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.

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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; Urbieta 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 and Čížek, 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 and Čížek, 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

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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; Hédl 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 et al., 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 (BR) 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 (Fig. 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: Děvín Wood (400 ha covering most of Děvín Hill) and Milovice Wood (2500 ha). The limestone slopes of Děvín Hill (with altitudes from 260 to 549 m a.s.l.) represent a sharp environmental gradient (Fig. 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; Hédl and Rejšek, 2007). The gently undulating loess plateau of Milovice Wood (altitudes of 180–324 m a.s.l.) is covered by luvisols and represents one of the largest compact complexes of subcontinental oak forests in the region (Hédl 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
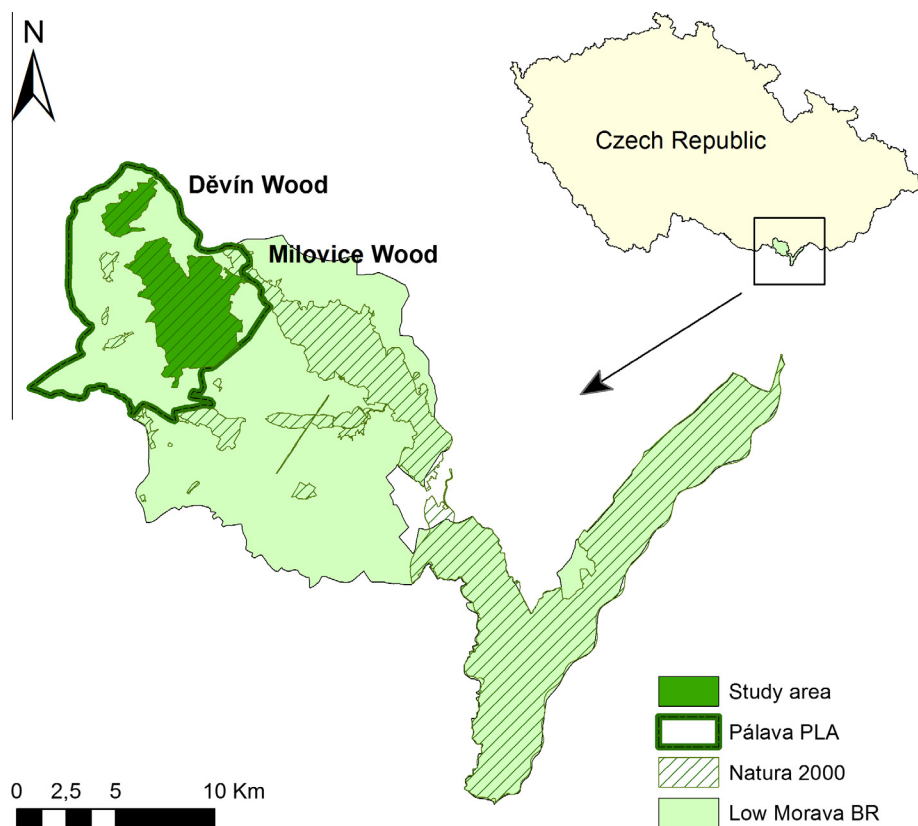

Fig. 1. Map of the study area with all type of protection marked (PLA = Protected Landscape Area, BR = Biosphere Reserve).
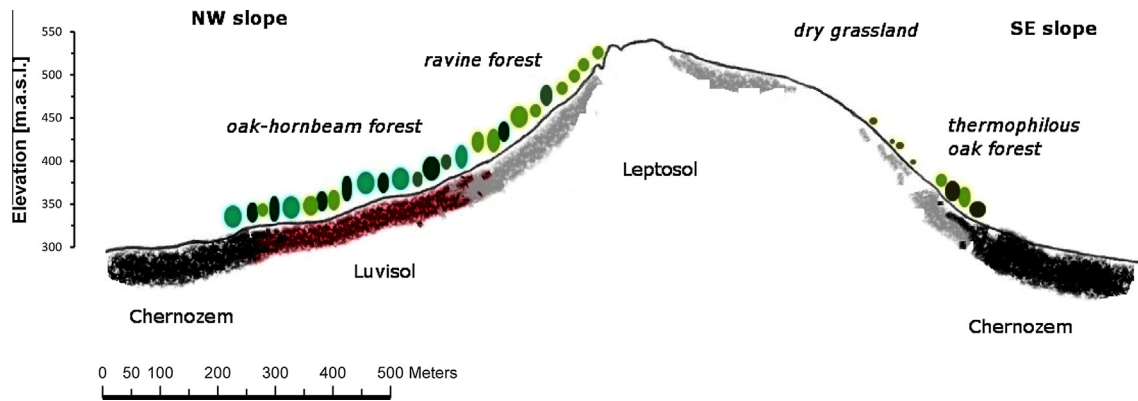
Fig. 2. Environmental gradient of the Děvín Hill. NW–SE section shows four main vegetation types including three ecologically and floristically distinct forest types, confined to specific environmental conditions defined by topography and soils.

were also intensively used for game keeping in certain periods. The first game preserve was established on the Děvín 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 Děvín 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 Děvín game preserve was closed in 1996, while the other two in Milovice forest are still active. In 2003, the Lower Morava Biosphere Reserve (354 km^2) 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 (Fig. 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. Děvín 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 Děvín Wood. The quantitative analyses of species abundance changes was therefore carried out in Děvín 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 inexactly localized species-plots was applied, an approach increasingly termed 'resurvey of semi-permanent plots' (Baeten et al., 2009; Hédl et al., 2010; Kopecký and Macek, 2015). Two sets of data from the 1950s were used, both by the same author (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 Děvín Wood (Hédl, 2005; Kopecký et al., 2013) and in 2006 for Milovice Wood (Komárek, 2008; Hédl 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 Děvín Wood, plot size most commonly varied between 200 and 400 m^2, in Milovice Wood it was 500 m^2. All vascular plant species in the tree, shrub, herb and woody juvenile (seedlings and saplings) layers were recorded in Děvín 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 Děvín 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 Děvín 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, Inc., 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 Děvín 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 and 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 Děvín 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 Děvín Wood, oak showed increasing abundance, while hornbeam decreased and lime and ash remained stable (Fig. 3a). Other species, such as elm, maple, black pine, and black locust 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 1–16 %). 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 (Fig. 3b).

Although the detail of historical sources is limited (for example *Q. pubescens* and *Q. petraea* cannot be separated), the sharp environmental gradient on Děvín Hill from NW to SE (Fig. 2) is recognizable in historical tree species composition (Fig. 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 Děvín Hill on previously unforested shallow rocky soils (10 ha), and some in Milovice Wood. Currently 5% of Děvín 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 Děvín 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 Děvín 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. Děvín Wood was dominated with lime (mostly *T. platyphyllos*), ash, maples, hornbeam and mesophilous (mostly *Q. 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 Děvín Wood. Total tree diversity in Milovice Wood is only half of that for Děvín 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. *C. mas*, *P. mahaleb*, *Q. cerris* (planted),

Table 1
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.

(a) Milovice Wood

17th century [2]	1692 [1]	1808 [4] [a]			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	

(b) Děvín Wood

17th century [2]	1808 [4] [a]		1885 [6]	1901 [8]	1833–36 [9]	1948 [11]		1971 [13]			2010 [15]	
	Standards	Underwood	Underwood	Underwood	Underwood	Standards	Underwood	Standards	Underwood			
Oak	Hornbeam 41%	Oak	Oak	Oak	Oak	Oak 50%	Lime 38%	Oak 81%	Lime 43%		Lime	42%
Ash	Oak 40%	Hornbeam	Lime	Ash	Lime	Ash 19%	Black pine 10%	Ash 21%		Ash	23%
Hornbeam	Ash 9%	Lime	Ash	Lime	Ash	Lime 15%	Hornbeam 19%	Ash 4%	Hornbeam 17%	Oak	17%
Lime	Lime 7%	Maple	Maple	Hornbeam	Hornbeam	Black pine 9%	Oak 8%	Lime 4%	Oak 10%	Hornbeam	10%
	Elm 2%	Ash	Hornbeam	Maple	Elm	Hornbeam 3%	Maple 4%	Spruce 1%	Black locust 4%	Black pine	5%
	Aspen 1%	Hazel	Elm	Elm	Maple	Maple 2%	Elm 3%	Black locust	Elm 3%	Maple	4%
		Elm	Hazel	Horse chestnut	Black pine	Elm 2%	Black locust 1%		Poplar 1%	Horse chestnut	1%
		Aspen	Aspen	Hazel	Black locust		Rowan		Horse chestnut 1%	Elm	1%
		Dogwood	Black locust	Rowan	Birch		Hazel		Maple	Aspen	1%
			Horse chestnut	Black pine	Spruce				Aspen	Birch	1%
			Birch	Larch	Horse chestnut				Willow	Black locust	1%
			Alder	Birch						Sweet cherry	
			Rowan	Black locust						Spruce	
			Black pine							Apple	
			Larch							Larch	
										Rowan	
										Tree of heaven	

[a] Sources until 1971 covered only app. 2/3 of Milovice Wood (northern and southern part).

P. 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 (Fig. 5a and 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 Děvín Wood, $p < 0.01$ in Milovice Wood) and elm (significant only in Děvín Wood, $p < 0.01$). Oak decreased in Děvín 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 Děvín 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, Fig. 6), the resulting picture in Děvín 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 Děvín Wood. The overwhelming dominance of oak (change n.s.) partly
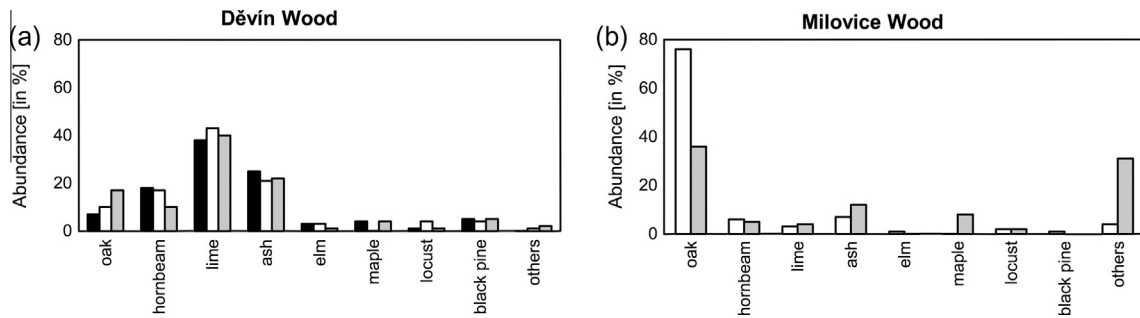
Fig. 3. Changes in underwood tree abundances in Děvín (a) and Milovice (b) Woods based on archival forestry data. Black bars represent abundance in the 1950s, white ones in the 1970s and grey ones in 2010. For Milovice Wood, only 1970–2010 data were available.
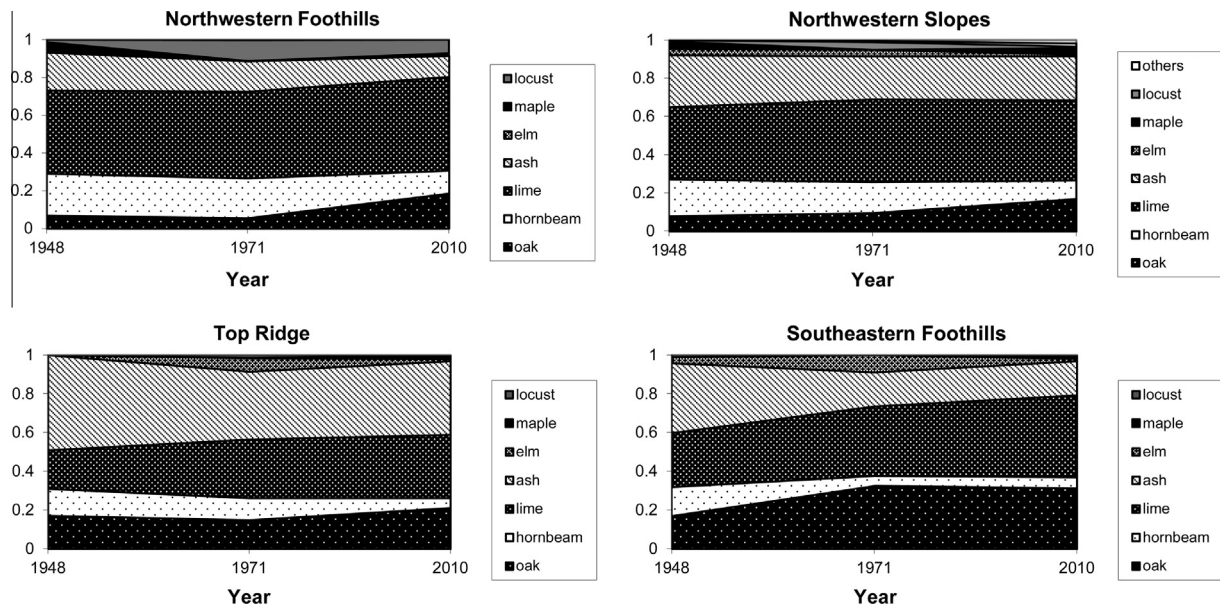

Fig. 4. Environmental gradient of the Děvín Hill from NW to SE reflected in shifts in tree abundances during the last sixty years.

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.

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

Table 2 (continued)

| Species	Děvín Wood (N = 122)		Milovice Wood (N = 46)	
	1953–1964	2002–2003	1953	2006
Ulmus glabra	44	16	0	0
Ulmus laevis	2	0	0	0
Ulmus minor	22	2	4	4
Number of species	22	22	13	10
(b) Woody undergrowth species (includes shrubs and woody juveniles)				
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
Robinia pseudacacia	6	3	2	2
Rosa canina agg.	64	37	33	13
Salix caprea	1	0	0	0
Sambucus nigra	7	10	2	4
Sorbus aucuparia	2	0	13	0
Sorbus danubialis	2	0	0	0
Sorbus domestica	0	1	46	7
Sorbus torminalis	18	8	22	13
Staphylea pinnata	18	24	0	0
Tilia platyphyllos + cordata	74	86	2	0
Ulmus glabra	37	64	9	2
Ulmus laevis	2	0	0	0
Ulmus minor	36	13	20	4
Viburnum lantana	16	9	7	0
Number of species	44	34	33	24
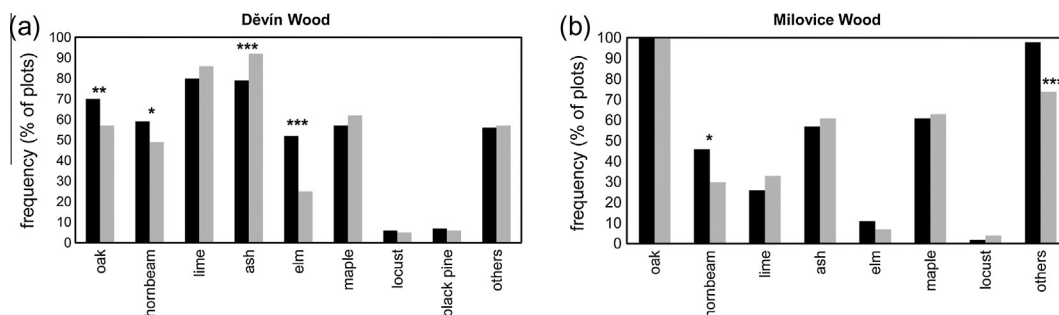
Fig. 5. Changes in the presence of tree species based on resurveyed vegetation plots in Děvín (a) and Milovice (b) Woods. Tree and shrub layers were merged. Black bars represent frequency (% of plots with a species) in the 1950s and grey ones in the 2000s. Black pine is missing in the plots from Milovice Wood. Significance codes are 0.001 '***', 0.01 '**', 0.05 '*'.
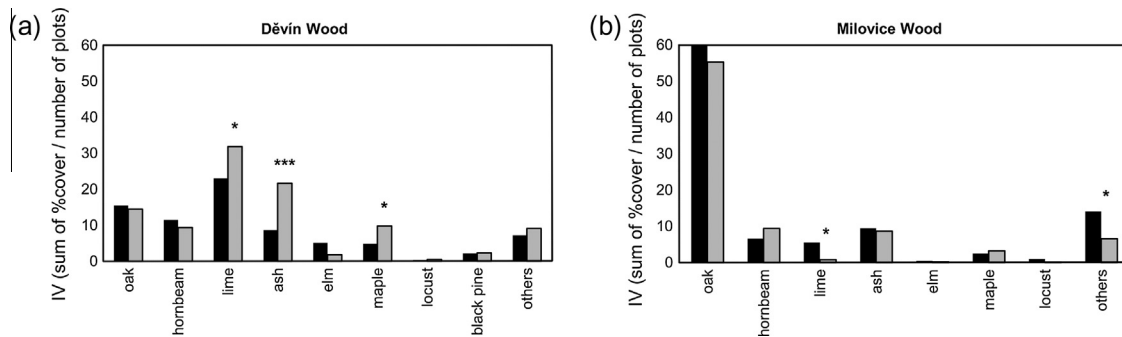
Fig. 6. Changes in average Importance Value of tree species based on resurveyed vegetation plots in Děvín (a) and Milovice (b) Woods. Graph design is same as in Fig. 4. Significance codes are 0.001 '***', 0.01 '**', 0.05 '*'.

obscured the performance of other, less abundant species: lime (decreased at $p < 0.05$), hornbeam, maple and especially elm (all three changes n.s.); Fig. 6b. The category 'others' decreased significantly at $p < 0.05$. By contrast, in Děvín 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 Děvín Wood was the increase of lime, ash and maple (Fig. 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*, *P. mahaleb*, *R. cathartica*, *Sorbus domestica*, *S. torminalis* and *Viburnum lantana*) or generally shrubby species of open habitats (*Cornus sanguinea*, *C. avellana*, *Crataegus* sp., *Prunus spinosa*, or *Rosa canina* agg.). Oaks (*Q. petraea*, *Q. pubescens*) failed to regenerate, decreasing by more than half at both sites. Elms either decreased (*U. minor*) or increased (*U. glabra* – in Děvín), probably reflecting the differing regeneration ecologies of the species. Similar differences can be observed for the regeneration of mesophilous maples (*A. platanoides*, *A. pseudoplatanus*), for which an increase was recorded in the increasingly mesic forests of Děvín and a decrease in the dry, ungulate-browsed forests of Milovice Wood. Lime (*T. platyphyllos* and *T. cordata*), another species of dark and moist forests, showed increasing regeneration in Děvín 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 Děvín 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 Děvín 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 Děvín 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 Děvín 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 (Fig. 7). Species richness estimated by rarefaction showed a striking difference in Děvín Wood between the old and new surveys; it was significantly lower in the new survey (Fig. 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 (Fig. 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 Děvín 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 (Fig. 9b) than in Děvín Wood (Fig. 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 Děvín Wood than in Milovice Wood, and so is the number of endangered species and their occurrences in plots.
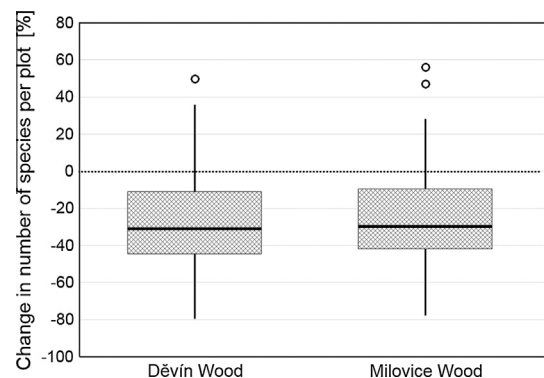

Fig. 7. Change in species richness in herbaceous layer of two studied forests. Plotwise difference between the number of species in new and old sample is calculated as % of the number of species in the old sample. Boxes show median and interquartile range, vertical bars are non-outlier range and circles outlier values. Three values exceeding the upper range of displayed change are not shown. Changes in both sites are statistically significant at $p < 0.001$.
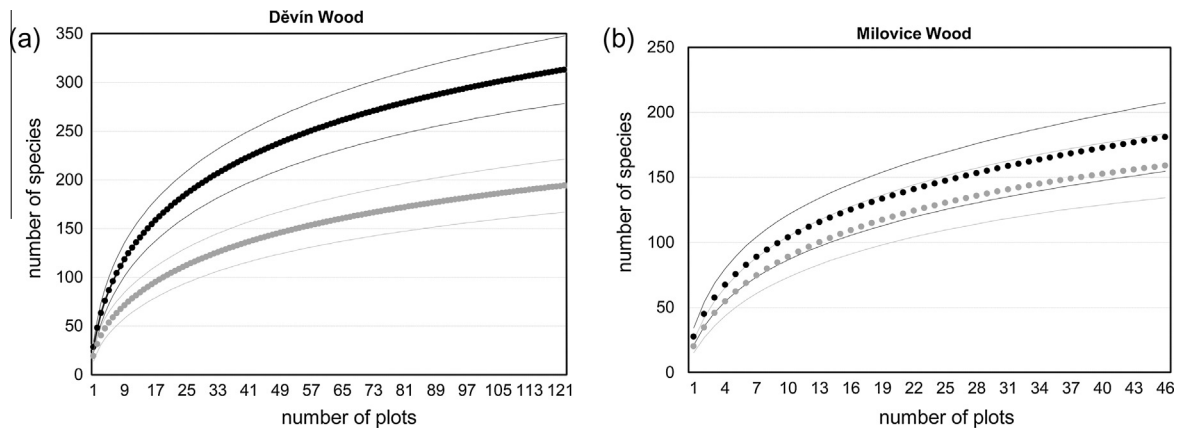
Fig. 8. Estimation of species richness by rarefaction curves for Děvín (a) and Milovice (b) Woods. Black symbols and lines are for the 1950s vegetation surveys, grey colour is used for the 2000s surveys. Mean species richness is by rows of circles, 95% confidence intervals are by lines accompanying means.
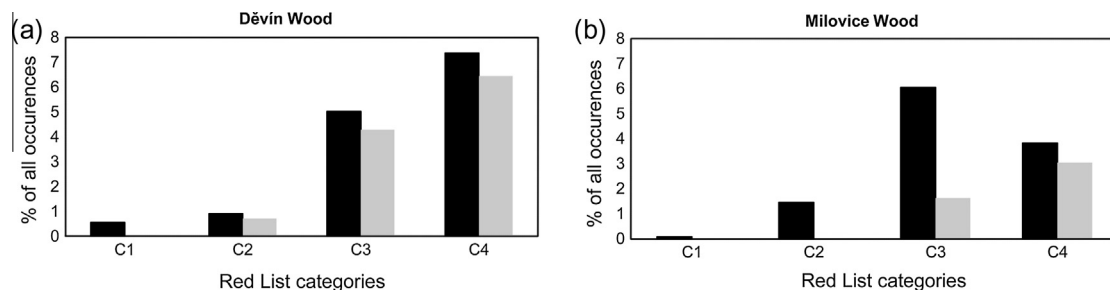

Fig. 9. Changes in endangered herb layer species for Děvín (a) and Milovice (b) Woods. Relative occurence (percentage) of the Red List species for the Czech Republic from the occurence of all species in the datasets. Differences between the old and new samples were statistically insignificant (at *p* < 0.05).

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 (Děvín) 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 Děvín 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 Děvín 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 Děvín 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 Děvín Wood concurs with the expansion of this species in the ecologically similar Bohemian Karst (Hofmeister et al., 2004; Střeštík 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 Děvín 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 Děvín 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 et al., 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. Děvín 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 (Děvín 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 Děvín 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 Děvín 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; Hédl 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 Děvín 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; Kopáček 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. Bartha 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 *A. 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 *U. 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 Děvín 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 *I. parviflora* did it on a larger scale in Děvín 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 socioeconomic 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 and Čížek, 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 resprouting ability for coppice stools after long periods of neglect. Furthermore, Leonardsson and Götmark (2015) found no effect of stool diameter on sprouting after conservation thinning in southern Sweden.

On the NE slopes of Děvín 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 (Hédl, 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 Děvín Wood are also susceptible to expansion by nitrophilous species, such as *Alliaria petiolata*, *Campanula rapunculoides* or *I. 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 Děvín game preserve was abolished in 1996, mouflons and deer still live here in high densities (Riedl, 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).

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2015.02.003.

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