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Coppice abandonment and its implications for species diversity in forest vegetation

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Abstract

Coppicing, once a common type of management in European broadleaved forests, was abandoned in many places after WWII. This form of management provided a variety of structural and microclimatic conditions for tree and understorey vegetation. After the abandonment of this intensive management, succession towards mature close forests ensued, and suitable habitats for species ecologically connected to coppicing were reduced. In our study, we chose a region in central Europe where coppicing was the dominant type of forest management until the first half of the 20th century but was abandoned after WWII. We investigated long-term changes in both woody and herbaceous species composition in the Lower Morava UNESCO Biosphere Reserve using historical sources and vegetation plot resurveys from the 17th to the 21st century. The impact of coppice abandonment on vegetation composition and on the conservation value of forests was evaluated. Dominant tree species appeared to be very stable throughout the past four centuries, but changes occurred in their proportions. A shift from species rich oak-hornbeam woodland towards species poorer communities with increasing proportions of lime, ash and maple was observed after the abandonment of coppicing. The observed tendencies partly differed according to site and data source. The conservation value of forests was measured as the occurrence of red-list species, which were considerably reduced after coppice abandonment. To stop the process of biodiversity loss and support the goals of nature conservation, the re-establishment of coppice management is proposed.

Keywords

conservation; forest management; history; forest species composition; resurvey of semi-permanent plots; vegetation diversity

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1 Introduction

Although forest vegetation patterns generally depend on the demands and interactions of species along environmental gradients, in Europe they were co-shaped by human activities at various spatio-temporal scales (Buckley 1992; Peterken 1993; Sanderson et al. 2002; Rackham 2003). Centuries of human management in European forests have modified species composition both by introducing certain species and genotypes, and by favouring certain species in selective cutting (e.g. Gil et al. 2004; Urbietá et al. 2008). Long-term anthropogenic impacts of various intensities are considered to be key factors in forest structure and species composition in regions with long human history in Europe (e.g. Decocq et al. 2004; Dambrine et al. 2007; De Frenne et al. 2011) and elsewhere (e.g. Ross and Rangel 2011).

In central Europe, broadleaved forests were coppiced for centuries. After fossil fuels became widely available, coppicing lost its importance. By the end of WWII, this form of management was almost completely abandoned. In a few decades, whole landscapes once covered with open woodlands were transformed into closed forest areas, which caused massive losses for biodiversity conservation (Miklín andřízek 2014). Most coppice woods have been transformed into high-forests either by replanting or by reducing the underwood to one or two large trunks ('singling out') (Peterken 1996; Van Calster et al. 2008, Rackham 2008). In coppice woods, a fine mosaic of differently-aged forest patches and the presence of scattered old trees provided favourable conditions for a variety of invertebrates (e.g. saproxylic beetles, Vodka andřízek 2013), macrofungi (Diamandis and Perlerou 2001) or herbaceous plants (Bartha et al. 2008). While coppicing forms a dynamic mosaic supporting high species diversity, after the transformation to high-forest lighter phases and permanent open areas are reduced with significant consequences for forest flora and fauna. Species dependent on cyclic changes (adapted to early successional stages) become threatened and gradually disappear from the landscape (Beneš et al. 2006, Freese et al. 2006, van Swaay et al. 2006, Van Calster et al. 2008, Baeten et al. 2009, Hédľ et al. 2010, Kopecký et al. 2013).

In recent decades, interest in the reintroduction of coppicing in order to protect endangered species (Fuller 2013, Vild et al. 2013) and obtain a sustainable source of energy (European Parliament 2009, McKenney 2011) has been steadily increasing in many regions of Europe, including England, Germany, Switzerland and the Czech Republic (EEA 2006). For the successful restoration and sustainable management of coppice forests, detailed knowledge on the influence of management on species composition and biodiversity is needed. The assessment of relationships between management changes and subsequent species replacement can bring insights into factors driving species distribution and abundance.

Our study concerns the Pálava Protected Landscape Area (PLA), part of the Lower Morava UNESCO Biosphere Reserve in the southeastern part of the Czech Republic. In this study, we investigated changes in tree species composition and changes in herbaceous layer composition and diversity. Trees were studied through the past four centuries, and species of the herbaceous layer (following Gilliam 2007) through the past five decades by focusing specifically on changes following coppice abandonment. Two types of information were used – archival forestry data and resurveys of semi-permanent plots in the 1950s and 2000s.

On the basis of information on historical changes in tree species composition, our main goal was to test the hypothesis that the abandonment of coppicing caused significant changes in both tree and understorey species composition and affected the conservation value of forests protected within national, EU and international legislatives.

2 Materials and methods

2.1 Study area

The study area (Figure 1) is situated in southern Moravia, in the northwestern corner of the Pannonian Lowland. It is the warmest and driest part of the Czech Republic with an average annual temperature of 9.6°C, average annual precipitation of 524 mm, and large seasonal variability. Valuable natural areas have been preserved in the midst of the intensively cultivated landscape. Apart from a few isolated segments, there are two larger forests: D vín Wood (400 ha covering most of D vín Hill) and Milovice Wood (2500 ha). The limestone slopes of D vín Hill (with altitudes from 260 to 549 m a.s.l.) represent a sharp environmental gradient (Figure 2). The northwestern (NW) slopes have deep and fertile luvisols and leptosols. They are almost fully covered by thermophilous to mesophilous oak-hornbeam and ravine lime forests. The top and the southeastern (SE) slopes are exposed to sun and wind, soils are poorly developed and vegetation is mostly dry grassland with relatively small extents of ravine forests and thermophilous oak forests (Horák 1969, Hédli and Rejšek 2007). The gently undulating loess plateau of Milovice Wood (altitudes of 180 to 324 m a.s.l.) is covered by luvisols and represents one of the largest compact complexes of subcontinental oak forests in the region (Hédli et al. 2010). Small-scale plantations of non-native black pine (*Pinus nigra*), and scattered black locust (*Robinia pseudoacacia*) are also present.

For centuries, forests in this area were managed as coppice or coppice-with-standards. The coppice cycle was gradually lengthened from 7 years in the Middle Ages to 30–40 years in 1938. In the middle of the 20th century coppicing was abandoned in the whole area, resulting in a forest age structure unseen for at least seven centuries (Müllerová et al. 2014). Forests in the study area were also intensively used for game keeping in certain periods. The first game preserve was established on the D vín Hill in 1885 (300 ha, 80% of the hill). Because of its high ecological value, a strict nature reserve with non-intervention management (however subjected to high intensity game browsing) was established on the D vín Hill (184.6 ha) in 1946. Milovice Wood has been managed as a high-forest since the abandonment of coppicing after WWII. In 1965/6, two additional game preserves were established in Milovice forest (1700 ha, 80% of the site; Szabó 2010; Müllerová et al. 2014). In 1976, the Pálava Protected Landscape Area (8017 ha) Woods was set up, which included both study sites. In 1986, protection was increased by the creation of the Pálava UNESCO Biosphere Reserve. Due to the browsing damage from deer and muflon in the most valuable parts of the protected area the D vín game preserve was closed in 1996, while the other two in Milovice forest are still active. In 2003, the Lower Morava Biosphere Reserve (354 km²) was created, which includes the Pálava PLA as well as the neighbouring Lednice-Valtice area and the floodplain forests at the confluence of Dyje and Morava rivers. To further protect this major European biodiversity hotspot, several large Sites of Community

Importance under Natura 2000 were designated in 2005 in the Lower Morava UNESCO Biosphere Reserve (Figure 1).

2.2 Data sources, processing and analyses

2.2.1 Archival forestry sources—For a qualitative assessment of changes in tree species composition during the past four centuries, forest surveys and forest management plans were analysed (Appendix S1, numbers in square brackets refer to individual sources in Appendix S1). The first two forest surveys were from the 17th century [1, 2]. These included general descriptions of species composition, especially as regards standard trees. More detail was provided by the Forest Management Plan (FMP) of 1807–1808 [3, 4], which recorded the age and species composition of underwood as well as the composition and number of standard trees in each compartment. FMPs from 1885 [6], 1901 [8] and 1933–1936 [9] dealt only with underwood, while FMPs from 1948 [11] and 1971 [13] contained data on both standards and coppice underwood. In the 2010 source [15] standards and underwood were once again treated together. Dvín Wood was covered by all sources, but, as far as more detailed sources are concerned, Milovice Wood was covered entirely only by the most recent sources (1971 and 2010 FMPs, [13, 15]).

For quantitative analyses of changes in species abundances after the abandonment of coppicing, large-scale forest maps (FM) containing precise information on forest extent and age, and the accompanying FMPs describing forest structure and management were used. These were produced in 1947/8 [10 and 11], 1971 [12 and 13] and 2010 [14 and 15]. Historical forest maps were scanned, georeferenced, digitized and analysed in a GIS environment using ArcGIS 9.2 (ESRI 2006). The first two sources provided details on the proportion of species of both standards and coppice underwood, whereas in the latest source (2010) standards and coppices were not differentiated and only overall species composition was given. Because of the dominance of underwood over standards in the study area, we considered the 2010 non-differentiated data to refer to underwood. The 1948 source referred only to tree genera and covered only Dvín Wood. The quantitative analyses of species abundance changes was therefore carried out in Dvín Wood in all three time periods, whereas in Milovice Wood only 1971 and 2010 data were taken into account. Species abundances were calculated from relative cover multiplied by the area of each plot.

2.2.2 Resurvey of semi-permanent plots—To assess the impact of 20th-century changes on the conservation value of forests, vegetation resurveys were undertaken. Pairwise resampling of inexact localized species-plots was applied, an approach increasingly termed ‘resurvey of semi-permanent plots’ (Baeten et al. 2009, Hédli et al. 2010, Kopecký and Macek 2015). Two sets of data from the 1950s were used, both by the same author (J. Horák 1969; hereafter referred to as ‘old’ sample). Sampling plots were scattered over the whole area of both forests. Plots were originally located subjectively during fieldwork to cover the variability of forest types for management planning. As a result, the entire environmental and vegetation variability of forests in the 1950s was documented. The resampling of the original plots was performed in 2002–2003 for Dvín Wood (Hédli 2005, Kopecký et al. 2013) and in 2006 for Milovice Wood (Komárek 2008, Hédli et al. 2010; hereafter referred to as ‘new’ sample). Individual plots were localized following original

maps scaled 1:10,000 and descriptions of terrain configuration from the original field notebooks. Information about tree species composition for plot re-location was used with precaution, giving priority to maps and terrain descriptions. In Dvín Wood, plot size most commonly varied between 200 and 400 m², in Milovice Wood it was 500 m². All vascular plant species in the tree, shrub, herb and woody juvenile (seedlings and saplings) layers were recorded in Dvín Wood. In Milovice Wood, tree and shrub seedlings (i.e. woody juveniles) were not distinguished from saplings and shrubs (cf. Chytrý and Danihelka 1993), and they formed a broadly defined ‘shrub’ layer. Similarly to some archival forestry sources, the tree layer included both standards and coppice underwood at both sites. Species relative representation was estimated using cover scales that were transformed into the corresponding cover-abundance grades of Braun-Blanquet scale. In addition to the analysis of the herbaceous layer, we used the data to analyse tree species composition at both sites and compared the results with data derived from archival forestry sources (cf. chapter 2.2.1). Sampling resulted in the independent analyses of 122 resurveyed plots in Dvín Wood and 46 plots in Milovice Wood. These datasets can be considered representative of the two woods regarding vascular plant species composition and relative coverage.

The analysis of changes in woody species composition used presence and estimated cover. To enable direct comparison with the results of tree species analysis from archival forestry resources, individual species belonging to the same genus were merged, and occurrences of these species in the ‘tree’ and ‘shrub’ layers were also merged. Thus, oak included *Quercus petraea* agg., *Q. robur*, *Q. pubescens* and *Q. cerris*, lime included *Tilia cordata* and *T. platyphyllos*, maple included *Acer campestre*, *A. platanoides* and *A. pseudoplatanus*, and elm included *Ulmus glabra*, *U. minor* and *U. laevis*. The category ‘others’ included *Aesculus hippocastaneum*, *Betula pendula*, *Cornus mas*, *Corylus avellana*, *Crataegus* spp., *Populus alba*, *Populus tremula*, *Prunus avium*, *Prunus mahaleb* and *Sorbus torminalis*. Two statistical parameters of the old vs. new samples were compared using bar graphs and chi-square tests. Frequency (percentage of plots with a species) and importance value (calculated as sum of percentage cover of a species divided by the total number of plots) were computed separately for Dvín and Milovice woods. The statistical significance of the null hypothesis – that number of plots or importance values for individual species do not differ between the old and new surveys – were calculated as chi-square statistics, where values from the new sample were taken as ‘observed’, and values in the old sample as ‘expected’. Presences and absences for individual species were the categories entering the chi-square statistics computation.

The analysis of the herbaceous layer focused on i) changes in the diversity of all herbaceous species with a height up to 1.3 m, and ii) changes in the occurrence of rare and endangered herbaceous species (Grulich 2012). Based on species lists in plots, we compared the total and average number of species in the old and new datasets, and the number of species present in both or in only one dataset. Changes in species richness at the plot level were tested by a Wilcoxon pair test (old vs. new sample per plot) and graphically presented using boxplots separately for the two sites. Rarefaction analysis (Colwell et al. 2004) was used to estimate species richness by randomly drawing a given count from the pool of plots. Average numbers of species and confidence intervals were then computed. Plot count was increased stepwise from 1 to N where N is the number of plots in the dataset. Following the

categorization suggested in the Red List of vascular plant species of the Czech Republic (Grulich 2012), we classified species into five categories: C1 – critically threatened, C2 – endangered, C3 – vulnerable, C4 – lower risk, and others. The relative occurrence of species in categories C1 to C4 was calculated as the sum of occurrences of the species in the respective Red List category divided by the sum of all species occurrences in the respective part of the dataset, i.e. old and new surveys separately for both sites. The statistical significance of the null hypothesis that no difference exists between the occurrences in old and new samples was tested for each of the four Red List categories using a chi-square test (see above). Statistical inference was computed in STATISTICA, version 12 (StatSoft 2013).

3 Results

3.1 Tree species composition

3.1.1 Archival forestry data—Throughout history, tree species composition in the study area remained remarkably stable (Table 1). Dominant species were oak, lime, ash and hornbeam. However, the two woods differed markedly. Whereas in D vín Wood dominant species were oak, lime, ash and hornbeam, in Milovice Wood oak constituted a consistent majority for both standards and underwood. Other species formed only a minority (Table 1a, b). While coppicing was active (until WWII, 30–35-year rotation cycle), both woods showed remarkable stability in species composition with only minor changes, although in D vín Wood the share of lime and ash standards grew at the expense of hornbeam during the period 1808–1948. Following the abandonment of coppicing, the abundance of dominant species changed, showing slightly different trends in the two. In D vín Wood, oak showed increasing abundance, while hornbeam decreased and lime and ash remained stable (Figure 3a). Other species, such as elm, maple, black pine, black locust etc. were relatively infrequent and stable. In Milovice Wood, the time span was shorter (only 40 years) and did not cover the period immediately after the last coppicing. Here we observed a marked decrease in the abundance of the dominant oak underwood, a considerable expansion of ash and maple, and an increase in horse chestnut (from less than 1 to 16 %). This tree was planted extensively in the game preserves of Milovice Wood in the 1980s to feed game on conkers. Other underwood species (hornbeam, lime) remained stable (Figure 3b).

Although the detail of historical sources is limited (for example *Q. pubescens* and *Q. petraea* cannot be separated), the sharp environmental gradient on D vín Hill from NW to SE (Figure 2) is recognizable in historical tree species composition (Figure 4). In the past half a century, the most abundant tree species differed along this environmental gradient. However, similar trends in lime dominance, as well as a remarkable decrease in hornbeam could be observed in all positions. The above-mentioned increase in oak and decrease in ash happened mainly on the NW slopes, and were less pronounced on the SE foothills.

Several non-native tree species were planted or occur spontaneously in the area. Black pine and black locust were both first mentioned in the 1885 FMP [6]. Around the turn of the 19th and 20th centuries, black pine plantations were established in the eastern part of D vín Hill on previously unforested shallow rocky soils (10 ha), and some in Milovice Wood. Currently 5% of D vín Wood and less than 1% of Milovice Wood is dominated by black pine. Black locust grows in low to very low densities on the NW foothills of D vín Wood (1%), and in

low to high densities on 2% of Milovice Wood. Larch, today present on a very small area in both woods, was also first mentioned in the 1885 FMP of D vln Wood [6]. More recent alien tree species are Douglas fir (in Milovice Wood), two oak species (*Q. cerris* in low abundances in both woods; and *Q. rubra* in low abundances in Milovice Wood), tree of heaven (*Ailanthus altissima*, in low abundances in both woods), and ash-leaved maple (in low abundances in Milovice Wood).

3.1.2 Vegetation resurvey data—In total 26 species were recorded in the tree layer in the two woods (Table 2a). The woody undergrowth, consisting of shrubs and woody juveniles, was even richer with at least 53 species recorded (Table 2b). Considerable differences between the woods can be observed in the dominant tree species. D vln Wood was dominated with lime (mostly *Tilia platyphyllos*), ash, maples, hornbeam and mesophilous (mostly *Quercus petraea*) as well as thermophilous (*Q. pubescens*) oaks. Milovice Wood, on the other hand, was an oak forest (almost exclusively *Q. petraea*) with moderate proportions of species that dominated in D vln Wood. Total tree diversity in Milovice Wood is only half of that for D vln Wood, which is reflected also in the diversity of understory woody species (Table 2b). Many thermophilous species are absent or nearly absent in Milovice Wood, e.g. *Cornus mas*, *Prunus mahaleb*, *Quercus cerris* (planted), *Pinus nigra* (planted), *Rhamnus cathartica*, *Sorbus danubialis* or *Staphylea pinnata*.

Changes in the occurrence of woody species (tree and shrub layers merged) showed similar trends in both woods (Figures 5a, b). From the six major species (taxonomically mostly representing respective genera), the ones with decreasing frequency of presence in individual plots were hornbeam (chi-square test, $p < 0.05$ in D vln Wood, $p < 0.01$ in Milovice Wood) and elm (significant only in D vln Wood, $p < 0.01$). Oak decreased in D vln Wood ($p < 0.01$), while it remained in all plots in Milovice Wood. Species with increasing frequency were lime (n.s. at either site), ash (significant only in D vln Wood, $p < 0.01$), and maple (n.s. at either site). Other species were infrequent and changed relatively little (black pine, black locust) or gave ambiguous results ('others'; decrease in Milovice Wood, $p < 0.01$). Regarding abundance weighted by coverage in plots (importance value of species, Figure 6), the resulting picture in D vln Wood was similar to the above described pattern in presence frequency, although with a somewhat different statistical significance of changes. Decreases in oak, hornbeam and elm were not significant, while increases in lime and maple were significant at $p < 0.05$. In Milovice Wood the results partly differed from D vln Wood. The overwhelming dominance of oak (change n.s.) partly obscured the performance of other, less abundant species: lime (decreased at $p < 0.05$), hornbeam, maple and especially elm (all three changes n.s.); Figure 6b. The category 'others' decreased significantly at $p < 0.05$. By contrast, in D vln Wood species composition was more even, at least relative to species frequency. A remarkable difference could be observed in species abundance (importance value): the main feature of the changes in tree species composition in D vln Wood was the increase of lime, ash and maple (Figure 6a).

An additional insight into forest regeneration processes was provided by frequency change in understory woody species (Table 2b). In both woods, the total number of species decreased by approximately one quarter. The frequency of most species decreased while only several species became more frequent. The heaviest losses affected thermophilous

shrubs and trees (*Euonymus verrucosa*, *Ligustrum vulgare*, *Prunus mahaleb*, *Rhamnus cathartica*, *Sorbus domestica*, *Sorbus torminalis* and *Viburnum lantana*) or generally shrubby species of open habitats (*Cornus sanguinea*, *Corylus avellana*, *Crataegus* sp., *Prunus spinosa*, or *Rosa canina* agg.). Oaks (*Quercus petraea*, *Q. pubescens*) failed to regenerate, decreasing by more than half at both sites. Elms either decreased (*Ulmus minor*) or increased (*U. glabra* – in D vín), probably reflecting the differing regeneration ecologies of the species. Similar differences can be observed for the regeneration of mesophilous maples (*Acer platanoides*, *A. pseudoplatanus*), for which an increase was recorded in the increasingly mesic forests of D vín and a decrease in the dry, ungulate-browsed forests of Milovice Wood. Lime (*Tilia platyphyllos* and *T. cordata*), another species of dark and moist forests, showed increasing regeneration in D vín Wood.

3.2 Herb species composition

Changes in forest herb species over the second half of the 20th century were considerable. Out of 325 species recorded in D vín Wood, 313 occurred in the old survey, while only 194 were present in the new one. 183 species (56%) were present in both surveys. A striking 130 species (40%) were observed only in the old survey, compared with only 12 species (4%) unique for the new survey. We recorded a similar situation for Milovice Wood with 234 species in total, out of which 104 (45%) were common in both datasets, 75 (32%) were exclusive to the old dataset and 54 (23%) were exclusive to the new dataset. Species exclusive to either dataset were mainly recorded only once. These rare species constituted 47% of species in the old and 75% of species in the new dataset in D vín Wood, and 57% and 43%, respectively, in Milovice Wood. On the other hand, only a few species showed marked increase. No species could outcompete the performance of the alien *Impatiens parviflora* in D vín Wood, which increased from ‘absent’ in 1953 to 56% of the plots fifty years later. In Milovice Wood, *Urtica dioica*, not present in the old survey, was recorded in 57% of plots in 2006.

Almost identical trends were observed in average species richness per plot. In D vín Wood, average species richness per plot decreased from 28.4 to 19.3 (Wilcoxon pair test, $p < 0.001$); in Milovice Wood, from 27.7 to 20.3 ($p < 0.001$). This trend of species diversity decline was very similar at both sites (Figure 7). Species richness estimated by rarefaction showed a striking difference in D vín Wood between the old and new surveys; it was significantly lower in the new survey (Figure 8a). However, in Milovice Wood, the estimated number of species was only slightly lower in the new survey and averages stayed within the confidence intervals of the other survey (Figure 8b). Both estimates showed a continuously increasing trend in rarefaction curves, which indicates that there were probably still species in forest vegetation at both sites that were not present in the plots, particularly in D vín Wood in the old sample. The rarefaction analysis illustrates the character of the studied vegetation with many rare species as indicated by the high proportion of singleton species mentioned above.

The occurrence of rare and endangered species decreased at both sites. This trend was more pronounced in Milovice Wood (Figure 9b) than in D vín Wood (Figure 9a). However, change in neither of the Red List categories was statistically significant at $p < 0.05$. Critically endangered species (category C1) have completely disappeared from the resurveyed plots;

strongly endangered (C2) and endangered species (C3) suffered higher losses in Milovice Wood, probably as an effect of the game preserves. Note the relative expression of the results; the absolute number of species is higher in D vín Wood than in Milovice Wood, and so is the number of endangered species and their occurrences in plots.

4 Discussion

4.1 Changes in woody species composition

Detailed historical information on tree species composition is relatively sparse. Generally speaking, quantitative data are more copious for species of standards, whereas only presence/absence was usually given for species of underwood, especially in older periods. This reflects partly the long-term interests of landowners in standards and partly business practices. From the Middle Ages onwards, standards were sold by the piece (different species had different prices) and therefore tended to be recorded as such, whereas underwood was marketed by the area and irrespective of species. In our case, archival forest sources contained detailed information on the proportions of underwood species only since 1948 (D vín) or 1971 (Milovice). This roughly overlaps with the period covered by the vegetation surveys, which enabled us to examine the changes following coppice abandonment comparing the two kinds of sources.

Unlike vegetation resurveys, archival forestry records often referred to underwood and standard composition separately. Whereas underwood was harvested all at once, the composition of standards was subject to selective cutting and the promotion of desirable species. From the observed strong reduction of standard density in D vín Wood in 1948–2011 (Altman et al. 2013) as well as from the rapid changes in standard composition in the period from 1948 to 1971, we can infer that standard felling happened mainly during the period of transformation to high-forests. Oak standards were often left while others (hornbeam, lime and ash) were mostly felled. In the 2010 FMP [15] underwood and standards were not separated, and because of the dominance of underwood we assumed species composition to be comparable with the vegetation resurveys. This assumption could play a role in the inconsistency of the two information sources. Instead of oak increase, the shifts in species dominance recorded in archival records could refer to the reduction of standards of other tree species through selective felling, and could therefore not be explained by forest successional dynamics.

The differences observed between archival forestry data and vegetation resurvey results may also be due to sampling methodology. Forestry records typically refer to entire forest compartments of considerable sizes (Bürgi 1999). By contrast, vegetation resurveys used sets of relatively small plots scattered on a small fraction of the studied forests and therefore provide higher spatial resolution but smaller spatial extent. No statistically random selection of vegetation resurveys was carried out. However, bias towards under or overestimation of common species was probably not high (Hédl 2007, Michalcová et al. 2011), and the spatial layout of plots was balanced, albeit subjective. The methodology of forestry data acquisition certainly experienced slight changes in time and was not always applied properly (from areas not covered in this paper we know of examples when instead of re-measuring in the field, data were simply copied from the previous FMP changing only the age of the forest).

For example today the composition of tree species in FMPs is derived from medium tree height and diameter using growth tables, and therefore if the trunks of the individuals of a species at a site are thicker than the average, the abundance of that species is overestimated. In our case, this may hold true especially for oaks on the NW foothills of Dvín Hill, which have large trunks and recorded the biggest increase in oak abundances.

Dominant tree species composition in the study area appeared to be very stable throughout the past four centuries, despite the lengthening of the coppice cycle (Szabó 2010), the fluctuating number of standards and the recent shift from coppice to high-forest management. These dominants were oak, lime, ash and hornbeam for both standards and underwood. However, their proportions changed and the observed tendencies differed partly according to the data source (forest records or vegetation resurvey) and between the sites. The observed shifts were connected mostly to changes in forest management.

From the changes of tree species composition we can infer the influence of shifts in management intensity from intensive coppicing to neglect although the archival and vegetation records did not always correspond. After the abandonment of coppicing, oak generally decreased, although in the case of Dvín Wood archival forestry records showed the opposite trend. This inconsistency could possibly be explained by the overestimation of oak abundance in forestry survey due to large trunks, discussed above. Ash and maple increased in both archival forestry records and vegetation resurveys. Congruent results were obtained for hornbeam, which generally decreased, and for lime and ash, which increased or fluctuated. A similar decline in light-demanding oak and increase in nutrient-demanding shady species (maple, hazel) were observed in resurvey data in Belgium (Vanhellemont et al. 2014), suggesting that such trends are common in European temperate lowland forests. The expansion of ash in Dvín Wood concurs with the expansion of this species in the ecologically similar Bohemian Karst (Hofmeister et al. 2005, Stěpík and Šamonil 2006). Elsewhere in Europe, ash is in decline (e.g. Vanhellemont et al. 2014), largely due to the pathogen fungus *Chalara fraxinea* (Kowalski 2006), now observed in most European regions including the Czech Republic (Jankovský and Holdenrieder 2009). Our former conclusions for Milovice Wood that the forests have changed from oak and hornbeam dominated stands to forests dominated by mesophilic species (Hédl et al. 2010) can be extended to Dvín Wood where this change is even more pronounced, probably because of topography and soil conditions. This change may not be reversible due to poor oak regeneration observed in Dvín Wood both in our resurveys and in the reconstruction of oak recruitment by Altman et al. (2013).

4.2 Changes in herb species diversity and composition

Decline in biodiversity and species richness in particular is recognized as a global process (Brooks et al. 2006; Butchart et al. 2010) threatening the functioning of ecosystems (Isbell et al. 2011) and human well-being (Díaz et al. 2006; Cardinale 2012). Biodiversity decline at a global scale may not necessarily be paralleled at local scales because of species migrations; locally extinct species can be replaced by newly arrived ones resulting in zero net change. Reliable assessment of species richness change and its linking to environmental changes at a local scale can be achieved by using resurveys of semi-permanent plots (Chytrý et al. 2014,

Kopecký and Macek 2015). Increasing numbers of time series of diversity data allow for wider generalizations, such as the meta-analyses recently published by Vellend et al. (2013) or Dornelas et al. (2014). The former study used an extensive dataset of resurveyed vegetation plots from a range of the Earth's biomes and detected no overall decline in species richness; the departure from zero change was not significant. Slight increases in species richness appeared in forests and after canopy closure; post-disturbance succession (which was not confined to forests in this meta-analysis) resulted in marked species richness increase.

Following the classification in Vellend et al. (2013), our two sites are distinct examples of canopy-closure post-disturbance succession forests. However, the observed changes in species richness were in contrast to the findings of Vellend et al. (2013). Both forests underwent a marked plot-level decrease of species richness. D vín and Milovice woods are formed by typical successional forest communities where active coppicing with frequent disturbances was replaced by high-forests with less frequent disturbances. Both study sites (D vín and Milovice woods) have been subject to ungulate pressure. Deer and mouflon impact is very complex. Unfortunately, currently there is not enough data for the assessment of the browsing effect. However, we can see a similar effect on vegetation in both forest complexes although in D vín Wood the game preserve was established long before coppice abandonment whereas in Milovice Wood only in the 1960s. So it is obvious that the changes in game numbers did not have the same pattern at both sites and therefore we can infer the game browsing was not the driving element of vegetation change. In D vín Wood, disturbances strongly decreased after the site was designated as a strict reserve shortly before the old vegetation records were made. In Milovice Wood, ground-disturbances by ungulates contributed to an increase of ruderal herbs, but at the same time they slowed down the process of biotic homogenization in the past decades. However, the succession from coppice to high-forest was probably the decisive element in the process of species richness decline (Chytrý and Danihelka 1993; Hédli et al. 2010).

One of the reasons behind the differences between the results of the global meta-analysis and our study can be the time lag between the surveys. In our case the temporal distance between the old and new surveys is 53 years for Milovice Wood and ca. 50 years for D vín Wood. By contrast, in Vellend et al. (2013) over half of the cases comprised plot resurveys after less than 25 years, and ca. 25% after 10 years or less. Climate change and pollution have affected vegetation composition and diversity well before the time span of such relatively short-term resurveys. In Europe and North America, the major impact of air pollution by acidic compounds happened between the 1960s and 1990s (Menz and Seip 2004; Kopá ek and Veselý 2005) whereas the negative impact of nitrogen depositions on global biodiversity persists (Wamelink et al. 2009; Bobbink et al. 2010). The crucial distinction between the short and long-term comparisons can be due to the long-term cumulative impact of these factors.

Forest succession, as an ecological consequence of the conversion of coppices to high-forests or in general of coppice abandonment, was considered to be the cause of vegetation diversity decline by many studies (e.g. Barthá et al. 2008; Baeten et al. 2009; Van Calster et al. 2008). The impact of deer and other ungulates represents another long-term factor in

temperate forests, although its consequences over longer time periods were rarely documented (Chytrý and Danihelka 1993). Most studies inferred vegetation change under the influence of deer for no longer than two decades (Rooney 2009; Nuttle et al. 2014). In the case of Milovice Wood, however, deer have interacted with forest succession after coppice abandonment for at least four decades, arguably preventing taxonomic homogenization via heterogeneous soil surface disturbances and by keeping the expansion of shrubs (mainly *Acer campestre*) under control (Hédl et al. 2010).

The influence of deer is relatively unexpected but may be more common than previously thought. Resurveys from former coppices in the Czech Republic indicated that understory vegetation homogenization had not taken place at sites where deer was kept in high densities (our own unpublished results). However, deer clearly causes an increase of nitrogen-demanding, shade-tolerant species (ruderals), such as *Urtica dioica* in Milovice Wood. The prevention of homogenization is probably due to the expansion of ruderals, because many threatened species have locally disappeared. In both Dvín and Milovice woods, species richness decrease was not due to the strongly negative effect of invasive species reported for example by Vellend et al. (2013). Only a few species invaded the forests and only *Impatiens parviflora* did it on a larger scale in Dvín Wood. Even this, however, had little effect on the native flora, which was subdued rather by the succession towards shadier forest conditions (Kopecký et al. 2013).

All in all, generalizations about species richness change can provide different stories in different situations because i) factors driving species richness change operate at various temporal scales, many of which are longer than a few decades, ii) the impact of the long-term factors is typically cumulative, iii) causality can be more complex than or even different from what simple categorizations would allow, iv) last but not least, resurvey data contain inherent errors, in particular authorship bias, which can corrupt the results.

5 Implications for management

The ancient landscape of Pálava and adjacent river alluvia, now protected as the Lower Morava UNESCO Biosphere Reserve, has been co-formed by humans for millennia. We believe that its exceptional ecological value is partly due to long-term human influences and disturbances. The relative influence of ecological versus socio-economic driving forces can be very complex and can involve the long-lasting effects of management decision making, as shown for the area by Szabó and Hédl (2013). Traditional forest management, including coppicing, was abandoned due to socio-economic changes as well as a misunderstanding of the tasks and goals of nature protection. In the past, nature protection was understood either as the enlightened and centralized manipulation of ecosystems towards a predefined state (Chase 1986) or as the protection of natural processes (the ‘wilderness’ or ‘non-intervention’ paradigm) (Cronon 1995; Nelson and Callicott 2008; for coppice forests, see Evans and Barkham 1992). The Pálava example clearly shows the contradictions between non-intervention policies and the role of humans in maintaining ecosystem biodiversity. When foresters lost interest in managing the forests and nature protection took over the territory, non-intervention became the official rather than the default policy. Reinforcing the findings of earlier research (Chytrý and Danihelka 1993; Beneš et al. 2006; Vodka et al. 2009; Hédl

et al. 2010; Kopecký et al. 2013; Miklín andřížek 2014; Müllerová et al. 2014), our study demonstrated that non-intervention alone is ineffective in protecting biodiversity in the Lower Morava UNESCO Biosphere Reserve.

Despite the long neglect, forms and structures created by historical management are still preserved in the study area, and recently conservation efforts have been put in place to re-establish traditional management. Although it is often argued that the restoration of neglected coppices is technically problematic, Pyttel et al. (2013) and Matula et al. (2012) showed good re-sprouting ability for coppice stools after long periods of neglect. Furthermore, Leonardsson and Götmark (2014) found no effect of stool diameter on sprouting after conservation thinning in southern Sweden.

On the NE slopes of Dvín Hill 21.6 ha of overgrown coppices were harvested in 2009–2013 and further thinning is planned to reduce the density of shoots by 60%. Field observations from spring 2014 (R. Hédľ, unpublished) showed two opposing development trajectories. On the one hand, new occurrences of thermophilous species such as *Polygonatum odoratum*, *Carex michelii* and *Vincetoxicum hirundinaria*, and regeneration of oak from seedlings indicate the positive impact of coppice restoration from the conservation perspective. Freshly created open-woodland habitats in Dvín Wood are also susceptible to expansion by nitrophilous species, such as *Alliaria petiolata*, *Campanula rapunculoides* or *Impatiens parviflora*. The risk of release of soil-accumulated nitrogen after canopy opening seems to have concrete manifestations (Verheyen et al. 2012). In general, through the expansion of ruderal and invasive species to freshly cut areas, coppice restoration can pose a threat to the conservation value of forests (Radtke et al. 2013; Vild et al. 2013; Ambrass et al. 2014).

Another challenge connected to attempts at coppice restoration is grazing pressure. Although the Dvín game preserve was abolished in 1996, mouflons and deer still live here in high densities (V. Riedľ, personal communication), causing damage by overgrazing and preventing natural regeneration from coppice stools (cf. Chytrý and Danihelka 1993). In Milovice Wood the two game preserves are still active and high numbers of ungulates would make coppice re-establishment practically impossible.

Both non-native tree species, black pine and black locust, although relatively rare in the study area, pose problems for nature conservation. Whereas black pine occurs only in plantations and does not spread spontaneously, black locust, an invasive species listed in the DAISIE database (<http://www.europe-aliens.org/>) as one of the 100 most aggressive invaders of the world, has the ability to spread fast both generatively and vegetatively, eventually altering the environmental characteristics of particular sites. Together with another alien, tree of heaven, which is already present in the area, it can soon become a real threat to nature conservation (Radtke et al. 2013).

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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References

- Altman J, Hédli R, Szabó P, Mazurek P, Riedl V, Müllerová J, Kopecký M, Doležal J. Tree-rings mirror management legacy: dramatic response of standard oaks to past coppicing in Central Europe. *PloS ONE*. 2013; 8:e55770.doi: 10.1371/journal.pone.0055770 [PubMed: 23405213]
- Ambrass S, Radtke A, Zerbe S, Fontana V, Ammer C. Dispersal and management of heaven and black locust in coppiced forests-results of a case study in Southern Tyrol. *Naturschutz und Landschaftsplanung*. 2014; 46:45–51.
- Baeten L, Bauwens B, De Schrijver A, De Keersmaecker L, Van Calster H, Vanderkerkhove K, Roelandt B, Beekman H, Verheyen K. Herb layer changes (1954-2000) related to the conversion of coppice-with-standards forest and soil acidification. *Applied Vegetation Science*. 2009; 12:187–197. DOI: 10.1111/j.1654-109X.2009.01013.x
- Bartha S, Merolli A, Campetella G, Canullo R. Changes of vascular plant diversity along a chronosequence of beech coppice stands, central Apennines, Italy. *Plant Biosystems*. 2008; 142:572–583. DOI: 10.1080/11263500802410926
- Beneš J,řížek O, Dovala J, Konvička M. Intensive game keeping, coppicing and butterflies: The story of Milovický Wood, Czech Republic. *Forest Ecol Management*. 2006; 237:353–365. DOI: 10.1016/j.foreco.2006.09.058
- Bobbink R, Hicks K, Galloway J, Spranger T, Alkemade R, Ashmore M, et al. De Vries W. Global assessment of nitrogen deposition effects on terrestrial plant diversity: a synthesis. *Ecological Applications*. 2010; 20:30–59. DOI: 10.1890/08-1140.1 [PubMed: 20349829]
- Brooks TM, Mittermeier RA, da Fonseca GA, Gerlach J, Hoffmann M, Lamoreux JF, Mittermeier CG, Pilgrim JD, Rodrigues ASL. Global biodiversity conservation priorities. *Science*. 2006; 313:58–61. DOI: 10.1126/science.1127609 [PubMed: 16825561]
- Buckley, GP., editor. *Ecology and management of coppice woodlands*. Chapman & Hall; London, UK: 1992.
- Bürgi M. A case study of forest change in the Swiss lowlands. *Landscape Ecology*. 1999; 14:567–575.
- Burchart SH, Walpole M, Collen B, van Strien A, Scharlemann JP, Almond RE, et al. Watson R. Global biodiversity: indicators of recent declines. *Science*. 2010; 328:1164–1168. DOI: 10.1126/science.1187512 [PubMed: 20430971]
- Cardinale BJ, Duffy JE, Gonzalez A, Hooper DU, Perrings C, Venail P, et al. Naeem S. Biodiversity loss and its impact on humanity. *Nature*. 2012; 486:59–67. DOI: 10.1038/nature11148 [PubMed: 22678280]
- Chase, A. *Playing God in Yellowstone: the Destruction of America's First National Park*. The Atlantic Monthly Press; Boston: 1986.
- Chytrý M, Danihelka J. Long-term changes in the field layer of oak and oak-hornbeam forests under the impact of deer and muflon. *Folia Geobot Phytotax*. 1993; 28:225–245. DOI: 10.1007/BF02853510
- Chytrý M, Tichý L, Hennekens SM, Schaminée JH. Assessing vegetation change using vegetation-plot databases: a risky business. *Applied Vegetation Science*. 2014; 17:32–41. DOI: 10.1111/avsc.12050
- Colwell RK, Mao CX, Chang J. Interpolating, extrapolating, and comparing incidence-based species accumulation curves. *Ecology*. 2004; 85:2717–2727. DOI: 10.1890/03-0557
- Cronon, W. *The trouble with wilderness; or, getting back to the wrong nature*. *Uncommon Ground: Rethinking the Human Place in Nature*. Cronon, W., editor. New York: W. W. Norton & Co.; 1995. p. 69-90.

- Dambrine E, Dupouey JL, Laüt L, Humbert L, Thion M, Beaufils T, Richard H. Present forest biodiversity patterns in France related to former Roman agriculture. *Ecology*. 2007; 88:1430–1439. DOI: 10.1890/05-1314 [PubMed: 17601136]
- De Frenne P, Baeten L, Graae BJ, Brunet J, Wulf M, Orczewska A, et al. Verheyen K. Interregional variation in the floristic recovery of post-agricultural forests. *J Ecol*. 2011; 99:600–609. DOI: 10.1111/j.1365-2745.2010.01768.x
- Decocq G, Aubert M, Dupont F, Alard D, Saguez R, Wattez-Franger A, De Foucault B, Delelis-Dusollier A, Bardat J. Plant diversity in a managed temperate deciduous forest: understory response to two silvicultural systems. *J Applied Ecology*. 2004; 41:1065–1079. DOI: 10.1111/j.0021-8901.2004.00960.x
- Diamandis S, Perlerou C. The mycoflora of the chestnut ecosystems in Greece. *For Snow Landsc Res*. 2001; 76:499–504.
- Díaz S, Fargione J, Chapin FS III, Tilman D. Biodiversity loss threatens human well-being. *PLoS Biology*. 2006; 4:e277.doi: 10.1371/journal.pbio.0040277 [PubMed: 16895442]
- Dornelas M, Gotelli NJ, McGill B, Shimadzu H, Moyes F, Sievers C, Magurran AE. Assemblage Time Series Reveal Biodiversity Change but Not Systematic Loss. *Science*. 2014; 344(6181):296–299. [PubMed: 24744374]
- EEA. How much bioenergy can Europe produce without harming the environment? EEA Report No 7/2006. European Environment Agency; Copenhagen: 2006.
- ESRI [Environmental Systems Research Institute]. ArcGIS 9.2. ESRI; Redlands, California, USA: 2006.
- European Parliament. Directive 2009/28/EC of the European Parliament and of the Council of 23 April 2009 on the promotion of the use of energy from renewable sources and amending and subsequently repealing Directives 2001/77/EC and 2003/30/EC. 2009.
- Evans, MN., Barkham, JP. Coppicing and natural disturbance in temperate woodlands - a review. *Ecology and Management of Coppice Woodlands*. Buckley, GP., editor. Chapman & Hall; London, UK: 1992. p. 79-98.
- Freese A, Beneš J, Bolz R,řízek O, Dolek M, Geyer A, Gros P, Konvička M, Liegl A, Stettmer C. Habitat use of the endangered butterfly *Euphydryas maturna* and forestry in Central Europe. *Animal Conservation*. 2006; 9:388–397. DOI: 10.1111/j.1469-1795.2006.00045.x
- Fuller RJ. Searching for biodiversity gains through woodfuel and forest management. *J Applied Ecology*. 2013; 50(6):1295–1300. DOI: 10.1111/1365-2664.12152
- Gil L, Fuentes-Utrilla P, Soto A, Cervera MT, Collada C. Phylogeography: English elm is a 2,000-year-old roman clone. *Nature*. 2004; 431:1053.doi: 10.1038/4311053a [PubMed: 15510138]
- Gilliam FS. The ecological significance of the herbaceous layer in temperate forest ecosystems. *Bioscience*. 2007; 57:845–858. DOI: 10.1641/B571007
- Grulich V. Red List of vascular plants of the Czech Republic. *Preslia*. 2012; 84:631–645.
- Hédl, R. Comparison of forest ecosystems in Devin Nature Reserve, after 50 years of natural succession. PhD. Thesis, Mendel University; Brno: 2005.
- Hédl R. Is sampling subjectivity a distorting factor in surveys for vegetation diversity? *Folia Geobotanica*. 2007; 42:191–198. DOI: 10.1007/BF02893885
- Hédl R, Kopecký M, Komárek J. Half a century of succession in a temperate oakwood: from species-rich community to mesic forest. *Diversity Distribution*. 2010; 16:267–276. DOI: 10.1111/j.1472-4642.2010.00637.x
- Hédl R, Rejšek K. Soil changes after 40 years of succession in an abandoned coppice in the Czech Republic. *Acta Agronomica Hungarica*. 2007; 55:453–474. DOI: 10.1556/AAgr.55.2007.4.6
- Hofmeister J, Mihaljevič M, Hošek J. The spread of ash (*Fraxinus excelsior*) in some European oak forests: an effect of nitrogen deposition or successional change? *Forest Ecol Management*. 2004; 203:35–47. DOI: 10.1016/j.foreco.2004.07.069
- Horák J. Waldtypen der Pavlovské kopce (Pollauer Berge). *Acta Sc Nat Brno*. 1969; 3(7):1–40.
- Isbell F, Calcagno V, Hector A, Connolly J, Harpole WS, Reich PB, et al. Loreau M. High plant diversity is needed to maintain ecosystem services. *Nature*. 2011; 477:199–202. DOI: 10.1038/nature10282 [PubMed: 21832994]

- Jankovský L, Holdenrieder O. *Chalara fraxinea* – ash dieback in the Czech Republic. Plant Protection Science. 2009; 45:74–78.
- Komárek, J. Long-term changes in vegetation of the Milovický Wood. MSc thesis, Palacký University; Olomouc: 2008.
- Kopálek J, Veselý J. Sulfur and nitrogen emissions in the Czech Republic and Slovakia from 1850 till 2000. Atmospheric Environment. 2005; 39:2179–2188. DOI: 10.1016/j.atmosenv.2005.01.002
- Kopecký M, Hédli R, Szabó P. Non-random extinctions dominate plant community changes in abandoned coppices. J Appl Ecol. 2013; 50:79–87. DOI: 10.1111/1365-2664.12010
- Kopecký M, Macek M. Vegetation resurvey is robust to plot location uncertainty. Diversity and Distribution. 2015; doi: 10.1111/ddi.12299
- Kowalski T. *Chalara fraxinea* sp. nov. associated with dieback of ash (*Fraxinus excelsior*) in Poland. Forest Pathology. 2006; 36:264–270. DOI: 10.1111/j.1439-0329.2006.00453.x
- Leonardsson J, Götmark F. Differential survival and growth of stumps in 14 woody species after conservation thinning in mixed oak-rich temperate forests. European Journal of Forest Research. 2014; in press. doi: 10.1007/s10342-014-0843-1
- Matula R, Svátek M, Křivá J, Úradník L, Kadavý J, Kneifl M. The sprouting ability of the main tree species in Central European coppices: implications for coppice restoration. European Journal of Forest Research. 2012; 131(5):1501–1511. DOI: 10.1007/s10342-012-0618-5
- McKenney DW, Yemshanov D, Fraleigh S, Allen D, Preto F. An economic assessment of the use of short-rotation coppice woody biomass to heat greenhouses in southern Canada. Biomass and Bioenergy. 2011; 35(1):374–384. DOI: 10.1016/j.biombioe.2010.08.055
- Menz FC, Seip HM. Acid rain in Europe and the United States: an update. Environmental Science & Policy. 2004; 7:253–265. DOI: 10.1016/j.envsci.2004.05.005
- Michalcová D, Lvoňák S, Chytrý M, Hájek O. Bias in vegetation databases? A comparison of stratified-random and preferential sampling. J Vegetation Science. 2011; 22:281–291. DOI: 10.1111/j.1654-1103.2010.01249.x
- Miklín J, Hájek L. Erasing a European biodiversity hot-spot: Open woodlands, veteran trees and mature forests succumb to forestry intensification, succession, and logging in a UNESCO Biosphere Reserve. Journal for Nature Conservation. 2014; 22:35–41. DOI: 10.1016/j.jnc.2013.08.002
- Müllerová J, Szabó P, Hédli R. The rise and fall of traditional forest management in southern Moravia: A history of the past 700 years. Forest Ecol Management. 2014; 331:104–115. DOI: 10.1016/j.foreco.2014.07.032
- Nelson, MP., Callicott, JB., editors. The Wilderness Debate Rages On: Continuing the Great New Wilderness Debate. University of Georgia Press; Athens: 2008.
- Nuttall T, Ristau TE, Royo AA. Long-term biological legacies of herbivore density in a landscape-scale experiment: forest understoreys reflect past deer density treatments for at least 20 years. Journal of Ecology. 2014; 102:221–228. DOI: 10.1111/1365-2745.12175
- Peterken, GF. Woodland conservation and management. 2nd Ed. Chapman & Hall; London: 1993.
- Peterken, GF. Natural woodland: Ecology and conservation in northern temperate regions. Cambridge University Press; Cambridge: 1996.
- Pyttel PL, Fischer UF, Suchomel C, Gärtner SM, Bauhus J. The effect of harvesting on stump mortality and re-sprouting in aged oak coppice forests. Forest Ecol Management. 2013; 289:18–27. DOI: 10.1016/j.foreco.2012.09.046
- Rackham, O. Ancient woodlands, Its History, Vegetation and Uses in England. 2nd Ed. Castlepoint Press; 2003.
- Rackham O. Ancient woodlands: modern threats. New Phytologist. 2008; 180:571–586. DOI: 10.1111/j.1469-8137.2008.02579.x [PubMed: 18771472]
- Radtke A, Ambraß S, Zerbe S, Tonon G, Fontana V, Ammer C. Traditional coppice forest management drives the invasion of *Ailanthus altissima* and *Robinia pseudoacacia* into deciduous forests. Forest Ecol Management. 2013; 291:308–317. DOI: 10.1016/j.foreco.2012.11.022
- Rooney TP. High white-tailed deer densities benefit graminoids and contribute to biotic homogenization of forest ground-layer vegetation. Plant Ecology. 2009; 202:103–111. DOI: 10.1007/s11258-008-9489-8

- Ross NJ, Rangel TF. Ancient Maya agroforestry echoing through spatial relationships in the extant forest of NW Belize. *Biotropica*. 2011; 43:141–148. DOI: 10.1111/j.1744-7429.2010.00666.x
- Sanderson EW, Jaiteh M, Levy MA, Redford KH, Wannebo AV, Woolmer G. The human footprint and the last of the wild. *BioScience*. 2002; 52:891–904. DOI: 10.1641/0006-3568(2002)052[0891:THFATL]2.0.CO;2
- StatSoft, Inc. STATISTICA (data analysis software system), version 12. 2013. www.statsoft.com
- St ešťík S, Šamonil P. Ecological valence of expanding European ash (*Fraxinus excelsior* L.) in the Bohemian Karst (Czech Republic). *Journal of Forest Science*. 2006; 52:293–305.
- Szabó P, Hédl R. Socio-economic demands, ecological conditions and the power of tradition: Past woodland management decisions in a Central European landscape. *Landscape Research*. 2013; 38:243–261. DOI: 10.1080/01426397.2012.677022
- Szabó P. Driving forces of stability and change in woodland structure: A case-study from the Czech lowlands. *Forest Ecol Management*. 2010; 259:650–656. DOI: 10.1016/j.foreco.2009.11.026
- Urbíeta IR, Zavala MA, Marañón T. Human and non-human determinants of forest composition in southern Spain: evidence of shifts towards cork oak dominance as a result of management over the past century. *J Biogeography*. 2008; 35:1688–1700. DOI: 10.1111/j.1365-2699.2008.01914.x
- Van Calster H, Baeten L, Verheyen K, De Keersmaecker L, Dekeyser S, Rogister JE, Hermy M. Diverging effect of overstorey conversion scenarios on the underground vegetation in a former coppice-with-standards forest. *Forest Ecol Management*. 2008; 256:519–528. DOI: 10.1016/j.foreco.2008.04.042
- van Swaay C, Warren M, Lois G. Biotope use and trends of European butterflies. *Journal of Insect Conservation*. 2006; 10:189–209. DOI: 10.1007/s10841-006-6293-4
- Vanhellemont M, Baeten L, Verheyen K. Relating changes in understorey diversity to environmental drivers in an ancient forest in northern Belgium. *Plant Ecology and Evolution*. 2014; 147:22–32. DOI: 10.5091/plecevo.2014.921
- Vellend M, Baeten L, Myers-Smith IH, Elmendorf SC, Beauséjour R, Brown CD, et al. Wipf S. Global meta-analysis reveals no net change in local-scale plant biodiversity over time. *Proceedings of the National Academy of Sciences*. 2013; 110(48):19456–19459. DOI: 10.1073/pnas.1312779110
- Verheyen K, Baeten L, De Frenne P, et al. Driving factors behind the eutrophication signal in understorey plant communities of deciduous temperate forests. *Journal of Ecology*. 2012; 100:352–365.
- Vild O, Role ek J, Hédl R, Kopecký M, Utínek D. Experimental restoration of coppice-with-standards: Response of understorey vegetation from the conservation perspective. *Forest Ecol Management*. 2013; 310:234–241. DOI: 10.1016/j.foreco.2013.07.056
- Vodka Š, ížek L. The effects of edge-interior and understorey-canopy gradients on the distribution of saproxylic beetles in a temperate lowland forest. *Forest Ecol Management*. 2013; 304:33–41. DOI: 10.1016/j.foreco.2013.04.007
- Vodka Š, Konvi ka M, ížek L. Habitat preferences of oak-feeding xylophagous beetles in a temperate woodland: implications for forest history and management. *Journal of Insect Conservation*. 2009; 13:553–562. DOI: 10.1007/s10841-008-9202-1
- Wamelink GWW, Van Dobben HF, Mol-Dijkstra JP, Schouwenberg EPAG, Kros J, De Vries W, Berendse F. Effect of nitrogen deposition reduction on biodiversity and carbon sequestration. *Forest Ecol Management*. 2009; 258:1774–1779. DOI: 10.1016/j.foreco.2008.10.024

Figure 1.
Map of the study area with all type of protection marked (PLA = Protected Landscape Area, BR = Biosphere Reserve).

Figure 2. Environmental gradient of the Děvín Hill. NW-SE section shows four main vegetation types including three ecologically and floristically distinct forest types, confined to specific environmental conditions defined by topography and soils.

Figure 3.

Changes in underwood tree abundances in Děvín (a) and Milovice (b) Woods based on archival forestry data. Black bars represent abundance in the 1950s, white ones in the 1970s and grey ones in 2010. For Milovice Wood, only 1970-2010 data were available.

Figure 4.
Environmental gradient of the Děvín Hill from NW to SE reflected in shifts in tree abundances during the last sixty years.

Figure 5.

Changes in the presence of tree species based on resurveyed vegetation plots in Děvín (a) and Milovice (b) Woods. Tree and shrub layers were merged. Black bars represent frequency (% of plots with a species) in the 1950s and grey ones in the 2000s. Black pine is missing in the plots from Milovice Wood. Significance codes are 0.001 '***', 0.01 '**', 0.05 '*'.

Figure 6.

Changes in average Importance Value of tree species based on resurveyed vegetation plots in Děvín (a) and Milovice (b) Woods. Graph design is same as in Fig. 4. Significance codes are 0.001 '***', 0.01 '**', 0.05 '*'.

Figure 7.

Change in species richness in herbaceous layer of two studied forests. Plot-wise difference between the number of species in new and old sample is calculated as % of the number of species in the old sample. Boxes show median and interquartile range, vertical bars are non-outlier range and circles outlier values. Three values exceeding the upper range of displayed change are not shown. Changes in both sites are statistically significant at $p < 0.001$.

Figure 8.

Estimation of species richness by rarefaction curves for Dĕvín (a) and Milovice (b) Woods.

Black symbols and lines are for the 1950s vegetation surveys, grey colour is used for the 2000s surveys. Mean species richness is by rows of circles, 95% confidence intervals are by lines accompanying means.

Figure 9.

Changes in endangered herb layer species for Děvín (a) and Milovice (b) Woods. Relative occurrence (percentage) of the Red List species for the Czech Republic from the occurrence of all species in the datasets. Differences between the old and new samples were statistically insignificant (at $p < 0.05$).

Changes in tree species composition in Milovice Wood (a); and Děvín Wood (b). Species are ordered by abundance, divided into standards/coppice underwood with proportion of species is marked (if known). Numbers in brackets refer to individual sources in Appendix S1.

17th century [2]	1692 [1]	1808 [4] *	1971 [13]				2010 [15]			
	standards	standards		underwood	standards		underwood			
oak	oak	oak	87%	oak	oak	95%	oak	76%	oak	36%
	aspen	pine	6%	hornbeam	black pine	2%	ash	7%	horse chestnut	16%
	elm	elm	4%	hazel	ash	1%	hornbeam	6%	ash	13%
		hornbeam	2%	dogwood	larch	1%	lime	3%	maple	8%
	maple	1%	elm	black locust	1%	aspen	2%	hornbeam	5%	
			lime	elm		black locust	2%	lime	4%	
		maple	hornbeam		birch	1%	apple	3%		
		ash	Douglas fir		hazel	1%	black locust	2%		
		aspen			elm	1%	poplar	2%		
		willow			alder		birch	1%		
		blackthorn			poplar		willow	1%		
		hawthorn			maple		aspen	1%		
					walnut		rowan			
					willow		larch			
					beech		sweet cherry			
					horse chestnut		alder			
							tree of heaven			
							walnut			
							pear			
							black pine			
						spruce				
						elm				
						beech				
						Douglas fir				

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Changes in tree species composition in Milovice Wood (a); and Děvín Wood (b). Species are ordered by abundance, divided into standards/coppice underwood with proportion of species is marked (if known). Numbers in brackets refer to individual sources in Appendix S1.

b) D vln Wood

17th century [2]	1808 [4] *	1885 [6]	1901 [8]	1833-36 [9]	1948 [11]	1971 [13]	2010 [15]
	standards	underwood	underwood	underwood	standards	underwood	
oak	hornbeam	oak	oak	oak	lime	lime	lime
ash	oak	lime	ash	lime	ash	ash	ash
hornbeam	ash	ash	lime	ash	hornbeam	hornbeam	oak
lime	lime	maple	hornbeam	hornbeam	lime	oak	hornbeam
	elm	hornbeam	maple	elm	maple	black locust	black pine
	aspen	elm	elm	maple	black locust	elm	maple
		hazel	horse chestnut	black pine	elm	poplar	horse chestnut
		hazel	hazel	black locust	elm	horse chestnut	elm
		aspen	aspen	black locust	maple	maple	aspen
		dogwood	rowan	birch	larch	aspen	birch
			black pine	spruce		willow	black locust
		birch	larch	horse chestnut			sweet cherry
		alder	birch				spruce
		rowan	black locust				apple
		black pine					larch
		larch					rowan
							tree of heaven

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Table 2

Change in woody species composition from repeated sampling of vegetation plots in the 1950s and 2000s. Numbers are frequency (% of species occurrence in the datasets). Two oak and two lime species were merged because of high risk of misidentification.

a) Tree species

Species	D vín Wood (N=122)		Milovice Wood (N=46)	
	1953-1964	2002-2003	1953	2006
<i>Acer campestre</i>	18	20	17	37
<i>Acer platanoides</i>	20	16	2	0
<i>Acer pseudoplatanus</i>	34	34	0	0
<i>Aesculus hippocastanum</i>	0	1	0	0
<i>Betula pendula</i>	0	6	7	0
<i>Carpinus betulus</i>	57	49	30	26
<i>Cornus mas</i>	3	1	0	0
<i>Corylus avellana</i>	3	3	0	0
<i>Crataegus species</i>	1	1	0	0
<i>Fraxinus excelsior</i>	73	87	33	46
<i>Pinus nigra</i>	7	6	0	0
<i>Populus alba</i>	1	0	0	0
<i>Populus tremula</i>	2	3	2	0
<i>Prunus avium</i>	7	3	7	2
<i>Prunus mahaleb</i>	4	0	0	0
<i>Quercus cerris</i>	4	1	0	0
<i>Quercus petraea+robur</i>	52	40	98	96
<i>Quercus pubescens</i>	25	22	15	9
<i>Robinia pseudacacia</i>	5	5	2	4
<i>Sorbus torminalis</i>	13	10	7	2
<i>Tilia cordata+platyphyllos</i>	79	84	20	28
<i>Ulmus glabra</i>	44	16	0	0
<i>Ulmus laevis</i>	2	0	0	0
<i>Ulmus minor</i>	22	2	4	4
Number of species	22	22	13	10

Change in woody species composition from repeated sampling of vegetation plots in the 1950s and 2000s. Numbers are frequency (% of species occurrence in the datasets). Two oak and two lime species were merged because of high risk of misidentification.

b) Woody undergrowth species (includes shrubs and woody juveniles)

Species	D vin Wood (N=122)		Milovice Wood (N=46)	
	1953-1964	2002-2003	1953	2006
Acer campestre	60	57	59	54
Acer platanoides	46	69	20	4
Acer pseudoplatanus	38	51	2	0
Aesculus hippocastanum	0	1	0	0
Berberis vulgaris	1	0	0	0
Betula pendula	0	0	2	0
Carpinus betulus	56	30	33	24
Cornus mas	37	29	11	28
Cornus sanguinea	27	15	52	17
Corylus avellana	30	13	35	13
Cotoneaster integerrimus	0	1	0	0
Crataegus species	57	41	39	28
Euonymus europaea	15	4	2	7
Euonymus verrucosa	29	11	13	11
Frangula alnus	0	0	2	0
Fraxinus excelsior	92	82	54	46
Juglans regia	4	1	0	0
Ligustrum vulgare	17	11	65	35
Lonicera caprifolium	1	0	2	0
Lonicera xylosteum	15	6	13	4
Malus species	4	0	0	0
Pinus nigra	2	0	0	0
Populus alba	1	0	0	0
Populus tremula	6	4	2	0
Prunus avium	22	13	7	4
Prunus domestica+insititia	0	0	2	0
Prunus fruticosa	1	0	0	0
Prunus mahaleb	16	6	0	2
Prunus spinosa	1	0	20	0
Prunus tenella	2	0	0	0
Pyrus communis agg.	4	7	2	2
Quercus cerris	4	1	0	0
Quercus petraea+robur	52	20	87	35
Quercus pubescens	23	16	15	2
Rhamnus cathartica	11	2	0	0
Ribes uva-crispa	1	0	0	0

Species	D vín Wood (N=122)		Milovice Wood (N=46)	
	1953-1964	2002-2003	1953	2006
<i>Robinia pseudacacia</i>	6	3	2	2
<i>Rosa canina</i> agg.	64	37	33	13
<i>Salix caprea</i>	1	0	0	0
<i>Sambucus nigra</i>	7	10	2	4
<i>Sorbus aucuparia</i>	2	0	13	0
<i>Sorbus danubialis</i>	2	0	0	0
<i>Sorbus domestica</i>	0	1	46	7
<i>Sorbus torminalis</i>	18	8	22	13
<i>Staphylea pinnata</i>	18	24	0	0
<i>Tilia platyphyllos</i> + <i>cordata</i>	74	86	2	0
<i>Ulmus glabra</i>	37	64	9	2
<i>Ulmus laevis</i>	2	0	0	0
<i>Ulmus minor</i>	36	13	20	4
<i>Viburnum lantana</i>	16	9	7	0
Number of species	44	34	33	24