely managed as coppices (Figure 3A). Additionally, the proportion of *Quercus* spp. increases while *Fagus* decreases with increasing mean diameter of wood used in the charcoal kilns (Figure 3B).

3.2 | Changes in understorey vegetation

The overall species composition shifted to vegetation dominated by *Fagus* (Figure 4). Shade-tolerant species increased their frequency, while light-demanding species relatively increased only if they had high nutrient demands (nitrophytes); the remaining majority of relatively light-demanding species did not change on average (Figure 5).

Vegetation heterogeneity decreased by 25% between the surveys (Figure 4). While average plot distance to the multi-variate median was 0.39 in the baseline survey, it was only 0.29 in the resurvey and this taxonomic homogenisation was highly significant ($F = 38.3$, $p = 0.001$).

More species significantly increased than decreased their frequency between the surveys (31 winners compared to four losers). Species that declined were light-demanding thermophilous herbs like *Astragalus glycyphyllos*, *Polygonatum odoratum*, *Ajuga genevensis* and graminoids including oligotrophic species

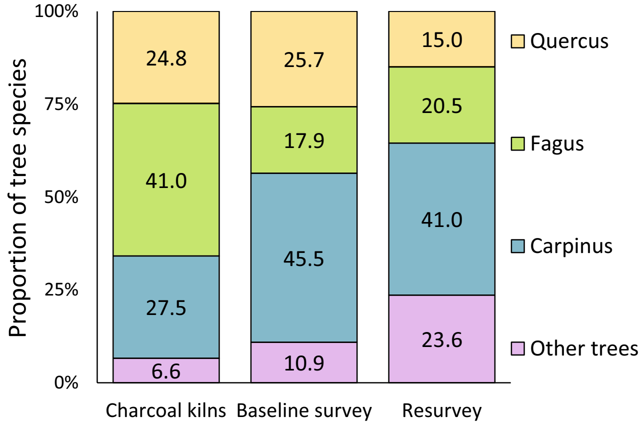

FIGURE 2 The proportion of tree species in 28 charcoal kilns (most likely dating from the 18th and 19th centuries) located nearby 28 vegetation plots sampled in 1975 (baseline survey) and re-sampled in 2013–2015 (resurvey). For the vegetation plots, only the proportion of species in tree layers was used

typical for open oak-dominated forests, like *Dactylis glomerata* agg., *Festuca heterophylla* or *Luzula luzuloides* (Table 1). The more shaded conditions below a denser tree canopy resulted also in a decrease of light-demanding shrubs, particularly *Cornus mas*.

Winner species also indicated the community's shift to mesic stands. They were species typical of beech forests, for example, *Sanicula europaea*, *Pulmonaria obscura*, *Viola reichenbachiana + rivininana* and *Galeobdolon luteum* agg. Geophytes (e.g. *Isopyrum thalictroides*) and myco-heterotrophs (e.g., *Neottia nidus-avis*) also adapted to closed canopies and a thick litter layer. Several nutrient-demanding herb species also significantly increased, for example, *Galium aparine*, *Alliaria petiolata*, *Mercurialis perennis* and *Moehringia trinervia*. Interestingly, saplings of many tree and shrub species also increased significantly, possibly indicating less intense forest management (Table 1). Apart from the juveniles of the tree layer dominants, the frequency of juveniles of originally rare eutrophic tree species also increased (*Acer* spp., *Fraxinus excelsior*, *Tilia* spp., *Ulmus glabra*).

4 | DISCUSSION

4.1 | Historical charcoal burning affected tree species composition

Our results suggest that *Fagus sylvatica* was historically more abundant in the Slovak Karst and that charcoal burning associated with massive iron production was probably the main cause of the decline of *Fagus* during recent centuries. These results are in line with local paleoecological evidence (Němejc, 1936; Wiezik *et al*., 2019) and findings from other regions with a history of intensive charcoal production (Knapp *et al*., 2015; Deforce *et al*., 2018).

Climatic conditions in the Slovak Karst are highly suitable for *Fagus*, which colonised this region earlier than previously thought (Wiezik *et al*., 2019). This early spread might be related to probable glacial microrefugia of *Fagus* in this region (Magri, 2008; Hájek *et al*., 2016; Jamrichová *et al*., 2017). Although there is a lack of suitable environment for organic matter sedimentation in this drained karst region, the available records in travertine deposits also support our findings that *Fagus* was historically more abundant (Němejc, 1936; Krippel, 1957).

The intensity of charcoal production in the studied area is well illustrated by the density of burning platforms of around 75 per 1 km^2. Similar or even higher densities have been reported from other central European regions where wood charcoal was used for iron production (Schmidt *et al*., 2016; Dupin *et al*., 2017; Rutkiewicz *et al*., 2019; Schneider *et al*., 2020). Since 1885, the consumption of charcoal by blast furnaces probably slowly declined due to the change to coke fuel and also the serious decline of iron production at the beginning of 20th century (Petrík and Mihok, 2007). Therefore, the information from charcoal kilns represents mainly the period of the 18th and the 19th century.

According to anthracological analyses, the diameter of wood used in charcoal kilns in the Slovak Karst was generally lower than the reference diameter of wood from coppiced forests in Germany (Nelle, 2003). Despite these values being only relative and not specifying the actual size of the burnt wood, the predominantly low diameter values found in Slovak Karst confirm that forests were managed mainly as coppice during the time of charcoal production. Even now, the stand structure with multiple stems, particularly of *Quercus* spp., is often recognisable in the field (Appendix S3). Similarly, studies from other regions in Europe also identified a link between coppice management and charcoal production (e.g., Deforce and Haneca, 2015; Paradis-Grenouillet *et al*., 2015). The heterogeneity of wood diameter measurements does, however, also suggest that the forest structure and the frequency of cutting were variable in space and time. It may be related to terrain conditions, since flat and more easily accessible areas were preferred (Nelle, 2002; Rutkiewicz *et al*., 2019). Moreover, the low meanD values also suggest that kilns were probably used repeatedly (Knapp *et al*., 2015; Dupin *et al*., 2017). Thinner wood diameters could possibly also be explained by the selective use of bigger trunks for timber. We suppose this to be rather unlikely because of the high demand for charcoal by the iron industry and unselective burning of all available wood in the kiln vicinity reported by many studies (e.g. Ludemann *et al*., 2004; Knapp *et al*., 2015; Ludemann *et al*., 2017). Moreover, bigger trunks which were certainly needed for wooden constructions, could be produced from the standards, from solitary trees that were kept over several cutting periods. This so-called coppice-with-standards management was a typical historical management approach that aimed to produce both wood for fuel and for timber (e.g. Altman *et al*., 2013; Becker *et al*., 2017). Such tree standards were certainly present also in the studied region as documented by historical aerial photography from 1950 and old tree standards found in the field (Figures S3, S4).

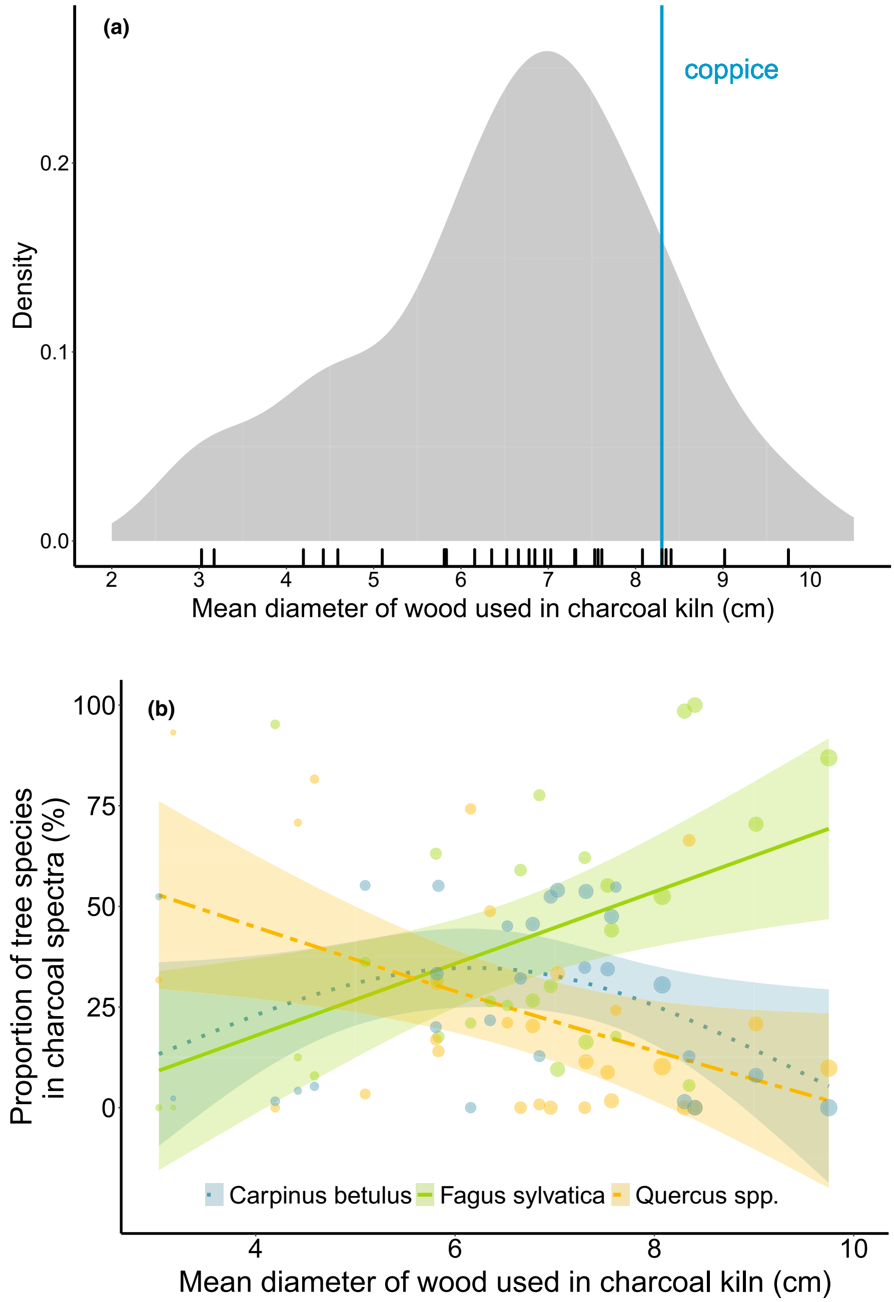

FIGURE 3 Structural parameters of forest stands harvested for charcoal production in 28 surveyed kilns. (a) The kernel density of the mean wood diameter (meanD) used in the kilns (shaded area) and meanD for each sampled kiln (bottom rung). For comparison, the blue line shows meanD from a charcoal kiln built with wood exclusively from coppice (Nelle, 2003). (b) The relationship between the meanD and the proportion of the three most abundant tree species in charcoal spectra; points are scaled by the maximum diameter of charcoal in a particular kiln. Trend lines were fitted with generalised additive models

Our finding of a higher *Quercus* spp. proportion in kilns with lower meanD values together with negative effects of systematic coppicing on *Fagus sylvatica* in central Europe (Leuschner and Ellenberg, 2017) suggests that frequent cutting with short rotation periods promoted *Quercus* spp. over *Fagus*. In Slovakia in the first half of the 20th century, the typical rotation period of coppices for fuel purposes was 30–40 years (Sigotský *et al.*, 1953), but even shorter cycles were historically used in central Europe (e.g. Szabó, 2010). Therefore, we suppose that forests before the charcoal production had possibly been even more dominated by *Fagus* than was shown by the charcoal spectra. A similar shift in forest domination from *Fagus* to *Quercus* was reported from Belgium (Deforce *et al.*, 2018), where early mediaeval kilns were dominated by *Fagus*, while younger by *Quercus*. Further, Knapp *et al.* (2015) found less *Fagus sylvatica* charcoal remains in younger layers accompanied by lower meanD values and supposed that repeated burning resulted into lower numbers of *Fagus* trees in the vicinity of kilns. Species composition in the charcoal spectra including a higher abundance of *Fagus* could be theoretically affected by a preference for certain species in charcoal production, but this is unlikely due to the above-mentioned non-selective burning of all available wood. Moreover, similar patterns of reducing *Fagus* dominance and increasing *Quercus* and other light-demanding tree species due to charcoal production was found also in other regions of Europe (Tolksdorf *et al.*, 2015; Dupin *et al.*, 2017; Deforce *et al.*, 2018). A specific study by Gocel-Chalté *et al.* (2020) identified a similar situation. These authors found a higher

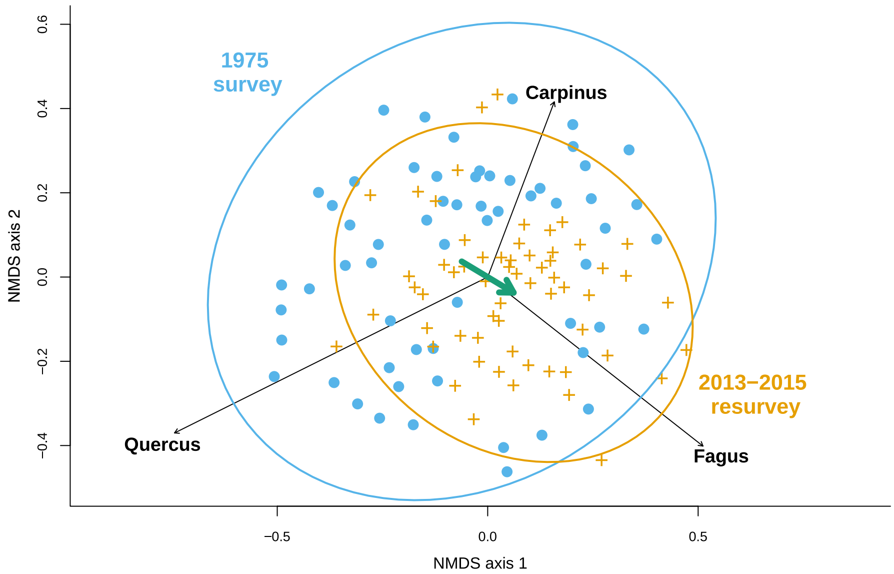

FIGURE 4 Understorey vegetation changes on 60 quasi-permanent plots visualised with Non-metric Multi-dimensional Scaling ordination (NMDS). The understorey vegetation was significantly more heterogeneous in the 1975 survey (blue dots and 95% dispersion ellipse) than in the 2013–2015 resurvey (gold crosses and 95% dispersion ellipse). The green arrow connects multi-variate centroids of both surveys and shows the overall vegetation shift toward the flora typical for *Fagus sylvatica*-dominated forests. The passively projected black arrows show the increasing proportion of dominant tree species in the tree layer regardless of the vegetation survey period

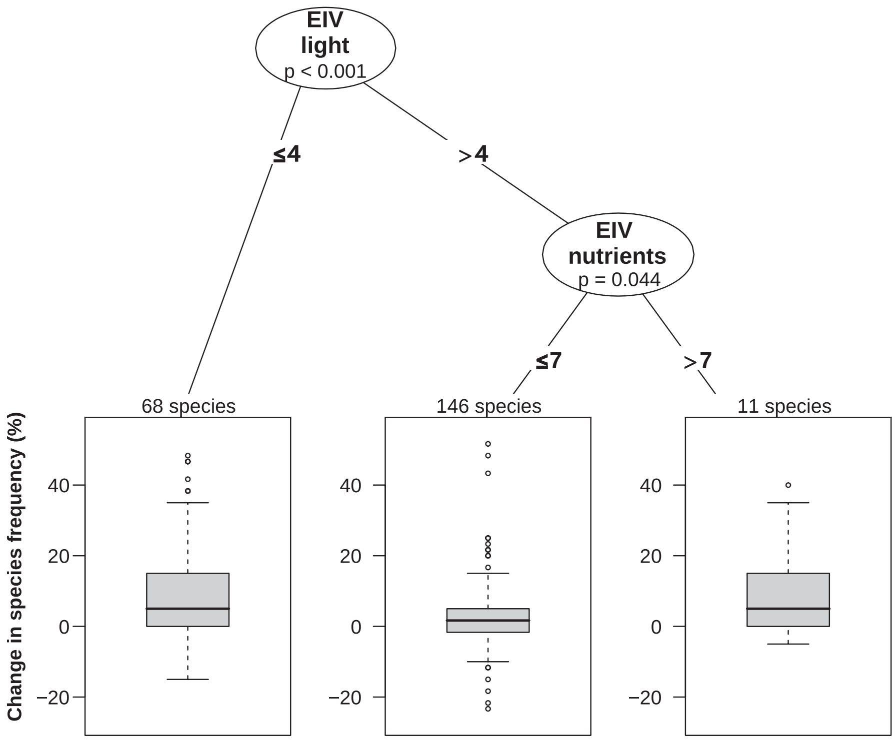

FIGURE 5 Ellenberg indicator values (EIV) structuring the changes in species frequency between the vegetation surveys. The response variable (summarised as box-plot) is the percentage change in each species frequency between the baseline and resurvey. Values below zero indicate declining species and values above zero expanding species. Each split of the tree is described by the EIV used at the split, its permutation-based significance and the EIV value at which the split occurs. The number of species (*n*) is given at each terminal node. While shade-tolerant species (EIV light ≤4) generally increased, species demanding more light (EIV light >4) remained unchanged with the exception of light-demanding nitrophytes (EIV nutrients >7), which increased

abundance of *Fagus* in the charcoal kiln spectra compared to current vegetation and concluded that this reflected natural woodland composition two centuries ago. Interestingly, in these other regions, the historical charcoal production was also associated with coppicing, therefore supporting our interpretation that forest stands in the Slovak Karst were coppiced for charcoal production.

Shifts in woodland composition are certainly related to trees' ability to regenerate under heavy and frequent disturbances that are associated with coppicing and charcoal burning. While pioneer species could benefit from bare and disturbed soil, this could be a disadvantage for others with large and heavy seeds like *Quercus* spp. or *Fagus sylvatica*. Moreover, *Fagus* seeds germinate

TABLE 1 Shortened synoptic table showing only species with a change in frequency above 5% between baseline and resurvey

Species	Layer	Frequency (%)		*p*-value
		Baseline survey	Resurvey	
Species with decrease of frequency (losers)				
Cornus mas + Swida sanguinea	**Tree regeneration**	**63**	**40**	**0.0195**
Astragalus glycyphyllos	**Herb layer**	**30**	**12**	**0.0215**
***Dactylis glomerata* agg.**	**Herb layer**	**68**	**47**	**0.0260**
Polygonatum odoratum	**Herb layer**	**23**	**8**	**0.0441**
Ajuga genevensis	Herb layer	7	1	0.0603
Luzula luzuloides	Herb layer	17	8	0.0663
Clinopodium vulgare	Herb layer	11	4	0.0866
Brachypodium sylvaticum	Herb layer	20	12	0.1399
Festuca heterophylla	Herb layer	12	6	0.1995
Vicia spp.	Herb layer	13	7	0.2178
Veronica chamaedrys	Herb layer	23	16	0.2228
Geranium robertianum	Herb layer	17	11	0.2599
Campanula trachelium	Herb layer	24	18	0.3071
Species with increase of frequency (winners)				
Acer platanoides	Tree regeneration	38	85	0.0002
***Quercus petraea* agg.**	Tree regeneration	22	70	0.0002
Euonymus verrucosus	Tree regeneration	15	67	0.0002
Fagus sylvatica	Tree regeneration	25	72	0.0002
Fraxinus excelsior	Tree regeneration	27	73	0.0002
Galium aparine	Herb layer	20	60	0.0002
Isopyrum thalictroides	Herb layer	2	27	0.0002
Neottia nidus-avis	Herb layer	3	38	0.0002
Polygonatum multiflorum	Herb layer	22	70	0.0002
***Tilia cordata + platyphyllos* + spp.**	Tree regeneration	40	83	0.0002
Ulmus glabra	Tree regeneration	10	52	0.0002
Alliaria petiolata	Herb layer	33	68	0.0004
Carpinus betulus	Tree regeneration	37	75	0.0004
Cerasus avium	Tree regeneration	20	58	0.0004
Roegneria canina	Herb layer	0	15	0.0034
Acer pseudoplatanus	Tree regeneration	27	53	0.0044
Acer campestre	Tree regeneration	53	78	0.0068
***Crataegus* spp.**	Tree regeneration	63	87	0.0070
***Galeobdolon luteum* agg.**	Herb layer	20	43	0.0076
Malus sylvestris	Tree regeneration	0	12	0.0118
Anemone ranunculoides	Herb layer	0	12	0.0120
Moehringia trinervia	Herb layer	2	15	0.0159
***Rosa canina* agg.**	Tree regeneration	20	42	0.0169
***Lonicera* spp. (cf. *L. xylosteum*)**	Tree regeneration	63	83	0.0195
***Fallopia convolvulus + dumetorum* + spp.**	Herb layer	7	23	0.0211
Cephalathera damasonium	Herb layer	12	30	0.0260
Lathyrus vernus	Herb layer	83	97	0.0280
Pulmonaria obscura	Herb layer	38	60	0.0292
Sanicula europaea	Herb layer	7	22	0.0378

(Continues)

TABLE 1 (Continued)

Species	Layer	Frequency (%)		p-value
		Baseline survey	Resurvey	
Viola reichenbachiana + riviniana	Herb layer	47	67	0.0412
Asplenium trichomanes	Herb layer	5	18	0.0429
Melica nutans	Herb layer	10	20	0.0507
Campanula rapunculoides	Herb layer	48	56	0.0531
Mercurialis perennis	Herb layer	29	40	0.0641
Hedera helix	Herb layer	23	34	0.0686
Chaerophyllum temulum + Torilis japonica	Herb layer	11	20	0.0958
Viola mirabilis	Herb layer	7	15	0.0990
Lilium martagon	Herb layer	24	34	0.0996
Cardamine impatiens	Herb layer	15	24	0.1096
Galium odoratum	Herb layer	36	45	0.1115
Geum urbanum	Herb layer	21	30	0.1316
Dryopteris filix-mas	Herb layer	16	24	0.1692
Mycelis muralis	Herb layer	13	20	0.2045
Dentaria bulbifera	Herb layer	46	52	0.2281
Waldsteinia geoides	Herb layer	29	36	0.2452
Vincetoxicum hirundinaria	Herb layer	10	16	0.2454
Tithymalus amygdaloides	Herb layer	31	38	0.2532
Bromus ramosus + benekenii+spp.	Herb layer	25	32	0.2535
Ligustrum vulgare	Tree regeneration	14	20	0.2895
Carex digitata	Herb layer	24	30	0.3200

Note: Species are ordered by the level of significance of the change expressed by *p*-value. Significant change is highlighted in bold. Species with uncertain taxonomic determination between surveys were merged (indicated by "+").

substantially worse on soils affected by charcoal burning than on control soils (Carrari *et al*., 2018). Although pioneer tree species should benefit from disturbances, we found a low proportion of other tree species in the charcoal spectra. That could be a consequence of underestimation of their proportion due to the specific taphonomy of charcoal from these species (Scott and Damblon, 2010), but their low abundance in historical forests is also shown in the vegetation records from the 1975 survey. The great ability of *Quercus* spp. and *Carpinus betulus* to resprout after coppicing (Matula *et al*., 2012; Leonardsson and Götmark, 2014) could also contribute to the observed decrease of *Fagus* in favour of *Quercus* spp. and *Carpinus*. The highest relative levels of *Carpinus betulus* in charcoal kilns were found around mean of meanD values, indicating that *Carpinus* was supported by coppicing of medium intensity. Frequent cutting was likely more favourable for *Quercus* spp., while in stands with longer rotation periods *Carpinus* could be outcompeted by *Fagus*. Therefore, the current higher abundance of more shade-tolerant tree species and an increasing abundance of *Fagus* is probably a direct result of the abandonment of coppicing and reduced management intensity during recent decades (Collet *et al*., 2008). This gradual succession is a natural process, but it has serious consequences for plant biodiversity (Kopecký *et al*., 2013; Chudomelová *et al*., 2017).

4.2 | Understorey homogenisation and shifts in species composition

Spatial heterogeneity in understorey species composition significantly decreased between the surveys. This taxonomic homogenisation was reported also from other regions in temperate Europe (Keith *et al*., 2009; Heinrichs and Schmidt, 2017; Prach and Kopecký, 2018) and suggests a more general trend. Indeed, our results support the hypothesis that the historical management created and maintained small-scale vegetation heterogeneity in temperate lowland forests (Kopecký *et al*., 2013). This small-scale heterogeneity was probably maintained by highly variable management, often applied with different intensity in space and time (Gimmi *et al*., 2008; Prach and Kopecký, 2018).

The most important historical driver of vegetation heterogeneity in our study region seems to be charcoal burning associated with coppicing. Other forms of historical management like grazing of domestic animals or litter raking probably also played important roles (Nagy, 2008). Abandonment of all these practices during the 20th century triggered significant vegetation changes. We found that loss of vegetation heterogeneity was caused by ecologically non-random species gains and losses resulting in compositional shift along a successional gradient. Forest understorey changed towards more shade-tolerant, mesic and nutrient-demanding in accordance with other studies of abandoned coppices (e.g. Hédl *et al*., 2010; Becker *et al*., 2017). That was likely driven by increasing canopy closure due to the expansion of shade-casting species and cessation of regular disturbances associated with coppicing (Kopecký *et al*., 2013). Short rotation periods also kept the canopy more open, stand height lower and understorey temperatures consequently less buffered (Fabbio *et al*., 1996; Kovács *et al*., 2018). These conditions possibly supported light-demanding and more thermophilous plants. Indeed, studies of vegetation changes along coppice chronosequences showed that particularly light and soil moisture conditions affect understorey dynamics in coppiced stands (Bartha *et al*., 2008; Campetella *et al*., 2011). Moreover, the decreasing abundance of beech in the Slovak Karst has likely increased local plant diversity since *Fagus sylvatica* is a strongly competitive species suppressing many understorey species (Mölder *et al*., 2008).

Legacy effects of historical charcoal burning can affect current vegetation not only by changing tree-species proportions, but also through affecting topsoil conditions. To create oxygen-reduced conditions needed for charcoal production, large amounts of tree litter mixed with topsoil were used to cover wood piles (Krebs *et al*., 2017). Raking of litter from the surroundings of charcoal platforms might further influence the diversity of vegetation (Douda *et al*., 2017; Vild *et al*., 2018). By comparison to the situation during historical management, the currently observed higher amounts of litter are likely to have a negative effect on diversity (Verheyen *et al*., 2012) and this process can also contribute to the observed increase of geophytes and saprophytes.

The expansion of several nutrient-demanding species between vegetation surveys could also be associated with nitrogen depositions (Staude *et al*., 2020). However, the local amount of nitrogen input from air pollution is rather low (6–11 $kg.ha^{-1}.yr^{-1}$, Krupová *et al*., 2018) and does not reach the levels that are considered to affect the diversity of temperate forests (Bobbink *et al*., 2010). Therefore, the compositional shift to tree species with more nutrient-rich litter and general canopy closure are more probable drivers of the observed understorey eutrophication (Verheyen *et al*., 2012; Maes *et al*., 2019).

5 | CONCLUSION

Vegetation homogenisation and the decline of light-demanding plant species is currently observed in many lowland forests in Europe. Combining data from historical charcoal kilns and vegetation resurveys, we showed that the biologically diverse forests in the Slovak Karst are changing in a similar way.

These vegetation changes could be associated with forest succession reflecting the shift from historical coppicing to high-forest management. Long-term data on tree-species composition and structure suggest that the recent vegetation changes of the past four decades constitute a natural process leading back to the forests more dominated by *Fagus sylvatica*. This natural succession is however leading also to local extinction of light-demanding species, an increase of mesic species and to spatially more homogeneous vegetation of the forest understorey. This long-term process poses serious issues with major implications for nature conservation and close-to-nature forest management within the Slovak Karst National Park.

Overall, our study showed the potential of combining vegetation plot resurveys with anthracological analyses of historical charcoal kilns. Such a combination can help in understanding the links between the current biological patterns and processes and the legacies of historical land use and management.

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AUTHOR CONTRIBUTIONS

All authors conceived research idea, designed the research and collected field data. PB performed anthracology. MK and FM analysed the data. FM and MK wrote the first draft and all authors contributed to its revision.

DATA AVAILABILITY STATEMENT

The vegetation resurvey data are stored in the Database of Typological Representative Plots of the Slovak forest vegetation survey (Vladovič and Máliš, 2008). The vegetation resurvey data will be deposited in the forestREplot database (www.forestreplot.ugent.be) and accessible under the conditions of forestREplot data policy.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

Appendix S1. Species taxonomy

Appendix S2. Examples of historical vegetation survey field forms and permanent plot marking

Appendix S3. Figures documenting historical forest and land use

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